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DIVERSITY AND DISTRIBUTION OF ASCIDIANS (TUNICATA) AT TWIN CAYS, BELIZE

BY

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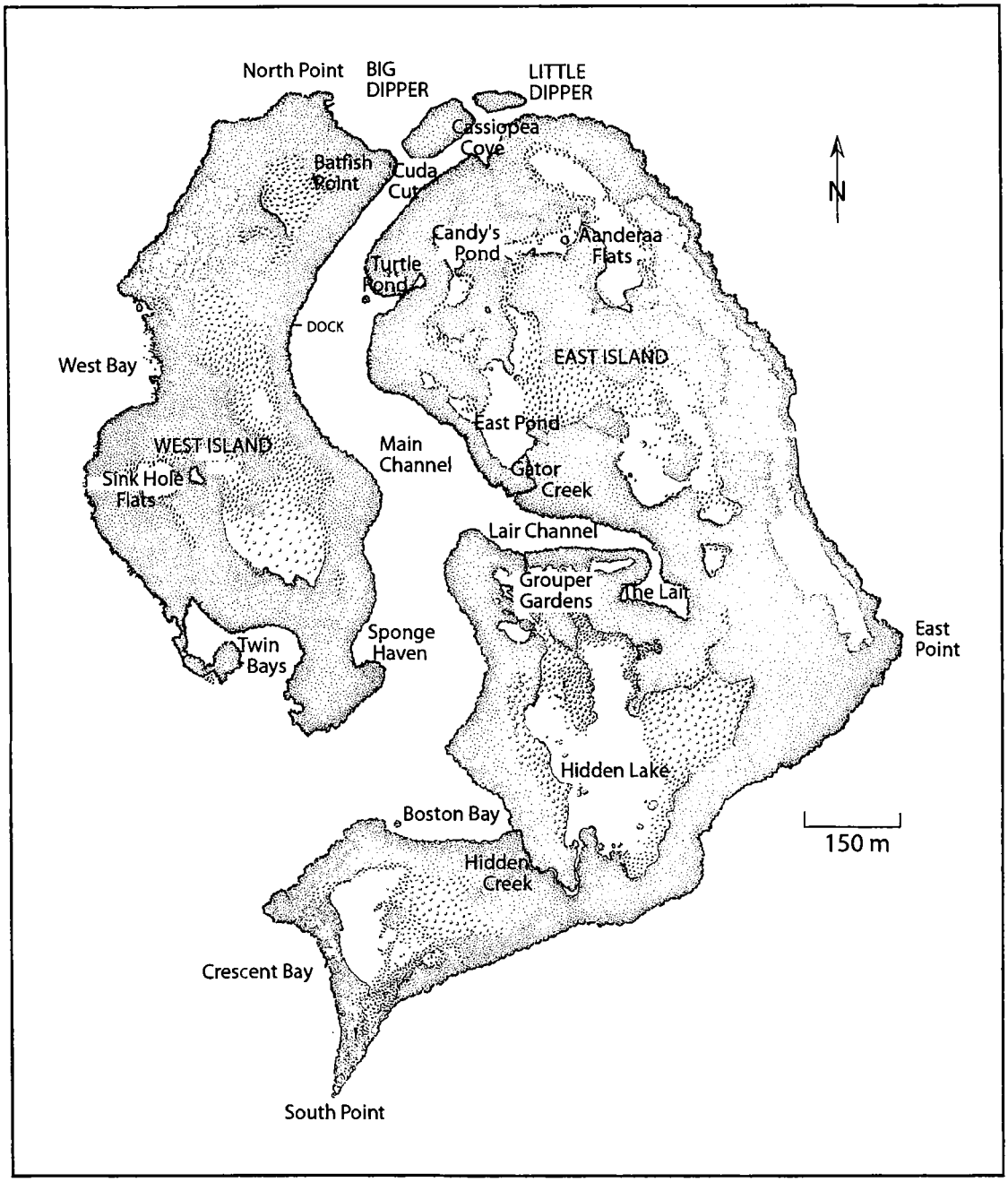

Figure 1. Twin Cays index map

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ABSTRACT

Forty species of ascidian in nine Families have been recorded from Twin Cays during a ten-year period of study. Twin Cays is the type locality for three of these species. Colony-forming species, notably those in the families Didemnidae, Polycitoridae and Perophoridae, predominate over solitary species which are poorly represented. The distribution in Twin Cays and habitat requirements of these different species are considered and the composition of the fauna is compared with that of other well documented mangrove environments in the Caribbean Basin. It is suggested that several other species of ascidian may colonize Twin Cays in years to come if the environment alters significantly. Notable among these are two species of *Ecteinascidia* which have breeding populations within a few kilometers distance from Twin Cays.

INTRODUCTION

Twin Cays, Belize is a mangrove-covered cay of about 75 ha., divided into two islands by a north-to-south channel opening at either end to the open sea. Detailed descriptions of the system are given elsewhere in this issue of the Bulletin. (Rützler et al., 2004; Rodriguez and Feller, 2004).

Forty species of ascidian have been identified from the area. Most species are found growing on the adventitious hanging roots of the red mangrove tree (*Rhizophora mangle*), while a few species are characteristic of bottom sediments. The *Rhizophora* roots provide an excellent growing surface for a variety of sessile marine invertebrates. As this community matures it becomes a fiercely competitive environment in which sponges and ascidians are the dominant living organisms. One attribute of the environment is that new space is constantly being created by growth of the root tips. Under favorable circumstances, growth of an individual root tip may exceed 0.2 to 0.4 mm per day *(pers. obs.)*. Secondary space is also important in the form of bivalve (*Isognomon alatus*) shells, algal filaments and benthic seagrasses (*Thalassia testudinum).* Another feature of the environment is that most parts of the system are regularly flushed by diurnal tidal rhythms producing fast water flows in narrow channels (e.g. Hidden

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Creek, Gator Creek) and more sluggish transport in broader channels (e.g. Lair Channel). These currents, fast or slow, renew supplies of suspended particulate matter on which the sessile community depends for food. In addition, when the tide rises it floods across the swamp floor and during neap tide the water carries decomposed organic matter back into the channels and ponds further replenishing food resources. All of these attributes of the environment are exploited by ascidians according to their individual needs resulting in a species-rich assemblage over a relatively small linear distance. The total linear measure of mangrove fringe along which sessile communities grow on *Rhizophora* roots is in the order of 4.63 kilometers. (Rodriguez and Feller, 2004).

METHODOLOGY

During a 10-year period between 1984 and 1994, I made 20 visits to Belize to work from the Carrie Bow Cay laboratory. Each visit lasted 2-to-3 weeks and during each visit daily trips were made to Twin Cays for the purpose of surveying and studying the ascidian fauna. All seasons of the year were covered during the overall period of study. Observations were made by free swimming with a mask and snorkel and all observations were recorded on an underwater slate to be transferred to written notebooks after return to the laboratory at Carrie Bow. Where continuous observation of individual ascidians or colonies was required, the site was marked by attaching a small plastic numbered label to the relevant mangrove root with a tie-wrap. To follow growth and change in colonial species a photographic record was made using Nikonos II and III underwater cameras with flash heads. Every accessible site in Twin Cays was covered by this survey with particular attention paid to the Main Channel, Twin Bays, Hidden Creek, Lair and Lair Channel, Turtle Pond and Channel, Candy's Pond, Grouper Gardens and Gator Creek. A few observations were also carried out in the open-water shallow areas to east and west of the two Cays. To the east the sea floor is mostly covered by *Thalassia* beds growing in soft sediments while to the west is a mixture of *Thalassia,* coarse sands and broken coral rock (Figure 1).

SPECIES COMPOSITION

A total of 40 species of ascidian have now been recorded from Twin Cays (Table 1) and of this number three species have been described as new taxa during the course of the study. It will be seen from the table that there is a preponderance of clonal species belonging to a few Families, notably Didemnidae, Polycitoridae Perophoridae and Styelidae. To simplify the presentation of information I have chosen to treat the fauna family-by-family rather than species by species. General taxonomic information on most species will be found in Van Name (1945) and additional information on individual families will be found in the literature cited with each family. A previous account of ascidian diversity elsewhere on the Barrier Reef in Belize is given in Goodbody (2000). Eleven species at Twin Cays are sufficiently common and prominent in the sessile community to warrant designation as key species. These are marked with an asterisk (*)

in Table 1. Voucher specimens of all species referred to as occurring at Twin Cays have been deposited in the U.S. National Museum of Natural History. The habitat distribution of different species at Twin Cays is summarized in Table 2. See Plate 1.

Family **Polyclinidae** (F. Monniot 1972, 1983b) Unlike at many other sites in the Caribbean this family is poorly represented in Twin Cays. A single specimen of *Aplidium antillense* was found overgrowing the test of *Ascidia interrupta* in Twin Bays on November 17, 1984 and on several occasions an algal-bearing polyclinid was seen on the peat bank near the north end of the Main Channel. No specimen survived collecting and the identity of the animal is unknown. The presence of algae in a polyclinid is unusual. *Aplidium exile* occurs on *Rhizophora* roots at the nearby Blue Ground Range and is of regular occurrence in lagoons at the Pelican Cays and on nearby reefs (Goodbody, 2000). Hence it is possible that it may colonize Twin Cays in the future.

Family **Didemnidae** (F. Monniot, 1983a) The Didemnidae are an abundant family in most marine environments throughout the tropics. Twin Cays is no exception. By virtue of their ability to replicate rapidly and form sheet-like colonies, they are found overgrowing most types of substrate. The inclusion of white calcareous spicules within the test substance makes many species conspicuous members of sessile communities. For a detailed account of the family characteristics the reader is referred to Kott's (2001) excellent monograph on Australian species.

Of the seven species recorded from Twin Cays (Table 1), only two species can be regarded as Key species in the sessile community. *Didemnum conchyliatum* (Plate 1a) is one of the most common didemnids throughout the Caribbean. In Twin Cays it is ubiquitous, functioning as a primary colonizer on fresh root tips, panel surfaces and other bare space. It is recorded from most habitats (Table 2) but seems to exhibit a preference for relatively quiet environments such as those along the margins of the Lair Channel and in Twin Bays. Throughout the Caribbean *D. conchyliatum* occurs in several color morphs, orange, white, gray (Goodbody, 2000). At Twin Cays a bright orange morph predominates.

Diplosoma glandulosum (Plate 1b) is another key species forming massive gelatinous colonies in many parts of the system. It is particularly abundant in the North Channel close to Cuda Cut and Batfish Point. In this area it hangs as drapes from the roots of *Rhizophora.* It is also abundant in the Lair Channel where it flourishes on the upper surface of the blades of *Thalassia* plants. In contrast, it is absent from Hidden Creek and Gator Creek where water flow is fast at times. Colonies occur in a number of different color morphs including marbled black and white, gray, green, white, brown. Many colonies have very large common cloacal openings on the upper surface and sometimes along the colony margin. Frequently, colonies are found which appear to be clasping a root from the back suggesting a tendency for larvae to settle on the back of the root where light intensity will be least. *D. glandulosum* releases larvae around the noon-day meridian (Goodbody, 1995) thus providing the larva with opportunity to select the most favorable conditions of shade for settlement. The related species *Diplosoma listerianum* occurs throughout Twin Cays but is neither as common nor as conspicuous as *D. glandulosum. D. listerianum* is usually a drab grey color with orange spotting due to

the bright orange stomach of individual zooids showing through the thin test substance. The species forms smaller colonies than its congener and often occurs filling spaces between other sessile organisms in the community.

The remaining four species of didemnid at Twin Cays are less common than those mentioned above. *Lissoclinum fragile* is usually snowy white growing in flat sheets spreading over roots or shell surfaces in a very few places, notably in Twin Bays where it is relatively common. The related, but poorly known, *Lissoclinum abdominale* seems confined to a single location in the North Channel close to Cuda Cut where it grows as gelatinous sheets on the vertical face of the peat bank at a depth of about one meter. *L. abdominale* is one of a number of ascidians on the Barrier Reef which contain symbiotic algae in the cloacal canals. While *Prochloron* has been identified as the symbiont in *Diplosoma virens* (Goodbody, 2000), the symbiont in *L. abdominale* has not been investigated; nevertheless it gives a greenish tinge to the otherwise gray-colored colony. *Didemnum psammathodes* forms small flat colonies, muddy brown in color. The color is due to the accumulation of faecal pellets in the test substance; white spicules are thinly distributed in the test but insufficient to give the colony the usual white color found in other species of the genus. The species is rare in Twin Cays; colonies are recorded from the Main Channel (Dock), Hidden Creek, Twin Bays and the Lair. The only other didemnid found at Twin Cays is a single record of *Tridemnum cyanophorum*, another algal-bearing species collected by Klaus Rützler in about 0.5m depth off the northwest tip of the island on May 14, 1989.

Family **Polycitoridae** (F. Monniot, (1972, 1983c) This important family is represented by four species. *Eudistoma olivaceum* (Plate 1d) is widespread throughout the system but is not particularly conspicuous. The species tends to frequent the shaded portions of *Rhizophora* root clusters usually close to the peat bank and within half a meter of the water surface. In this habitat, it is common along the northern shore of the Lair Channel and in many locations along the main channel. The species occupies a similar habitat in the Port Royal mangrove, Jamaica (Goodbody, 2003). At Twin Cays it is also abundant in portions of Candy's Pond close to areas of drainage from the swamp. Electron-micrographs of the gut contents of this species collected from Candy's Pond suggest that it may feed largely on bacteria. Both heterotrophic bacteria and cyanobacteria are recognizable in the micrographs of the gut contents. The preference shown by this species for settling in sites close to the peat bank may be a mechanism for exploiting a situation rich in bacteria draining off the swamp floor. The gut contents are not exclusively bacterial and larger photosynthetic organisms such as dinoflagellates, diatoms and single-cell chlorophytes are visible in the micrographs.

Two other species, *Eudistoma capsulatum and Eudistoma obscuratum*, have been recorded in the Main Channel at Twin Cays. These species are usually reef-dwelling species and have previously been found in mangrove ponds elsewhere on the Barrier Reef at Pelican Cays (Goodbody, 2000). Unlike colonies of the species found at North Lagoon Cay, colonies *of Eudistoma obscuratum* in Twin Cays are relatively small and except for their intense black coloration, are inconspicuous elements of the sessile community. Most specimens were seen at the north end of the Main Channel close to Cuda Cut and Batfish Point. The fourth member of the Family Polycitoridae occurring in

Twin Cays is *Distaplia corolla* (Plate 1c) which forms conspicuous orange-colored colonies all through the system. There are two focal points in its distribution in Twin Cays, one at the eastern end of the Lair Channel on the southern shore just before the junction of the channel with the Lair. The other focus is in the eastern half of Twin Bays where it was common along the northern shore. While these sites are foci of abundance, the species is widely distributed along the Main Channel but is absent from areas of fast-moving water as in Hidden Creek, Gator Creek or Turtle Channel. *D. corolla* occurs in two color morphs at Twin Cays, one bright orange and the other purple. The orange morph is more common than the purple. It is of particular interest to note at this point that there is no confirmed record of the occurrence at Twin Cays of *Cystodytes delle chiajei,* a polycitorid common throughout the mangrove ponds at Pelican *Cays.*

Family **Pycnoclavellidae** (Goodbody, 1996) A single species, *Pycnoclavella belizeana,* is the only member of this genus known to occur in the Western Atlantic. Originally described from specimens collected near Batfish Point in the Main Channel, the species subsequently has been found to be of fairly widespread distribution on the edge of the peat bank along both sides of the northern end of the Main Channel and in Grouper Gardens. Zooids are only about 1.0 mm in length and hence are difficult to discern unless the bank is carefully studied. The species has also been found at Fisherman's Cay in the Pelican Cays (Goodbody, 2000) and it is likely that it will be found to be widespread along the Barrier Reef in Belize wherever suitable habitat exists.

Family **Perophoridae** (Goodbody, 1994; Goodbody & Cole (*in press*) Based on abundance this exclusively colonial family is the most successful group of ascidians in Twin Cays. Four dominant species in the genus *Perophora* and two species in the genus *Ecteinascidi*a occur throughout the ponds and channels. Twin Cays is the type locality for two species of *Perophora, P. regina* (Plate 1e) and *P. carpenteria* (Plate 1f), which were first described during the course of this study. *P. regina* is a large and active species exhibiting strong muscular activity and a constant dancing motion throughout the colony. This suggests that the animal may have high metabolic demands for food and oxygen and, in keeping with this, the species is most frequently encountered in those parts of Twin Cays where there is strong-to-moderate water flow such as in Hidden Creek, Turtle Pond and Turtle Channel and in parts of the northern end of the Main Channel. *P. carpenteria* is one of a group of three very similar small species which are difficult to separate from one another in the field. *P. carpenteria* is the most abundant of these small species, so much so that it is here considered as a key species. Colonies overgrow other elements of the sessile community, the peat bank itself and the species is common everywhere growing over the upper surface of the blades of Turtle Grass (*Thalassia testudinum*).

Perophora viridis is less common and is usually found growing along the stems of Bryozoan colonies or on macroalgal stems. I have never found *P. viridis* growing on the peat bank or on grass blades as does *P. carpenteria* and it is suggested that in habitat selection *P. viridis* may seek a location raised above the substratum or above the sessile community in general.

The fourth species in this group is *Perophora bermudensis* which tends to grow in loose clusters of zooids often hanging down into a stream of relatively fast moving water.

A colony of this sort has been recorded frequently at the western side of the entrance to the Lair where it is exposed to the flow of water passing this point at tidal oscillations. An almost identical situation exists in the Port Royal mangroves in Jamaica where colonies of this species hang into a similar tidal flow (Goodbody, 2003). *P. bermudensis* does not always grow in these loose hanging colonies and may also be found growing as a creeping sessile colony along the margins of the peat bank. For further discussion of these growth forms see Goodbody (1994). Another small species, *Perophora multiclathrata*, occasionally occurs in mangrove environments in the Caribbean and has once been recorded at Twin Cays: a small colony was collected from a mangrove root at the Big Dipper on May 8, 1986. *P. multiclathrata* also occurs at Carrie Bow Cay where it is found under slabs of coral rock.

There are two species of *Ecteinascidia* occurring at Twin Cays. *E. styeloides* (Plate 1g), is an erect form growing usually as clusters of grey-green zooids. It is found throughout the system but is only common in the Lair and Hidden Creek. The second species, *E. minuta* (Plate 1h), is much smaller, more like a species of *Perophora* in external appearance but growing either as recumbent colonies on mangrove roots or other substrata or growing as diffuse colonies of small erect zooids. The recumbent form is the dominant form in Twin Cays and is found throughout the system but particularly in the inner more stressed areas such as in Candy's Pond, the Lair, Turtle Pond and in Hidden Lake and the upper reaches of Hidden Creek (Fig. 1). It frequently makes use of secondary space for settlement and in Hidden Creek is specially abundant on the shells of the oyster *Isognomon alatus*. Two other species of *Ecteinascidia, E. turbinata and E. conklini* occur elsewhere in the Southwater Reserve and it is surprising that neither has colonized Twin Cays. For further information on these species of *Ecteinascidia* see Goodbody and Cole (*in press*) and the discussion at the end of this paper.

Family **Ascidiidae** (C. Monniot, 1973, 1983a.) Animals in this large and important family usually grow as solitary zooids, not colonies. Nevertheless, under favorable conditions clusters of solitary zooids may grow close together as occurs with *Ascidia curvata* in Jamaican mangrove lagoons (Goodbody, 2003). At Twin Cays the family is represented by six species, none of which is common. *Phallusia nigra* has been found occasionally on roots in the Main Channel close to Batfish Point and also on roots in Twin Bays. By virtue of its glossy black color, *P. nigra* is readily recognized in the field whereas other species that are less conspicuous may often be overlooked. *Ascidia interrupta* is another large (5-10 cm) solitary form common throughout the Caribbean on reefs and in mangroves. At Twin Cays *A. interrupta* was occasionally found in Twin Bays and Lair Channel (Fig. 1), usually as isolated zooids and not in clusters. *Ascidia tenue* is a small (2-3 cm) poorly known species. The only record from Twin Cays is of four zooids collected from a settlement panel at the north end of the Main Channel on May 8, 1986. *Ascidia correloides* is another small species (1-2 cms) normally associated with reef environments. A single specimen was collected from the peat bank at the north end of the Main Channel in Twin Cays on May 23, 1986. *Ascidia curvata* is a medium-sized species in which the test is often very transparent. It has only once been recorded from Twin Cays: a single zooid collected on February 16, 1984 from the peat bank on the east side of the Main Channel. *Ascidia sydneiensis* is the largest species in the genus

found on the Belize Barrier Reef. It is usually benthic in habitat living buried in soft sediments with two greenish-yellow siphons protruding above the sediment surface. Twin Cays is an ideal environment for this species but it has only once been recorded--- a 9-cm long specimen collected in the Main Channel on March 30, 1981.

Family **Styelidae** (Sloot, 1969; C. Monniot, 1983b) This is another large family which contains both clonal and aclonal species some of which are very common at Twin Cays. *Botrylloides nigrum* (Plate 1i) is a colony-forming species growing as bright-orange to brick-red sheets covering mangrove roots, overgrowing other sessile organisms and very occasionally growing on the peat bank itself. It is abundant throughout the Main Channel but less common in other parts of the system. Among these colonies are other very similar colonies which I have assigned to the Indo-Pacific species *Botrylloides perspicuum* that is characterized by the presence of vascular ampullae arranged in rows in the test between the rows of zooids. Colonies assigned to this species were also found commonly at Pelican Cays in southern Belize (Goodbody, 2000). This apparent overlap of two such closely related species (Kott and Goodbody, 1982) deserves more intensive research than has been possible during this project. *Botryllus tuberatus* (formerly known as *Botryllus primigenus*) has only been recorded once at Twin Cays on *Thalassia* leaves in Hidden Lake in February 1984. This species is widespread but nowhere common on the Barrier Reef in both mangrove and reefal environments. *Botrylloides magnicoecum* and *Botryllus planus* have only been found rarely (Table 2).

Polyandrocarpa tincta is a colony-forming species normally associated with reefal communities rather than mangroves. Nevertheless, colonies are occasionally found in mangrove areas and the species is recorded once from Twin Cays. A colony was collected from a *Rhizophora* root on the east side of the Main Channel just north of Crescent Bay in February 1984. This area of the channel is not otherwise heavily populated by ascidians or other sessile community growth. It is possible, therefore, that special ecological conditions prevail along this shoreline which promote survival of a normally reef-dwelling species but do not support growth of the usual mangrove-root community. These ecological conditions have not been investigated.

Styela canopus is a solitary species found commonly throughout Twin Cays in most habitats. It is frequently found as erect zooids amongst other elements of the sessile community, easily recognized by characteristic yellow and brown stripes on the inner surface of the siphons. An alternative growth form is squat and rounded found frequently on the shells of the bivalve *Isognomon alatus*. *Styela plicata* is a solitary species only rarely encountered in Caribbean mangroves. Two specimens were recorded growing on oyster shells in the North Channel in March 1981.

The remaining species in the Family Styelidae all belong to the genus *Polycarpa*. *Polycarpa spongiabilis* is one of the largest (5cm) members of the genus found in the Caribbean. It is often abundant in mangrove lagoons living either attached to mangrove roots or buried in sediments with only the siphons visible at the surface. At Twin Cays I have found it only occasionally within the mangrove system. Specimens have been recorded from the Main Channel and Turtle Pond; small specimens have been found embedded among roots of *Thalassia testudinum* in West Bay. *Polycarpa arnoldi* and *Polycarpa cartilaginea* are both small (2cm) reef-dwelling species that have occasionally

been found in West Bay but never in the mangrove system. It is also of interest that *Polycarpa aurita*, which is common in some lagoons at Pelican Cays (Goodbody, 2000), has never been seen at Twin Cays, and no species in the genus *Symplegma* has ever been seen at Twin Cays whereas two species S. *brakenhielmi and S. rubra* are found in lagoons at the Pelican Cays.

Family **Pyuridae** (C. Monniot, 1983c) *Microcosmus exasperatus* is a large (3 to 5cm) species common in mangrove lagoons throughout the Caribbean. It has only rarely been seen at Twin Cays, records including specimens in Twin Bays, Lair Channel and several sites in the Main Channel. There are no confirmed records of either *Pyura vittata* or *Herdmania momus* at Twin Cays although both species are normally common in mangrove systems of this sort.

Family **Molgulidae** (C. Monniot, 1983c) *Molgula occidentalis* is the only member of this family recorded from the Barrier Reef. Although Van Name (1945) records specimens of 6 cm in length, most specimens collected in Belize are about 2 cm in maximum length. The species is common in parts of the Pelican Cays (Goodbody, 2000) but has seldom been seen at Twin Cays. Specimens have been collected from among *Thalassia* roots at West Bay and from settlement panels in the Main Channel. Because the animal is often embedded in other elements of the sessile community, and sometimes embedded in the peat bank, it is difficult to see and hence may be more common at Twin Cays than appears to be the case.

DISCUSSION

In terms of species richness, the diversity of ascidians at Twin Cays is not especially notable. Table 3 shows the number of ascidian species recorded in various mangrove habitats throughout the Caribbean. Pond A at the Pelican Cays in Belize (42 species) is comparable to Twin Cays (40 species) but Twin Cays and Pond A are both richer than the Fort Rocky Lagoon at Port Royal, Jamaica (25 species). These differences are merely differences in number; species composition is of much more interest from an ecological point of view. The outstanding feature at Twin Cays is the relative paucity of solitary species of ascidian and the abundance of colony-forming species. At Port Royal and at Pelican Cays, colony-forming species are important but solitary species, especially in the Families Ascidiidae, Styelidae, and Pyuridae, are conspicuous elements of the ascidian fauna. In all of these locations, three families of colony-forming ascidian (Didemnidae, Polycitoridae and Perophoridae) contribute significantly to the fauna.

Attention should be focussed on the Perophoridae. Twin Cays is the type-locality for *Perophora regina*, a conspicuous and large member of the genus considered here to be a key species at Twin Cays. Up to the time of writing, this species has only been recorded from two other locations in the Caribbean: Pond B in the Pelican Cays, 15 kilometers south of Twin Cays, and in an isolated lagoon at Blue Ground Range a few kilometers southwest of Twin Cays. No comparable species has been recorded from any other biogeographical region and one is led to speculate as to whether *P. regina* evolved

in Twin Cays and, if so, what were the ecological forces that induced such a development. Wherever the species evolved, it appears to be endemic to the Meso-American Region. Another significant point about the Perophoridae at Twin Cays is the complete absence of *Ecteinascidia turbinata* and *Ecteinascidia conklini. E. turbinata* is a widely distributed and common species throughout the Caribbean and is a characteristic inhabitant of eutrophic environments such as Fort Rocky Lagoon, Jamaica and Piscadeera Baai in Curaçao. *E. turbinata* has been found in submerged peat hollows close to Tobacco Range a few kilometers from Twin Cays and has also been recorded at 100 meters depth on the fore-reef at Carrie Bow Cay, hence opportunity for colonization of Twin Cays exists. Similarly, the rare *Ecteinascidia conklini* occurs in some abundance at Blue Ground Range close to Twin Cays but the species has not colonized Twin Cays. It is to be expected that it may do so at some time in the future.

Considering the Caribbean as a whole, it is apparent that members of the Family Perophoridae are a characteristic element of the fauna of mangrove lagoons throughout the region. They are more abundant in mangrove environments than they are in reefal environments. This apparent linkage between mangroves and perophorids is probably associated with two significant features of most members of the family. They are stress resistant, particularly with reference to extremes of salinity and temperature, and they have an ability to regenerate entire colonies or groups of zooids from undifferentiated material residing in stolonic networks or fragments of such networks (cf. Goodbody and Cole, *in press* and Por and Dor, 1975). At Twin Cays the species of this family that are present have a wide distribution occupying almost all habitats (Table 2). It is significant that, as a group, they are especially abundant in Hidden Creek which is a stressed environment subject to strong water flow and considerable fluctuations in temperature (Rützler et al., 2004). In contrast, in the environment of Candy's Pond where changes in temperature and salinity are the important stress factors, only one species in the family, *Ecteinascidia minuta,* has been observed. In this instance it is of further interest that *Perophora regina*, which is abundant in nearby Turtle Pond does not occur in Candy's Pond. It is not possible to throw further light on this pattern of distribution until such time as we learn a great deal more about the ecophysiology of these species.

In the Family Polycitoridae two species, *Distaplia corolla* and *Eudistoma olivaceum*, are considered to be key species in Twin Cays. *Distaplia corolla* was originally described from the Azores (F. Monniot, 1974). Until recently the species was poorly recognized in the Caribbean fauna. It now transpires that it is widely distributed in mangrove environments along the Belize Barrier Reef. I have also found the species in reefal environments in Belize and in Jamaica, but only as small colonies (1 to 2 cm) whereas in some mangrove environments (e.g. pond H at Pelican Cays) it forms large colonies (c.10 cm) and dominates the sessile community. The other key species in the Polycitoridae, *Eudistoma olivaceum,* is common in mangrove environments throughout the Caribbean. It has already been noted above that the species shows a preference for settling in shaded areas at the back of the hanging root complex where it is also close to drainage from the floor of the swamp. It is further suggested that bacteria may be an important element in their diet and that water draining from the swamp floor may provide a rich source of such bacteria. Notwithstanding any preference for shaded areas close to the peat bank, *Eudistoma olivaceum* is widely distributed throughout Twin Cays and at

times has been found to be abundant in the stressed environment of Candy's Pond which appears to provide a reservoir of constantly breeding populations. Although quantitative data are not available, it is apparent that the populations of *E. olivaceum* in Candy's Pond fluctuate and change rapidly from time-to-time. Frequently, mangrove roots in the pond are densely populated by large colonies in which individual heads are large, long and tightly packed with larvae. On other occassions only small populations of newly settled, nonbreeding animals are present. One such occasion occurred in February 1988 after a period of heavy rain storms, thus suggesting that freshwater flooding and reduced salinity may have caused a mass mortality in the population followed by a new settlement of larvae.

Settlement and growth in these populations is maximal in the upper half meter of the water column. As a consequence, the populations will be particularly vulnerable to surface conditions such as freshwater or warm-water influx from the swamp. These populations must be sustained by some particular food supply derived from the enclosed nature of the pond. In the light of what has been recorded earlier about the presence of bacteria in the food cord of *E. olivaceum,* it seems reasonable to postulate that the high level of organic detritus in the pond may support high levels of bacterial production which in turn provide a food source for the ascidians. Whatever the truth is, it is abundantly clear that Candy's Pond is an environment that deserves close attention from future researchers. The channel leading in and out of Candy's Pond and connecting it with Turtle Pond is also an area of interest as very large colonies of *E. olivaceum* occur at either end and occasionally large colonies occur along the length of the channel. Why should such large colonies, 100cm^2 and more in area, develop at either end of the channel? Presumably it is a function of food supply and water flow. In February 1988 in Turtle Pond there was a relatively rich growth of *E. olivaceum* gradually decreasing in size from the mouth of the channel leading to Candy's Pond toward the entrance to Turtle Channel on the western side of Turtle Pond. In the series of colonies in Turtle Pond, large colonies were replaced by smaller colonies around the margin of the pond further suggesting that the strong flow of food-rich water from Candy's Pond is an important ingredient in encouraging growth and replication of *E. olivaceum.* Its effectiveness is rapidly dissipated as the water mixes with water in Turtle Pond which is influenced also by inflow from The Main Channel of Twin Cays.

At a site in the Lair Channel, which is 65 meters to the east along the north shore from the entrance to Gator Creek, growth of *E. olivaceum* was relatively similar to that in Turtle Pond. There were a lot of medium-sized colonies sheltered on roots with overhanging canopy and on roots hanging away from the peat bank. These colonies were in the size range of 5 to 20 heads each. It is of interest that only a few very small colonies of *E. olivaceum* have been found in the Lair itself so that this pond does not appear to be a focal point for the species in the way that Candy's Pond is a focus. Why? The Lair receives direct drainage from the swamp and is semienclosed. The difference between it and Candy's Pond is the size of the channel through which the pond is flushed. The Lair is less isolated than Candy's Pond and, in consequence, may have less opportunity to develop bacterial populations than seems to be the case in Candy's Pond. In Gator Creek, colonies grow in fairly large numbers on the peat walls of the creek as is also the case in Hidden Creek. Throughout the remainder of the Twin Cays channel system *E. olivaceum*

occurs only sporadically here and here on roots, usually where other sessile organisms do not have a strong presence, often occurring towards the tops of roots and always in small colonies, usually 5 to 10 heads. A site just north of the dock on the west bank of the main channel is representative of this situation. Formerly I considered that competition with other sessile organisms was the main factor controlling the distribution and abundance of *E. olivaceum* but the situation in Turtle Pond (and Candy's Pond) leads me to believe that food is the most important factor. If food is an important limiting factor, the abundance and status of the Lair Channel population may be explained by food resources entering the channel from Gator Creek close to the site in question. We may conclude, therefore, that *E. olivaceum* is an adaptable species and is one which deserves much closer study from an ecological and physiological point of view.

It is of interest at this point to notice that no species in the Family Clavelinidae has been found at Twin Cays, whereas at Pelican Cays, 15 km further south, two species, *Clavelina picta* and *C. puertosecensis,* are abundant in many of the lagoons. *C. picta* also occurs at Blue Ground Range a few kilometers southwest of Twin Cays and *C. puertosecensis* has been found on the fore-reef slope at Carrie Bow Cay, so there is potential for both species to colonize Twin Cays at some time in the future. The closely related Family Pycnoclavellidae is represented at Twin Cays by *Pycnoclavella belizeana* which forms colonies of tiny zooids along the edge of the peat bank in the Main Channel. By virtue of size and abundance, the species can have little ecological significance in the sessile community but nevertheless its presence is of biogeographical interest since no other member of the family is recorded from the Caribbean.

At present there is a fairly comprehensive knowledge of the diversity and distribution of ascidians in the Caribbean as a result of the work of many specialists (Traustedt, 1882, 1883; Sluiter, 1898; Van Name, 1921, 1945; Monniot and Monniot, 1984; Millar, 1962; Millar and Goodbody, 1974; Goodbody, 2000, 2003). Only a few local details need to be resolved. At the time of this writing, we can confirm the presence of 117 species in 39 genera in the Caribbean representing about 5% of known species worldwide. It is time to seek explanations for this diversity and there are some compelling questions for which we need answers. At the community level we should be asking how it is that so many different species of filter-feeding organisms are able to compete for similar resources in the mangrove environment and continue to survive. The same question arises again at the species level and is well illustrated in the genus *Perophor*a. Three very closely related species, *P. viridis*, *P. carpenteria*, and *P. bermudensis*, live in close proximity to one another in the sessile communities of Twin Cays apparently competing for the same resources. Ecological theory suggests that there must be significant differences in their requirements--- otherwise one or more species would be eliminated by competition. It is to questions like this that we should now be directing research through study of single-species ecology. This information is needed to understand the complexity of the whole sessile community. Attention should be focused on other aspects of population growth and regulation in these communities. Apart from competition, the question of predation arises as a force controlling ascidian populations in mangrove environments. My observations at Twin Cays have thrown little light on sources of predation. Species of the gastropod *Diodora* are occasionally seen grazing on colonial ascidians as are also the Polyclad Turbellarians *Thysanozoon nigrum* and

Pseudoceros crozieri. An unidentified nudibranch and a species of *Thais* have been seen grazing on Dis*taplia corolla.* With a few exceptions fishes seem uninterested in feeding on ascidians. Angelfish *(Pomacanthus sp)* and the Spadefish (*Chaetodipterus faber)* have been seen grazing on sessile communities and include small perophorids in their diet.

CONCLUSION

On the basis of my observations in mangrove environments throughout the Caribbean I believe we may generalize and make a number of postulates about the factors that control the distribution and abundance of ascidians in Twin Cays and other mangrove systems.

- Ascidians are hard substratum limited. In mangrove systems this restricts them to living on mangrove roots and other biota such as oyster shells. In the few cases (e.g. *Polycarpa spongiabilis*) in which they live in bottom sediments, it will usually be found that there is the remnant of a shell or other hard object attached to the posterior of the zooid; this probably is the original substrate on which the larva settled.

- Ascidians are inhibited by high sediment loading in the water column. In consequence ascidians survive best where water exchange is good and suspended sediments are removed by water flow before they can resettle on and suffocate the sessile community.

- Long roots hanging in shallow water often reach to the bottom sediments; during windy conditions such roots drag on the bottom disturbing the sediment. In consequence ascidians are usually found growing where roots hang clear of the bottom sediments.

- Ascidians are inhibited by close proximity of certain sponges, e.g. *Tedania ignis.*

- Most ascidians, but not all, are sensitive to stress, particularly lowered salinity (Goodbody, 1961). Mangrove swamps seasonally collect large volumes of rainwater which drains laterally through the root fringe giving rise to a surface layer of low-salinity water that inhibits ascidian growth in the upper portion of the roots. This upper zone becomes dominated by the oyster *Isognomon alatus*, which is apparently resistant to low-salinity stress. When normal salinity is restored, fast growing opportunist species of ascidian, such as *Ecteinascidia minuta*, subsequently use the oyster shell as a substrate for settlement.

- Temperature may not be important in defining local distribution but may affect reproductive processes. At Twin Cays, warm-water fluxes due to daytime heating periodically drain through the root system, e.g. in Hidden Creek (Rützler et al., 2004), and several species of ascidian survive in this environment (See Table 2).

The distribution of ascidians at Twin Cays may be explained in terms of these general postulates. A main focus of ascidian growth occurs at the north end of the Main Channel where water exchange is good, driven into the channel by the prevailing northeast wind. Water flow at this north end has caused deep erosion of the peat bank in this area so that mangrove roots are long and hang well clear of the peat bank. A similar but less obvious situation occurs at the southern end of the channel in the vicinity of Sponge Haven.

The lower end of Hidden Creek has rich communities of ascidians, especially members of the Perophoridae. This may be attributed to the strong flow of water that keeps sedimentation to a minimum and has eroded the peat bank in such a way as to enable mangrove roots to hang free from the bank. A negative factor in Hidden Creek is the temperature fluctuation already referred to above.

Twin Bays is different from any other environment at Twin Cays because of its sheltered position at the leeward end of the island. It nevertheless seems to experience sufficient flushing to prevent the accumulation of high levels of organic detritus such as occur in the closed environment of Candy's Pond. The most significant ascidian presence in Twin Bays was the population of *Distaplia corolla* but there is insufficient information on the ecology of this species to suggest why it should thrive at this site.

In general we may postulate that, at Twin Cays and elsewhere, the drainage of organic material from the swamp floor into the aquatic system must be a major element in maintaining sessile communities on the mangrove roots. Finally, the population structure of ascidians at Twin Cays should not be regarded as stable. The proximity to reefal communities elsewhere in the Southwater Reserve provides ample opportunity for opportunistic colonization in Twin Cays by species normally associated with reef environments. Such species (e.g. *Ascidia corelloides)* may colonize and survive but fail to reproduce and form stable populations in Twin Cays. Nevertheless, once a species does establish a breeding population, opportunity exists for that species to spread throughout the ecosystem and colonize wherever suitable habitat exists. In consequence, the diversity and distribution of species as described in this paper may alter from time-to-time as new colonists invade and existing colonists change their distribution with the passage of time and changing ecological conditions.

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Table 1. List of Ascidian Species Recorded from Twin Cays
Total recorded species = 40 * = key species

FAMILY: Polyclinidae
Aplidium antillense (Gravier, 1955)
FAMILY: Didemnidae
Tridemnum cyanophorum Lafargue et Duclaux, 1979
**Didemnum conchyliatum* (Sluiter, 1898) (Plate 1a)
Didemnum psammathodes (Sluiter, 1895)
Lissoclinum abdominale F. Monniot, 1983
Lissoclinum fragile (Van Name, 1902)
**Diplosoma glandulosum* F. Monniot, 1983 (Plate 1b)
Diplosoma listerianum (Milne-Edwards, 1841
FAMILY: Polycitoridae
**Distaplia corolla* Monniot F., 1974 (Plate 1c)
Eudistoma capsulatum (Van Name, 1902)
Eudistoma obscuratum (Van Name , 1902)
**Eudistoma olivaceum* (Van Name, 1902) (Plate 1d)
FAMILY: Pycnoclavellidae
Pycnoclavella belizeana Goodbody, 1996 (Type locality)
FAMILY: Perophoridae
**Perophora bermudensis* Berrill, 1932
**Perophora carpenteria* Goodbody, 1994 (Type locality) (Plate 1f)
Perophora multiclathrata (Sluiter, 1904)
**Perophora regina* Goodbody & Cole, 1987 (Type locality) (Plate 1e)
Perophora viridis Verrill, 1871
**Ecteinascidia minuta (=E. tortugensis)* Berrill, 1932 (Plate 1h)
**Ecteinascidia styeloides* (Traustedt, 1882) (Plate 1g)
FAMILY: Ascidiidae
Ascidia corelloides (Van Name, 1924)
Ascidia curvata (Traustedt, 1882)
Ascidia interrupta Heller, 1878
Ascidia sydneiensis Stimpson, 1855
Ascidia tenue Monniot, 1983
Phallusia nigra (=Ascidia nigra) Savigny, 1816
FAMILY: Styelidae
Botrylloides magnicoecum (Hartmeyer, 1912)
**Botrylloides nigrum* Herdman, 1886 (Plate 1i)
Botrylloides perspicuum Herdman, 1886
Botryllus planus (Van Name, 1902)
Botryllus tuberatus Ritter et Forsyth, 1917
Polyandrocarpa tincta Van Name, 1902
Polycarpa arnoldi Michaelsen, 1915
Polycarpa cartilaginea (Sluiter, 1898)
Polycarpa spongiabilis Traustedt, 1883

Table 1 cont'd
**Styela canopus* (=*S. partita)* Savigny, 1816
Styela plicata (Lesueur, 1823)

FAMILY: Pyuridae
Pyura munita (Van Name, 1902)
Microcosmus exasperatus Heller, 1878
FAMILY: Molgulidae
Molgula occidentalis Traustedt, 1883

Table 2. The Distribution of Ascidian Species in Different habitats at Twin Cays
a = abundant: + = present: - = absent: o = occasional: r = rare.
Key species are indicated in bold
tb = Twin Bays, c = Main channel, nc = North Channel, lc = Lair Channel
l = Lair, hc = Hidden Creek, hl = Hidden Lake, tp = Turtle Pond, cp = Candy's Pond, gg = Grouper Gardens, gc = Gator Creek, w = West Bay, op = Outer Perimeter

Species	tb	c	nc	lc	l	hc	hl	tp	cp	gg	gc	w	op
Aplidium antillense	r	-	-	-	-	-	-	-	-	-	-	-	-
Trididemnum cyanophorum	-	-	-	-	-	-	-	-	-	-	-	-	r
Didemnum conchyliatum	+	+	+	+	+	+	-	+	-	o	-	-	-
Didemnum psammathodes	r	r	-	r	r	o	-	r	-	-	-	-	-
Lissoclinum abdominale	-	-	+	-	-	-	-	-	-	-	-	-	-
Lissoclinum fragile	+	-	-	-	-	-	-	-	-	-	-	-	-
Diplosoma glandulosum	-	o	a	a	-	-	-	-	-	-	-	-	-
Diplosoma listerianum	-	+	+	+	+	-	-	-	-	-	-	-	-
Distaplia corolla	a	+	o	a	-	-	-	-	-	o	-	-	-
Eudistoma capsulatum	-	o	r	-	-	-	-	-	-	-	-	-	-
Eudistoma obscuratum	-	o	o	-	-	-	-	-	-	-	-	-	-
Eudistoma olivaceum	o	o	o	+	+	+	-	+	a	-	+	-	-
Pycnoclavella belizeana	-	+	+	-	-	-	-	-	-	+	-	-	-
Perophora bermudensis	-	o	o	+	a	+	-	-	-	o	-	-	-
Perophora carpenteria	+	+	+	+	+	+	-	-	-	+	-	-	-
Perophora multiclathrata	-	-	r	-	-	-	-	-	-	-	-	-	-
Perophora regina	-	o	+	-	-	a	-	a	-	-	-	-	-
Perophora viridis	-	-	-	o	o	+	-	+		r	-	-	-
Ecteinascidia minuta	+	o	o	+	+	+	+	+	+	-	-	-	-
Ecteinascidia styeloides	-	o	o	o	+	a	-	-	-	o	-	-	-
Ascidia corelloides	-	-	r	-	-	-	-	-	-	-	-	-	-
Ascidia curvata	-	r	-	-	-	-	-	-	-	-	-	-	-
Ascidia interrupta	o	-	-	o	-	-	-	-	-	-	-	-	-

Table 2 con'td

Ascidia sydneiensis	-	r	-	-	-	-	-	-	-	-	-	-	-
Ascidia tenue	-	-	r	-	-	-	-	-	-	-	-	-	-
Phallusia nigra	o	-	o	-	-	-	-	-	-	-	-	-	-
Botrylloides magnicoecum	-	r	-	-	-	-	-	-	-	-	-	-	-
Botrylloides nigrum	-	a	+	-	-	o	-	-	-	-	-	-	-
Botrylloides perspicuum	-	+	+	-	-	-	-	-	-	-	-	-	-
Botryllus planus	-	r	-	o	-	-	-	-	-	-	-	-	-
Botryllus tuberatus	-	-	-	-	-	-	r	-	-	-	-	-	-
Polyandrocarpa tincta	-	r	-	-	-	-	-	-	-	-	-	-	-
Polycarpa arnoldi	-	-	-	-	-	-	-	-	-	-	-	r	-
Polycarpa cartilaginea	-	-	-	-	-	-	-	-	-	-	-	r	-
Polycarpa spongiabilis	-	r	-	-	-	-	-	r	-	-	-	o	-
Styela canopus	-	o	o	o	o	o	-	-	-	-	-	-	-
Styela plicata	-	-	r	-	-	-	-	-	-	-	-	-	-
Pyura munita	-	-	-	-	-	-	-	-	-	-	-	o	-
Microcosmus exasperatus	r	r	r	r	-	-	-	-	-	-	-	-	-
Molgula occidentalis	-	o	-	-	-	-	-	-	-	-	-	r	-

Table 3. The number of Species of Ascidian occurring at different mangrove locations in the Caribbean

Site	# Ascidian Species	Reference
Jamaica, Fort Rocky	25	Goodbody, 1993
Curacao, Pisadera Baai	23	Goodbody, 1984
Bonaire, Lac	15	Goodbody, 1984
Belize, Pelican Cays Pond A	42	Goodbody, 2000
Pond C	39	Goodbody, 2000
Pond H	27	Goodbody, 2000
Twin cays	40	This work

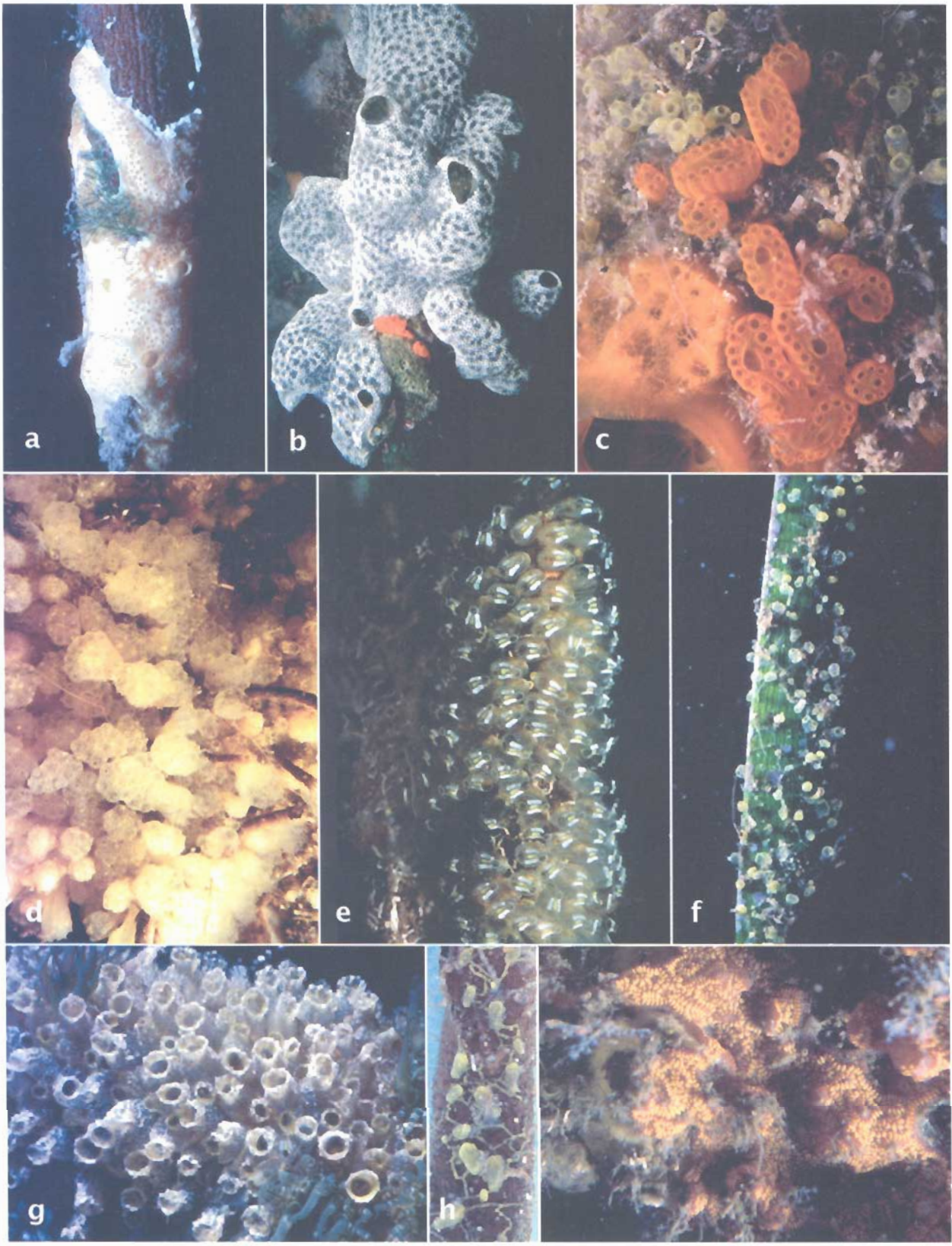

Plate 1. Representative species of ascidians at Twin Cays in situ: *a, Didemnum conchyliatum; b, Diplosoma glandulosum; c, Distaplia corolla; d, Eudistoma olivaceum; e, Perophora regina; f, P. carpenteria; g, Ecteinascidia styeloides; h, E. minuta; i, Botrylloides nigrum.*