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ECHINODERMS OF THE RHOMBOIDAL CAYS, BELIZE: BIODIVERSITY, DISTRIBUTION, AND ECOLOGY

BY

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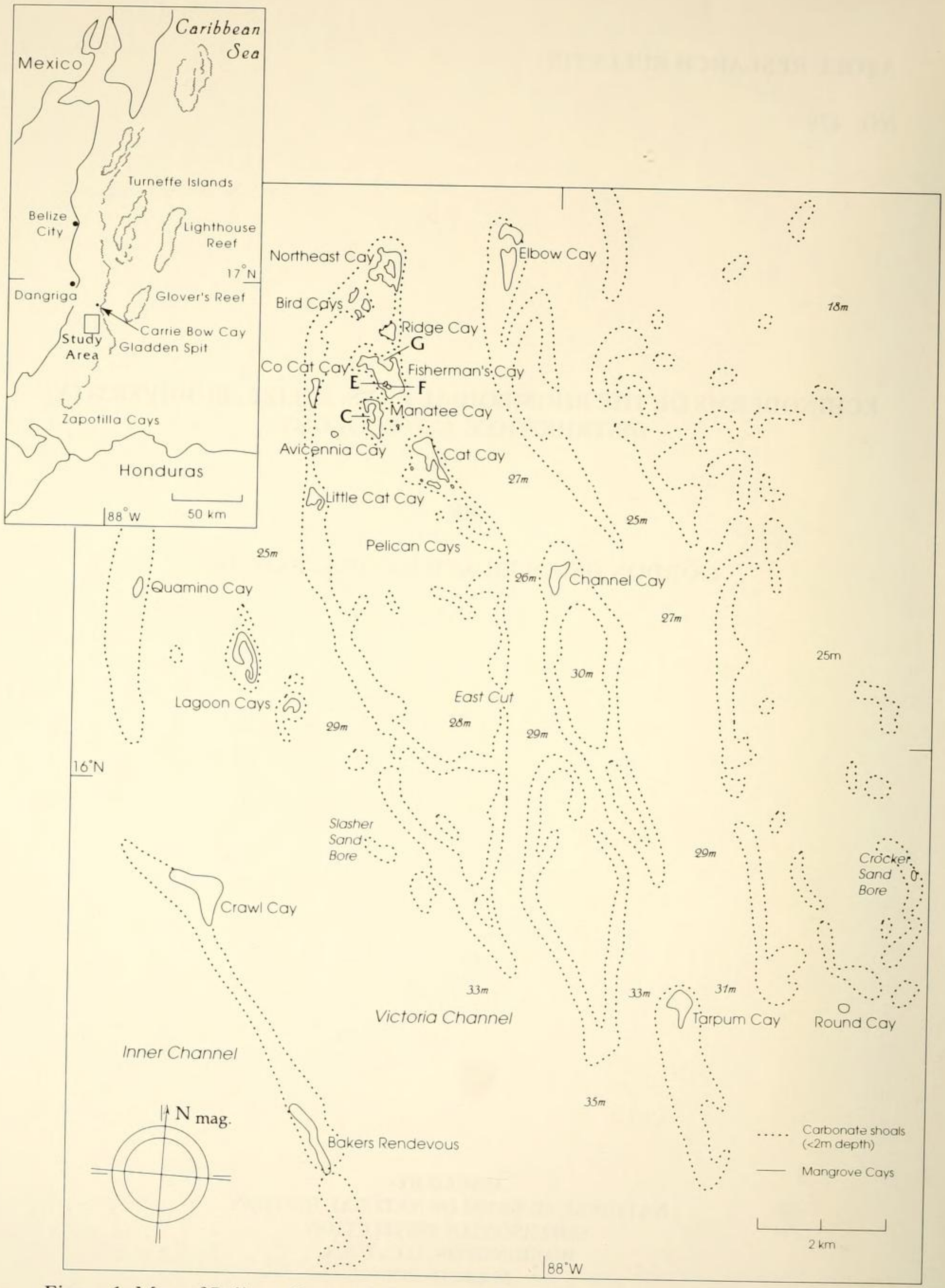

Figure 1. Map of Pelican Cays and the surrounding rhomboidal cays that were surveyed for echinoderms.

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ABSTRACT

Fifty-two species of echinoderms were found in a preliminary survey of 13 sites in the Pelican Cays and the nearby rhomboidal cays in the southern region of the Belize Barrier Reef lagoon. Most are a subset of the 86 species known from the barrier reef and offshore atolls. More species of echinoderms are associated with coral and rubble on the shelf and slope around the cays than in the bays and ponds. Some echinoderms may be excluded from the cays by the low diversity of corals and consequent lack of habitat complexity, the lack of solid substrate and the reduced water flow in protected embayments, and physical stresses, including extreme temperatures and salinities.

Ten species found at the cays have not previously been reported from Belizean waters. Among them are *Ocnus suspectus* and *Thyone pseudofusus*, the first dendrochirote sea cucumbers reported from Belize. It is suggested that the cays offer suitable substrates, calm waters, and possibly a refuge from predation for some species that are cryptic on, or completely excluded from, reef habitats. *Ophioderma cinereum* and *Ophioderma appressum* of unusually large size and dark coloration adopt exposed positions on mangrove peat banks, whereas in reef habitats they are cryptic. *Echinometra viridis*, which shelters beneath rubble in turbulent reef habitats, takes exposed positions at the cays. Its putative role in shaping the composition of coral communities such as the cays is discussed. *Ophiophragmus pulcher* and *Amphipholis* cf. *januarii,* the first long-armed burrowing amphiurid brittle stars reported from Belize, and *Ophiopsila riisei*, typically found in rocky reef substrates, are associated with soft, peat bank substrates.

At the cays, the first instance of *Oreaster reticulatus* feeding on a living coral was noted. Its prey, *Agaricia tenuifolia*, is a dominant species on the steep slopes of the cays. Since *Oreaster* recruits to seagrass beds on the cays, it may be a potential threat to the long-term stability of local coral communities. *Synaptula hydriformis* is reported to be the only echinoderm present in a pond on Elbow Cay, where its success may depend on its capabilities for colonization, its lack of planktonic larvae, and its physiological tolerance of environmental extremes. The pond population of *S. hydriformis* might be a relict from the soft-bottom and coral community that formerly occupied the site or may be of recent origin. The species is a viviparous, self-fertilizing hermaphrodite and potentially a proficient colonist.

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INTRODUCTION

Two notable features of the Pelican Cays, in the southern part of the Belize Barrier Reef lagoon, are the remarkably high species diversity of certain taxa and the abundance of some typically rare and cryptic organisms (Goodbody, 1995; Littler and Littler, 1997). Their unusual ecology is attributed to: the occurrence of coral, mangrove, and seagrass communities in intimate proximity; oligotrophic lagoon habitats with an ample circulation of oceanic seawater; and minimal sediment resuspension. The sensitive habitats probably have been preserved thanks to negligible human visitation to these islands.

Studies of the Pelican Cays habitats are warranted because they have a unique and poorly understood ecology, they are highly susceptible to degradation through natural and anthropogenic disturbance, and a better understanding of the cays is needed to promote their conservation (Goodbody, 1995). Thus, in 1997 Klaus Rützler, Director of the Smithsonian Institution's Caribbean Coral Reef Ecosystems (CCRE) program, invited the authors to conduct a survey of the Pelican Cays echinoderms in order to bolster efforts to preserve their habitats. The present report describes our findings for 1997 and our prior observations in the Pelican group and surrounding cays in 1986 and 1990, which were made in connection with a more extensive survey of the Belizean echinoderm fauna that is in progress.

We summarize the published records for the distribution of Belizean echinoderms and contrast them with our results for the Pelican Cays. In addition, we discuss the species composition and noteworthy characteristics of the echinoderms occurring at the Pelican group. Information is also presented concerning the surrounding islands, including Elbow, Lagoon, Quamino, Bakers Rendezvous, and Tarpum cays because all, like the Pelican group, are parts of "atoll-like" rhomboidal shoals (Fig. 1). Throughout this report, the latter cays and the Pelican group are referred to collectively as the rhomboidal cays.

METHODS

As indicated in Table 1, eight sites in the Pelican group and five neighboring cays were surveyed for echinoderms in 1986, 1990, and 1997. One or two localities were examined at each island. Before 1997, the cays were reached by inflatable boats and whalers that were too small to carry passengers and scuba gear for long distances, and so observations were made using snorkel. Even in calm seas, the trip from Carrie Bow Cay to Elbow Cay took 45 minutes and almost 3 hours to the Lagoon Cays, limiting the time available for fieldwork. In 1997, several localities in the Pelican Cays and vicinity were surveyed with a larger, faster fiberglass boat, permitting scuba observations on several island slopes. Nevertheless, the diversity of habitats examined and the intensity of sampling were limited by time constraints and by efforts to minimize destructive sampling.

Aerial photographs of the cays were taken on March 15, 1989, in the late morning, from an altitude of approximately 500 m.

Most of the species discussed herein are conspicuous epifauna or are associated with large pieces of rubble or small corals that could be easily overturned. Soft bottom and peat bank substrates were sampled sporadically when signs of infauna were noted. In some cases, samples of algae and sponge that were carefully examined and pieces of rubble that were accidentally collected yielded species of echinoderms that would otherwise have been overlooked. However,

DISCUSSION

Composition of the Echinoderm Fauna on the Rhomboidal Cays and Barrier Reef

Belize has a rich shallow-water echinoderm fauna with more than 90 species (Table2; representative species, Fig. 7). The present study suggests that the greatest diversity, comprising approximately 86 species, occurs on coral reef habitats of the Barrier Reef and offshore atolls. Fewer species are associated with the cays of the Barrier Reef lagoon. Most are a subset of the reef-associated fauna, although some have not been found on the reef. A distinctive suite of species is restricted to soft-sediment benthic habitats near the mainland. Only a few mainland species have been reported, which may be attributed to a lack of sampling along the coast and to the influence of terrigenous sediments, river runoff, and other environmental factors. However, several species listed herein for the Barrier Reef environs—including *Paraster doederleini*, *Moira atropos*, and *Brissopsis elongata*—were found exclusively in a mud field within the lagoon (see Kier, 1975) and might better be categorized with the mainland group once their distribution is charted. Kier (1975) found *Paraster* cf. *Paraster floridiensis* in the mud field, and tests of the species were found in shallow water at Bird and Little Cat cays in this study, suggesting it may be more eurytopic than the other mud flat spatangoids.

In the present study, 7 echinoderm species that had not been found on barrier reef and atoll environments were collected from the rhomboidal cays. Kier (1975) reported several sea urchins, listed in Table 2 as belonging to the barrier reef and environs (*Lytechinus variegatus*, *Arbacia punctulata*, and *Clypeaster rosaceus*), as occurring exclusively in the *Thalassia* beds east of Twin Cays, a lagoonal mangrove cay. The occurrence of the same 3 species at the rhomboidal cays, and the 7 species found exclusively at the cays, suggests that there is a distinctive Belizean mangrove cay fauna composed of at least 10 species. However, it is not readily apparent why the species are absent from the barrier reef. The 7 species that were found only at the rhomboidal cays have all been reported from reef and seagrass habitats elsewhere in the Caribbean; only *Echinaster echinophorus* has previously been reported from mangrove habitats (Hendler et al., 1995).

Ocnus suspectus, *Thyone pseudofusus*, and *Pseudothyone belli,* which were found in the rhomboidal cays, represent the first Belizean records of holothuroids in the order Dendrochirotida. Pawson (1976) noted that the absence of dendrochirote sea cucumbers in collections from Carrie Bow Cay was inexplicable, given the importance of the group at other Caribbean localities. Thus the discovery of Belizean dendrochrotes in this study is not surprising, but the reason for their apparent restriction to the cays in the barrier reef lagoon is an enigma. It may be significant that *T. pseudofusus* is unusual among dendrochirotes in that it is a facultative deposit-feeder. It is not known how *O. suspectus* and *P. belli* feed.

As noted above, 10 species present at Pelican Cays localities were not found at the other 5 rhomboidal cays surveyed, and 10 species found at the other rhomboidal cays were absent from the Pelican group. The discrepancies are probably an artifact of sampling, since many of the species are small and easily overlooked, most of them were represented at only one sampling station, and some occurred in substrates that were not systematically sampled. With 44 species of echinoderms, the Pelican group scarcely has greater species richness than the surrounding rhomboidal cays, where 43 species were found.

There are similarities and striking differences between the ophiuroid species that were

Table 1. Localities and dates for surveys of echinoderms at the Pelican group and surrounding cays. Collecting mode, approximate time devoted to the survey, and station numbers are provided for each collection.

Location	Survey Dates						
	7 Apr 86	10 Jun 90	15 Jun 90	5 Sep 97	8 Sep 97	10 Sep 97	11 Sep 97
Elbow Cay	CBC86-24 (bay) snorkel	CBC90-2 (pond) snorkel	CBC90-12 (bay) snorkel CBC90-13 (pond) snorkel			CBC97-19 (bay) snorkel	
Northeast Cay			CBC90-10 snorkel				
Bird Cays			CBC90-11 snorkel				
Fisherman's Cay						CBC97-24 (Frenchy's Ponds, inner cove) CBC97-25 (outer cove) Snorkel 1 hr CBC97-26 (Great Bay) snorkel	
Manatee Cay				CBC97-4 snorkel 1 hr			
Manatee Cay Shoal				CBC97-5 scuba 12 m 1 hr			
Cat Cay				CBC97-3 scuba 18 m 1 hr			
East Cut					CBC97-15 scuba 15 m 1 hr		
Little Cat Cay	CBC86-25 CBC86-26 snorkel 1 hr						
Lagoon Cays	CBC86-27 (outer bay) snorkel ½ hr					CBC97-21 CBC97-22 (slope) scuba 18 m 1 hr CBC97-23 (inner bay) snorkel	
Quamino Cay					CBC97-12 Snorkel 1 hr		
Tarpum Cay					CBC 97-14 snorkel		
Bakers Rendezvous Cay					CBC97-13 scuba 18 m 1 hr		

substrates that serve as microhabitats for small cryptic species were not systematically examined. When habitats were resampled, novel species were found, and others seen previously at the locality were overlooked, indicating that the sampling methodology was not altogether exhaustive.

RESULTS

The Distribution of Belizean Echinoderms

Echinoderm species from Belize reported in reliable sources and those found in the present study are listed in Table 2. The sole records for the mainland of Belize are for Belize Harbor and Stann Creek (= Dangriga) (John and Clark, 1954; Kier, 1975). Information for Turneffe Islands, Lighthouse Reef, and Glover's Reef atolls is based on Devaney (1974) and Boone's (1928) report of *Meoma ventricosa* from Glover's Reef. Records for the barrier reef are derived from surveys at Carrie Bow Cay and environs for echinoids (Kier, 1975), holothuroids (Pawson, 1976), crinoids (Macurda, 1982), ophiuroids (Hotchkiss, 1982; Hendler, 1984, 1988, 1995; Hendler and Miller, 1984; Hendler and Littman, 1986; Hendler and Turner, 1987; Hendler and Peck, 1988; Hendler et al., 1995), and asteroids (Miller, 1984). Additional species of Belizean echinoderms were noted by Hendler et al. (1995), but only their records for specific locales (e.g., Carrie Bow Cay) are considered here.

A total of 88 shallow-water species were previously recorded (Table 2). Three species are reported only from the mainland: *Leodia sexiesperforata*, *Luidia clathrata,* and *Amphipholis gracillima.* The latter two have not been found elsewhere in Belize. Thirty-one species are reported for the offshore atolls, and *Astropecten duplicatus* has been found only there. The richest locale, and the most intensively sampled, is Carrie Bow Cay and environs, where 83 species are known. Twenty-eight species were found there exclusively. They include species limited to the deep fore reef (*Ophiobyrsa serpens*, *Ophionereis vittata*, *Ophioderma ensiferum*, *Sigsbeia conifera*), species associated with reef-dwelling hosts (*Ophiactis quinqueradia*, *Ophiothrix lineata*), and a suite of species typical of exposed Caribbean reef habitats (Crinoidea, *Copidaster lymani*, *Poraniella echinulata*, *Ophioderma anitae*, *O. guttatum*, *O. phoenium*, *Echinometra lucunter*), as well as three species of *Leptosynapta* that are endemic to Carrie Bow Cay.

The survey of the 13 rhomboidal cays sites yielded 53 species. Forty-four species were found at the Pelican Cays localities, and 43 species on the nearby reefs. Eight species occurring on the cays had not been found at the barrier reef or offshore atolls: *Echinaster echinophorus*, *Ophiophragmus pulcher*, *Amphipholis* cf. *januarii*, *Asterina folium*, *Ocnus suspectus*, *Thyone pseudofusus*, *Pseudothyone belli*, and *Holothuria floridana*. The latter 6 species are new records for Belizean waters. Ten species found at the Pelican Cays were not found at the 5 rhomboidal cays nearby, and 10 species found at the latter cays were not collected in the Pelican group.

General Characteristics of the Cays and of the Echinoderms at Each Site

This section provides a description of each cay (see Fig. 1) and of the echinoderms based on field observations. The echinoderm species occurring at each cay are listed in Table 2.

Table 2. Distribution of the echinoderm species found in Belizean waters. Data for the mainland coast (M), offshore atolls including Turneffe Islands, Lighthouse, and Glover's Reef atolls (A), and the Belize Barrier Reef in the vicinity of Carrie Bow Cay (BR) are based on literature cited in Results. Data for the cays surveyed in the present study are listed from north to south: Elbow Cay (EL), Northeast Cay (NE), westernmost of the Bird Cays (B), Fisherman's Cay (FM), Manatee Cay (MN), Manatee Cay shoal (MS), Cat Cay (CA), East Cut (EC), Little Cat Cay (LC), northernmost of the Lagoon Cays (LG), Quamino Cay (Q), Tarpum Cay (TP), and Bakers Rendezvous Cay (BR). X indicates species for which voucher specimens were collected, # indicates non-vouchered records from field notes, and ? denotes field identifications deemed questionable.

Echinoderm Species	M	A	BR	EL	NE	B	FM	MN	MS	CA	EC	LC	LG	Q	TP	BA
Class Crinoidea																
Order Comatulida																
Family Comasteridae																
*Davidaster rubiginosus**		X	X							#						
Davidaster discoideus			X													
Family Colobometridae																
Analcidometra armata			X													
Family Antedonidae																
Ctenantedon kinziei			X													
Class Asteroidea																
Order Paxillosida																
Family Luidiidae																
Luidia clathrata	X															
Family Astropectinidae																
Astropecten duplicatus		X														
Order Valvatida																
Family Asterinidae																
Asterina folium									X							
Family Ophidiasteridae																
Copidaster lymani			X													
Linckia guildingii		X				X										
Family Asteropseidae																
Poraniella echinulata			X													
Family Oreasteridae																
*Oreaster reticulatus**	X			#	#		X	#	X	#		X	#	#	X	
Order Spinulosida																
Family Echinasteridae																
Echinaster (Othilia) echinophorus				X			X					X	X			
Class Ophiuroidea																
Order Phrynophiurida																
Family Gorgonocephalidae																
*Astrophyton muricatum**			X							X	X	X				
Family Ophiomyxidae																
Ophioblenna antillensis			X							X		X		X		
Ophiobyrsa serpens			X													
Ophiomyxa flaccida	X	X	X	X	X	X		X		X	X	X	X			X
Order Ophiurida																
Family Ophiuridae																
Ophiolepis gemma			X								X					
Ophiolepis impressa	X	X	X	X	X	X		X		X	X	X	X			X
Ophiolepis paucispina	X	X														
Ophiolepis pawsoni			X													
Family Ophiocomidae																
Ophiocoma echinata	X	X	X	X	X	X		X				X	X			
Ophiocoma paucigranulata	X	X														
Ophiocoma pumila	X	X	X		X			X				X		#		
Ophiocoma wendtii	X	X	X							X	X	X	X			X
Ophiocomella ophiactoides			X													

Table 2.–continued

Echinoderm Species	M	A	BR	EL	NE	B	FM	MN	MS	CA	EC	LC	LG	Q	TP	BA
Ophiopsila riisei			X	X		X			X	X	X	X	X			X
Family Ophionereididae																
Ophionereis olivacea			X									X	X			
Ophionereis reticulata		X	X	X	X	X	X		X	X		X	X	#		X
Ophionereis squamulosa			X													
Ophionereis vittata			X													
Family Ophiodermatidae																
Ophioderma anitae			X													
*Ophioderma appressum**		X	X	X	X	X	X	X	X	X		X	X	X		
Ophioderma brevicaudum		X	X											X		
Ophioderma brevispinum			X	X								X	X			
Ophioderma cinereum		X	X	X	X	X		X	X	X	X	X	X	#		X
Ophioderma ensiferum			X													
Ophioderma guttatum			X													
Ophioderma phoenium		X	X													
Ophioderma rubicundum		X	X	X		X	X		X	X	X	X	X			X
Ophioderma squamosissimum			X													
Ophiurochaeta littoralis		X	X													
Family Hemieuryalidae																
Sigsbeia conifera			X													
Family Ophiactidae																
Ophiactis algicola			X									X	X			
Ophiactis quinqueradia			X						X							
Ophiactis savignyi		X	X	X			X									
Family Amphiuridae																
Amphiodia pulchella			X	X												
Amphipholis gracillima	X															
Amphipholis cf. *januarii*								X								
Amphipholis squamata			X	X												
Amphiura fibulata			X													
Amphiura stimpsonii			X	X									X			
Ophiophragmus pulcher				X				X								
Ophiostigma isocanthum			X	#												
Ophiostigma siva			X								X		X			
Family Ophiotrichidae																
Ophiothrix angulata		X	X	X			X		X	X	X	X	X			X
Ophiothrix lineata		X	X													
Ophiothrix orstedii		X	X	#	X					X		X	X			X
Ophiothrix suensonii		X	X	X	X		X		X	X	X	X	X			X
Class Echinoidea																
Order Cidaridae																
Family Cidaridae																
Eucidaris tribuloides		X	X			#							#			
Order Diadematoida																
Family Diadematidae																
Diadema antillarum		X	X									#				
Order Arbaciidae																
Family Arbaciidae																
Arbacia punctulata			X	X							X		X			
Order Temnopleuroida																
Family Toxopneustidae																
Lytechinus variegatus		X	X	X	X	X	#					#	X		X	
Lytechinus williamsi			X													X
Tripneustes ventricosus		X	X													
Order Echinoida																
Family Echinometridae																
Echinometra lucunter			X													
*Echinometra viridis**		X	X	X	#	#	X		#	#		X	X	X	X	X

Table 2.–continued

Echinoderm Species	M	A	BR	EL	NE	B	FM	MN	MS	CA	EC	LC	LG	Q	TP	BA
Order Clypeasteroida																
Family Clypeasteridae																
Clypeaster rosaceus			X	#								#	#			
Clypeaster subdepressus			X			X						?	X			
Family Mellitidae																
Leodia sexiesperforata	X		X													
Order Cassiduloida																
Cassidulus caribboearum			X													
Order Spatangoida																
Family Schizasteridae																
Agassizia excentrica			X													
Moira atropos		X	X													
Paraster doederleini			X													
Paraster cf. *P. floridiensis*			X			X						X				
Family Brissidae																
Brissopsis elongata			X													
Brissus unicolor																
Meoma ventricosa		X	X													
Plagiobrissus grandis			X													
Class Holothuroidea																
Order Dendrochirotida																
Family Cucumariidae																
Ocnus suspectus						X										
Family Sclerodactylidae																
Euthyonidiella destichada			X													
Pseudothyone belli													X			
Family Phyllophoridae																
Thyone pseudofusus				X												
Order Aspidochirotida																
Family Stichopodidae																
Isostichopus badionotus			X	X	X		#			X		X	X			
Isostichopus macroparentheses			X													
Family Holothuriidae																
Actinopyga agassizi			X	?				?	?	X			X	?		
Holothuria (Cystipus) cubana			X		X	X						X	X	X		
Holothuria (Halodeima) floridana				X		X						X	X	X		
*Holothuria (Halodeima) mexicana**			X	X	#		#	X	X			X	X	#	?	
Holothuria (Thymiosycia) arenicola			X											X		
Holothuria (Thymiosycia) impatiens			X	X			?		X	X		X	X			X
Holothuria (Thymiosycia) thomasi			X		X				X		X	X				
Order Apodida																
Family Synaptidae																
Euapta lappa		X	X													
Leptosynapta imswe			X													
Leptosynapta nannoplax			X													
Leptosynapta roseogradia			X													
Synaptula hydriformis			X	X												
Family Chirodotidae																
Chirodota rotifera			X													

*See Figure 7

Elbow Cay. This elongate island is at the northern tip of an extensive rhomboidal shoal that lies west of the Pelican group (Fig. 2). Its large stands of mangroves partly encircle several bays and completely enclose a small pond (Figs. 2, 4). Features of the island—its deeply indented shoreline, bays with protective sills, and enclosed pond—are similar to those of the Pelican Cays.

In aerial views the outline of the island resembles the reticulate shape of the neighboring rhomboidal shoals. The appearance of Elbow and Pelican cays suggest that mangroves, once established on a rhomboidal shoal, may form bays by overgrowing shallow portions of the reef, and may form ponds by obstructing the mouths of bays. In time, the bays could give rise to ponds, and ponds could give rise to bays or fill with mangrove swamp, depending on the advance and retreat of the mangroves and corals that colonize the shoals. As noted below, corals and burrowing and boring bivalves are buried in the unconsolidated sediment in the Elbow Cay pond. They are apparently the remnants of a now defunct soft-bottom coral community, which is consistent with the view that the site was formerly an open embayment (Fig. 5).

The sites examined were the large, west-facing and small, east-facing bays and the pond near the northern end of the island. The western bay is approximately 15 m deep, with a sill across its mouth reaching within less than 1 m of the surface. The seaward slope of the sill is covered with rubble, and colonized by calcareous algae and gorgonians. Within the bay the slope is covered with coarse sediment and a little *Thalassia*. Shallow, hard-bottom areas within the large bay have small coral heads scattered over the surface, including *Siderastrea*, clumps of branching *Porites* and *Millepora*, along with gorgonians, rubble, *Thalassia*, and sediment with many *Halimeda* flakes. Areas of exposed mangrove peat have a cover of seagrass, algae (including *Padina*), sponge, and some patches of *Halimeda* flakes. In places where the peat banks are steep and undercut, there are free-hanging mangrove roots covered with sponge, *Clavelina*, *Caulerpa* and *Lobophora*, and a few with large, stacked plates of *Porites astreoides*. Near the south edge of the large bay a sandy ridge rises to within 2.5 m of the surface. *Porites* rubble and sponge (*Spheciospongia*?) is present on the top of the ridge. Seagrass grows on the crest and on both flanks of the ridge. Spadefish, grunts, and snapper were seen in the large bay.

The eastern bay is 9 m deep and is separated from the larger bay by a shallow sill. The hard bottom nearby has scattered corals and sponge, and the sand bottom had *Thalassia* and *Syringodium*. The reef slope seaward of the east bay had a *Thalassia* cover and a few large sponges (*Spheciospongia*?).

The enclosed pond, at most 5 m deep, is separated from the large bay by a stand of mangrove approximately 30 m wide (Fig. 3). The bottom of the pond is covered with unconsolidated sediment about 0.6 m thick, composed largely of microscopic fecal pellets of unknown origin. Near the center of the pond there is a thinly covered framework of dead coral, the bivalves *Chione cancellata* and *Gastrochaena hians*, and peat (Fig. 5). Visibility in the pond ranges from 3 to 5 meters horizontally. The murkiness is due to suspended fine particulates, the mixing of water with different densities, and possibly the presence of tannins. Temperature and salinity measurements indicate that the exchange of water between the pond and sea and mixing within the pond are limited. After a brief rainstorm on June 10, 1990, refractometer readings indicated the surface salinity in the pond was 31 ppt and the bottom salinity was 36 ppt. On June 15, 1990, the water temperature at a depth of 0.3 m inside the pond was 32°C, whereas in the bay it was 30°C. An open channel to the reef was not seen, but cooler and warmer parcels of water were felt by Hendler while snorkeling in the pond.

Figure 2. Elbow Cay: oblique aerial view showing the small eastern bay, larger western bay, and the enclosed pond at the northern end of the island. Reef surrounding the island forms a shallow sill at the mouths of the bays and joins a rhomboidal shoal which is seen to the south of the cay.

Figure 3. Elbow Cay: dense stand of *Rhizophora mangle* surrounding the enclosed pond.

Figure 4. Elbow Cay: enclosed pond, overview. Thick mats of filamentous green algae entangled in the prop roots of red mangrove trees float at the waterline.

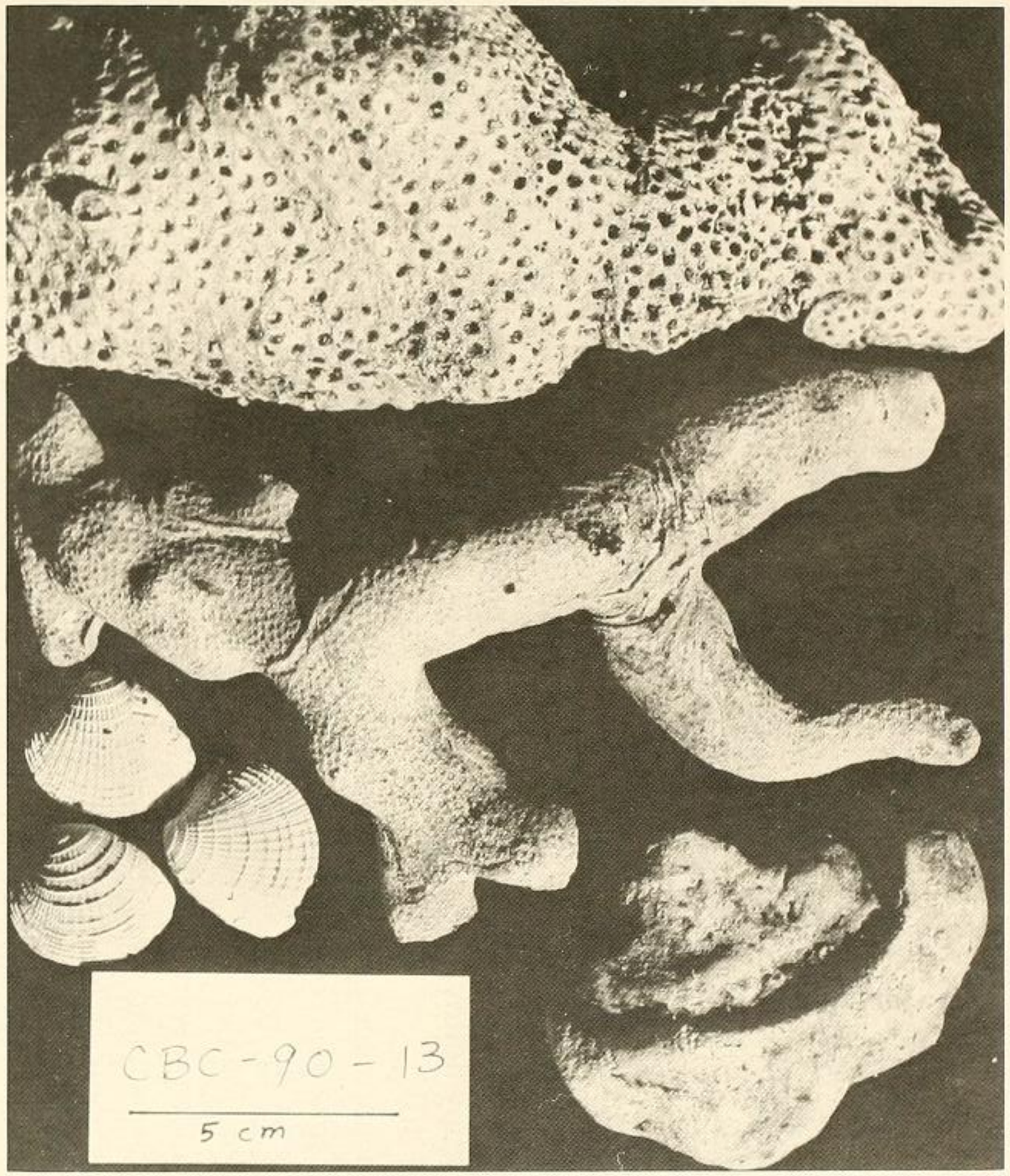

Figure 5. Elbow Cay: fragments of corals and the bivalve *Chione cancella* from the center of the enclosed pond.

At the edge of the pond there are floating mats of filamentous algae (Fig. 4), and mangrove roots thickly covered by *Caulerpa verticillata* and other algae, dangling a meter into the water. Other conspicuous biota associated with the roots include extremely numerous sabellids and actinarians, various sponges and gastropods, with a bullid snail in abundance, oysters, a green colonial ascidian, tanaids, and shrimps. The soupy sediment is covered with patches of white microbial mat near the shore, and elsewhere with a thin layer of greenish material (cyanobacteria and/or diatoms?) supporting a rich meiofauna. Barracuda, snappers, silvery schooling fish, and mosquitofish were seen in the pond.

The peat banks in the western bay have a distinctive echinoderm fauna, including *Ophiopsila riisei*, a long-armed brittle star that typically nestles in coral interstices at reef habitats. Hendler et al. (1995) stated that it lives in mangrove peat banks after observing a dense population of the species in the large bay at Elbow Cay in 1986, and again in 1997. Individuals do not extend their arms during the day and are presumably active nocturnally. Those excavated from peat occupy hollow cavities such as those found in decomposing twigs, with their arms enfolding the disk.

The occurrence of two species of small nestling amphiurid brittle stars is also notable. *Amphipholis squamata* occurs in a wide range of microhabitats, and *Amphiodia pulchella* is usually found on the reef in soft sediment or in association with algae and corals (Hendler and Littman, 1986; Hendler et al., 1995). *Ophioderma cinereum*, *Ophiolepis impressa*, *and Ophiomyxa flaccida* were found under clumps of *Millepora* and sponge, and *Ophioderma brevispinum* in peat and mangrove leaves and under rubble amid seagrass. An orange sponge, *Mycale laevis*, yielded 249 specimens of *Ophiactis savignyi*. They were nearly all small and fissiparous; only one among the few large individuals had five arms. In 1990, *Echinometra viridis* was noted to be much more common than *Lytechinus variegatus*. In 1997, at the same locality, small *L. variegatus* were particularly abundant under rubble; *E. viridis* was again common and was sometimes found under the same pieces of rubble as *Arbacia punctulata*.

The only echinoderm species seen in the Elbow Cay pond is *Synaptula hydriformis*. In Bermuda the species is usually mottled brown and white, and green and white individuals have been noted at Carrie Bow Cay (Pawson, 1976, 1986). The living individuals at Elbow Cay are brown and turn red when preserved in ethanol.

Northeast Cay, Pelican Cays. The southwest part of the cay has an exposed sandy coastline with *Thalassia* and *Syringodium* near the shore. Barnacles grow on mangrove roots along the shore. In the bay nearby, cover for echinoderms is provided by rubble, sponge, a small amount of *Acropora cervicornis*, *Millepora*, zoanthid mats, gorgonians, and *Padina*. Clumps of *Agaricia* can be seen along the crest and flank of the slope outside the bay, but the lower part of the slope is sandy. Mounds of conch shells and clumps of *Halimeda* occur in the water near a fish camp. One *Lytechinus variegatus* was seen in the bay, with its peristomial region and viscera missing, but with the spines on the test still moving. It is not known if the urchin was preyed upon by a boxfish seen nearby.

Bird Cays, Pelican Cays. Large brain corals were seen at the collecting site on the westernmost part of the Bird Cays. Echinoderms were collected from rubble, *Millepora*, and coral occurring in the shallows near the island, which were dominated by *Thalassia*.

Fisherman's Cay and Ponds E and F, Pelican Cays). Some details can be added to a previous description of the habitats at Fisherman's Cay (Littler and Littler, 1997). Ctenophores were observed carried by the current into the larger (outer) Pond E but the water was relatively still in the smaller (inner) Pond F. Evidently, it is only at the mouths of the two ponds that water currents sweep the bottom clean and expose firm sediment. Pen shells are embedded in sediment near the entrance to the outer pond. Elsewhere the sediment is soupy, with white microbial patches in places. Pendent mangrove roots support huge masses of *Caulerpa verticillata* and *C. racemosa*, *Halimeda opuntia*, ascidians, various sponges, and an abundance of small sabellid worms. A dense bed of *Thalassia* is present in the outer cove.

The sessile fauna is strikingly different on the hard shelf immediately outside Frenchy's Ponds E and F. There, large gorgonians and sponges, and large plates of coral (*Montastrea* or *Porites*?), grow on *Rhizophora* roots. The steep shelf slope is densely populated with sponge, gorgonians, and living *Agaricia*. The northern side of the cay, at the mouth of Great Bay, is the site of a broad shoaling *Thalassia* flat with many clumps of *Millepora* and *Porites*, some overgrown by zoanthids. The wall of the seaward slope has a cover of coral rubble and sponge.

Oreaster reticulatus was the only echinoderm seen in Pond E. In the field, a superficial examination of algae in the inner cove was unproductive, but a one-gallon sample of *Halimeda opuntia* from the outer cove studied in the laboratory yielded two specimens of *Ophiothrix angulata*. The undercut peat banks might have harbored echinoderms, but a cursory search for them was unproductive. In contrast to the pond, the cay's shelf and slope support a profusion of *Ophiothrix suensonii*, as well as *Isostichopus badionotus*, *Holothuria mexicana*, and *Lytechinus variegatus*. *Echinometra viridis* is abundant at Great Bay. *Echinaster echinophorus* occurs in the open on sandy algae-covered sediment, and *Ophiopsila riisei* is common in the clumps of algae growing on the top of the slope at the mouth of the embayment.

Manatee Cay, Pond C, and Manatee Cay Shoal, Pelican Cays. In Pond C, the surface water is very warm and a reddish color. Mangrove roots on the northern side of the pond are heavily overgrown with sponge, algae, and colonial tunicates. In places the peat banks are 2 m high and strongly undercut. Sponges cover the ceiling of the undercuts; patches of decomposing mangrove leaves cover areas of the soft-sediment floor. French angel fish and barracuda were seen in the pond.

A dive was made on both sides of a shoal at the south end of the island. *Acropora cervicornis* was found growing sparsely on the summit of the ridge. A dense cover of *Agaricia* fouled by sponges and fine sediment, together with some large coral shelves (*Montastrea annularis*?), is present on both flanks. One section of the shoal is free of living coral and thickly covered with rubble.

In Pond C, burrowing amphiurid brittle star arms can be seen on the surface of the mud. *Ophiophragmus pulcher* and *Amphipholis* cf. *januarii* were collected from soft sediment beneath the overhanging peat banks. They were the only echinoderms seen in Pond C. In the seagrass bed surrounding the island, *Ophioderma appressum* and *O. cinereum* were collected from beneath coral rubble and large *Holothuria mexicana* and *Oreaster reticulatus* were observed in the open. The latter was also found on the reef slope, and an individual was seen with its arms clasping a colony of *Agaricia tenuifolia*. Beneath the extruded stomach of the sea star, tissue of the coral was dissolving and white skeleton was exposed. *Echinometra viridis* was found to be common on the shoal, on coral, and on rubble-dominated portions of the slope. *Actinopyga agassizi* and

Holothuria mexicana were collected from the rubble-covered area, and a small individual of *Asterina folium* was collected on a piece of rubble gathered with the sea cucumbers.

Cat Cay and East Cut, Pelican Cays. The wall on the northeast slope of the cay and the southern side of the opening at East Cut were observed while using scuba. The latter site is a break near the middle of a shoal that extends southward for approximately three kilometers from Cat Cay. Off Cat Cay, at depths of 4 to 6 m, there is a narrow shelf with rubble cover and small corals, large brain corals, and *Rhipocephalus* brushes. The steep wall of the slope consists of silty sediment colonized by colonies of *Agaricia tenuifolia*, plates of large agariciids, and shingled brain corals, along with some *Halimeda*, delicate sponges, gorgonians, and antipatharian wires. The slope at East Cut is similar, with rubble overgrown by *Lobophora*, *Agaricia tenuifolia*, agariciids, and scattered gorgonians and antipatharian wires being the predominant cover. A brief boat reconnaissance at Channel Cay, due east, indicated that coral cover is sparser there than at East Cut.

The echinoderm fauna on the shallow shelf is fairly diverse; exposed *Oreaster reticulatus* is present, along with *Ophioderma* spp., *Ophioblenna antillensis*, and *Ophionereis reticulata* associated with corals and rubble. *Echinometra viridis* is very abundant on the slope, and *Ophiothrix suensonii* and *Ophiocoma wendtii* are fairly common. At a depth of 9 m, a juvenile *Astrophyton muricatum* was found entwined in a gorgonian. The only ophiuroids seen at depths >9 m were large *Ophioderma cinereum* and *Ophioderma rubicundum*. *E. viridis* was not recorded at East Cut, but *Arbacia punctulata* was collected there.

Little Cat Cay, Pelican Cays. *Thalassia* grows close to the mangrove roots in shallow water at the southeast corner of the cay. A reef flat with coral, rubble, and sponges occurs where the bottom slopes gradually to a depth of approximately 1 m. A long shoal extending southward from the island has a steeply sloping western flank reaching more than 15 m in depth. Hard-bottom areas in the bight on the southwest side of the island are composed of densely packed *Porites* rubble. Mangroves roots are embedded in a thin layer of peat and sand. A ridge crest occurs several meters from the mangrove shoreline. It is occupied primarily by clumps of *Agaricia* and *Millepora*, some overgrown with algae, sponge, or zoanthid, and by some thickets of *Acropora cervicornis*. Sandy slumps occur between the coral patches. The sandy slope of the ridge is strewn with rubble, scattered sponges, and gorgonians. It drops at a 45° angle, to a depth of more than 15 m, onto a gently sloping sand bottom.

Acropora cervicornis on the ridge crest is densely covered with climbing *Echinometra viridis* at one site, and at another the branches are overgrown with a greenish-brown sponge. Clumps of *Agaricia* were found to harbor *Ophiomyxa flaccida*, *Ophioderma appressum* and *O. rubicundum*, and *Ophioblenna antillensis*; *Ophiothrix angulata* and *Ophionereis reticulata* were found in *Halimeda*. Many large blue and yellow individuals of *Ophiothrix suensonii* were conspicuous on the slope of the ridge. *Ophiopsila riisei* was found at Little Cat Cay, but in less abundance than at Elbow Cay. A small individual of *Astrophyton muricatum* at the site had an associated shrimp, *Periclimenes perryae*. Three large individuals of *Diadema antillarum* were noted on a peat bank; this was the only sighting of the species in rhomboidal cays.

Lagoon Cays. The northerly cay (Fig. 6) was first surveyed in 1986, and the small outer cove of the bay was examined at that time. The reef flat was occupied by gorgonians with dead

branch tips that may have been killed by exposure, and by coral heads of moderate size. A bed of *Thalassia* with short blades grew on a densely packed coral rubble bottom that was covered with a thin layer of sand. The bed extended to the shore, where mangrove roots were fixed in the sand and there was a very shallow peat bank. In 1997, seagrass was noted on the southeast coast of the island, outside the bay.

Figure 6. Lagoon Cays: oblique aerial view showing the larger northern cay, smaller southern cay, and surrounding shoals. The northern cay has an enclosed pond, which was not explored, and a bay with a large, deep cove and a small shallow cove.

In 1997, we examined the deep inner pond of the bay. The mangrove roots hanging from high, steep peat banks were thickly covered with oysters, and abundant *Ascidia nigra* and other solitary tunicates with associated sabellid worms. At that time, 5% of the *A. nigra* were turning white and disintegrating. Beneath the bank, terebellid tentacles extended from the soft sediment and in other areas there were accumulations of *Halimeda* flakes. Seaward of the bay there was a silty slope on the flank of the cay, with little coral cover.

On the northeast side of the cay, near the crest of the reef, the shelf at 6 m depth is dominated by seagrass, with gorgonians, clumps of *Porites*, moderate-sized coral heads, and a few large brain corals. The reef slope is covered with soft sediment and scattered living *Agaricia*

and agariciid plates, gorgonians, and antipatharian wires. At 12 m depth, the cover is provided by algae; much of the *Agaricia* there is dead. At a depth of 18 m, the bottom is composed largely of silty soft sediment, except for occasional coral clumps and *Halimeda*.

At Lagoon Cays, the presence of *Ophioderma cinereum* and *Ophioderma appressum* in exposed positions on the tops of high peat banks is noteworthy, since both species are invariably cryptic wherever they occur in reef habitats (Hendler et al., 1995). Most of the individuals were large. Among those collected were an *O. cinereum* (disk diameter, 35.7 mm; arm length, 163 mm) and an *O. appressum* (disk diameter, 25.3 mm; arm length, 125 mm) approaching the maximum size known for the two species (Hendler et al., 1995). Orange-red individuals of *Echinaster echinophorus* were found in the open on the walls of the peat bank. The arms of burrowing amphiurids were not observed in or near the bank, but individuals of *Ophionereis reticulata* extended their arms from the sediment below the banks and anchored their disks in the branches of buried *Porites* rubble. *Ophiothrix angulata* was perched on top of epiphytic *Ascidia nigra* and was found along with *Ophiopsila riisei* in the shallow mangrove peat bank near the outer part of the bay. Several species of holothuroids, *Ophionereis olivacea*, *Ophiocoma echinata*, and *Arbacia punctulata*, which were collected in 1986 but not in 1997, were found amid rubble near the outer part of the bay.

The density and abundance of echinoderms on the reef slope was greatest near the crest and decreased downslope. At 18 m only a few individuals of *Ophioderma* and *Ophiocoma* were found associated with coral rubble. However, *Amphiura stimpsonii*, *Ophiothrix angulata*, *Ophiactis algicola*, and juvenile *Ophiopsila riisei*, *Ophiostigma* cf. *siva*, and *Echinometra viridis* were found in a sample of *Halimeda*. A full-grown specimen of *O. siva* was found on a piece of rubble collected along with holothuroids.

Most species occurring in the inner bay—including *Echinometra viridis*, *Ophioderma cinereum*, *O. appressum*, *O. reticulata*, *Ophiopsila riisei*, *Ophiolepis impressa*, and *Ophiothrix angulata*—are a subset of those collected on the reef slope at the Lagoon Cays. However, *Lytechinus variegatus*, *Echinaster echinophorus*, and *Isostichopus badionotus* are restricted to the bay. *Ophiomyxa flaccida*, *Ophioderma rubicundum*, *Ophiocoma wendtii*, *Ophiostigma siva*, *Ophiothrix suensonii*, *O. oerstedii*, *Ophiactis algicola*, *Actinopyga agassizii*, and *Holothuria impatiens* only occur on the reef slope.

Quamino Cay. Quamino Cay occupies the northeast end of a narrow rhomboidal shoal that borders the inner channel of the Belize barrier reef lagoon and lies to the west of Little Cat Cay. During a brief snorkeling reconnaissance, a *Thalassia* bed was seen abutting the mangroves on the eastern edge of the island. A shallow shelf extending from the northeast corner of the cay has considerable sponge and algae cover, *Siderastrea* and heads of brain coral, clumps of *Agaricia*, and sparse *Acropora cervicornis*. Whenever a piece of rubble was turned, a dense cloud of fine sediment spread through the water. The reef slope also has a thick cover of silty sediment and scattered *Agaricia* and gorgonians.

Most of the echinoderms collected at Quamino Cay live in dead clumps of *Agaricia* and in large pieces of rubble, which are overgrown with algae. The most common species on the shallow shelf are *Ophioderma cinereum*, *Ophionereis reticulata*, and *Ophiocoma pumila*. The latter two typically nestle in rubble-covered sediment at back-reef habitats such as Carrie Bow Cay.

Tarpum Cay. The cay is at the northern end of a group of rhomboidal shoals to the southeast of the Pelican Cays. Observations made from the boat indicated there was sparsely distributed *Agaricia* on the silty slope around the island. The survey was made while snorkeling in the island's south-facing bight. There, peat banks along the mangrove-lined shoreline are shallow and very hard. Exposed roots bear meager algae and sponge cover and, in pools between the roots, there are accumulations of decomposing leaves and white microbial mat. The fine white sand beyond the mangroves covers mangrove roots and fallen trunks, and has a sparse growth of *Thalassia* and *Caulerpa*. Further from shore, where the depth is 1 to 3 m, the bottom is composed of fine white silt with numerous mounds and burrows, and individuals of *Cassiopea* are numerous. In places at Tarpum Cay, the water washing out of mangroves is an intense brownish color, presumably from tannins in solution.

The site is relatively unproductive, in part because there is hardly any rubble to shelter echinoderms, and the sand bottom and peat are too hard-packed for most burrowing species. An effort to locate burrowing brittle stars in the peat banks was not successful. However, purely epifaunal organisms were found, including *Holothuria mexicana* and *Oreaster reticulatus*.

Bakers Rendezvous Cay. The cay is south of Quamino Cay and southwest of Tarpum Cay and the Pelican group. It is situated on a very long narrow shoal that separates Victoria Channel from the broad Inner Channel of the barrier reef lagoon. The dive site was located on the steeply sloping face of the island to the east of the gap between the two main stands of mangroves on the cay. As at Quamino Cay, the water was murky and the bottom very silty. At a depth of 6 m, there is a shelf covered by a *Thalassia* bed; at greater depths on the slope *Agaricia tenuifolia* appears, along with some large agariciid plates, gorgonians, antipatharian wires, and a few small brain corals.

Echinometra viridis was very common at this site. A single individual of *Lytechinus williamsi* was found, the only one seen in the rhomboidal cays. The individuals of *Ophioderma cinereum* (max. 23.4 mm) and *Ophioderma rubicundum* (max. 14.5 mm in disk diameter) that were collected were of typical size.

Characteristics of the Mangrove Cay Fauna

Table 3 compares the dominant ophiuroid species from the rhomboidal cays and the barrier reef. It shows that the cays fauna are more similar to that of the shallow rubble habitats on the barrier reef than to that of the living substrates in shallow water on the barrier reef and the fore-reef slope. The comparison is inexact, as it is based on the number of sites, of a possible maximum of 13, at which the rhomboidal species occur, versus an actual percentage of the population represented by each species at three Barrier Reef habitats.

Among the echinoderms found at five or more localities in the rhomboidal cays were 13 ophiuroids, *Echinometra viridis*, *Lytechinus variegatus*, *Oreaster reticulatus*, *Holothuria mexicana*, *H. impatiens*, *H. cubana*, *H. floridana*, and *Isostichopus badionotus* (Table 3). The most widespread echinoderms were *Ophioderma cinereum* and *Echinometra viridis*, both of which were found at 11 localities. *Ophiomyxa flaccida*, *Ophionereis reticulata*, *Ophioderma appressum* and *Ophiolepis impressa* were almost as common; each was found at 10 of the 13 surveyed localities in the rhomboidal cays.

Table 3. Frequency of occurrence of the most widespread rhomboidal cays echinoderms compared with the most numerically abundant barrier reef ophiuroids. Rhomboidal cays species are listed in the order of the number of sites (out of 13) at which each was observed. The 10 most common ophiuroids at the rhomboidal cays fall above the dashed line. The ophiuroids that were among the 10 most common at the barrier reef, and are also among the most widespread in the rhomboidal cays, are indicated by an X. Their ranking was calculated in terms of the percentage of the population each species comprised at 3 different habitats at Carrie Bow Cay (based on Hendler and Peck, 1988: 414).

	Rhomboidal Cays (all taxa)	Barrier Reef (ophiuroids only)		
Species	Number of sites (descending)	Shallow reef (in living substrata)	Shallow reef (in rubble)	Fore-reef slope
Ophioderma cinereum	11			
Echinometra viridis				
Ophiomyxa flaccida	10			X
Ophionereis reticulata			X	
Ophioderma appressum			X	X
Ophiolepis impressa			X	
Oreaster reticulatus				
Ophioderma rubicundum	9	X	X	X
Ophiothrix suensonii				
Ophiopsila riisei	8			X
Ophiothrix angulata		X		
Holothuria mexicana				
Ophiocoma echinata	7	X	X	

Lytechinus variegatus				
Ophiocoma wendtii	6	X	X	X
Ophiothrix orstedii		X	X	
Holothuria impatiens				
Isostichopus badionotus				
Ophiocoma pumila	5	X	X	
Holothuria cubana				
Holothuria floridana				

Several species of ophiuroids found at the rhomboidal cays were distinguished from their reef-dwelling conspecifics by differences in size and pigmentation. As detailed in the treatment of Lagoon Cays, individuals of *Ophioderma cinereum* at the rhomboidal cays are also unusually large. Reef-dwelling individuals of *O. cinereum* are characteristically pale gray. Those at the cays are typically brown or grayish-brown, with a tendency for small individuals to be grayish and large individuals to be dark brown. *Ophiolepis impressa* collected from the cays were sometimes a deeper brown color than individuals from the Barrier Reef habitat. The individuals of *Ophionereis reticulata* at the cays have a less distinct and contrasting netted pattern on the disk than those from many coral reefs.

DISCUSSION

Composition of the Echinoderm Fauna on the Rhomboidal Cays and Barrier Reef

Belize has a rich shallow-water echinoderm fauna with more than 90 species (Table2; representative species, Fig. 7). The present study suggests that the greatest diversity, comprising approximately 86 species, occurs on coral reef habitats of the Barrier Reef and offshore atolls. Fewer species are associated with the cays of the Barrier Reef lagoon. Most are a subset of the reef-associated fauna, although some have not been found on the reef. A distinctive suite of species is restricted to soft-sediment benthic habitats near the mainland. Only a few mainland species have been reported, which may be attributed to a lack of sampling along the coast and to the influence of terrigenous sediments, river runoff, and other environmental factors. However, several species listed herein for the Barrier Reef environs—including *Paraster doederleini*, *Moira atropos*, and *Brissopsis elongata*—were found exclusively in a mud field within the lagoon (see Kier, 1975) and might better be categorized with the mainland group once their distribution is charted. Kier (1975) found *Paraster* cf. *Paraster floridiensis* in the mud field, and tests of the species were found in shallow water at Bird and Little Cat cays in this study, suggesting it may be more eurytopic than the other mud flat spatangoids.

In the present study, 7 echinoderm species that had not been found on barrier reef and atoll environments were collected from the rhomboidal cays. Kier (1975) reported several sea urchins, listed in Table 2 as belonging to the barrier reef and environs (*Lytechinus variegatus*, *Arbacia punctulata*, and *Clypeaster rosaceus*), as occurring exclusively in the *Thalassia* beds east of Twin Cays, a lagoonal mangrove cay. The occurrence of the same 3 species at the rhomboidal cays, and the 7 species found exclusively at the cays, suggests that there is a distinctive Belizean mangrove cay fauna composed of at least 10 species. However, it is not readily apparent why the species are absent from the barrier reef. The 7 species that were found only at the rhomboidal cays have all been reported from reef and seagrass habitats elsewhere in the Caribbean; only *Echinaster echinophorus* has previously been reported from mangrove habitats (Hendler et al., 1995).

Ocnus suspectus, *Thyone pseudofusus*, and *Pseudothyone belli,* which were found in the rhomboidal cays, represent the first Belizean records of holothuroids in the order Dendrochirotida. Pawson (1976) noted that the absence of dendrochirote sea cucumbers in collections from Carrie Bow Cay was inexplicable, given the importance of the group at other Caribbean localities. Thus the discovery of Belizean dendrochrotes in this study is not surprising, but the reason for their apparent restriction to the cays in the barrier reef lagoon is an enigma. It may be significant that *T. pseudofusus* is unusual among dendrochirotes in that it is a facultative deposit-feeder. It is not known how *O. suspectus* and *P. belli* feed.

As noted above, 10 species present at Pelican Cays localities were not found at the other 5 rhomboidal cays surveyed, and 10 species found at the other rhomboidal cays were absent from the Pelican group. The discrepancies are probably an artifact of sampling, since many of the species are small and easily overlooked, most of them were represented at only one sampling station, and some occurred in substrates that were not systematically sampled. With 44 species of echinoderms, the Pelican group scarcely has greater species richness than the surrounding rhomboidal cays, where 43 species were found.

There are similarities and striking differences between the ophiuroid species that were

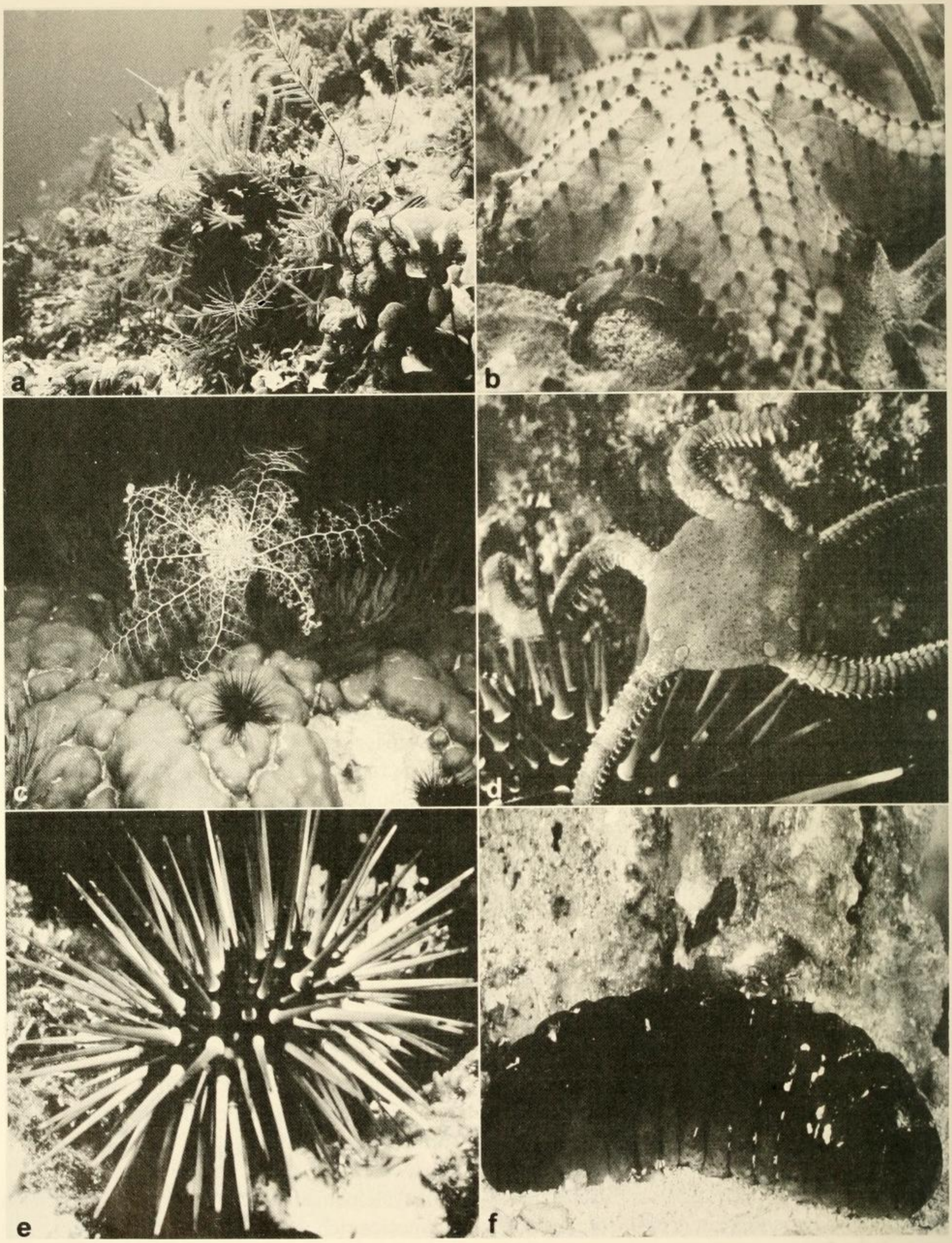

Figure 7. Common representatives of echinoderms in situ in Belize: a, Feather star, *Davidaster rubiginosa* (Crinoidea), top arrow, among gorgonians on slope of coral ridge near Cat Cay, 5 m; ophiuroid (lower arrow) arms protruding from lettuce coral *(Agaricia)* in right foreground (photo I.G. Macintyre). b, Cushion sea star, *Oreaster reticulatus* (Asteroidea) (photo K. Rützler). c, Basket star, *Astrophyton muricatum* (Ophiuroidea) (photo C. Clark). d, Brittle star, *Ophioderma appressum* (Ophiuroidea) on top of sea urchin (photo G.M. Miller). e, Sea urchin, *Echinometra viridis* (Echinoidea) (photo G.M. Miller). f, Sea cucumber, *Holothuria mexicana* (Holothuroidea) (photo K. Sandved).

most widespread at the rhomboidal cays, and the species that are most abundant on the barrier reef at Carrie Bow Cay (Table 3). A list of the 10 most widespread ophiuroid species from the rhomboidal cays includes 8 of the most abundant species found by Hendler and Peck (1988) in 3 barrier reef habitats near Carrie Bow Cay (i.e., *Ophiomyxa flaccida*, *Ophionereis reiculata*, *Ophioderma appressum*, *Ophiolepis impressa*, *Ophioderma rubicundum*, *Ophiopsila riisei*, *Ophiothrix angulata*, and *Ophiocoma echinata*). *Ophioderma rubicundum*, which was the most numerous species on the fore-reef slope of the barrier reef, was relatively widespread in the rhomboidal cays. However, ophiuroid species at the barrier reef that were most numerous in shallow-water reef rubble *(Ophiocoma echinata*) and in shallow-water living substrates (*Ophiocoma pumila)* were not particularly widespread at the rhomboidal cays. Moreover, the most widespread ophiuroid at the rhomboidal cays (*Ophioderma cinereum*) was relatively rare on the reef (Hendler and Peck, 1988) and thus is not listed for the barrier reef in Table 3.

Because so little is known about their natural history, it is difficult to explain why some species have been successful in the rhomboidal cays and others have not though they are abundant on the barrier reef (Hendler et al., 1995). It is possible that the population density and distribution of rhomboidal cays echinoderms generally hinge on coincidental, stochastic events in population recruitment and extinction. It is also possible that their success depends on crucial adaptations in reproductive mode, behavior, competitive capabilities, or physiology, and on environmental factors peculiar to the cays. The alternative explanations should be tested, since the results might provide a better understanding of the rhomboidal keys and of large-scale changes on Caribbean reefs.

Presence, Absence, and Impact of Echinoderm Species in the Rhomboidal Cays

E. viridis is one of the most widespread echinoderms of the rhomboidal cays. Our observation of large numbers of *E. viridis* climbing on the branches of *Acropora cervicornis* in 1986 at Little Cat Cay may have been a typical occurrence at that time, and *E. viridis* has persisted as a dominant herbivore throughout the rhomboidal cays (Aronson and Precht, 1997). It is replaced on reefs exposed to heavy wave action by congeneric *E. lucunter*, which is capable of excavating galleries in coral rock. *E. viridis* typically occurs in coral and rubble on reefs, but can also be found in the open on mangrove prop roots and branching corals, and it has been suggested that its cryptic behavior may be a response to water turbulence or to predation (Hendler et al., 1995).

It has been proposed that *E. viridis* played an important role in the drastic transformation of the rhomboidal cays reefs from a coral community that was dominated by *Acropora cervicornis* for at least 3,800 years, to one dominated by *Agaricia tenuifolia* (Aronson and Precht, 1997). Aronson and Precht indicate that the transition occurred in the 1980s because *A. cervicornis* succumbed to mass mortality from white-band disease. They speculate that the subsequent dominance of *A. tenuifolia* was abetted by *E. viridis* herbivory, citing Sammarco's (1982) demonstration that *E. viridis* promotes the settlement and successful growth of *Agaricia* spp. They contend that the *Acropora-Agaricia* transition occurred in Belize and not elsewhere in the Caribbean because of an exceptionally high population density of *E. viridis*. Aronson and Precht (1997) also suggest that its abundance could have resulted from the mass mortality of a competing species, *Diadema antillarum*. However, Lessios (1995) has shown that a release from competition with *D. antillarum* has not benefited *E. viridis*. Furthermore, the present-day density

of *E. viridis* in Belize is not greater than at other Caribbean localities (e.g., Lessios, 1995) and is considerably lower than the density of the echinoids monitored by Sammarco (1982) that improved the success of *Agaricia* spp. Whether herbivory by *E. viridis* controls the composition of the rhomboidal cays coral community remains to be confirmed.

Oreaster reticulatus may pose a potential threat to the integrity of the *Agaricia* community that dominates the rhomboidal keys slopes at present. Our observation of the starfish feeding on *Agaricia tenuifolia* on the slope of Manatee Cay is the first evidence that *O. reticulatus*, which was known to have a fairly generalized diet, is a potential coralivore (Hendler et al., 1995). Agariciids, which constitute the dominant coral cover on the slopes of the rhomboidal reefs, represent a potential windfall for a coral predator. Most of the rhomboidal cays have shallow water seagrass beds, to which *O. reticulatus* recruits. Should there be a large, successful recruitment of the sea star, the adults would in all likelihood move downslope to feed on *Agaricia*, perhaps initiating another large-scale transformation of the coral community.

The widespread distribution and the large body size of *Ophioderma cinereum* in the rhomboidal cays contrast with the characteristics of the populations at Carrie Bow Cay reef and the barrier reef. It is not clear why the species is relatively uncommon on the barrier reef, especially since it is a major component of the reef-flat ophiuroid fauna in Panama (Hendler, unpublished observation). However, the large size and the exposed position adopted by individuals on high peat banks indicate that individuals in mangrove habitats are responding to abundant resources or less predation and may be long-lived or fast-growing. It is less clear why the large individuals commonly hide in the interstices of coral and rubble on the reef slopes of several cays, but the same factors may be involved. The rarity of populations on peat banks, and the possibility that large individuals have a long life-span, are indications that experimental manipulations of those populations should be avoided.

Another interesting aspect of *O. cinereum* is the contrast in pigmentation noted above, between individuals living on the mangrove cays and those on the reef. Presuming that the coloration is not strictly under genetic control, their integument probably incorporates pigmented material from the environment or accumulates it from their diet as they grow.

Several species of burrowing brittle stars provide further examples of contrasting ecologies between reef-dwelling and rhomboidal cay populations. Large, long-armed, burrowing amphiurid brittle stars such as *Ophiophragmus pulcher* have not been found on the reef and seagrass habitats in Belize, although they occur in those habitats elsewhere in the Caribbean (Hendler et al., 1995). The presence of *O. pulcher* at Elbow Cay, and at Manatee Cay with a smaller burrowing species, *Amphipholis* cf. *januarii*, suggests that the mangrove peat banks provide a more suitable environment than the soft sediment habitats near the barrier reef. The other amphiurid brittle stars that occur on the reef are all diminutive species that do not burrow deeply.

The occurrence of numerous *Ophiopsila riisei* burrowing in the peat banks at Elbow, Lagoon, and Little Cat cays was unexpected, as noted above, because the species is typically restricted to hard substrates on the barrier reef. Evidently, mangrove peat is a suitable substrate for some burrowing brittle stars, including *O. pulcher*, *A.* cf. *januarii*, and *O. riisei*, whether they live in hard or soft substrates elsewhere. However, the occurrence of burrowing brittle stars in the rhomboidal cays that do not occur in soft substrates at the barrier reef may be due to negligible turbulence and other environmental factors in the cays, or to the influence of biological factors such as curtailed competition and predation. Thus the factors potentially affecting the success of

burrowing brittle stars in the rhomboidal cays are the same ones thought to influence *E. viridis* and *O. cinereum*.

The occurrence of large numbers of *Synaptula hydriformis*, a small apodan sea cucumber, in the Elbow Cay pond indirectly sheds light on the absence of other species from the habitat. The pond is a small body of water with sluggish circulation and at times higher temperatures and more extreme salinities than in the barrier reef lagoon. It is likely that echinoderms rarely recruit to the pond because the surrounding mangrove swamp is a barrier to adult individuals and planktonic larvae. Quite possibly, high water temperatures and salinity in the dry season and low salinity in the rainy season are stressful to adults and lethal to larval echinoderms. Those conditions would make it difficult for echinoderms with a planktonic larval stage to maintain viable populations in the pond. The success of *S. hydriformis* may be due in part to its viviparous reproduction, which could protect its embryos from environmental stress. Or the population in the pond may be descended from individuals that inhabited the soft-bottom coral community, which we suggest previously occupied the same site. However, its capabilities as a self-fertilizing hermaphrodite would increase the likelihood that a single individual could successfully invade and reproduce, even in an isolated pond (Hendler et al., 1995; Frick, 1998). The situation at Elbow Cay is similar to that in Bermuda, where *S. hydriformis* inhabits isolated salt ponds (Pawson, 1986).

The level of environmental stress in enclosed ponds must be more severe than that in the more open bays, but even in some bays of the rhomboidal cays temperature and salinity stresses probably exclude some sensitive organisms. At Elbow Cay, where only one echinoderm inhabits the pond, the nearby bay has more than 30 species. Physical stress and competition for space probably account for the absence of corals from localities such as Ponds E, F, and C. At those sites, accumulations of unconsolidated soft sediment and the absence of living corals are obstacles for the many echinoderms that require hard substrate or that are obligate symbionts of coral and other reef fauna. Thus it is not surprising that the richness of echinoderm species was markedly lower in the embayments at Manatee and Lagoon cays, in comparison with the adjacent reef slope.

Even on the reef slopes at the rhomboidal cays coral diversity and spatial complexity are limited. As a result, this area has failed to attract species restricted to conditions on the deep fore-reef slope or specific to hosts living only on the barrier reef. In the absence of those species, echinoderm diversity at the cays has remained lower than on the barrier reef.

The general trends in diversity that we have described are presumably reliable, although the figures for species richness at certain localities are not precise. Our findings are preliminary and limited to the more conspicuous components of the echinoderm fauna. The biodiversity of echinoderms at the rhomboidal cays is undoubtedly greater than known at present. To produce a more definitive taxonomic list of Belizean echinoderms, additional localities must be explored and their microhabitats must be examined systematically.

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