

# Obvious Invaders and Overlooked Infauna: Unexpected Constituents of the Decapod Crustacean Fauna at Twin Cays, Belize

*Darryl L. Felder, Peter C. Dworschak, Rafael Robles, Heather D. Bracken, Amanda M. Windsor, Jennifer M. Felder, and Rafael Lemaitre*

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**ABSTRACT.** Decapod crustaceans in the vicinity of Carrie Bow Cay and Twin Cays, Belize, have been under study for more than 25 years. Large collections have been assembled, and new species have been discovered. The effort has included photographic documentation of coloration, yielding characters of value in identification of problematic tropical taxa. Measurements of diversity have been markedly enhanced by extraction corer (yabby pump) sampling in shallow subtidal sediments, especially at Twin Cays. This technique revealed species, genera, and families of thalassinidean decapods not previously known from the region. Studies continue on the ecological roles of these burrowers, dominant bioturbators in seagrass beds where they produce conspicuous mounds of sediment and constitute a major infaunal biomass at Twin Cays. By contrast, familiar large reptant decapods typically dominate shallow rocky substrates. Within the past four years, however, the nonindigenous portunid crab *Charybdis hellerii* has extensively invaded large portions of hard substrates at Twin Cays. In 2007, it was found to dominate cavities under coral heads in survey areas along the northeastern and southwestern shorelines, possibly displacing populations of large *Mithrax*, *Menippe*, *Callinectes*, and *Panulirus* previously found there in abundance.

## INTRODUCTION

Fieldwork centered on Carrie Bow Cay and surrounding habitats, including a variety of settings at Twin Cays. The effort continues work by the first author in collaboration with the late Ray Manning in 1983, as well as work by the late Brian Kensley during the 1980s and early 1990s (Kensley, 1981, 1996). Early efforts produced abundant grass-bed and reef-crest species generally identifiable with known Caribbean taxa, along with small cryptic forms obtained by cutting open sponges, breaking rubble, poisoning in situ, or using several narcotants to drive out small decapods from rubble isolated in containers. Rich collections that have accumulated in the the Smithsonian Institution's National Museum of Natural History were fixed in formalin, limiting their value in genetic analyses. Efforts in 2002 and 2007 shifted emphasis to varied intertidal and subtidal habitats of Twin Cays and to resampling the regional fauna to obtain alcohol-fixed materials for molecular genetic analyses.

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Darryl L. Felder, Rafael Robles, Heather D. Bracken, Amanda M. Windsor, and Jennifer M. Felder, Department of Biology and Laboratory for Crustacean Research, University of Louisiana at Lafayette, Lafayette, Louisiana 70504-2451, USA. Peter C. Dworschak, Naturhistorisches Museum in Wien, Burgring 7, A-1014 Wien, Austria. Rafael Lemaitre, Department of Invertebrate Zoology, National Museum of Natural History, MRC 163, Smithsonian Institution, Washington, D.C. 20013-7012, USA. Corresponding author: D. Felder (dlf4517@louisiana.edu). Manuscript received 13 May 2008; accepted 20 April 2009.



Concerted effort has been made to photographically document coloration of fresh specimens, given the value of color in the identifications of tropical species and the long-term goal of producing a guidebook for the regional decapod fauna (DLF and RL, in progress). More than 260 decapod species have been enumerated in our collections from the Carrie Bow Cay region, some yet to be named. Under U.S. National Science Foundation ATOL "Decapod Tree of Life" support, molecular and morphological systematic studies are under way concerning alpheid and other caridean shrimps, paguroid hermit crabs, thalassinidean shrimps, and panopeid, portunid, grapsoid, pinnothetid, and majoid crabs, as well as family-level relationships among all major decapod groups. Work incorporating porcelain crab collections from the region has been published (Rodríguez et al., 2005, 2006) as has work by other investigators on some alpheid shrimp groups (Duffy, 1996; Duffy and Macdonald, 1999; Duffy et al., 2000, 2002; Macdonald et al., 2006; Ríos and Duffy, 2007). Previous collections of upogebioid thalassinidean shrimp from Belize were included in Williams (1993). Several descriptions of new species from our Belize collections have also appeared (Goy and Felder, 1988; Manning and Felder, 1996; Felder and Manning, 1997), but many species remain to be described. The second author has been involved in several ecological studies of the infaunal decapods of the region (Dworschak and Ott, 1993; Abed-Navandi and Dworschak, 2005; Dworschak et al., 2006).

Our protracted field sampling program has in some cases allowed us to observe apparent changes in community composition. In a striking example, shallow subtidal habitats at Twin Cays have been recently invaded by the nonindigenous swimming crab *Charybdis hellerii* (A. Milne-Edwards, 1867), previously unreported from Belize. Recurrent trips have also provided opportunities for shallow subtidal sampling and burrow-casting of fossorial infauna in turtle grass (*Thalassia*) beds along shorelines of Twin Cays, revealing unexpected thalassinidean diversity. A brief account of these latest efforts is our present focus, preliminary to more comprehensive treatment of the full decapod assemblage.

## MATERIALS AND METHODS

Sampling included the breaking of dead coral and conch shell rubble, netting, extraction of sediments, and sorting through hard-surface fouling organisms, but sampling of large crabs such as *Charybdis hellerii* (Brachyura)

and its macrocrustacean associates was a targeted effort. These decapods were captured from under pieces of dead subtidal coral and debris that were lifted while snorkeling over and adjacent to seagrass (*Thalassia*) beds in water 1–2 m deep. Sampling of most thalassinideans and related decapod burrowers was accomplished with a suction extractor (yabby pump) and bag-sieve while wading, snorkeling, or SCUBA diving in water 0.5–4 m deep. In addition to collections of *Glypturus acanthochirus* (Callianassidae) by suction extractor, some specimens of this species were obtained with "weighted line" traps (de Vaugelas, 1985). Specimens of *Axiopsis serratifrons* (Axiidae) were obtained by baiting animals to the apertures of their burrows, where they were captured by cutting off the burrow or by spearing the specimens. Casts of burrows were made as described by Dworschak and Ott (1993). Specimens were immobilized by immersion in chilled seawater or by narcotization with clove oil before photography. Photographs of specimens immersed in a pan of seawater were made with a Fuji Fine Pix S1Pro digital camera equipped with a 60 mm macrolens while the subject was lighted by a combination of direct and reflected sunlight or high-intensity 5000°K fluorescent photographic lamps. All specimens were subsequently preserved in several exchanges of 95% nondenatured ethanol and then stored in 75% nondenatured ethanol. Photographic voucher specimens were archived in the Zoological Collections of the University of Louisiana at Lafayette (ULLZ), and most other materials were deposited in the Smithsonian Institution–National Museum of Natural History (USNM). Some collections by the second author (especially thalassinideans) were deposited in the Naturhistorisches Museum in Wien, Austria (NHMW) and the Muséum National d'Histoire Naturelle, Paris, France (MNHN). For figured specimens, size is indicated as carapace width (cw) or carapace length (cl).

## RESULTS AND DISCUSSION

### INVASION BY *CHARYBDIS HELLERII*

Large bottom debris (waterlogged wood, discarded building materials, dead coral heads) typically provides cover for large reptants such as spiny lobsters (*Panulirus* spp.), swimming crabs (*Callinectes* spp.), stone crabs (*Menippe* spp.), and large spider crabs (*Mithrax* spp.), especially in shallow well-lighted waters. Sampling of these environments at both Carrie Bow Cay and Twin Cays in October 2002 revealed no large decapods other than these genera. That same year, however, a small specimen of the



nonindigenous portunid crab *Charybdis hellerii* was found in an empty conch shell on the inshore side of Carrie Bow Cay, the first such occurrence recorded in our sampling program.

In April 2007, sampling under large pieces of cover at Twin Cays was undertaken to obtain fresh materials of the aforementioned resident genera for genetic analyses. Initial sampling centered in the vicinity of the "Fisheries Camp" on the southeastern end of Twin Cays, where a storm had scattered sheets of metal building siding from the shoreline to depths of nearly 2 m. Inspections beneath 20 such sheets across this entire range of depths revealed none of the target species but at least seven variously sized individuals of the nonindigenous swimming crab *C. hellerii*.

Sampling was thereafter shifted to dead coral heads scattered among turtle grass beds on the northeast side of Twin Cays. A crude survey was there undertaken for coral heads in 1–1.5 m depths, each head roughly 0.5–0.7 m in diameter and separated from one another by roughly 6–15 m. Of the 25 coral heads inspected, 13 were uninhabited by large reptant decapods, 8 harbored large specimens of *C. hellerii* (Figure 1b), and four harbored only *Menippe nodifrons* Stimpson, 1859 (Figure 1a). Large single individuals of *C. hellerii* were found under 6 of the 25 heads that were lifted, a mating pair of *C. hellerii* was found under a single head, and a specimen of *C. hellerii* together with a large specimen of *M. nodifrons* was found under another head. No specimens of *Mithrax* spp., *Callinectes* spp.,

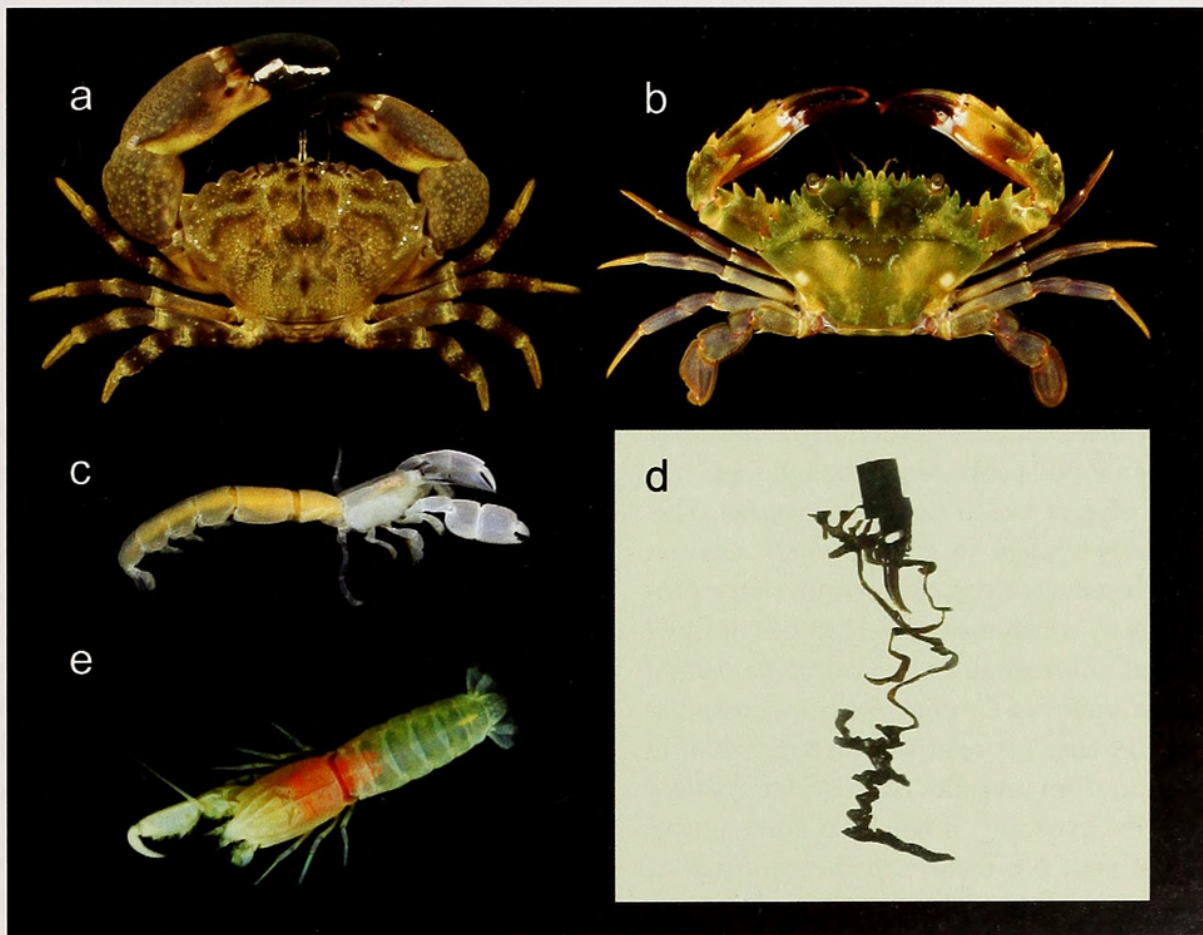


FIGURE 1. a, Stone crab *Menippe nodifrons*, male, 69.7 mm carapace width (cw), Twin Cays, Belize 10 April 2007, ULLZ 8991. b, Invasive Indo-Pacific swimming crab *Charybdis hellerii*, male, 75.3 mm cw, Twin Cays, Belize, 10 April 2007, ULLZ 8990. c, Callianassid *Eucalliax* sp., female, 8.3 mm carapace length (cl), South Water Cay, 22 October 2002, ULLZ 9230. d, Polyester resin burrow cast from Twin Cays, probably assignable to *Axianassa australis*, cast length 85 cm, made by PCD, Twin Cays, Belize, August 1989, NHMW 24001. e, Laomediid *Naushonia* sp. female, 5.8 mm cl, Carrie Bow Cay, Belize, 3 April 2007, ULLZ 8895. ULLZ, University of Louisiana at Lafayette; NHMW, Naturhistorisches Museum Wien. Photographs a–c and e by DLF; photograph d by PCD.



or *Panulirus* spp. were observed, despite these taxa being commonly found in such settings during 1983 and 2002.

Small or immature specimens of *Charybdis hellerii* are easily confused with *Cronius ruber* (Lamarck, 1818) and to a lesser extent with *Achelous tumidulus* Stimpson, 1871, both of which also occur in Belize and adjacent waters of the Caribbean, Gulf of Mexico, and other areas of the warm temperate Atlantic. This similarity led us to initially question the identity of the single small specimen collected in 2002, but it was confirmed to be *Charybdis hellerii* by 16S mtDNA sequence analysis by comparing to other sequence data for the species (Robles et al., 2007; Mantelatto et al., 2009). Widely used diagnostic morphological characters that apply well to full-sized adults do not readily facilitate identification of juveniles among these three species, and records of subadults could easily be in error if based on presently limited descriptions. At the very least, *A. tumidulus* differs from both *C. ruber* and *Charybdis hellerii* by lacking a striking posterior or posterodistal meral spine on the fifth pereopod (swimming leg) in all crab stages. *Cronius ruber* and *Charybdis hellerii*, however, share a strongly spined fifth pereopod, albeit with the spine usually occupying a relatively more distal position and being less posteriorly directed on the merus of *Cronius ruber*. The relative position of the spine is, however, difficult to distinguish in small juveniles. These two species also share the presence of small spinules bordering the posterior margin of the fifth pereopod propodus, although these spinules are of relatively larger size in *Charybdis hellerii*. This characteristic is readily evident in adults, where setation obscures small acute granules along the margins of the propodus in *Cronius ruber*, which are unlikely to be confused with the well-formed adult spinules of *Charybdis hellerii* (see Figure 1b). In juveniles of *Cronius ruber*, microspination of this propodal margin is relatively stronger than in adults, and distinction from juveniles of *Charybdis hellerii* is somewhat subjective, especially if one lacks comparative specimens of similar size. No feature in the carapace of early crab stages (Dineen et al., 2001: fig. 24) appears to separate small individuals of these species.

Recent observations have revealed an ongoing invasion of *C. hellerii* into coastal western Atlantic locations, and its documented distribution must now include Belize along with Brazil, Venezuela, Colombia, Cuba, the Yucatán shelf of Mexico, both coasts of Florida, and other northern Atlantic U.S. coastal habitats through at least the Carolinas (Campos and Türkay, 1989; Gómez and Martínez-Iglesias, 1990; Hernández and Bolaños, 1995; Lemaitre, 1995; Calado, 1996; Mantelatto and Dias, 1999; Dineen et al., 2001; Mantelatto and Garcia, 2001;

Mantelatto et al., 2007; Robles et al., 2007; McMillen-Jackson, 2008; Felder et al., 2009). Clearly, the foregoing chronology of reports reveals continued western Atlantic range expansion for *C. hellerii*, although the potential trophic impacts of this invader remain poorly documented. The first author has on two occasions observed individuals of *C. hellerii* in the Indian River Lagoon, Florida, feeding (inside shallow cavities of hard substrates that they occupied) on soft-shelled, postmolt individuals of native species of large decapods (one *Callinectes*, one *Panulirus*), and in another instance feeding on small mussels. As in the present report, all such observations and inferences of this invader's potential competitive and predatory impacts in the western Atlantic remain very limited and anecdotal, but they serve to justify a call for controlled experimental studies.

#### THALASSINIDEANS

Our collections of cryptic burrowing thalassinideans from various habitats in the vicinity of Carrie Bow and Twin Cays, along with the few previously reported records, include at least 17 species representing the families Callianassidae, Laomediidae, Thomassiniidae, Axianassidae, Axiidae, and Upogebiidae. The species of these often overlooked groups are presented in the following list, with collection sites indicated as TC (Twin Cays), CB (Carrie Bow Cay), SW (South Water Cay), and SL (shorelines near Dangriga); catalogue numbers are shown for archived specimens.

#### INFRAORDER THALASSINIDEA SENSU LATO

##### CALLIANASSIDAE (Ghost Shrimps)

*Corallianassa longiventris* (A. Milne-Edwards, 1870)—TC, CB: NHMW 6774, 6775, 15352–15355; ULLZ 4228–4230, 6083, 8997.

*Eucalliax* sp.—TC, SW: ULLZ 9230.

*Glypturus acanthochirus* Stimpson, 1866—TC, CB: NHMW 6765–6770, 15338–15342; MNHN Th 1181, Th 1185; ULLZ 8993–8995, 9233; USNM 266241–266244.

*Lepidophthalmus richardi* Felder and Manning, 1997—SL [near river mouths]: NHMW 15343–15349; ULLZ 3577, 5186–5188, 8992; USNM 277777–277779.

*Neocallichirus grandimana* (Gibbes, 1850)—TC, CB, SW: NHMW 6796–6799, 15356–15367; MNHN Th



1182–1184; ULLZ 8998, 9235–9237, 9239–9241, 9243, 9244.

*Neocallichirus maryae* Karasawa, 2004—TC: ULLZ 9234, 9238.

#### LAOMEDIIDAE

*Naushonia* sp.—CB: ULLZ 8895, 8915.

#### AXIANASSIDAE

*Axianassa australis* Rodrigues and Shimizu, 1992—TC [identified by burrow cast]: NHMW 24001.

#### THOMASSINIIDAE

*Mictaxius thalassicola* Kensley and Heard, 1991—TC: ULLZ 9246.

#### UPOGEBIIDAE (Mud Shrimps)

*Pomatogebia operculata* (Schmitt, 1924—CB: ULLZ 9231.

*Upogebia acanthura* (Coelho, 1973)—?CB: USNM 251246.

*Upogebia omissa* Gomes Corrêa, 1968—TC, SL: ULLZ 5165.

*Upogebia* sp.—CB: ULLZ 9232.

#### AXIIDAE (Lobster Shrimps)

*Axiopsis serratifrons* (A. Milne-Edwards, 1873)—CB: NHMW 6771–6773, 15350–15351; ULLZ 4232, 4233, 5827, 8996; USNM 18905, 18907, 18908.

*Coralaxius nodulosus* (Meinert, 1877)—CB: USNM 170856, 171764–171766, 243431–243434.

*Paraxiopsis hispida* Kensley, 1996—CB: USNM 211462.

*Paraxiopsis spinipleura* Kensley, 1996—CB: USNM 211451.

Sediments in lower intertidal to subtidal seagrass beds at Twin Cays are densely populated by *Neocallichirus grandimana*, *Glypturus acanthochirus*, *Corallianassa longiventris*, *Neocallichirus maryae*, *Mictaxius thalassicola*, and *Eucalliax* sp., often burrowing more than 1 m into

sediments. Dworschak and Ott (1993) previously analyzed burrow morphologies and distributions for three of these species, as well as for *Axiopsis serratifrons* and two species of pistol shrimp. Their food sources were investigated by stable isotope studies (Abed-Navandi and Dworschak, 2005). Among the species from Twin Cays, *M. thalassicola* has not previously been reported from the northern Caribbean, and *Eucalliax* sp. (Figure 1c) represents an undescribed taxon presently known only from Belize.

The newly reported *Neocallichirus maryae* is a replacement name for the more familiar *N. rathbunae* (Schmitt, 1935), which proved to be a junior primary homonym of a different fossil species (Karasawa, 2004). Although Sakai (2005) placed *N. raymanningi* Blanco Rambla and Lemaitre, 1999, in synonymy with *N. rathbunae* (Schmitt, 1935), and *N. raymanningi* would thus predate recent establishment of *N. maryae*, we do not accept the presently limited evidence for this synonymy.

Ejecta from burrows of these thalassinideans dominates bottom topography in intertidal to shallow subtidal seagrass beds of this area, but along intertidal muddy shorelines at Twin Cays, especially those immediately adjacent to mangroves, it appears that the axianassid *Axianassa australis* also occurs. As no specimens have been captured, this can be deduced only from highly characteristic ejecta patterns and spiraled burrow casts (see Dworschak and Rodrigues, 1997; Felder, 2001), the latter obtained by the second author in 1989 (Figure 1d).

*Neocallichirus grandimana* appears to be the most widely distributed callianassid among sites sampled in the vicinity, inhabiting both vegetated and nonvegetated sediments. Together with *Eucalliax* sp., it densely populates sparsely vegetated calcareous sands of shallow shoals bordering South Water Cay in addition to sites at Twin Cays. At South Water Cay, upper reaches of its burrows are commonly inhabited by *Processa* sp. and early juvenile stages of *Callinectes* sp., the latter being uniquely pigmented an opaque bluish-black. *Glypturus acanthochirus* and *Corallianassa longiventris* range into deeper grass beds, where they appear to draw grass blades into their burrows. Distributions of all the collected thalassinideans depend on sediment characteristics, depths, vegetation, and water quality, whereas characteristic burrow architectures are both diagnostic of species and suggestive of ecological adaptations (Dworschak and Ott, 1993, Abed-Navandi and Dworschak, 2005; Dworschak et al., 2006). Less conspicuous evidence of sediment ejecta characterizes areas among seagrasses that are burrowed primarily by nonthalassinidean decapods such as the *Alpheus* spp. reported by Dworschak and Ott (1993). Surface features of these burrows can be all



but indistinguishable from those made by what appear to be several species of *Upogebia*, including *U. omissa*.

The assemblage of upogebiids in the Carrie Bow Cay region remains poorly understood. It appears that *Upogebia omissa* ranges widely here, from the shoreline along the mainland to offshore cays, and the first author has identified specimens taken as "pests" from commercial penaeid shrimp farms on the mainland. General treatment of western Atlantic upogebiids by Williams (1993) included records of *U. acanthura* from a patch reef southwest of Carrie Bow Cay and *U. brasiliensis* Holthuis, 1956 from more distant shoreline areas of Belize, although our collections have produced no additional specimens. Two other species listed by Williams (1993) from nearby coastal environments of Quintana Roo (*U. corallifora* Williams and Scott, 1989 and *U. vasquezi* Ngoc-Ho, 1989) could also be expected in Belize, although we have yet to find them. Specimens of this genus from coralline rubble just off the reef crest at Carrie Bow Cay (ULLZ 9232) and other uncatalogued specimens from Twin Cays (in areas also burrowed by alpheid shrimp) cannot confidently be assigned to known species and warrant further study. Generally found in deeper subtidal habitats (Felder et al., in press), the upogebiid *Pomatogebia operculata* ranges into waters as shallow as 2 m depth off Carrie Bow Cay and likely occurs elsewhere between cays in appropriate deeper calcareous rubble habitats; these have been collected by breaking open highly eroded pieces of coralline rubble to expose the muddy interstices and cavities occupied by this upogebiid.

Axiids are also found in association with rubble and reef structures of outer cays, as, for example, at Carrie Bow. The widely distributed *Coralaxius nodulosus*, a small-sized species inhabiting cavities in subtidal coralline rubble from the fore-reef (see also Kensley, 1994), is routinely found along with the upogebiid *Pomatogebia operculata* in interstices of broken rubble retrieved from depths greater than 2 m. By contrast, the large and strongly armed *Axiopsis serratifrons* is widely distributed between pieces of coarse coral rubble in back-reef flats of Carrie Bow (0.5–2 m depths), there positioned to ambush prey from its somewhat concealed burrow aperture. In addition, two new species of *Paraxiopsis* described by Kensley (1996) both range into reef habitats of Carrie Bow Cay. Although *P. spinipleura* was originally found there in shallow (1.5 m) back-reef rubble, we have not encountered additional specimens. We have also not found additional materials of *P. hispidus*, previously collected at the reef drop-off in depths greater than 20 m.

A remarkable thalassinidean find at Carrie Bow was the April 2007 discovery of a laomediid assignable to

*Naushonia* sp. (Figure 1e). Two specimens were captured, both from cavities of empty conch shells in shallow (<1.5 m) subtidal waters. These individuals appear to also represent an undescribed species of a rarely encountered genus in the northern Caribbean region. To date known only from Carrie Bow Cay, they are currently being described.

The thalassinidean fauna of the general region also includes an abundant nearshore species, *Lepidophthalmus richardi*, adapted to euryhaline waters and muddy sand shorelines of the Stann Creek District (Felder and Manning, 1997). This species has not been found in habitats immediately associated with Twin Cays or Carrie Bow Cay, despite intensive search.

These collections have allowed us to update and expand the burrow distribution schemes for Belize given by Dworschak and Ott (1993). We herewith add additional taxa and habitat distributions (Figure 2) to underscore the overlooked diversity of infaunal macrocrustaceans, some of which are dominant bioturbators.

#### NOTE ADDED IN PRESS

Additional sampling in Belize was conducted in February 2009. Observations in shallow waters at Twin Cays confirmed that populations of *Charybdis helleri* remained as seen in 2007. Further sampling for thalassinideans supported accounts on the preceding pages, with noteworthy additions. Sampling among shoreline mangrove roots at Twin Cays produced the first specimens of the Axianassidae, representing new records for *Axianassa intermedia* Schmitt, 1924. Five such specimens were extracted by yabby pump from beneath a surface area of no more than 0.25 m<sup>2</sup> at low tide, but less productive adjacent sampling suggested heterogeneous patterning. Given the small size of these specimens, we question whether this species accounts for burrows provisionally attributed to *A. australis* on the basis of castings mentioned on the preceding pages. From these same habitats at Twin Cays, the first specimen of the callianassid *Biffarius fragilis* (Biffar, 1970) was captured, along with a specimen of the same *Naushonia* sp. reported from Carrie Bow Cay on preceding pages. Finally, the first specimen of the family Callianideidae, *Callianidea laevicauda* Grill, 1959, was taken from intertidal rubble of the exposed reef crest at Carrie Bow Cay. These latest efforts confirm presence of at least one species of the family Axianassidae, add a seventh thalassinidean family to our report, and bring the documented number of thalassinidean species in our survey to at least 19.



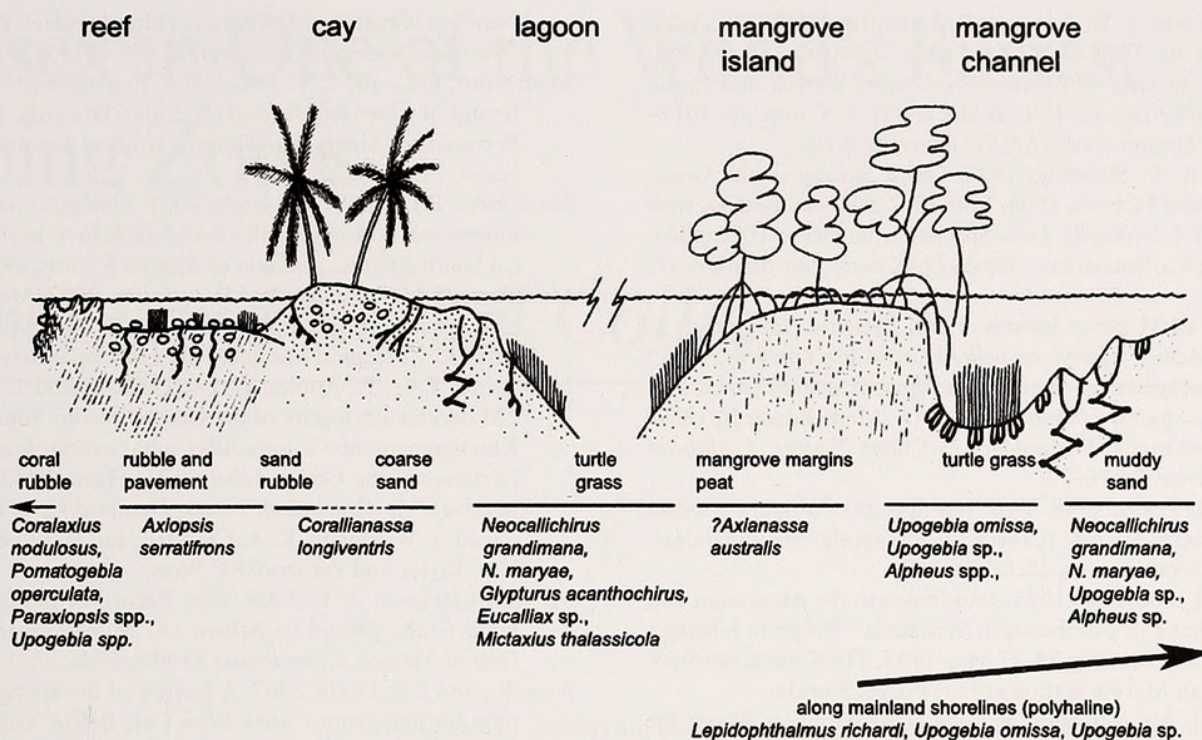


FIGURE 2. Schematic of thalassinidean distributions in channel and back-reef environments near Carrie Bow Cay and Twin Cays, Belize. Modified from Dworschak and Ott (1993:fig. 9).

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