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**THE DINOFLAGELLATES OF TWIN CAYS, BELIZE: BIODIVERSITY,
DISTRIBUTION, AND VULNERABILITY**

BY

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Twin Cays, Belize

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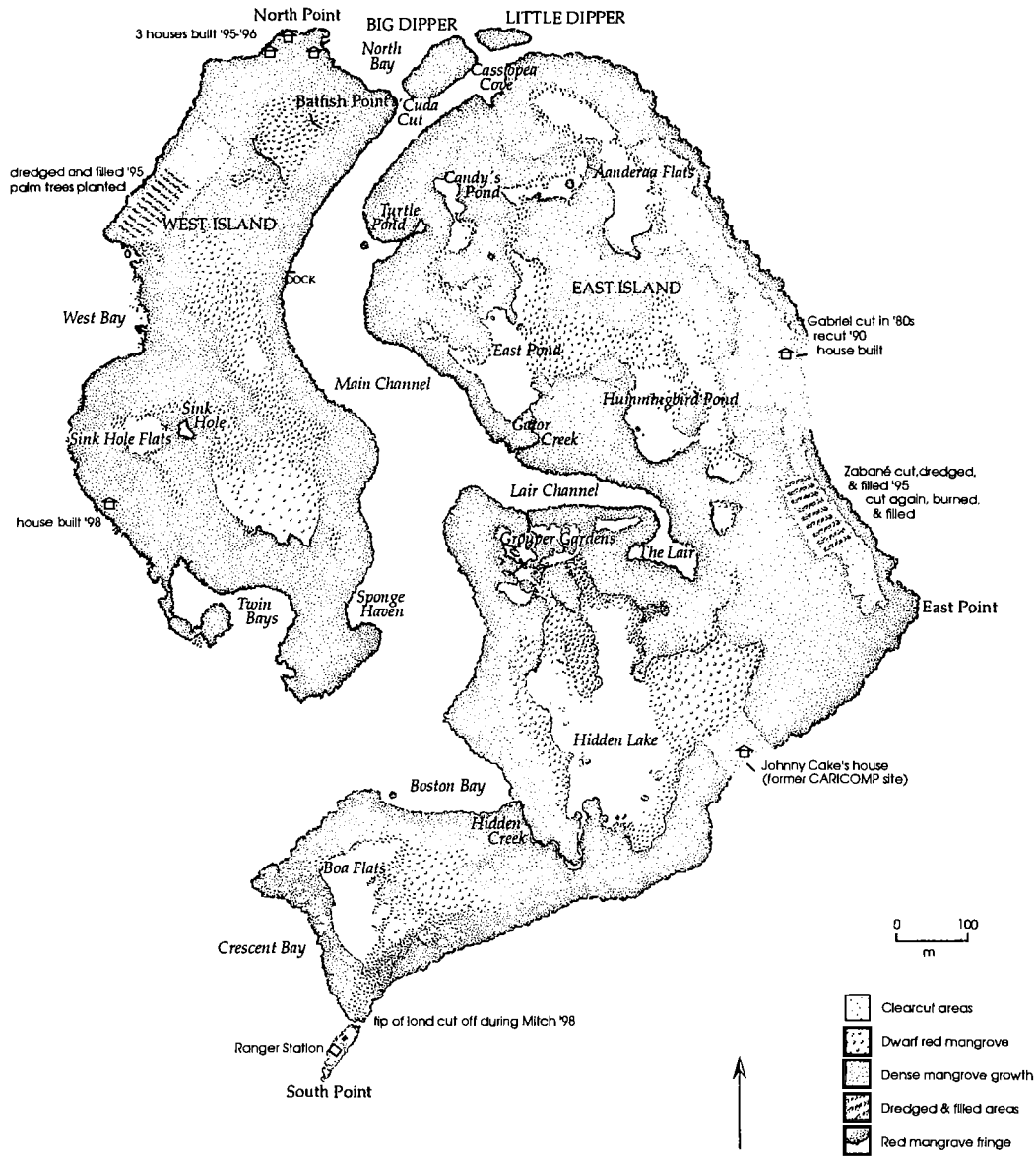


Figure 1. Location Map of Twin Cays showing collection sites: Main Channel, The Lair, Boston Bay and Hidden Lake, Belize.

THE DINOFLAGELLATES OF TWIN CAYS, BELIZE: BIODIVERSITY, DISTRIBUTION, AND VULNERABILITY

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ABSTRACT

Floating detritus, a unique microcosm, acts as a reservoir of diverse microalgae and meiofauna in mangrove areas found in Twin Cays, Belize. The Lair, Boston Bay, Hidden Creek and Main Channel, four locations within Twin Cays, were used as the study sites. Large suspended detrital aggregates are specialized environments where benthic photosynthetic and heterotrophic organisms thrive as suspended free-floating cells in the water column. On the water surface, patches of detritus, a combination of benthic organisms, dinoflagellates, diatoms, cyanobacteria and dinoflagellate cysts, are enclosed in a matrix of fibers. Heterotrophic organisms are also numerous in floating detritus. Phagotrophic fauna, along with nematodes, ciliates, copepods and crustacean larvae, rely on small algal forms in detritus as their food source. Vertical distribution and species composition of microalgae and associated meiofauna in rising and sinking detritus aggregates are reported using water-depth and time-series studies. The biodiversity of dinoflagellates included a total of 38 species, 15 potentially harmful species, and eight neritic species. Populations of benthic dinoflagellates in floating detritus were measured against total cell counts and found to represent 28-43 % in the Lair and 18-68 % in Boston Bay. The highest concentration of dinoflagellate species were identified as being: *Bysmatrum subsalsum*, *Prorocentrum caribbeanum*, *Prorocentrum elegans* and *Prorocentrum mexicanum*. All other dinoflagellates were one to two orders of magnitude lower in cell numbers. Dominant meiofauna organisms were nematodes and ciliates in detritus. Illegal dumping of domestic waste in the Lair caused dinoflagellates to disappear from floating detritus and their recovery is briefly described.

INTRODUCTION

Shallow subtropical warm waters serve as habitats for assemblages of microalgae, and zooplankton (Frenchel, 1988). Mangrove detritus is relatively high in organic matter (Leichfried, 1988) allowing bacteria (Alongi, 1994), microalgae and meiofauna to thrive within the nutrient-rich environment. In addition, mangrove detritus serves as the food source for fish and shell fish (Robertson, 1987; Boto et al., 1989). However, perceiving microscopic aspects of this environment is just becoming better known with regard to biodiversity and distribution of microalgae and meiofauna assemblages.

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In shallow mangrove embayments at Twin Cays, Belize, physical relationships exist between pelagic and benthic environments. On the sediment surface, amorphous aggregates and partially decomposed plant matter accumulates. Floating mangrove detritus represents a benthic habitat that is suspended in the water column as it moves vertically upward responding to oxygen gas generated by the attached microalgae. Patches of detritus increase on the water surface as the day progresses and sink out of sight in the late afternoon (Faust, 1996). Mangrove detritus in protected marine habitats, located at depths of 2 to 4 m, is a rising-sinking platform of various microorganisms in the microscopic food web. Benthic microalgal populations are able to maintain high biodiversity in floating detritus, and are the daily food source for the heterotrophic meiofauna organisms.

I investigated the associations of microalgae and meiofauna in floating detritus at the mangrove island, Twin Cays, to show the changing patterns of these organisms in the microscopic marine food web in long-term studies. In addition, I examined temporal and spatial patterns of benthic microorganisms to illustrate their proliferation and functional role in the tropical mangrove detritus.

METHODS

Study Area

Floating detritus samples were collected at Twin Cays, Belize (16°48' 88°05' W), an intertidal mangrove island (Fig. 1), a section of the barrier reef on the western Caribbean extending 220 km from the Mexican border north to the Gulf of Honduras (Ruetzler and Feller, 1988). Twin Cays has distinct habitats such as lagoons, channels, lakes, and mud flats. Floating detritus samples were collected in the Lair, a 2-3 m-deep enclosed embayment containing high amounts of organic matter originating from the red mangrove, *Rhizophora mangle* Linnaeus and anaerobic sediments. In contrast, Boston Bay and Hidden Lake are 0.5 to 1.5 m deep and Main Channel 3-4 m deep with carbonate silt, mud, sand and meadows of turtle grass, *Thalassia testudinum* Bank ex Konin. The water is high in organic detritus as result of plant and animal decay associated with peat and siliceous skeletons derived from diatom, calcareous algae and sponges.

Sampling

Detritus samples were collected in the center of the Lair with 250 ml plastic bottles opened and closed at a given depth and positioned on a 4 m-PVC pipe four times a day: 06:00, 11:00, 15:00 and 18:00. Samples were collected at three different stations approximately 5 m apart and three depths in the water column (below surface, mid-water and bottom) in May, 1991-1995. Time-series samples from the three stations were pooled for each depth and composite samples were used to minimize biological patchiness within detritus and to collect a manageable number of samples for cell counts and organism identification. A detritus sample was then concentrated to 40 ml and fixed with glutaraldehyde to a final concentration of 2% for enumeration of microorganisms (Faust, 1990).

Physical Parameters

Temperature, salinity and irradiance were measured in the water column at three depths with the following instruments: a Yellow Spring Instrument (YSI) 33 S-C-T Meter; a YSI oxygen analyzer Model 57; a YSI 5739 oxygen probe; and a YSI5795A portable, batter-operated submersible stirrer. Irradiance was estimated by the integrating quantum scalar irradiance meter, Biospherical Instruments # QSI-140 meter. Light intensity varied between 150 and 200 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. During the study the water temperature ranged from 27.1 to 30.8°C, salinity from 22.2 to 30 psu, and dissolved oxygen from 2.2 to 7.5 ppm. Rainfall was 0.2 to 20 mm/day and wind speed ranged from 7.8 to 9.8 $\text{m}\cdot\text{s}^{-1}$. Nutrient concentrations in the Lair water column were: urea (4 to 6 $\text{nmole}\cdot\text{L}^{-1}$); ammonium (1 to 1.5 $\mu\text{mole}\cdot\text{L}^{-1}$); nitrate and nitrite (0.3 to 1.0 $\mu\text{mole}\cdot\text{L}^{-1}$); and dissolved organic phosphorus (0.15 to 0.22 $\mu\text{mole}\cdot\text{L}^{-1}$) (Ambler, 1991). Floating detritus had a total nitrogen (TN) content of 18.5 $\text{mg}\cdot\text{g}^{-1}$ and total particulate organic carbon (POM) content of 34.3 $\text{mg}\cdot\text{g}^{-1}$ (Leichfried, 1988).

Enumeration and Identification of Organisms

To enumerate microalgae the following procedure was used: 1 ml fixed detritus sample was sonicated for 15-20 s, diluted to 10 ml volume with filtered seawater, centrifuged with an International Clinical Centrifuge at top speed for 10 min, supernatant discarded and sample volume adjusted to 2 ml. Cell concentrations were estimated at 100X magnification in a Palmer-Maloney cell chamber (Stein, 1973) and examined under differential interference contrast illumination with Carl Zeiss Axiophot microscope. Abundance of microalgae was enumerated and calculated for dinoflagellates, diatoms, cyanobacteria and dinoflagellate cysts. Relative abundance of microorganisms was determined as the proportion of organisms present in a total of 500 cells. For plate pattern identification, cells were stained with Calcofluor White (Fritz and Triemer, 1985) and observed under the same microscope equipped with an ultraviolet mercury lamp and a Zeiss 01 filter set. The proportion of diatoms and cyanobacteria appeared underrepresented in the data because both form chains or colonies making exact enumeration of populations difficult. Sonication for 15-20 s did not affect the morphology of fixed-cell populations. To enumerate meiofauna, the following procedure was used: the day before counting, 0.2 ml of 1% rose Bengal solution was added to a 20 ml fixed detritus sample from each station-to-strain organism (Higgins and Thiel, 1988). Samples were sonicated (3-5 min) just prior to counting to loosen zooplankton from attached detritus particles. Samples were counted in a 10 x 10 cm square plastic plate. Concentrations of organisms were estimated at 40x magnification using a Carl Zeiss dissecting microscope. Abundance of heterotrophs was calculated for ciliates, copepods, Crustacea, and crustacean larvae. Meiofaunal assemblages are considered underrepresented due to relatively small sample sizes.

Kofoidian nomenclature was used for identifying dinoflagellate species (Kofoid, 1909). Samples of this investigation are deposited in the Dinoflagellate Collection of the U.S. National Herbarium, Department of Botany, NMNH, Smithsonian Institution, Washington, D.C. 20560, United States.

RESULTS

Floating Detritus

In the shallow waters of the Lair, Hidden Lake and Boston Bay, patches of detritus float upward to the water surface on sunny days. Detritus is composed of a loosely composed aggregate of associated organisms, organic fibers, mucus, fecal pellets, silt, and brown humus-like particulates. The abundance of floating detritus increases in the water column with sunrise, peaking in mid-afternoon and declining by sunset. Slight variations in light levels and temperature affect the metabolic activity of microbial assemblages within mangrove detritus fibers. Near the sediment surface of the water column, light level is low and water temperature is cool. From this location detritus floats vertically to the water surface via oxygen bubbles (Lewis and Gattie, 1990) generated by the photosynthesis of diverse, attached microalgae. Once the detritus reaches the water surface, cells are exposed to warmer temperatures and higher light levels which induce rapid growth of organisms. Large patches of forming detritus become visible to the human eye on the water surface by early afternoon. These patches can be dispersed by wind or heavy rain which transports the organisms to other habitats.

Physical Parameters

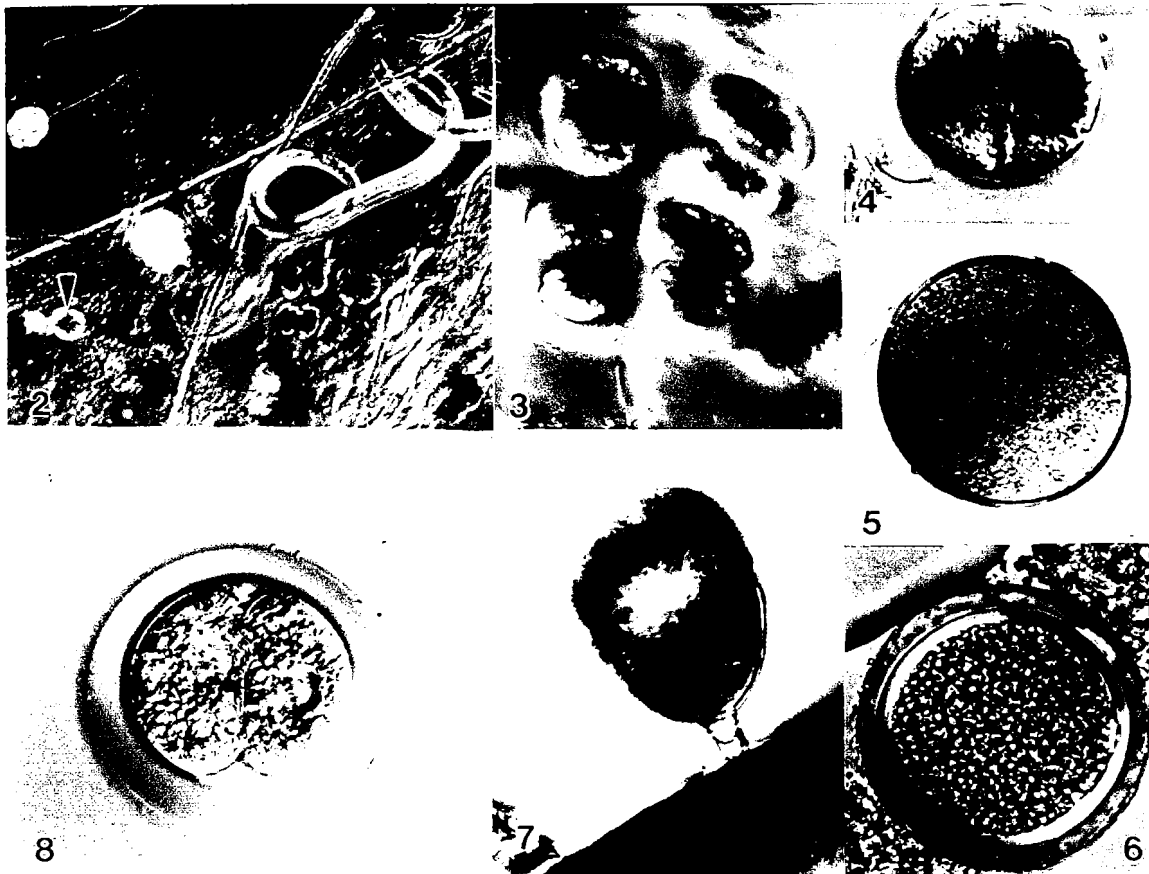
Table 1. Daily mean water temperature, salinity and dissolved oxygen levels for a six day time-series in the Lair habitat measured on May, 1995. Each value is the daily mean of 12 measurements taken at three depths

Parameters	Sampling days					
	1	2	3	4	5	6
Temperature (°C)	29.45	29.45	29.65	29.84	29.52	29.27
Salinity (psu)	35.39	33.69	31.73	28.98	30.04	28.30
Oxygen (ppm)	4.99	4.51	5.45	4.11	5.64	6.18

Temperatures ranged at the water surface from 26.6 to 30.3°C; at mid-water from 28.0 to 30.3°C; and the bottom from 28 to 30.8°C. Temperatures were the lowest at 06:00 at sunrise and the highest at 14:00, declining by 18:00 before sunset. Salinity values ranged at the surface from 22.2 to 35.0 psu, at midwater from 26.7 to 35.8 psu and at bottom from 25.8 to 35.8 psu. Salinity values remained relatively similar from 06:00 to 18:00 but varied daily. Dissolved oxygen concentrations varied within the vertical water column depth from day-to-day. Dissolved oxygen concentrations were the lowest at sunrise 3.5-4.5 O₂ ppm, at 06:00 at the sediment surface and the highest, 6.4 -7.3 O₂ ppm, at 17:00 at 1.5 m depth within the water column.

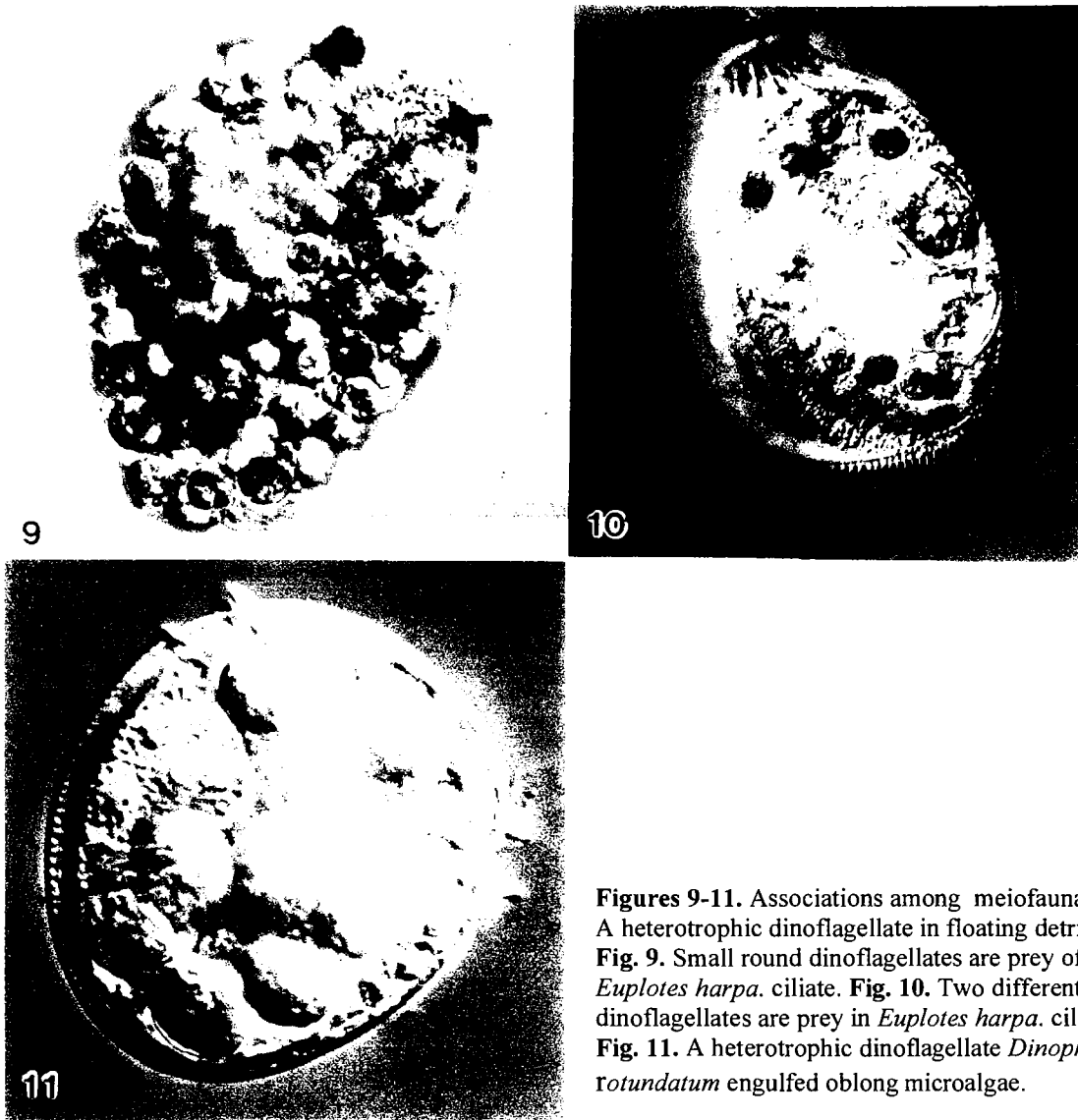
Association of Microscopic Organisms in Detritus

Detritus provides a protective environment which acts as a nursery for diverse species of toxic and nontoxic dinoflagellates and meiofauna. The following light micrographs illustrate the life-cycle stages of dinoflagellates in detritus (Figs 2-8).



Figures 2-8. Life cycle stages and related associations among benthic dinoflagellates present in floating detritus.

Floating detritus showing loosely bound fibrous aggregates and life-cycle stages viewed at low (100x) magnification (Fig. 2). Photographs were taken at 1000x magnification. Cell pairs of *Prorocentrum* ssp. is embedded in mucilage (Fig. 3). Daughter cells of *Amphidinium* sp. is in a division cyst (Fig. 4). Temporary cyst of *Prorocentrum lima* (Fig. 5). Round, triple-layered dormant cyst of *Prorocentrum foraminosum* has unique granulated cytoplasm (Fig. 6). Prominent stalk of a dinoflagellate sp. attached to plant detritus (Fig. 7). Dividing cell pair of *Prorocentrum* sp. embedded in a ring of mucilage (Fig. 8).



Figures 9-11. Associations among meiofauna and A heterotrophic dinoflagellate in floating detritus. **Fig. 9.** Small round dinoflagellates are prey of an *Euplotes harpa*. ciliate. **Fig. 10.** Two different sized dinoflagellates are prey in *Euplotes harpa*. ciliate. **Fig. 11.** A heterotrophic dinoflagellate *Dinophysis rotundatum* engulfed oblong microalgae.

Examples of dinoflagellates as prey of ciliates and heterotrophic dinoflagellates in floating detritus are in the following light micrographs illustrated at 400x magnification: *Euplotes harpa*. exhibits captured small round dinoflagellates (Fig. 9). A second *Euplotes harpa* shows engulfed large and small dinoflagellate as prey (Fig. 10). *D. rotundatum* heterotrophic dinoflagellate, consumed small, oblong microalgal preys (Fig. 11).

Time-series Study: Microalgae

Floating detritus samples were collected from three levels within the water from the Lair and Boston Bay on May 12, 1991 (Fig. 12). The relative abundance of microorganisms varied with time and collection site. At the Lair, 28 % to 43 % of the floating microorganisms were dinoflagellates whereby in Boston Bay the quantities of dinoflagellates recorded was 18 % to 60 % of the total cell numbers, reaching the highest value at mid-afternoon, 15:00 h. Diatoms were also present in high proportional numbers;

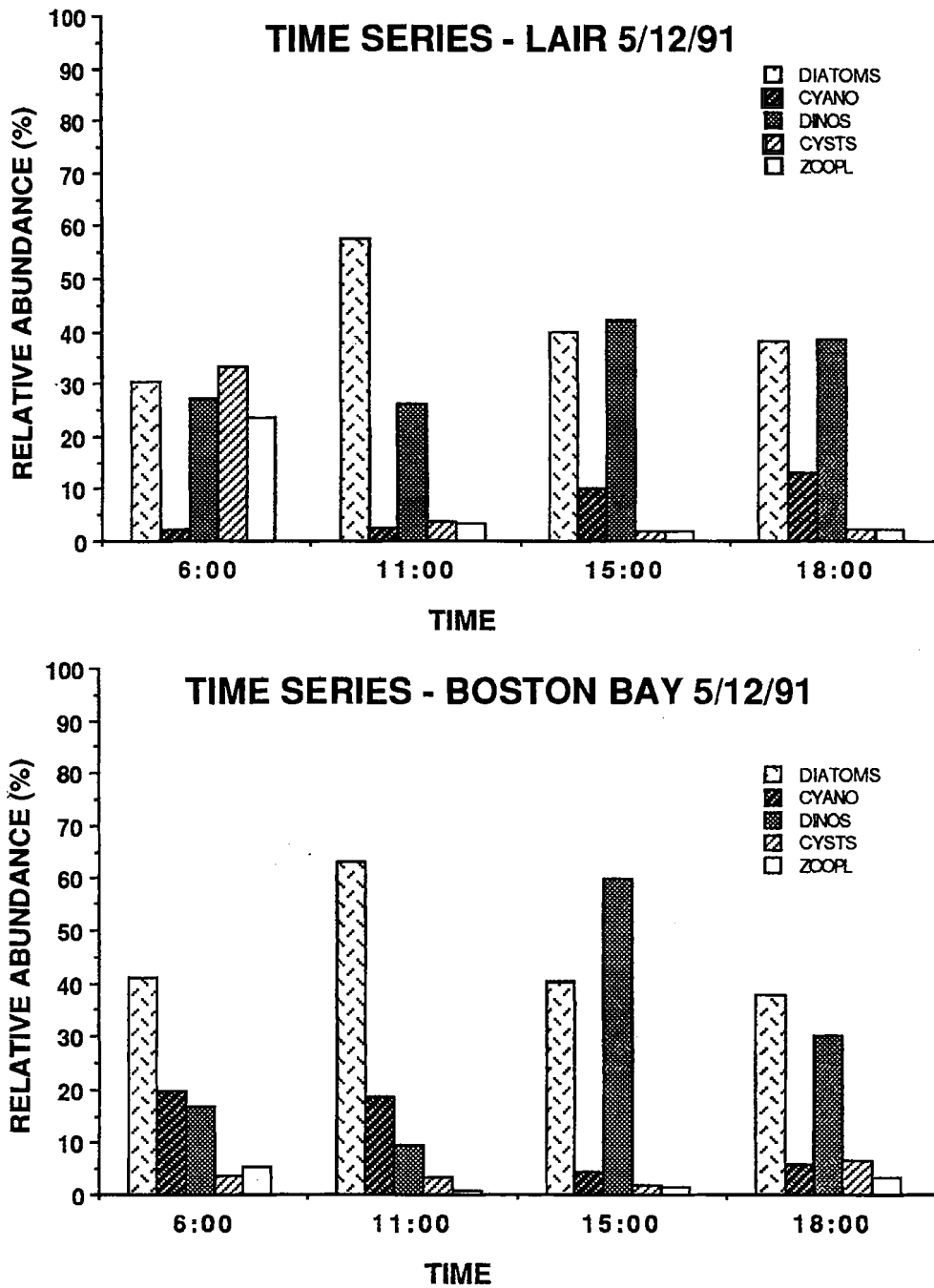


Figure 12. Relative abundance of diatoms, cyanobacteria, dinoflagellates and cysts of dinoflagellates and zooplankton in floating detritus in a time series experiment.

30 % to 68 % at the Lair and 42 % to 65 % in Boston Bay where they the most abundant. Recording was made in the late morning, 11:00 h. Cyanobacteria represented less than 20 % in the samples. Populations increased during time series studies at the Lair whereas decreased in Boston Bay. Benthic cysts represented approximately 35 % of the detritus collected at the Lair at 6:00 h and their numbers rapidly declined from 11:00 h to 18:00 h. In contrast, cysts remained low at Boston Bay from 6:00 h to 18:00 h. Zooplankton

numbers were the lowest at both sampling sites. Dinoflagellates and diatoms were the dominant component in the mangrove detritus, whereas only minor populations of zooplankton were counted.

Table 2. Dinoflagellate species distribution listed as cell numbers present in 500 total cells counted per detritus sample collected in the Lair and Boston Bay on May 12, 1991.

Dinoflagellate species	Samples Taken (Time and Stations)							
	6h		11h		15h		18h	
	L	BB	L	BB	L	BB	L	BB
<i>Amphidinium carterae</i>	0	0	3	4	11	169	29	2
<i>A. operculatum</i>	0	0	11	0	46	15	0	0
<i>Ceratium furca</i>	8	17	6	1	21	2	0	64
<i>Gambierdiscus toxicus*</i>	13	5	18	0	10	9	7	2
<i>Gonyaulax grindleyi</i>	0	57	28	19	50	215	67	61
<i>Ostreopsis lenticularis*</i>	0	0	0	1	3	2	0	3
<i>Bysmatrum subsalsum</i>	41	1	9	3	0	0	14	5
<i>Prorocentrum lima*</i>	0	3	0	0	0	1	0	0
<i>P. mexicanum*</i>	5	3	26	5	12	12	5	2
<i>P. concavum*</i>	0	0	3	0	0	0	0	0
<i>P. emarginatum</i>	2	0	5	1	0	2	0	0
<i>P. ruetzlerianum</i>	0	0	3	0	2	1	4	0
<i>P. norrisianum</i>	66	9	11	1	3	2	18	6

Abbreviations: L = The Lair; BB = Boston Bay; * toxic species

Detritus collected at the Lair and Boston Bay exhibited diverse dinoflagellate species (Table 2). Cell numbers differed at the collection sites and were found to be less in the early morning at 6:00 h. and highest at 15:00 h. These findings directly coincided with the abundance levels of less floating detritus with the least observed at 6:00 h. and the most seen at 15:00 h. Species of *Amphidinium carterae*, *A. operculatum*, Claparède et Lachmann, *Gonyaulax grindleyi* Reinecke, *Prorocentrum mexicanum* Tafall, and *P. norrisianum* Faust were the most numerous in the samples. Several toxins-producing species were also present in low numbers: *G. toxicus* Adachi et Fukuyo, *O. lenticularis* Fukuyo, *P. lima* (Ehrenberg) Dodge, *P. mexicanum* and *P. concavum* Fukuyo. One planktonic species, *Ceratium furca* (Ehrenberg) Claparède et Lachmann, was recognized.

Cell populations of the microalgae in suspended detritus varied daily with time and depth as observed at the Lair study site. Vertical distribution of dinoflagellates, diatoms, cyanobacteria and cysts was compared as a relative percentage of total cells. Three depths (below surface, mid-water, bottom) were examined over a six-day time period in May 1994. In Figure 13, vertical distribution of dinoflagellates, diatoms, cyanobacteria, and dinoflagellate cysts is compared via a relative percentage of total number of cells. The resulting distribution is the following: dinoflagellates represent 50-90 %, diatoms 5-15 %, cyanobacteria 3-25 %, and dinoflagellate cysts 1-7 % of the total cells in floating detritus.

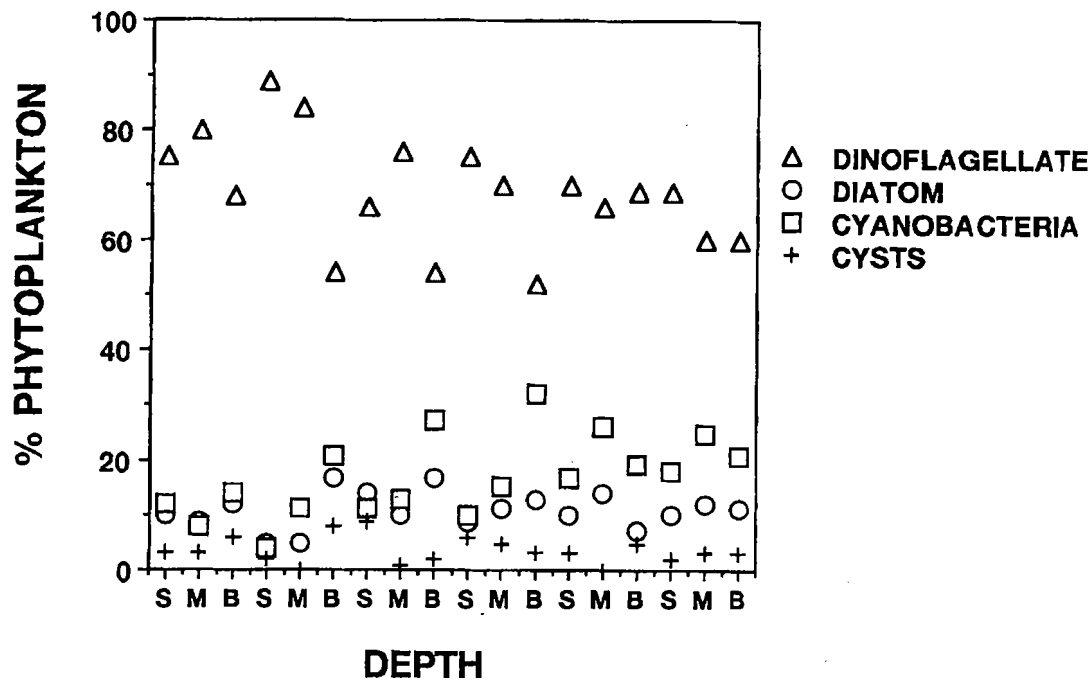


Figure 13. Vertical distribution of dinoflagellates, diatom, cyanobacteria, and cysts of dinoflagellates expressed as relative percentage of total cells in detritus of six-days time series experiment. S, surface; M, midwater; B, bottom detritus.

Vertical distribution and patterns of microalgae in floating detritus for day three are illustrated as one example in (Figure. 14 A). Cell numbers were the highest in surface and bottom of samples and lowest in mid-water with their numbers increasing with time. In bottom detritus samples cysts with a red body were present (Fig. 2), whereas in mid-water and surface detritus samples division cyst enclosed in hyaline membrane (Figs 4-5) were observed. During their journey in rising detritus, cysts became metabolically active and divided (Figs 2-4, 8). The freshly divided microalgae provide an abundant food source for meiofauna that follow.

Composition of meiofauna in floating detritus is diverse. Dominant taxa include nematodes, ciliates, copepods and crustacean-larvae (Fig. 14 B). Meiofauna cell densities in detritus varied with depth and time. Most numerous taxa in surface and bottom detritus were nematodes, crustacean-larvae, and ciliates and copepods were more abundant in mid-waters. Usually meiofauna assemblages in mid-water detritus samples were few.

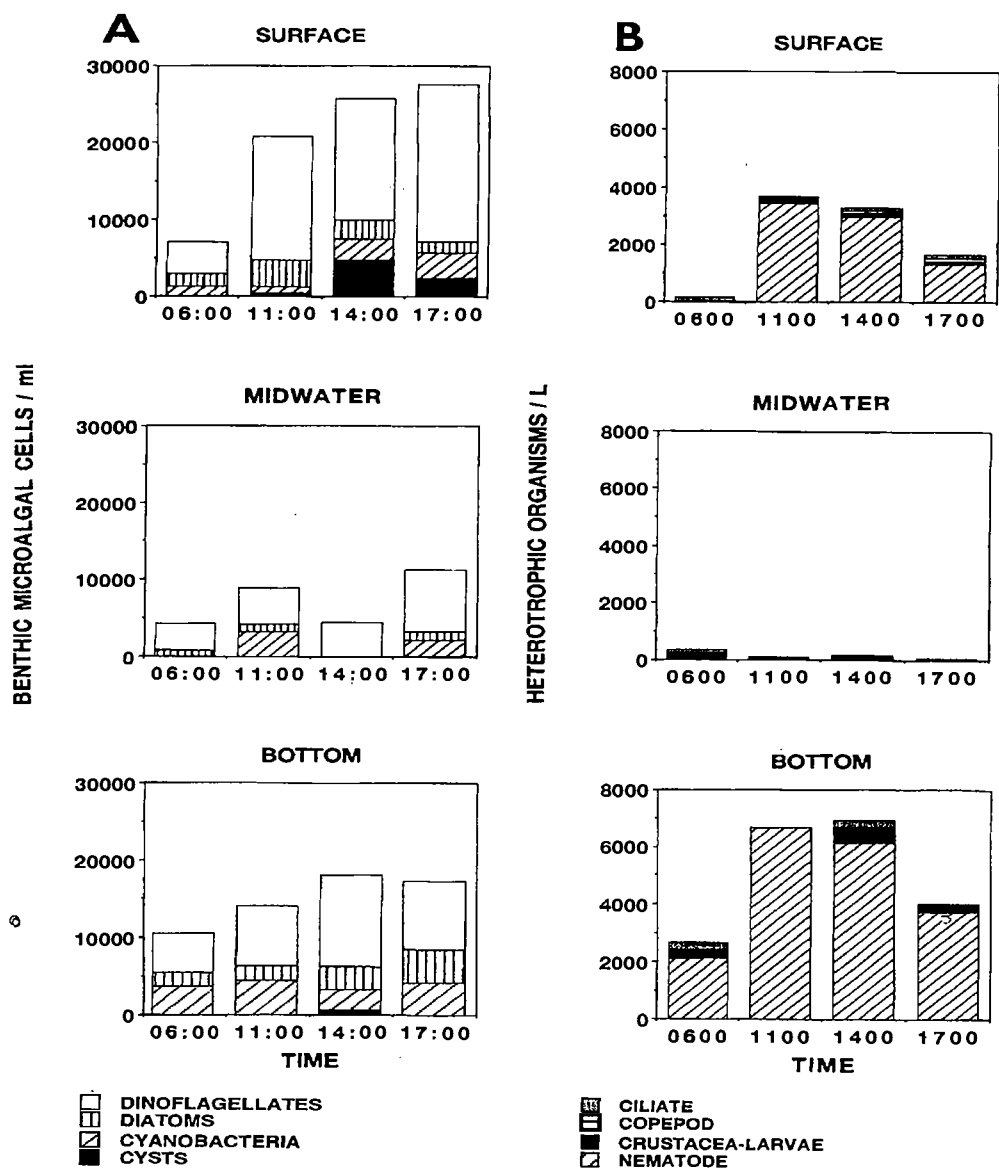


Figure 14. Vertical distribution of microalgae (A) and meiofauna (B) assemblages in floating detritus samples collected at surface, midwater and bottom floating detritus samples from sunrise to sunset in time series

Biodiversity of Dinoflagellates

The biodiversity of dinoflagellates in floating detritus at the Lair, Boston Bay, Hidden Lake, and Main Channel include 38 species, 15 toxins producing species (*) and 8 neritic species (Table 3).

Table 3. Biodiversity of dinoflagellate species in detritus from the Lair (L), Boston Bay (BB), Hidden Lake (HL) and Main Channel (MC), Twin Cays, * toxic species, and species in detritus (D), sediment (S) and plankton (P) are presented.

Dinoflagellate species	L	BB	HL	MC	Ecology
<i>Amphidinium carterae</i> *	+	+	+	-	DS
<i>A. operculatum</i>	-	-	+	-	D
<i>Bysmatrum capony</i>	+	-	-	-	D
<i>B. subsalsum</i>	+	+	+	+	DSP
<i>Ceratium furca</i>	+	-	-	+	P
<i>C. hircus</i>	+	-	-	+	P
<i>C. lineatum</i>	+	-	-	+	P
<i>Cochlodinium polykrikoides</i> *	+	-	-	+	P
<i>Coolia monotis</i> *	+	+	+	+	DSP
<i>Dinophysis caudata</i> *	-	-	-	+	DP
<i>D. mitra</i>	-	-	-	+	DP
<i>D. rotundatum</i> *	-	-	-	+	DP
<i>Gambierdiscus toxicus</i> *	+	-	+	+	DSP
<i>Gonyaulax grindleyi</i> *	+	+	-	+	DSP
<i>G. polyedra</i>	+	-	-	+	PD
<i>G. polygramma</i>	+	-	-	+	PD
<i>G. spinifera</i>	-	-	-	+	PD
<i>Gymnodinium sanguineum</i>	+	+	+	+	P
<i>G. estuariale</i>	+	+	+	+	P
<i>Ostreopsis lenticularis</i> *	+	+	-	+	DPS
<i>O. ovata</i> *	+	+	-	+	DPS
<i>Plagodinium belizeanum</i>	+	-	-	+	DPS
<i>Prorocentrum belizeanum</i> *	+	+	+	+	DPS
<i>P. caribbeanum</i>	+	+	-	-	DS
<i>P. concavum</i> *	+	+	+	+	DS
<i>P. elegans</i>	+	+	-	-	PD
<i>P. emarginatum</i>	+	+	+	-	DS
<i>P. formosum</i>	+	+	+	-	P
<i>P. foraminosum</i>	+	-	+	-	DS
<i>P. hoffmannianum</i> *	+	+	+	+	DSP
<i>P. lima</i> *	+	+	+	+	DS
<i>P. maculosum</i> *	+	+	+	-	DS
<i>P. mexicanum</i> *	+	+	+	+	DSP
<i>P. norrisianum</i>	+	+	+	-	DP
<i>P. ruetzlerianum</i>	+	+	+	-	DSP
<i>Pyrodinium bahamense</i>	-	-	-	+	P
<i>Scrippsiella trochoidea</i>	+	+	+	+	PD
<i>Synophysis microcephalus</i>	+	-	+	-	SD

Most numerous species were benthic dinoflagellates associated with detritus and sand, and eight species considered planktonic/neritic (Table 4). Detritus samples with high species counts were collected in the Lair and Main Channel. Collections of detritus samples were relatively few from Boston Bay and Hidden Lake which may limit the assessment of the biodiversity of dinoflagellates.

Table 4. Concentrations of benthic and neritic dinoflagellate species within floating detritus in the Lair collected at two different dates, May 1991 and 2003, are compared.

Dinoflagellate species	Concentrations (cells. 10^{-3} . L ⁻¹)	
	1991	2003
Benthic		
<i>Amphidinium carterae</i>	3.01	0.15
<i>Bysmatrum subsalsum</i>	18.45	0.25
<i>Coolia monotis</i> *	4.24	
<i>Dinophysis caudata</i> *	0.31	
<i>D. rotundatum</i> *	0.28	
<i>Gambierdiscus toxicus</i> *	0.25	
<i>Gonyaulax grindleyi</i> *	2.72	0.06
<i>Ostreopsis lenticularis</i> *	0.72	
<i>O. ovata</i> *	0.37	
<i>Plagodinium belizeanum</i>	4.75	0.20
<i>Prorocentrum belizeanum</i> *	2.26	0.32
<i>P. caribbeanum</i>	10.52	
<i>P. concavum</i> *	0.06	
<i>P. elegans</i>	80.23	0.88
<i>P. emarginatum</i>	1.56	0.08
<i>P. formosum</i>	1.69	
<i>P. foraminosum</i>	1.52	
<i>P. hoffmannianum</i> *	1.12	
<i>P. lima</i> *	0.81	
<i>P. maculosum</i> *	0.75	
<i>P. mexicanum</i> *	27.84	0.16
<i>Synophysis microcephalus</i>	0.07	
Neritic		
<i>Ceratium furca</i>	1.83	
<i>Gonyaulax grindleyi</i>	2.72	
<i>Cochlodinium polykrikoides</i>	3.14	
<i>G. polyedra</i>	3.11	
<i>Gymnodinium sanguineum</i>	2.32	
<i>G. estuariale</i>	0.42	
<i>Protoperidinium quinquecorne</i>	0.32	
<i>Scrippsiella trochoidea</i>	2.87	

Dinoflagellate concentrations in floating detritus from the Lair illustrate the distribution of species collected in early afternoon in May 1994 (Table 4). Four dinoflagellates reached the highest populations: *Bysmatrum subsalsum* (Ostenfeld) Faust et Steidinger 1998, *Prorocentrum caribbeanum* Faust 1993, *P. elegans* Faust 1993, and *P. mexicanum* Tafall 1942. Thirteen toxic species were also present in the samples which are marked with the * symbol. The majority of other species were one-two orders of magnitudes lower in cell numbers. *Dinophysis caudata* Saville-Kent 1881 and *D. rotundatum* (Claparède and Lachmann) Kofoid and Michener 1911 are heterotrophic void of chloroplasts whereas all other species are photosynthetic.

Concentrations of dinoflagellates in detritus varied with species (Table 4). The highest concentration of dinoflagellate species were identified as being: *Bysmatrum subsalsum*, *Prorocentrum caribbeanum*, *P. elegans*, and *P. mexicanum*. All other dinoflagellates were one-to-two orders of magnitude lower in cell numbers. Dinoflagellate assemblages in floating detritus at the Lair totaled 22 benthic species, 13 toxin-producing species, and eight neritic species. Among the dinoflagellates, nine were new species described from Twin Cays and also reported for the first time from a coral reef-mangrove habitat: *Plagodinium belizeanum* Faust et Balech 1993, *Prorocentrum hoffmannianum* Faust 1990, *P. maculosum* Faust 1993, *P. formosum* Faust 1993, *P. ruetzlerianum* Faust 1990, *P. belizeanum* Faust 1990, *P. foraminosum* Faust 1993, *P. elegans*, and *P. caribbeanum*. *Sinophysis microcephalus* Nie et Wang 1944.

Illegal dumping of domestic waste occurred in the Lair beginning in 1995. The next four years, 1997 to 2000, dinoflagellates disappeared from floating detritus. The first sign of recovery of dinoflagellate was noted in 2001; since then eight species were identified in floating detritus in 2003. Note the low cell numbers as shown in Table 4.

DISCUSSION

Floating Detritus: a Specialized Environment

In Twin Cays, floating detritus is a unique microcosm in protected mangrove habitats. It consists of organic fibers, decomposed organic matter, and various taxa of photosynthetic microalgae and heterotrophic meiofauna (Faust, 1995). Patches of detritus originate at the sediment-water interface and appear floating on the water surface visible to the human eye. Detritus dislodges from sediment where dissolved oxygen and light levels are low and organic matter high (Amble, 1991). Benthic microorganisms enclosed in aggregates move upward, and re-enter the water column daily. As the sun rises, microalgal photosynthesis increases generating oxygen gas bubbles clearly visible as patches of detritus float upward to the water surface propelled by the buoyant force. Microalgal assemblages proliferate in rising detritus aggregates where they receive optimum light to photosynthesize, grow and sexually reproduce (Faust, 1993). During this journey detrital aggregates exhibit dividing microalgae that are consumed by the meiofauna (Faust and Gullledge, 1996). Once the patches reach the water surface, cells are exposed to warmer temperatures and higher levels of light induce excystment of dinoflagellates and rapid bacterial growth (Herndl, 1991). These adhering organisms in the detritus can be reintroduced into the water column or detritus patches can be broken

up and dispersed by high winds and heavy rains. The observation described in Twin Cays is less complementary to the formation and sinking aggregates of shallow coastal waters (Sherr et al., 1986) or of deep ocean (Alldredge, 1989).

Dinoflagellate-adhering surface relationships may involve physical and chemical interactions as well as structural and surface interactions (Bomber et al., 1985). Bomber et al., (1985) referred to the attachment of dinoflagellates to microalgal surfaces. In the detritus-dinoflagellate interaction the detritus probably supplies nutrients and provides a stabilizing structure for colonization. Because detritus patches are easily broken up by the water movement, cells are nourished and benthic organisms become free floating. In this situation, detritus patches serve as a nursery for dinoflagellate populations as well as other associated microorganisms. When such dinoflagellate populations are producers of toxins, floating detritus in mangrove embayments, near-shore areas and coral reefs may be extremely important to the balance of this ecosystem.

Twin Cays mangrove ecosystem is a unique floating detritus habitat and a masterpiece of nature (Along, 1998; Newel, 1984). In the protected quiescent physical habitats found at the Lair, Boston Bay and Hidden Lake, low-wave energy enables mangrove leaves to decompose and facilitate development of soft sediments (Faust, 1996). Floating detritus is processed and recycled rapidly through the aquatic food chain and controlled by hydrodynamic forces, temperature, light and nutrient availability. Assemblages of microalgae including dinoflagellates proliferate in rising detritus aggregates. On the sediment surface, unfavorable environmental conditions hinder microalgal proliferation and their number is further reduced by the grazing activities of nematodes, ciliates and other consumer organisms (Fig. 14B). These microbial communities are highly dynamic undergoing rapid population changes that are measured in hours (Fig. 14A). At the bottom, detritus predation of nematodes may regulate population size of dinoflagellates similarly to phagotrophic protozoa (Sherr et al., 1986). In surface detritus where predator populations were lower, dinoflagellates developed into densities two-three orders of magnitude higher than found in bottom detritus. As part of the microbial community, microalgae produced new cells and dissolved oxygen for heterotrophs residing in the mangrove food webs.

Benthic food chains in mangroves obtain their sustenance not only from detritus but also from a variety of living nutritious microalgae (Alongi, 1998). Floating detritus acts as a vehicle that transports benthic microbial assemblages daily into the suspended pelagic tropical waters where they become actively dividing populations and, as a consequence, a continuous shift exists between actively growing and inactive cell populations. These phototrophs, such as cyanobacteria, dinoflagellates and diatoms, are a quality food source of meiofauna (Porter et al., 1985, Sherr et al., 1986), microfaunal assemblages (Frenche, 1988), and large particle feeders including crustaceans and juvenile fish (Stoner and Zimmerman, 1988). Suspended floating detritus provide physical surfaces where microorganisms can attach and grow rapidly in an environment highly enriched and protected from predators. In detritus the proliferation of benthic microbial communities occur, a nutrient-enriched environment, resulting in diverse microalgal and meiofaunal populations and dinoflagellate life-cycle events (Faust, 1993, 1991).

Microbial Associations and Biodiversity

Microorganisms in floating detritus at Twin Cays represent assemblages that are associated in benthic planktonic habitats (Tables 3 and 4). Dinoflagellates are the most dominant microalgae, with nematodes and ciliates as the most common consumers. Benthic assemblages of microalgae in a time series are illustrated in Figure 14. The biodiversity of dinoflagellates at four collection sites included a total of 38 species, 15 toxins-producing species (designated by * symbol), and eight neritic species. Dinoflagellate populations were most numerous in floating detritus. Smetacek (1985) proposed that aggregation is an adaptation-promoting sedimentation of diatoms out of warm, nutrient-depleted water into cold water resulting in the formation of resting spores. The result of this study illustrates a similar occurrence where benthic dinoflagellate assemblages of resting cysts reenter the water column and form new surface dinoflagellate populations beginning at sunrise via floating detritus. Floating detritus containing dinoflagellates in late afternoon sink down from warm surface water into colder nutrient-enriched bottom waters to produce resting stages with sunset. This floating platform of mangrove detritus creates microhabitats for a variety of benthic organisms within the water column. This aggregated platform has its own diverse microbial assemblages, nutrient gradients on solid-liquid interfaces as illustrated in ecological analogies of the aggregated micro-environments (Alldredge and Youngbluth, 1985; Sherr et al., 1986; Aldredge and Silver, 1988; Stoner and Zimmerman, 1988; Caron, 1991; Alongi, 1994, 1992).

Functional Roles

Floating mangrove detritus at Twin Cays has microbial assemblages that include photosynthetic and heterotrophic organisms that form the base of benthic food webs. Large suspended aggregates are specialized environments rich in communities of bacteria, cyanobacteria and photosynthetic eukaryotes constituting patches of highly elevated abundances of prey for many species of protozoa (Porter et al., 1985), ciliates (Sherr et al., 1986) and flagellates (Caron, 1991). In mangrove detritus, phytoplankton exudates in the form of dissolved nutrients (organic carbon and nitrogen) that may provide nutrients for heterotrophs as described for marine snow (Alldredge, 1979) and mangrove detritus (Boto et al., 1989). Mangrove detritus creates a specialized environment where mixed species of organisms exist. Benthic microorganisms may grow at different rates, in part depending on whether they are free-living motile species in the water or aggregated in biofilms (Lewis and Gattie, 1990).

Nematodes were by far the most abundant heterotroph in the floating detritus samples. They were most abundant at 11:00 in bottom detritus (Fig. 14B) when algal densities were relatively low. Nematodes were less abundant in surface detritus where algal densities were more prominent (Fig. 14A). This is similar to the findings of Alongi and Christoffers, (1992) who reported comparable numbers of nematodes in near-bottom mangrove sediments of the Great Barrier Reef, Australia. In this study, 15-25 engulfed dinoflagellates were often observed in a nematode indicating that they are important consumers of benthic dinoflagellates in Twin Cays mangroves. The slender, flexible body structure of a nematode allows it to move easily between detrital fiber-webs in search of food. They may be the major predators of benthic dinoflagellates. Nematode densities

also varied significantly with depth in Australian sediments at Queensland (Alongi and Christoffers, 1992).

Dinoflagellate-ciliate prey associations are complex. Ciliate species exhibited size-specific dinoflagellate-prey preferences (Figs 9-10). Certain ciliates capture only small dinoflagellates, but other ciliates have a more diverse food preference (Faust and Gullledge, 1996). Ciliates also have some advantage in floating detritus; they are small and readily navigate within detritus fibers and often consume small centric diatoms readily available. In floating detritus the movements of calanid copepods are restricted due to their larger size and feed primarily on attached bacteria (Herndl, 1991). Heterotrophic dinoflagellates were the major consumers of small dinoflagellates in floating detritus (Fig. 11).

The function of floating mangrove aggregates appears to be somewhat similar to marine snow (Alldredge and Silver, 1988; Alldredge, 1989; Jackso, 1993) as observed in Twin Cay mangrove habitats. It is difficult, however, to make exact comparison between the ecology and dynamics of these two marine aggregates. One major difference is that in the shallow water column, mangrove aggregates rise and sink daily and have a short residence time in water measured in hours. 'Marine snow' aggregates in deep oceans have a long residence time and move downward in the water and sink to the sea floor in a matter of months (Alldredge, 1989).

This study suggests that floating mangrove detritus is a location where food sources are generated for meiofauna. Regeneration of algae and the predation cycle repeated daily in the water column regulate benthic assemblages of organisms. Detrital aggregates are sites of active algal and bacterial production (Alongi, 1994; Gotschalk and Alldredge, 1989) that serve as the food source for a variety of heterotrophic organisms (Sherr et al., 1986; Alongi, 1990). The main function of floating mangrove detritus is as a highly effective, self-sufficient microhabitat for a variety of benthic taxa, somewhat similar in function to marine snow for pelagic microorganisms.

Vulnerability of Dinoflagellates

Illegal dumping of domestic waste in black plastic bags in shallow waters of the Lair, Twin Cays was discovered during field studies. Waste disposal took place beginning in 1995 and continued for three years. Released pollutants during the decomposition process resulted in dramatic loss of phytoplankton populations diverse in these waters. First sign of population recovery occurred in May 2001 when benthic dinoflagellates were again seen attached to floating detritus. However, species composition and cell density were significantly reduced after to dumping of domestic waste (Table 4).

While dinoflagellates have little economic value, indirectly they may signal change in the health of an undisturbed aquatic ecosystem as illustrated in Twin Cays. Mangrove swamps indeed constitutes an extremely delicate natural ecosystem. Three years of waste disposal in Twin Cays significantly altered dinoflagellate assemblages, greatly changing the microscopic food web of this habitat. Continuation of waste disposal would probably have caused irreversible harm. The effect of household waste ultimately could have resulted in a loss of habitat for microscopic food web organisms and, in turn, the loss of a food source for marine fish and shell fish. Our knowledge is limited in

understanding the effect of household waste on the microscopic biodiversity of shallow, slow-flowing mangrove environments.

CONCLUSIONS

Long-term studies at the Twin Cays mangrove forest provided the opportunity to examine not only spatial differences in assemblages of microalgae and meiofauna in floating detritus but also to document temporal changes in abundance, biodiversity and distribution in the microscopic food web. Floating detritus aggregates are specialized protective environments and significantly affect the productivity of mangroves, where benthic organisms sweep into the water column as free-floating photosynthetic and heterotrophic organisms. On the water surface microalgae proliferate in light and provide the food source for the meiofauna grazers and in turn, maintain nursery for fish and shellfish. Detritus is a nutrient-enriched microcosm for toxic dinoflagellates and a possible site for ciguatera outbreaks. When dinoflagellate populations are ciguatoxicogenic, the existence of floating detritus originating in mangrove waters may take on extreme importance to near-shore areas and coral reefs. Illegal dumping of domestic waste in the Lair for four years caused the disappearance of dinoflagellates. Our knowledge is limited in understanding the effects of household waste on microscopic aquatic organisms. This report is the first to provide empirical data on this topic.

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