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**DINOFLAGELLATE DIVERSITY AND ABUNDANCE IN TWO
BELIZEAN CORAL-REEF MANGROVE LAGOONS: A TEST OF
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Research Area of Twin Cays and Douglas Cay

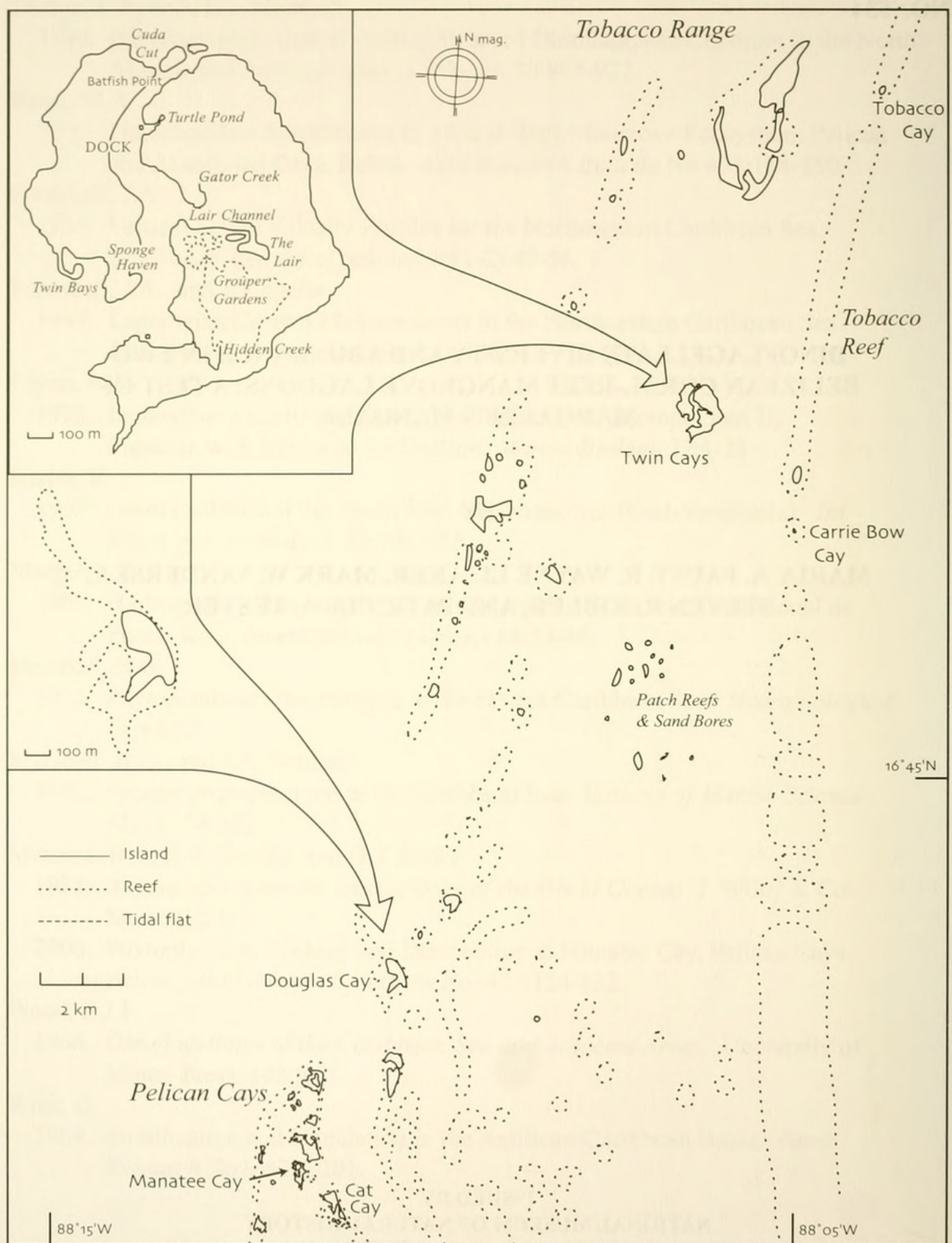


Figure 1. Map showing The Lair at Twin Cays, and Douglas Cay sample sites and surrounding cays.

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ABSTRACT

Dinoflagellates are frequently abundant in the coral-reef mangrove lagoons off the coast of Belize. Margalef predicted that marine environments with low turbulence and high nutrient inputs would favor dinoflagellates. A long-term study of coral-reef mangrove embayment cays of Belize, including this study, has shown that these systems contain abundant dinoflagellate species. Consistent with Margalef's prediction, these habitats are protected from wind mixing, show a high degree of stratification, and have restricted water exchange with surrounding oligotrophic waters of the open barrier-reef system. This limited water exchange favors retention of dinoflagellate cells and the trapping of nutrient rich organic material that is rapidly recycled providing a relatively high-nutrient environment. Species-specific blooms are a common feature of these systems. In the study, the ecology and diversity of dinoflagellate species from two nutrient-enriched habitats, Douglas Cay and The Lair at Twin Cay, were examined in detail. A comparison of the species composition from both sites showed that Douglas Cay contained coastal planktonic and offshore oceanic dinoflagellates while The Lair at Twin Cay contained mainly benthic dinoflagellates. A total of 19 bloom-forming species were observed in these systems during three two-week studies. The morphology of eight of these bloom-forming species is illustrated in Scanning Electron Microscopy (SEM) photographs. These include *Bysmatrum caponii*, *Dinophysis caudata*, *Gonyaulax grindleyi*, *Peridinium quinquecorne*, *Gonyaulax polygramma*, *Gonyaulax spinifera*, *Lingulodinium polyedrum*, and *Pyrodinium bahamense* var. *bahamense*. Approximately half of the bloom-forming dinoflagellates are known toxin producers. The congruence between Margalef's prediction and the distribution of dinoflagellates in these naturally eutrophic systems suggests that increased nutrient inputs in oligotrophic portions of the Caribbean will favor a shift in species dominance toward dinoflagellate species. The effect will be most pronounced in bays or other regions where turbulence is likely to be reduced. This species shift may have consequences for food web dynamics and the prevalence of dinoflagellate toxins in the food chain.

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INTRODUCTION

Dinoflagellates constitute one of the dominant groups of oceanic phytoplankton and are responsible for a significant portion of overall primary productivity. Many species are bloom formers, and a subset of these is known to produce potent toxins that accumulate in the food chain causing mass mortalities of fish, birds and mammals, as well as human illness and death. These blooms frequently reach densities sufficient to discolor the water and can release enough organic material to result in hypoxia or other forms of water-quality degradation including noxious odors and unsightly foams. Occurrences of harmful algal blooms (HABs) near shore regions cause severe economic impact, have major environmental and human health problems, and cause losses to fisheries and tourism operations (Smayda, 1997; Ajani et al., 2001). Often these blooms are characterized by the proliferation and dominance of a particular species (Hallegraeff, 1993). Globally, HABs are increasing in scale and frequency and currently threaten most coastal regions of the world. Many reasons for this increase in bloom frequency have been postulated, ranging from anthropogenic nutrient inputs to increased awareness and improved surveillance (Pitcher and Cockcroft, 1996).

Extensive research has been conducted to identify the physical, chemical and biological mechanisms responsible for dinoflagellate bloom formation (Smayda, 1997). One of the earliest and most robust hypotheses put forward is Margalef's Mandala (Margalef, 1978; Margalef et al., 1979). This hypothesis predicts that low turbulence and high nutrient environments favor dinoflagellate dominance. Work with mid- and upper- latitude species does indeed seem to confirm that substantial nutrient inputs and low turbulence conditions coincide with dinoflagellate blooms. These conditions also include blooms that are enhanced by accumulation in stable frontal zones which represent regions of lowered turbulent dispersion. There is, however, a paucity of available information about HAB dinoflagellate blooms that occur in tropical regions including the Atlantic barrier coral-reef mangrove ecosystems of Belize (Hernández-Becerril and Becerril, 2004). Preliminary surveys have found that although some HAB dinoflagellates are found in low abundance throughout the Belizean barrier-reef system, the greatest diversity and highest number of bloom-forming species appear restricted to mangrove cay embayments or similar environments (Faust, 2000, 2004; Morton and Villareal, 1998; Morton, 2000). In this publication, we report the occurrence of 59 dinoflagellate species from two lagoonal embayments located at Douglas Cay and Twin Cays, Belize. Fifteen of the species identified formed substantial blooms. The ecology and morphology of eight of these are described in detail and an evaluation of how well the prevailing conditions and dinoflagellate abundance agree with the predictions of Margalef's Mandala is presented.

METHODS

Study Area

Douglas Cay, Belize is situated north of The Pelican Cays ($16^{\circ} 42.5' \text{ N } 88^{\circ} 10.3' \text{ W}$, Figure 1) and is part of the largest barrier-reef mangrove ecosystem in the new world (Macintyre and Rützler, 2000). The reefs in this system are characterized by channels that form a number of shelf atolls (James and Ginsburg, 1979) which are separated by an unusual network of reef ridges, both submerged and exposed, which were formed during the Holocene (Macintyre et al., 2000). Many of these lagoon reefs have been colonized by red mangroves, *Rhizophora mangle* Linnaeus (Purdy, 1994). When the morphology of these lagoonal reefs is favorable, the developing mangrove islands will encompass an internal lagoon like that found at Douglas Cay. These lagoons range from 1-10 m depth at their center. They have eroded peat banks around the margin with an abundant growth of mangrove prop roots. The entrance to these lagoons is frequently characterized by a sill or other morphological feature that restricts water exchange with the surrounding oceanic fore-reef systems. As a result, these lagoons are considered separate water masses and are characteristically warmer and more saline than the open waters of the surrounding central lagoon (Villareal et al., 2000). The mangrove prop roots that line the edge of these lagoons are colonized by abundant corals, sponges and tunicates (Rützler and Feller, 1996). The hydrographic isolation of these systems, and low tidal amplitude ($<20 \text{ cm}$) allows retention of nutrient and carbon-rich detrital material supplied by the surrounding mangrove trees. These conditions promote a high microbial biomass and the rapid rates of nutrient recycling.

Twin Cays, the second system studied (located 7 km north of Pelican Cays ($16^{\circ} 49.4' \text{ N } 88^{\circ} 6.1' \text{ W}$), consists of a shallow intertidal mangrove island characterized by a series of lagoons, channels, mud flats and ponds. The "Lair", the specific location where samples were taken, is a shallow lagoon (0.5 to 3 m deep) located at the end of The Lair channel. Though The Lair has a poorly developed sill, the $<20 \text{ cm}$ tide and long narrow Lair channel which separates The Lair from surrounding waters, help restrict water exchange with the surrounding waters. Overall water exchange, however, is greater than observed for Douglas Cay (Kibler et al., 2005). The Lair is also high in organic matter originating from mangroves, meadows of turtle grass, *Thalassia testudinum* Bank ex Konin, as well as benthic production associated with the soft sediments.

Physical Parameters and Chlorophyll a Biomass

Temperature, salinity, dissolved oxygen and irradiance were measured in the water column at three depths with a Yellow Spring Instrument profiling unit (model 6600). Irradiance was estimated by the integrating quantum scalar irradiance meter, Biospherical Instruments # QSI-140 meter (Tester et al., 2003). Ammonia was measured fluorometrically using the method of Holmes et al. (1999). Samples for chlorophyll a analysis were vacuum-filtered through 25mm GF/F filters ($< 10 \text{ cm Hg}$) and were immediately frozen in liquid nitrogen. Samples were subsequently extracted with 7.5

ml 90% acetone and were macerated with a tissue grinder before being analyzed using the acidification method for chl *a* described by Parsons et al. (1984). The water column conditions at Douglas Cay and The Lair were similar in 2002, 2003 and 2004. In 2004, we formally quantified stratification at each station using the Brunt-Väisälä frequency (*N*), which describes the oscillation that results when the pycnocline is displaced (Mann and Lazier, 1996). This metric was calculated at mid-depth in the water column using the expression $N \text{ (rad s}^{-1}\text{)} = (g/\bar{\rho}/\bar{\rho}_z)^{1/2}$, where *g* is the gravitational constant (m s^{-2}) and $\bar{\rho}$ is density (Kg m^{-3}). To simplify comparisons, *N* was converted to units of cycles h^{-1} using $N/2\pi$. Strong stratification is indicated by frequencies in excess of 20 cycles. h^{-1} (Macintyre et al., 2002).

Dinoflagellate Sampling

The dinoflagellate assemblages were characterized annually at both Douglas Cay and Lair habitats during a two-week period in each May from 2002 to 2004 (Fig. 1). A total of 42 water samples were collected from Douglas Cay and 20 water samples were collected from The Lair. Subsurface water was collected using a 20 μm pore size nylon plankton net towed by a small boat operating at its lowest speed for 1-2 minutes. Large pieces of floating detritus were also collected (Faust, 2004). Samples were concentrated to 100 ml volume and fixed with glutaraldehyde at 1% final concentration for light microscopy and SEM species identification (Faust, 1990). Both the Douglas Cay and "Lair" habitats were characterized by a diverse community of dinoflagellates (Faust, 2004).

Enumeration and Identification of Dinoflagellates

To enumerate microalgae, cell concentrations of three replicates for each water sample were estimated at 100x magnification in a Palmer-Maloney cell chamber or in settling chambers (Guillard, 1973). Dinoflagellates were identified under differential interference contrast illumination with Carl Zeiss Axiophot microscope. The relative abundance of dinoflagellates was determined as the proportion of organisms present in a total of 500 cells.

For SEM, glutaraldehyde (1% concentration)-preserved dinoflagellates were isolated using a capillary pipette under a compound microscope. Cells were concentrated onto a polycarbonate filter at room temperature, rinsed six to eight times with deionized water, dehydrated in a graded series of ethanol concentrations and critical point dried. The preparation was coated with carbon and by a layer of gold-palladium (Faust, 1990). Cell dimensions were determined from SEM photographs of at least 10 cells; values given represent the mean. Kofoidian nomenclature was used for identifying dinoflagellate species (Kofoid, 1909). Samples of this investigation are deposited in The Dinoflagellate Collection of the U.S.A. National Herbarium, Smithsonian Institution, Washington D.C.

RESULTS

Physical environment

Both temperature and salinity were high in Douglas Cay and The Lair and varied only slightly over the course of all three May study periods (Table 1). Both lagoons were protected from prevailing winds by the surrounding mangrove trees. Stable temperature and salinity conditions, low tidal exchange and reduced wind mixing resulted in a low turbulence environment (Table 2).

Table 1. Range of environmental variables measured in Douglas Cay and The Lair, Twin Cays during the three two week study periods.

Study Site	Dissolved NH_4^+ $\mu\text{mole.L}^{-1}$	Temperature $^{\circ}\text{C}$	Salinity psu	Dissolved O_2 ppm	Light $\mu\text{E.m}^{-2}.\text{s}^{-1}$	Chlorophyll a $\mu\text{g.L}^{-1}$
Douglas Cay	0.6-6.0	28.3-29.3	35.6-36.1	2.2-6.5	1500-2000	5.0-15.0
The Lair	0.1-0.8	29.1-31.2	37.5-38.0	2.0-5.0	1200-2000	0.8-15.0

Table 2. Brunt-Vaisala frequency calculated at Douglas Cay and at The Lair

The Lair 2004		
Date	Time	B-V Frequency (cycles h^{-1})
12 May 04	1530	37.6
13 May 04	0800	23.5
13 May 04	1415	34.2
17 May 04	0830	28.3
17 May 04	1430	33.8
18 May 04	1000	34.3
18 May 04	1615	40.7

Douglas Cay 2004		
Date	Time	B-V Frequency (cycles h^{-1})
10 May 04	0630	10.3
11 May 04	0645	25.0
11 May 04	1400	48.6

Dissolved oxygen varied from hypoxic to supersaturated depending on the time of day. This fluctuation is due to the balance between bacterial respiration and photosynthetic oxygen production. In these shallow systems, midday photosynthetically active radiation is sufficient to saturate photosynthesis in the water column (Table 1) and at the benthic surface as well. Dissolved NH_4^+ is higher in Douglas than in The Lair, but both are on

average approximately an order of magnitude greater than concentrations found in the surrounding oligotrophic lagoon. The Brunt-Väisälä numbers exceeded 20 cycles h^{-1} during each period measured except one, indicating that the water column is highly stable (Table 2).

Distribution and Diversity of Dinoflagellates Observed in Douglas Cay and The Lair

The dinoflagellate assemblage present in Douglas Cay during 2002 was quite diverse. There were 45 dinoflagellate species present. Twenty-one of these were planktonic, 11 benthic and 5 benthoplanktonic. Thirty-three of the species are known autotrophs, 6 were heterotrophs and 3 mixotrophs. Fifteen are known to form toxic blooms in other regions (Table 3). A comparison of the dinoflagellate species present in Douglas Cay and The Lair in 2004 demonstrated that dinoflagellate communities were similarly diverse to that observed in 2002, and that they shared approximately 65% of the species in common. Overall, benthic species were common in The Lair than in Douglas Cay (Tables 3 and 4). A compilation of the data from all three years identified a total of 19 bloom-forming species from Douglas Cay and The Lair (Table 5). Some of these species were more persistent in time and space than others. Of these 19 species, 11 are known toxin producers (Table 6). A detailed description of the ecology and morphology for 8 of these 19 bloom-forming species follows:

Gonyaulax grindleyi Reinecke 1967

Synonym: *Protoceratium reticulatum* (Claparède & Lachmann) Bütschli, 1885: p. 1000, pl. 52.

Figures 2-6

Morphology: Cells conical with a rounded hypotheca; cells (30-45 μm L, and 28-43 μm W) (Fig. 2). Surface is deeply areolate (Fig. 3). Apical pore complex is oblong with the apical pore in the center covered by a mucus plug (Fig. 4). Sulcus is oblong and narrow (Fig. 5). Morphology of the dissociated plates is in line drawings (Fig. 6): species-specific feature the intercalary plate 1a and the ventral pore situated in right margin on apical plate 1' (Fig. 6b). Forms cysts.

Ecology: Cells present in Cat Cay, Douglas Cay, Elbow Cay, and Manatee Cay (Faust, 2000). Bloom of 9.85×10^4 cells L^{-1} caused brown water discoloration at Tobacco Range (Fig. 1) in May 2000. Cysts in the sediment germinate that initiated the bloom (Reinicke, 1967).

Distribution: neritic, estuarine; cold temperate to subtropical waters.

Toxicity: Producer of paralytic toxin affecting shellfish beds (Table 6).

Peridinium quinquecorne Abé 1927

Synonym: *Protoperidinium quinquecorne* (Abé) Balech, 1974: p. 59.

Figures 7-10

Morphology: Epitheca is conical with a pointed apex, cells (23-40 μm L and 20-36 μm W) (Fig. 7); Hypotheca is angular, 4 antapical spines variable in length. Intercalary plates 1a pentagonal and 2a heptagonal (Fig. 8). Apical plate is a round chamber with a Po plate and X canal plate (Fig. 9). Cell shape is rhomboid (Fig. 10b- c). Red eye-spot present.

Ecology: Identified in floating detritus at Douglas Cay and The Lair, cell shape, and length variable. Forms red tides (1.15×10^4 cells L^{-1}), cells adapted to both benthic and planktonic shallow-tropical waters. Cells tolerate high temperatures (38 to 42 $^{\circ}\text{C}$). Present in tropical tide pools (Horiguchi and Pienaar, 1991).

Toxicity: During very high cell numbers this species can cause anoxia and fish kills (Fukuyo et al., 1990).

Bysmatrum caponii (Horiguchi et Pienaar) Faust and Steidinger 1998
 Synonym: *Peridinium gregarium* Lombard et Capon, 1971a: p. 184-187.

Figures 11-12

Morphology: Epitheca is conical and hypotheca trapezoidal; epitheca and hypotheca almost equal (Fig. 11). Cells are 35 μm L to 30 μm W and cell surface vermiculate. Hypotheca is indented (Fig. 12a). Apical intercalary plates 1a and, 2a adjacent and 3a separated (Fig. 12b). Apical pore complex is chamber-like (Fig. 12b). Sulcus is wide four sulcal platelets present (Fig. 12c). Red stigma is present.

Ecology: Species is a new red tide-forming dinoflagellate from Belize. Cell concentrations, 1.85×10^2 cells L^{-1} , observed in Douglas Cay. Cells also present in Elbow and Manatee Cays (Faust, 2000). Species sand dwelling, attach to particles via mucus strands emerging from the apical pore (Po).

Distribution: coastal, warm, tropical and estuarine tide pools.

Toxicity: Not toxic (Table 6).

Dinophysis caudata Saville-Kent 1881
 Synonym: *Dinophysis homunculus* Stein, 1883: p. 3, 24, pl. 21, figs. 5-7.

Figures 13-14

Morphology: Epitheca very small and hidden, cells flattened and 110 μm L to 80 μm W (Fig. 13). Hypotheca is prominent with a long ventral finger-like projection. Left sulcal list extends the length of the main body; right sulcal list is shorter. Cell surface is delicately areolated. Cells may occur in pairs, dorsally attached (Fig. 14).

Ecology: Species is a new red tide-forming dinoflagellate species from Belize. Concentrations of *D. caudata* $2.8\text{-}3.2 \times 10^2$ cells L^{-1} observed in Douglas Cay, and 550-

2010 cells L⁻¹ in Manatee Cay (Morton, 2000); dinoflagellates also present in Cat Cay and Fisherman Cay (Faust, 2000). The 'bloom' population in Douglas Cay may suggest that high organic nutrients enhanced growth of *D. caudata* to a red tide level in Douglas Cay that is an unusual occurrence (Maestrini, 1998).

Distributions: Neritic and estuarine in warm temperate to tropical waters worldwide except in cold water, cosmopolitan.

Toxicity: Producer of ichthyotoxins that may cause massive fish mortality (Table 6).

***Gonyaulax polygramma* Stein 1883**

Figures 15-18

Morphology: Cell elongate with tapered epitheca; epitheca angular with a short horn (Fig. 15). Cell size (42-65 µm L and 26-56 µm W). Hypotheca rounded or truncate (Fig. 16) with three short antapical spines. Theca is ornate with reticulae, longitudinal ridges and striae (Fig. 17). Line drawings of plates are characterized by longitudinal raised and serrated reticulae extending from apex to antapex (Fig. 18).

Ecology: Species is a new red tide-forming dinoflagellate species from Belize. Cell concentrations 1.2 x 10³ cells L⁻¹ observed in Douglas Cay. The first reported of a dense red tide of 3.5 x 10⁶ cells L⁻¹ and caused brown discoloration of the water in Manatee (Morton and Villareal, 1998).

Distribution: neritic, oceanic, cosmopolitan in cold temperate to tropical waters, worldwide distribution.

Toxicity: Non-toxin producing species (Table 6); causing anoxia and fish kills during the microalgal cells decomposition and release of high sulfide and ammonia concentrations (Koizumi et al., 1996).

***Gonyaulax spinifera* (Claparède et Lachmann) Diesing 1866**

Synonym: *Peridinium spiniferum* Claparède et Lachmann, 1859: p. 405, pl. 20, figs 4-5.

Figures 19-22

Morphology: Epitheca elongate, conical with a short apical horn (Fig. 19), cells (35-40 µm L and 21-33 µm W). Cell and hypotheca rounded; two short antapical spines present (Fig. 20). Apical pore complex is oblong, Po elliptical. Apical plate 1' bears a ventral pore (Vp) (fig. 22a). Cingulum is excavated, descending with an overhang (Fig. 21). Cell surface is ornate, characterized by reticulae, extending from the apex to antapex. Striae associated with round trichocyst pores. Thecal plate morphology illustrated in line drawing (Fig. 22). The shape of *G. spinifera* is variable and difficult to identify. Forms cysts.

Ecology: *Gonyaulax spinifera* formed red tide 1.5 x 10³ cells L⁻¹ in Douglas Cay, was also

observed in Cat Cay, Manatee Cay and Lagoon Cay reef-mangrove ponds.

Distribution: neritic, oceanic, estuarine, cosmopolitan.

Toxicity: Non-toxic (Table 6).

Lingulodinium polyedrum (Stein) Dodge 1989

Synonym: *Gonyaulax polyedra* Stein, 1883: p. 13, pl.4, figs. 7-9.

Figures 23-26

Morphology: Cells polyhedral shaped without antapical spines and apical horn (Fig. 23). Cell size (40-50 μm L and 37-53 μm W). Epitheca is pointed and hypotheca round to flat; sulcus long, narrow and excavated (Figs. 24, 26a). The APC oblong and the apical pore plate Po appears as a lattice inside with raised ridge (Fig. 25). Surface of thecal plates sculptured, reticulation includes ring-shaped ridges round trychocysts pores in depressions (Fig. 25). Line drawings describe morphology of thecal plates (Fig. 26). Forms cysts.

Ecology: Species is a new red-tide-forming dinoflagellate from Belize. *L. polyedrum* formed red tides 1.8×10^3 cells L^{-1} outside Douglas Cay, and species present in Cat Cay, Fisherman Cay and Manatee Cay (Faust, 2000). Cells during the night display brilliant phosphorescence.

Distribution: neritic oceanic coastal warm temperate to tropical waters.

Toxicity: Species producer of paralytic shellfish poison and saxitoxin (Table 6).

Pyrodinium bahamense* var. *bahamense Plate 1906

Figures 27-30

Morphology: Cell shape nearly round, epitheca and hypotheca about equal in size; prominent apical horn and apical spine with a list (Fig. 27). Cell size (33-47 μm L and 37-52 μm W); in bloom condition cell size larger (34-77 μm L and 38-67 μm W). Apical pore plate triangular shaped and composed of the Po plate and closing plate (cp) (Fig. 30). Cingulum equatorial, lists well developed (Fig. 27). Plate sutures with a crest arising between plates (Fig. 29); and thecal surface laced with spinulae of round tip (Fig. 28). Forms cysts.

Ecology: Species formed red tide 2.5×10^3 cell L^{-1} outside the Douglas Cay and species present outside Cat Cay, Fisherman Cay and Manatee Cay. This species may confine to mangrove-fringed coastal waters of the Atlantic and Indo-West Pacific and causes red-brown water discoloration under bloom condition (Hallegraeff, 1993).

Distribution: Species present worldwide in Caribbean, Atlantic and Pacific Oceans in subtropical to tropical waters.

Toxicity: *P. bahamense* var. *bahamense* producer of DSP and paralytic shellfish poison (Table 6).

Table 3. Characteristics of the 45 dinoflagellate species identified in 2002 at Douglas Cay.

Dinoflagellate species	Benthic, Planktonic or Both	Autotroph Heterotroph, or Mixotroph	Bloom Forming
<i>Akashivo sanguinea</i>	Both	Autotroph	-
<i>Amphidinium carterae</i>	Benthic	Autotroph	+
<i>Bysmatrum caponii</i>	Both	Autotroph	+
<i>Ceratium furca</i>	Planktonic	Autotroph	+
<i>Ceratium pulchellum</i>	Planktonic	Autotroph	-
<i>Ceratium trichoceros</i>	Planktonic	Autotroph	+
<i>Ceratium tripos</i>	Planktonic	Autotroph	-
<i>Cochlodinium polykrikoides</i>	Planktonic	Mixotroph	+
<i>Coolia monotis</i>	Benthic	Autotroph	-
<i>Dinophysis caudata</i>	Planktonic	Autotroph	-
<i>Dinophysis rotundata</i>	Planktonic	Mixotroph	-
<i>Diplopelta symmetrica</i>	Planktonic	Mixotroph	-
<i>Diplosalis bomba</i>	Planktonic	Mixotroph	-
<i>Gambierdiscus australes</i>	Benthic	Autotroph	-
<i>Gambierdiscus polynesiensis</i>	Benthic	Autotroph	-
<i>Gambierdiscus toxicus</i>	Benthic	Autotroph	-
<i>Goniodoma sphaericum</i>	Planktonic	Autotroph	-
<i>Gonyaulax digitale</i>	Benthic	Autotroph	-
<i>Gonyaulax grindleyi</i>	Both	Autotroph	+
<i>Gonyaulax. polygramma</i>	Planktonic	Autotroph	+
<i>Gonyaulax. spinifera</i>	Planktonic	Autotroph	+
<i>Gonyaulax verior</i>	Planktonic	Autotroph	-
<i>Heterocapsa triquetra</i>	Planktonic	Autotroph	+
<i>Lingulodinium polyedrum</i>	Planktonic	Autotroph	+
<i>Ostreopsis labens</i>	Benthic	Mixotroph	-
<i>Ostreopsis lenticularis</i>	Benthic	Mixotroph	-
<i>Ostreopsis ovata</i>	Benthic	Autotroph	-
<i>Ostreopsis siamensis</i>	Planktonic	Autotroph	-
<i>Peridinium quinquecorne</i>	Planktonic	Autotroph	+
<i>Peridinium venestrum</i>	Planktonic	Heterotroph	+
<i>Plagonidium belizeanum</i>	Benthic	Autotroph	-
<i>Prorocentrum caribbeanum</i>	Benthic	Autotroph	-
<i>Prorocentrum elegans</i>	Planktonic	Autotroph	+
<i>Prorocentrum hofmanianum</i>	Benthic	Autotroph	-
<i>Prorocentrum lima</i>	Benthic	Mixotroph	-
<i>Prorocentrum mexicanum</i>	Both	Autotroph	-
<i>Prorocentrum rhathymum</i>	Both	Autotroph	+
<i>Proto-peridinium depressum</i>	Planktonic	Heterotroph	-
<i>Proto-peridinium divergens</i>	Planktonic	Heterotroph	-
<i>Proto-peridinium oblongum</i>	Planktonic	Heterotroph	-
<i>Proto-peridinium oceanicum</i>	Planktonic	Heterotroph	-
<i>Proto-peridinium pallidum</i>	Planktonic	Autotroph	-
<i>Proto-peridinium steidingeriae</i>	Planktonic	Heterotroph	-
<i>Pyrodinium bahamense</i> v. <i>b.</i>	Both	Autotroph	+
<i>Pyrophacus steinii</i>	Planktonic	Autotroph	-

Table 4. Biodiversity of dinoflagellates in detritus at Douglas Cay and The Lair, Twin Cays (2004) including whether species producing toxin (*) were present (+) or (-) absent.

Dinoflagellate species	Douglas Cay	The Lair	Benthic, Planktonic or Both	Autotroph, Heterotroph or Mixotroph
<i>Akashiwo sanguinea</i>	+	+	Both	Autotroph
<i>Alexandrium balechii</i>	-	+	Planktonic	Autotroph
<i>Bysmatrum caponii</i>	-	+	Both	Autotroph
<i>Bysmatrum subsalsum</i>	-	+	Benthic	Autotroph
<i>Ceratium furca</i>	+	-	Planktonic	Autotroph
<i>Ceratium pulchellum</i>	+	-	Planktonic	Autotroph
<i>Ceratium trichoceros</i>	+	-	Planktonic	Autotroph
<i>Ceratium tripos</i>	+	-	Planktonic	Autotroph
<i>Cochlodinium polykrikoides</i> *	+	-	Planktonic	Autotroph
<i>Coolia monotis</i> *	+	+	Benthic	Autotroph
<i>Coolia tropicalis</i>	-	+	Planktonic	Autotroph
<i>Dinophysis accuminata</i> *	-	+	Planktonic	Autotroph
<i>Dinophysis caudata</i> *	+	+	Planktonic	Autotroph
<i>Dinophysis rotundata</i> *	+	-	Planktonic	Mixotroph
<i>Gambierdiscus belizeanus</i> *	-	+	Benthic	Autotroph
<i>Gambierdiscus polynesiensis</i> *	-	+	Benthic	Autotroph
<i>Gambierdiscus toxicus</i> *	+	+	Benthic	Autotroph
<i>Gonyaulax grindleyi</i>	+	-	Benthic	Autotroph
<i>Gonyaulax monocanta</i>	+	-	Planktonic	Autotroph
<i>Gonyaulax reticulatum</i> *	+	-	Planktonic	Autotroph
<i>Gonyaulax polygramma</i> *	+	-	Planktonic	Autotroph
<i>Gonyaulax spinifera</i>	+	-	Planktonic	Autotroph
<i>Heterocapsa triquetra</i>	+	+	Planktonic	Autotroph
<i>Ostreopsis labens</i> *	+	+	Benthic	Mixotroph
<i>Ostreopsis marina</i>	-	+	Benthic	Mixotroph
<i>Ostreopsis siamensis</i> *	+	-	Benthic	Mixotroph
<i>Peridinium quinquecorne</i>	+	+	Planktonic	Autotroph
<i>Peridinium quinquecorne</i>	+	+	Planktonic	Autotroph
<i>Peridinium venestrum</i>			Planktonic	Heterotroph
<i>Plagodinium belizeanum</i>	+	+	Planktonic	Autotroph
<i>Prorocentrum belizeanum</i> *	+	+	Benthic	Autotroph
<i>Prorocentrum elegans</i>	-	+	Planktonic	Autotroph
<i>Prorocentrum emarginatum</i>	+	-	Benthic	Autotroph
<i>Prorocentrum hoffmannianum</i> *	-	+	Benthic	Autotroph
<i>Prorocentrum mexicanum</i> *	+	+	Both	Autotroph
<i>Prorocentrum micans</i>	+	-	Planktonic	Autotroph
<i>Prorocentrum lima</i> *	+	-	Benthic	Autotroph
<i>Prorocentrum rathymum</i>	-	+	Both	Autotroph
<i>Prorocentrum ruetzlerianum</i>	-	+	Benthic	Autotroph
<i>Prorocentrum tropicalis</i>	-	+	Benthic	Autotroph
<i>Protoceratium spinulosum</i>	+	-	Planktonic	Autotroph
<i>Proto-peridinium crassipes</i>	+	+	Planktonic	Heterotroph
<i>Pyrodinium bahamense</i> v. <i>b</i>	+	-	Planktonic	Autotroph
<i>Scrippsiella trochoidea</i>	-	+	Planktonic	Autotroph
<i>Scrippsiella tiftida</i>	+	+	Planktonic	Autotroph

Table 5. Relative abundance of bloom-forming dinoflagellate species at Douglas Cay and The Lair, Twin Cays in different years. * Cell concentrations L-1 are: cells + (<10²), ++ (<10³) and +++ (<10⁴). * Species present (+) and species absent (-).

Dinoflagellate species	Douglas Cay		The Lair Twin Cays		Reference
	2002	2003	2003	2004	
<i>Akashivo sanguinea</i>	-*	++	++	++	Faust, M.A., 2004
<i>Bysmatrum caponii</i>	++	+	-	+	Faust M.A. & K.A. Steidinger, 1998
<i>Bysmatrum subsalsum</i>	-	++	++	++	Faust M.A. & K.A. Steidinger, 1998
<i>Ceratium furca</i>	-	-	-	++	Steidinger K.A. & K. Tangen, 1996
<i>Cochlodinium polykrikoides</i>	+	++	++	++	Sournia, A., 1986
<i>Coolia monotis</i>	+	+	-	+	Faust, M.A., 1992
<i>Dinophysis caudata</i>	+	++	+	+	Balech, E., 1988
<i>Gonyaulax grindleyi</i>	+	++	-	-	Balech, E., 1988
<i>Gonyaulax polygramma</i>	+	++	-	-	Balech, E., 1988
<i>Gonyaulax spinifera</i>	+	+	-	-	Balech, E., 1988
<i>Heterocapsa triquetra</i>	-	-	++	+	Horiguchi, T. & Pienaar, R. N., 1991
<i>Lingulodinium polyedra</i>	+	++	-	-	Dodge, J.D., 1989
<i>Peridinium quinquecorne</i>	+++	++	++	++	Horiguchi, T. & Pienaar, R.N., 1991
<i>Plagodinium belizeanum</i>	++	-	-	++	Faust M.A. and E. Balech, 1993
<i>Prorocentrum belizeanum</i>	-	+	-	+	Faust, M.A., 1993
<i>Prorocentrum caribbeanum</i>	+	-	++	+	Faust, M.A., 1993
<i>Prorocentrum elegans</i>	++	++	+++	+	Faust, M.A., 1993
<i>Prorocentrum mexicanum</i>	+	++	++	++	Martin, G.W., 1929
<i>Pyrodinium bahamense</i>	++	++	-	-	Steidinger, K.A., 1983

Table 6. Toxin and non-toxin producing dinoflagellates at Douglas Cay and The Lair, Twin Cays. Abbreviations: DSP=diarrhetic shellfish poisoning; FAT=fast acting toxins; PSP=paralytic shell-fish poisoning; and STX=saxitoxin.

Dinoflagellate species	Produced Toxins	Reference
<i>Akashivo sanguinea</i>	Ichthyotoxins	Carlson, R.D. & D.R. Tindall, 1985
<i>Bysmatrum caponii</i>	Non toxic	Faust, M.A. & K.A. Steidinger, 1998
<i>Bysmatrum subsalsum</i>	Non toxic	Faust, M.A. & K.A. Steidinger, 1998
<i>Ceratium furca</i>	Non toxic	Steidinger, K.A. & T. Tangen, 1996
<i>Cochlodinium polykrikoides</i>	Ichthyotoxins	Yuki, K. & S. Yoshimatsu, 1989
<i>Coolia monotis</i>	Cooliatxin	Holmes M.J. et al., 1995
<i>Dinophysis caudata</i>	Ichthyotoxin, DSP	Okaichi, T., 1967
<i>Gonyaulax grindleyi</i>	Paralytic toxin	Reinecke, P., 1967
<i>Gonyaulax polygramma</i>	Fish kills due to anoxia	Koizumi, Y. et al., 1996
<i>Gonyaulax spinifera</i>	Non toxic	Steidinger, K.A. & K. Tangen, 1996
<i>Lingulodinium polyedrum</i>	PSP toxins; STX	Bruno, M.P. et al., 1990
<i>Peridinium quinquecorne</i>	Fish kills due to anoxia	Fukuyo, Y. et al., 1990
<i>Plagodinium belizeanum</i>	Non toxic	Faust, M.A. & E. Balech, 1993
<i>Prorocentrum belizeanum</i>	DSP toxins: DTXI, OA	Morton, S.L. et al., 1998
<i>Prorocentrum caribbeanum</i>	Non toxic	Faust, M.A., 1993
<i>Prorocentrum elegans</i>	Non toxic	Faust, M.A. & E. Balech, 1993
<i>Prorocentrum mexicanum</i>	FAT	Tindall D.R. et al., 1984
<i>Pyrodinium bahamense</i>	DSP, Ichthyotoxin	Hallegraeff, G.M. 1993

DISCUSSION

Mandala's Prediction Validated for Tropical Mangrove Lagoons

The hydrographic and residual ammonia data from both Douglas Cay and The Lair are consistent with these lagoonal systems being stable, low turbulence environments with high rates of nutrient regeneration (Fig. 2, Tables 1-2, Kibler et al., 2005). Elevated nutrients in these systems likely result from the rapid recycling of organic matter by bacteria (Chróst and Faust, 1999). This organic matter is contributed by the surrounding mangrove forest, seagrasses, macroalgal meadows and the dense assemblage of filter-feeding invertebrates and sponges that colonize the peat walls and mangrove prop roots (Rützler and Feller, 1996). These relatively higher nutrient levels are reflected in the 4 to 40 times higher chlorophyll *a* biomass in the lagoons compared to the surrounding oligotrophic waters of the central Belizean reef system which are generally $<0.2 \mu\text{g chl } a \text{ L}^{-1}$ (Table 1). Both lagoons are also protected from wind mixing due to prevailing winds by the surrounding mangrove trees which further promote the stability of the water column. Margalef's Mandala predicts that these low-turbulence, high-nutrient environments would favor dinoflagellate species (Margalef, 1978; Margalef et al., 1979; Smayda, 1997; Smayda and Reynolds, 2001).

The reason is rooted in the basic biology of these organisms. Dinoflagellates are sensitive to physical disturbance with turbulence regimes disrupting their basic metabolism resulting in a significant decrease in division rates relative to other species such as diatoms (Sullivan et al., 2003). Dinoflagellates are also known to have slower growth rates at low nutrient concentrations than many other algal groups (Broekhuizen and Oldman, 2002). It is only at relatively higher nutrient concentrations that dinoflagellates have a competitive growth advantage. The low turbulence, high nutrient environment lagoons sampled in this study would therefore represent ideal environments for dinoflagellates.

Consistent with this prediction, both the Douglas Cay and Lair lagoons contained a rich assemblage of dinoflagellates with a total of 52 species being identified from Douglas Cay and 30 from The Lair (Tables 3-5). Interestingly, only 15 species were identified from both environments (Tables 4 and 5). Planktonic and autotrophic species common to more oceanic environments were dominant in Douglas Cay and include representatives from 7 genera: *Ceratium*, *Cochlodinium*, *Dinophysis*, *Gonyaulax*, *Lingulodinium*, *Peridinium*, and *Pyrodinium* (Tables 3 and 4). Of these, the armored dinoflagellate species were the most common with unarmored species such as *Akashiwo sanguinea*, *Amphidinium carterae*, *Cochlodinium polykrikoides*, and *Heterocapsa triquetra* representing a minor component (Table 3). In contrast, benthic dinoflagellates composed a greater proportion of the species observed in The Lair (Tables 3 and 4). Because dinoflagellates tend to be niche specialists (Smayda, 1997), the large diversity of dinoflagellate species recovered from both Douglas Cay and The Lair imply that these environments contain a diverse array of temporally and spatially varying niches. That a majority of species are unique to each environment also implies that there are different source populations for Douglas Cay and The Lair, or that the selection regime is significantly different.

Differences in the water exchange in these semienclosed mangrove lagoons may account to some extent for these observed differences in species composition (Levasseur et al., 1984). Douglas Cay has a predominant sill that may restrict exchange to a greater extent than occurs in Lair which is mainly restricted due to the length of The Lair Channel and the low tidal amplitude (<20 cm) (Macintyre and Rützler, 2000). A lower rate of exchange in Douglas would favor retention of dinoflagellate cells (Villareal et al., 2000) and a larger portion of incoming organic matter, thereby increasing the nutrient recycling capacity of the system. Douglas Cay is also a larger lagoon with a more complicated geomorphology (unpublished data). Furthermore, Douglas Cay received nutrient inputs from the abundant pelicans that come to fish in the lagoon and roost in the mangroves. Trees surrounding the lagoon were consequently streaked with guano. These highly mobile pelican populations feed on a wide range of food sources and thus import nutrients daily to the lagoon. All these conditions combine to foster the greater diversity of dinoflagellate species in Douglas Cay. Despite the richer environment, Douglas Cay still provides sufficient confinement and nutrient supply to enhance the proliferation of species-specific dinoflagellate blooms (Table 5; Smayda and Reynolds, 2001). The observed diversity is also higher than generally reported at any given time for the deep offshore waters of the Eastern Caribbean Sea (Halim, 1967; Hulburt, 1968; Marshall, 1973).

Another low-turbulence, high-nutrient microenvironment, which exists to a much larger extent in The Lair than in the Douglas Cay, are the loose detrital mats which cover much of the benthos. These flocculent mats sit on top of the sediments where nutrient fluxes are likely to be high. Evidence for this nutrient flux can be found in the rich assemblage of dinoflagellate and other algal species that occupy these mats. In the afternoon, oxygen production by algae in the mat causes large sections to detach and begin floating upward in the water column. This floating biodebris carries large numbers of dinoflagellates into the water column and can account for the higher proportion of benthic dinoflagellates observed in The Lair compared to those in Douglas Cay, where the benthos is dominated to a greater extent by attached macrophytes and sea grasses (Tables 3 and 4; Faust, 2004).

Bloom-forming Dinoflagellates

In addition to high diversity, we observed a number of dinoflagellate blooms in both lagoonal systems. In Douglas Cay, 14 bloom-forming species were observed in 2002 and 15 in 2003. The Lair experienced a slightly smaller number of blooms involving 9 species in 2003 and 13 in 2004 (Table 5). The most intense bloom-forming species were *Peridinium quinquecorne* in Douglas Cay and *Prorocentrum elegans* in The Lair. Blooms of *Gonyaulax grindleyi* in Douglas Cay were also sufficiently high to discolor the water. Similar *G. polygramma* blooms have been reported in Manatee Cay (Morton and Villareal, 1998; Morton, 2000). Previous studies in Douglas Cay conducted in May 1997, 1999 and 2000 also found one or more >20 μm dinoflagellates bloomed in each of these studies reaching cell concentrations in excess of 1×10^3 cells L^{-1} . Frequent blooms therefore can be considered a persistent feature of these systems from year-to-year during the May study period.

Of the 19 bloom-forming species observed, the most consistent species between sites were *Akashivo sanguinea*, *Bysmatrum subsalsum*, *Cochlodinium polykrikoides*, *Dinophysis caudata*, *Peridinium quinquecorne*, *Prorocentrum elegans* and *P. mexicanum*. Blooms typically varied in intensity and duration with many lasting only a few days. A potential reason for the rapid decline of many of these blooms is predation by the large number of heterotrophic ciliates, nematodes, and dinoflagellates such as the *Proto-peridinium* species. Mixotrophic species, such as those that belong to the genera *Prorocentrum* and *Ostreopsis*, were also common and are known to feed heterotrophically on other small microalgae (Faust, 1998). The rapid growth and decline of these blooms, in conjunction with elevated nutrient concentrations, may imply a tight coupling between bottom-up nutrient driven growth and top-down control by predators.

Toxin-producing Species

Approximately half of the 19 bloom-forming species found in either Douglas Cay or The Lair are known toxin producers (Table 6). This implies that the natural eutrophication present in these lagoons favors selection of toxic bloom formers. It is not currently known if these potentially toxic bloom-forming species actually are producing toxin. There is growing evidence that HAB toxins can serve an anti grazing function (Teegarden et. al., 2001). This would lead to the prediction that, in instances of intense grazing pressure, blooms producing toxin will be favored. Further research is needed to address this possibility. If grazers find these species unpalatable or toxic, it can lead to significant and often adverse alterations of the food web (Pitcher and Cockcroft, 1996). It should be noted that all the toxic bloom-forming species were phototrophs as are most reported HAB taxa (Smayda and Reynolds, 2001).

Margalef's Madala, and the results for Douglas Cay and The Lair, also have profound implications for ecosystem health. Both the theory and the species found in these naturally eutrophied systems (Tables 3-5) would predict that as anthropogenic inputs into the oligotrophic waters of the Caribbean increase, so will the proportion of dinoflagellates in the assemblage. This species shift would likely be most pronounced in sheltered bays or other regions where turbulence and hydrodynamic dilution are minimized and in the very regions most likely to be receiving increased nutrient inputs. (Smayda, 1997). If the toxic dinoflagellate species are favored due to selective grazing pressures or other factors, their toxins will likely accumulate in the food web. It is now known that all trophic compartments of marine food web are vulnerable to the chronic, sublethal impacts of these HAB toxins (Hallegraeff, 1993). In cases where toxin accumulation is significant, acute impacts including alteration of food-web dynamics sufficient to result in trophic dysfunction, as well as adverse effects on fisheries and human health, can result.

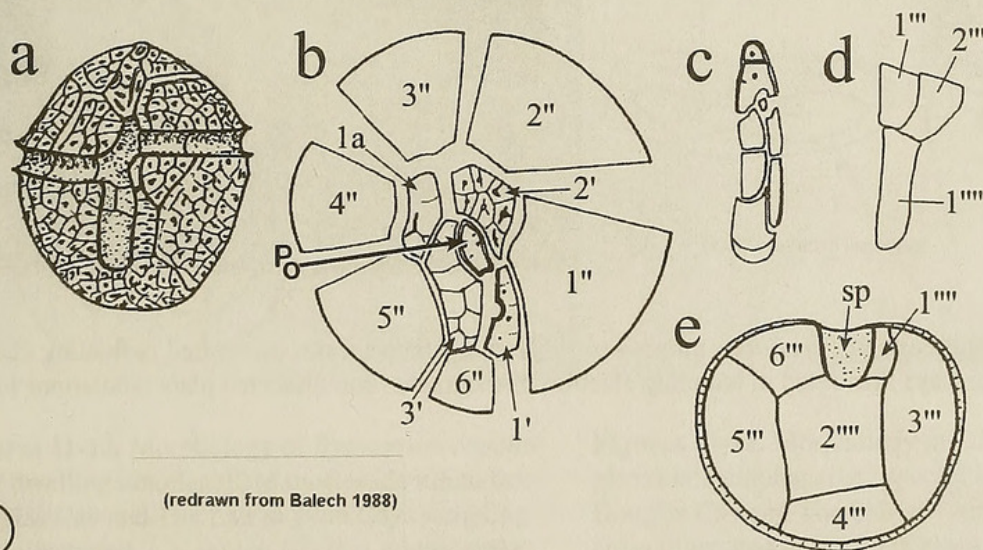
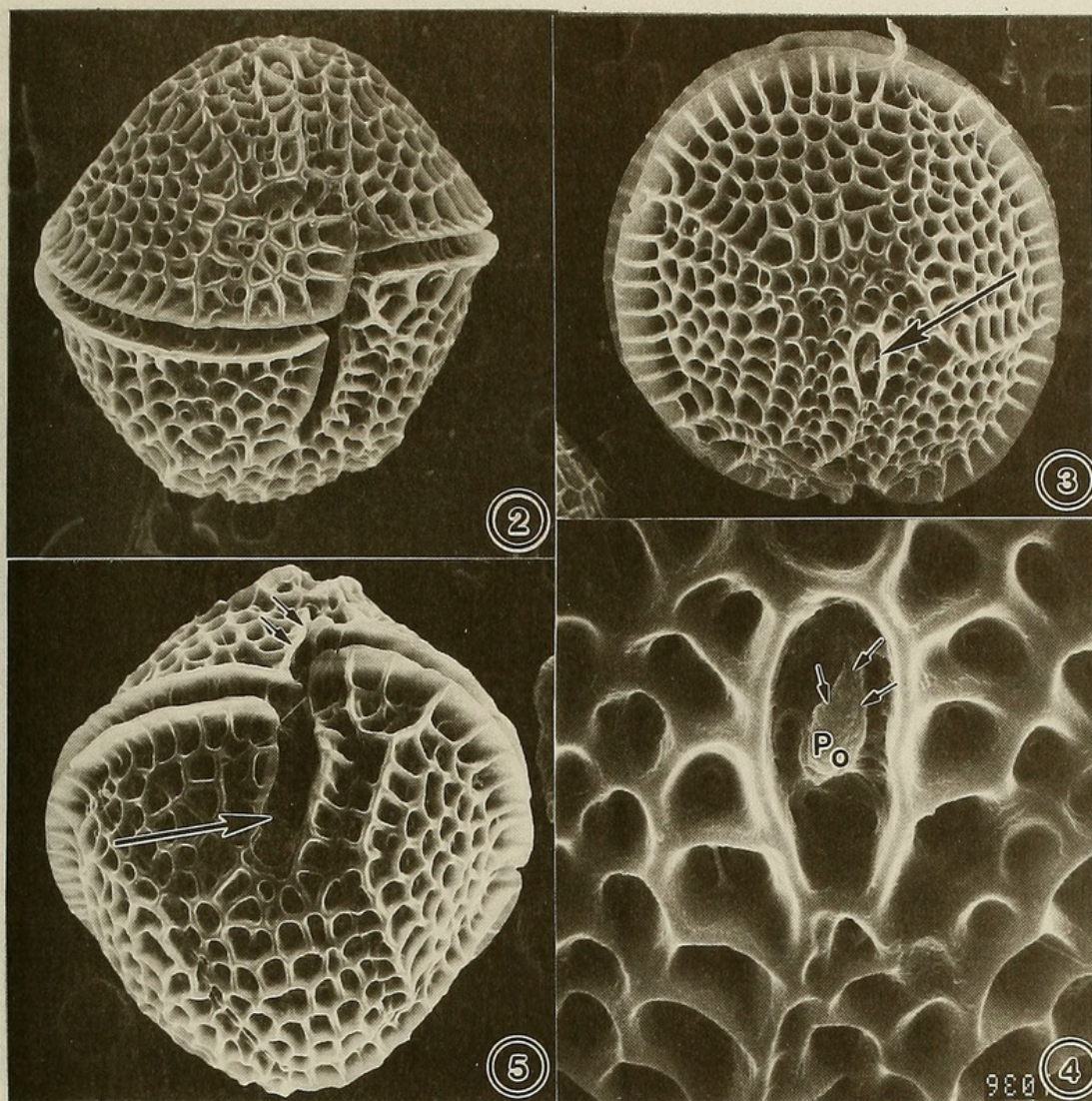
Even if the nontoxin-producing bloom-forming dinoflagellates come to predominate, they can still cause problems (Alongi, 1998). Though these blooms pose no serious threat in the environment, they often discolor the water and are considered to be aesthetically unpleasant and noxious. Anoxia formation resulting from the degradation of organic-rich material derived from phytoplankton blooms can also cause fish kills (Pitcher and Cockcroft, 1996; Koizumi et al., 1996). High ammonia concentration released after cell lysis can adversely affect fish as well (Ajani et al., 2001).

CONCLUSIONS

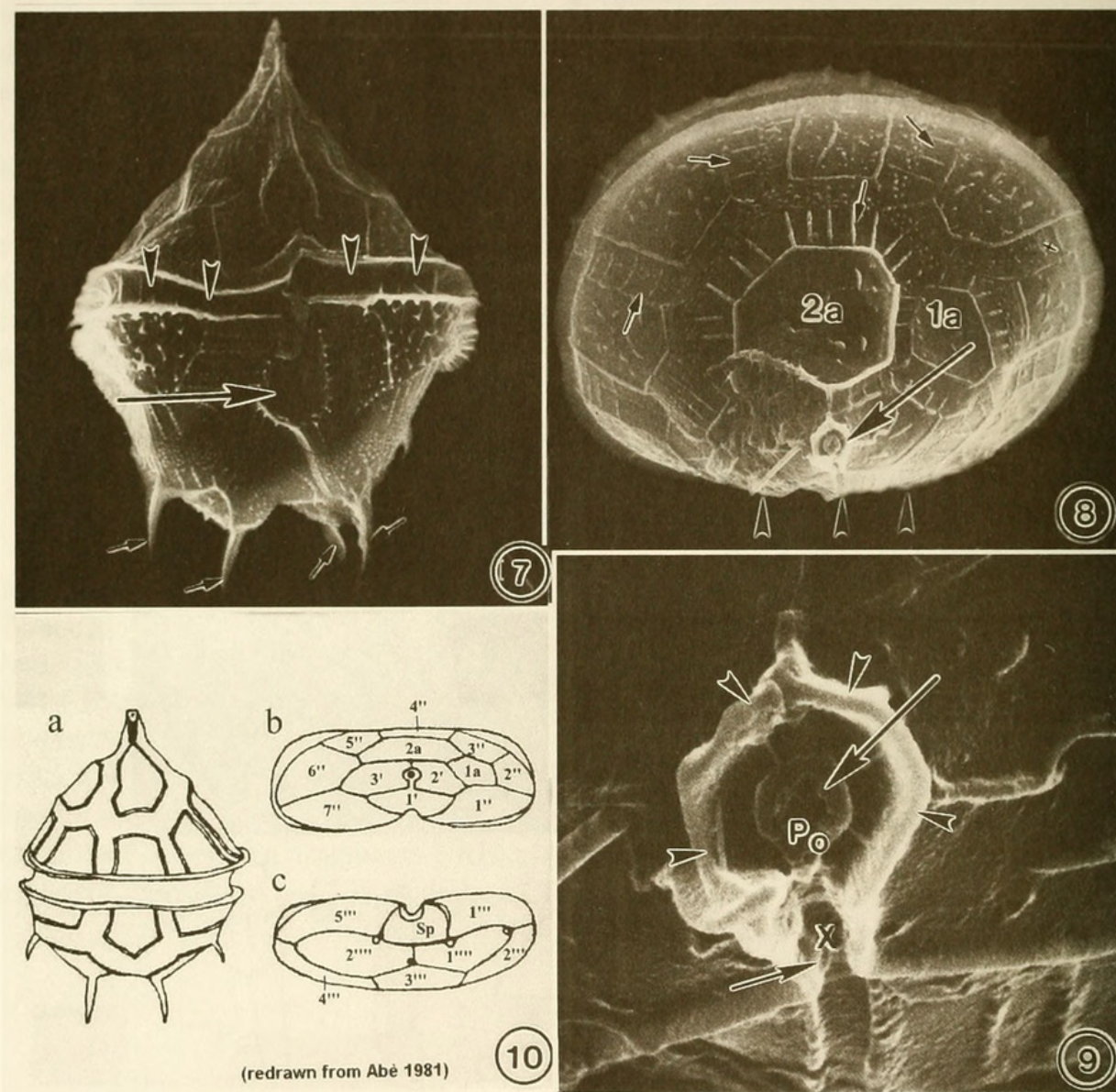
The results of this study demonstrate that the phytoplankton species composition of two naturally eutrophic lagoonal systems in the Belizean Barrier Reef system conform to the predications of Margelf's Mandala. This theory predicts that high nutrient, low turbulence marine environments, such as those examined in this study, will favor the diversity and abundance of dinoflagellates. Consistent with this prediction, a rich assemblage of dinoflagellates is found in both lagoonal systems. Approximately 19 of these species were consistent bloom formers, and of these bloom formers, approximately half were known toxin producers. The ecology and taxonomy of eight of these bloom formers were described in detail. If the predictions of Margalef's Mandala hold true, then increased anthropogenic nutrient inputs into the oligotrophic Caribbean waters may favor a shift in species composition toward potentially toxic dinoflagellate species. This shift could profoundly alter the food-web dynamics as well as adversely affecting fisheries and human health.

ACKNOWLEDGEMENTS

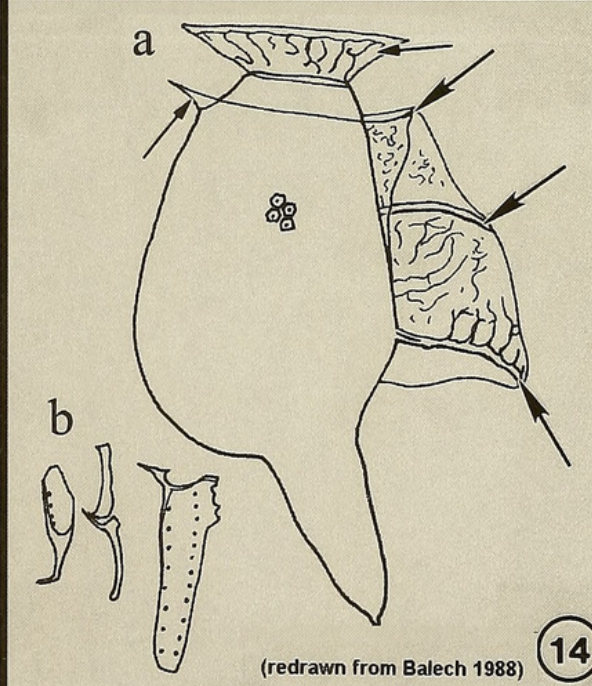
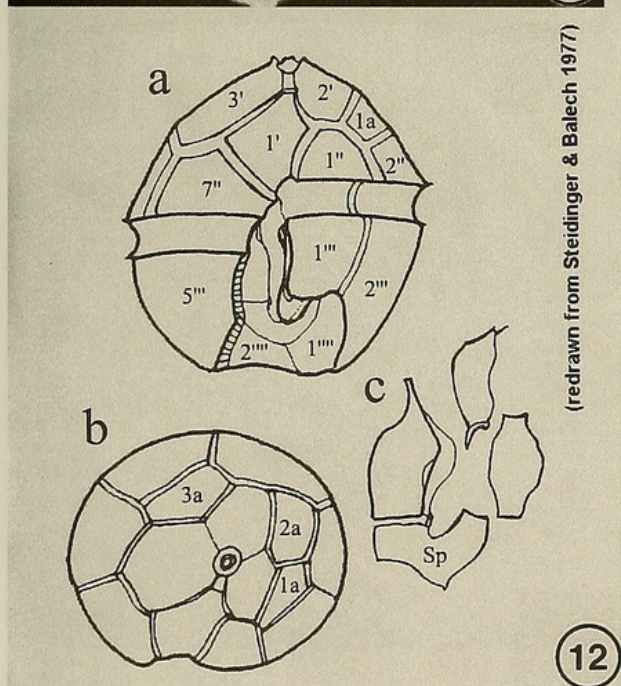
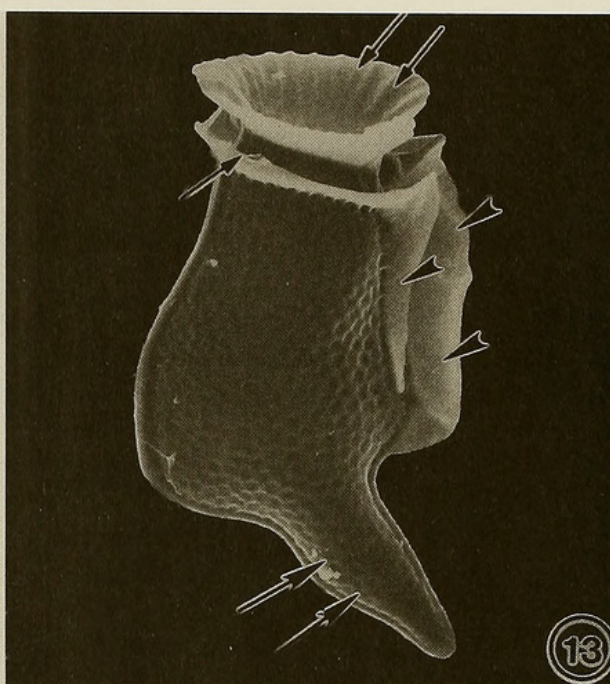
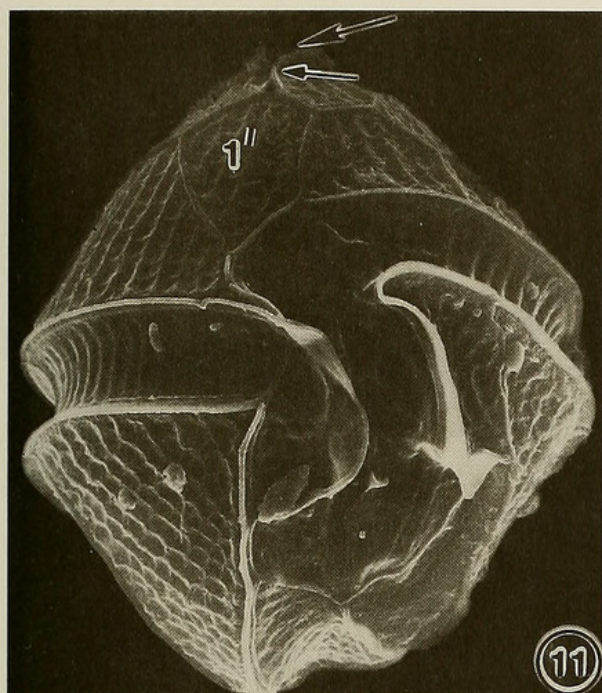
We thank Dr. Klaus Rützler at the National Museum of Natural History (NMNH), Smithsonian Institution, for use of the facilities at Carrie Bow Cay Field Station, Belize. We are also grateful to numerous individuals who contributed to its success and deserve credit here: Dr. Ian G. Macintyre for his valuable comments on this manuscript; Ms. Molly Ryan for her artwork and graphics; and Mrs. Judit A. Quasney for photographic layouts that paved the way for publishing this research paper. I convey a special thanks to Scott Whitaker in the SEM laboratory for technical assistance and Mike Carpenter for logistic support, NMNH. This investigation was supported by grants from the Caribbean Coral Reef Ecosystem program (CCRE) at the National Museum of Natural History. This paper is Contribution No. 729 from the CCRE Program.



Figures 2-6. Morphology of *Gonyaulax grindleyi* dinoflagellate species causing water discoloration in sampling areas illustrated in scanning electron micrographs, and dissected plate tabulations in line drawings.

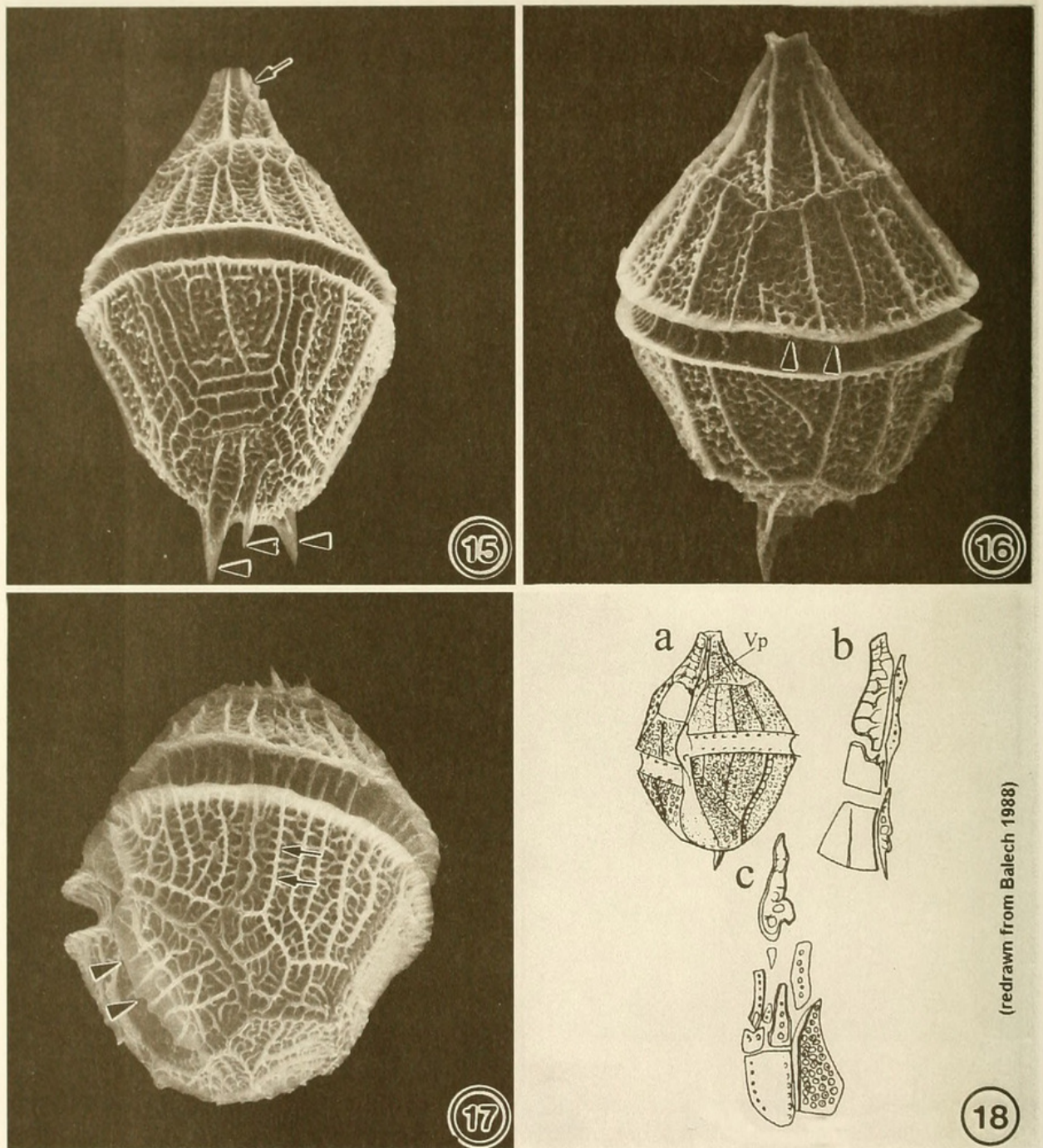


Figures 7-10. Morphology of *Peridinium quinquecorne* dinoflagellate species associated in floating detritus in The Lair at Twin Cays illustrated in scanning electron micrographs, and dissected plate tabulations in line drawings.

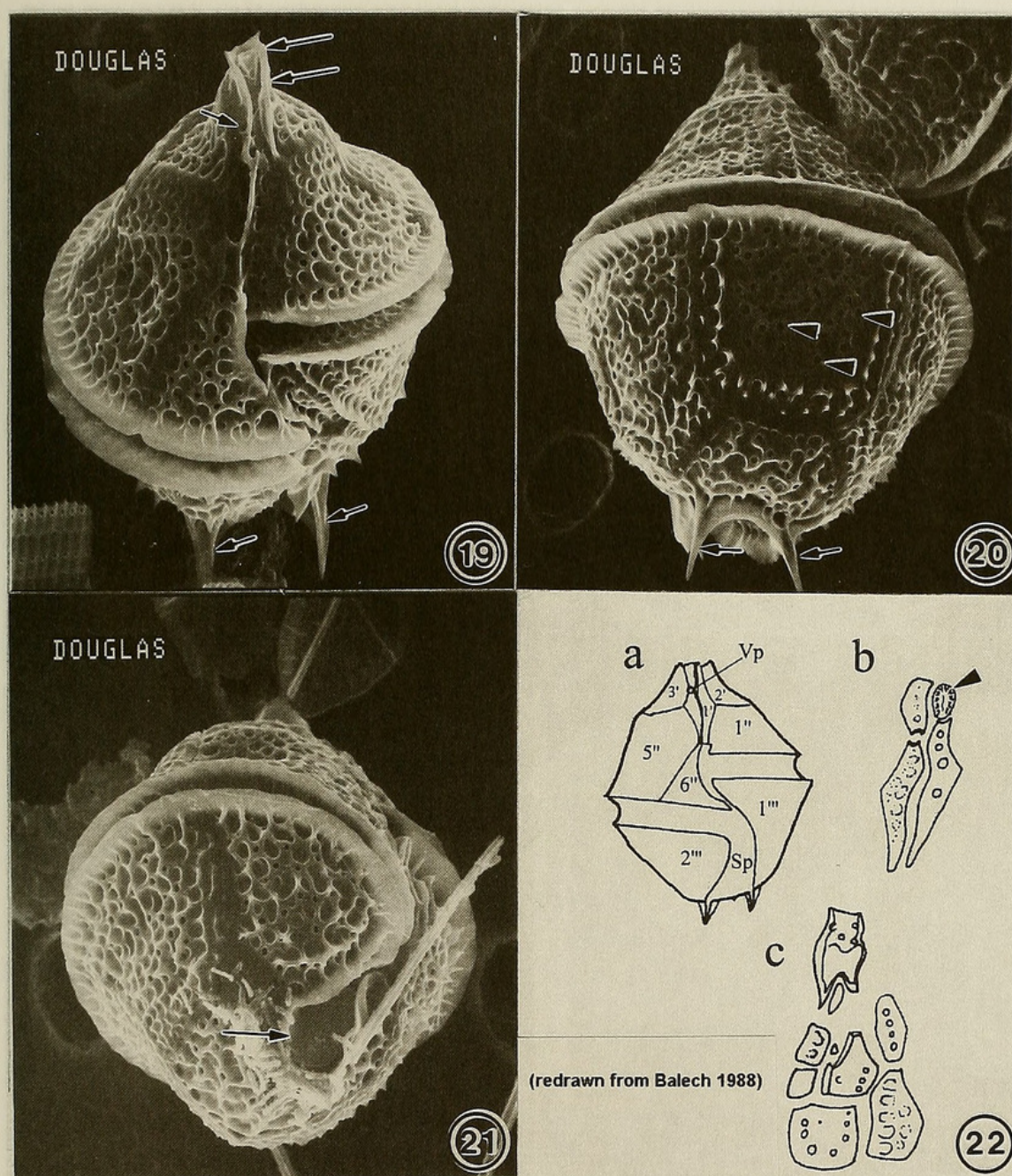


Figures 11-12. Morphology of *Bysmatrum caponii* sand dwelling dinoflagellate species identified from Douglas Cay and The Lair at Twin Cays sampling areas illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.

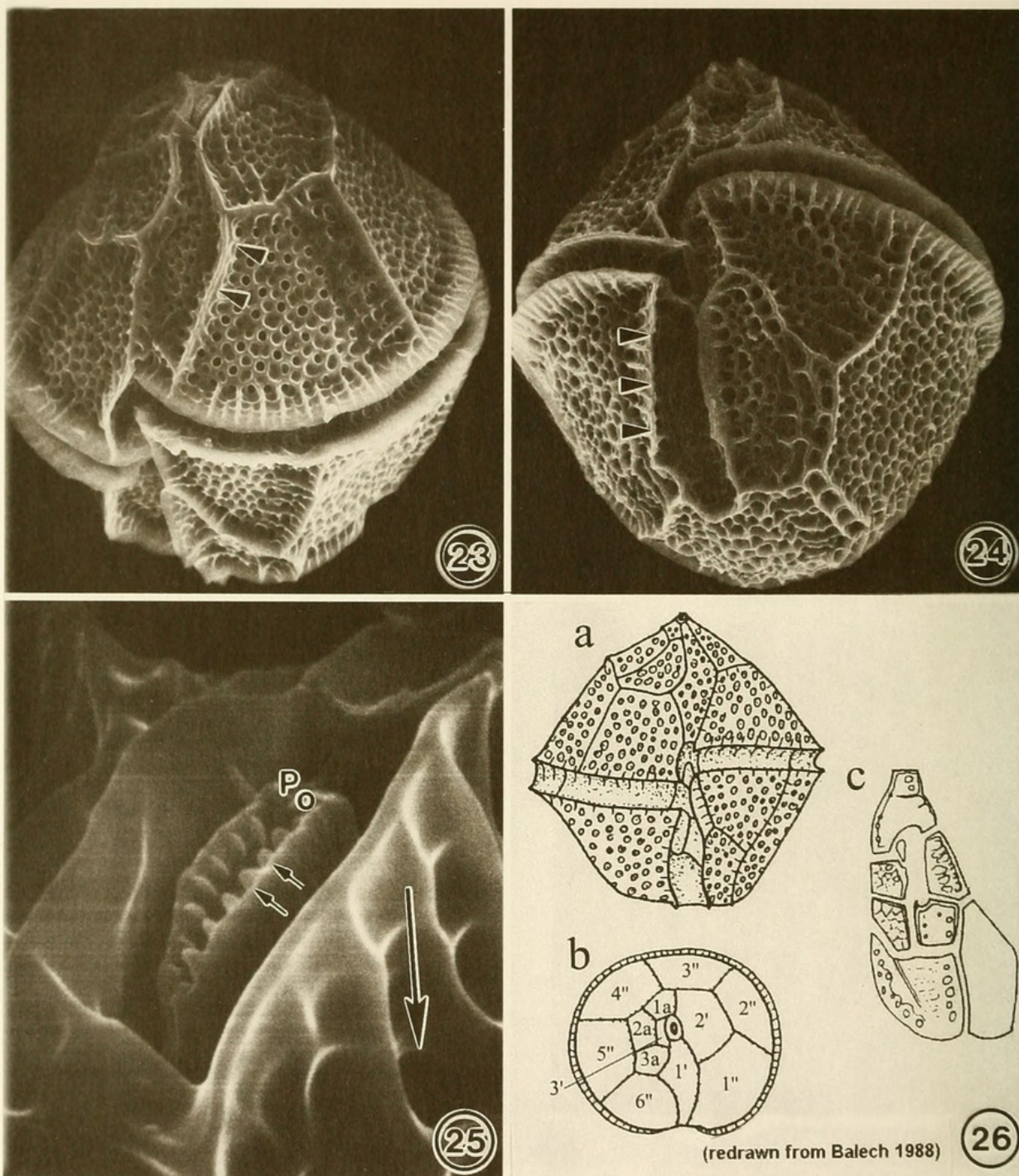
Figures 13-14. Morphology of *Dinophysis caudata* planktonic dinoflagellate species identified from Douglas Cay and The Lair at Twin Cays sampling areas illustrated in scanning electron micrographs, and dissected plate tabulations in line drawings.



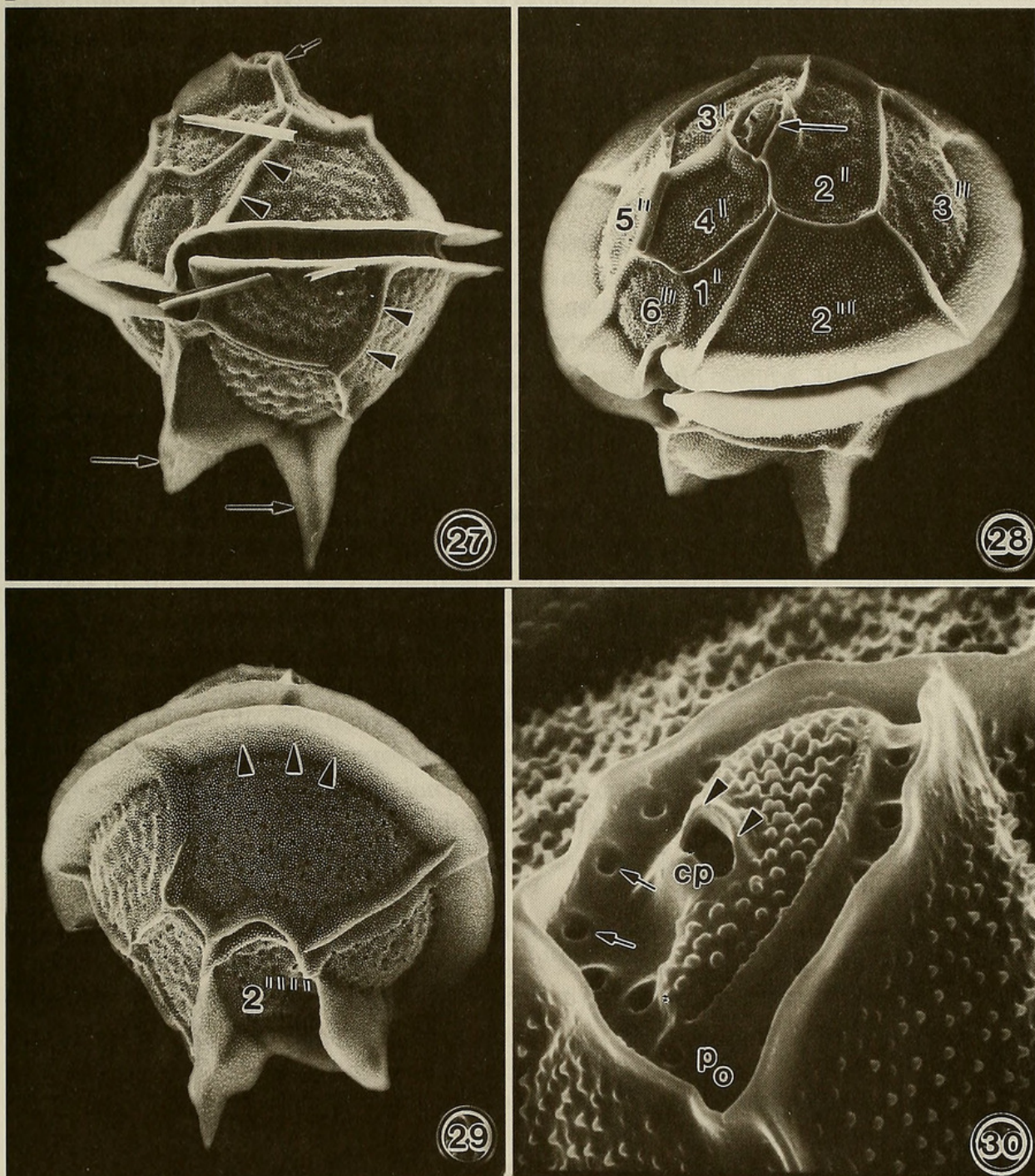
Figures 15-18. Morphology of *Gonyaulax polygramma* cosmopolitan oceanic, red-tide dinoflagellate species identified from Douglas Cay illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.



Figures 19-22. Morphology of *Gonyaulax spinifera*, an oceanic red-tide dinoflagellate species identified from Douglas Cay sampling area, illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.



Figures 23-26. Morphology of *Lingulodinium polyedrum* oceanic bioluminescent dinoflagellate species identified from Douglas Cay sampling area illustrated in scanning electron micrographs and dissected plate tabulations in line drawings.



Figures 27-30. Morphology of *Pyrodinium bahamense* var. *bahamense* planktonic worldwide distributed dinoflagellate species identified from Douglas Cay sampling area illustrated in scanning electron micrographs.

REFERENCES

- Ajani, P., G.M. Hallegraeff, and T. Pritchard
2001. Historic overview of Algal blooms in marine and estuarine waters of the New South Wales, Australia. *Proceedings of the Linnean Society, of New South Wales* 123:1-22.
- Alongi, D.M.
1998. *Coastal Ecosystem Processes. Marine Science Series*, 1-419, New York: CRE Press.
- Broekhuizen, N., and J. Oldman
2002. Marine Ecosystems: Between-individual variations modify phytoplankton dynamics. *Water and Atmosphere* 10:10-12.
- Chróst, R. ., and M.A. Faust
1999. Consequences of solar radiation on bacterial secondary production and growth rates in subtropical coastal water (Atlantic Coral Reef off Belize, Central America). *Aquatic Microbial Ecology* 20:39-48.
- Faust, M.A.
2004. The Dinoflagellates of Twin Cays: Biodiversity, Distribution, and Vulnerability In *The Twin Cays Mangrove Ecosystem, Belize: Biodiversity, Geological History, and Two Decades of Change* , edited by K.R Ruetzler, I.C. Feller, and I.G. Macintyre, 1-21, Special Volume, *Atoll Research Bulletin* 515:1-20.
2000. Dinoflagellate associations in a coral reef-mangrove ecosystem: Pelican and associated Cays, Belize. *Atoll Research Bulletin* 473:133-149.
1998. Mixotrophy in tropical benthic dinoflagellates. In *Harmful Algae*, edited by B. Reguera, J. Blanco, L. Fernandez, and T. Wyatt, 390-394. Paris: Xunta de Galicia & Intergovernmental Oceanographic Commission of UNESCO.
1990. Morphologic details of six benthic species of *Prorocentrum* (Pyrrophyta) from a mangrove island, Twin Cays, Belize. *Journal of Phycology* 26:548-558.
- Fukuyo, Y., H. Takano, M. Chihara, and K. Matsuoka
1990. *Red Tide Organisms in Japan - An Illustrated Taxonomic Guide*, 430. Tokyo: Uchida Rokakuho Press.
- Guillard, R.R.L.
1973. Division rates. In *Handbook of Phycological Methods. Culture Methods and Growth Measurements*, edited by J. Stein, 289-311. New York: Cambridge University Press.
- Hallegraeff, G.M.
1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32:79-99.
- Hernández-Becerril, D.U., and A. Almazán Becerril
2004. Especies de dinoflagelados del género *Gambierdiscus* (Dinophyceae) del Mar Carib mexicano. *Review Biology Tropical* (Supplement 1) 52:77-87.
- Holmes, R.M., A. Aminot, R. Kerouel, B.A. Hooker, and B.J. Peterson.
1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. *Can. J. Fish. Aquat. Sci.* 56:1801-1808.

- Horiguchi, T., and R.N. Piennar
1991. Ultrastructure of a marine dinoflagellate, *Peridinium quinqueforme* Abé (Peridinales) from South Africa with particular reference to its chrysophate endosymbiont. *Botanica Marina* 34:123-131.
- Halim, Y.
1967. The phytoplankton of Venezuela. International Reviews *Hydrobiologia* 52:701-755.
- Hulburt, E.M.
1968. Phytoplankton observations in the Western Caribbean Sea. *Bulletin of Marine Science* 18:388-399.
- James, N.P., and R.N. Ginsburg
1979. *The seaward Margin of Belize Barrier and Atoll Reefs: Morphology, Sedimentology, Organism Distribution and late Quarternary History*, Special publication of the International Association of Sediments, Volume 3.
- Kibler, S.R., M.A. Faust, M.W. Vandersea, S.M. Varnam, R.W. Litaker, and P.A. Tester
2005. Water column structure and circulation in the main channel, Twin Cays, Belize. *Atoll Research Bulletin* (submitted).
- Kofoed, C A.
1909. On *Peridinium steinii* Jörgensen, with note on the nomenclature of the skeleton of Peridinidae. *Archiv für Protistenkunde* 16:25-47.
- Koizumi, Y., J. Kohno, N. Matsuyama, T. Uchida, and T. Honjo
1996. Environmental features and the mass mortality of fish and shellfish during the *Gonyaulax polygramma* red tide occurring in and around Uwajima Bay, Japan in 1994. *Nippon. Suis. Gakki*. 62:217-224.
- Levasseur, M., J.C. Therriault, and L. Legendre
1984. Hierarchical control of phytoplankton succession by physical factors. *Marine Ecology Progress Series* 19:211-222.
- Macintyre, I.G., and K. Rützler
2000. Natural History of the Pelican Cays, Belize. In *Atoll Research Bulletin*, edited by Macintyre, I. G., and K. Rützler 466-480:1-333. Washington D.C. Smithsonian Institute Press.
- Macintyre, I.G., W.F. Precht, and R.B. Aronson
2000. Origin of the Pelican Cays ponds, Belize. *Atoll Research Bulletin* 466:1-15.
- MacIntyre, S., J.R. Romero, and G.W. Kling
2002. Spatial-temporal variability in surface layer deepening and lateral advection in an embayment of Lake Victoria, East Africa. *Limnology and Oceanography* 47:656-671.
- Maestrini, S.Y.
1998. Bloom Dynamics and ecophysiology of *Dinophysis* spp. In *Physiological Ecology of Harmful Algal Blooms*, edited by D. M. Andersen, A. D. Cembella, and G.M. Hallegraeff, NATO ASI Series 41:243-265. Berlin Heidelberg: Springer-Verlag.
- Mann, K.H., and J.R.N. Lazier
1996. Biological – Physical interaction in the oceans. In *Dynamic of Marine*

- Ecosystems*, edited by Mann, K.H., and J.R.N. Lazier, 394. Cambridge: Blackwell Science.
- Margalef, R.
1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* 1:493-509
- Margalef, R., M. Estrada, and D. Blasco
1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In: *Toxic Dinoflagellate Blooms*, edited by D. Taylor and H. Seliger, 89-94. New York: Elsevier.
- Marshall, H.G.
1973. Phytoplankton observations in the Eastern Caribbean Sea. *Hydrobiologia* 41:45-55.
- Morton, S.L.
2000. Phytoplankton ecology and distribution at Manatee Cay, Pelican Cay, Belize. *Atoll Research Bulletin* 472:123-134.
- Morton, S.L., and T.A. Villareal
1998. Bloom of *Gonyaulax polygramma* Stein (Dinophyceae) in a coral reef mangrove lagoon, Douglas Cay, Belize. *Bulletin of Marine Science* 63:1-4.
- Parsons, T.R., Y. Maita, and C.M. Lalli
1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*, 173 pp. Oxford: Pergamon Press.
- Pitcher, G.C., and A. Cockcroft
1996. Noxious *Gymnodinium* species in South African waters. In *Harmful Algae News*, edited by T. Wyatt, 15:1-3. Paris: Intergovernmental Oceanographic Commission of UNESCO.
- Purdy, E.G.
1994. Karst-determined facies patterns in British Honduras: Holocene carbonate dimentation model. *American Associations of Petroleum Geologists* 58:825-855.
- Reinicke, P.
1967. *Gonyaulax grindleyi* sp. nov., a dinoflagellate causing red tide at Elands Bay, Cape Province, in December 1996. *Journal of South African Botany* 33:157-160.
- Rützler, K., and I.C. Feller
1996. Caribbean mangrove swamps. *Scientific American* 274:94-99.
- Smayda, T.J.
1997. Harmful algal blooms: Their ecolophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography* 42:1137-1153.
- Smayda, T.J., and C.S. Reynolds
2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J. Plank. Res.* 23:447-461.
- Sullivan, J.M., E. Swift, P.L. Donaghay, and J.E.B. Rines
2003. Small-scale turbulence affects the division rate and morphology of two red-tide dinoflagellates. *Harmful Algae* 2:183-199.

Teegarden, G.J., R.G. Campbell, and E.G. Durbin

2001. Zooplankton feeding behavior and particle selection in natural plankton assemblages containing toxic *Alexandrium* spp. *Marine Ecology Progress Series* 218:213–226.

Tester, P., S.L. Kibler, W. Litaker, M.W. Vandersea, W. Sunda, and S. Varnam

2003. Douglas Cay: A model for the effects of eutrophication on tropical marine ecosystems, 9. CCRE Project Summary.

Villareal, T.A., S.L. Morton, and G.B. Gardner

2000. Hydrography of a semi-enclosed mangrove lagoon, Manatee Cay, Belize. *Atoll Research Bulletin* 470:87-104.



Faust, Maria A et al. 2005. "Dinoflagellate diversity and abundance in two Belizean coral-reef mangrove lagoons: A test of Margalef's Mandala." *Atoll research bulletin* 531-542, 103-131.

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