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PRIMARY PRODUCTION IN TAMPA BAY, FLORIDA: A REVIEW

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INTRODUCTION

The Tampa Bay system is a nitrogen and phosphorus enriched shallow estuary supporting, seasonally, extremely high phytoplankton biomass and productivity. Seagrass beds in less than 2 m depth, attached and drift macroalgae, and benthic microflora also add to the total primary production of the bay system. Additionally, the system is fringed by limited mangrove stands and marsh areas, which contribute detrital litter and consequently particulate and dissolved substrates.

Primary production data for Tampa Bay is very limited. The phytoplankton component has received the greatest study effort; however, even knowledge of this group is limited and biased by the lack of area-wide and long-term studies, and the use of questionable methodologies. This review will summarize historical primary production data; discuss methodologies and their shortcomings; outline future research needs for understanding the carbon cycle of the Tampa Bay system; and discuss the carbon cycle in relation to trophic dynamics.

HISTORICAL DATA

The first measurement of primary production in the Tampa Bay system was by Pomeroy (1960) in May and September of 1958. He compared the relative production of seagrasses, benthic microflora, and phytoplankton in Boca Ciega Bay (Fig. 1). The only other study of that type, with more than one production component, was not performed until 1981 when Gibson (Harbor Branch Foundation, pers. comm.) initiated a multi-component productivity study of the shallow waters of Lassing Park, in the Middle Tampa Bay region (Fig. 1). In addition to the components measured by Pomeroy, Gibson distinguished between productivity of the seagrasses themselves and their epiphytes. These two studies will be discussed in detail later in this review.

Other studies on primary production of the Tampa Bay system have mostly involved phytoplankton measurements. Only two phytoplankton production studies, to this date, have been of sufficient duration to estimate seasonal cycles in production. These two studies are those by the U.S. Fish and Wildlife Service (FWS) from 1962 through 1973 (Saloman et al. 1964; Dragovich and Johnson 1966; Finucane and Dragovich 1966; May 1966; Kelly and Johnson 1967; McNulty 1968, 1969; Saloman and Taylor 1968, 1971a, b, 1972; Taylor and Saloman 1968; McNulty et al. 1970; Taylor 1970; Saloman 1973, 1974; Collins and Finucane 1974; Saloman and Collins 1974) and the study by the City of Tampa (COT) from 1978 to present (Johansson

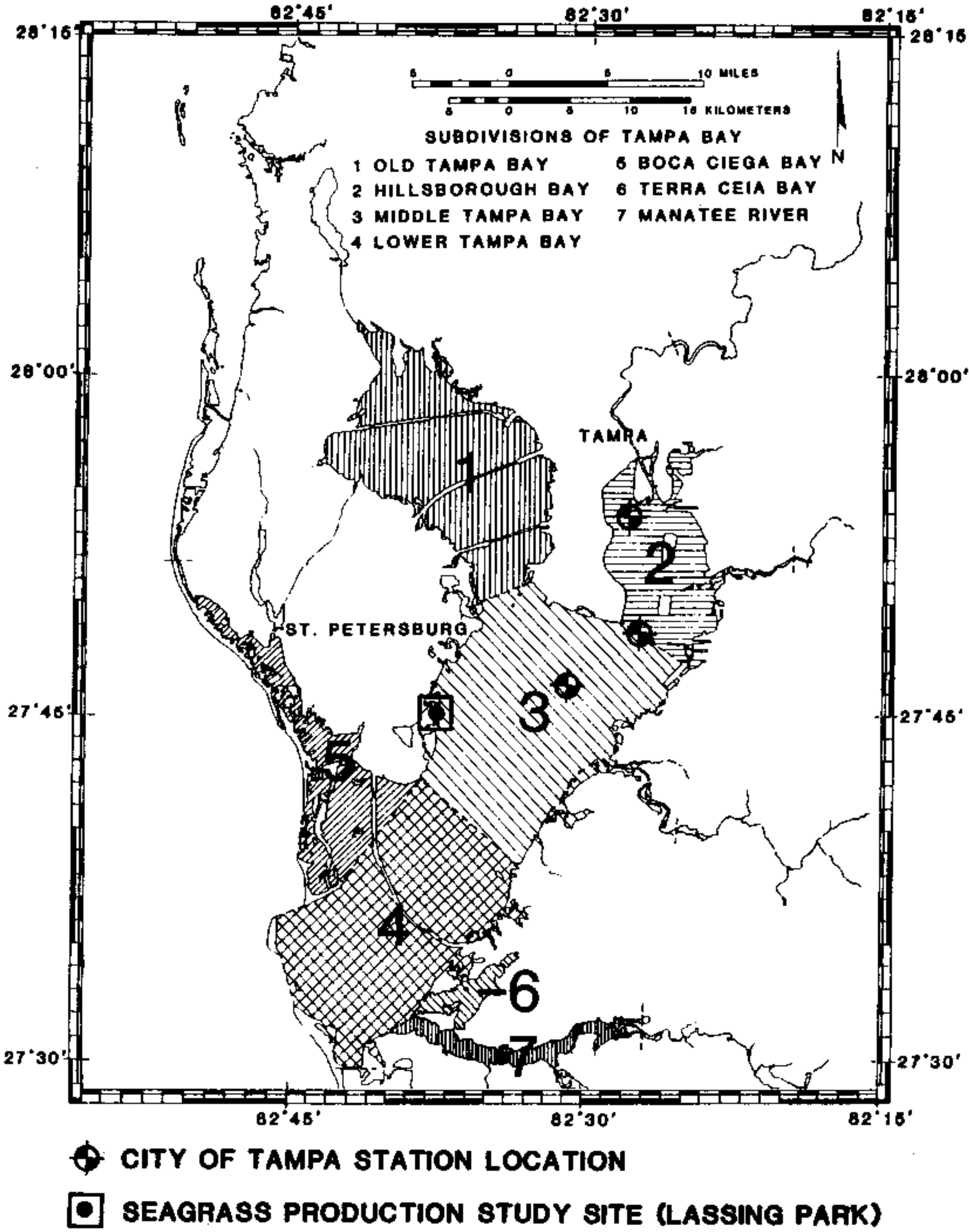

Figure 1. Sites of productivity studies.

and Carpenter, in prep.). However, only the FWS study had stations in all major parts of the bay; the COT study has stations in Hillsborough Bay and Middle Tampa Bay only. Therefore, no phytoplankton production information on the bay system as a whole has been generated since 1973. Further, most of the production data from FWS was estimated from the chlorophyll and light method of Ryther and Yentsch (1957), which does not involve any direct measurements of photosynthetic rates. The lack of comparative production information based on rate measurements between different parts of the bay is a serious shortcoming in the total data base.

The FWS study, in addition to the chlorophyll and light method, also measured phytoplankton production from the dissolved oxygen technique using the light and dark bottle method (Gaarder and Gran 1927) during 1964-1968. The FWS group compared the two methods. The COT study group estimates phytoplankton production from the ^{14}C method (Steeman-Nielsen 1952).

The FWS annually summarized production information by reporting an average monthly rate for each of the four major sections of the bay (Old Tampa Bay, Hillsborough Bay, Middle Tampa Bay, and Lower Tampa Bay). To reduce the data further for this review, only seasonal averages are presented for both FWS and COT data. Monthly values from June, July, August and September are grouped into a wet season category, and the remaining months represent the dry season. Forty years of rainfall data from the Tampa area were used to separate months according to season.

Figure 2 shows the FWS seasonal production data estimated from the chlorophyll and light method. Similarly, Figure 3a shows FWS light and dark bottle estimates of production and Figure 3b shows ^{14}C production measurements of COT. The chlorophyll and light data indicate a weak seasonal pattern with highest production rates during the wet season. There are no obvious long term trends present for Lower Tampa Bay; however, for other parts of the bay, rates increased in 1969 and remained relatively high until the termination of the study (Fig. 2). No explanation for the sudden and long-lasting increase in phytoplankton production, which started in 1969, was offered by the original authors.

Gross production, measured by the oxygen method concurrent with the chlorophyll and light method, was about 2.5 times greater than production estimated from chlorophyll and light data. Further, the oxygen method shows a much clearer seasonal pattern in all areas except the lower bay (Fig. 3a).

Phytoplankton production measured by the ^{14}C method clearly shows a very distinct seasonal pattern with the highest values, as expected, in the wet season which is coincident with the highest water temperatures. These recent measurements by COT appear higher than rates measured by FWS. Whether these differences are due to different methods used, and/or actual differences in production, cannot be determined.

Discussion of the Chlorophyll and Light Method of Estimating Phytoplankton Production

Lack of a strong seasonal pattern in FWS chlorophyll and light estimates was probably due to the extraction technique and specifically, not grinding the filters and phytoplankton residues. Grinding was recommended by SCOR-UNESCO (1966) and has subsequently been adopted by most researchers.

Figure 4 shows the long term record of chlorophyll a concentration for Tampa Bay. Data from the period 1974-1981 have been collected by the Hillsborough County Environmental Protection Commission (HCEPC) and have been added to the records of FWS. The HCEPC chlorophyll data is available from the STORET data storage system. There is little known variation between FWS and HCEPC data sets, since both do not incorporate grinding of filters. The COT has measured chlorophyll a concentrations from filter-ground samples, in Hillsborough Bay and Middle

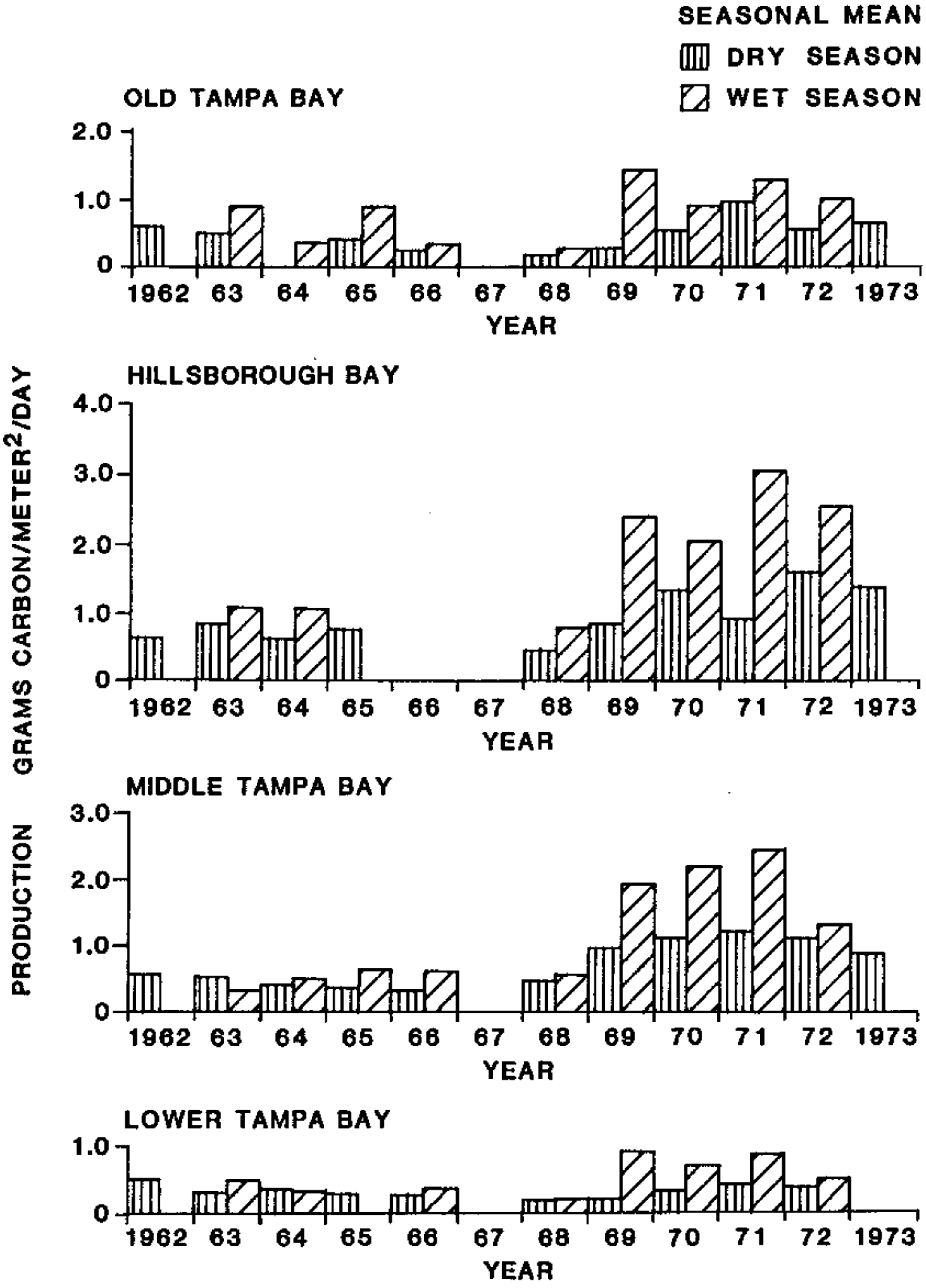

Figure 2. FWS data, chlorophyll + light.

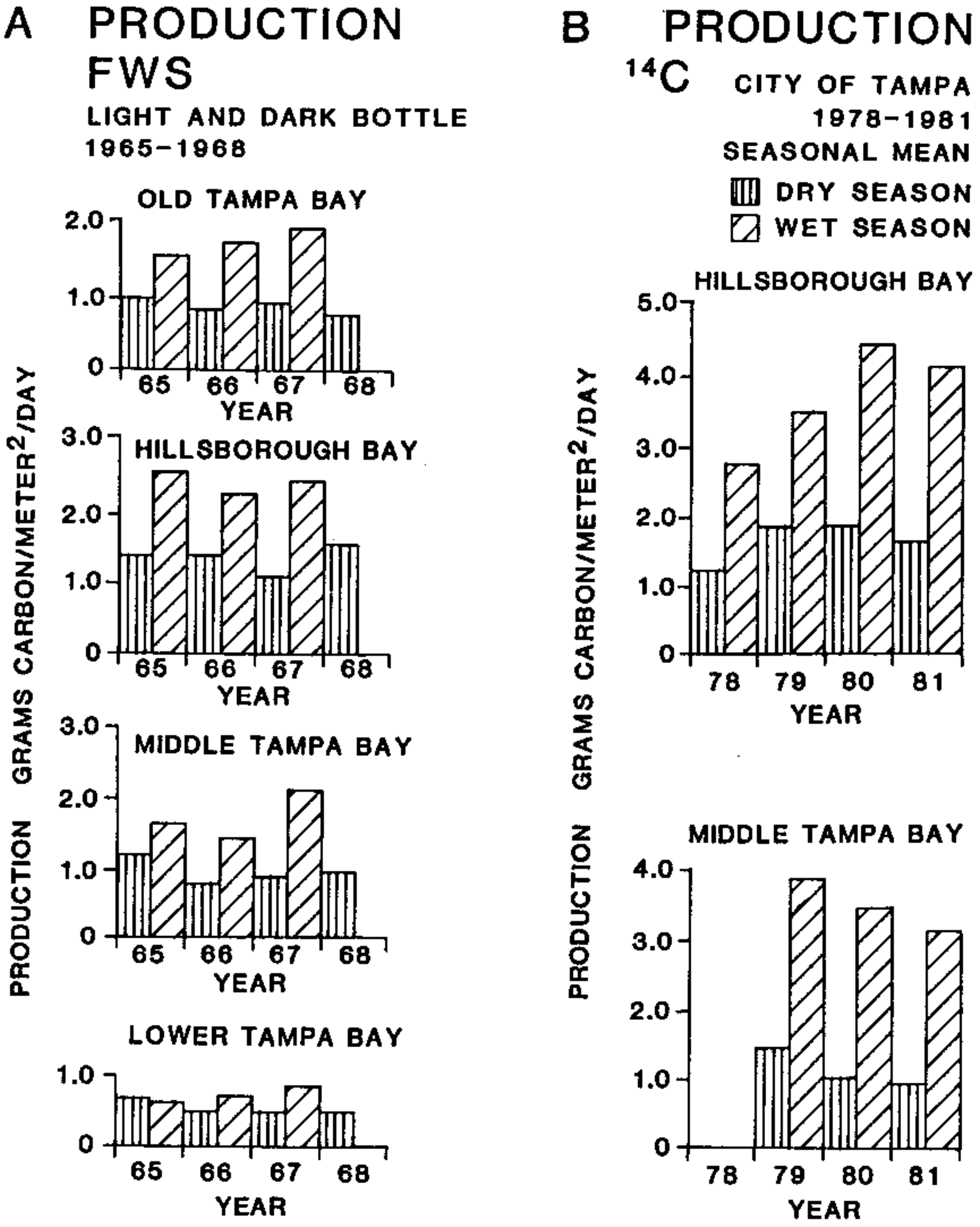

Figure 3. A - FWS data, light & dark bottle; B - COT data, ^{14}C.

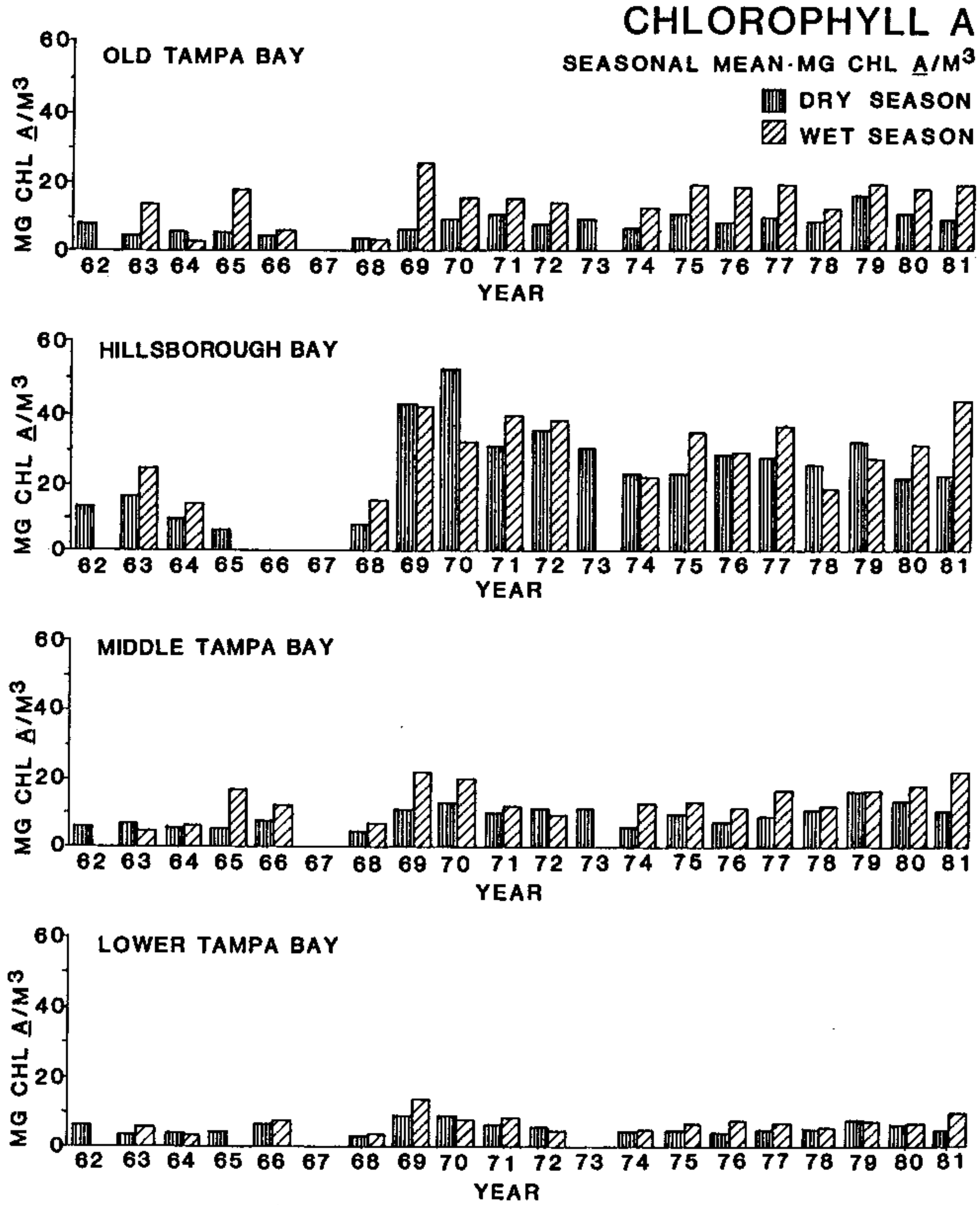

Figure 4. Chlorophyll a, FWS and HCEPC data.

Tampa Bay, since 1978 and 1979, repsectively. These data are presented in Figure 5. Marked seasonal patterns and generally higher concentrations found in the COT data are in clear contrast to the data collected by FWS and HCEPC in Hillsborough Bay and Middle Tampa Bay.

Not grinding chlorophyll samples has been shown to underestimate chlorophyll a concentrations (Fig. 6). Particularly large errors occur during periods when blue-green algae are abundant (Yentsch and Menzel 1963). The blue-green Schizothrix calcicola has been the dominant phytoplankton, both in terms of abundance and biomass, in Hillsborough Bay from late summer to early winter every year of the COT sampling program (1978-1982). Other records (HCEPC pers. comms. and Tampa Electric Co. 1973) indicate that blue-greens (probably S. calcicola) were present in Hillsborough Bay prior to the COT study. Dense concentrations of blue-greens have also been found in Old Tampa Bay and Middle Tampa Bay by the COT. Long-term and area-wide phytoplankton records, generated by FWS from the chlorophyll and light method, may therefore be of limited value for the following reasons: 1) phytoplankton production was calculated from a method which does not involve any direct measurement of photosynthetic rates, and 2) production rates for the eutrophic upper reaches of Tampa Bay may have been greatly underestimated during periods of high blue-green algae abundance due to the lack of sample grinding. The large difference between ground and unground chlorophyll a concentrations in Hillsborough Bay and Middle Tampa Bay is clearly demonstrated in Figures 4 and 5.

Discussion of the ^{14}C Technique

Of the different techniques currently used for plankton primary productivity estimates, ^{14}C is the most widely pursued in oceanic and inshore waters because it can be an effective physiological tracer. However, over the last ten years potential and actual problems with the application of the method have received critical discussion, e.g. bottle confinement, incubation time, heterotrophic uptake, photoinhibition, dark respiration and photorespiration in relation to balanced growth over time, phased assimilation, sample preservation, filter retention and ^{14}C-DOC, autotrophic size components retained and measured, and other facets associated with theory and practice (cf. Steidinger 1973; Eppley et al. 1977; Savidge 1978; Gieskes et al. 1979; Lean and Burnison 1979; Peterson 1980; Platt 1981; Redalje and Laws 1981; Li et al. 1983). Oceanic sampling practices and data assumptions appear to present the most problems by giving underestimates, because of the previously assumed low generation times and size composition of phytoplankton in oligotrophic waters. The ^{14}C method would appear to be more accurate for nutrient-rich inshore waters, yet many of the above problems can still apply. Additionally, bottle incubation and O_2 evolution measure gross production by incorporating respiratory activities (assuming equal respiration rates in light and dark) while ^{14}C incubations can measure gross or net productivity depending on the length of incubation, and grazers and bacteria present.

Annual Phytoplankton Production Estimates

Estimated annual phytoplankton production rates of the four major areas of Tampa Bay are presented in Table 1. Also shown in this table are comparisons of the three different methods of estimating phytoplankton production. The increase in chlorophyll and light estimated production after 1968, discussed above, is very evident when the period 1963-1968 is compared to the period of 1969-1972. Annual rates from the latter period are approximately twice the rates from the preceding period for all parts of the Bay. Methodological differences between the chlorophyll and light method and the oxygen method are reflected in the large discrepancies of estimated production

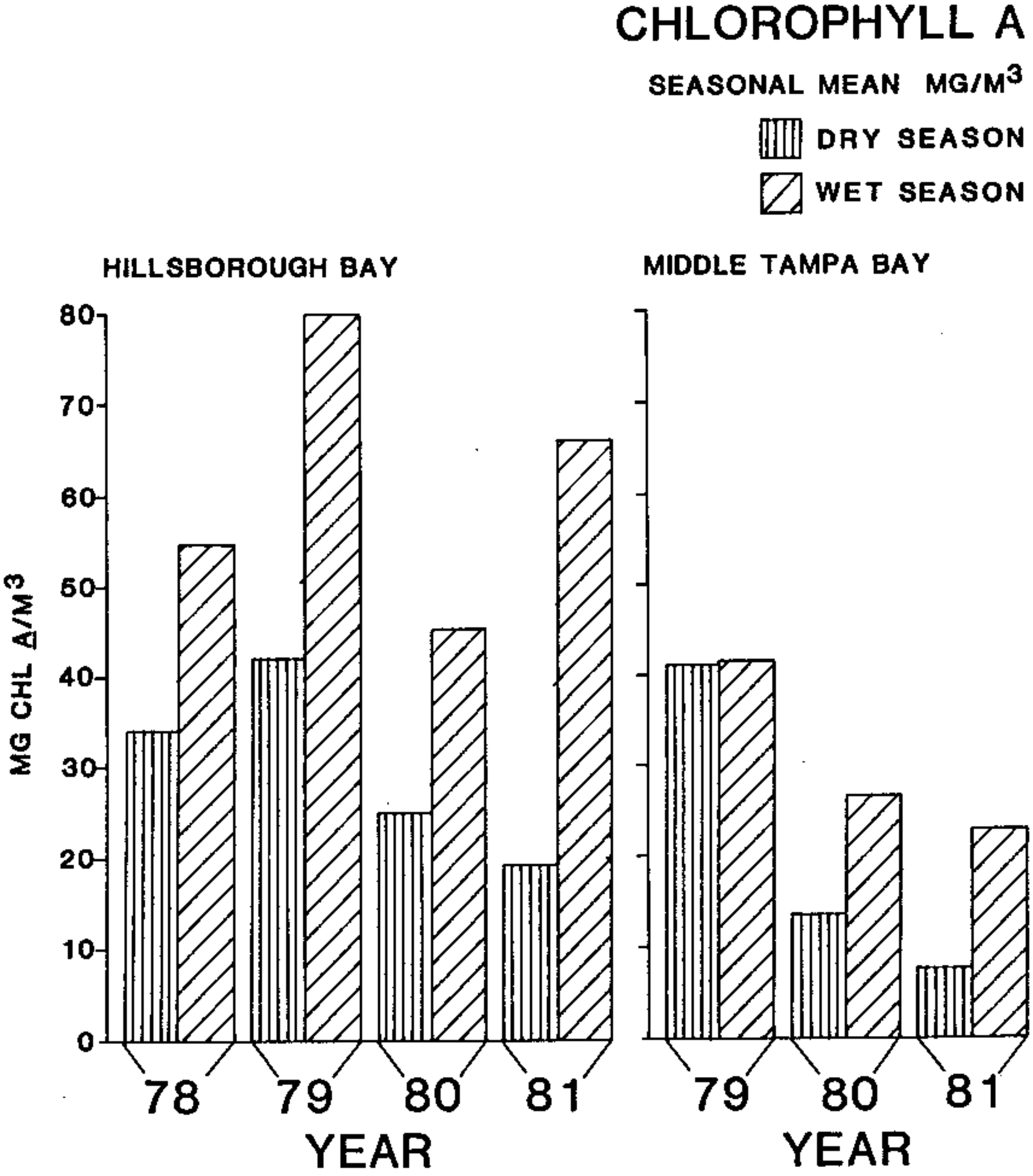

Figure 5. Chlorophyll a, filter-ground samples, COT data.

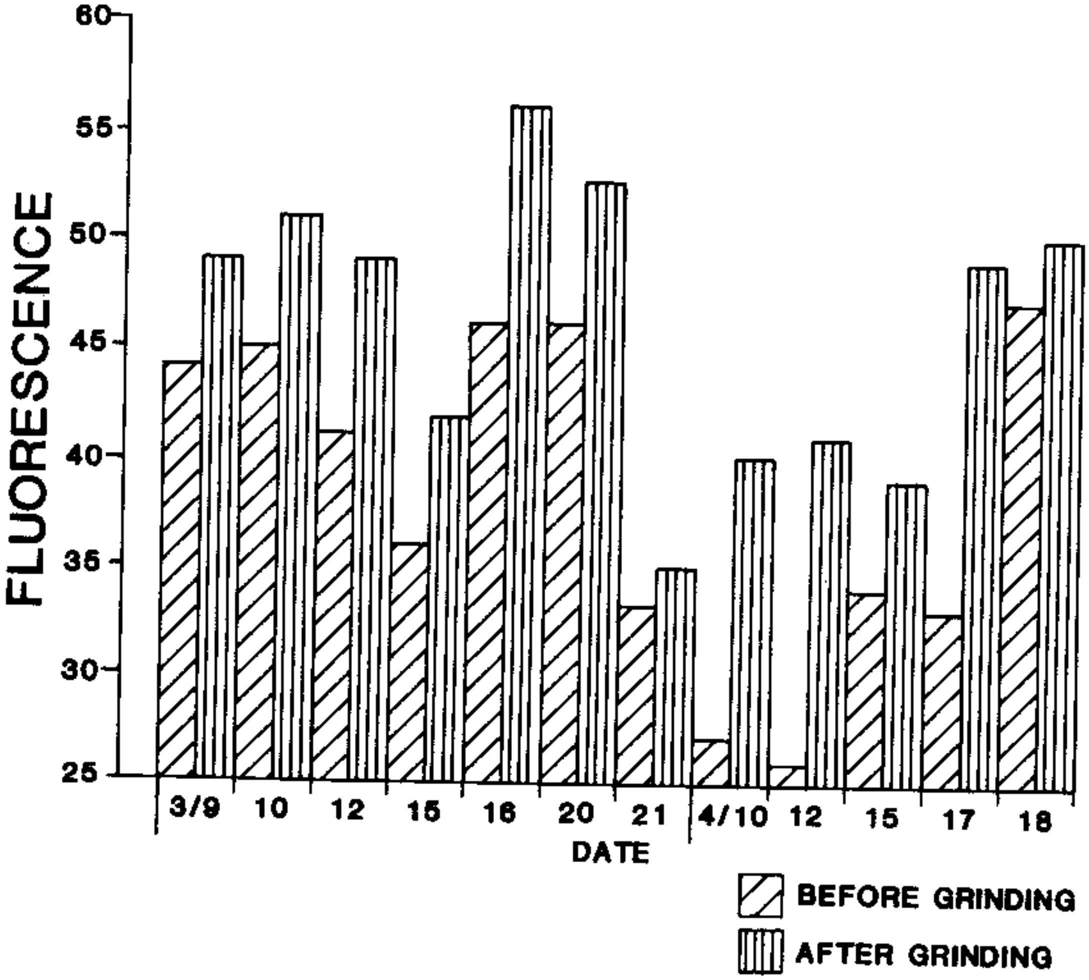

Figure 6. Comparison of fluorescence in 85% acetone extracts of natural phytoplankton in Woods Hole waters before and after grinding. (From Yentsch and Menzel 1963).

Table 1. Estimated annual phytoplankton production rates in the Tampa Bay system (g $C/m^2/yr$)

	Old Tampa Bay	Hillsborough Bay	Middle Tampa Bay	Lower Tampa Bay
1963-1968, chlorophyll + light	170	270	170	120
1965-1967, O_2	430	610	440	220
1969-1972, chlorophyll + light	290	580	490	180
1978-1983, ^{14}C	...	620	620	...

rates during the earliest periods of measurements.

Annual rates calculated from the ^{14}C method are only available for Hillsborough Bay and Middle Tampa Bay. These regions had similar rates during the period 1978-1983; however, the distribution of production in the water column was different. In Hillsborough Bay, a proportionally large amount of carbon was fixed near the surface, while production was more evenly distributed over the water column in the Middle Tampa Bay reigon.

Comparisons between annual rates calculated from the O_2 method and the ^{14}C method (Hillsborough Bay and Middle Tampa Bay) show that ^{14}C-measured production for the period 1978-1983 was similar to O_2-measured production for the period 1965-1967 in Hillsborough Bay. During the same period, ^{14}C-measured production in Middle Tampa Bay was approximately 1.4 times greater than production measured from the O_2 method. It is not known if these differences in production are true or artifacts caused by the use of different methods. It is reasonable to assume, however, that phytoplankton production in Tampa Bay has increased as a response to eutrophication of the bay system and reduced flushing. The suggested almost constant production in Hillsborough Bay since 1965-1967 may indicate that this portion of Tampa Bay has reached a level of maximum phytoplankton production.

Comparison of Primary Producing Components

Above, we discussed some of the shortcomings of the phytoplankton production information available for the Tampa Bay system. Phytoplankton data, however, appear plentiful when compared to information available on other primary producing components (i.e. seagrasses, macro- and microalgae, mangroves and salt marshes). To this date, there have not been long-term and area-wide production studies of any of these components.

Two studies (Pomeroy 1960 and Gibson, pers. comm.) have measured the production of several benthic components and both studies compared benthic production to planktonic production. Pomeroy compared the relative importance in production of the seagrass *Thalassia*, the benthic microflora, and the phytoplankton in Boca Ciega Bay (Fig. 7). He concluded that the relative importance of the three components was a function of water depth. In water less than 2 m, which was 75% of Boca Ciega Bay in 1958, the three groups were of approximately equal importance. Benthic plants became unimportant in deeper waters where all production was assumed to be planktonic.

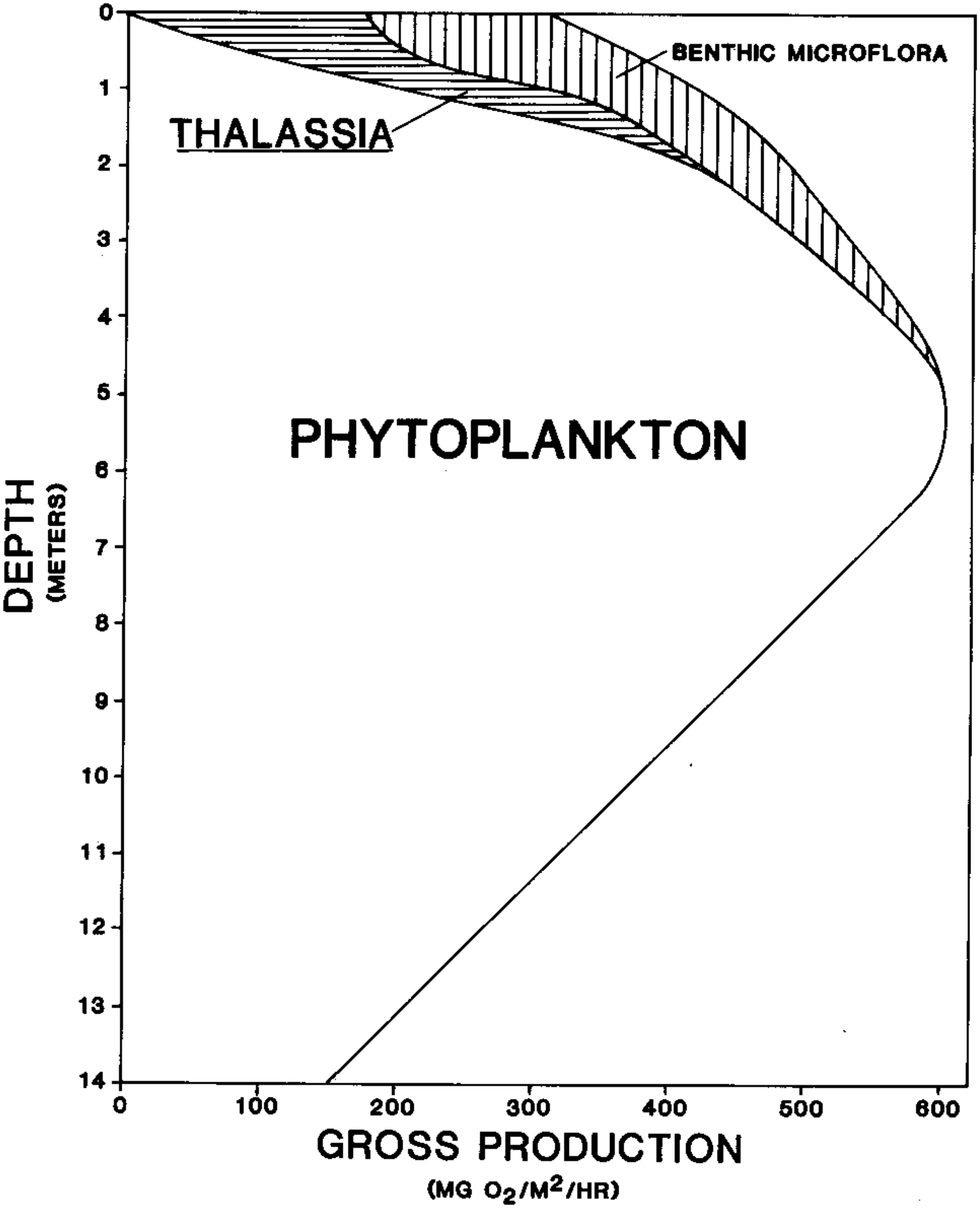

Figure 7. Variation with depth of the relative primary production of the plant populations in Boca Ciega Bay. Most of the bay is less than 2 m deep. (From Pomeroy 1960).

In 1981, Gibson initiated a quarterly investigation of seagrass and epiphyte production. He also measured production of benthic microflora and phytoplankton near the seagrasses. Preliminary results of this study indicate that seagrass beds are highly productive on a per m^2 basis. However, due to the limited coverage of seagrasses in Tampa Bay (Lewis *et al.*, this volume), he suggests that the phytoplankton community is much more important in terms of carbon production than the seagrasses with epiphytes and the benthic microflora. His report will be published in full elsewhere.

Table 2 was constructed in order to discuss the relative importance of production by selected primary producer groups and also to calculate a crude estimate of total annual primary production for the system. Mangrove and salt marsh production are not listed in this table. Although these components have high primary production, little is known of their importance to the bay system. These producers supply organic matter to the bay proper, but could possibly be consumers or net importers of organic carbon from the bay (Haines 1979).

The data in Table 2 are presented as possible primary production by selected components and are not intended to give a complete carbon budget. It should also be emphasized that areal coverage of macroalgae and benthic microalgae are crude estimates. The City of Tampa and Mangrove Systems, Inc. have been conducting studies of biomass, and species and chemical composition of macroalgae in Tampa Bay, with emphasis on Hillsborough Bay. Large drifts of *Gracilaria*, *Ulva* and *Chaetomorpha* are common in the shallows of Hillsborough Bay. These studies will yield a biomass estimate of the macroalgae; however, little is known of their productivity. Hoffman and Dawes (1980) measured the productivity of *Gracilaria* during the summer at the Weeki Wachee River. The authors caution about extrapolating their single season rates to an annual rate, but for the purpose of Table 2 this has been attempted and the annual rate resulting was approximately 70 g C m^{-2}. This rate is generally lower than rates reported from other areas, but Hoffman and Dawes suggest their value is more realistic since they accounted for diel fluctuations in production. Macroalgae production in Tampa Bay may possibly be greater than at Weeki Wachee due to higher nutrient concentrations present.

The seagrass plus epiphyte production rate in Table 2 is an annual average of the Lassing Park seagrass bed (Gibson, pers. comm.). This rate is low in comparison with rates from Biscayne Bay (Jones 1968), but is similar to rates measured during the summer by Bittaker

Table 2. Estimated annual production of selected primary producers based on areal coverage in the Tampa Bay system.

		Production g C/m^2/yr	Area 10^6 m^2	Total Production g C/yr x 10^9	Percent Total
Seagrasses & epiphytes		130	57.5	7.5	2.3
Macroalgae		70	100	7.0	2.1
Benthic microalgae		80	200	16.0	4.9
Phytoplankton	deep area	340	864	293.8	89.3
	shallow area	50	96	48	1.5

and Iverson (1976) in northeastern Gulf of Mexico Thalassia beds. The latter study, however, did not account for epiphyte production.

Benthic microalgae production rates measured by Gibson are close to rates reported in the literature, which usually range between 100-200 g C m^{-2} yr^{-1}.

Phytoplankton productivity in Tampa Bay, according to the data presented in Table 2, accounts for 91% of the production by the selected primary producers. Similarly, Gibson (pers. comm.) found that the phytoplankton in the Indian River estuary contributed 93% of the annual production. McNulty (1969) first calculated the total production of phytoplankton, seagrasses and benthic microalgae in Tampa Bay on an area coverage basis. He concluded that the combined annual production by benthic algae and grasses was 2-3 times greater than the annual production by the phytoplankton. His calculations are in stark contrast to ours.

Annual Recurring Blue-Green Algae Bloom in Hillsborough Bay

Records of annual blue-green blooms (Schizothrix calcicola) in Hillsborough Bay date back to 1975 (see above). There are also reports of dense blue-green blooms in Tampa Bay from the 1960s (Saunders et al. 1967). The COT study has found S. calcicola to dominate the ultra and net (greater than 2 um) phytoplankton community from August through November every year of the study (1978-1982). Schizothrix calcicola displaces Skeletonema costatum and other small diatoms from dominance at the peak of summer temperatures (30°C and above). It reaches maximum concentrations of approximately 80,000 filaments per ml later in the summer and early fall. By the end of the year, S. costatum and other small diatoms again dominate the phytoplankton and S. calcicola becomes less abundant. The blue-green is virtually absent from the phytoplankton community between late winter and early summer.

The annual curve of phytoplankton in Hillsborough Bay (Figs. 8a and 8b) generally follows the temperature curve, which is a common phenomenon for shallow estuaries (Eppley 1972). However, maximum production does not occur when S. calcicola and chlorophyll a are at maximum concentrations (Figs. 8c and 8d). The blue-green is therefore a relatively inefficient producer of organic carbon. The primary productivity to chlorophyll a ratio (assimilation number) further illustrates the inefficency of S. calcicola (Fig. 8e). The phytoplankton community of Hillsborough Bay is least efficient when the blue-green is at maximum abundance. The greatest efficiency occurs in early summer when the bay has a "typical" estuarine community of small photosynthetic flagellates, S. costatum, and other small diatoms. Similar succession of phytoplankton groups, including filamentous blue-green algae, and associated seasonality in efficiency of carbon assimilation have been reported by others (e.g. Revelante and Gilmartin 1981).

Little is known about the food value of Schizothrix calcicola, although blue-greens generally are considered undesirable as food (Forsskahl et al. 1982). Therefore, if blue-greens compete with and replace better food species such as small diatoms, less particulate organic carbon will be available to secondary production. More fixed carbon will be lost to export, the sediments, and bacterial remineralization processes, and as a result the ecological efficiency of the system will be lowered.

CARBON FLOW AND TROPHIC DYNAMICS

A realistic limitation with any primary productivity measurement is its usage in trophic and energy flow schemes. Questions such as how is the resultant POC used, or lost and recycled, and what trophic level benefits, and at what cost to ecological efficiency, are not addressed. Carbon flow is indeed not

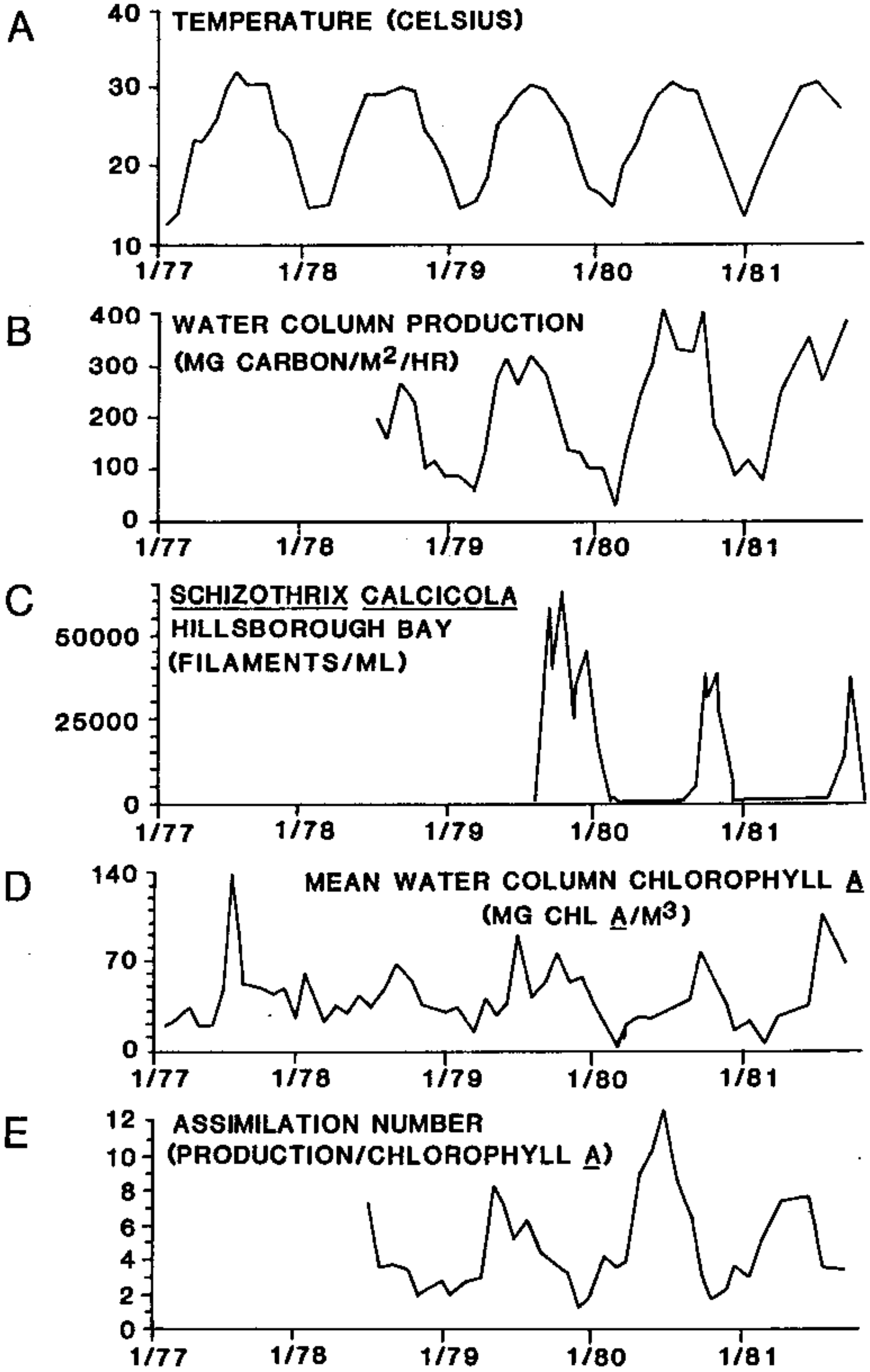

Figure 8. Hillsborough Bay water temperature (A), production (B), *Schizothrix calcicola* filaments (C), chlorophyll *a* (D) and assimilation number (E), 1977–1981.

unidirectional as Peterson (1980) stressed. He also made statements that 10 years ago would have been considered radical:

> I think the most significant advance of the last few years in interpreting the meaning of ^{14}C-CO_2 uptake has been the realization that our conceptual model of carbon flow has been too simple. The idea that simply calculating the fraction of the inorganic carbon pool converted to POC and DOC in a 4 hr incubation is a sufficient measure of primary production is no longer valid ... It seems unacceptable to guess at the proper interpretation of ^{14}C data ... We need to know how much of the carbon fixed in photosynthesis is available to grazers and other heterotrophs in aquatic systems ... The ^{14}C method will surely help in reaching this goal, but it may not be sufficient unless coupled with other tools now available to aquatic ecologists. (Peterson 1980, p. 376-377).

Although Peterson's comments were directed primarily to open pelagic realms, they also apply to estuarine areas where planktonic values are complicated by nonphytoplankton detrital inputs, benthic macro- and microphytes, and monospecific blooms that are not grazed but often cause decomposition and anoxia when developing in a restricted water mass.

System Production

The Tampa Bay system has high phytoplankton standing stock and primary productivity. The system is fringed by limited mangrove stands and marsh areas, and has submerged seagrasses and micro- and macroalgae which constitute other primary producers. Major inorganic nutrients would not appear to be limiting primary productivity, particularly in upper and middle reaches, and the system probably has a high nitrogen turnover rate. Consequently, the Tampa Bay system is considered enriched and "productive".

The most limiting factors to total primary production for the system, therefore, would be water clarity and temperature, particularly in the upper reaches such as Hillsborough and Old Tampa Bays. Water clarity, or rather turbidity, has restricted benthic macrophytes to shoreline areas of less than 2 m depth in those areas that still support submerged vegetation. These shallow depths represent about 10% of the bay system. Although primary productivity of seagrasses and their epiphytes in many subtropical and tropical areas can be high (Jones 1968), and micro- and macroalgae also can be significant primary producers, their limited surface area coverage reduces the total contribution when compared to phytoplankton productivity based on integrated m^2 calculations for total area (see Table 2). If primary productivity was used as an hourly or yearly per m^2 value alone, then seagrasses and their epiphytes would have the highest values, followed by benthic macroalgae and planktonic microalgae in shallow estuaries and specifically the Tampa Bay system. When the total bay area is used, assuming that the benthic components are limited to less than 2 m, then planktonic microalgae dominate as primary producers and always have because of the bathymetry and size (960 km^2) of the bay system. It is not that the system is changing from one dominated by seagrasses to one dominated by phytoplankton; rather, where seagrasses have been removed or destroyed (81% of the grassbeds have been lost since 1876; Lewis et al., this volume), phytoplankton now dominate the system's shallow perimeter as well as deeper water.

Even though benthic primary producers, such as seagrasses and macroalgae, assimilate inorganic carbon and photosynthesize, their immediate particulate organic carbon (POC) contribution is unquantified. Seagrass leaves in the Tampa Bay area are rarely grazed directly, although seagrass epiphytes are; however, leaves detach and become drift twice yearly and this POC contributes to detrital and remineralization cycles. Also, massive amounts of drift Gracilaria and Ulva can dominate aquatic biomass and primary productivity, yet their contribution also is principally to particulate detrital and dissolved nutrient cycles. In addition to these detrital inputs, mangrove leaf and twig litter from fringing trees and saltmarsh plant detritus contribute POC and DOC that support some estuarine food webs or portions thereof. Grazers, such as amphipods, further break down the vegetation into smaller particles (Fenchel 1970) and these animals contribute DOC, nutrients, and fecal matter to the system which is then recycled, thus building in a time lag to total production, injecting a lower trophic level, and decreasing ecological efficiencies. Microcolonizers of detrital particles utilize these substrates and release DOC and nutrients in addition to increasing the nutritional value (e.g. protein) of the total detrital biomass. Again, carbon flow is not unidirectional. As Pomeroy stated, "In the real world there are other energy pathways involving such entities as microorganisms, detritus, and dissolved organic materials (DOM)" (Pomeroy 1979, p. 165). Consequently, there are direct and indirect trophic pathways. For many of Florida's recreational and commercial fishes, e.g. tarpon, redfish, spotted seatrout, snook, black mullet, black drum, gag grouper and others, food items vary with a fish's age and habitat. Fenchel (1972) suggested that detrital-based trophic systems acted as energy reservoirs or reserves, making seasonally fixed carbon or sporadic allochthonous carbon inputs available for longer time periods to herbivores and carnivores.

Recommendations for Future Primary Production and Trophic Studies

Sackett (in press), in a review of stable carbon isotope studies and applications, stated "... the carbon isotope composition of an organism is a weighted average of the isotopic composition of its organic carbon food intake." This was further supported by Fry and Parker (1979) and Haines and Montagne (1979) where carbon pathways, particularly those based on microalgae/phytoplankton and vascular plant sources, were differentiated by analyzing tissue from higher animal trophic levels. However, stable values for a given group, or even a given species, can vary 14°/oo because of natural fluctuations in lipid metabolism and reserves, photosynthetic pathways, temperature, season, geographic location, plant part if vascular, and decomposition (Gormly and Sackett 1977; McMillan et al. 1980; Fry 1981; McMillan and Smith 1982; Sackett, in press). Hughes and Sherr (1983) pointed out that ^{13}C was selectively biomagnified at each trophic level because ^{12}C is respired; therefore, higher trophic levels are ^{13}C enriched with each step increasing 0.5 to 1.5°/oo. Since there are recognized problems with the overlap in and interpretation of $^{13}C/^{12}C$ ratios, other stable isotopes, e.g. $^{15}N/^{14}N$ and $^{35}S/^{34}S$, are being pursued because they are subject to little change with trophic levels (cf. Macko et al. 1982; Fry et al. 1982). Another stable isotope being used to trace food webs is deuterium/hydrogen (cf. Estep and Dabrowski 1980). Using a combination of stable isotopes, researchers can differentiate between phytoplankton, seagrass, macroalgae, and mangrove sources as primary production components in food webs.

Based on the above discussion of isotope ratios and how these techniques can be applied to food webs with both auto- and allochthonous inputs, this approach could be taken to compartmentalize and identify the significance of various detrital sources at succeeding levels of food webs in the Tampa Bay system. Primary productivity measurements for potential major direct pathways, e.g. planktonic and benthic microalgae and epiphytes, could still be pursued, but interpretation of resultant data must be correlated with herbivores or omnivores, secondary production, and system dynamics. Are the potential direct sources actually used as POC or is DOC more significant in food webs? What is the significance and contribution of planktonic bloom events. What is the yearly production of benthic microalgae and what does it support? What time lag is built into total system production because of detrital and DOC utilization? In other words, we may need to determine the major inputs and their form before a sampling and analytical strategy can be properly designed to evaluate and quantify primary and secondary production in relation to carbon flow, trophic pathways and interactions in such a diverse system. Secondary production, depending on definition, would appear to be multilevel, while much of the primary production is lost as sedimented POC and recycled, thus introducing additional trophic levels. Such an approach requires a "rethinking" of the value and application of primary production measurement as carbon per area per time interval as they relate to systems production and trophic structures.

REFERENCES

Bittaker, H. F. and R. L. Iverson. 1976. Thalassia testudinum productivity: a field comparison of measurement methods. Mar. Biol. 37:39-46.

Collins, A. L. and J. H. Finucane. 1974. Hydrographic observations in Tampa Bay and adjacent waters, May 1971 through April 1973. Natl. Mar. Fish. Serv. Data Rept. 87. 146 pp.

Dragovich, A. and L. Johnson, Jr. 1966. Chemical environment project. Pp. 16-17 in Report of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida, fiscal year 1965. U.S. Fish Wildl. Serv. Circ. 242.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fishery Bull. 70:1063-1085.

Eppley, R. W., W. G. Harrison, S. W. Chisholm and E. Stewart. 1977. Particulate organic matter in surface waters off southern California and its relationship to phytoplankton. J. Mar. Res. 35(4):671-696.

Estep, M. F. and H. Dabrowski. 1980. Tracing food webs with stable hydrogen isotopes. Science 209:1537-1538.

Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass Thalassia testudinum. Limnol. Oceanog. 15:14-20.

Fenchel, T. 1972. Aspects of decomposed food chains in marine benthos. Verh. Dtsch. Zool. Ges. 65:14-22.

Finucane, J. H. and A. Dragovich. 1966. Hydrographic observations in Tampa Bay, Florida and the adjacent Gulf of Mexico, 1963. U.S. Fish Wildl. Serv. Data Rept. 14. 81 pp.

Forsskahl, M., A. Laakonen and J.-M. Leppanen. 1982. Seasonal cycles of production and sedimentation of organic matter at the entrance to the Gulf of Finland. Netherlands J. Sea Res. 16:290-299.

Fry, B. 1981. Natural stable carbon isotope tag traces, Texas shrimp migrations. Fish. Bull. 79:337-345.

Fry, B. and P. L. Parker. 1979. Animal diet in Texas seagrass meadows: ^{13}C evidence for the importance of benthic plants. Estuar. Coast. Mar. Sci. 8:499-509.

Fry, B., R. S. Scalan, J. K. Winters and P. L. Parker. 1982. Sulphur uptake by salt grasses, mangroves, and seagrasses in anaerobic sediments. Geochem. Cosmochim. Acta 46:1121-1124.

Gaarder, T. and H. H. Gran. 1927. Investigations of the production of plankton in the Oslo Fjord. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer. 42:1-48.

Geiskes, W. W., G. W. Kraay and M. A. Baars. 1979. Current ^{14}C methods for measuring primary production: gross underestimates in oceanic waters. Netherlands J. Sea Res. 13(1):58-78.

Gormly, J. R. and W. M. Sackett. 1977. Carbon isotope evidence for the maturation of marine lipids. Pp. 321-339 in R. Campos and J. Gori (eds.), Proceedings of the 7th Annual Meeting on Organic Geochemistry. Rev. Espanola Micropaleontol. Endadimsa, Madrid.

Haines, E. B. and C. L. Montagne. 1979. Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios. Ecology 60(1):48-56.

Hoffman, W. E. and C. J. Dawes. 1980. Photosynthetic rates and primary production by two Florida benthic red algal species from a salt marsh and a mangrove community. Bull. Mar. Sci. 30:358-364.

Hughes, E. H. and E. B. Sherr. 1983. Subtidal food webs in a Georgia estuary: ^{13}C analysis. J. Exp. Mar. Biol. Ecol. 67:227-242.

Jones, J. A. 1968. Primary productivity by the tropical marine grass, Thalassia testudinum Konig and its epiphytes. Ph.D. dissertation, Univ. of Miami. 196 pp.

Kelly, J. A., Jr. and L. Johnson, Jr. 1967. Chemical environment project. Pp. 11-12 in Report of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida, fiscal year 1966. U.S. Fish Wildl. Serv. Circ. 257.

Lean, D. R. S. and B. K. Burnison. 1979. An evaluation of errors in the ^{14}C method of primary production measurement. Limnol. Oceanogr. 24(5):917-928.

Li, W. K. W., D. Subba Rao, W. G. Harrison, J. L. Smith, J. J. Cullen, B. Irwin and T. Platt. 1983. Autotrophic picoplankton in the tropical ocean. Science 219:292-295.

Malko, S. A., W. Y. Lee and P. L. Parker. 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. J. Exp. Biol. Ecol. 63:145-149.

May, B. Z. 1966. Chemical environment project. Pp. 15-16 in Report of the Bureau of Commercial Fisheries Biological Station, St. Petersburg Beach, Florida, fiscal years 1962-1964. U.S. Fish Wildl. Serv. Circ. 239.

McMillan, C., P. L. Parker and B. Fry. 1980. $^{13}C/^{12}C$ ratios in seagrasses. Aquatic Bot. 9:237-249.

McMillan, C. and B. W. Smith. 1982. Comparison of ^{13}C values for seagrasses in experimental cultures and in natural habitats. Aquatic Bot. 14:381-387.

McNulty, J. K. 1968. Plankton ecology project. Pp. 8-10 in Report of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida, fiscal year 1967. U.S. Fish Wildl. Serv. Circ. 290.

McNulty, J. K. 1969. Plankton ecology project. Pp. 22-24 in Report of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Fl., fiscal year 1968. U.S. Fish Wildl. Serv. Circ. 313.

McNulty, J. K., L. Johnson, Jr., E. A. Anthony and W. N. Lindall, Jr. 1970. Plankton ecology project. Pp. 20-22 in Report of the Bureau of Commercial Fisheries Biological Laboratory, St. Petersburg Beach, Florida, fiscal year 1969. U.S. Fish Wildl. Serv. Circ. 342.

Peterson, B. J. 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: a history of the productivity problem. Ann. Rev. Ecol. Syst. 11:359-385.

Platt, T. (ed.). 1981. Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210. 346 pp.

Pomeroy, L. R. 1960. Primary productivity of Boca Ciega Bay, Florida. Bull. Mar. Sci. Gulf Carib. 10:1-10.

Pomeroy, L. 1979. Secondary production mechanisms of continental shelf communities. Pp. 163-186 in R. J. Livingston (ed.), Ecological Processes in Coastal and Marine Systems. Plenum Press, N.Y.

Redalje, D. G. and E. Laws. 1981. A new method for estimating phytoplankton growth rates and carbon biomass. Mar. Biol. 62:73-79.

Revelante, N. and M. Gilmartin. 1982. Dynamics of phytoplankton in the Great Barrier Reef Lagoon. J. Plankton Res. 4:47-75.

Ryther, J. H. and C. S. Yentsch. 1957. The estimation of phytoplankton production in the ocean from chlorophyll and light data. Limnol. Oceanogr. 2:281-286.

Sackett, W. M. In press. Stable carbon isotope studies on organic matter in the marine environment. In Handbook of Environmental Isotope Geochemistry. Elsevier, Holland.

Saloman, C. H. 1973. Hydrographic observations in Tampa Bay, Florida - 1970. Natl. Mar. Fish. Serv. Data Rept. 77. 246 pp.

Saloman, C. H. 1974. Hydrographic and meteorological observations from Tampa Bay and adjacent waters - 1971. Natl. Mar. Fish. Serv. Data Rept. 84. 554 pp.

Saloman, C. H. and L. A. Collins. 1974. Hydrographic observations in Tampa Bay and adjacent waters - 1972. Natl. Mar. Fish. Serv. Data Rept. 90. 176 pp.

Saloman, C. H., J. H. Finucane and J. A. Kelly. 1964. Hydrographic ovservations in Tampa Bay, Florida, and the adjacent waters, August 1961 - December 1962. U.S. Fish Wildl. Serv. Data Rept. 4. 112 pp.

Saloman, C. H. and J. L. Taylor. 1968. Hydrographic observations in Tampa Bay, Florida, and the adjacent Gulf of Mexico - 1967. Natl. Mar. Fish. Serv. Data Rept. 24. 393 pp.

Saloman, C. H. and J. L. Taylor. 1971a. Hydrographic observations in Tampa Bay and the adjacent Gulf of Mexico - 1967. Natl. Mar. Fish. Serv. Data Rept. 55. 64 pp.

Saloman, C. H. and J. L. Taylor. 1971b. Hydrographic observations in Tampa Bay and the adjacent Gulf of Mexico - 1968. Natl. Mar. Fish. Serv. Data Rept. 63. 204 pp.

Saloman, C. H. and J. L. Taylor. 1972. Hydrographic observations in Tampa Bay, Florida. Natl. Mar. Fish. Serv. Data Rept. 73. 82 pp.

Saunders, R. P., B. I. Birnhak, J. T. Davis and C. L. Wahlquist. 1967. Seasonal distributions of diatoms in Florida inshore waters from Tampa Bay to Caxambas Pass, 1963-1964. Pp. 48-78 in Red Tide Studies, Pinellas to Collier Counties, 1963-1966. Fl. Board Conserv. Marine Lab., St. Petersburg. Prof. Pap. Ser. no. 9. 141 pp.

SCOR-UNESCO. 1966. Determination of photosynthetic pigments in seawater. Monographs on Oceanographic Methodology, UNESCO, Paris. 1:11-18.

Savidge, G. 1978. Variations in the progress of ^{14}C uptake as a source of error in estimates of primary production. Mar. Biol. 49:295-301.

Steeman Nielsen, E. 1952. The use of radioactive carbon (^{14}C) for measuring organic production in the sea. J. Cons. Int. Expl. Mer. 18:117-140.

Steidinger, K. A. 1973. Phytoplankton ecology: a conceptual review based on eastern Gulf of Mexico research. CRC Crit. Res. Microbiol. 3:49-68.

Tampa Electric Company. 1973. Ecological surveys of the Big Bend area - supplement. Tampa Electric Co. 3. 137 pp.

Taylor, J. L. 1970. Coastal development in Tampa Bay, Florida. Mar. Poll. Bull. 1:153-156.

Taylor, J. L. and C. H. Saloman. 1968. Some effects of hydraulic dredging and coastal development in Boca Ciega Bay, Florida. U.S. Fish Wildl. Serv. Fish. Bull. 67:213-241.

Yentsch, C. S. and D. W. Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep Sea Res. 10:221-231.