INTRODUCTION
Phytoplankton in brackish and marine habitats, such as estuaries, consists of four principal microalgal groups: phytomicroflagellates (7 or more classes), diatoms, dinoflagellates, and blue-green algae. These groups are representative of several size classes: pico plankton (0.2 to 2 µm), ultraplankton (less than 5 µm), nannoplankton (3 to 20 µm or less than 20 µm), and microplankton (20 to 200 µm). Occasionally, there are larger species such as Noctiluca, which can be 1-2 mm in diameter. These algal groups can be found in both the water column and sediments of estuaries, yet specific species are usually planktonic or benthic in the prevailing vegetative stage. Benthic microalgal communities (epi- and endolithic, epipsammic, epiphytic) can be significant components of an estuary in diversity and biomass. Hustedt (1955) described 89 new species out of 319 species identified in just two mud samples from North Carolina. Bader and Roessler (1971) gave a biomass figure of 50-630 mgC/m² for a Florida bay (based on chlorophyll conversions) and Round (1971), in a benthic diatom review, gave 420 mg Chl a/m². Benthic microalgae can serve as food sources for a variety of heterotrophs, act as sediment stabilizers, and often become tychoplanktonic in turbulent events.

Phytoplankton less than 20 µm often dominate the water column, particularly in temperate and subtropical waters; dominance can be both numerical and by biomass, and/or productivity (Fogg 1965; Loftus et al. 1972; Tundisi 1971, Herbland and Bouteiller 1981, and others). Photosynthetic microorganisms less than 20 µm, even less than 2 µm, can account for 20-90% of the planktonic inorganic C uptake, but at the same time they can have high respiration rates and function in remineralization cycles, thus being important in detrital food webs because of their dissolved organic uptake capabilities (Pomeroy 1974, Li et al. 1983). Number of species and associated abundance trends in estuaries usually reveal an inverse relationship horizontally with increasing salinity from the head to the mouth (Hulburt 1965; Kinne 1967, and others). Defelice and Lynts (1978) also noted an increase in benthic diatom diversity from terrestrial influences to open waters in upper Florida Bay. Many phytoplankters are cosmopolitan and endemic populations are rare, particularly in estuaries (Lackey 1967; Wood 1965; Steidinger 1973); however, brackish or marine microalgal assemblages (planktonic and benthic) may be distinct areally and seasonally. Most species are "neritic" and represent an estuarine/neritic grouping although there are periodic invasions of limnetic or oceanic/neritic species due to freshwater discharge or oceanic intrusions respectively (Wood 1965).

Estuaries are dynamic because of physical, chemical, and biological interactions. The system is a fluctuating, and at times unstable, environment. This affects which species are present as well as total production,
temporally and spatially. Such a system tends to limit planktonic and benthic populations to those that have wide ranges in physiological and reproductive strategies, e.g., most are euryhaline and eurythermal and have "regenerative" or "resting stage" cycles. Additionally, many species have varied nutritional requirements with adaptive assimilation rates, particularly nannoplankters.

Environmental factors limiting phytoplankton occurrence, diversity, and abundance interact synergistically and principally involve light (water clarity), temperature (metabolic processes, division rates), salinity (osmoregulation), micro- and macronutrients or growth factors, and circulation patterns. The influence of light intensity on primary production is simply demonstrated by the existence of productivity formulae involving solar radiation, extinction factors, and chlorophyll (Ryther and Yentsch 1957; Small et al. 1972; Bannister 1974, and others) which are still used today with some reservations. Although light is required, high levels can cause photoinhibition and bleaching of surface restricted organisms. High light intensities can also cause organisms to seek a lower level in the water column. Diatoms are light saturated at lower light intensities than dinoflagellates (Riley and Chester 1971), while blue-greens do best at highest light intensities. Therefore, adaptations to light intensity and wavelengths can effect competitive advantages. In addition, photosynthetic organisms have phased uptake and metabolic functions in both light and dark cycles (see Eppley 1981). Light also acts to concentrate positively phototactic flagellates in the euphotic zone so that there are diurnal or diel vertical migration patterns associated with time of day, light intensity and water clarity. Benthic microalgal communities are likewise affected by light, although the association may be indirect due to substrate preference and its cyclic availability, or circadian rhythms. Most photosynthetic benthic microflora can chromatically adapt to varying light intensities because of efficient accessory pigments.

Temperature has always been used as a primary factor in distribution and seasonal occurrence (Braarud 1961; Eppley 1972; Raymont 1980). Many pelagic marine plants and animals are classified geographically by temperature regimes, e.g. boreal, polar, temperate, and tropical, yet most estuarine phytoplankters appear to be cosmopolitan. Temperature extremes and daily differentials can affect division rates (doublings per day = 0.85c 0.631 at a Q10 of 1.88; Eppley 1972), nutrient availability and uptake, photosynthetic rates, respiration, assimilation numbers (mg C mg chl a-1 hr-1) with the relationship being Aν = 1.43e 0.0801 at a Q10 of 2.23 (Smayda 1976), and consequently successional patterns because of interspecific competitive adaptations.

Phytoplankton dynamics, whether it be in the estuary or in neritic or oceanic waters, have historically been equated to availability of macronutrients. If nitrates, phosphates, silicates and the like are in insufficient amounts they are considered limiting, yet growth is a function of cellular nutrient pools and enzymatic capabilities and not necessarily external levels (Healey 1973). Also, ambient levels of basic nutrients such as NH4-N, NO3-N, and PO4-P at specific times do not reflect turnover rates and cycling by bacteria, nannoplankters, and animals. Theoretically, macronutrients could be growth limiting, particularly during seasonal bloom periods, with nitrogen being considered the limiting macronutrient in temperate North Atlantic estuaries (Smayda 1976). However, phytoplankton have varied nutritional strategies and adaptations in relation to availability and uptake, stored resources, organic N and P utilization, and growth factor requirements, e.g., vitamins, trace metals, and chelators. Laws and Bannister (1980) stated "... phytoplankton have mechanisms for regulating uptake of each element and ... these
mechanisms are used to maintain composition and achieve balanced growth." Even in oligotrophic oceanic waters, nutrients appear to be nonlimiting (see Platt 1981; Hubert 1970; McCarthy and Goldman 1979) with growth rates up to three or more doublings per day. In contrast, eu- and mesotrophic areas (e.g., Koblentz-Mishke and Vedernikos 1976; Redalje and Laws 1981) would appear to have lower growth (doublings per day), suggesting physiological saturation inefficiencies in relation to higher nutrient availability and "threshold" growth, or other factors. Smayda (1976), in discussing Narragansett Bay data, stated

In 1974, 42% of the annual production of 310 g m⁻² occurred during July and August when nitrogen remained at very low concentrations. Rapid nutrient recycling was necessary to sustain this production. That it must have occurred is consistent with the elevated assimilation numbers found during the summer despite very low ambient nutrient concentrations... phytoplankton dynamics during the summer in this bay, however, are not clearly limited physiologically by nutrient limitation or grazing. While nutrition levels and the recycling rate may set the magnitude (yield) of the population pulses, the underlying factors regulating the fluctuations in abundance remain unknown.

Smayda (1974) had demonstrated earlier that bioassays of natural waters would give more reliable data on limiting factors and successional dynamics; he concluded that "...natural phytoplankton growth conditioned the surface waters of Narragansett Bay" and that "...chemical changes in situ important to the occurrence, growth, and succession of phytoplankton species would not be detected by the routinely used nutrient and biological analyses."

Although there may be correlations between final yield and nitrogen and phosphorus levels as suggested by Margalef (1971) and shown for some studies, the macrocomponents do not regulate the fine structure of planktonic systems. As an example, Provasoli (1971) considered vitamin requirements an important regulatory agent in occurrence and succession of species. Since the 1960s it has been shown that various phytoplankters, besides bacteria, produce vitamins, e.g., B₁₂, thiamin and biotin, as well as vitamin inhibitors or binders. Recently, Messina and Baker (1982), using axenic cultures of Skeletonema costatum, Gonyaulax tamarensis and Cyclotella cryptica and their filtrates, showed that G. tamarensis and C. cryptica in the exponential growth phase produced high molecular weight ectoclines that inhibited S. costatum growth responses, thus effecting a competitive advantage. The growth response could be "normalized" by addition of excess vitamin B₁₂ or by autoclaving the active filtrate prior to testing. Others, (Keating 1978, for freshwater; Freeberg et al. 1979 and Kayser 1981, for marine waters) also have used culture filtrates to demonstrate species succession patterns and that they were mediated by competitive inhibition. Provasoli (1979) pointed out that laboratory experiments with axenic cultures may produce biased results because marine bacteria are capable of enzymatically degrading binders. Provasoli (1979) also discussed nutrient competition and the importance of chelators, such as hydroxamates, and trace metals (e.g., ferric and cupric ions) in relation to species succession and preconditioning of water masses. Using S. costatum as an example again (it is the dominant diatom in temperate and tropical estuaries, including Tampa Bay), Morel et al. (1978) showed that this species was relatively insensitive to Cu⁺⁺ activity, yet some other diatoms and phytoplankters are sensitive and trace metal availability or sequestering has been used to project species successions. Such potential species interactions are particularly significant in estuarine areas with poor flushing, confined water masses, or frontal boundaries where biological conditioning
and species interactions are accentuated.

Ketchum (1954), among others, first pointed out the association of estuarine circulation with phytoplankton accumulation and growth; where there is less exchange there can be higher standing stock because loss due to mixing and export is minimal. Casper (1967) also reported that plankton can remain in the same water mass for long periods because of low flushing and mixing—particularly in upper reaches of estuaries. Later observations and studies have emphasized the significance of circulation patterns in transport and/or concentration of phytoplankton at a density or tidal boundary, motility, and life history stages (e.g., Tyler and Seliger 1981; Tyler et al. 1982). Most of these studies deal with long estuaries (more than 100 miles) and vertically stratified events associated with pycnoclines. Wind and tidal action alone can concentrate surface organisms by accumulation at convergences; with wind direction and/or intensity changes and tidal changes, patches can be diluted by mixing and dispersion. Venrick (1978a) stated, "In general, one may expect greater phytoplankton heterogeneity in regions of rapid growth and high standing crop as well as in regions of environmental heterogeneity." Plankton patches can be on the scale of meters to hundreds of kilometers and are influenced by turbulence and other convective processes, growth rates versus diffusion, grazing, and community structure. Platt et al. (1977) suggested that patches less than 100 m diameter were controlled by turbulence.

The Tampa Bay Estuary

The Tampa Bay System is a shallow, vertically mixed, coastal plain estuary (about 400 mi²) with a mean depth of 3.3 m (see Simon 1974 and this volume for reviews). The system consists of eight named subunits: Old Tampa Bay, Hillsborough Bay, McKay Bay, Middle and Lower Tampa Bay (more than 50% of the system area), Boca Ciega Bay, Terra Ceia Bay, and Manatee River (see Lewis and Whitman, this volume). Three of these geographic subunits connect directly to Lower Tampa Bay which opens to the Gulf of Mexico through barrier islands.

Major freshwater tributaries (Hillsborough, Alafia, Little Manatee, and Manatee Rivers) are located on the eastern side and have an average total discharge of about 1350 cfs with peak periods usually from June through September. Other freshwater drainage enters the bay system through creeks, streams, ditches, canals, effluent pipes, and excessive land runoff. Mean salinities for the system reflect lower runoff for Old Tampa Bay and the western side of the system with the greatest influence from the eastern side due to river discharge. Salinities increase from an average of 20.8 °/oo at the upper reaches (Hillsborough Bay) to 26.5 °/oo mid-bay to 32.2 °/oo inside of Egmont Key; Gulf salinities just outside the system average 34.1 °/oo (McNulty et al. 1972). Because of drainage in upper reaches and wind-induced sediment suspension in shallow waters, there are associated lower water clarity and higher turbidity values which increase or decrease, respectively, toward the bay mouth. Turbidity also can be due to plankton blooms.

Mixing of bay waters is tidal or wind-induced with a flushing time of months in upper reaches. The predominately diurnal tides, with occasional semi-diurnal cycles, create an average tidal range of 2.3 ft, yet because of natural and man-made constrictions such as bridges and causeways, circulation and mixing in upper reaches of the system, i.e. Old Tampa Bay and Hillsborough/McKay Bay, is poor. Poor circulation and slow mixing contribute to long residency times for water masses and the biota they support. For this reason, the upper reaches of the estuary often act as nutrient or particulate "sinks." Such conditions can lead to massive algal blooms, anoxia, and the release of H2S.
HISTORICAL ACCOUNT OF PHYTOPLANKTON STUDIES

1. Marshall, N., 1952-1953. Marshall (1956) made some important preliminary observations regarding phytoplankton standing stock in Tampa Bay. "The greatest concentrations, toward the head of the estuaries studied, were probably associated with low dispersal rates and with mixing of benthic forms into the plankton of shallow water ... the retention of phytoplankton populations, permitting recruitment and growth, may be regarded as the more fundamental of these reasons for such contrasts in production." Although sampling of the bay was not synoptic and represented only several stations, one or two days during five months in 1952-53, there was a north to south trend towards higher salinities and lower chlorophyll a values which is substantiated in later, more comprehensive studies.

2. Pomeroy, L. R., 1958. Pomeroy (1960) assessed the "relative" contribution of seagrasses and their epiphytes, phytoplankton and benthic microflora in Boca Ciega Bay to primary production using the O₂ light-dark bottle method or changes in dissolved O₂ in a bell jar. Phytoplankton and benthic microflora were not identified or enumerated. Measurements were made on 5 different days in May and September, 1958; chlorophyll varied from 0.8 to 3.5 mg/m³ for water column phytoplankton, and benthic microflora accounted for an average of 130 ± 30 mg O₂/m²/hr. He concluded that in waters deeper than 2 m, only phytoplankton were important primary producers in Boca Ciega Bay.

3. U.S. Bureau of Commercial Fisheries (later National Marine Fisheries Service), St. Petersburg Beach, Florida, 1954 to 1973 (see Dragovich, Kelly, Finucane, Rounsefell, Proctor, Sykes and McNulty references). These coastal and estuarine studies were initiated in response to data needs for assessing Florida west coast red tides and physical, chemical, and biological correlations, both inshore and offshore. Number of stations ranged from 4 to 30 for the Tampa Bay system. Variables measured included salinity, temperature, major nutrients, D.O., pH, turbidity, chlorophyll, primary production (chlorophyll-light or O₂ light-dark bottle), Pychodiscus brevis (= Gymnodinium breve) counts, and limited phytoplankton identifications and enumerations. Not all variables were measured at all times for all studies; most hydrologic collections were monthly. Their data showed higher standing stock as total chlorophyll a in upper bay reaches with bay system peaks in spring and summer. Taylor (1970) stated, "The overabundance of phytoplankton in Hillsborough Bay is a consequence of high nutrient levels, and is reflected in high figures for chlorophyll a and primary production. Actually, phytoplankters are the only important primary producers in Hillsborough Bay because turbidity has reduced light in the littoral zone to such a degree that seagrasses now survive only in small, scattered patches."

Dragovich and Kelly (1964; 1966) identified limited phytoplankton species during a 1963-64 study. Of the diatoms identified, Skeletonema costatum and Asterionella glacialis were dominant species with S. costatum prevalent from February to May. They also reported concurrent dinoflagellate blooms in the upper system during April 1963; Ceratium hircus (= C. furca var. hircus), P. brevis, Prorocentrum micans, and Gonyaulax diegensis (?). Dragovich and Kelly (1964) reported that microflagellates of less than 12 um dominated Tampa Bay collections during a portion of 1963. Later, Dragovich et al. (1965) noted 4-7 um flagellates in a 1964 Ceratium hircus bloom in Hillsborough Bay.

McNulty et al. (1970) associated spring phytoplankton peaks with temperature and nutrients and summer peaks with salinity and nutrients. Rounsefell and Dragovich (1966) found no statistical correlation with the occurrence of P. brevis (1959-1961) in Florida waters and NO₃-N, NO₂-N, NH₃-N, PO₄-P, TON and TPO₄-P, but did find
correlations with temperature, salinity, onshore winds (greater than 7 kts), and the previous months' P. brevis counts. Physicochemical variables in relationship to standing stock and primary productivity are presented by Johannsson et al., this volume.

4. Florida Board of Conservation (later the Florida Department of Natural Resources), St. Petersburg, Florida, 1963 to present. These phytoplankton studies were also initiated in response to data needs for assessing Florida's west coast red tides and physical, chemical, and biological correlations. Eldred et al. (1964) reported on the 1963 Tampa Bay red tide and shellfish toxicity in relation to P. brevis counts and were the first to associate a cause-effect relationship which was later confirmed by McFarren (1965) using mouse bioassays.

Saunders et al. (1967) and Steidinger et al. (1967) studied diatoms and dinoflagellates from Tampa Bay to Caxambas Pass in 1963-1964 at 20 stations; four Tampa Bay stations were sampled monthly, three were sampled weekly and all stations but two were less than 2 m deep. Taxa lists included 43 diatom genera with 68 identified species, 21 dinoflagellate genera with 28 identified species, 5 blue-green genera and many unidentified forms. The most dominant component of these unpreserved samples were microflagellates less than 15 um. Diatoms usually were encountered at 1 x 10^6 cells/liter while dinoflagellates were less than 20,000/liter except during blooms. Skeletonema costatum numerically dominated except during late spring and summer. In these months, larger species of Rhizosolenia, Chaetoceros, and Bellerocrhea (B. horologicalis) dominated the biomass, particularly in lower reaches. El-Sayed et al. (1972) stated, "The Tampa Bay region has perhaps the most distinct diatom flora of the entire Gulf. Unusual members of the genera Cyclotella, Porosira, Amphipora, Chaetoceros and Bacteriastrum are known ... certain species dominate the phytoplankton communities regularly ... Hemidiscus hardmanianus and Bellerocrhea sp. at times constitute over 90% of total plankton surface area in the lower bay." As expected, recorded species (live specimens) tolerated wide temperature and salinity ranges. Comparison of weekly versus monthly collections showed dramatic weekly (and daily) dinoflagellate species composition changes. These data, plus offshore data, (Steidinger and Williams 1970) demonstrate that monthly phytoplankton collections smooth out or miss major short-term fluctuations and successional patterns.

Steidinger (1973) stated:

... assemblages that characterize eastern Gulf estuarine conditions including the diatoms Skeletonema costatum, Chaetoceros spp., Rhizosolenia stolterfothii, R. setigera, Cylindrotheca closterium, Cyclotella spp., Thalassiosira spp., Thalassio nitzschioidea, Cerataulina pelagica, Bacillaria paradoxa, Asterionella japonica, Paralia sulcata, Bacte riastrum spp., Nitzschia seriata (?), Leptocylindrus danicus, Bellerocrhea sp., and the dinoflagellates Ceratium hiricus, Gymnodinium splendens, small Gymnodinium and Gyrodinium spp., Polykrikos spp., Peridinium spp., (e.g. P. quinquecorne), Gonyaulax spp. (e.g. G. spinifera), Tordionium spp., Prorocentrum micans, and P. gracile ...

An overview of estuarine, coastal (continental shelf) and open Gulf phytoplankton reveals four broad types of assemblages: 1) estuarine, 2) estuarine and coastal, 3) coastal and open Gulf, and 4) open Gulf ... Many of the diatoms and dinoflagellates listed above for estuaries also occur in coastal waters but usually in lesser numbers and lower frequency ... No doubt if we were to carefully identify the small microflagellates, unarmed dinoflagellates, and diatoms, we would be better able to distinguish an estuarine assemblage; however, as Saville (1966) mentioned, estuaries have few endemic species and are influenced by freshwater and marine forms ... Tampa Bay is also rather
distinct in that at times it can have coincident dinoflagellate blooms, e.g. Gymnodinium breve, Gonyaulax monilata (both toxic species, one of coastal origin), Cochlodinium citron, Gymnodinium splendens, Gonyaulax spinifera and Peridinium quinquecornic.

To this list should be added: Ceratium hircus, Prorocentrum micans, P. gracile, Peridinium foliaceum, Amphidinium carterae, Gonyaulax diacantha, G. digitalis, Pyrodinium bahamense var. bahamense, and Noctiluca. Up to five species can be co-blooming in the Bay system with two to three in the same general area, particularly the upper reaches; blooms can be monospecific or mixed. Gonyaulax monilata typically blooms in August and September in Old Tampa Bay or mid-bay and is rarely found during the rest of the year because the species forms a benthic hypnozygote which "overwinters" in the upper 1-5 cm of sediment. This species and others that have dormant benthic stages form seed beds; consequently, water column blooms recur in the same area and are usually seasonal. Recently, Walker and Steidinger (1979a) were the first to induce and document the complete sexual life history of a marine dinoflagellate - G. monilata - using Tampa Bay vegetative and zygotic isolates. Steidinger and Ingle (1972) recounted the 1971 Tampa Bay red tide and Steidinger (1975a) stated.

Salinities of less than 25 0/oo are typically limiting to P. brevis (= G. breve). Steidinger (1975a) also pointed out that "Gymnodinium breve during these two outbreaks originally gained access to mid-Tampa Bay via the ship channel ... once in Tampa Bay ... winds and tides were instrumental in transporting and dispersing blooms."

Surface counts of P. brevis in several instances in back Boca Ciega canals were 10^7 cells/l due to southwest winds and incoming tides, then on the turn of the tide counts were 10^9/l throughout the water column. Prior to 1973, researchers believed that red tides started inshore near passes, e.g. off Egmont, and were initiated by previous freshwater drainage, but a reanalysis of offshore and inshore data suggested red tides started 10-40 miles offshore (Steidinger 1973, 1975a, b) and may be associated with offshore benthic seed beds in a discrete zone. Offshore initiation has since been demonstrated by Haddad and Carder (1979), Steidinger and Haddad (1981) and Haddad (1982), and has been associated with intrusions of oceanic water on the broad continental shelf. Walker (1982) recently documented the sexual cycle of P. brevis from gamete formation through planozygotes in culture and is working on induction of hypnozygotes. Other coastal bloom species, e.g. the blue-green alga Oscillatoria erythraea, can also be transported into inshore areas and bays. Most monospecific blooms in Tampa Bay are dinoflagellates or blue-greens (e.g. Schizothrix calcicola) that initiate in the bay itself.

Other studies by this agency on phytoplankton occurring in Tampa Bay include: taxonomic treatments (e.g. Pyrodinium bahamense, Steidinger et al. 1981; Scrippsiella, Steidinger and Balech 1977; Gonyaulax, Steidinger 1968, 1971); culture studies (e.g. Prorocentrum minimum (= P. marie-lebourae), Birnacak and Farrow 1965; Guinardia flaccida, Birnacak et al. 1967; Ceratulina pelagica, Saunders 1968; Chaetoceros galvestonensis, Britton and Farrow 1965; Rhodomonas baltica, Detweiler et al.
1965); documentation of dinoflagellate cyst or hypnozygote stages, particularly in bloom species (Walker, unpublished); and benthic microalgal production of gas bubbles that resuspend and transport sediment particles. Durako et al. (1982) demonstrated that dense populations of microalgae, e.g. *Peridinium foliaceum* and *Gyrodinium fssum* in Tampa Bay grass flat sediments produced 307.9 ml of gas/m²/24 hrs with the highest production during daylight hours. At night, there was a 75% reduction in bubble production. During the day, oxygen constituted more than 90% of the gases; at night there was an increase in CO₂ composition. These bubbles of benthic origin were capable of resuspending sediments by adsorption of particles.

5. University of South Florida (Department of Marine Science, St. Petersburg), 1968 to present. Various thesis topics and contract work involving phytoplankton, standing stock, associated physicochemical variables, and/or primary productivity have been completed or are underway for the Tampa Bay area and other nearshore and coastal areas, e.g. Anclote basin, Crystal River, Charlotte Harbor, and Gulf waters. These are in addition to unpublished and uncirculated short-term class projects or laboratory reports, e.g. vertical stratification in Bayboro Harbor due to runoff and the associated temporary separation of freshwater and marine plankters; the effects of Tampa Bay power plant cooling systems on phytoplankton and standing stock and production; and others. Both the Department of Biology and the Department of Marine Science use Tampa Bay as a study site.

Phytoplankton thesis topics based on Tampa Bay and offshore Tampa Bay have included: description of a new species and distribution of *Gonyaulax* (Steidinger, 1971); phytoplankton distribution, abundance and seasonality in relation to physicochemical variables (Turner, 1972); oceanic intrusions in relation to offshore initiation of red tides (Haddad, 1982), and vertical distribution of chlorophyll *a* and its degradation products in intertidal sediments (Buckley, 1982). Of these, Turner's work was the most extensive as regards number of stations (55) and variables measured, but sampling was quarterly from fall 1969 to summer 1971, thus missing short-term fluctuations and masking seasonal trends. In addition, the samples were preserved in formalin, thus distorting or lysing most of the unarmored dinoflagellates and other fragile phytococflagellates. Turner measured species occurrence, cell counts, biomass, total chlorophyll *a*, salinity, temperature, turbidity, depth, water color, total seston, PO₄-P, NO₃-N, NH₄-N, and SiO₂-Si but found no consistent significant correlation among biological and physicochemical variables for most of the collections. Even for the fall 1971 synoptic samples of the bay system (66 samples) Turner stated, "The absence of significant correlation among factors in the synoptic data of fall 1971 indicates that synoptic sampling may not reduce many of the problems encountered in phytoplankton study." In total, 42 diatom and 23 dinoflagellate taxa were recorded. *Skeletonema costatum* was the most abundant diatom in fall and spring, particularly in upper reaches; diatoms predominated in spring both numerically and in biomass. Maximum cell counts were recorded in fall with a second maximum in winter. Summer 1970 had a dinoflagellate maximum. Phytoplankton abundance and nutrients generally decreased toward the mouth of the bay. Turner pointed out Platt et al.'s (1970) work on spatial heterogeneity of phytoplankton where they demonstrated up to a 70% coefficient of variation (CV) for chlorophyll values between closely spaced stations (0.5 n mi). The same has been reported for chlorophyll differences over one tidal cycle with higher CVs in other areas.

Turner's recording of oceanic *Ornithocercus* species at salinities of 16.7 to 26.9 °/oo and counts of up to 200,000 cells/l was in error (Turner, pers. comm.). The speculation that the Tampa
Bay system may be nitrogen limited solely based on NO₃⁻PO₄⁴ ratios (Turner and Hopkins 1974) is beyond the data base as outlined in the introduction because of unknown in situ turnover rates, use of other N sources, such as NH₃ and urea, and excess PO₄-P values due to natural phosphate beds and mining activities (Johannson et al., this symposium).

Buckley (1982) reported chlorophyll a values for 19 sediment samples from Lassing Park as 18.3-209.6 mg/m² and phaeopigments from 13.7-60.9 mg/m²; little chlorophyll a was detected below 20 cm. Chlorophyll a peaked in early fall. Since most samples were from mud and the chlorophyll a values are less than some other areas, substrate type, e.g. firm sand vs. mud, no doubt could influence maxima obtained, as could sampling time in relation to tide and other factors, although Buckley found no distinct vertical migration with simulated tidal cycles.

More recently, Dr. Gabriel Vargo, a phytoplankton physiological ecologist, has been studying N and P metabolism in a Tampa Bay intruder - P. brevis. His interests are nitrate and urea uptake, phosphatases, photosynthetic capacity and efficiency, respiration, and vertical migration. He has conducted several laboratory and field trials to date and has verified varied N utilization as well as a population migration (partial) for this species.

6. University of South Florida (Department of Biology and Department of Chemistry), Tampa, 1967 to present. Various theses and contract work involving marine phytoplankton have been completed or are underway. Most of these studies have concentrated on toxic dinoflagellates causing red tides and have reported on ultrastructure (Davis 1969; Steidinger 1979), growth requirements (Olander 1968); growth and toxicity (e.g. Doig 1973; McCoy 1977; Eng-Wilmot 1978; Martin and Martin 1976), and ecological impacts (Smith 1978). One study, unrelated to red tides, documented the identity and occurrence of phytoflagellates in Tampa Bay (Gardiner 1982). The latter study is of the most interest to this review.

In a year-long nanoplanктon flagellate study, Gardiner (1982) sampled five stations in Tampa Bay twice monthly; one of the stations, Cockroach Bay, was sampled for both water and sediment. Live samples were processed within 24 hours of collection and relative abundance of species was estimated.

At least 25 species were recorded including representatives of the following algal classes:

- Chloromonadophyceae
- Chlorophyceae
- Chrysophyceae
- Cryptophyceae
- Dinophyceae
- Euglenophyceae
- Prasinophyceae
- Prymnesiophyceae

This number is conservative, since many such species superficially resemble others when examined with light microscopy. Accordingly, many of the listed taxa, such as Prymnesium disomata, may include two or more morphologically indistinguishable species. Six species were encountered year-round including Bipedinomonas rotunda, Calycomonas ovalis (non-photosynthetic), Chroomonas pluricocca, Amphidinium carterae (in sediments of Cockroach Bay), Prymnesium disomata, Eutreptiella marina, Katodinium rotundatum, Gyrodinium estuariale and Prorocentrum minimum. Prymnesium parvum is reported to cause fish kills when it reaches densities exceeding 100,000/ml in England coastal waters (Holdway et al. 1978).

Other species of interest which were found include the chlomonad Horniella marina and the chrysophyte Olisthodiscus luteus which are morphologically similar bloom species. All species identified are between 5 and 20 um except for Horniella which is about 50 um, and larger Amphidinium carterae. In addition to the above work, two clones of Gyrodinium estuariale (spring and fall) were tested for growth
responses in relation to varied light, temperature, and salinity regimes. No substantial differences in growth rates were detected.

7. Tampa Electric Company, Big Bend site, (under contract to Conservation Consultants, Inc., Palmetto, Florida), 1970 to 1977. Monthly or more frequent (e.g. every 19 days) water samples for chlorophyll, phytoplankton occurrence and abundance, and certain physicochemical variables were collected from 1970-1977 using various field and laboratory techniques at several sites in Hillsborough Bay. From 1972-1975, 20 liter samples for phytoplankton were concentrated using a 135 um mesh net; later, a 35 um net was used. Net samples were preserved (glutaraldehyde) in one liter; live samples were additionally used in 1972-1975. In total, 46 dinoflagellate species and 17 genera, 137 diatom species and varieties and 61 genera, and 3 blue-green genera were identified (Hughes and Parks 1977). Using the 35 um data, diatoms had primary peaks in winter with secondary peaks in late summer/fall. Skeletonema costatum was common and dominant with peaks in fall and winter as was Rhizosolenia sp. cf. delicatula with peaks in early winter, late summer and late fall. Skeletonema costatum abundance biased the species diversity index (H1); highest diversity occurred at times of lowest S. costatum abundance. This was also demonstrated by Walker and Steidinger (1979b) for Florida east coast samples and would apply to monospecific phytoflagellate bloom events as well. Other dominants were Hemialus sinensis, Oscillatoria sp. (Schizothrix?), Ceratium hircus, Asterionella glacialis, Gonyaulax polygramma, Rhizosolenia setigera, Chaetoceros spp, and Nitzschia spp. This dominance for 15 months is not necessarily representative of the system since bloom events could influence maximum counts and dominance, and such events can represent different species during different years. Oscillatoria sp. (Schizothrix?) was abundant from late summer through fall which agrees with City of Tampa data for Schizothrix calcicola. Dinoflagellates dominated during spring and summer but were in low concentrations during the rest of the 15 month study; bloom species were Gonyaulax polygramma, G. balechii, Gymnodinium nelsonii (= G. splendens in part), and P. brevis.

8. Hillsborough County Environmental Protection Commission (HCEPC) Tampa, 1972 to present. Hillsborough County personnel have been sampling the Tampa Bay system since 1972; their 50 to 54 stations in marine waters were sampled for up to 42 water quality parameters including salinity, temperature, basic nutrients, chlorophyll, turbidity, dissolved oxygen, light penetration, and algal blooms. Sampling has been monthly and since 1975, surface, mid-depth, and bottom samples have usually been collected. This data base is available through HCEPC and is summarized annually in reports; stored raw data is also available on computer tapes through the Department of Environmental Regulation. Although chlorophyll as chlorophyll a is available, the procedure followed does not include grinding and therefore data points may be underestimated, particularly during diatom peaks or blue-green algal blooms. Yet chlorophyll trends show north to south decreases. Typically upper Old Tampa Bay and Hillsborough/ McKay Bay have chlorophyll a values greater than 20 mg/m$^3$ and some data points exceed 100 mg/m$^3$ during bloom events. The lower reaches of the system have less than 10 mg/m$^3$. The average chlorophyll a concentration for those stations sampled between 1972-79 was the highest in 1979 with a mean of 18 mg/m$^3$. The lowest for this period was a mean of about 10 mg/m$^3$ in 1972. The high chlorophyll a levels for upper reaches are often coincident with lower salinity/higher turbidity and lower light penetration levels. Algal blooms of dinoflagellates, blue-greens and occasionally diatoms are recorded, but in some instances taxa are only identified to genus or basic taxonomic grouping,
e.g. filamentous algae, diatom. Nutrients from this database are discussed separately in this volume (Fanning and Bell).

9. City of Tampa, 1976 to present. The City of Tampa (CT) has been monitoring primary production and standing stock since 1976. The data from 1978 to present are used in J. O. R. Johansson et al. (this volume) and include 14C for planktonic primary productivity, chlorophyll a, temperature, salinity, secchi depth, nutrients and dissolved oxygen. From 1978 to 1981 they occupied 2 stations in Hillsborough Bay and sampled surface and 3 m depths for phytoplankton occurrence and abundance (Lugol-preserved) and the variables listed above. From 1979 to 1981, another station in mid-Tampa Bay was added and sampling strategy was the same except subsurface depth was 4 m. In 1981, sampling changed to monthly collections. Seventy-five diatom species and 39 genera, 31 dinoflagellate species and 14 genera, 4 blue-green genera (including two Schizothrix species), 8 microflagellate species, and various unidentified forms have been recorded to date. Peak chlorophyll biomass is usually in fall which corresponds with Schizothrix blooms. Nannoplankters (less than 20 um) typically dominate except during monospecific blue-green or larger dinoflagellate blooms. There is a general decrease in standing stock seaward with increasing salinities. Schizothrix calcicola usually dominates Hillsborough Bay from July/August to October or later and represents high biomass but low productivity. The blooms are associated with anoxia and benthic fauna mortalities. These blooms also occur in parts of Old Tampa Bay, sometimes coincident with the Hillsborough Bay events. Previous studies (Saunders et al. 1976, HCEPC) list Oscillatoria or filamentous algae blooms for the same time period and these are assumed to be Schizothrix calcicola blooms. Other bloom events, e.g. Noctiluca, have also been documented with analysis of successive feeding strategies of this heterotroph underway. The City of Tampa data base is the most comprehensive available based on techniques and variables measured but it is limited to Hillsborough Bay and one station mid-bay.

In addition to their monitoring efforts, Johannson and Carpenter are conducting quarterly natural plankton enrichment studies to evaluate nitrogen and phosphorus limitation. Data to date show that PO4-P is not limiting (all data provided by J. O. R. Johannson, pers. comm.).

DISCUSSION AND SUMMARY

Phytoplankton studies in the Tampa Bay system and surrounding coastal waters were initiated to determine the occurrence and distribution of the red tide organism Pychodiscus brevis (= Gymnodinium breve) in relation to environmental variables, e.g. salinity, temperature, and major nutrients, following the 11 month 1946-47 red tide outbreak. Since then, a number of specific studies or theses have been pursued by federal, state, county, city, university, and private organizations as outlined above.

The findings of these studies can be summarized by seven major headings: north to south gradients in the system; dominance of nannoplankton; number of species and biogeographic classification; planktonic versus benthic assemblages; bloom events; short-term fluctuations and seasonality; and sampling strategy and analytical procedures.

North to South Gradients: Studies, even those of short duration, showed that a north to south, or head to mouth, gradient existed for salinity (lower to higher). They also showed increased water clarity, mixing of water, and species "diversity" from lower to higher salinities within the Old Tampa Bay, Hillsborough Bay/McKay Bay, Tampa Bay system. Contrarily, standing stock as chlorophyll a or cell counts and the location and frequency of bloom events (autochthonous) decreased from the head to the mouth of this large, shallow estuary. These trends are obvious regardless of sampling frequency (e.g.
weekly, monthly, quarterly, sporadic) or analytical techniques (e.g. chlorophyll a derived with or without grinding of the concentrated samples). Intuitively, these specific associations would be suspected because of freshwater inputs, the shallowness of the bay, and poor circulation and mixing in the upper reaches where residency of water masses may be months. These trends are classical associations as expressed by Hulburt (1965), Casper (1967), Kinne (1967), and others.

Dominance of Nannoplankton (5-20 um): As early as 1965, Fogg recognized that at least half of planktonic photosynthesis was due to microalgae that passed through a 35 um mesh net and that even though the smaller size classes were the most productive, they went unstudied. Since then there have been numerous studies showing the importance of pico-, ultra- and nannoplankters and their contributions to biomass and primary production in estuaries, coastal waters, and even open oceanic waters, both in tropical and temperate regions. Smaller size classes have higher turnover and uptake rates and are metabolically very active.

Again, Tampa Bay is not an exception to the general rule of nannoplankters dominating microplanktonic microalgae, except seasonally when monospecific blooms of blue-greens (Schizothrix) or dinoflagellates (e.g. Gymnodinium nelsonii, Ceratium hircus, Prorocentrum micans, Gonyaulax spp., and others) dominate certain water masses in the upper or middle reaches of the system. Nannoplankters, such as small diatoms and microphytoflagellates, often less than 15 um, have been reported to dominate water samples since 1963. However, not until Gardiner's (1982) dissertation work has this group been studied in any quantitative detail. Prior to Johannson (pers. comm.) and Gardiner, few researchers attempted generic or species identification because of size and taxonomic difficulties.

Nannoplankters not only dominate the water column but can be a significant component of benthic populations, e.g. Amphidinium carterae, an unarmored dinoflagellate. No one has yet attempted quantitative benthic and epiphytic community studies of microalgae in Tampa Bay or other major estuaries in Florida even though biomass as chlorophyll a suggests high standing stocks, and casual personal observations suggest rich communities of diatoms, dinoflagellates and other flagellates.

Number of Species and Classification: In total, 272 taxa identified to species or varieties have been recorded from the Tampa Bay system (see Appendix). If unidentified forms were added, the list would exceed 300 taxa. Benthic studies would further increase the list and no doubt reveal new, undescribed taxa. Of the 272 species/varieties identified, 167 were diatoms, 78 were dinoflagellates, four were blue-greens, and 25 were microphytoflagellates (Table 1).

Table 1. Number of Tampa Bay system phytoplankton species/varieties and genera by major grouping (see Appendix for species lists and references).

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
<th>Genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>diatoms</td>
<td>167</td>
<td>65</td>
</tr>
<tr>
<td>dinoflagellates</td>
<td>76</td>
<td>28</td>
</tr>
<tr>
<td>blue-greens</td>
<td>-</td>
<td>7</td>
</tr>
<tr>
<td>microflagellates*</td>
<td>25</td>
<td>18</td>
</tr>
</tbody>
</table>

*exclusive of dinoflagellates
Comparison of the Tampa Bay system assemblage to other geographic areas shows that 23.5% to 70% of the diatoms from 10 other studies, except two, were also recorded from the Tampa Bay area (Table 2). The lower the total number of species recorded, the higher the percentage in common. The two exceptions were a North Carolina estuary and Florida Bay where benthic diatoms dominated. Comparing dinoflagellates from nine of these same studies and another listing (Table 2), 11.3% to 38.1% of the dinoflagellates were in common. These lower percentages for dinoflagellates, as compared to diatoms, reflect differences in temperate versus tropical or subtropical assemblages. Tampa Bay is strongly influenced by a subtropical assemblage. In comparing Gulf of Mexico dinoflagellates (El Sayed et al., 1972), 36% of Japanese coastal dinoflagellates were recorded from Gulf waters whereas only 11.3% were in common for the Tampa Bay system. The 11 phytoplankton studies cited in Table 2 represent comprehensive studies of either long duration or intensive sampling effort, but techniques differed (e.g. live vs. preserved, different sized nets) as did sampling frequency and depth. Consequently, a direct comparison for similarity indices or association/matrix analyses was not possible nor warranted based on these differences and the lack of benthic sampling.

Smayda’s (1978) biogeographical classification scheme based on records for 379 planktonic species outlined twelve proposed distribution types. Tampa Bay phytoplankton falls into two of his cosmopolitan classes - temperate and warm waters, and warm waters. Most species are cosmopolitan except for those that had been recently described in the last 10 years, e.g. Beijerina horologicalis, Gonyaulax balechii, and Protoperidinium steidingerae. Even though many phytoplankters are cosmopolitan in distribution, most species represent different physiological strains with different environmental tolerances and growth responses. In at least one species complex (Cryptocodinium cohnii), Beam and Hines (1982) identified over 28 sibling species and the likelihood of other species complexes among cosmopolitan phytoplankters certainly exists.

Planktonic versus Benthic Assemblages: Planktonic phytoplankton have been well studied world-wide both taxonomically and as primary producers. However, benthic microalgal assemblages are not well known even though they represent a significant primary production component of an estimated 100-200 g C/m²/yr. The lack of these data from a systems study approach represents a major gap in our knowledge of diversity, function, and energy flow. Diatoms, dinoflagellates, and microphytoplankton can be epipelic, epipsammic, and epiphytic. Some can attach by stalks or filaments to a variety of substrates; others live in close association with various plant and inorganic materials. Hustedt (1955) identified 319 diatom species from just two North Carolina mud samples; 89 species were new to science. Diatoms, both vegetative and reproductive stages, can be found down to at least 5 cm as can dinoflagellates, and even down to 10 cm (Round 1971; Buckley 1982; D. Anderson, Woods Hole Oceanographic Institution, pers. comm.). Vertical distribution is associated with rhythmic migrations or biological and physical reworking of sediments. Benthic cryptomonads, chrysomonads, diatoms, and dinoflagellates can be significant components of estuarine phytoplankton as pointed out by Wood (1965), Saville (1966), Round (1971) and others. Benthic dinoflagellates, such as certain species of Prorocentrum, Amphidinium, Thecamoeba, Polykrikos, Gymnodinium, Gyrodinium, Scrippsiella, Peridinium, Ostreopsis, and Protoperidinium, can be dense and metabolically active in their vegetative stages both in temperate and tropical areas. For example, Durako et al.’s (1982) study on benthic dinoflagellate gas production in a Tampa
Table 2. Number of species of diatoms and dinoflagellates in common between other geographical areas and the Tampa Bay system. Collection methods, handling methods, numbers of stations, frequency of sampling, and other factors variable.

<table>
<thead>
<tr>
<th>Study</th>
<th>DIATOMS</th>
<th></th>
<th></th>
<th></th>
<th>DINOFLAGELLATES</th>
<th></th>
<th></th>
<th></th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># species</td>
<td>% (#) in</td>
<td># species</td>
<td>% (#) in</td>
<td></td>
<td>Reference</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Tampa Bay</td>
<td></td>
<td>Tampa Bay</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Guadeloupe, West Indies (tropical)</td>
<td>196</td>
<td>23.5 (46)</td>
<td>28</td>
<td>35.7 (10)</td>
<td>Ricard &amp; Delesalle 1979</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>India (tropical)</td>
<td>164</td>
<td>40.0 (66)</td>
<td>111</td>
<td>24.3 (27)</td>
<td>Subrahmanyan &amp; Sarma 1960</td>
<td></td>
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<td></td>
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<tr>
<td>Mozambique (tropical)</td>
<td>345</td>
<td>29.6 (102)</td>
<td>189</td>
<td>14.8 (28)</td>
<td>Sournia 1970</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Lebanon (warm temperate)</td>
<td>100</td>
<td>54.0 (54)</td>
<td>148</td>
<td>16.9 (25)</td>
<td>Lakkis &amp; Novel-Lakkis 1980</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NW Atlantic (warm temperate/tropical)</td>
<td>81</td>
<td>63.0 (51)</td>
<td>31</td>
<td>32.3 (10)</td>
<td>Marshall 1971</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>North Carolina (temperate)</td>
<td>187</td>
<td>12.8 (24)</td>
<td>65</td>
<td>29.2 (19)</td>
<td>Campbell 1973</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Narragansett Bay (cold temperate)</td>
<td>50</td>
<td>70.0 (35)</td>
<td>21</td>
<td>38.1 (8)</td>
<td>Pratt 1959</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>English Channel (temperate)</td>
<td>64</td>
<td>60.9 (39)</td>
<td>38</td>
<td>42.1 (16)</td>
<td>Maddock et al. 1981</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Japan (temperate)</td>
<td>250</td>
<td>36.0 (90)</td>
<td>239</td>
<td>11.3 (27)</td>
<td>Yamaji 1966</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Florida Bay (tropical)</td>
<td>160</td>
<td>13.8 (22)</td>
<td>-</td>
<td>-</td>
<td>Defelice &amp; Lynts 1978</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>British Isles (cold temperate)</td>
<td>-</td>
<td>-</td>
<td>124</td>
<td>31.5 (39)</td>
<td>Dodge 1981</td>
<td></td>
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</tbody>
</table>
Bay seagrass bed suggests high diurnal metabolic activity that may indirectly influence sediment transport by resuspension via adsorption to bubbles.

In addition to benthic vegetative cells, this environment harbors a variety of resting stages of planktonic forms, e.g. hypnozygotes, hypnocysts, and resting cells that can influence the diversity and seasonality of planktonic diatoms, dinoflagellates, and microphytoflagellates. These stages, under the right conditions, e.g. temperature and photoperiod, act as seed beds for future planktonic production, particularly in estuaries and coastal waters. These "resting" stages have lowered metabolic activity and often represent dimorphic life history stages. In essence, there are probably few truly holoplanktonic estuarine phytoplankton; most are probably meroplanktonic.

Even though benthic phytoplankton can be high in biomass, primary production and species diversity, they have principally been studied as tychoplankton, incidental in water column collections. This is an unfortunate oversight. On an areal basis, primary production of benthic microalgae could equal planktonic production values yearly, yet trophically, benthic microalgae may represent a more direct food source to herbivores such as ciliates, small crustaceans, and filter or other suspension feeders than phytoplankton or detritus from the water column. Not only are there few production values, but turnover rates, intra- and interspecific competition and interaction, food webs, morphological and physiological adaptations, habitat preference or tolerance, life histories, diversity, successional patterns and other factors remain relatively unknown. Such studies should be a high priority for phytoplanktonologists (or phycologists working with microalgae or systems ecologists if there is a conceptual problem with the term "plankton").

**Short-term Fluctuations and Succession/Seasonality:** The most dominant planktonic species is *Skeletonema costatum*, an estuarine and neritic chain-forming diatom, followed by *Rhizosolenia* spp., *Chaetoceros* spp. and seasonal dominants such as *Bellerochea horologialis*, *Schizothrix calcicola*, and dinoflagellates. *Skeletonema* numerically dominates the water column in January to April/May and again in fall. *Bellerochea* and *Rhizosolenia* can dominate in late spring and summer as can *Chaetoceros*. Dinoflagellate blooms, mixed or monospecific in water masses of long residency in upper and middle reaches of the bay, dominate in summer, fall and even late spring, depending on environmental factors such as salinity, light, temperature, micronutrients, and organics. These blooms and *Schizothrix* in upper reaches can lead to oxygen depletion in the shallow water column and cause fish and invertebrate mortalities. The broad successional pattern, and therefore seasonality, that emerges is small diatoms to larger diatoms to dinoflagellates to blue-greens. Margalef (1967) presented a temperate successional pattern of small diatoms and flagellates to *Chaetoceros* to *Rhizosolenia* (both larger diatom groups) to coccolithophorids and dinoflagellates. Even though there are year to year fluctuations in species occurrence and abundance, succession infers that major seasonal events, e.g. freshwater inputs, temperature, photoperiod, organic conditioning agents, and life history strategies (e.g. benthic resting stages), are more important than macronutrient regimes, at least in estuaries. Factors regulating succession, for example temperature, affect growth responses and maximum reproductive rate. A species that has a high division rate (e.g. 2-3 divisions per day or more), even at the extremes of its temperature tolerance or at a narrow band of high temperatures, can outcompete another species within a water mass. Such a productive advantage may explain the *Schizothrix* biomass. Blue-greens have the highest tolerance to high light and temperature, followed by dinoflagellates, then diatoms. Smayda's (1974) bioassay work suggests that microconstituents
produced as ectocrines and acting as either growth inhibitors or stimulators regulate succession rather than any measurable inorganic variable such as nitrate, nitrite, ammonia, and orthophosphates. It is also conceivable that light, temperature, and salinity influence the breaking of dormancy in benthic resting stages and that ectocrines and circulation patterns influence dominance and abundance of planktonic stages - at least for dinoflagellates. For example, *Gonyaulax monilata* can bloom July through September in Tampa Bay and elsewhere in the Gulf of Mexico; it is usually absent from the water column in other months. This species has known seed beds that inoculate the water column in Old Tampa Bay.

Weekly, monthly, quarterly, or sporadic sampling misses short-term fluctuations that occur daily and tidally. As an example, sampling on an incoming tide in back shallow areas should reveal a higher composition of tychoplanktonic pennate diatoms. Seven to tenfold differences in biomass have been recorded within one tidal cycle and this may be due, at least in part, to turbulence and suspension of benthic microflora. Sampling at different times of the day, regardless of tidal cycle, may, at least in summer and fall, show different vertical distribution for flagellates because of light adaptations. Night sampling may even reveal migration patterns. Species composition differences occur at "stations" on a daily basis during nonbloom events because a station is a fixed location while plankton are transient and water masses are rarely tracked. In poorly flushed areas of long residency, such differences can be negligible. Because of daily and weekly differences, seasonality, abundance peaks, and successional patterns can be masked by sampling infrequency.

**Auto- and Allochthonous Bloom Events** A phytoplankton bloom represents cell densities above background levels, usually greater than 50,000 cells/liter. Such blooms can be mixed and then monospecific by competitive inhibition or exclusion, or remain mixed. Those that become monospecific or almost monospecific often are associated with upper, poorly flushed areas and may last months, or at least several weeks. Blooms of *Ceratium hircus*, *Prorocentrum micans*, *P. gracile*, *Gonyaulax digitalis*, *Pytdiscus brevis*, *Schizothrix calcicola*, and others have lasted several months. Most bloom species are autochthonous and originate in the bay system either from a benthic or planktonic inoculum. Two exceptions are *P. brevis* and *Oscillatoria erythraea* which are oceanic/coastal "invaders" and of allochthonous origin. Blooms of the toxic dinoflagellate *P. brevis* originate 10-40 miles offshore, in association with oceanic events, not near passes as previously suspected, and can be transported shoreward by currents and winds. Between 1946 and 1982, various portions of the Tampa Bay system were exposed to this invader at least 12 times, usually in the lower reaches. In two outbreaks, 1963 and 1971, *P. brevis* penetrated the upper reaches and in one instance, this species dominated for over three months. The only reason *P. brevis* was able to establish itself in the upper portion of the system was because of higher than normal salinity regimes (up to 31 °/oo) due to drought conditions at the time of the outbreak. In 1963, with the lowering of salinities due to rainfall, the species quickly disappeared, but in 1971 there was no or minimal rainfall during its bloom duration. The species does not survive in waters of less than 25 °/oo.

There are several factors regulating bloom occurrence and duration; some are: seeding of an inoculum, salinity regimes, low mixing of bay waters, ectocrines, competitive growth rates, and lack of predators. These same factors probably account for the *Schizothrix* blooms, except that the importance of salinity is replaced by temperature and light. Again, monospecific blooms of photosynthetic microalgae, whether the species produces a toxin or not, can lead to oxygen depletion and animal mortalities.
particularly in early morning hours due to high respiration activity at night.

**Sampling Strategy and Analytical Procedures:** Each study should have a sound experimental design prior to initiation (see Venrick 1978a, b, c, d). This planning phase may involve preliminary sampling and analyses to establish minimal sample size in specific areas or under specific conditions and gear type. Sample size can relate to volume of field samples, number of field replicates, number of subsamples as replicates, and whether seawater volume or cell counts should serve as the sample in setting size limitations. When analyzing standing stock as chlorophyll or total cell volume, the initial sample size may be in ml or liters when unconcentrated, but it may be tens of m$^3$ if nets are used. When performing diversity or cluster analyses, then subsample size may relate to cell numbers, e.g. 400 cells per subsample or aliquot with a precision of ± 10% of the mean. Different techniques or approaches may even be used within this breakdown. The number of replicates when pooled, or total volume of subsample, can determine the lower level of detection if an entire sample is not analyzed, e.g. if ten one ml replicates (or 10 ml) are used, the limit of detection is $10^4$ cell/liter or $10^5$ cells/m$^3$. If only one ml is analyzed, the sensitivity is decreased to $10^3$ cells/liter or $10^6$ cells/m$^3$. Water column samples, in addition to being just "trapped" and not concentrated, can be sedimented, centrifuged, or filtered and the living or preserved concentrate subsampled. Again, pooled subsamples or total subsample size influences the level of detection and reported abundance or biomass. Turner's (1972) level of detection was 1 cell = 100,000 cells/liter. Lack of adequate sample or subsample size can obviously bias numerical data and presence or absence of less abundant forms that may be part of a characteristic assemblage. The advantage of individual replicates over a total subsample volume lies in being able to determine subsample variation, for example, with the coefficient of variation (CV) which does not require a normal distribution of data points around the mean.

Initial sample size and sampling techniques are important to any quantitative study because plankton distribution is not homogenous, rather it is "patchy" and among sample variation is very high (CV greater than 50%). Again, depending on the study goals and subsequent strategies, different gear types that represent continuous sampling, e.g. pumps or nets, may be warranted, or large volume point samples can be pooled and concentrated on board. In reviewing past Tampa Bay system studies, most programs probably had inadequate sample and subsample sizes for quantifying abundance or cell volume, and counts should have been expressed in orders of magnitude ranges for relative abundance for among area comparisons using nonparametric statistics.

Microscopic examination for identifications and abundance may require different volume subsamples because of magnification limitations. Many of the smaller forms have to be identified and counted under high dry or oil immersion with limited working distance, depending on available optics.

In addition to sample size and spatial heterogeneity of plankton, fixed station data can be misleading; the growth medium and the plankton are transitory. In essence, each collection, even at the same site, represents a new area or stations which would theoretically necessitate new sample size determinations. Only in a discrete water mass which was being tracked or a water mass that was physically retained, or even a small lake, would the concept of initial sample size have any carryover meaning for statistical reliability. Another problem with sampling stations is whether they should be random or source/influence related, e.g. stratified random sampling. For example, in Tampa Bay: upper reaches and southern boundary areas have freshwater inputs; water mass residency in Old Tampa Bay
and Hillsborough Bay can be 5-27 months; shallow areas can contribute substantial typhoplanktonic components from tidal, wind or storm influence, etc. Should sampling be synoptic and at what depths? There are no simple answers to "station" locations, number of stations, or sample and subsample sizes. There are other variables such as sampling frequency, gear type, plankton size categories, handling techniques and strata sampling that also need to be addressed depending on project goals and hypotheses being tested. The questions raised above not only apply to phytoplankton but to zooplankton, bacteria, nutrients, turbidity, suspended particles, and other aspects of water column investigations.

Sampling frequency and timing have historically been based on human and financial resources, sample processing time, and the convenience of the investigator. How many planktonologists do night sampling unless it is in relation to 24 hour, tidal, or limited cruise sampling? Should sampling be at a specific tidal phase, e.g. high tide, or can sampling be considered as random when tidal phases are ignored? Does sampling every second Monday of the month mask daily and weekly fluctuations; does it ignore rainfall and runoff events and system responses? Quarterly sampling for certain benthic sessile or infaunal populations may be adequate, but quarterly sampling for water column plankton is inadequate unless the investigator is looking at specific within-sample correlations and variables in a large enough data base.

From past and current Tampa Bay system phytoplankton studies, it is obvious that water column nanoplankton numerically dominate net plankton. Yet this fraction is usually ignored for its presence and contribution to standing stock as chlorophyll or primary production. Many of the nanoplankters are delicate phytomicroflagellates that do not fix well and therefore are lost to even baseline data. To understand phytoplankton "diversity", biomass, production, succession, and dynamics, the nanoplankton fraction between 5-20 um, as well as the pico- and ultraplankton fraction less than 5 um, must be studied quantitatively. Also, there are few investigators trained in the taxonomy of these small organisms. By definition, ecology is based on the study of biotic and abiotic system components; biotic aspects relate to communities and therefore populations. Populations are made up of individuals and consequently, systematics is the grassroots of ecology. It is an indispensable tool that unfortunately is looked upon as more of an art than a science. Systematic and taxonomic studies are receiving reduced funding at a time when species complexes and an expanded concept of "species" are just being realized.

Most phytoplanktonologists working in the Tampa Bay system and elsewhere have been preoccupied with water column microalgae and the dynamics of planktonic interactions and responses, ignoring the microalgal component in the benthos. Actually, the two realms are coupled through life histories, vertical migrations and sinking, and yet there are few even qualitative benthic analyses. Those benthic studies that are quantitative have been selective, concentrating on the diatom assemblage, the cyst or spore assemblage, or just biomass as chlorophyll in sediments. Such studies cannot be integrated into a plankton dynamics system approach because of missing compartments.

Quantitative sampling of benthic microalgae, vegetative or reproductive stages, usually follows techniques used for infauna, e.g. replicate core samples; sampling could be less frequent than water column collections, but it should take into account rhythms in response to tides, light, or other environmental cues. Analyses should be such that living and dead material can be differentiated quantitatively, e.g. by vital staining or fluorescence microscopy, since the benthos is a detrital reservoir, and fragile, unpreservable forms should be identified. This necessitates that samples be live and handled within a
short time frame to avoid decomposition and succession. Cores can be cut for different depths, weighed, sediments resuspended in filtered seawater letting the heavier particles settle out, and finally the supernatant size fractioned to remove larger inorganic fractions. This procedure would bias the data toward the removed episamnic assemblage. Or, sediments from different depths can be resuspended in filtered seawater of a known volume from the site and subsampled with a wide bore pipette. Sampling water column phytoplankton with all the associated problems is technologically easier than sampling benthic populations. Round (1971), Round and Hickman (1971) and Dale (1979) gave benthic sampling techniques and strategies for diatoms and dinoflagellate cysts and there are several accounts for measuring chlorophyll in sediments. Even presence or absence without quantitative sampling would be meaningful data for associations, seasonality, and life history strategies since the data gap is so extensive, as would total standing stock as active chlorophyll. Recently, Moed and Hallegraeff (1978) and Riemann (1978) have emphasized pH problems with spectrophotometric determinations of pheopigment concentrations in the water column. The same problems would apply to benthic samples, if not more so. Therefore, it may be best to use chromatographic separation techniques for benthic samples.

The above discussion on sampling strategy and analytical procedures is superficial at best because it does not recommend a final Tampa Bay system study design for phytoplankton or more appropriately, microalgae. Such a study would take a team effort of specialists and a variety of sampling strategies that should address stratified random sampling in the water column and benthos over a period of years at a frequency adequate to characterize natural fluctuations. Funding and human resources would necessarily restrict design and scope of such studies and thus limit the usefulness of the data base.

ACKNOWLEDGEMENTS

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APPENDIX
PHYTOPLANKTON SPECIES LIST FOR THE TAMPA BAY SYSTEM, FLORIDA

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4. Turner 1972
5. Steidinger, personal observations
6. Gardiner, personal observations
7. Dragovich and Kelly 1964
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DIATOMS (BACILLARIOPHYCEAE)

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*R. setigera Brightwell
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A. klebsii Kofoid & Swezy
A. spp.
Ceratium furca (Ehrenberg) Claparede & Lachmann
REFERENCES

*C. fusus (Ehrenberg) Dujardin
*C. hircus Schroder (= C. furca var. hircus)
C. massiliense (Gourret) Karsten
C. trichoceros (Ehrenberg) Kofoid
*G. tripus var. atlanticum (Ostenfeld) Paulsen
C. spp.
Cochlodinium citron
D. spp.
Coolia monotos Meunier
Dinophysis caudata f. acutiformis Kofoid & Skogsberg
D. caudata var. pedunculata (Schmidt)
D. spp.
Diplopsalis lenticula Bergh
Fragilidium heterolobatum Balech ex Loeblich
F. spp.
Gonyaulax balechii Steidinger
G. diacantha (Meunier) Schiller
G. diegensis Kofoid
*G. digitalis (Pouchet) Kofoid
G. grindleyi Reinecke (= Protoceratium reticulatum)
*G. monilata Howell
G. polygramma Stein
G. scrippsae Kofoid
*G. spinifera (Claparede & Lachmann) Diesing
G. "A"
*Gymnodinium nelsonii Martin
(= G. splendens in part)
?G. aurantium Campbell n. sp.
G. spp.
Gyrodinium estuarii Huburt
G. fissum (Levander) Kofoid & Swezy
G. spirale (Bergh) Kofoid & Swezy
G. spp.
Heterocapsa niei (Loeblich) Morrill & Loeblich
(= Cachonhia niei)
Katodinium rotundatum (Lohmann) Loeblich
K. glaucum (Lebour) Loeblich
Nectilius scintillans (Macartney) Kofoid & Swezy
Oblea rotunda (Lebour) Balech ex Sournia
(= Diplopsalis rotundum)
Oxyrrhis marina Dujardin
Oxytoxum scolopax Stein
O. spp.
Protothecidium abei (Paulsen) Balech
*P. claudicans (Paulsen) Balech
P. conicum (Gran) Balech
P. crassipes (Kofoid) Balech
P. deficiens Meunier
*P. depressum (Bailey) Balech
P. divergens (Ehrenberg) Balech
P. excentricum (Paulsen) Balech
P. nipponicum (Abe) Balech

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REFERENCES

*P. pellucidum Bergh
P. pentagonum (Gran) Balech
*P. quinquecorne (Abe) Balech
P. spiniferum (Schiller) Balech
*P. steidingerae Balech (= P. oblongum in part)
P. striatum (Bohm)
(= P. leonis (Pavillard) Balech in part)
P. subinerme (Paulsen) Balech
P. tubum (Schiller) Balech
P. 'A'
F. spp.
Peridiniopsis asymmetrica Mangin
Peridinium foliaceum (Stein) Biecheler
P. aciculiferum Lemmermann
P. 'A'
P. 'B'
P. 'E'
P. 'N'
*Polykrikos hartmannii Zimmermann
P. kofoidii Chatton
*P. schwartzii Batschli
P. spp.
Prorocentrum compressum (Ostenfeld) Abe
*P. gracile Schutt (= P. redfieldii in part)
P. mexicanum Tafall (= P. maximum in part)
*P. micans Ehrenberg
(= P. marie-lebouriae in part)
P. oblongum (Pavillard) F. J. R. Taylor
P. triestinum Schiller
Ptychodiscus brevis (Davis) Steidinger
(= Gymnodinium breve)
Pyrodinium bahamense var. bahamense Plate
Pyrophacus horologium Stein
*P. steini (Schiller) Wall & Dale
P. vancampoae (Rossignol) Wall & Dale
Scrippsiella subsalsa (Ostenfeld) Steidinger & Balech
*S. trochoidea (Stein) Loeblich
*Torodinium robustum Kofoid & Swezy
T. teredo (Pouchet) Kofoid & Swezy
Triadinium polyedricum (Pouchet) Dodge
(= Goniodoma polyedricum)
Warnowia spp. (= Pouchetia spp.)
?Ornithocercus steini Schutt (misidentified)
?O. thumii (Schmidt) Kofoid & Skogsberg
(misidentified)
NANNOPLANKTON FLAGELLATES (exclusive of Dinophyceae)

CHLOROPHYCEAE

Dunaliella primolecta Butcher

CHRYSOPHYCEAE

Apedinella spinifera (Throdsen) Throdsen
Dictyocha fibula Ehrenberg
Olisthodiscus luteus Carter
Olisthodiscus carterae Hulburt
Mailomonopsis elliptica Matwienko

CRYPTOPHYCEAE

Chroomonas esopus (Conrad & Kuff) Butcher
Chroomonas pluricocca Butcher
Cryptomonas curvata (Ehrenberg) Penard
Hillea serpens (Conrad & Kuff) Butcher

EUGLENOPHYCEAE

Eutreptia lanowii Steur
Eutreptiella marina da Cunha
E. gymnastica Throdsen

PRASINOPHYCEAE

Bipedinomonas rotunda Carter
Pyramimonas amylifera Conrad
P. disomata Butcher
Tetraselmis apiculata (Butcher) Butcher
T. carteriformis Butcher
T. gracilis (Kylin) Butcher
T. tetrahele (West) Butcher

PRYMNESIOPHYCEAE

Chrysochromulina spp.
Pavlova salina (Carter) Green
Prymnesium parvum Carter
Hymenomonas carterae (Braarud and Faegerl.) Braarud

CHLOROMONADOPHYCEAE

Horniella marina Subrahmanyan

REFERENCES

6
BLUE GREENS

Agmenellum spp. (= Merismopedia)
Anabaena spp.
Anacytis aeruginosa Drouet & Daily
Oscillatoria erythraea (Ehrenberg) Kützing
Oscillatoria spp.
Schizothrix calcicola (Agardh) Gomont
S. mexicana Gomont
Spirulina spp.

ADDED IN PROOF: Dr. Grethe Hasle (pers. comm.) has identified the following additional diatoms from Tampa Bay: Nitzschia pseudodelicatissima Hasle, Cymatosira belgica Grunow, C. lorenziana Grunow, Skeletonema menzelii Guillard, Carpenter & Reimann, Thalassiosira tenera Proshkina & Laurenko, T. mala Takaro, T. allenii Takaro, and Minutocellus sp. In addition, Dr. Hasle pointed out the following synonymies: Thalassiosira leptopus (=Casciodiscus lineatus), T. angustelineata (=Coscinosira polycorda), and Leptocylindrus mediterraneus (=Dactylosolen mediterraneus).

REFERENCES

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