PHYTOPLANKTON PRODUCTIVITY AND STANDING CROP IN THE ANCLOTE ESTUARY, FLORIDA

by

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Certificate of Approval - Master's Thesis

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Tampa, Florida

CERTIFICATE OF APPROVAL

MASTER'S THESIS

This is to certify that the Master's Thesis of

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with a major in Marine Science has been approved by the Examining Committee as satisfactory for the thesis requirement for the Master of Science degree at the convocation of December 10, 1975.

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INTRODUCTION

The Department of Marine Science, University of South Florida, has been conducting a comprehensive environmental study of the Anclote Estuary on the west central coast of Florida near the town of Tarpon Springs since 1970. This study was primarily designed to characterize the marine environment prior to the construction and operation of a Florida Power Corporation generating plant and, subsequently, to evaluate impact of its construction and operation on the environment. Phytoplankton productivity and standing crop were investigated from March, 1973 through February, 1974 as a part of the multi-disciplinary study.

Gibson and Hopkins (1973) initially reported on diatoms found in Anclote surface waters and subsequently presented a quantitative treatment of all major groups of phytoplankton found in this area (Gibson and Hopkins, 1974). Primary productivity at a reference station located in the Anclote Anchorage has also been discussed by Johansson and Hopkins (1973). The present study characterizes phytoplankton production in different regions of the Anclote Estuary and examines relationships among phytoplankton standing crop, composition, and production. This represents one of the few extensive seasonal studies of phytoplankton production and ecology on the Florida west coast. The only comparable studies along this coast are those of Putnam (1966) and Gorman (unpubl. data) who investigated the Waccasassa and Crystal River Estuaries, respectively.

THE ANCLOTE ESTUARY

The Anclote Estuary forms a shallow coastal lagoon occupying approximately 48 km^2 between latitudes 28°09' - 28°13' North and longitudes 82°47' - 82°51' West. To the west it is separated from the Gulf of Mexico by 5 km of narrow barrier islands (Anclote Key, Dutchman Key, and North Anclote Keys). Confluence with the Gulf of Mexico occurs around the north and south ends of these keys. The depth of the estuary is estimated to be less than 2 m over approximately 70% of its area.

The sediments consist of fine to medium quartz sand with scattered sandy clay beds (Mohler, 1962). Seagrasses occupy approximately 40% of the submerged bottom and are generally restricted to depths not exceeding 1.5 m (mean low water) (Zimmerman et al., 1973).

The Anclote region is influenced predominately in spring and summer by tropical air masses from the south and southeast, and by cold air masses from the continent in late fall and winter (Jordan, 1973). Average monthly air temperatures in the summer months are approximately 28°C and in the winter 22°C (Jordan, 1973). Annual rainfall averages about 1300 mm, with usually more than 50% of the precipitation occurring in the period of June-September (Jordan, 1973).

The tidal cycle of the region is predominately semi-diurnal and tidal amplitudes usually range between 0.3 and 0.9 m. Water currents in the estuary are tidally and wind driven, the latter the stronger factor when winds are in excess of 6.7 m s^{-1} (Carder and Klausewitz, 1973). Mean

monthly wind speeds in this region, however, seldom exceed 5 m s^{-1} (Jordan, 1973).

The Anclote River, having a drainage area of 290 km^2 (Mohler, 1962), is the major contributor of fresh water to the Anclote Estuary. River discharge is low during most of the year, averaging 2.2 m^3 s^{-1} at Elfers, 26 km upstream from the mouth of the river (U.S. Geological Survey, 1973; see also Figure 4A of the present study for 1973-1974 discharge data). The river water flows into the anchorage primarily towards the north during flood tide (Carder and Klausewitz, 1972).

METHODS

Sampling Program

Surface water was sampled monthly from March, 1973 through February, 1974 at eleven stations in the Anclote Estuary (Figure 1).

Aliquots were taken from surface bucket samples for the following determinations: salinity and dissolved nutrients (0.5 liter), phytoplankton pigments (2 liters), and primary productivity (4 liters). Additional aliquots (4 liters) were obtained from stations 50, P, and 13, in the Gulf, anchorage, and river, respectively, for phytoplankton abundance, biomass, and taxonomic analyses. Further, at station P 10 liters of surface water were collected for *in situ* primary productivity studies.

At each sampling, time of collection was recorded and surface water temperature was obtained. Also Secchi depth was measured, with a white 20 cm diameter disk. At station P, submarine irradiance measurements were made at 0.5 m depth intervals using a Tsurumi-Seiki Simple Submarine Illuminance Meter.

Primary Productivity Procedures

Primary productivity was measured using a modification of the ^{14}C technique of Steemann Nielsen (1952). Water samples were initially filtered through a 202 µm mesh gauze to remove the larger zooplankton (Strickland, 1960). Four 130 ml Pyrex BOD bottles (three clear and one light-proofed with tape) were filled with water from every station for surface primary productivity determinations. The sample bottles were

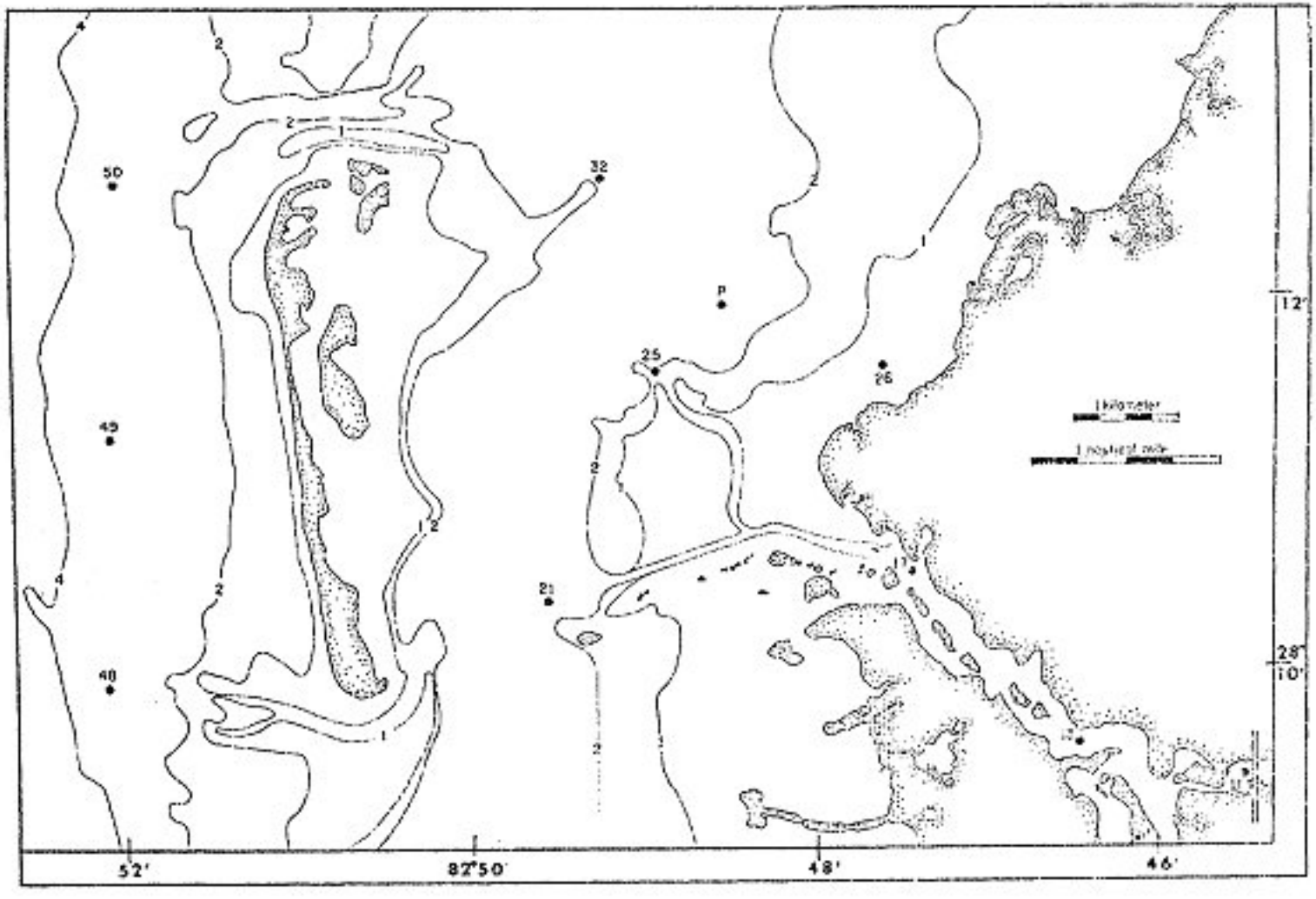


Figure 1. Phytoplankton sampling stations in the Anclote Estuary, 1973-1974. Contours indicate approximate depth in meters.

inoculated with 1 ml of $Na_2{}^{14}CO_3$ solution containing 4 μc of ^{14}C using a 2 ml Brinkman Dispenser. The radioactive solution was drawn from a reservoir sufficiently large to ensure that all samples would be inoculated from the same well-agitated source. Black bottles were then covered with two layers of aluminum foil to ensure exclusion of light and all sample bottles were covered with a dark cloth until the initiation of the incubation period.

The surface samples from the eleven stations were incubated under natural light for 4 to 6 hr starting at local noon at a location in the Anclote River near the University of South Florida marine field station. These samples were temperature controlled by immersing the bottles in river water. From March through August, samples were placed in a deck incubator on shore and a submersible pump was used to deliver the river water for temperature control. After August, a floating incubator, anchored in the river, was used. Regardless of what incubation procedure was employed, the samples received unshaded sunlight throughout the incubation period and the two procedures are considered comparable.

Each month an in situ experiment was conducted at station P to estimate productivity in the water column and to serve as a reference or calibration point for the surface samples. At this station five sets of BOD bottles were filled with surface water. The introduction of the ^{14}C tracer and the period of incubation were as above, however, the samples were attached to holders (a modified version of the one described by Schindler and Holmgren, 1971), one holder with one set of bottles for each 0.5 m depth increment from surface to 2.0 m.

At the end of the incubation period, sample bottles were retrieved and covered with a dark cloth and brought to the field station. Each

productivity sample was vacuum-filtered at 130 mm Hg through a prenumbered 47 mm HA 0.45 µm Millipore membrane filter. The filters were wet with filtered seawater prior to filtration in order to reduce retention of unfixed ^{14}C material by the filters (see below), as suggested by Williams, Berman, and Holm-Hansen (1972). The filtration process took place under dim light (Vollenweider, 1974). At the termination of filtration, each filter was rinsed with approximately 10 ml of filtered sea water and 2 ml of isotonic ammonium formate solution, and then coiled along the wall (residue to the inside [Crouzet, 1972]) of a 20 ml glass liquid scintillation vial. At the laboratory of the Department of Marine Science of the University of South Florida in St. Petersburg, the filters were dried over silica gel in a desiccator for at least 4 days. Possible losses of radioactivity occurring during desiccation, as reported by Wallen and Geen (1968) and Ward and Nakanishi (1971, 1973), were not determined. These losses are probably variable and therefore not easily corrected for. After desiccation, 20 ml of 0.5% PBD (phenylbiphenyloxadiazole-1, 3, 4) (Amersham/Searle Corp.)-toluene scintillation cocktail were added to each vial, and the vials were wiped with lint-free tissue paper before counting (Thomas, 1971).

Scintillation induced by ß-radiation was measured in a Nuclear Chicago "Isocap 300" counter for 10 minutes or until 2×10^5 counts were reached. Counts per minute were transformed to disintegrations per minute (DPM) using a sample channels ratio (SCR) versus efficiency curve. This curve was generated according to the procedure of measuring counting efficiency of heterogeneous samples as described by Pugh (1970, 1973). In contrast to Pugh's procedure, however, in the present study 50 to 300 ml of sea water containing natural phytoplankton were filtered onto 12

membrane filters and 50 µl of a ^{14}C-sucrose solution (specific activity 0.25 µc ml^{-1}) was pipetted using a microsyringe onto the filter surfaces. These samples were counted as described above.

Loss of cellular ^{14}C activity during filtration has been regarded as a major source of error in the ^{14}C technique by Arthur and Rigler (1967), Schlinder and Holmgren (1971), Schindler, Schmidt, and Reid (1972). This effect has been examined in later studies by Nalewajko and Lean (1972), McMahon (1973), and Stadelmann, Moore, and Pickett (1974). They found that the error probably is not caused by cell breakage as first stated by Arthur and Rigler (1967), but is mainly the result of retention by the filter of unfixed ^{14}C-labeled substances present in the incubation water. They also found that by increasing the volume filtered, the relative importance of the error decreased, suggesting that the losses first described by Arthur and Rigler (1967) were artifacts due to small sample size (5-25 ml). McMahon (1973) stated that filtering a volume of 100 ml or more and washing the filtered sample with 100 ml of nonradioactive water reduced this error to an insignificant level. Gibson, Johansson, and Gorman (unpubl. data) found that the use of smaller volumes of rinse water (filtered sea water), 10 to 15 ml, decreased retention of unfixed ^{14}C-labeled material of the filter to a minimum level.

The $Na_2{}^{14}CO_3$ solution was prepared by diluting high specific activity material with a Na_2CO_3 solution (final pH: 10.6) as recommended in Strickland and Parsons (1968). The solution was stored in autoclaved rubber-stoppered 100 ml glass bottles. The specific activity of the solution used for each determination of primary productivity was measured in triplicate in the liquid scintillation counter by adding 50 µl of solution to a vial containing 10 ml of a PCS-NCS (Amersham/Searle Corp.)

scintillation solubilizer. The samples were agitated and counted for at least 8×10^5 counts. Counting efficiency was determined by using the external standards ratio (ESR) in conjunction with a set of chemically quenched homogeneous standards (Amersham/Searle Corp.).

The total carbonate content of the surface samples was determined in a Beckman Model 915 Total Carbon Analyzer as described in Hopkins et al. (1972).

Primary productivity was calculated as the hourly average production over the incubating period using the following formula:

$$P = \frac{R_s \times W \times 1.05}{R \times N}$$

where P is the primary productivity (mg C m^{-3} hr^{-1}), R_s is the radioactivity of the filter (DPM), R is the absolute activity of the $Na_2{}^{14}CO_3$ solution (DPM), W is the total carbonate content of the water sample (mg C m^{-3}), N is the duration of the incubation period (hr), and 1.05 is an isotope correction factor suggested by Strickland (1960). Primary productivity of the water column at station P in the anchorage was calculated from the following modification of the formula given by Jitts (1965):

$$P = 0.5(P_0 + P_{0.5})\ (D_{0.5} + D_0) + \ldots\ldots + 0.5(P_{1.5} + P_{2.0})\ (D_{2.0} + D_{1.5})$$

where P is the primary productivity (mg C m^{-2} hr^{-1}), and P_i is the primary productivity (mg C m^{-3} hr^{-1}) at depth i (D_i) (m).

Corrections for dark uptake of radioactive carbon based on dark bottle counts were recorded for future reference, but were not applied in this study because of arguments presented by Morris, Yentsch, and Yentsch (1971). They suggested that dark uptake corrections should be disregarded until better understood. Also, exudation of ^{14}C-labeled organic metabolites (see Anderson and Zeutschel, 1970 and Thomas, 1971) was not cor-

rected for and the calculated productivity rates might best be interpreted as estimates of net production of particulate carbon as suggested by Antia et al. (1963), McAllister, Shah, and Strickland (1964), Eppley and Sloan (1965), Ryther and Menzel (1965a), and Strickland et al. (1969). In addition, in this laboratory it has been determined, through the use of Cyclotella nana cultures, that a ^{14}C method similar to the one employed in this study measured close to particulate carbon formation (Gunn, unpubl. data).

Phytoplankton Abundance and Biomass Procedures

Phytoplankton samples collected at stations 50, P, and 13 for taxonomic analyses were preserved immediately after collection in a weak mercuric chloride solution. Less than 24 hr after sampling, the phytoplankton in the raw sample was concentrated into a few ml of water using a Dodson filtration tube (Dodson and Thomas, 1964). The tube was fitted with a 28 µm mesh gauze rather than with the Whatman No. 42 filter paper used by Dodson and Thomas. Gibson et al. (1974b) showed through comparative counts that up to 93% of cell numbers can be lost through the gauze. However, virtually all of the cells passing through the gauze were "naked" flagellates which rupture in usual preservation procedures (5% formaldehyde solution) and thus, in any event, escape detection in most investigations. Also the biomass loss is small constituting only 2% of the total standing crop. Aliquots of the concentrated samples were placed in a shallow 0.12 ml counting chamber and examined under a Zeiss Standard RA microscope at 400x magnification. During the counting procedure, cells containing refractive chloroplasts were identified to major higher taxa. The dominant forms were generally identified at least to genus.

Total cell numbers were calculated according to the following equation:

$$C = N \frac{V_c}{V_r \times V_1}$$

where C is total cell numbers (cells m^{-3}), N is cells counted (cells), V_c is the volume of the concentrated sample (ml), V_r is the volume of the raw sample (m^3), and V_1 is the counted volume (ml).

Cell dimensions for biomass determinations were measured along major axes. The average dimensions of ten cells were used for abundant types, while every cell of the less abundant forms was measured. Biomass of individual cells was then estimated by converting the average linear dimensions into the appropriate geometric volume formulas (i.e., sphere, ellipsoid, and cylinder) and substituting this volume into the Mullin, Sloan, and Eppley (1966) equation below:

$$\log C = 0.76 \log V - 0.29$$

where C is the cell carbon (pg C) and V is the cell volume (μm^3). The value of cell carbon was multiplied by the respective value of cell number per unit volume of water to obtain biomass for each cell type. Total cell biomass for the sample was then determined by cumulating the biomass data on all types.

Chemical Analyses

Dissolved nutrient samples, containing 400 ppm of mercuric chloride for preservation purposes, were filtered immediately after collection through Nucleopore filters at the field laboratory in Tarpon Springs. The samples were analyzed for the following nutrients in a Technicon Autoanalyzer II at the laboratory in St. Petersburg: PO_4-P (Murphy and Riley, 1962; Chan and Riley, 1966), NO_3-N (Wood, Armstrong, and Richards, 1967; Armstrong, Stearns, and Strickland, 1967), NH_3-N (Solorzano, 1969; Head, 1971), and SiO_2-Si (Maynard, unpubl.). The SiO_2-Si method used in

our laboratory resembles the one described by Brewer and Riley (1966) however, in the present analysis, a silico-molybdate complex is reduced in acidic solution by ascorbic acid.

Surface salinity was analysed in a Beckman induction salinometer at the laboratory in St. Petersburg.

Phytoplankton pigment samples were filtered at the field laboratory through Type A glass fibre filters (Fisher Scientific Co.) for chlorophyll *a* and phaeopigment determinations. To prevent degradation of chlorophyll *a* through acidification, approximately 0.5 ml magnesium carbonate suspension was added to the filter surface at the termination of filtration. The filter was next trimmed of excess membrane which showed no phytoplankton deposit. The trimmed filters were then placed in covered centrifuge tubes containing 5 ml of 90% acetone. The tubes were stored for 24 hr of darkness in a refrigerator (4°C) at the laboratory in St. Petersburg and subsequently centrifuged for 15 minutes. The supernatant liquid was decanted into 1 cm pathlength spectrophotometer cells. The extinction of the liquid was measured in a Hitachi Perkin-Elmer 139 UV-VIS spectrophotometer at the wave lengths 750, 665, 645, and 630 nm. Chlorophyll *a* concentrations were calculated using the equation of Parsons and Strickland (Strickland and Parsons, 1968) and phaeopigments according to Lorenzen (1967).

Turbidity Analysis

Turbidity was calculated from Secchi depth using the formula:

$$k = \frac{1.6}{Z_{sd}}$$

where k is the extinction coefficient (m^{-1}) and Z_{sd} is the depth of disappearance of the Secchi disk (m). The constant 1.6, derived from

submarine irradiance measurements at station P in the Anclote Anchorage, was found more suitable in this area than constants suggested by Poole and Atkins (1929), Jones and Wills (1956), and Holmes (1970).

Special Collections

Primary productivity throughout the water column at stations 50 and 13 was measured on single occasions using the *in situ* procedure described above, though an additional set of bottles was added at 2.5 m due to the greater depth of these stations.

Also, station P was sampled on a separate occasion in a more precise study of vertical distribution of primary productivity. In this experiment, water was collected from the 5 depths mentioned above rather than from the surface only as in the routine monthly *in situ* experiments. Subsurface water samples were collected using 2 Niskin sampling bottles. The samples were then incubated *in situ* at the depth of collection. Ancillary information was also obtained on temperature, salinity, and nutrients for each depth, and phytoplankton pigments, abundance, and biomass for the surface and the 2.0 m depth.

Daily variations of photosynthetic capacity were investigated on May 25 at station P. Surface productivity samples collected before sunrise were incubated from sunrise until noon and samples collected just prior to noon were incubated from noon until sunset. Physical, chemical, and phytoplankton pigment data were obtained for both the morning and afternoon experiments.

Statistical Analyses

Programs from the Biomedical Computer Program (Dixon, 1973) were used in the statistical analyses. These programs are stored in the IBM

360 Computer System of the University of South Florida. Correlation coefficient statistics were applied to test relationships between primary productivity, phytoplankton standing crop measurements, and selected physical-chemical variables. Analysis of variance and Duncan's New Multiple Range Test (Steel and Torrie, 1960) were used to group stations into regions of the Anclote Estuary and to combine monthly data into seasonal units.

Climatological and Hydrological Data

Climatological and hydrological data for the period of study were obtained from the following sources:

Solar radiation, air temperature, and wind speed at Tampa International Airport: U.S. Weather Bureau, Tampa, Florida.

Daylength at Tampa: The Nautical Almanac Office, U.S. Naval Observatory, Washington, D.C.

Tides at South Anclote Key and Tarpon Springs: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, D.C.

Rainfall at Tarpon Springs: U.S. Department of Commerce, National Climatic Center, Ashville, North Carolina.

Anclote River discharge at Elfers: U.S. Geological Survey, Tampa, Florida.

RESULTS

Seasonal and Regional Description

Hopkins *et al.* (1972), in their study of nutrients in the Anclote Estuary, found that the year 1971 could be readily divided into two dry periods, January to June and October to November, and one wet season, July to September. While 1973 could not be as easily divided into seasons on this basis, it was possible to partition the year using water temperature. Analysis of variance of water temperature over the sampling period indicated that cool seasons extended over seven months, March to May, 1973 and November, 1973 to February, 1974, and a warm season extended, for five months, June through October, 1973. In the present investigation an analysis of variance using 1973-1974 data on salinity, silicate, chlorophyll *a*, and primary productivity revealed that the three river stations were significantly different ($\alpha = 0.05$) from the remainder of the stations in the anchorage and the Gulf. It was also possible with salinity data alone to separate stations located on the Gulf of Mexico side of the Anclote Keys from those within the Anclote Anchorage. The same regions were recognized by Gibson and Hopkins (1974) and, in the subsequent text, tables, and figures, data from the stations sampled in this study will be grouped as in Table 1.

Table 1. Stations included in average data for the three regions of the Anclote Estuary.

Region	Stations
Gulf of Mexico	50 49 48
Anclote Anchorage	32 21 25 P 26
Anclote River	17 13 11

Physical and Chemical Data

Solar radiation for the period March, 1973 through February, 1974 was least during the cooler months, the lowest values occurring in December; maximum values were recorded for May (Figure 2A). In the latter part of the summer, when higher values would be expected, increased cloud cover associated with thunder storms reduced incident light. Monthly averages of physical and chemical factors for the three regions of the Anclote Estuary are listed in Table 2, and annual averages in Table 3.

Water turbidity was generally low in the winter, indicating a reduced suspended particle load. Values were higher in the summer during phytoplankton blooms and during periods of high wind velocity in both seasons (e.g., December 12 field trip).

Water temperature in the estuary ranged from 11.8 ^{o}C at station 26 in December to 30.5 ^{o}C at station 11 in July, representing an annual range of 18.7 ^{o}C (Figure 2B). Differences among the eleven stations for a specific month, however, were quite small.

Surface salinities ranged between 12.3 ^{o}/oo at station 11 in January and 36.6 ^{o}/oo at station 48 in July (Figure 3). As would be expected the greatest annual variation (19.6 ^{o}/oo) was recorded at station 11 in the river and the least (4.0 ^{o}/oo) in the Gulf at station 49. In general, salinity increased with increasing temperature and was highest in July. The sudden decrease in August, which was especially apparent at the river stations, resulted from heavy rainfall in late July and early August (Figure 4A).

Dissolved nutrients (i.e., PO_4-P, NO_3-N, NH_3-N, and SiO_2-Si) generally occurred in highest concentrations in the Anclote River (Tables

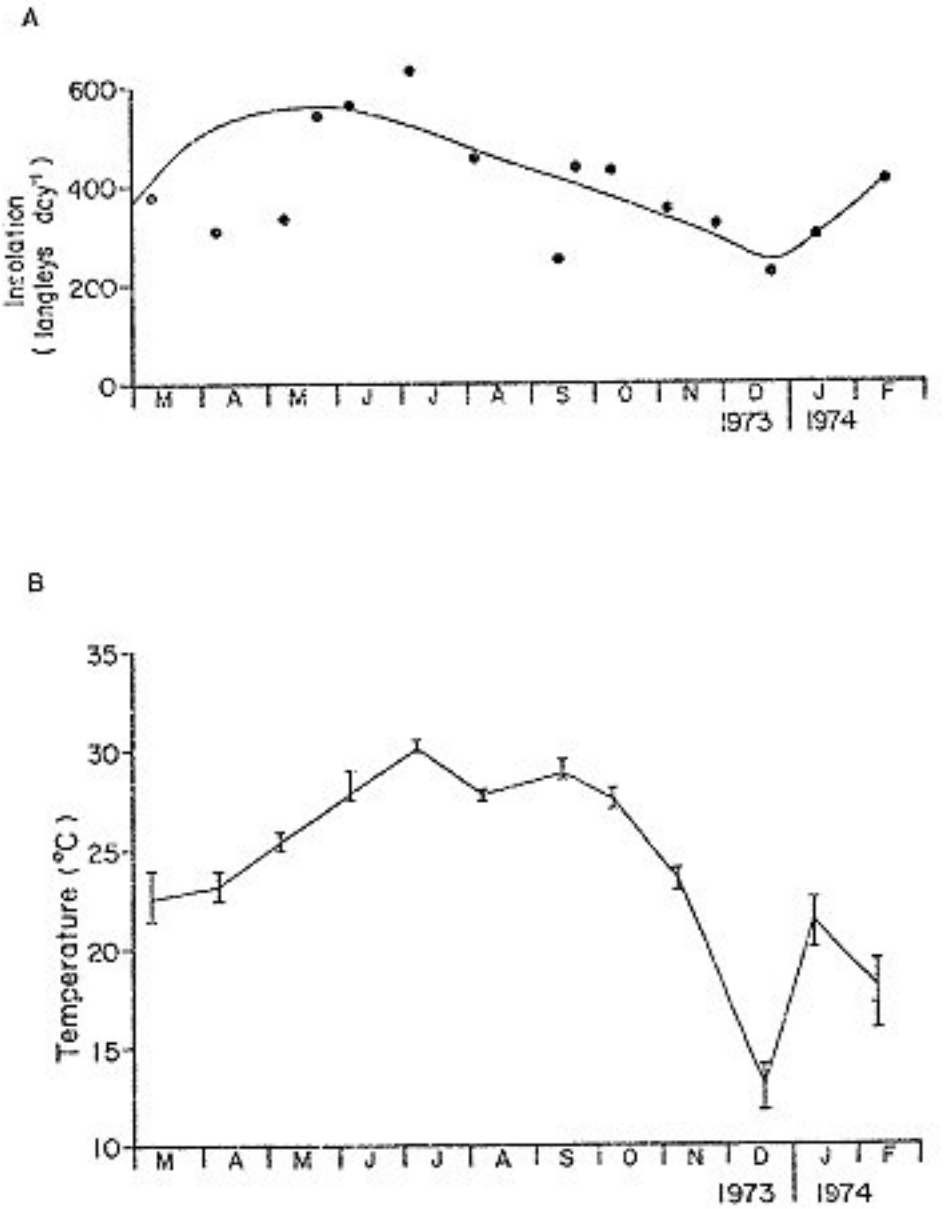


Figure 2. Seasonal variation of insolation and surface water temperature, 1973-1974.

A. Curve of insolation at Tampa International Airport based on weekly averages. Totals for each sampling date are shown as closed circles.

B. Monthly average surface water temperature for the Anclote Estuary. Temperature ranges for sampling dates are shown as vertical bars.

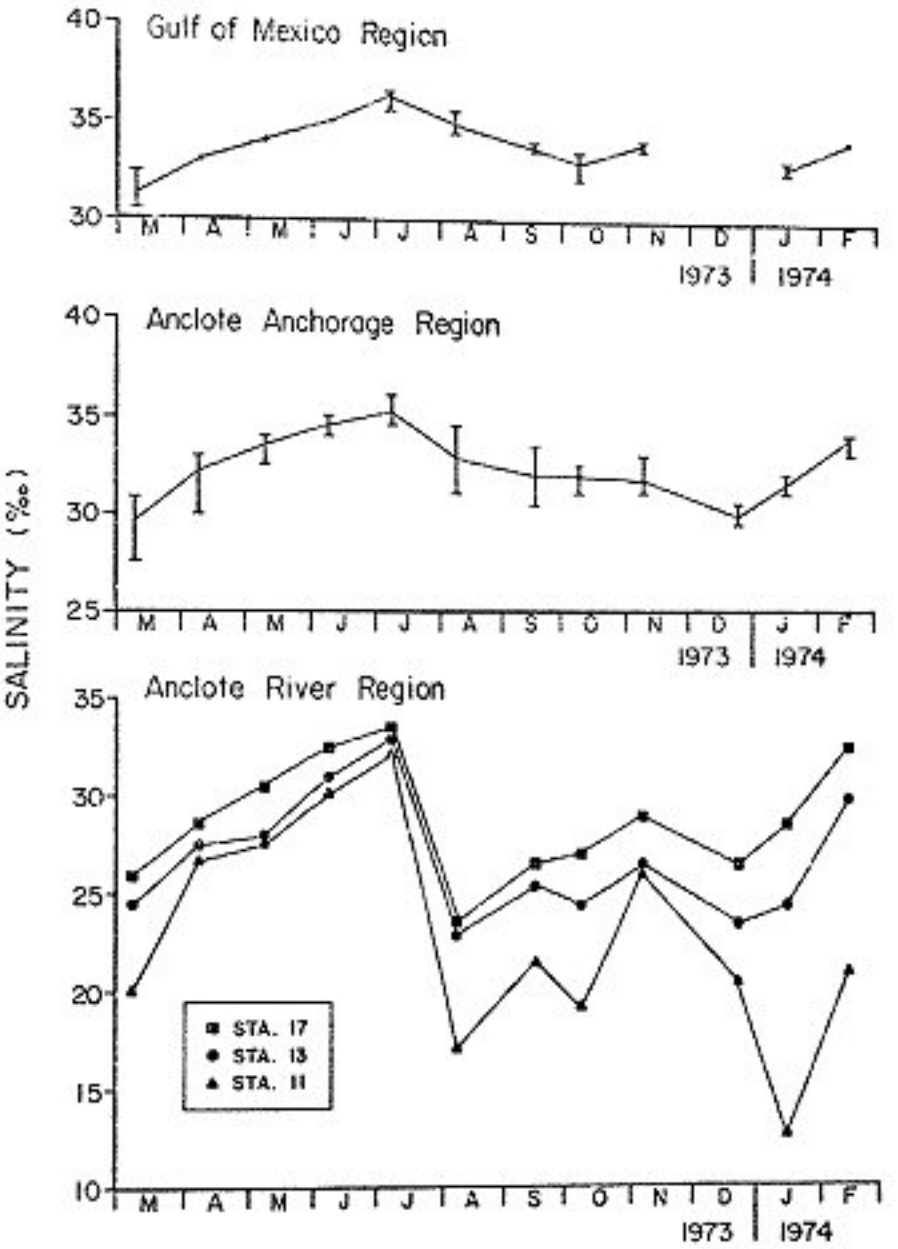


Figure 3. Seasonal variation of surface salinity, 1973-1974. Salinity curves for the Gulf of Mexico and Anclote Anchorage regions are based on monthly averages for each region; ranges are indicated as vertical bars. Curves for individual Anclote River stations are plotted separately.

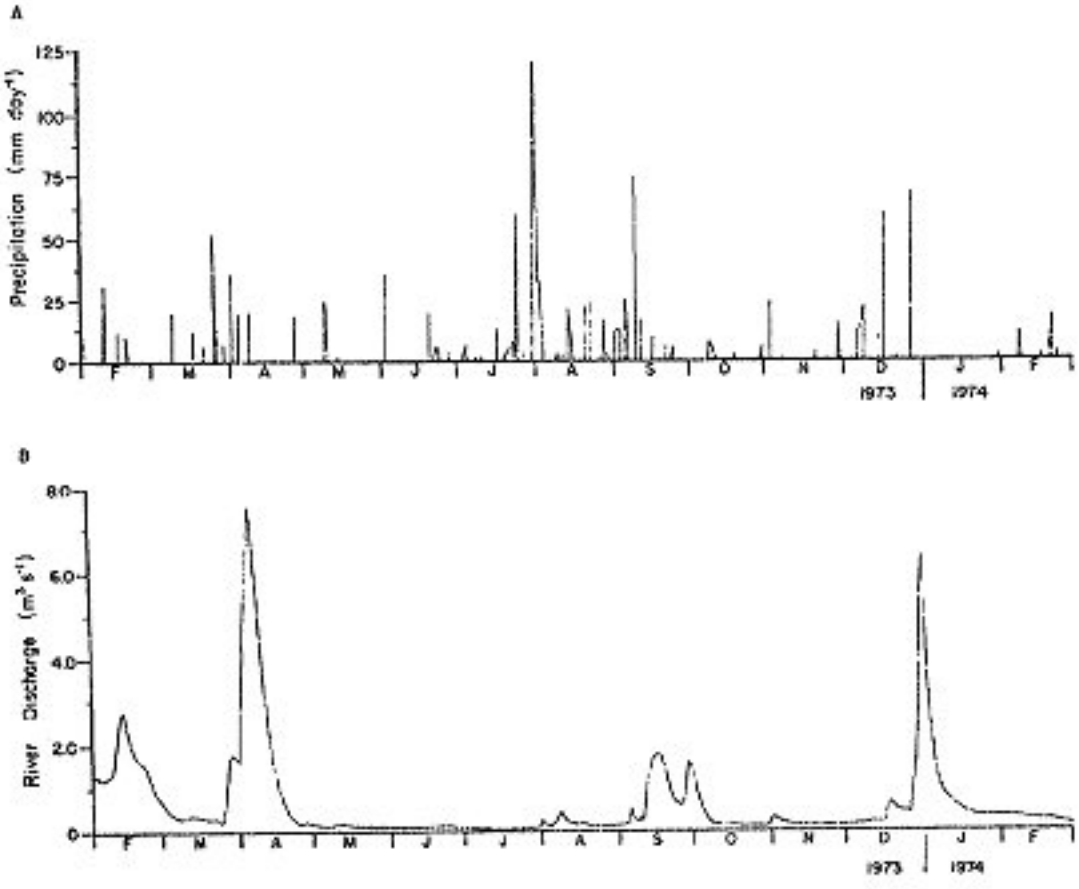


Figure 4. Seasonal variation of daily precipitation at Tarpon Springs and Anclote River discharge at Elfers, 1973-1974.
A. Precipitation.
B. River discharge.

Table 2. Monthly averages of physical and chemical data for the three regions of the Anclcte Estuary, 1973-1974.

Date		March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Salinity	Gulf of Mexico	31.4	33.2	34.1	34.9	36.2	34.9	33.6	33.0	33.8	--	32.8	34.1
(°/oo)	Anclote Anchorage	29.7	32.2	33.6	34.6	35.2	33.0	32.0	32.0	31.7	29.9	31.3	33.8
	Anclote River	23.6	27.5	28.7	31.2	32.7	21.1	24.5	23.3	27.1	23.3	21.7	27.7
Temperature	Gulf of Mexico	21.6	22.7	25.0	28.2	29.9	27.9	28.6	27.6	22.9	--	20.5	19.2
(°C)	Anclote Anchorage	22.2	23.1	25.3	27.5	29.9	27.6	29.1	27.6	23.0	12.8	21.6	17.9
	Anclote River	24.0	23.9	25.8	28.4	30.4	27.8	29.0	28.8	24.0	13.7	22.3	17.8
Turbidity	Gulf of Mexico	0.68	0.78	0.57	0.48	0.69	1.25	1.07	0.54	0.50	--	0.59	1.50
(m^{-1})	Anclote Anchorage	0.52	0.97	0.59	0.96	0.73	1.47	0.91	0.91	0.53	2.67	0.75	1.54
	Anclote River	0.66	1.09	0.74	0.98	0.89	1.21	0.89	1.15	0.69	0.75	1.11	1.32
PO_4 - P	Gulf of Mexico	0.162	0.093	0.010	0.014	0.015	0.058	0.018	0.008	0.020	--	0.029	0.169
(ppm)	Anclote Anchorage	0.159	0.036	0.018	0.016	0.016	0.071	0.015	0.008	0.015	0.025	0.029	0.155
	Anclote River	0.160	0.054	0.075	0.038	0.034	0.150	0.044	0.077	0.030	0.006	0.045	0.107
NO_3 - N	Gulf of Mexico	0.001	0.004	0.002	0.002	0.002	0.001	0.008	0.001	0.010	--	0.004	0.001
(ppm)	Anclote Anchorage	0.001	0.005	0.002	0.002	0.002	0.002	0.006	0.002	0.013	0.011	0.001	0.001
	Anclote River	0.011	0.004	0.008	0.010	0.007	0.053	0.035	0.027	0.032	0.136	0.036	0.014
NH_3 - N	Gulf of Mexico	0.010	0.032	0.005	0.004	0.005	0.013	0.019	0.018	0.005	--	0.011	0.009
(ppm)	Anclote Anchorage	0.005	0.159	0.005	0.020	0.007	0.004	0.028	0.021	0.005	0.001	0.007	0.012
	Anclote River	0.026	0.047	0.009	0.024	0.015	0.228	0.231	0.082	0.015	0.093	0.063	0.022
SiO_2 - Si	Gulf of Mexico	0.090	0.036	0.034	0.047	0.047	0.061	0.049	0.038	0.046	--	0.042	0.041
(ppm)	Anclote Anchorage	0.112	0.042	0.049	0.043	0.234	0.367	0.110	0.053	0.053	0.066	0.101	0.058
	Anclote River	0.842	0.201	0.287	0.330	0.296	0.995	0.489	0.969	0.216	0.600	1.001	0.392

Table 3. Physical and chemical data for the Anclote Estuary by station (1973-1974 average values).

Station	50	49	48	32	21	25	P	26	17	13	11
Salinity (°/oo)	33.6	34.0	33.9	32.7	32.9	32.7	32.4	31.7	28.6	26.9	22.7
Temperature (°C)	25.2	25.0	24.9	24.0	24.1	25.0	24.9	23.8	24.3	24.6	24.8
Turbidity (m^{-1})	0.73	0.63	0.70	1.11	0.97	0.77	0.90	1.06	0.77	0.77	0.87
PO_4 - P (ppm)	0.048	0.057	0.055	0.053	0.051	0.054	0.045	0.047	0.154	0.079	0.091
NO_3 - N (ppm)	0.002	0.003	0.005	0.004	0.003	0.003	0.004	0.004	0.015	0.033	0.045
NH_3 - N (ppm)	0.027	0.008	0.012	0.036	0.009	0.035	0.031	0.009	0.056	0.052	0.105
SiO_2 - Si (ppm)	0.052	0.045	0.049	0.090	0.096	0.100	0.127	0.096	0.306	0.475	0.877

2 and 3). Levels in the anchorage tended to be lower and were often similar to those in the Gulf of Mexico, however, silicate was found at intermediate levels in the anchorage. All three regions had high phosphate concentrations in February and March and high nitrate levels in November and December. During the remaining months, phosphate and nitrate values were relatively low in all three regions. Ammonia levels were high in surface waters throughout the area in late summer, and high in river water in December and January. Unusually high concentrations of ammonia were found at stations 50, 32, 25, and P in April, and at station 17 in September. Contamination by atmospheric ammonia may account, in part, for these anomalous values (Hopkins et al., 1972).

Silicate levels were relatively constant at stations in the Gulf. Concentrations in the anchorage and at river stations 17 and 13 were generally similar to those of the Gulf, but differed from the latter during July and August when high values were recorded. Concentrations at station 11, on the other hand, were considerably higher than those found at other stations. Peak values were observed in January, March, August, and October. In view of the inverse relationship between salinity and silicate levels demonstrated by Hopkins et al. (1972), it comes as no surprise that station 11, which is farthest upriver, has the highest average silicate concentration of all stations.

Primary Productivity

Seasonal and Regional Variations

Phytoplankton productivity in surface waters of the Gulf of Mexico adjacent to the Anclote Keys was highest in August and September (Figure 5; Table 4). During the remainder of the year, productivity was rather low with minimum rates occurring in February and March. The Anclote

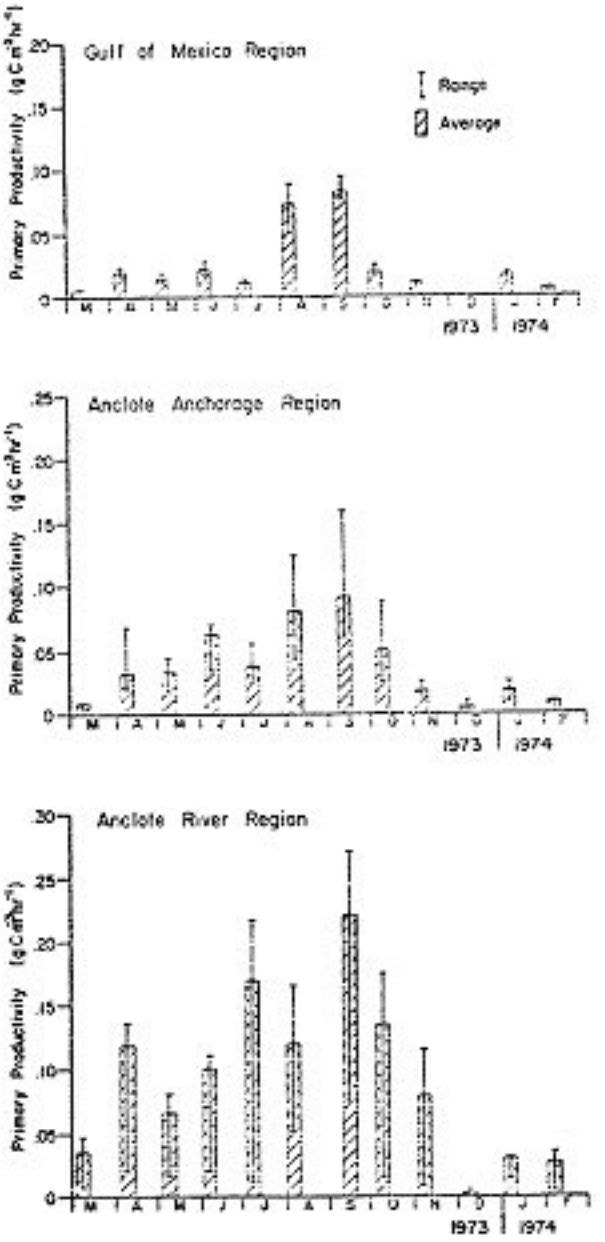


Figure 5. Seasonal variation of surface primary productivity in the Anclote Estuary, 1973-1974

Table 4. Monthly averages of primary productivity, chlorophyll *a*, and phaeopigments for the three regions of the Anclote Estuary, 1973-1974.

Date		March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Primary productivity ($mg\ C\ m^{-3}\ hr^{-1}$)	Gulf of Mexico	6.66	22.70	16.63	22.00	11.67	72.20	82.10	18.73	11.35	--	14.89	5.60
	Anclote Anchorage	8.70	30.78	31.24	61.08	39.36	83.94	92.10	49.46	18.52	5.91	19.82	8.77
	Anclote River	33.53	117.83	65.23	101.53	169.33	119.63	220.67	135.07	77.30	2.35	29.15	26.01
Chlorophyll *a* ($mg\ m^{-3}$)	Gulf of Mexico	1.98	2.79	2.35	2.29	3.86	17.31	15.33	3.74	1.68	--	2.32	3.18
	Anclote Anchorage	1.70	4.28	4.38	6.95	5.79	10.91	10.31	8.90	3.03	9.41	3.44	4.35
	Anclote River	5.29	11.57	6.44	8.83	11.63	10.15	21.33	15.38	6.13	3.75	5.22	10.09
Phaeopigments ($mg\ m^{-3}$)	Gulf of Mexico	0.55	2.97	0.92	0.34	1.45	7.53	13.21	3.04	0.88	--	1.04	2.55
	Anclote Anchorage	1.53	4.61	1.13	1.35	2.21	5.29	6.13	6.83	1.25	3.08	1.52	2.96
	Anclote River	2.48	4.91	2.81	2.79	5.61	3.98	8.67	7.29	3.72	0.17	2.44	5.30

Table 5. Primary productivity, chlorophyll a, and phaeopigments in the Anclote Estuary by station (1973-1974 average values).

Station	50	49	48	32	21	25	P	26	17	13	11
Primary productivity (mg C m^{-3} hr^{-1})	28.10	22.13	27.84	27.07	31.63	44.72	33.57	50.00	98.85	93.31	78.62
Chlorophyll a (mg m^{-3})	5.96	4.22	5.38	4.55	5.87	7.00	6.08	6.90	11.50	9.46	7.86
Phaeopigments (mg m^{-3})	3.25	2.91	3.58	2.29	3.35	4.08	3.00	3.27	4.60	4.03	3.76

Anchorage was generally most productive during the warm months of June through October, and the highest rates occurred most frequently in the latter part of this period. Lowest rates in the anchorage were found in February, March, and December. In the Anclote River, relatively high productivity persisted from April through November, the annual maxima occurring in July and September. The lowest rates for the river were recorded in December. In general, seasonal fluctuations in surface productivity were most noticeable at the river stations and least obvious in the Gulf.

Vertical Distribution

Results of the *in situ* experiments at stations P, 50, and 13 are presented in Figures 6 and 7. *In situ* surface productivity at station P average 1.5 times greater than productivity just above the bottom at 2.0 m suggesting that turbidity of the water column on most occasions reduced productivity in the deepest samples. On every sampling date, however, measurable photosynthesis occurred at all depths indicating that, during the time of incubation, the compensation depth (i.e., the depth where gross photosynthesis and respiration balance) was always greater than 2.0 m. Single *in situ* experiments at station 50 and 13 also indicated a net productivity at all depths during the period of incubation.

As determined in previous studies (Johansson and Hopkins, 1973), a rather constant relationship was found at station P between surface productivity and total productivity for the water column. In both studies surface productivity multiplied by a factor of 1.9 approximated values for the total production under a square meter of water, as determined by integration of rates obtained from *in situ* experiments. Single *in situ*

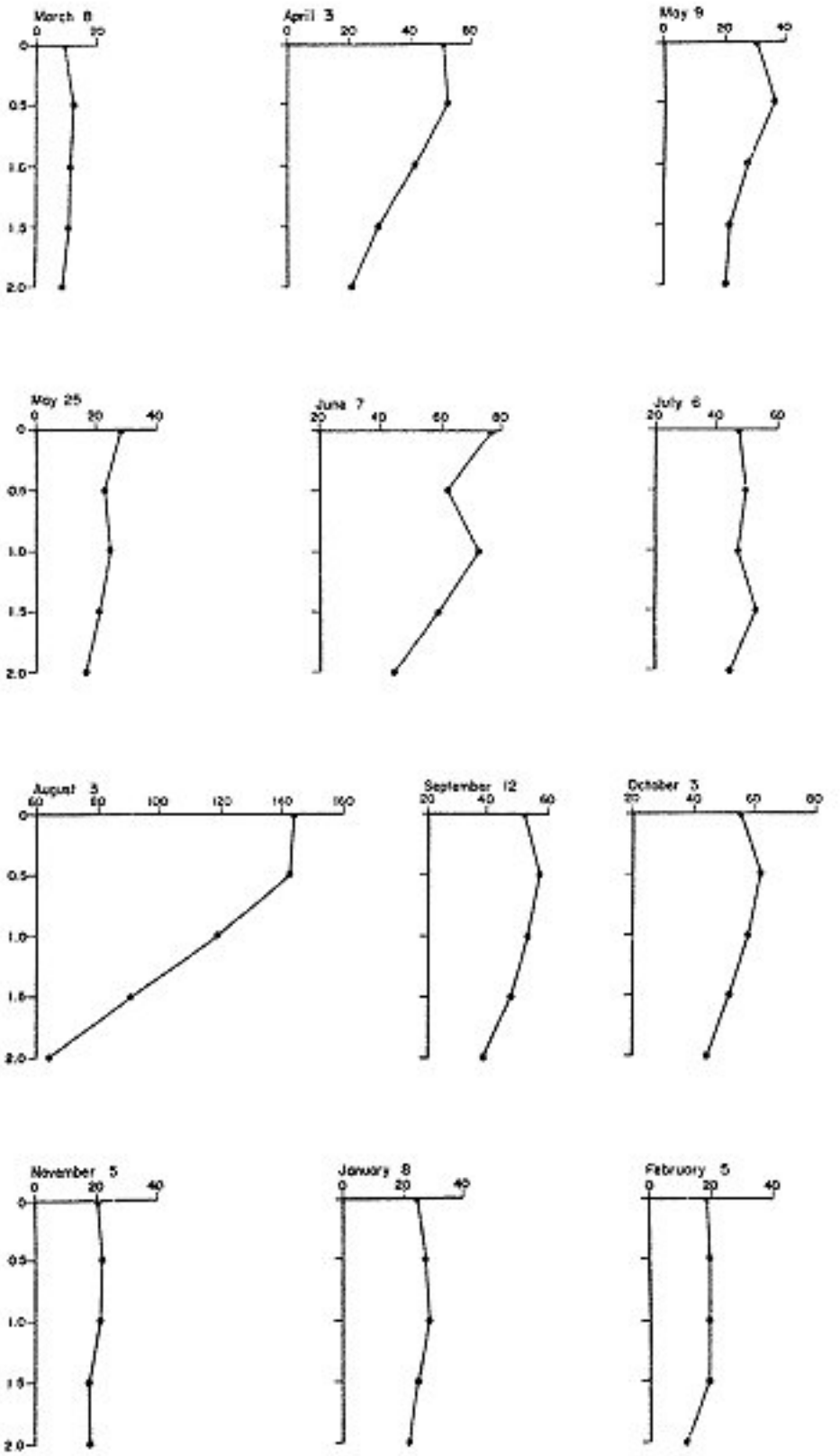
measurements at stations 50 and 13 in the Gulf and river yielded factors of 2.8 and 1.4, respectively. Integrated productivity at station P over the sampling period is presented in Figure 8.

As stated in the methods section, productivity samples collected monthly at the surface at station P were suspended at various depths of the water column for estimations of vertical distribution of photosynthesis and total production under a square meter. This procedure is reliable only if the phytoplankton population is homogeneously distributed with depth and not photosynthetically adapted to light conditions found at a specific depth.

Measurements of temperature and salinity by Carder and Klausewitz (1972, 1973) indicate that the Anclote Anchorage generally is well mixed. Therefore vertical stratification of the phytoplankton would not be expected on most sampling occasions. Steemann Nielsen and Park (1964) suspended surface phytoplankton adapted to high light intensities at the depth of 5% incident light and the plankton required three days to photosynthetically adapt to the lower light intensities. In view of the shallowness of the study area and the strong tidal forces acting in the estuary (Humm et al., 1971), it can be assumed that the rate of total vertical mixing is less than three days. Differentiation into physiologically distinct surface and subsurface plankton populations, then, would not be expected (Steemann Nielsen and Hansen, 1959). Further, on May 25 an experiment was conducted at station P in which water collected from the 5 standard depths (rather than the usual procedure of using only surface water) was incubated in situ. In this experiment surface productivity multiplied by a factor of 1.6 equaled the total production of the water column, a value close to the average of all in situ experiments at station

Figure 6. Vertical distribution of primary productivity at station P in the Anclote Anchorage, 1973-1974.

Primary Productivity
(mg C m^{-3} hr^{-1})



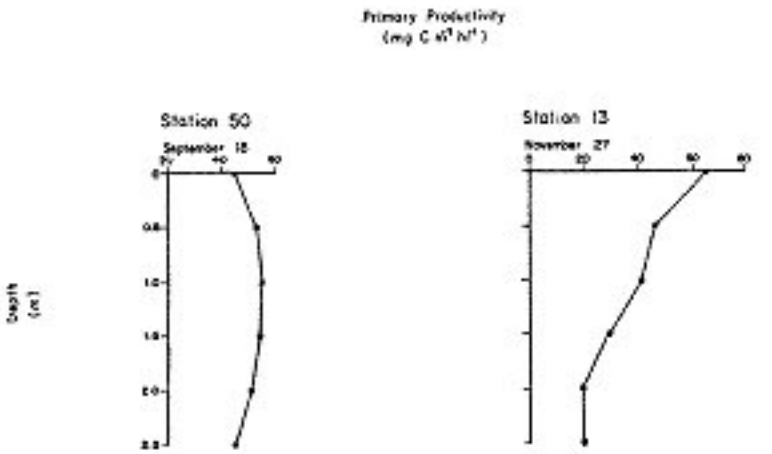


Figure 7. Vertical distribution of primary productivity at station 50 in the Gulf of Mexico and station 13 in the Anclote River, 1973.

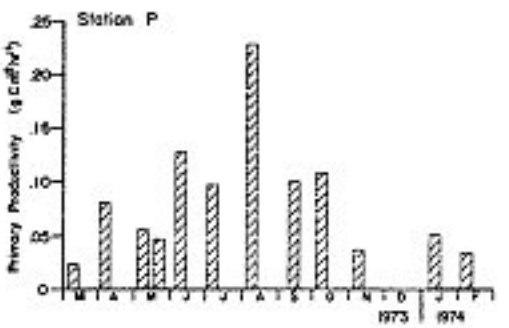


Figure 8. Seasonal variation of integrated primary productivity at station P in the Anclote Anchorage, 1973-1974.

P (see above). In addition, temperature, salinity, nutrients, and phytoplankton standing crop data showed no apparent trends with depth on this sampling date. This particular experiment, then, substantiates the validity in this shallow area of incubating surface samples at different depths of the water column.

In situ surface productivity rates for station P were an average 1.3 times greater than incubator rates (Figure 9). The greatest difference between the two techniques resulted when the in situ sample was collected a few meters away from the incubator sample, possibly suggesting that patchiness of the phytoplankton population was a major cause of the variation. Cassie (1962) found in a study of natural and cultured phytoplankton that any two water samples collected more than 10 cm apart were likely to show a statistically significant difference in primary productivity. Obtaining samples from one relatively large and well-agitated source generally gave close agreement between the two techniques (see regression line C in Figure 9). Also excluded from this regression calculation were data from an improperly incubated sample.

Annual surface productivity of the three Anclote regions, derived by integrating the area under the seasonal curve, was as follows:

Gulf of Mexico: 120 g C m^{-3} yr^{-1}

Anclote Anchorage: 170 g C m^{-3} yr^{-1}

Anclote River: 420 g C m^{-3} yr^{-1}

Estimates of annual productivity for the water column at stations 50, P, and 13 were:

Station 50: 340 g C m^{-2} yr^{-1}

Station P: 370 g C m^{-2} yr^{-1}

Station 13: 610 g C m^{-2} yr^{-1}

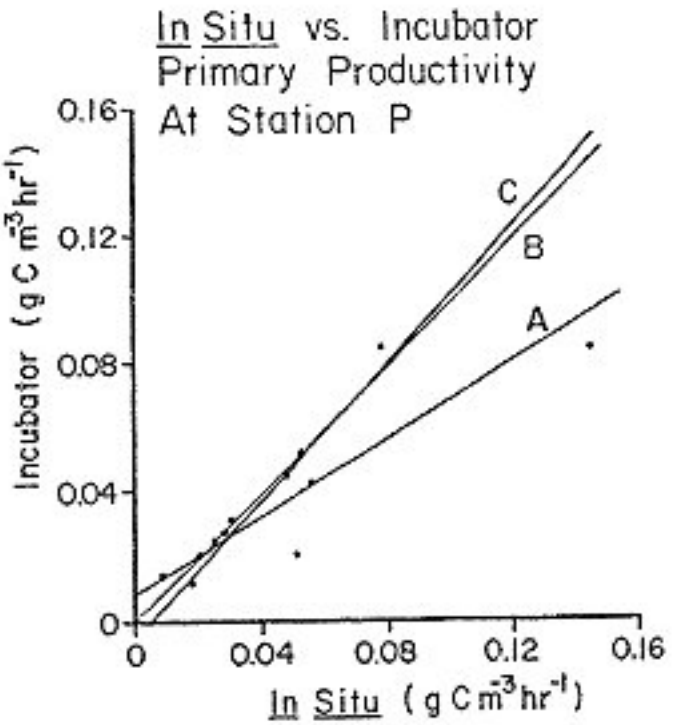


Figure 9. In situ versus incubator surface primary productivity at station P in the Anclote Anchorage.
Regression line A represents the measured relationship.
Regression line B represents the expected theoretical relationship.
Regression line C represents the relationship with three points excluded (see text).

The 1973-1974 value for annual productivity under a square meter at station P in the Anclote Anchorage was approximately twice that reported for the same station in 1971-1972 (Johansson and Hopkins, 1973).

Phytoplankton Pigments

High chlorophyll a (chlorophyll a + phaeopigments) concentrations in surface waters of all three regions occurred during the summer, the annual maxima most often recorded in the latter part of this season (Figure 10; Table 4). Relatively high values were also found in April for most stations and in December for the anchorage region. Phaeopigments followed the seasonal patterns of chlorophyll a rather closely, although annual variations in phaeopigments were greater than those of chlorophyll a.

Average annual chlorophyll a and phaeopigment concentrations for the three Anclote regions were:

Chlorophyll a:	Gulf of Mexico:	5.2 mg m^{-3}
	Anclote Anchorage:	6.1 mg m^{-3}
	Anclote River:	9.6 mg m^{-3}
Phaeopigments:	Gulf of Mexico:	3.3 mg m^{-3}
	Anclote Anchorage:	3.2 mg m^{-3}
	Anclote River:	4.1 mg m^{-3}

Average concentrations by station are listed in Table 5. The 1971 average of chlorophyll a concentrations for all stations in the Anclote Estuary (Gibson and Hopkins, 1974) was 1.3 times that of the present study, while the 1971-1972 average for station P (Johansson and Hopkins, 1973) was only 0.6 the 1973-1974 value.

Phytoplankton Abundance and Biomass

Seasonal patterns of phytoplankton abundance, biomass, and taxonomic

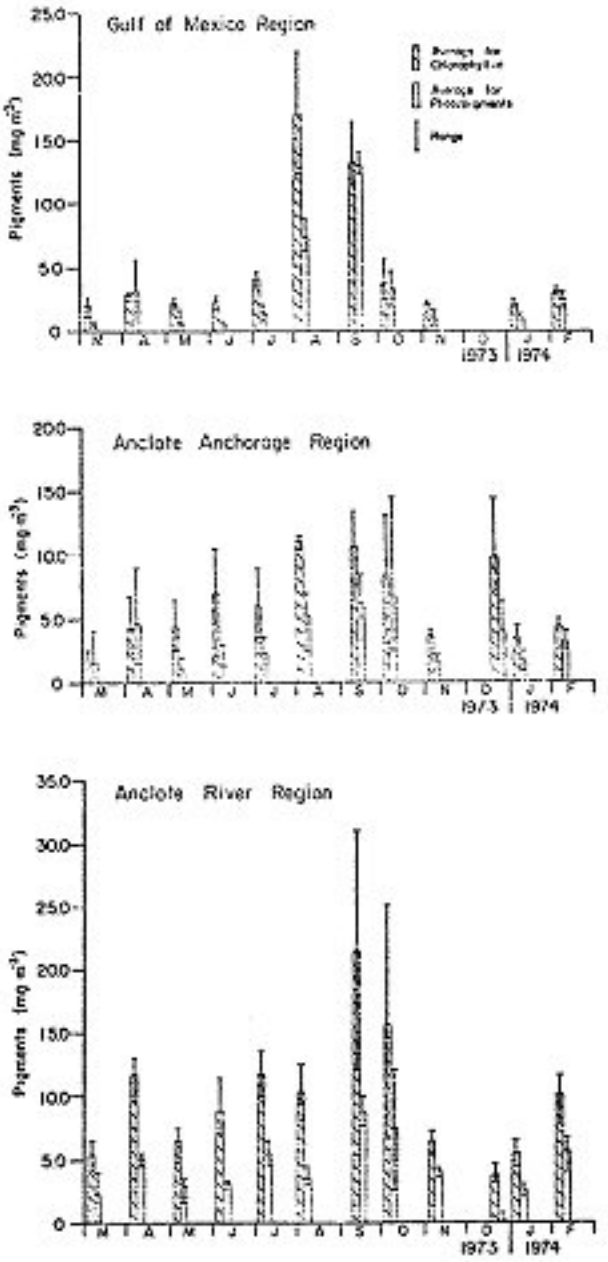


Figure 10. Seasonal variation of chlorophyll a (chlorophyll a + phaeopigments) and phaeopigment concentrations in the Anclote Estuary, 1973-1974.

composition were similar for the three reference stations (50, P, and 13) (Figure 11; Tables 6 and 7). Phytoplankton cells were most abundant between June and November, with maximum numbers occurring in September at all three stations. Relatively low cell counts were recorded for December through May. Planktonic diatoms were most important in terms of abundance, averaging 84.5% of total cell numbers. The principal diatom genera of the summer season were Skeletonema, Chaetoceros, and Nitzschia; during the winter Rhizosolenia, Leptocylindrus, and Chaetoceros were most abundant. Benthic diatoms, dinoflagellates, and other phytoplankton were of minor importance, with the exception of the filamentous bluegreen algae Trichodesmium sp. which was abundant at stations 50 and P during the summer.

The seasonal pattern of phytoplankton biomass followed closely that of cell numbers, though peaks were not always concurrent. Planktonic diatoms constituted the largest fraction of total phytoplankton biomass, averaging 80.9% and, generally, the principal forms were the same as those contributing most heavily to cell numbers. Benthic diatoms were more important in terms of biomass than of numbers. Their share of total biomass averaged 11.8%, while representing only 1.3% of total number of cells. Occasionally dinoflagellates were abundant; a bloom of the dinoflagellate Ceratium hircus, for instance, constituted the major portion of phytoplankton biomass at stations 50 and P in January. In terms of total biomass over the sampling period, however, neither dinoflagellates nor other phytoplankton, exclusive of diatoms, were of major importance in the phytoplankton detectable with our procedures.

Annual averages of phytoplankton abundance and biomass for the three stations were:

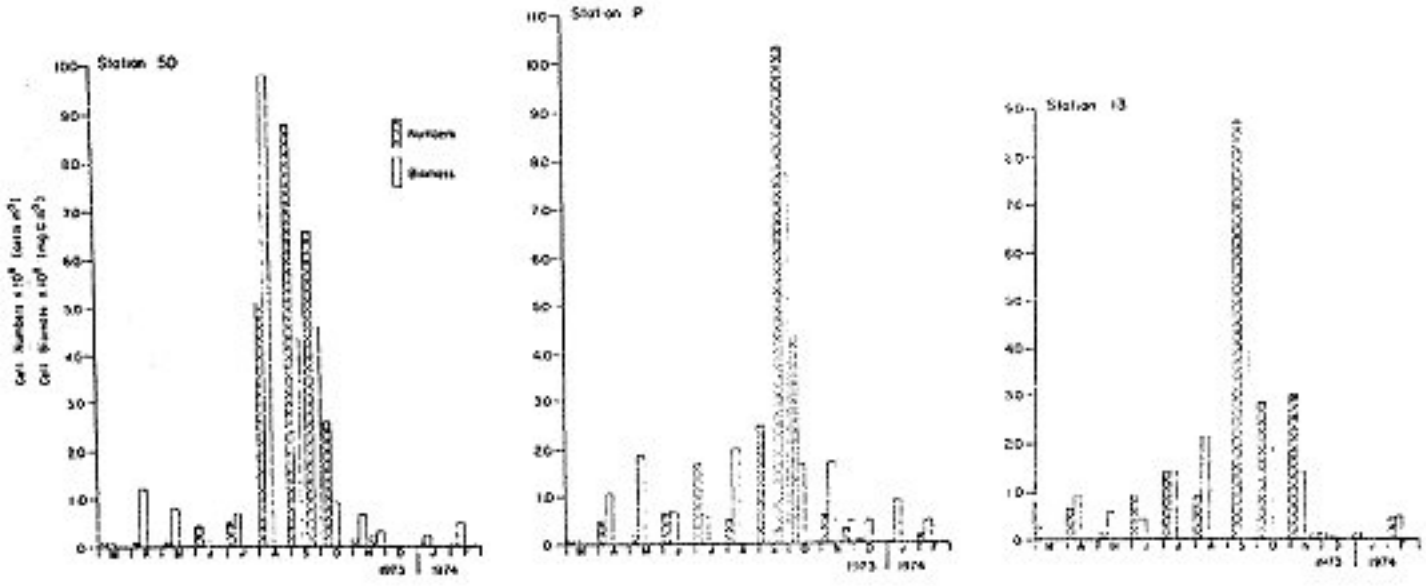


Figure 11. Seasonal variation of phytoplankton abundance and biomass at stations 50, P, and 13 in the Anclote Estuary, 1973-1974.

Table 6. Seasonal distribution of phytoplankton abundance (cells x 10^6 m^{-3}) in surface waters of the Anclote Estuary, 1973-1974.

Date		March 8	April 3	May 9	May 25	June 7	July 6	August 3	September 12	September 18	October 3	November 5	November 27	December 12	January 3	February 5	Average, 1973-1974
Planktonic diatoms	Station 10	52.0	87.1	43.2	--	126.5	514.6	3197.5	7579.5	6132.5	2434.4	345.1	6.8	--	3.9	27.3	1436.0
	Station 9	30.6	459.8	104.0	360.1	330.2	949.4	276.4	1454.4	8564.3	3274.0	495.3	392.2	0	0.4	395.5	1203.4
	Station 13	61.1	425.3	48.6	—	856.1	1345.8	891.2	8515.2	--	2658.7	2959.7	48.2	16.9	4.5	377.6	1414.5
Benthic diatoms	Station 10	3.1	3.5	5.4	—	3.2	3.8	21.9	335.5	3.2	5.1	6.5	15.2	—	3.0	18.8	34.4
	Station 9	2.0	35.7	4.4	3.8	0	25.7	43.2	97.0	23.9	43.6	8.6	4.8	86.3	0.4	23.8	23.3
	Station 13	0	16.1	6.3	—	0	3.6	5.8	15.2	—	4.0	26.3	8.9	0.7	1.7	8.7	6.8
Dinoflagellates	Station 10	0	33.5	4.8	—	3.4	0	1	15.9	36.3	8.1	4.7	10.2	--	10.2	1.5	6.2
	Station 9	2.0	31.4	2.9	1.3	4.3	3.7	0	7	6.8	14.7	0	4.8	0	26.7	5.4	6.1
	Station 13	0	8.1	0	--	6.5	0	1.7	13.3	—	53.9	0	2.6	0	0	2.9	7.7
Other phytoplankton	Station 10	91.7	29.4	4.0	--	288.3	7.2	1875.0	843.3	501.3	1391.3	22.7	374.2	--	25.8	4.0	284.6
	Station 9	25.5	16.7	0	8.4	8.7	478.0	217.4	333.1	1205.4	729.2	53.7	33.7	75.4	11.6	3.3	293.4
	Station 13	213.3	17.5	70.6	--	32.0	30.1	11.7	116.4	--	95.6	33.4	83.5	6.8	153.4	30.4	62.6
Total	Station 10	145.4	150.7	56.4	—	319.6	521.6	5102.4	8769.6	6625.1	3945.6	384.2	395.3	--	42.0	43.6	2530.1
	Station 9	61.1	519.6	561.3	371.6	743.2	1356.9	581.2	2444.3	20021.1	4235.8	560.5	398.4	117.4	37.1	327.9	1482.9
	Station 13	275.9	567.0	135.4	--	891.7	1378.5	913.5	8676.1	--	3451.4	3704.6	131.3	23.5	59.6	419.6	1490.3

Table 7. Seasonal distribution of phytoplankton biomass (mg C m^{-3}) in surface waters of the Anclote Estuary, 1973-1974.

Date		March 8	April 5	May 9	May 25	June 7	July 6	August 3	September 13	September 18	October 3	November 5	November 27	December 17	January 8	February 5	Average, 1973-1974
Planktonic diatoms	Station 50	7.2	35.5	65.1	--	7.0	66.3	946.8	327.7	423.5	64.9	63.1	0.4	—	0.2	3.1	151.1
	Station F	8.7	40.5	183.2	36.3	56.6	21.0	95.6	73.5	681.3	142.2	171.9	43.9	0	0.2	18.1	104.7
	Station 13	0.4	64.0	7.3	--	35.6	141.5	201.6	335.5	--	168.2	135.4	3.4	1.0	0.2	38.8	89.3
Benthic diatoms	Station 50	1.4	40.9	11.9	--	1.4	3.4	37.8	54.3	0.3	4.5	1.5	23.9	—	1.9	39.7	19.4
	Station F	5.1	48.8	4.2	3.6	0	31.0	101.4	30.9	5.9	13.8	2.3	0.4	51.5	0	24.9	21.5
	Station 13	0	23.6	55.8	--	0	4.6	0.4	7.6	—	0.3	2.4	4.3	0	1.6	17.7	8.4
Dinoflagellates	Station 50	0	3.5	30.3	—	0.3	0	0	3.1	39.3	8.4	7.4	0.3	--	21.0	4.1	6.2
	Station F	0.3	21.5	3.0	8.1	17.6	3.0	0	0	2.0	4.8	0	6.0	0	80.3	32.0	10.4
	Station 13	0	5.0	0	--	1.4	0	3.9	5.2	—	28.7	0	0.5	0	0	3.8	3.2
Other phytoplankton	Station 50	1.0	0.2	0	--	1.3	3.9	7.3	7.7	31.4	9.6	0.8	1.5	--	0.1	0.1	4.3
	Station F	0.9	0.5	0	0.3	0.1	3.5	1.2	6.3	79.3	5.9	0.6	0.8	1.0	0.1	0	6.3
	Station 13	2.1	0.1	1.4	—	1.3	0.1	0.5	4.6	--	4.8	0.7	1.8	0.1	0.1	0.7	1.4
Total	Station 50	9.4	120.1	77.3	—	9.9	32.8	981.7	415.0	455.9	87.4	72.8	26.1	--	23.2	46.9	155.9
	Station F	15.0	111.3	191.4	46.1	74.3	58.3	190.2	117.7	767.4	168.7	174.8	51.0	53.5	90.5	56.0	144.0
	Station 13	7.1	92.1	64.5	--	38.3	144.4	212.6	357.1	—	109.8	131.1	9.0	1.1	2.1	45.2	102.2

Abundance: Station 50: 1910×10^6 cells m^{-3}

Station P: 1490×10^6 cells m^{-3}

Station 13: 1490×10^6 cells m^{-3}

Biomass: Station 50: 186 mg C m^{-3}

Station P: 145 mg C m^{-3}

Station 13: 102 mg C m^{-3}

Gibson and Hopkins (1974), in their earlier study, found approximately the same seasonal pattern and principal composition of the phytoplankton population for the three regions. The diatom genus Chaetoceros, though, was not as important in their samples as in the present study. Average biomass for the three regions was approximately the same, while average cell numbers, by contrast, were 5.3 times higher in the present investigation. This descrepancy may have resulted from the use of different sample preservation techniques. Small, fragile chain-forming diatoms, included in the present counts, may better withstand preservation in the weak mercuric chloride solution used in the present study than in the 10% buffered formaldehyde used by Gibson and Hopkins. Because of the small size of these diatoms, however, changes in their abundance probably contributed little of the year to year variation in phytoplankton biomass.

DISCUSSION

Phytoplankton Productivity and Environmental Factors

In order to gain insight to possible factors influencing phytoplankton dynamics in Anclote waters, statistical comparisons were made of phytoplankton characteristics and selected physical and chemical variables.

Correlation statistics (Table 8) indicate a positive, highly significant relationship ($\alpha = 0.01$) between primary productivity and surface water temperature for the three regions of the Anclote Estuary during the cool season. Other relationships were less apparent with the exception of productivity versus insolation in the Gulf and anchorage regions. The negative coefficients of the latter relationship are difficult to interpret. Light inhibition of photosynthesis in surface samples might be a possible factor, though the coefficient was still negative for data from *in situ* samples at station P obtained from the depth of maximum photosynthesis below the surface. A possible explanation might lie in the geographical separation between the points of data acquisition; insolation was measured at Tampa International Airport, which is approximately 100 km from the area of productivity measurements and more influenced by "inland" meteorological conditions. Putnam (1966) offers a similar explanation for poor correlation between productivity at the Waccasassa Estuary and insolation measured 80 km inland.

A number of the correlations between nutrient content and primary productivity were statistically significant ($\alpha = 0.05$; $\alpha = 0.01$) but may

Table 8. Correlation coefficients for relationships among log-transformed primary productivity data and physical and chemical variables in the three regions of the Anclote Estuary.

Season	Area	Degrees of Freedom (n-2)	Insolation	Water Temp.	Salinity	PO_4-P	NO_3-N	SiO_2-Si
WARM (June - Oct.)	Gulf of Mexico	13	-0.76**	-0.39	-0.35	0.57*	0.27	0.45
	Anclote Anchorage	23	-0.47*	-0.20	-0.42*	0.31	0.42*	0.12
	Anclote River	13	-0.33	0.38	0.29	-0.47	-0.23	-0.54*
COOL (Nov. - May)	Gulf of Mexico	16	-0.87**	0.61**	0.16	-0.67**	0.30	-0.50*
	Anclote Anchorage	32	-0.04	0.70**	0.36	-0.46**	-0.03	-0.15
	Anclote River	19	0.54*	0.88**	0.28	-0.15	-0.81**	-0.25

* Significant at $\alpha = 0.05$
** Significant at $\alpha = 0.01$

not reflect utilization-production relationships due to the large sampling interval (∿30 days). Loftus, Subba Rao, and Seliger (1972), for instance, found that a complete phytoplankton bloom cycle may be completed in a period of 21 days. In addition, these statistical analyses were weakened by unassayed variables known to affect primary productivity such as concentrations of iron and trace metals (Ryther and Guillard, 1959), humic acid (Prakash et al., 1973), vitamin B_{12} (Curl, 1962), nutrients in particulate form (Goering, Nelson, and Carter, 1973), and zooplankton grazing (Riley and Bumpus, 1946).

Relationships Among Phytoplankton Measurements

Correlation coefficient matrices of linear relationships among primary productivity, chlorophyll a, cell numbers, and biomass at stations 50, P, and 13 are listed in Table 9. A number of significant relationships ($\alpha = 0.05$; $\alpha = 0.01$) occurred during the summer months at stations 50 and 13, in the Gulf and river, respectively. In winter significant coefficients were only recorded for station 13.

The meaning of these regional and seasonal variations is not fully understood and more investigation is needed. For instance, it is not clear why significant relationships in the summer were found among most of the variables listed for station 13 in the river and station 50 in the Gulf, but not for intermediate station P in the anchorage. Putnam (1966) also reports that chlorophyll a was only related to surface productivity in the upper reaches of the Waccasassa River and in the Gulf of Mexico. Further, on the basis of the available data, it is difficult to interpret the meaning of the generally weaker correlations between these variables in winter than in summer.

Table 9. Correlation coefficient matrices for relationships among primary productivity, chlorophyll *a*, and phytoplankton standing crop at stations 50, P, and 13.

Season	Station	Degrees of Freedom (n-2)	Variables			
Warm (June - Oct.)	50	3		Chl. *a*	Cell no.	Biomass
			Prod.	0.99**	0.90*	0.87
			Chl. *a*		0.90*	0.90*
			Cell no.			0.62
	P	3		Chl. *a*	Cell no.	Biomass
			Prod.	0.74	-0.83	0.17
			Chl. *a*		-0.35	0.76
			Cell no.			0.19
	13	3		Chl. *a*	Cell no.	Biomass
			Prod.	0.94*	0.96**	0.90*
			Chl. *a*		0.96**	0.88*
			Cell no.			0.88*
Cool (Nov. - May)	50	4		Chl. *a*	Cell no.	Biomass
			Prod.	0.63	0.72	0.12
			Chl. *a*		0.57	-0.46
			Cell no.			0.11
	P	6		Chl. *a*	Cell no.	Biomass
			Prod.	-0.46	0.13	0.65
			Chl. *a*		-0.03	-0.30
			Cell no.			0.46
	13	6		Chl. *a*	Cell no.	Biomass
			Prod.	0.47	0.72*	0.91**
			Chl. *a*		0.13	0.49
			Cell no.			0.83*

* Significant at $\alpha = 0.05$
** Significant at $\alpha = 0.01$

The productivity-chlorophyll a relationship gave significant correlations ($\alpha = 0.01$) in the Gulf and anchorage regions in summer and in both seasons in the river (Table 10). The high correlations in all three areas during the summer months agree with recent findings from the Crystal River Estuary (Gorman, unpubl. data). The weaker winter coefficients between productivity and chlorophyll a suggest that a relatively large portion of inactive chlorophyll was present in the live phytoplankton cells or that perhaps relatively large quantities of chlorophyll a were associated with non-living detrital material (e.g., Ryther and Yentsch, 1957).

The mean annual rate of productivity and chlorophyll a concentration were highest for station 13 in the river whereas average phytoplankton biomass and cell numbers were greatest at station 50 in the Gulf. The unexpected distributional relationship of cell abundance and biomass with respect to productivity and chlorophyll a may derive from inaccuracies in cell enumeration techniques. As stated previously, the small, fragile species were largely unaccounted for. These cells, which may account for much of the productivity (e.g., Yentsch and Ryther, 1959; Malone, 1971a; Valkenburg and Flemer, 1974) may have been more abundant in the river than in the Gulf (e.g., Yentsch and Ryther, 1959; Loftus, Subba Rao, and Seliger, 1972; discussion below). Further, estimates for water column productivity at stations 50 and 13 were based on single in situ experiments.

Relationships Between Chlorophyll and Photosynthesis

The productivity index (i.e., photosynthetic rate per unit chlorophyll a) may be used as an indication of phytoplankton photosynthetic capacity (Strickland, 1960). Average indices for the present study were generally higher in summer than in winter in the Anclote Anchorage and

Table 10. Correlation coefficients for relationships between primary productivity and chlorophyll *a* in the three regions of the Anclote Estuary.

Season	Area	Degrees of Freedom (n-2)	Correlation Coefficient
Warm (June - Oct.)	Gulf of Mexico	13	0.90**
	Anclote Anchorage	23	0.72**
	Anclote River	13	0.83**
Cool (May - May)	Gulf of Mexico	15	0.27
	Anclote Anchorage	32	0.10
	Anclote River	19	0.61**

** Significant at $\alpha = 0.01$

River regions. No seasonal trend was apparent in the Gulf region adjacent to the Anclote Keys (Table 11). Similar findings were reported by Flemer (1970) who investigated primary productivity in the Chesapeake Bay. Stations located closest to the mouth of the bay did not show any seasonal variation in the productivity index, but, at stations farther up the bay, a seasonal pattern was clearly observed with highest values occurring during the warm months.

The index appears to be dependent on interrelationships among light conditions, water temperature, nutrients, and algal composition (Eppley, 1972). Correlation analyses between daily insolation and indices in the present study were weak in all cases, suggesting that light is not limiting surface productivity in the area studied. Talling (1955) stated that light saturation of photosynthesis normally occurs at intensities that are low relative to the intensity of surface incident radiation. Further, Steele and Menzel (1962) found in the Sargasso Sea, where the average daily radiation never falls below 200 g cal cm^{-2}, that insufficient light as a factor limiting photosynthesis of the surface phytoplankton population could be ignored. In the present study radiation below this value was never encountered (Figure 2A).

The seasonal pattern of the index in the Anclote Anchorage and River regions, is typical of shallow coastal estuaries (Eppley, 1972) with rapid nutrient regeneration processes. In such environments the productivity index is strongly correlated with temperature (Figure 12). Correlation coefficient analyses of Anclote Anchorage and River data indicate that approximately 84% of the variance of the index is related to variations in temperature. Similar agreement between the productivity index and temperature have been reported by Barlow, Lorenzen, and Myren

Table 11. Monthly average productivity indices (mg C [mg Chl a]$^{-1}$ hr^{-1}) for the three regions of the Anclote Estuary, 1973-1974.

Date	Gulf of Mexico	Anclote Anchorage	Anclote River
March	3.5	5.0	6.4
April	8.2	6.9	10.4
May	7.2	7.4	9.6
June	7.8*	7.8*	12.0
July	3.0	7.1	14.5
August	4.2	7.5	11.5
September	6.2	8.7	10.6
October	5.4	6.5	9.8
November	6.1	6.4	12.3
December	-	0.6	0.7
January	6.3	5.9	5.7
February	1.8	2.0	2.5
Mean	5.3	6.0	8.8

* One anomalously high value omitted from the average.

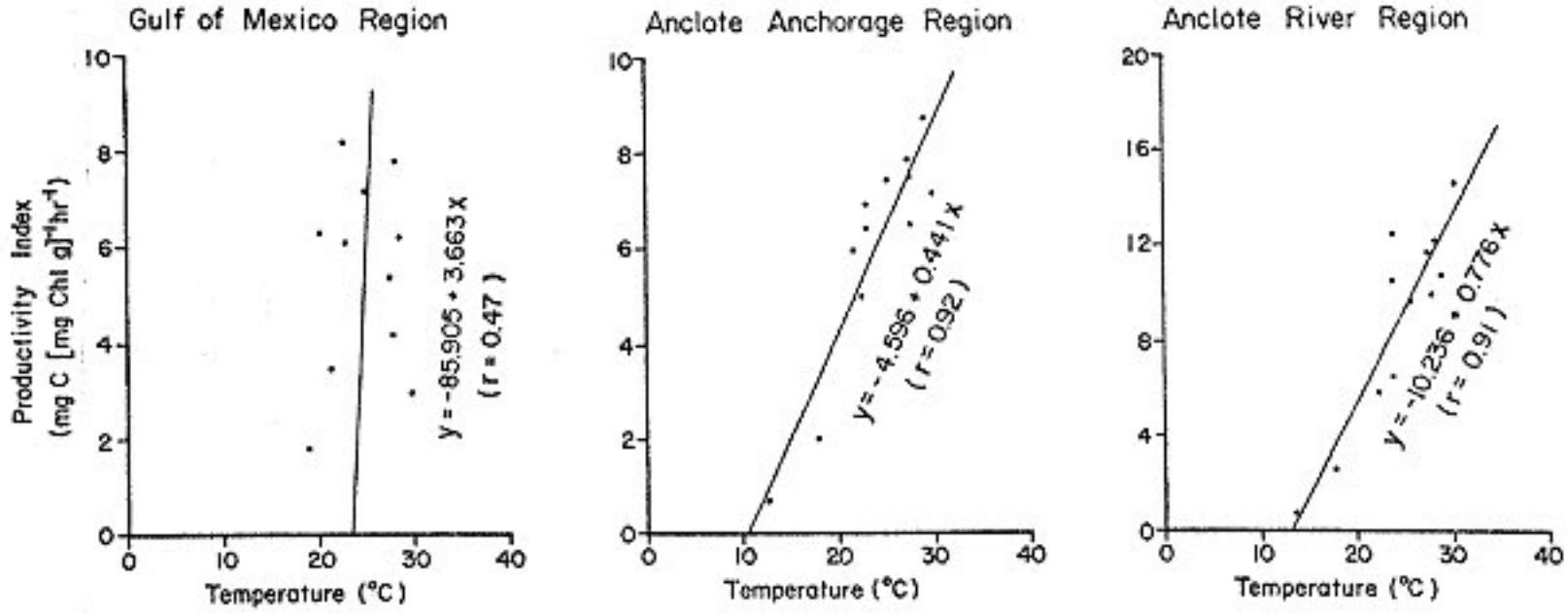


Figure 12. Linear relationships between the productivity index and water temperature in the Anclote Estuary.

(1963), Williams and Murdoch (1966), Ichimura (1967), Mandelli et al. (1970), and Valkenburg and Flemer (1974).

Williams and Murdoch (1966) derived an equation for prediction of surface primary productivity in a shallow estuary in North Carolina from chlorophyll a concentration and water temperature. Their calculated rates of daily productivity differed from measured rates by an average 26%. Accordingly, primary productivity in the Anclote Anchorage and River regions can also be predicted from the relationship between the productivity index and temperature (Figure 12):

$$\text{Anclote Anchorage:} \quad P = C(0.441T - 4.596)$$

$$\text{Anclote River:} \quad P = C(0.776T - 10.236)$$

where P is surface productivity (mg C m^{-3} hr^{-1}), C is surface chlorophyll a concentration (mg m^{-3}), and T is surface water temperature (^{o}C). Calculated rates differed from measured rates by an average 26 and 24% for the anchorage and river, respectively. Further, when measured rates were compared to those calculated from data at station P in the anchorage in 1971-1972 (Johansson and Hopkins, 1973) an average difference of 32% resulted.

The slope of the regression between the productivity index and temperature yielded temperature coefficients (Q_{10}) of 2.04 and 2.47 for the Anclote Anchorage and River regions, respectively. The Q_{10} for natural phytoplankton populations in field measurements was reported at approximately 2.3 by Talling (1955) and Williams and Murdoch (1966) and close to 2.0 by Ichimura (1967). Wassink et al. (1938) and Talling (1957) have shown that the average Q_{10} for light-saturated photosynthesis lies between 2.3 and 2.5.

The lack of apparent major influence of water temperature on the

productivity index in the Gulf region is puzzling. Possibly unassayed nutrients were limiting in this area. Curl and Small (1965) suggested that indices less than 3 indicate nutrient depletion, ratios between 3 and 5 a borderline deficiency, and ratios between 5 and 10 nutrient-rich waters. This was confirmed by Glooschenko and Curl (1971) in their subsequent study of Oregon coastal waters. Annual average ratios in the Anclote Anchorage and River regions were well above 5, but the ratio for the Gulf region was close to the suggested critical value of 5.

The nutrient observations of the present study do not provide sufficient information to draw conclusions on specific substances which might limit phytoplankton productivity. As stated previously, many nutrients known to affect primary productivity were not measured. Also, Ryther and Guillard (1959) and Loftus, Subba Rao, and Seliger (1972), among others, emphasize the importance of not basing conclusions of phytoplankton growth on instantaneous nutrient concentrations, in view of the presently inadequate understanding of nutrient utilization and remineralization rates. Nutrient enrichment and bioassay experiments would seem in order, then, in future research on primary productivity in the Anclote Estuary.

Daily variations in photosynthetic capacity of natural marine phytoplankton communities have been reported by Doty and Oguri (1957), Yentsch and Ryther (1957), Shimada (1958), Lorenzen (1963), and McAllister (1963). Malone (1971b) suggested that diurnal variations in the productivity index are related to the size composition of the primary producers and the availability of essential nutrients. In eutrophic tropical waters both netplankton and nannoplankton (i.e., phytoplankton retained and not retained, respectively, by a net with a mesh aperture size of 22 μm) had maximum indices in the afternoon. The measurement of diurnal periodicity

at station P (May 25) yielded a 9% higher productivity index for the morning incubation period. More data are necessary before a general statement can be made on diurnal variations in this area.

Estimated Growth Rates of the Phytoplankton

An average growth rate of the phytoplankton was calculated for every sampling of stations 50, P, and 13. The procedure used has been described in detail by Eppley (1972), who gave the following equation for calculations of specific growth rates:

$$\mu = \frac{1}{t} \log_2 \frac{C_o + \Delta C}{C_o}$$

where μ is doublings of cell carbon day^{-1} and t is the duration of light multiplied by a factor to equal growth during 24 hr (the growth rate is assumed proportional to the numbers of hours of light per 24 hr [Eppley, 1972]). The term C_o is the initial carbon content of the phytoplankton, as measured from cell volume, and ΔC is the daily rate of primary productivity, assumed to represent the net increase in particulate carbon. The assumption that the ^{14}C method of measuring primary productivity indeed measures net particulate carbon formation has been indicated by several laboratory studies which included two or more independant measures of phytoplankton assimilation rates (see above).

Estimated phytoplankton growth rates forthe three stations ranged from 0.2 to 3.5 doublings of cell carbon day^{-1}, with station 13 having the highest annual mean rate (Table 12). Seasonal trends were not clearly apparent, although relatively high rates occurred in late spring and early summer and lower than average rates in late summer and fall.

Eppley (1972) predicted the upper limit of growth rate to be expected for laboratory cultured unicellular algae at a given temperature (range:

Table 12. Estimated phytoplankton growth rates (doublings of cell carbon day^{-1}) at stations 50, P, and 13, 1973-1974.

Date	Station 50	Station P	Station 13
March 8	1.6	1.7	3.5
April 3	0.8	0.9	1.9
May 9	1.1	1.0	2.4
May 25	-	1.8	-
June 7	2.7	2.3	3.0
July 6	1.0	2.1	2.3
August 3	0.7	1.9	1.7
September 12	1.0	1.5	1.7
September 18	0.7	0.2	-
October 3	0.9	1.2	1.7
November 5	0.7	0.6	1.5
November 27	1.6	1.1	2.8
December 17	-	0.3	2.0
January 8	1.1	0.9	3.2
February 5	0.5	1.1	1.4
Mean	1.0	1.3	2.2

0-40 ^{o}C) with the equation:

$$\mu = 0.851\ (1.066)^{T}$$

where T is the water temperature (^{o}C). Estimated growth rates in the present study plotted against temperature were in all cases lower than the maximum expected value for that particular temperature. This was not unanticipated since the samples contained a mixture of phytoplankton with different optimum growth temperatures. Differences in temperature optima for growth of unicellular algae have been confirmed in the laboratory (e.g., Eppley and Sloan, 1966; Jørgensen, 1968).

Average growth rates at stations 50 and P were in close agreement with rates calculated (see Eppley, 1972) for nutrient-rich waters of the western Arabian Sea (Ryther and Menzel, 1965b) and off southwest Africa (Hobson, 1971), although productivity indices for the Gulf region indicate possible nutrient limitation. The average growth rate at station 13 in the river, however, was considerably higher than other values for natural phytoplankton populations reported in the available literature. This discrepancy may arise from an underestimation of cell biomass at station 13. As previously stated, virtually all small phytoplankton were lost due to the sample concentration technique employed. It is suspected that samples from station 13 contained more small phytoplankton than samples from stations 50 and P (see above). Conversely, primary productivity rates and chlorophyll _a_ concentrations on most occasions were considerably higher at station 13, while biomass at this station often was lower or equal to that at stations 50 and P. Similarly, Gibson and Hopkins in 1971 (Gibson and Hopkins, 1974) found an intermediate biomass for the Anclote River, while the average chlorophyll _a_ level was higher than those in the Anclote Anchorage and the adjacent Gulf of Mexico.

Anclote Estuary in Comparison to Other Areas

Primary productivity in surface waters of the Anclote Anchorage and Gulf of Mexico adjacent to the Anclote Keys was considerably greater than that observed in offshore waters of the Gulf of Mexico and from the southwest Florida shelf (Table 13). El-Sayed (1972) reported lower average surface phosphate concentrations from offshore Gulf waters and from the Florida shelf than were measured at the two Anclote regions mentioned above. Further, Kabanova (1966) found surface productivity in the southern part of the Gulf to be limited by nutrients.

The Crystal River Estuary, located approximately 75 km north of the study area, generally showed lower productivity than the Anclote Anchorage, although nutrient concentrations (phosphate and nitrate) often were equal or higher (Gorman, unpubl. data). The average chlorophyll *a* concentration for the Anclote Anchorage, however, was approximately twice that of the Crystal River Estuary. Also phytoplankton abundance in winter in the Anclote Anchorage was higher. Productivity measured in the Anclote River was considerably higher than that of the Crystal and Mississippi Rivers. The comparatively low productivity at the mouth of Crystal River was not unexpected in view of the high aquifer input at its lower portions. The productivity of Mississippi River may be low due to the high suspended load. Thomas and Simmons (1960) found that productivity decreased in the Mississippi River as the water became more turbid.

The Waccasassa Estuary, 25 km north of the Crystal River Estuary, had an average surface productivity similar to the Anclote Anchorage but greater than the adjacent Gulf of Mexico (Saville, 1966). Levels of phosphate were somewhat lower in the Anclote Anchorage as compared to the Waccasassa Bay, and nitrate in the anchorage was as much as an order of

Table 13. Phytoplankton productivity rates in various estuarine, coastal, and offshore waters of the Gulf of Mexico.

Area	Primary Productivity ($mg\ C\ m^{-\beta} hr^{-1}$)	($mg\ C\ m^{-2} hr^{-1}$)	Method	Season	Source
Offshore waters:					
Gulf of Mexico	0.01-4.46	1.32-28.22	^{14}C	All seasons	El-Sayed, 1972
Gulf of Mexico	0.29-0.47	32.3 -35.0	"	August	Hopkins, unpubl. data
Coastal waters:					
Northwest Coast of Cuba		12.5- 95.83	"	October	Kondratyeva and Sosa, 1967
Southwest of Florida Shelf	4.17-8.33		"	April, June	Kabanova, 1966
Gulf of Mexico Adjacent Anclote Keys	5.60-82.10		"	All seasons	Present study
Anclote Anchorage	5.91-92.10	23.4 -229.0*	"	" "	" "
Estuaries:					
Hillsborough Bay		20.83-109.17	O_2	July-Dec.	Taylor, 1970
Old Tampa Bay		9.17- 33.33	"	" "	" "
Upper Tampa Bay		17.50- 77.50	"	" "	" "
Lower Tampa Bay		18.33- 35.83	"	" "	" "
Boca Ciega Bay		10.83- 45.00	"	" "	" "
Anclote River	2.35-220.67		^{14}C	All seasons	Present study
Crystal River Estuary	1.71-101.25		"	Nov.-Sept.	Gorman, unpubl. data
Cross Florida Barge Canal	7.16-115.46		"	Dec.-Sept.	" "
Crystal River	1.46- 27.00		"	Feb.-Sept.	" "
Waccasassa Estuary	0.09-225		"	All seasons	Saville, 1966
Mississippi River	0 -13.80		"	" "	Thomas and Simmons, 1960

* Station P

magnitude lower. Putnam (1966) suggested that primary productivity in the Waccasassa Estuary appeared in part regulated by available nitrogen and phosphorus. These nutrients were usually in greatest demand in summer when photosynthesis was at maximum. There is some similarity in regional distribution of productivity between the Anclote and Waccasassa Estuaries. In these areas it appears that productivity reaches maximum values at the mouth of the rivers and decreases seaward and upriver (see, respectively, Table 5 of the present study and Putnam, 1966). A similar distribution of productivity was found by Williams (1966) in a system of shallow temperate estuaries in North Carolina. In the Anclote Estuary the average concentration of chlorophyll a followed the same regional pattern as that of productivity, though this relationship was not observed in the Waccasassa Estuary. The causes of increased productivity in the mouth of the Anclote River are not fully understood and require further investigation. Parsons and Takahashi (1973) suggested that high productivity in a seawater-freshwater mixing area may be caused by natural enrichment by nutrients from the river.

Integrated productivity at station P in the Anclote Anchorage during the warm season exceeded that reported for the other areas listed in Table 13. Winter rates at station P, however, were similar to the lowest rates in the upper sections of Tampa Bay and lower than rates listed for the central Gulf of Mexico during August. The comparatively low productivity reported for Tampa Bay is surprising when considering the high nutrient levels and the high phytoplankton standing crop reported in this area by Turner and Hopkins (1974). Integrated annual productivity at stations 50 and P were similar to the mean annual rate for coastal waters (approximately 370 g C m^{-2}) as reported by Koblentz-Mishke, Volkovinsky,

and Kabanova (1970). The value for station 13 in the river was considerably greater and approximates annual productivity measured in eutrophic lakes (Johnsen, Mathiesen, and Røen, 1962). A similar annual value was also reported from the highly productive Altamaha River mouth in Georgia by Thomas (1966).

The seasonal cycle of primary productivity in the Anclote Estuary is similar to general annual patterns observed in other shallow estuarine areas (e.g., Steemann Nielsen, 1958; Grøntved, 1960; Ryther, 1963; Putnam, 1966; Williams and Murdoch, 1966; Thayer, 1971) in having maximum productivity during warm periods and minimum productivity during cool periods. The increased productivity during summer in these areas is believed related, in part, to a greater availibility of nutrients through increased remineralization rates of organic compounds by heterotrophs at elevated temperatures.

Chlorophyll a concentrations (Table 14) in the Anclote Estuary appear intermediate between those of the nutrient-poor Gulf of Mexico and those of the enriched upper Tampa Bay regions. The average concentration in the Waccasassa Estuary (Saville, 1966) was approximately the same as that in the Anclote Estuary, while the average level in the Crystal River Estuary (Gorman, unpubl. data), as previously stated, was only half that in the Anclote Anchorage.

Average cell concentrations in Anclote waters during 1973-1974 were considerably greater than those in the central and eastern Gulf of Mexico. Concentrations similar to those recorded at Anclote were found in the upper regions of Tampa Bay and on the inner southwest shelf of Florida between Ft. Myers and St. Petersburg (Table 15). Cell abundances recorded in the Anclote River and Anclote Anchorage in early summer resem-

Table 14. Chlorophyll *a* concentrations in various estuarine, coastal, and offshore waters of the Gulf of Mexico.

Area	Chlorophyll *a* ($mg\ m^{-3}$)	Season	Source
Offshore waters:			
Gulf of Mexico	0.01- 2.35	All seasons	El-Sayed, 1972
Coastal waters:			
Gulf of Mexico Adjacent to Anclote Keys	1.88- 17.33	" "	Present study
Anclote Anchorage	1.70- 10.91	" "	" "
Estuaries:			
Hillsborough Bay	2.69- 56.47	" "	Turner and Hopkins, 1974
Old Tampa Bay	2.23- 28.23	" "	" "
Mid Tampa Bay	0.14-163.60	" "	" "
Lower Tampa Bay	0.52- 6.05	" "	" "
Anclote River	3.75- 21.33	" "	Present study
Crystal River Estuary	0.27- 21.44	Nov.-Sept.	Gorman, unpubl. data
Cross Florida Barge Canal	2.12- 16.73	Dec.-Sept.	" "
Crystal River	1.05- 4.82	Feb.-Sept.	" "
St. Andrew Bay System	0.52- 4.18	All seasons	Hopkins, 1966
Waccasassa Estuary	1.12- 38.83	" "	Saville, 1966

Table 15. Phytoplankton abundance in various estuarine, coastal, and offshore waters of the Gulf of Mexico.

Area	Abundance (cells x 10^6 m^{-3})	Season	Source
Offshore waters:			
Central and Eastern Gulf of Mexico	15.3	Nov., Dec.	Hulburt and Corwin, 1972
Coastal waters:			
Outer Shelf, St. Petersburg-Ft. Myers	8*	All seasons	Saunders and Glenn, 1969
Inner Shelf, St. Petersburg-Ft. Myers	1096*	" "	" "
Gulf of Mexico Adjacent Anclote Keys	1910	" "	Present study
Anclote Anchorage	1420	" "	Present study
Estuaries:			
Hillsborough Bay	1200	All seasons	Turner and Hopkins, 1974
Old Tampa Bay	1200	" "	" "
Mid Tampa Bay	800	" "	" "
Lower Tampa Bay	800	" "	" "
Anclote River	1490	" "	Present study
Crystal River Estuary	68	Nov.-April	Gorman, unpubl. data
Cross Florida Barge Canal	899	Dec.-April	" "
Crystal River	10	Feb.-April	" "
St. Andrew Bay System	800*	All seasons	Hopkins, 1966
Mississippi River	1588	May	Thomas and Simmons, 1960

*Diatoms

bled those recorded in May in the Mississippi River. As in the present study, Putnam (1966) and Gorman (unpubl. data) found that diatoms were the most abundant phytoplankton in the Waccasassa and Crystal River Estuaries.

A comparison of phytoplankton biomass (Table 16) indicates that the lower regions of Tampa Bay were similar to the Anclote Estuary, whereas the upper areas of Tampa Bay had a considerably greater standing crop. The Anclote Estuary in winter, in terms of cell biomass, was similar to the Crystal River Estuary and the central Gulf of Mexico.

The Anclote coastal environment can be described as a "flow-through" system where the plankton sampled at a particular station may in a period of 30 days (sampling interval) have been transported from a distant location (e.g., if a net longshore drift rate of only 0.1 m s^{-1} is assumed 260 km can be covered in 30 days). Leipper (1954) describes a counterclockwise current system off western Florida which transports nearshore waters northward with a speed of approximately 0.4 m s^{-1} during most of the year. It is assumed, then, that the seasonal patterns recorded in this study generally apply to vast stretches of coastal environment which potentially serve as source regions for the phytoplankton collected.

Considering a transport of nearshore waters along the west coast of Florida, a general similarity could be expected between phytoplankton measurements in the Anclote Estuary and other estuaries of this coast. Studies in this area most comparable with the present one are those conducted by Putnam (1966) and Gorman (unpubl. data) in the Waccasassa and Crystal River Estuaries, respectively. In the previous comparison it is found that phytoplankton measurements of the Anclote Estuary generally were slightly greater than those of the Crystal River Estuary, while most

Table 16. Phytoplankton biomass in various estuarine, coastal, and offshore waters of the Gulf of Mexico.

Area	Biomass (mg C m^{-3})	Season	Source
Offshore waters:			
Central Gulf of Mexico	35	Nov.	Hobson and Lorenzen, 1972
Coastal waters:			
Gulf of Mexico Adjacent Anclote Keys	186	All seasons	Present study
Anclote Anchorage	140	" "	" "
Estuaries:			
Hillsborough Bay	2686	All seasons	Turner and Hopkins, 1974
Old Tampa Bay	1312	" "	" "
Mid Tampa Bay	486	" "	" "
Lower Tampa Bay	145	" "	" "
Anclote River	103	" "	Present study
Crystal River Estuary	29	Nov., Dec.	Gibson et al., 1974a
Cross Florida Barge Canal	588	Dec.	" "

of the measurements from the Waccasassa Estuary compare quite well with those of the Anclote Estuary.

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SUMMARY

1. Phytoplankton was investigated monthly from March, 1973 through February, 1974 at 11 locations in the Anclote Estuary.
2. The principal phytoplankton genera in terms of cell numbers and biomass were Skeletonema, Chaetoceros, and Nitzschia in the summer, and Rhizosolenia, Leptocylindrus, and Chaetoceros in the winter.
3. Average phytoplankton concentrations of 1910, 1490, and 1490 cells x 10^6 m^{-3} were measured at station 50, P, and 13, respectively. Average biomass estimates for these stations were 186, 145, and 102 mg C m^{-3}.
4. Annual productivity rates of 420, 170, and 120 g C m^{-3} were calculated for surface waters of the Anclote River, Anclote Anchorage, and adjacent Gulf of Mexico, respectively.
5. Average surface chlorophyll a concentrations were 9.6, 6.1, and 5.2 mg m^{-3}, respectively, for these areas.
6. Primary productivity and phytoplankton standing crop followed a pronounced seasonal cycle with annual peaks occurring during the warmer months of June through October.
7. Correlation statistics indicate a positive, highly significant relationship ($\alpha = 0.01$) between primary productivity and surface water temperature during the cool season.
8. The average regional productivity index (mg C [mg Chl a]$^{-1}$ hr^{-1}) ranged from 0.6 to 14.5 and showed a high correlation with water

temperature in the Anclote Anchorage and River. This relationship was weaker in the adjacent Gulf of Mexico, possibly indicating that nutrients were more limiting in this area.

9. The phytoplankton growth rate in Anclote waters was estimated at 0.2 to 3.5 doublings of cell carbon day^{-1}, the highest yearly average occurring in the Anclote River. Clear seasonal trends were not apparent.

10. Surface productivity in the Anclote Anchorage and adjacent Gulf of Mexico was greater than that for the central Gulf of Mexico and the Crystal River Estuary but similar to rates in the Waccasassa Estuary. Productivity rates measured in the Anclote River were considerably greater than rates of the Crystal and Mississippi Rivers.

11. Phytoplankton abundance in Anclote surface waters was greater than in the central Gulf of Mexico but similar to cell numbers recorded for the inner southwest shelf of the Gulf and the upper regions of Tampa Bay.

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