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Further Studies on Reaeration and Metabolism of Texas Bays, 1958-1960[1]

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Abstract

123 diurnal curves of oxygen were obtained in 1959–60 to further outline the patterns of total photosynthesis and community metabolism of Texas bays. Examples were analyzed with nighttime variations in respiration, with changing reaeration constants, and with post-sunset artifacts in computational graphs. The area-based reaeration constant increased with depth, but the volume based reaeration coefficient was more constant at about 1.2 ppm per hr per 100% deficit. The volume-based constant increased with wind velocity. Peaks in the 4 yr seasonal pattern of metabolism in the grassy upper Laguna Madre were in phase with peaks of insolation with P and R remaining in relatively close balance from 0.5 gm/m²/day in winter to 20 gm/m²/day in summer. Planktonic systems of Corpus Christi bay were equally productive. Metabolism was slight in a winter cold regime and momentarily interrupted in a spring squall line passage. Hexadecanol had little effect on a salt pond, and inorganic fertilization caused increased metabolism temporarily. Metabolism during dredging was unbalanced towards respiration, and a case of high photosynthesis in flood regimes was reported. A very large diurnal oxygen range was reported in an algal film system with anaerobic nighttime conditions associated with blue-green dominants. Maximum production rates (30–40 gm/m²/day) were found in the clearest bay, the lower Laguna Madre, with values similar to those for some Texas sewage ponds indicating the effectiveness of natural, stabilized communities in recycling nutrients. Production measurements inside and outside of enclosures indicated the ability of turtle grass systems to maintain fairly normal metabolism for weeks following enclosure. Data from a Louisiana Bayou were similar to data from turbid bays of East Texas. Total phosphorus data indicated slightly higher values in hypersaline bays (2–4 mg-atom/m³) than in bays flushed with fresh water (0.8–2.4 mg-atom/m³). The larger bays were equally or more productive than the small sheltered sloughs and harbors of similar depth. Metabolism fluctuated from day to day in a small boat harbor, but conditions remained aerobic. Extinction coefficients were obtained for white light ranging from values typical of Gulf coastal water to those with a 1% compensation point at 0.5 m in turbid bays. Productivities during the summer in the various bays were correlated with clarity. Respiration often exceeded photosynthesis in the back bays where land run-off was more important. For maintaining maximum gross photosynthesis, management measures may be designed for obtaining water clarity and maximum light utilization, for holding stable salinity and nutrient water mass regimes, for conserving well developed bottom communities for holding nutrient cycles, and for controlling bottom depths to intermediate levels (1–2 m) for optimum combinations of light, circulation, and oxygen range.

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Introduction

The bays and estuaries along the ocean margins of the world are the frontiers where man's enterprise is now exploring new ways of using the sea. To carry out research, evaluate fertility, appraise pollution, predict biological events, manage production, develop resource yields, and farm the vast shallow oceans, one must be able to assay day by day the total photosynthesis and respiratory consumption of these ecosystems. Such assay is attempted with the diurnal curve method involving the measurement of oxygen, total carbon dioxide, and other metabolically active constituents through twenty-four hour periods. From such measurements one may seek to compute rates of turnover of chemical cycles, rates of uptake of radioactive substances, productivities, potentials for increased yields of marine products, and metabolic conditions of the bay systems.

In previous papers on the broad, fertile bays of Texas, data were presented indicating the suitability of the diurnal curve method for the determination of gross photosynthesis and total community respiration in Texas waters (Odum and Hoskin, 1959; Park, Hood, and Odum 1958; Bruce and Hood, 1959; Odum, 1960). To further elucidate the nature of total metabolism and reaeration in marine coastal ecosystems, 123 more diurnal curve measurements have been made in special situations, new areas, seasons, and experimental tests. Selected case histories and seasonal patterns are presented in this report in order to interpret the role of depth, light, temperature, turbidity, nutrients, areas, and agitation on production, respiration, and reaeration.

Methods

Oxygen analyses by the Winkler method were made on water samples collected at frequent intervals through 24-hour periods representing whole functional areas and water masses. Then rates of gross production, respiration, and reaeration were computed. Procedural details on the graphical analysis were presented in a preceding report (Odum and Hoskin, 1958). In other papers variations were described for some special situations (Odum, 1956, 1957, 1960; Odum, Burkholder, and Rivero, 1959). Several new refinements concerning the computation of diffusion and respiration are here described. These methods apply in thoroughly mixing shallow waters.

Phosphorus analyses were made by H. Bruce (Bruce and Hood, 1959) and R. Ward working with C. Oppenheimer using perchloric acid digestions followed by stannous-chloride-ammonium molybdate colorimetry.

Field measurements of foot candles were made with a General Electric Golden Crown Exposure Meter, Type PR 3 with an incident light attachment. The manufacturer supplied a foot candle calibration. Under conditions of rough field use, changing tensions on the spring, and other factors, the foot candle data must be considered approximate and relative.

Wind velocities were measured in the field with a hand anemometer Model MRF Florite from Bacharach Industrial Instrument Company, 200 W. Braddock Ave., Pittsburgh, Pa.

CORRECTIONS FOR CHANGING NIGHTTIME RESPIRATION

From studies by Beyers (1962) on microcosms, from data in some diurnal curves (Fig. 1 and 2), from diurnal data in Silver Springs (Odum, 1957), and from experiments on plant respiration as a function of oxygen content by Gessner and Pannier (1958) it is known that the respiration of oxygen after dark may exceed that just before dawn in many instances, especially when oxygen content is much higher at sunset than at sunrise. Wherever post-sunset respiration is higher than respiration later at night an error in the diffusion computation may be introduced ultimately causing a slight overestimation of of total community respiration.

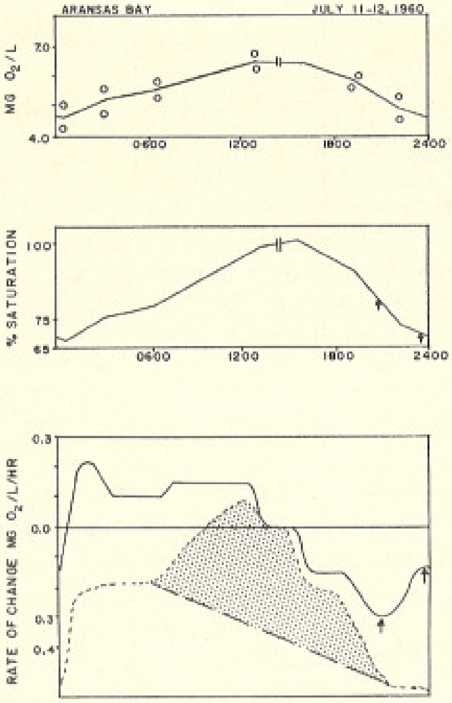

FIG. 1. Diurnal curve off Hunt's Pier, Rockport, Texas, in Aransas Bay, July 11–12, 1960; salinity, 21 ‰. This is an unusual curve in which the respiration decreases markedly during the night. The change in rate of nighttime oxygen decrease occurred even though the winds diminished from 18 mph at sunset to 7 mph at sunrise.

Recalling the procedure previously outlined in detail (Odum and Hoskin, 1958), one selected two points during the night from the rate of change graph. In the routine previously used the respiration was taken to be constant at both times of night and any difference in the rate of oxygen decrease was attributed and computed in ratio to the difference in per cent saturation of the water at the two times. Since both respiration and the tendency for diffusion out are greatest in the early part of the night (or tendency for diffusion inward is minimal), one attributed too much of the observed oxygen

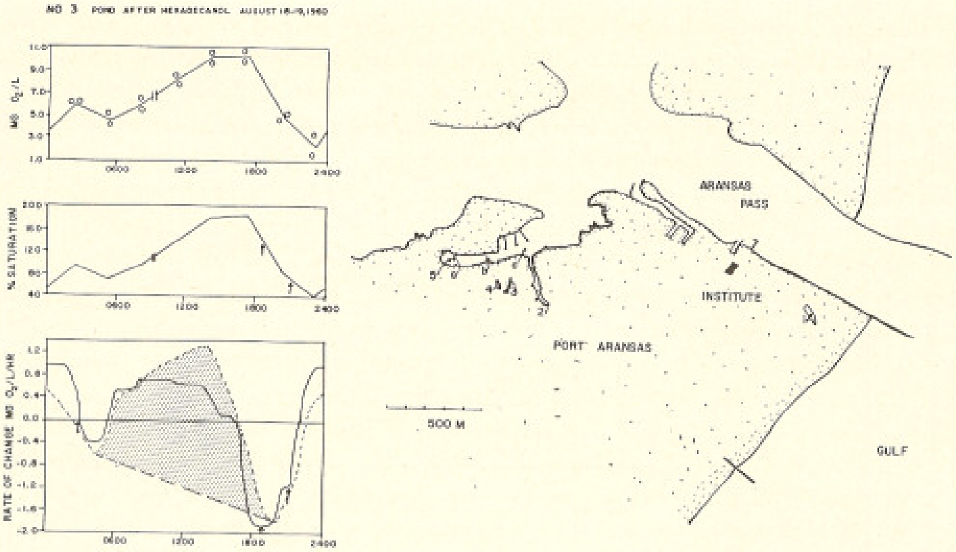

FIG. 2. Diurnal curve in a shallow slough (Pond No. 3) after addition of hexadecanol at noon, Aug. 18–19, 1960: salinity 33.6 ‰; wind with little variation through the night 0–6 mph. This curve shows a decrease in respiration during the night. Also included is a map of Port Aransas waterways showing ponds and sloughs: 1, beach pool; 2, shell shop pond; 3, Oppenheimer House pond; 4, ferry road algal mat; 5, city boat basin, stations a, b, and c.

decline at night to diffusion. The diffusion correction was overestimated. When the graphs were finally completed, the nighttime respiration was slightly overestimated and the P/R ratio too low.

In aerobic waters the magnitude of error is small judging by the small differences in nighttime oxygen respiration indicated in sources cited above. The large differences in Fig. 1 and 2 are unusual. In anaerobic waters, however, very large differences develop as recently reported (Odum, 1960) in cases in which oxygen consumption although rapid after sunset stops later at night as oxygen runs out. To some extent a localized anaerobic effect may always exist where the bottom ooze is in the euphotic zone with declining oxygen metabolism at night.

Data by Beyers (1962) on carbon metabolism of several types of balanced microcosms show the maximal nocturnal respiration at sunset suggesting a relation to the labile organic matter accumulating from the net production of the previous day. In his graphs respiration declines rapidly, perhaps logarithmically during early night. If the bays are behaving similarly, the diffusion constants obtained in this paper with the simple formula (R constant) are too large, since they include some of the change in respiration as change in diffusion. Were the change in respiration during the night between the two computational times known, the diffusion constant might be used as

$$k = \frac{(q_e - q_m) - (r_e - r_m)}{S_e - S_m}$$

where k is the volume based diffusion constant, q the rate of change, r the respiration, and S the saturation deficit.

Because the data on diurnal pH CO_2 curves for these bays (Park, Hood, and Odum, 1958) do not yet show systematic trends in nighttime respiration, it seems premature to attempt complex assumptions about respiration for estimating diffusion directly from the diurnal graphs. Thus in this paper the simple procedure has still been used, and the values for diffusion constant may be regarded as upper limits. Ultimately independent physical determinations of the reaeration constant may solve this problem with the night respiration and daytime net photosynthesis determined after subtraction of diffusion as independently determined.

In rate graphs analyzed in the previous paper (Odum and Hoskin, 1958), one line for "R" was drawn through the average nighttime respiration. In many of the graphs after diffusion corrections have been applied, there was observed a greater respiration after dark than before dawn even without the correction of the diffusion constant described above. Where pre-sunrise and post-sunset respiration differ in this paper, a dashed line is connected diagonally connecting dawn respiration rate to the sunset respiration rate on the rate of change graph. This line may be used for counting squares in estimating gross photosynthesis. How real the line may be as an indication of daytime respiration is not known.

Where the diurnal variation of respiration of oxygen is severe as in anaerobic systems, it seems best to use a reaeration (diffusion) constant that is approximated independently from k's in similar conditions of depth and mixing as measured under aerobic conditions (Fig. 3). For example, k or about 1 $gm/m^3/hr/100\%$ deficit is representative of the Texas bays under average conditions. After applying the assumed diffusion constant, one may use the corrected rate graph to indicate the course of night respiration.

REAERATION CONSTANTS AND WATER DEPTH

In streams the area-based reaeration coefficient increases with the rate of stirring and thus increases with current, wave action depth, and size of the water eddies (Phelps, 1944; O'Connor, 1958; Velz, 1939). Consider reaeration relationship to depth in the bays. Reaeration constants computed by the diurnal curve method for Texas bays have been plotted in Fig. 3 as a function of depth. Reaeration and the variation in reaeration increase with depth. Although the reaeration computations from diurnal curves are subject to many sources of variation and error, the data show a regression from values of 0.1 $gm/m^2/hr/100\%$ deficit in shallow water to values greater than 3 $gm/m^2/hr/100\%$ deficit in the deeper bays. The line in Fig. 3 may be used to estimate reaeration constants where night data are inadequate or where other complexities prevent the usual computation.

The volume based reaeration constant (k) in $gm/m^3/hr/100\%$ deficit is related to the area based constant (K) by the definition:

$$K = zk \text{ where z is depth in meters.}$$

The regression line for K from Figure 3 was converted into a line for k by dividing by depth as indicated in Fig. 3. The volume based constant is rather independent of depth in these bays.

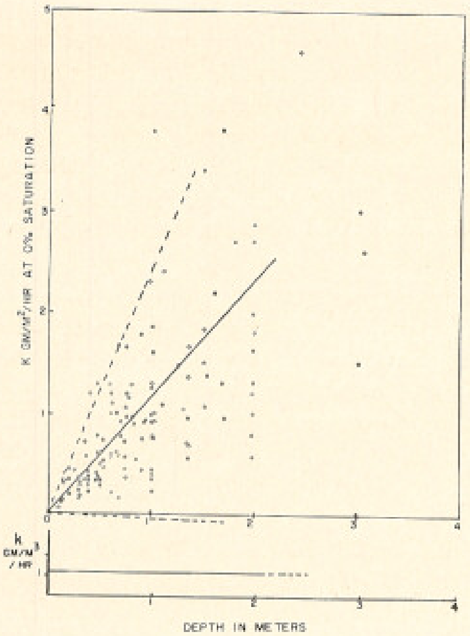

Fig. 3. Reaeration constants on an area basis (K in gm/m²/hr/100% deficit) as a function of the bottom depth (in meters). A linear regression line is plotted as computed from the data points. Dashed lines form boundaries for 95% confidence. Also plotted is the same regression line expressed as a volume basis (k = K/z in units mg/1/hr/100% deficit). Each point in this figure was computed from a diurnal curve using changing rates of change at night following the procedure of Odum and Hoskin (1958).

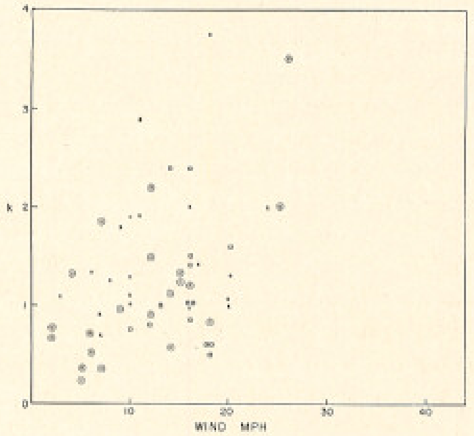

Fig. 4. Reaeration constants on a volume basis (k in units mg/1/hr/100% deficit) plotted as a function of average wind velocity during nighttime hours.

Values for reaeration in San Diego bay of about 0.12 gm/m³/hr/100% deficit (volume base) (O'Connor, 1958) and for the Thames estuary by Gameson and Barrett (1958) of 0.5 gm/m²/hr (area base) are within the range in Texas waters on the low side.

REAERATION CONSTANTS AND WIND VELOCITY

Because the passes are narrow and the Gulf tides small there is little tide in most of the bays and most of the stirring action is wind driven due to waves and wind-induced circulation. The reaeration coefficients as computed from the diurnal graphic analyses are plotted for environments of similar depth in Fig. 4 as a function of observed wind velocity during the night. Increasing reaeration coefficients can be observed with increasing winds. The graph in Fig. 4 has been used in several instances to compute diffusion corrections on days in which wind velocities varied markedly at different times. Estimates of wind velocity in the field were used to select a reaeration constant for each time of the day. Computation of reaeration rates from a diurnal graph can only be done if one has two periods with nighttime rate measurements in which wind velocities are fairly similar. Such data are plotted in Fig. 3 and 4.

POST-SUNSET DIFFUSION ARTIFACT

In the usual graphic analysis of diurnal curves, after selection or computation of k, the diffusion correction is applied for each hour of the day and night so that the final rate of change graph indicates only the photosynthetic and respiratory metabolic rates. When no allowance is made for changing constants and where there is a change of reaeration rate due to wind variation, some artifacts are produced. One of these artifacts has been observed frequently, a post-sunset bulge. Where this irregularity is recognized it may be allowed for in metabolic computations. Field measurements of wind velocity with a hand anemometer are now a standard part of the diurnal procedure.

In many localities on the Texas coast particularly in summer there is a marked seabreeze-landbreeze effect so that the prevailing southeast trades pulse with diurnal variation. The bay waters are much more vigorously mixed in the evening than in the early morning. There is a resulting diurnal change in the reaeration constant. Because many of the curves pass through saturation about sunset, the error is not great in most instances. However, if one uses one reaeration constant uniformly during a night, one introduces an artifact that looks like a burst of post-sunset photosynthesis (Fig. 5 and 6). This graphic artifact develops because one undercorrects for aeration early in the evening and overcorrects later. One may suspect this effect whenever the post-sunset oxygen curve is concave downward. To avoid the effect one may use a different k in the early evening from that used later at night using wind observations and Fig. 4 to estimate a suitable k.

Results

In the paragraphs that follow photosynthetic and respiratory data are presented for several situations and seasons with an interpretive emphasis on the special features discussed in each case as a natural experiment. P is gross production; R is total community respiration.

The various new refinements in analysis of these graphs have been applied to older data wherever used in this paper so that the values in Fig. 7 may not be exactly the same as previously published in some instances.

In presenting diurnal data from a 24 hour series, all items are arranged with noon in the middle of the graph even though the series began at any time of the day. The right side of the graph may be earlier in time than the left side. The time of start is indicated by a break in the line connecting the points. One should not compute a rate of change for the segment connecting the start to the end, as such a segment is not real. One may connect the points on the rate graph across such a gap in order to compute photosynthetic areas without affecting values appreciably.

SEASONAL CYCLES IN THE LAGUNA MADRE, A THIN-GRASS SYSTEM

With the help of many persons and as part of several related studies, diurnal curve measurements have now been made in the Laguna Madre over a period of 4 years including dry and wet years. The measurements in the first year were made in a slightly more inshore station inside Pita island than in later years when the curves were taken outside of Pita island. Data on photosynthesis, respiration, computed diffusion constants, salinity and temperature are reported in Fig. 7.

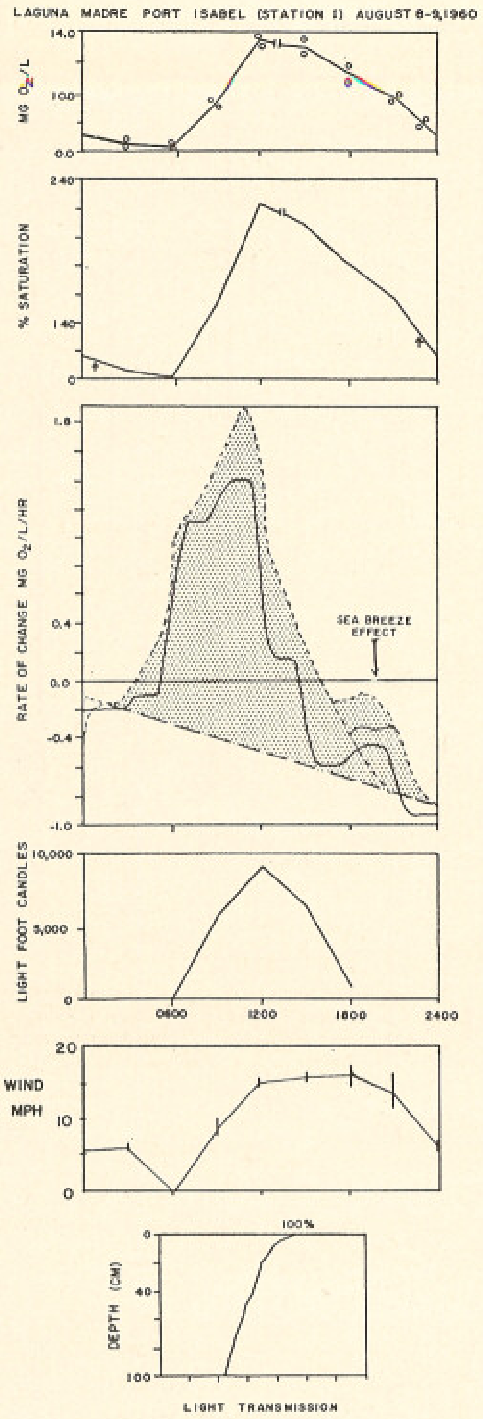

FIG. 5. Diurnal curve showing the post-sunset bulge artifact due to decreasing winds and aeration after dark frequently found in Texas due to seabreeze effects. Grass flats in the Lower Laguna Madre at Port Isabel, 1.4 m, salinity 36.7‰, wind velocities in mph.

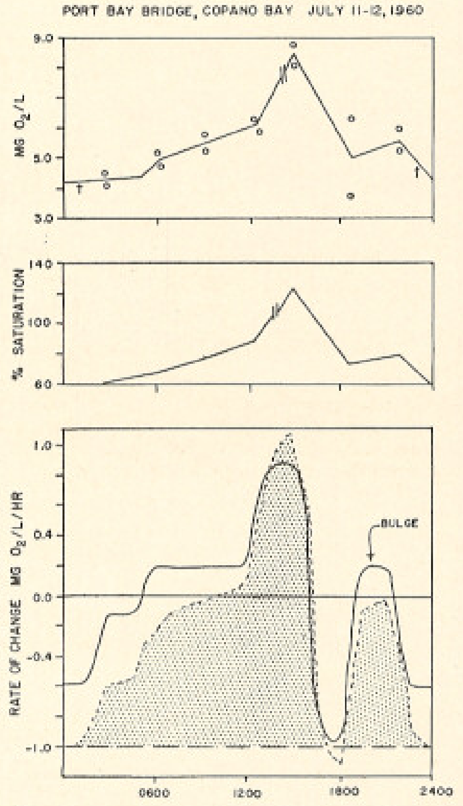

FIG. 6. Diurnal curve with post-sunset bulge artifact in Port bay, a low salinity arm of Copano Bay receiving Aransas River. Depth 0.92 m; salinity 13.6 ‰, July 11–12, 1960.

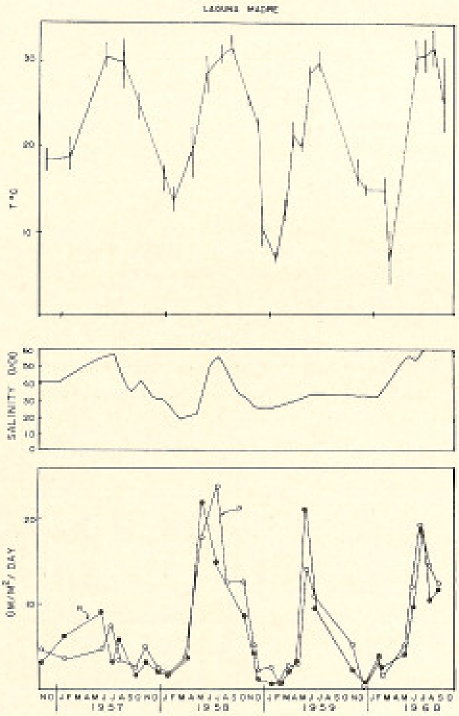

FIG. 7. Four year record of gross photosynthesis (P) and community respiration (R) in the Laguna Madre. Each point represents a diurnal curve on a particular day as indicated. Salinities and temperatures (daily ranges) are also plotted for the particular days of the 24 hr studies.

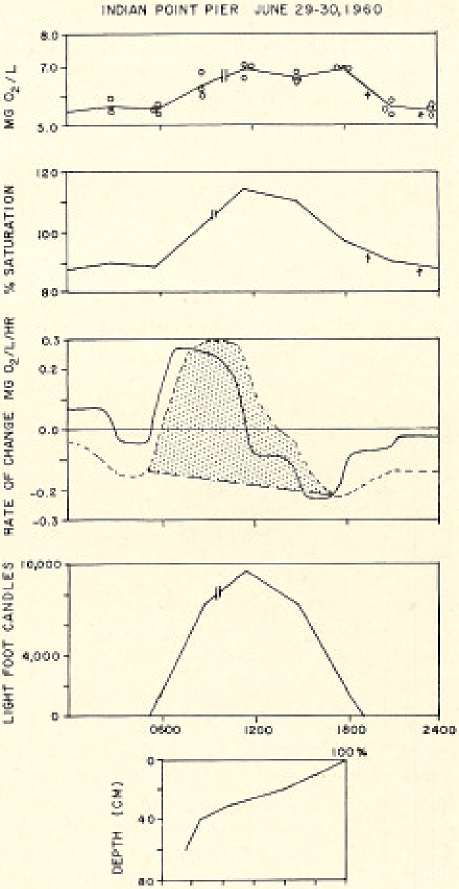

FIG. 8. Diurnal curve for Corpus Christi from Indian Point Pier, July 29–30, 1960. Salinity 34.6 ‰; water depth 3 m; temperature range 28 to 32° C; wind 7 to 14 mph. A typical graph for a deeper bay.

The upper Laguna Madre in the study area is carpeted with a firm bottom and fine grass in water about one meter in depth. In the dry years with the salinity above 40 ‰ this grass was almost exclusively composed of *Diplanthera wrightii*, but during the relatively wet year of 1959 considerable *Ruppia maritima* developed, diminishing again in 1960.

Only in summer 1960 were dense mats of dead grass observed accumulating. In general consumption and production were closely correlated. There was an immense difference between the winter and the summer (Fig. 7). Whereas 96,000 foot candle-hours were received on a representative summer day July 25, 1960, only 4500 foot candle-hours were received on a cloudy winter day Dec. 8, 1960, and 19,500 foot candle-hours on a clear day in winter, Dec. 28, 1961. The low winter photosynthetic productivities thus were correlated with winter cloudiness and short days. Unlike Florida at a similar latitude, the cloudiness in Texas was maximal in winter. There was thus a tremendous annual pulse in the energy entering the biological system. The observed photosynthesis reflects this cloudiness. The close correspondence of respiration with photosynthesis without lag suggests that the life cycles of the organisms are sufficiently adjusted to provide almost simultaneous increase and decrease of consumer populations to maintain equivalence of P and R. The migration of mullet, shrimp, crabs and other consumers from the Laguna (Hellier, 1962) is a part of this system which diminishes winter metabolism as the photosynthesis drops. There is relatively little lag.

The temperature sequence parallels photosynthesis only in part. Productivities fall rapidly after July whereas temperature does not diminish appreciably until November. See plot of temperature by Hellier (1962). Although the decrease in salinity produced some differences in plant type, gross photosynthesis was little affected.

METABOLISM IN CORPUS CHRISTI BAY, A PLANKTONIC SYSTEM

A very different type of ecosystem, the deeper bay, is represented by Corpus Christi Bay, a large moderately turbid system 3 to 4 m deep, in which wind and waves provide a strong circulation. Salinity studies such as that by Hood (1953) indicate a generally counterclockwise circulation as might be expected for a body receiving freshwater river flow. The salinity varies markedly between wet and dry years with values ranging from 10 to 45 ‰. The bay metabolism is based on a plankton system. The shade of the relatively deep and turbid water prevents growth of extensive grass areas. Several industrial effluents enter along the margins. A typical diurnal curve is given in Fig. 8.

Data were collected on Corpus Christi Bay over a period of several years as indicated in Table 1. In general the oxygen amplitude was slight and production usually relatively small per volume (one or two mg/1/day). In the total water column, however, combined production and respiration approached values for other bays. The diurnal curve for Indian Point Pier, June 29–30, 1960, (Fig. 8) is representative.

Along the waterfront at Corpus Christi is a protected area behind a breakwater. In this inner area there was calm water with some stagnation and opportunity for fertilizations and pollutions from boat activity. In this "T head" area an instance of high metabolism is reported (Table 1).

SYNOPTIC COMPARISON OF METABOLISM OF THE TEXAS BAYS IN SUMMER

During summer (June-August), 1960, an intensive effort was made to measure the metabolism of a number of the bays of Texas during the same summer season. The resulting values for gross photosynthesis and total respiration are plotted in Fig. 9. The grass and plankton types are represented as already described, but each bay has distinctive features.

The general high level of summer metabolism is again demonstrated as compared with values of 1 gm/m^2/day for the central oceans (Ryther, 1959). The back bays in drowned river valleys with values from 1 to 12 gm/m^2/day were somewhat less productive than some of the front bays along the beach barrier, not immediately part of the river valleys.

In general the back bays and those with river inflows receive more turbid drainages, more pollutions, more wind disturbances, more flushing, and more shocks of high and low salinity variation. These factors may be responsible for lower sustained photosynthesis values.

TABLE 1

Gross production, community respiration, and reaeration constants for Texas bays. Data for Redfish Bay and Laguna Madre are in Figures 7 and 21. An asterisk (*) indicates that data were not suitable for computing reaeration constant.

	Date	Depth m	Salinity ‰	Temperature °C	P gm/m^2/ day	R gm/m^2/ day	K gm/m^2/ hr at 0%
NUECES BAY							
Outlaw Bait Stand	July 30–31, 1959	0.25	15	28–33	2.7	2.2	0.4
Outlaw Bait Stand	July 16–17, 1960	0.61	35	29–33	12.9	7.9	0.6
Near East end of causeway	July 16–17, 1960	0.3	35	29–34	5.6	0.9	*
OSO BAY							
Under Bridge	June 30–31, 1959	0.6	22	26–34	6.8	2.4	1.0
SAN ANTONIO BAY							
Hynes Bay	July 11–12, 1960	0.5	2	27–35	4.2	9.3	0.8
Hoppers Landing	July 11–12, 1960	0.4	6	28–34	2.7	5.7	0.6
Gonzalez Camp	July 11–12, 1960	0.5	8	27–35	4.3	6.2	0.7
MESQUITE BAY							
Red Algal Bottom	July 22–23, 1957	0.7	15	28–31	3.7	7.3	0.7
Shell Bottom	July 22–23, 1957	1.0	16	28–31	2.1	5.8	0.8
Cedar Bayou	July 22–23, 1957	1.5	25	28–31	2.4	2.0	2.2
ARANSAS BAY							
Hunt's Pier, Rockport	May 19–20, 1957	2	21	26–28	10.0	9.6	*
Rockport Basin	Aug. 5–6, 1957	1.5	34	31–32	6.1	11.5	1.1
Hunt's Pier, Rockport	Oct. 20, 1957	1.3	19	22–26	6.1	7.8	1.8
A & J Pier, Rockport	July 10, 1959	1.0	20	29–32	3.6	2.4	1.0
Hunt's Pier, Rockport	July 11, 1960	2.0	21	28–32	6.8	10.9	2.7
LOWER LAGUNA MADRE							
Port Isabel, Sta. 1	Aug. 8–9, 1960	1.4	37	28–30	26.3	13.8	0.7
Port Isabel, Sta. 2	Aug. 8–9, 1960	1.4	37	28–30	30.0	19.7	1.0
Port Isabel, Sta. 3	Aug. 8–9, 1960	0.9	37	28–30	22.6	6.7	1.3
Port Mansfield, Sta. 1	July 25–26, 1960	0.9	36	28–31	11.7	4.3	0.7
Port Mansfield, Sta. 2	July 25–26, 1960	1.4	41	29–31	17.3	19.7	0.6
Port Mansfield, Sta. 3	July 25–26, 1960	1.4	39	29–31	22.5	21.4	1.4
BAFFIN BAY							
County Pier, Loyola	Feb. 4, 1957	1.0	79	23–25	16.6	9.6	2.3
County Pier, Loyola	June 12, 1957	1.0	45	29–32	4.2	12.9	1.0
County Pier, Loyola	July 26–27, 1957	0.9	57	28–33	7.8	13.8	0.9
County Pier, Loyola	Aug. 15–16, 1957	0.9	65	29–32	6.9	8.8	0.9
County Pier, Loyola	Nov. 14–15, 1957	1.7	78	15–20	7.1	4.0	1.0
County Pier, Loyola	Dec. 22–23, 1957	0.8	63	19–21	4.0	5.1	1.3
County Pier, Loyola	Sept. 3–4, 1958	1.0	42	28–31	2.4	3.4	0.8
County Pier, Loyola	June 18–19, 1959	1.3	30	28–31	12.2	25.3	1.3
County Pier, Loyola	Sept. 7–8, 1959	0.9	41	27–30	5.9	8.3	0.7
County Pier, Loyola	Dec. 1–2, 1959	1.0	49	14–17	1.7	1.8	1.5
County Pier, Loyola	Jan. 8–9, 1960	1.1	49	12–15	4.7	2.4	1.1
County Pier, Loyola	April 11, 1960	1.1	51	22–25	9.0	19.8	2.4
County Pier, Loyola	June 21, 1960	0.9	61	28–32	3.5	9.7	0.8
County Pier, Loyola	July 12, 1960	1.4	59	28–32	6.4	13.2	*
Off Riviera Beach	June 28, 1960	1.6	53	28–30	19.2	18.4	2.2
Middle Bay	July 5–6, 1960	0.8	51	28–31	4.3	8.3	0.4
Penescal Point	July 7–8, 1960	1.0	47	28–31	3.5	7.3	0.5
Alazan Bay	July 14, 1960	1.3	59	28–33	12.5	13.5	0.8
SEWAGE LAGOONS, TEXAS HEALTH DEPARTMENT DATA							
San Marcos	July 12, 1948	0.8	fresh	27–30	17	14	0.6
San Marcos	July 14, 1948	0.8	fresh	27–30	46	25	1.7
San Marcos	July 20, 1948	0.8	fresh	27–30	21	25	1.1
San Marcos	Aug. 5, 1948	0.8	fresh	27–30	32	27	0.5
SABINE BAY							
Port Arthur	June 27, 1960	2.0	15	27–31	8.8	11.3	2.0
CORPUS CHRISTI BAY							
Ingleside, Moores Pier	June 21–22, 1957	1.4	23	28–30	5.3	7.9	0.7
Indian Point Pier	June 26–27, 1959	3.0	28	28–29	6.8	9.4	*
Indian Point Pier, tropical storm	June 23–24, 1960	3.0	30	26–29	7.8	25	*
Indian Point Pier	June 29–30, 1960	3.0	35	28–32	9.6	12.3	3.0
T Head	June 15–16, 1960	3.1	33	27–30	20.4	21.6	*

TABLE 1—Continued

Gross production, community respiration, and reaeration constants for Texas bays. Data for Redfish Bay and Laguna Madre are in Figures 7 and 21. An asterisk (*) indicates that data were not suitable for computing reaeration constant.

	Date	Depth m	Salinity ‰	Temperature °C	P gm/m²/day	R gm/m²/day	K gm/m²/hr at 0%
North Beach, pier, tropical storm	June 23–24, 1960	2.4	31	26–29	3.8	18.4	*
North Beach, pier	June 29–30, 1960	2.4	34	27–29	13.4	13.7	4.6
Oso Pier	June 30–31, 1960	3.0	29	28–30	7.5	10.8	*
Oso Pier	July 5–6, 1960	3.7	34	28–32	26.6	18.6	*
COPANO BAY							
Bayside	Oct. 20–21, 1957	2.0	18	22–25	1.6	1.7	*
Route 35 bridge	May 19–20, 1957	1.0	13	26–29	5.0	7.2	3.8
Port Bay bridge	May 19–20, 1957	1.0	30	26–31	3.6	4.3	0.4
Bayside, pier	Aug. 8–9, 1957	1.5	12	30–32	5.0	14.7	3.4
Bayside, pier	July 11–12, 1960	1.5	6	28–31	10.5	24.1	2.7
Port Bay bridge	July 11–12, 1960	0.9	14	27–32	14.0	22.0	0.9
MATAGORDA BAY							
Lavaca Bay Bridge	June 17–18, 1957	1.5	5	29–30	1.0	7.8	1
Lavaca Bay Bridge	July 15–16, 1960	1.7	1	29–32	10.4	4.0	2
Tres Palacious, pier	June 17–18, 1957	1.0	4	29–31	3.8	5.8	0.8
Tres Palacious, pier	July 14–15, 1960	1.0	3	29–32	12.5	0.5	1
Caranchua Bay Bridge	July 4–15, 1960	0.9	1	28–34	6.0	4.4	0.6
SLOUGHS AND BOAT HARBORS, Port Aransas							
Shell Shop Pond, Fig. 2, No. 2	July 1–2, 1957	1.0	26	28–30	5.3	11.7	1.3
Shell Shop Pond	July 21–22, 1960	0.4	39	29–37	14.7	13.7	0.3
Shell Shop Pond	July 27–28, 1960	0.4	39	29–31	5.8	10.0	*
Shell Shop Pond	Aug. 3–4, 1960	0.4	39	29–35	12.0	5.5	0.3
Shell Shop Pond	Aug. 10–11, 1960	0.4	38	30–36	11.6	9.1	*
Shell Shop Pond	Aug. 16–17, 1960	0.4	36	30–34	10.6	6.1	0.4
Shell Shop Pond, after hexadecanol added	Aug. 18–19, 1960	0.4	36	30–35	11.0	7.4	0.3
Port Aransas Beach pool near jetty, Fig. 2, No.1	July 1–2, 1957	0.15	25	27–32	1.5	3.7	0.3
Pond, Fig. 2, No. 3	July 5–6, 1960	0.3	30	27–36	3.0	4.3	*
Pond, Fig. 2, No. 3, after fertilization	July 18–19, 1960	0.3	35	27–36	12.0	12.7	0.3
Pond, Fig. 2, No. 3	July 21–22, 1960	0.3	35	28–37	11.4	9.1	0.2
Pond, Fig. 2, No. 3	July 27–28, 1960	0.3	34	29–36	10.0	10.2	0.4
Pond, Fig. 2, No. 3	Aug. 3–4, 1960	0.3	30	28–36	7.1	6.5	0.2
Pond, Fig. 2, No. 3	Aug. 10–11, 1960	0.3	45	29–36	8.0	5.8	0.3
Pond, Fig. 2, No. 3	Aug. 16–17, 1960	0.2	34	30–36	3.2	1.7	0.5
Pond, Fig. 2, No. 3, hexadecanol added	Aug. 18–19, 1960	0.2	34	30–35	4.6	5.7	0.2
Ferry Road algal mat, Fig. 2, No. 4	July 5–6, 1960	0.13	35	27–37	2.9	2.2	0.16
Ferry Road algal mat, trace metals added	July 18–19, 1960	0.13	40	27–38	5.4	6.6	0.26
Ferry Road algal mat	July 21–22, 1960	0.13	40	27–39	6.6	6.6	0.27
Ferry Road algal mat, Fig. 2, No. 4	July 27–28, 1960	0.05	....	26–40	....	....	....
City Launching Basin, (by G. Kone) Fig. 2, No. 5, Sta. a	July 25–26, 1959	2	33	30–32	4.3	4.4	0.6
City Launching Basin, (by G. Kone), Sta. b	July 25–26, 1959	2	34	29–31	4.2	4.7	0.8
City Launching Basin, (by G. Kone), Sta. c	July 25–26, 1959	2	34	29–31	5.3	9.4	2.9
City Launching Basin	Aug. 10–11, 1959	2	34	30–32	9.8	9.6	1.6
City Launching Basin	July 5–6, 1960	2	32	29–32	6.8	9.7	1.2
City Launching Basin	July 18–19, 1960	2	38	30–32	18.0	9.7	1.8
City Launching Basin	July 21–22, 1960	2	39	29–33	3.8	1.4	1.3
City Launching Basin	July 27–28, 1960	2	39	30–33	....	....	....
City Launching Basin	Aug. 3–4, 1960	2	32	30–33	17.7	6.0	1.0

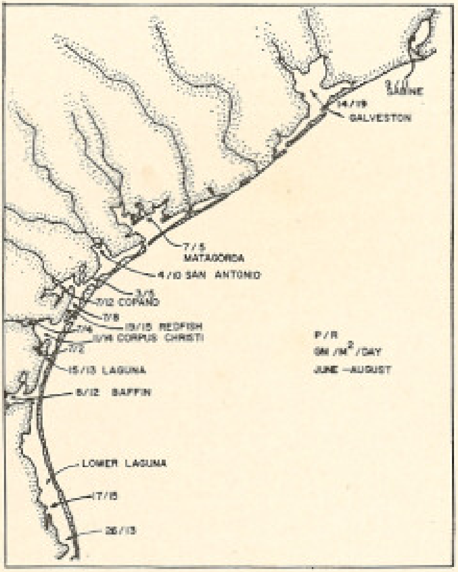

FIG. 9. Synoptic map of gross photosynthesis (P) and twenty-four-hour respiration (R) in Texas bays in June, July, and August, 1960. Each value is given in gm oxygen/m²/day. The upper value is gross photosynthesis; the lower value is total community respiration. Galveston values in 1961, July 15–19: Eagle Point, West Bay, and Lower-center of Trinity bay (field assistant, N. Vick). Each number is a mean of three.

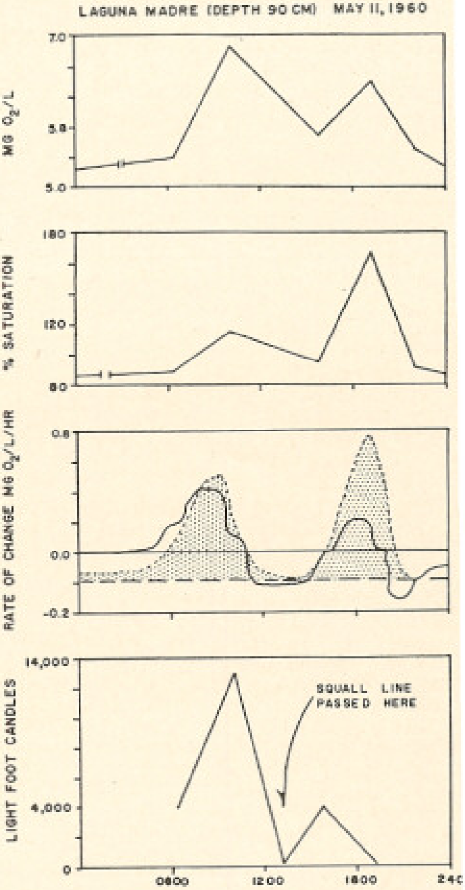

FIG. 10. Diurnal curve in the Laguna Madre May 11, 1959, showing the passage of a cold frontal squall line with a zone of heavy cloudiness in the middle of the day. Salinity 49 ‰, depth 0.9 temperature range 24 to 24°C, wind light except 60 mph during squall passage.

Whereas the front bays (Laguna Madre and Redfish Bay) are shallow and often grassy, the back bays tend to be deeper with insufficient light reaching the bottom for fully developed production. Where they can develop, the benthic communities are generally more fertile than the plankton communities as illustrated by data in Table 1.

High gross productivity is correlated with the establishment of a stable community with its self-contained nutrient cycle. Thus the very high salinity conditions of 40 to 70 ‰ in Baffin Bay and Laguna Madre although unfavorable to particular species are apparently not detrimental to overall production and respiration since highest values are obtained in these regimes. Where evaporating conditions are developing, nutrients are conserved, concentrated, and biota may be stabilized.

The general patterns of metabolism with time and space were outlined in Figs. 1–9. Next consider some special cases.

METABOLISM DURING PASSAGE OF A DENSELY-CLOUDY COLD FRONT

On May 11, 1959, a diurnal curve was taken in the Laguna Madre in which a norther passed in the middle of the day. The data are presented in Fig. 10. As indicated in the foot candle graph the frontal cloudiness was sufficient to reduce the light available to photosynthesis to 5% of that which preceded and followed the passage of the sharp frontal squall area. An interruption of photosynthesis was produced by the interruption of light. Similar instantaneous changes in photosynthetic rate have been observed with changes in cloud cover in many graphs.

METABOLISM DURING DAYS OF MINIMUM TEMPERATURE IN WINTER

In the seasonal record of metabolism in Fig. 7, the winter days reported are unrepresentatively high since the data were generally collected between cold spells on relatively sunny days and at times of higher temperature. In the series for Laguna Madre, February 24, 1960, however, a special effort was made to obtain data during one of the cold, cloudy periods accompanied by the strong north winds typical of winter northers in Texas.

Examination of the oxygen graphs in Fig. 11 shows the effect of temperature change in modyfying the oxygen content of the bay waters. With thirty mile per hour winds

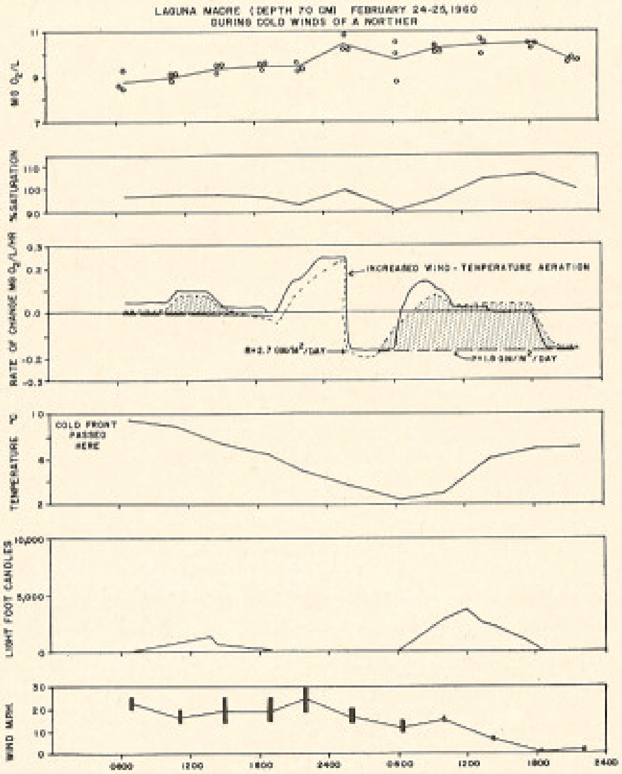

FIG. 11. Diurnal oxygen curves for Laguna Madre, February 24 and 25, 1960, during the weather regime associated with passage of a cold norther and later return to more normal temperatures. Salinity 31 ‰, depth 0.70 m.

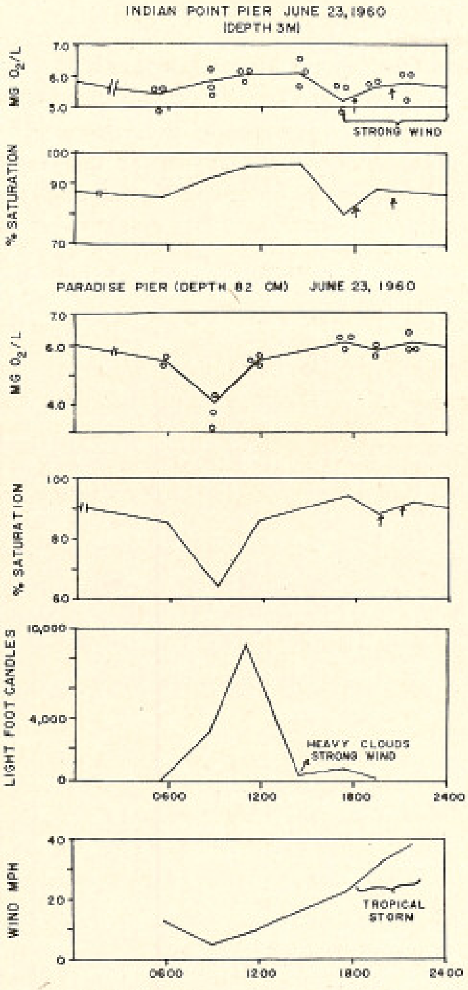

FIG. 12. Diurnal curves at two stations in Corpus Christi bay June 23, 1960, as a tropical storm approached, accelerating winds, and lowering heavy clouds. This is an example of the effect of an increasing reaeration rate during the course of the day.

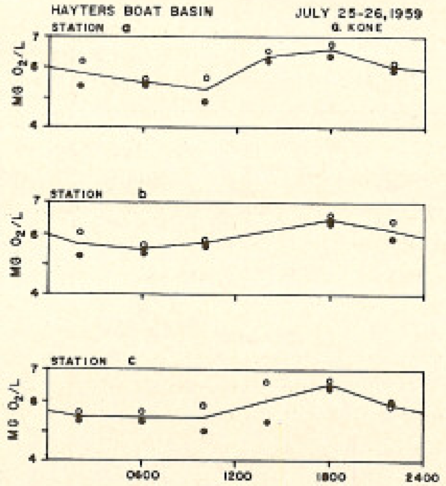

FIG. 13. Diurnal curves taken by Miss Gertrude Kone in a new small boat harbor, Port Aransas, Texas, July 25–26, 1959. Clear circles are surface samples; solid circles are bottom samples. See Fig. 2 for map showing stations a, b, and c.

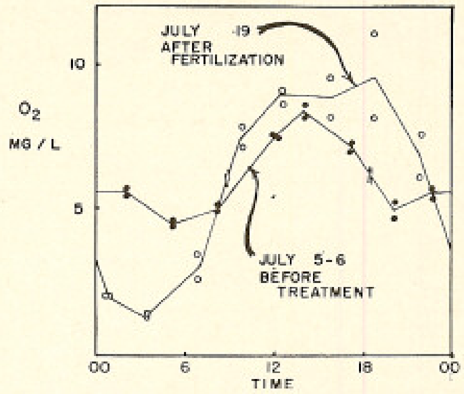

FIG. 14. Diurnal curves for the Oppenheimer House Slough before and after fertilization with nitrogen-phosphorus fertilizer. See Fig. 2, pond No. 3.

blowing polar air over bays 0.5 to 1 m deep there was a rapid fall of temperature of the water, corresponding increase in saturation capacity of the water, and influx of oxygen by diffusion. Under conditions of rapid diffusion due to wind agitation, conditions are not optimal for application of the diurnal curve methods. Nevertheless when the diffusion correction was applied in the usual manner and the oxygen that had diffused in was removed from the rate of change curve (Fig. 4), a definite though small photosynthesis was found. Even though temperature changes are large and rapid in the bays in winter, the metabolism and photosynthesis of the communitties does continue. Some acclimation is suggested by the greater respiration the second day.

During the same period a 24 hour dark-light experiment was run in triplicate with bottles at surface and bottom. On an area basis plankton metabolism estimated from bottles was 0.28 gm/m^2/day respiration and 0.49 gm/m^2/day gross photosynthesis. As in previous comparisons of bottle and freewater data, higher values in the freewater indicate importance of bottom components (Odum and Hoskin, 1958).

COMPARISON OF METABOLISM ON SUCCESSIVE CLEAR DAYS AND CLOUDY DAYS

In the *Thalassia-Diplanthera* grass of Redfish bay diurnal curves were taken for a pair of successive clear and coludy days in winter, January 31-February 1, 1957, and for a pair of successive clear and cloudy days in summer, August 10–11 and August 13–14, 1960. The data in Table 1 indicate a very large range in photosynthesis from day to day correlated with cloudiness. In winter the sunny day was 50% more productive: (clear day, $P = 6.3$ gm/m^2/day; overcast day, $P = 3.9$ gm/m^2/day); in the summer example 4 times more productive; (clear day, 10,000 foot candles at noon, $P = 38.5$, $R = 33.0$ gm/m^2/day; cloudy day, 3,000 foot candles at noon, $P = 8.5$, $R = 7.9$ gm/m^2/day). Apparently the respiration was a function of the photosynthesis since it diminished on the cloudy day. Beyers (1962) found a close correspondence between community respiration and community photosynthesis in microcosms from day to day, P depending on the preceding R and vice versa.

METABOLISM DURING APPROACH OF A TROPICAL STORM

On June 23, 1960 a diurnal curve was obtained at two stations in Corpus Christi Bay as a tropical storm moved in. Data are presented in Fig. 12 and diurnal computation made on the mean curve. The winds increased from early morning at 5 mph to 40 mph by sunset occompanied by lowering ceilings and heavy rain. Reaeration was maximal by evening with waters swirling around the bay at a great velocity in water about 3 m deep. By evening the changing reaeration constant was 2 to 3. In spite of the tremendous reaeration rate, the oxygen remained in equilibrium below saturation presumably due to increasing respiration. The computed respiration rate necessary to balance reaeration was higher than usual for Corpus Christi Bay as might be consistent with high temperature, extensive agitation, and resuspension of bay bottom materials under maximum winds. The photosynthesis was measurable in the morning while the light intensity was appreciable before the onset of heavy afternoon clouds. The analysis of this curve is an example of use of the diurnal methods in a complex situation. Complex analysis cannot yet be turned over completely to routine assay.

METABOLISM IN A SMALL BOAT HARBOR

In spring, 1959, a small boat harbor was dredged into the land of the bar island at Port Aransas producing a stagnant arm of the sea about 4 m deep, 30 m wide, and 300 m long (Fig. 2). Shortly after its formation in summer diurnal curves were run for 3 stations (Fig. 2: a, b and c) in this body by Miss Gertrude Kone as part of course requirement of General Marine Science with the results in Fig. 13. Data from the deeper of two sampling levels indicated a greater respiration than at the surface level, although stratification was not sharp. Computation of production was made with the mean of top and bottom samples.

After a year of heavy use by small boats, curves were again analyzed for the summer of 1960 with the results in Table 1. The use by the boats, fuel leakages, and other localized pollutions had apparently no great effect at that time. In spite of the considerable metabolism and sheltered nature of the basin, anaerobic conditions did not develop. There was considerable range in metabolism from day to day (1.4–18 gm/m^2/day).

METABOLISM OF SLOUGHS

On the margins of the bays are small hollows, depressions, and pools at intertidal level containing 0.1 to 1 m of water. Some of these are connected with the main water body; others are isolated from normal water exchange. A series of measurements of metabolism was made in these sloughs. These bodies generally lack the strong circulation of the wind driven motion of the broad days of similar depth, but some have special localized sources of nutrients from pollutions, land drainage, or other cause. Diurnal curves were run on some of these sloughs as reported in Fig. 2, 14–16, and Table 1.

Whereas the daily range of oxygen was maximal in these bodies because all of the metabolism was compressed into a very thin layer, with the exception of the shell shop pond, the total metabolism per area (3–9 gm/m^2/day) was not as great as in some of the larger bays that were better mixed and less disturbed such as Redfish Bay and Laguna Madre. All intertidal waters tended to be subjected to catastrophic drying during extremely low sets of the Gulf when water drained out of the bays for several days. Turbid flooding occurried at high tides, and fresh water flooded in during heavy rains.

During the period the shell shop pond was receiving fish offal and domestic pollution. Photosynthesis and respiration rates of that slough were greater than in the other littoral waters measured (5–15 gm/m^2/day, Table 1).

FERTILIZATION IN SLOUGHS

In Fig. 14 are graphs for Oppenheimer House Pond, a small slough in which 50 pounds of nitrogen and phosphorus fertilizer powders were added July 18, 1960. As in other fertilization work in fish ponds, there was an immediate stimulation of photosynthesis (Table 1). Apparently the concentration of trace nutrients being maintained by the internal P-R cycle in the slough was less than the new concentrations which developed when the fertilizer was added. Subsequent measurements indicated a reurn to prefertilization values by the end of August a month later (Table 1). Respiration values followed photosynthesis values.

METABOLISM IN A WATER FILM SYSTEM

One of the important ecosystems of the south Texas bay margins is the blue-green algal mat growing in films of water about 10 cm in depth. Diurnal curves in such systems as in the example in Fig. 15 provide some insight as to the kind of environment and productivity.

In spite of the extreme shallowness of the water, the range of oxygen was tremendous from anaerobic conditions to 240 per cent supersaturations in the course of the day. Contrary to expectations based on the theory that shallow waters are well aerated, the aeration is less effective in moderating the metabolism in the film community than in deeper systems. The action of metabolism tends to be concentrated in such

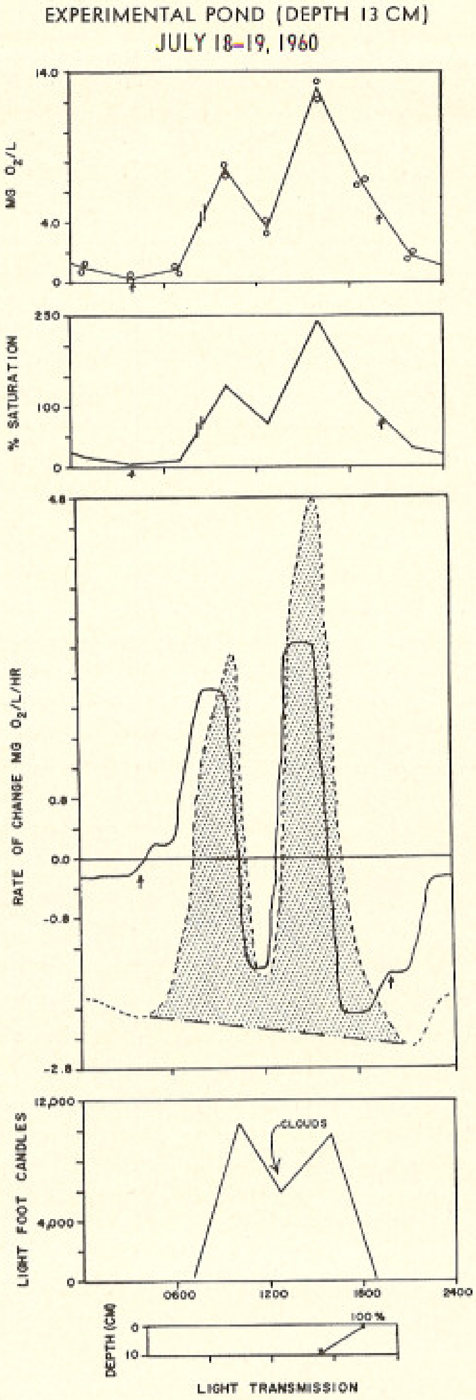

Fig. 15. Diurnal curve in a very shallow slough with 13 cm water over a benthic algal film community, along Ferry road, Port Aransas, July 18–19, 1960, salinity 39.6 ‰, wind 3–10 mph, uniform during period. See Fig. 2, No. 4.

a thin layer that diurnal changes are very large. The reaeration constant, on the other hand, on an area basis diminishes with depth (Fig. 3). In the example in Fig. 15, K is 0.25 gm/m^2/hr/100%, and aeration does not keep up with the wild swings of the concentrations in the film. For example just before noon, clouds diminished the light intensity as recorded in a drop from 10,000 to 6,000 foot candles. As instantaneous and marked drop in oxygen content occurred (Fig. 15).

It may be postulated that the reason for the dominance of the blue green algal mats in waters at 10 cm and not at greater depths is the anaerobic nighttime period in the film systems. Apparently the shallowest systems in the Texas bays are the only natural communities which regularly go anaerobic at night. The blue-greens survive.

The temperatures may also have a role in causing unusual biota. The diurnal range of temperature from 27 to 39°C in the very shallow waters and the wide fluctuation of oxygen contents tends to eliminate most consumer species thus favoring a net deposit of organic matter. The possible role of the algal mats in organic sedimentation has been already discussed (Fisk, 1959).

Hexadecanol Experiment in a Slough

Twelve pounds of hexadecanol were broadcast by hand on August 17, 1960, on water and marginal muds of each of two slough ponds (Fig. 2: Oppenheimer House Pond (No. 3) and Shell Shop Pond (No. 2) after diurnal curves had been made previously. Surface water ripples were visibly damped as the material was cast on the water in flakes, but by the end of the 24 hour period there was no sign of the hexadecanol over the water and the ripples were back to normal. Metabolic values were not markedly changed although there was possibly some increase in respiration over photosynthesis (Fig. 2 and Table 1). Harris and Meinke (1960) also reported an increase of bacterial action in sediments of fresh waters receiving hexadecanol due to metabolism of the solid alcohol material by the bacteria.

Metabolic Rates of Sewage Ponds

During World War II the Texas State Health Department made some studies of oxygen in experimental sewage lagoons. Some of these data were made available for the purpose of computing the total production and respiration. The data were derived from an unpublished report prepared by V. M. Ehlers, T. W. Ray, and E. C. Nelson in 1949.

The pond on the average was 0.75 m in depth, 41 m long, and 2.4 m wide. Supplementary lights were provided at one end. Some difference in oxygen values were found with about 1–4 ppm more oxygen in the lighted end. In recomputing the graphs for purpose of comparison with the natural bays, the data for the two ends of the long lagoon were averaged as presented in one series in Fig. 16. As included in Table 1 production ranged from 14 to 46 gm/m^2/day with respiration in a similar range. P exceeded R in 3 of the diurnal curves but R was in excess in the fourth.

Respiration Excess in Back Bays

The back bays extending away from the beach line and receiving rivers developed respiration in excess of photosynthesis (Table 4; Fig. 1, 6, 17 and 18) suggesting a consumption of organic matter from an imported or previously stored source. R was greater

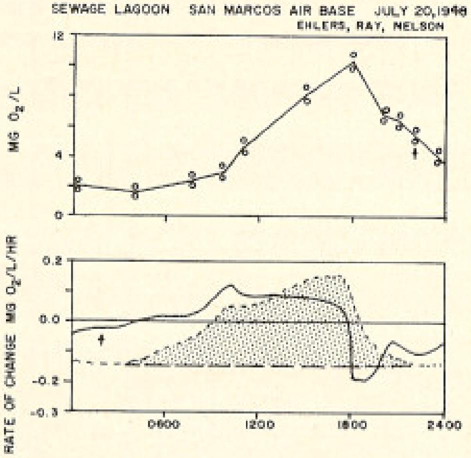

Fig. 16. Diurnal oxygen curve in a freshwater sewage lagoon, San Marcos, Texas, July 20, 1938. Data from Ehlers, Ray and Nelson. Depth 0.75 m; P, 21 gm/m²/day; R, 25 gm/m²/day. K = 1.05 gm/m²/100% deficit.

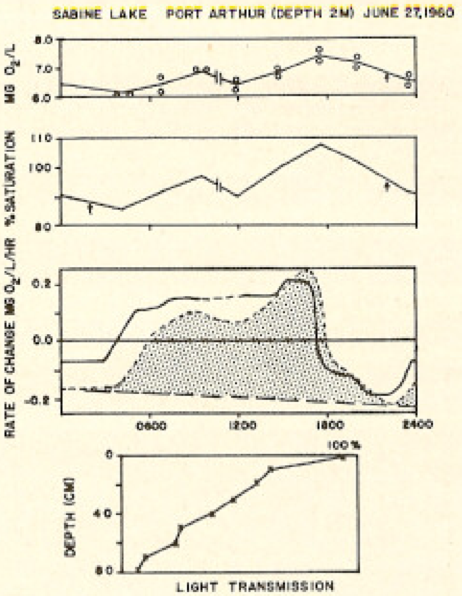

Fig. 17. Diurnal curve for Sabine Lake, Port Arthur, Texas, June 27, 1960. Salinity 15.4 ‰; depth 2 m.

than P at times of high turbidity both in low salinity conditions and in very high salinity conditions. Note frequent low P/R ratios for Baffin, Sabine, Lavaca, Corpus Christi, Copano and San Antonio Bays (Table 1). Baffin Bay is in a very arid area and was observed with an excess of respiration over photosynthesis for extended periods. The bay was continuously turbid suggesting a runoff of organic matter after cloudbursts over the arid lands of the surrounding King Ranch, little-covered with vegetation. Whereas the rains coming in floods were not frequent enough to equal evaporation, runoff was apparently adequate to supply the bay with enough particulate or other organic matter to maintain consumption in excess of photosynthesis.

Upper areas of San Antonio Bay at low salinity were observed with low P/R ratios near the bay delta of the Guadalupe River on two occasions also (Table 1). The Louisiana Bayou curves cited in a later paragraph are similar.

Metabolism after Floods

In 1960 a major flood developed in the Port Lavaca area with 15 inches rain causing the salinity of the arms of the Matagorda bay to fall to oligohaline amounts (less than 1 ‰). A diurnal curve measured in the headwater area during the flood runoff is presented in Fig. 19. Photosynthesis exceeded respiration. It is rather remarkable that photosynthesis was relatively high immediately after so sudden an upset. Apparently there are not always excesses in respiration in the runoffs. The quick recovery of the headwater producers was further established by Siler and Odum in an experimental pond microcosm with oysters and low salinity waters in which flooding rain waters were introduced. Photosynthesis returned to normal in several days.

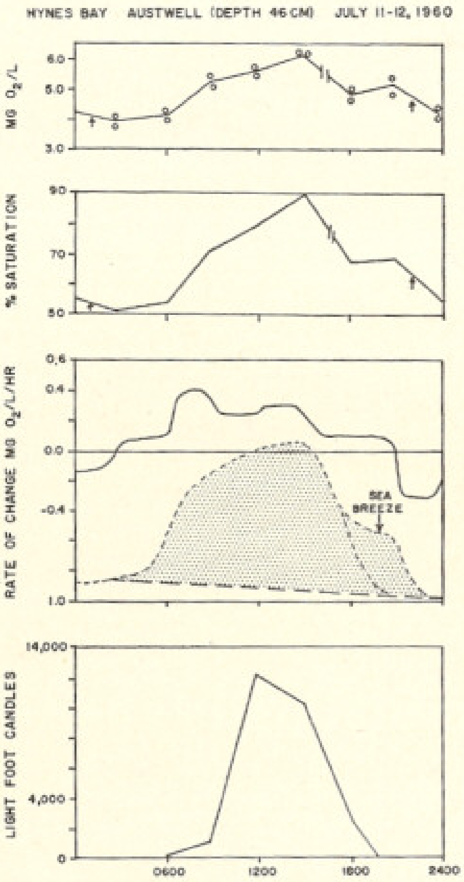

FIG. 18. Diurnal curve for Hynes Bay in San Antonio Bay, Texas, July 11–12, 1960. Salinity 1.8‰; depth 0.46 m; wind 12 to 15 mph in afternoon, 0 to 5 mph later at night.

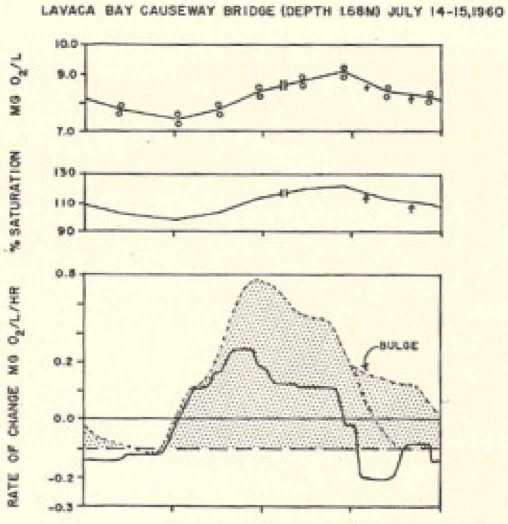

FIG. 19. Diurnal curve from causeway bridge in Lavaca Bay showing metabolism after a flood, July 14–15, 1960. Salinity 1.1‰, depth 1.7 m; wind 12–14 mph in the afternoon diminishing to calm in the morning.

METABOLISM AFTER DREDGING IN REDFISH BAY (Turtle Grass)

Another kind of inflow of turbid matter containing organic substrates occurred as a result of dredging of an intra-coastal channel near Redfish bay. Two diurnal curves were made during the dredging while the clouds of turbid water were drifting over the stations. The first off Bishop Pier in 2 m water March 10–11, 1959, at salinity 18.2‰ produced values: P, 3.0 gm/m^2/day and R, 12.4 gm/m^2/day. The second curve near Ransom island in 1 m depth Aug. 5–6, 1959, over grass flats at salinity 29.8‰ yielded values, P, 13.6 gm/m^2/day and R, 17.3 gm/m^2/day. Thus in both cases respiration much exceeded photosynthesis during the dredgings.

After the dredging a light layer of silt was deposited over the turtle grass flats as described elsewhere (Hellier and Kornicker, 1962). It is apparent that respiration exceeded photosynthesis, possibly due to the consumption of organic matter added with the spoil sediments.

The photosynthesis was not much diminished during or after dredging as compared with data from a previous year. The additional respiration due to extra organic matter did not apparently interfere with normal production. High production and dense grass found after dredging may have resulted from release of nutrients.

METABOLISM IN AN ENCLOSURE OVER TURTLE GRASS

In Redfish Bay in June 1958 a fiber glass enclosure was constructed with 3 fiber glass sheets each 3 m long arranged in a triangle so as to make a tank. This enclosure was set over the turtle grass beds in 0.5 m depth at station 2 in Redfish bay. On June 10 a diurnal curve was run on the inside and on the outside. The mean curves are similar as indicated in Fig. 20. Metabolism was similar outside the enclosure (P, 6.4 gm/m²/day; R, 11.8 gm/m²/day) to that inside the enclosure (P, 5.9 gm/m²/day; R, 11.1 gm/m²/day). The graph for the outside water was slightly more irregular probably due to some heterogeneity of water drifting over the flats. Respiration exceeded gross photosynthesis on this day as throughout the season following the first dredging in March that released a light layer of turbid materials into the grassy areas. During this period the wind ranged from 5 to 18 miles per hour.

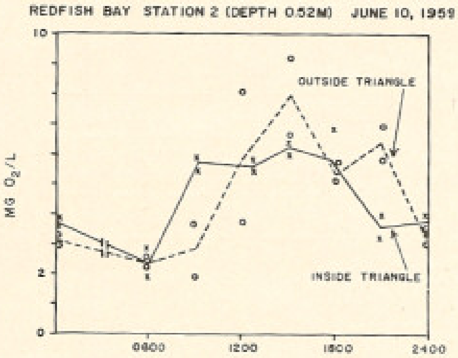

FIG. 20. Diurnal curves over turtle grass beds in Redfish Bay inside and outside a fiberglass enclosure, June 10, 1959. Salinity, 28 ‰; depth 0.5 m. Computations based on the inside curve yield: P, 5.9 gm/m²/day; R, 11.1 gm/m²/day. Computations from the outside curve are: P, 6.4 gm/m²/day; R, 11.8 gm/m²/day.

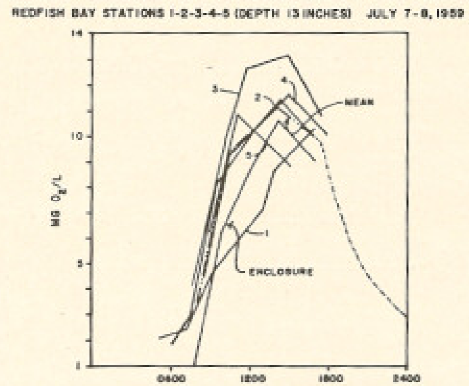

FIG. 21. Diurnal curves over turtle grass beds in Redfish Bay inside a fiberglass enclosure and in 5 outside stations July 7–8, 1959. In this figure each point is the mean of two separate Winkler analyses. Salinity, 32.8 ‰.

Later on July 7 during a period of extreme shallow water (0.3 m) in spite of difficulties in getting into the bay, measurements were taken at 5 bay stations and again in the enclosure. The data are indicated in Fig. 21 with each point based on duplicate samples. A computation for the whole bay based on the mean of all the data indicated a gross production of 13.8 gm/m²/day and respiration 12.3 gm/m²/day. The grass beds were prostrate preventing appreciable circulation. Temperatures in the afternoon reached 33–36°C. Oxygen levels were slightly lower in the enclosure especially at dawn indicating a slightly greater respiration relative to photosynthesis in the enclosure at this time, although production levels were still high.

These results indicate that enclosures can be placed over turtle grass beds for experimental purposes without immediately upsetting community metabolism.

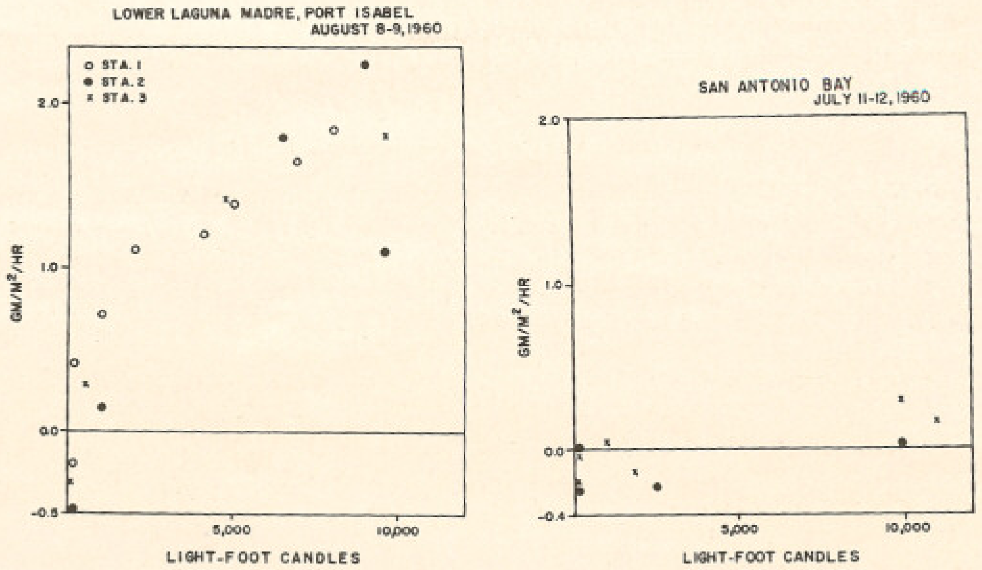

Fig. 22. Gross production as a function of light intensity in foot candles including data from different times of day. The left figure was taken from a grassy, relatively clear bay, Lower Laguna Madre, Aug. 8–9, 1960; the right figure was taken from a more turbid bay, San Antonio bay, July 11–12, 1960; solid circles, Hynes Landing; crosses, Gonzalez camp.

METABOLISM IN A LOUISIANA BAYOU

A pair of diurnal curves were made during sunny weather in a low salinity bayou at Hopedale, Louisiana, April 21, 1960 prior to dredging of the Mississippi River by-pass channel. The water in this area slides back and forth with the tide through small brackish lakes and channels among islands of marsh grass. One curve was taken at the margin of open water of Lake Borgne at about 1 ‰ and the other in Hopedale slightly more seaward at high salinity of 5–6 ‰. The oxygen change diurnally was very slight in both curves. Although the graphs were not as regular as those in more homogeneously mixed bays, there can be no doubt about the small amplitude of the metabolism. Computing metabolism for an average depth of 2 m, gross photosynthesis values found were 1.8 and 2.6 gm/m^2/day; respiration values were 3.8 and 2.4 gm/m^2/day. The waters were turbid with detritus from the marshes. The conditions were apparently similar to those extensively studied at the University of Georgia Marine Laboratory in which metabolism in the water was much less than that of the above-water marshes and dependent upon it (Ragotzkie, 1959).

Discussion

From the case histories presented in the previous section one may draw some inferences about the role of environmental factors in controlling the overall metabolism of estuarine ecosystems.

THE ROLE OF LIGHT, EFFICIENCY

The close correspondence between the diurnal variation in light and the diurnal variation in photosynthesis was illustrated in the previous paper (Odum and Hoskin, 1958).

Further evidence may be found in the 123 additional diurnal curves of photosynthesis, which have the general hump shape of the incident light. The sequence of productivity during passage of the clouded cold frontal zone during a time of relatively high productivity in May (Fig. 10) and the sequence of productivity on successive clear and cloudy days further indicate the close correspondence of oxygen production as measured in the free water and the incident light energy.

To further analyze the relationship of bay photosynthesis to bay light intensity, graphs were drawn of hourly photosynthesis as a function of light intensity as measured with a General Electric exposure meter with a foot-candle scale in the field (Fig. 22). The increase of efficiency with decrease of light intensity familiar in physiological studies of single plants is again verified as characteristic of whole ecosystems (Odum, McConnell, and Abbott, 1958). As discussed in the previous paper, as implied from free water data discussed by Verduin (1957), and as found in microcosm studies by Beyers (1961) the efficiencies in the morning are somewhat higher than in the late afternoon. This may be due to the diminishing nutrients available late in the day as demonstrated for phosphorus in these same bays by Bruce and Hood (1959).

Although one might expect a sewage lagoon (Fig. 16) with high nutrient levels to attain maximum possible efficiency in utilization of light, it may be noted that the natural and unpolluted grass flat systems of the Laguna Madre (Table 1 and Fig. 5, 7, 20, 21 and 22) have metabolism as high as the sewage lagoons. Where gross photosynthesis reaches a maximum at about 40 $gm/m^2/day$ in either a grass flat or sewage lagoon in south Texas in summer, the efficiency of utilization of light energy in available wave lengths is about 6%, based on usable incident radiation of 2850 kg/cal and an approximate conversion of 4 kg-cal/gm oxygen metabolized. Thus both the man made system which was started with abundant nutrients and the natural system that accumulated its own necessary nutrients in a system of geochemical recycling were equally efficient. These efficiencies are similar to those attained in other communities of maximum output elsewhere in the world, the coral reefs, the agriculture of maximum fertilization, the rain forest, the Silver Springs system and others (Odum and Odum, 1960).

Since the photosynthetic output is dependent on incident light reaching the plant cells, the amount of absorption and scattering by turbid materials and water controls the productivity. The higher yields of the relatively clear front bays as compared to the turbid back bays may be related to differences in light energy reaching plant cells. Note photosynthesis at the same light intensity comparing the lower Laguna and San Antonio bay (Fig. 22).

In Fig. 23 are plotted representative graphs of penetration of light with depth. In the very turbid back bays such as Baffin and Copano bay the bay bottoms, although shallow, are illuminated with less than 1% of surface light intensity. The very clear lower Laguna allows more light penetration than Gulf waters at times.

For plankton systems importance of the depth of the mixing layer as compared to the depth of light penetration (euphotic zone) was quantitatively described by Sverdrup (1953) and applied to conditions in turbid estuaries at Sapelo island by Ragotzkie (1959). Where the depth of mixing is great enough to carry the plankton cells into the shade too long for cell photosynthesis to exceed cell attrition, the phytoplankton population cannot survive. The layer is said to be below critical depth. Thus, as waters get deeper, photosynthesis of the grassy-algal bottoms is replaced with a phytoplankton sys-

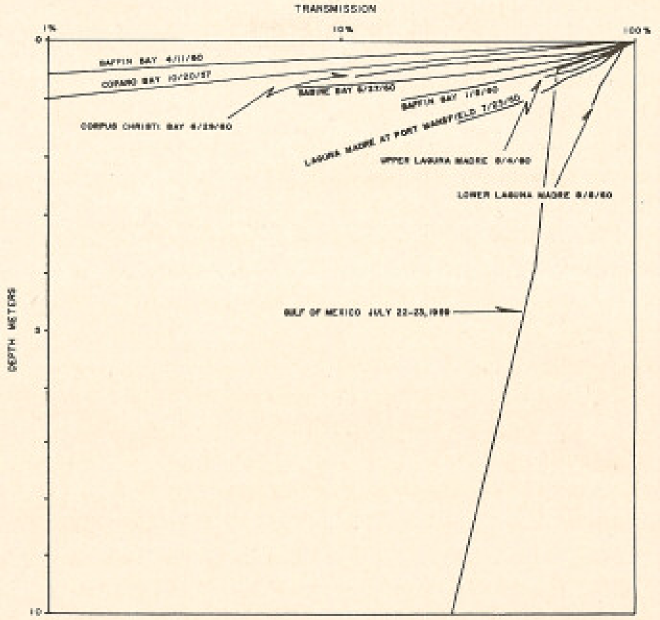

FIG. 23. Percent of surface visible light reaching bottom of Texas bays as a function of depth.

tem, and finally may practically disappear in turbid waters. Murphy (1962) has provided a graph quantitatively relating turbidity and depth according to the quantitative predictions of this theory.

Where the bottom is within the euphotic zone, high productivities are possible even with high turbidities. Waters circulating from deeper zones may not gain in net production except while they are passing over shallow bars. Under such circumstances the production of the whole bay may be a function of the ratio of area shallower than the critical depth to the area deeper than the critical depth.

Whereas turbidity is not disastrous in the shallow depths, it may essentially eliminate photosynthesis in the deeper waters. Fortunately, most of the bays of Texas are shallow enough and productive enough to be above the critical point much of the time. The first objective of any program for stimulating greater primary production in deeper Texas bays should be elimination of sources of turbidity.

THE ROLE OF TEMPERATURE AND COMMUNITY REGULATION

In the Texas bays both light and temperature undergo large annual and day to day variations between summer maxima and winter minima (Fig. 7). In Silver Springs, Florida, at constant temperature it was possible to attribute all of the annual range of photosynthetic production to the variation in incident light, but in the Texas bays some authors have been tempted to attribute some of the winter decline in biological stocks and activity to the decrease in temperature. What evidence there is, however, suggests a minor role for temperature. Low temperature (above freezing) does not in itself preclude high production rates. The basic photosynthetic process is not temperature dependent although temperature affects the output of whole plants studied (Stafelt, 1960).

High rates of photosynthetic and respiratory metabolism are known from adapted ecosystems in arctic climates in summer. Adaptations, successions, and evolutions in an ecosystem can occur to permit high metabolism at low temperature.

In the annual picture temperature does not begin to fall much until the cold fronts begin to pass through in November. The photosynthesis, however, begins to decline markedly (Fig. 7) as soon as the light income begins to decline in July.

As established by many authors the temperatures in the shallow bays follow that of the air masses that blow over them. There may be 15 degree centigrade range from one day to the next in winter. As illustrated in the case history presented for a February norther (Fig. 11), rapidly falling temperatures have a profound effect on the gas exchanges, but do not eliminate the metabolism.

The hypothesis is proposed that the system and its organisms are sufficiently organized in their activity to keep the total metabolism in phase with food conditions as developed seasonally from light energy. In the annual cycle the total community metabolism is somewhat independent of temperature. What proportion of this community regulatory activity may be controlled by the migratory behavior of populations and what proportion may take place within the physiological mechanisms of the single organisms is not known.

The diurnal range of temperature like the diurnal range of oxygen content is a function of the water depth with greater ranges in shallow water. In the water film communities the daytime temperature approaches the upper limit (40°C) for many organisms.

THE ROLE OF TURBID BOTTOM MATERIALS

The release of turbid materials is a dominant feature of the Texas area with organic laden silts and clays released in large quantity into the bays from the rivers, from dredging, from reagitation up from the bottom during storms, and from beach erosion. Turbid materials had two distinct effects on total metabolism as observed in this study. One effect of turbidity in reducing light penetration and thus reducing primary production was discussed in the previous section on light. The other effect was a stimulation of the community respiration apparently due to organic matter accompanying the inorganic turbidity.

In the turbid water of Baffin Bay, in San Antonio Bay, during dredging in two places in Redfish Bay, in the floodwaters in Matagorda Bay, in the Louisiana bay at Hopedale receiving marsh detritus, and in the back bays receiving rivers, respiration was often in excess of photosynthesis suggesting that the import of organic matter was supporting consumption in addition to that produced by plants in situ. In Fig. 24 are data for the hypersaline Baffin Bay in which R exceeded P frequently, especially when salinities fell following rains. These days were like the waters of the Neuse River, North Carolina, in which respiration of a stream exceeded its photosynthesis with much of the consumption supported by organic matter running off the land (Hoskin, 1959). Similar conclusions were drawn by Pomeroy (1959), Ragotzkie (1959), and Teal (1959) in their studies of the metabolism of the Sapelo Island marsh waters.

Although respiration was in excess of production in turbid water studies, the excess was not a large one. In nature respiration was not in excess of photosynthesis by more than a factor of 2. Larger excesses of respiration over photosynthesis have been recorded in marine bays with known pollutions (Odum, 1960).

A complicating aspect of the additions of turbid matter is the stimulus provided to photosynthesis indirectly through the excess of respiration over photosynthesis. Where R is in excess of P, inorganic nutrients accumulate stimulating photosynthesis. Thus the turbid mixtures of organic and inorganic matter both interfere with photosynthesis by shielding light and stimulate it by indirectly raising inorganic nutrient levels.

Studies by Wilson (1961) with the infra-red CO_2 analyzer method for assay of dissolved and suspended organic matter have demonstrated the relatively high concentrations of organic matter found in the Texas bays with greatest concentrations up to 80 mg/l in the turbid back bays so far studied including Baffin and Corpus Christi bays. Excess respiration over photosynthesis of 5 mg/l/day (Fig. 24) would consmue a storage of 80 ppm in about 16 days, but there is rarely decrease in respiration relative to photosynthesis. Apparently the inflow of extra-bay organic matter is keeping up with the consumption since the organic levels and excess respiration over photosynthesis are maintained particularly when the salinity is falling.

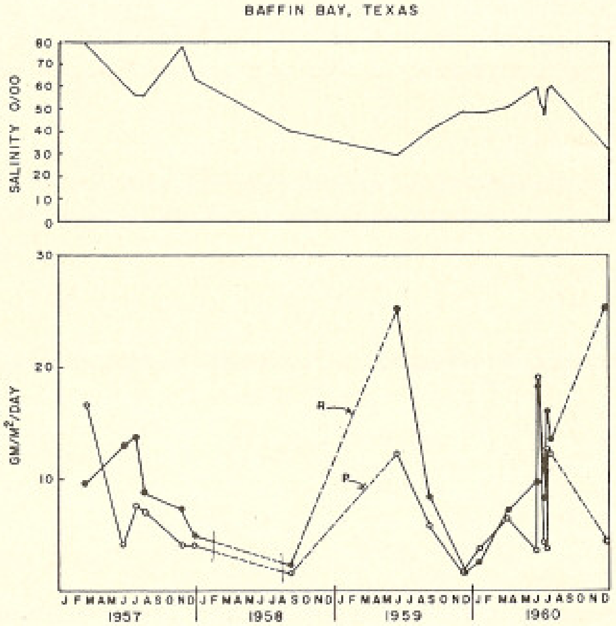

FIG. 24. Metabolic data from Baffin Bay, Texas, during dry and wet periods.

THE ROLE OF AREA AND AGITATION

Physical circulation is a normal requirement for many ecosystems supplying the nutrients for photosynthesis and redistributing the organic matter and oxygen as fuel for consumers. In the Texas bays the areal extent determines the amount of circulation that can develop under the strong winds usual for the area.

Armstrong Price (1947) and others have discussed the area of the bays as a controlling factor on the depth of the bottom. They indicate that in small bays, insufficient wave energy develops to keep the bottoms from filling in with sediment to shallow levels. In deep bays mixing favorable to photosynthesis is partially offset by greater equilibrium depth maintained by scouring in the larger bays. The role of agitation on metabolism is further masked by the rapid settling of the turbid materials during periods of relatively calm weather, when the additional penetration of light tends to offset any unfavorable aspect of diminished circulation. With the interplay of factors of area and agitation it is not easy to select natural experiments that delimit the factors.

A comparison may be made between the metabolism in the small shallow sloughs (Table 1) as compared with the larger but equally shallow bays like the Laguna Madre (Table 1, Fig. 7). Similarly metabolism of enclosed and less agitated boat harbors may be compared with that of the open, well mixed bays (Table 1) of similar depth.

In general the small littoral bodies of water, sloughs, and harbors, in spite of opportunities for nutrient supplement from littoral pollutions did not sustain greater production and metabolism than the larger wind-stirred, freely mixing bays.

THE ROLE OF NUTRIENTS

It is axiomatic that the maintenance of an adequate nutrient supply is essential to the maintenance of maximum gross production. Maintenance of nutrients is accomplished in some systems by the recycling of nutrients from the respiratory consumers. In some systems nutrients are regularly imported balancing those lost. Pomeroy, working in the estuary of the Altamaha river in Georgia (Pomeroy, 1960) showed that where bays receive flushing out of water with floods of low-nutrient, fresh water; accumulated nutrients tend to be flushed out. Such floods also kill off many of the larger organisms so that their stored nutrients are also lost. Hoese (1960) documented a case of such flushing for Mesquite bay.

In Texas bays studied it may be useful to propose three types of systems operating to supply adequate nutrients for high production rates: (a) hypersaline regimes, (b) bottom grass-algal systems, (c) systems near inflows of high nutrient concentrations.

(a) In the high salinity bays, the Laguna Madre and Baffin bay, after long periods of sustained high salinity, nutrients have an opportunity to be accumulated and recycled. As indicated in Table 2, high values of total phosphorus, 2 to 3 mg-atom/m^3, occur in

TABLE 2 Total phosphorus in Texas bays.
Groups of analyses are arranged in order of decreasing salinity.
Analyses by H. Bruce, R. Ward, and C. Oppenheimer

	Number of samples	mg-atom/m^3
HYPERSALINE BAYS, salinity, 50 to 70‰		
Baffin Bay, July 26, 1957	8	2.7–5.2
Baffin Bay, August 15, 1957	9	3.4–4.2
Upper Laguna Madre, July 23, 1957	4	1.4–3.2
Upper Laguna Madre, August 1, 1957	8	3.4–4.2
GULF OF MEXICO, salinity, 33 to 36‰		
Port Aransas jetties, July 15, 1957	8	2.0–2.2
Port Aransas jetties, July 23, 1957	1	1.8
Whistling buoy, Port Aransas, August 10, 1959	4	0.0–1.27
BOAT HARBORS, salinity, 28 to 34‰		
Corpus Christi T head Harbor, August 10, 1959	2	1.6–1.9
Rockport Basin, August 5, 1957	8	2.0–4.0
GRASS FLATS, salinity, 29 to 33‰		
Redfish bay, July 17, 1957	1	1.3
Redfish bay, August 10, 1959	8	0.62–1.38
PLANKTONIC BAY, TURBID, salinity, 10 to 28‰		
Copano Bay, August 8, 1957	8	1.6–2.4
Corpus Christi Bay, July 23, 1957	3	1.2–1.9
Corpus Christi Bay, August 10, 1959	6	0.80–0.97

dry years. The details of the daily uptake and regeneration have been shown by Bruce and Hood (1959). A similar high nutrient state has been established for inland waters in arid climates (Hutchinson, 1957).

Bays that are stable with little flushing are the ones thought to develop higher productivity and nutrients self-regenerated.

(b) In shallow water where bottom communities of grass and attached algae dominate the metabolism, flushing out of water due to floods or due to winter northers that drop the Gulf level are not so serious as in deeper bays, for much of the nutrient reservoir is not in the plankton but in the attached bottom materials. Providing the flushing does not kill the bottom system, the ecosystem can conserve nutrients for sustained high production.

(c) Where high nutrient levels in usable proportions are maintained in the inflowing water, flushing may not be detrimental to nutrient supplies. Nueces Bay and Oso Bay are examples of areas that often receive high nutrient contents due to municipal and industrial effluents.

It is not always possible in field analyses to show when nutrients levels are limiting metabolism or when the reverse is actually the initial cause and effect (inadequate biota and metabolism for storage and circulation of nutrients). If the production is limited by some non-nutrient factor, the impoverished biota may be unable to store high concentrations of nutrients in the geochemical recycling system. In any case, however, the nutrient level may be correlated with the gross production. In Table 2 the higher values of total phosphorus were associated with the areas of higher production in Baffin Bay and Laguna Madre whereas lower values, about one mg-atom/m^3, were found in Corpus Christi Bay.

As the many experiments on ponds indicate (Barrett, 1953; Hepher, 1959), adding concentrations of a nutrient like phosphorus may not have a sustained effect in many instances longer than the time for immediate uptake by the plants. The increase in photosynthesis in the fertilized slough (Table 1) followed by a decline in metabolism in subsequent weeks seemed to follow this pattern. Sustained increases in production require maintaining high rates of nutrient conservation and regeneration. Spot fertilization of the bays of Texas is likely to have the temporary effects found in fishpond work, but large sustained increases in fertility involve developing the nutrient conservation system like those already effective in some bays. Possible measures include development of hypersalinity by diversion of runoffs, the development of more grass flats by control of turbidity and depth, and the channeling of nutrients of municipality and industry into areas to balance rate of flushout.

The photosynthesis in the unfertilized natural grass beds around Port Mansfield (Table 1) was greater than the photosynthesis in the beds around the sewage outfall in Laguna grass flats near Ransom Island. It is doubtful if one can stimulate metabolism much by fertilizing an ecosystem if it already has P equal to R and a fully developed standing crop in stable steady state, geochemically recycling nutrients at rates equal to the maximum photosynthetic demand possible at the available light intensity.

For most of the Texas bays there is considerable opportunity to increase total production and consumption by changing the regime for nutrient supply. There is no reason why diversion of the flushing floods and sustained fertilization cannot maintain many bays much closer to the maximum productivities observed in the lower Laguna Madre in 1960. Such an action program may be expected to double biological output of a half million acres.

POTENTIAL YIELDS

The measurements of gross photosynthesis indicate the effectiveness of light in producing organic matter. In the natural aquatic communities of Texas P and R are often similar, and there is little net gain or loss of organic matter except for fish migrations and detritus export to the open Gulf. This balanced pattern may be changed by artificial management. If means similar to those of terrestrial agriculture can be employed to reduce respiration by weeding of consumers and if outside nutrients are added at a rate adequate to replace the normal supply from respiratory regeneration, then a great part of the gross production might be channeled into organic storage for harvest. Since the rates of maximum gross photosynthesis measured in the Texas bays are equivalent to maximum rates of gross photosynthesis in agriculture, the potentials for eventful harvest and use are about the same.

The grass flats because of their stability, nutrients conservation, and ease of manipulation can be the first of the large marine systems to be managed commercially either for increased fisheries and wildlife or for organized aquatic agriculture, harvesting plant matter.

In arid areas along sea coasts the farming of the sea waters has the advantage over terrestrial agriculture in not being limited by water shortage. The bay waters of arid south Texas are suitable for providing world leadership in management of marine waters for useful purposes.

Summary

1. Further studies were made on the photosynthesis and respiratory metabolism of the marine bays of Texas with the diurnal oxygen method. On the basis of 123 new curves, the characteristics of metabolism of the planktonic and grassy bays have been explored with emphasis on refinement of methods, natural experiments, and special situations. Measurements were included from 9 bays not heretofore studied metabolically. The bays included in this study are all continuously well mixed by the winds without vertical stratifications.

2. Photosynthesis and respiration were generally similar and often in phase although the annual metabolism in single bays ranged from 0.5 gm/m^2/day minimum in winter to 40 gm/m^2/day maximum in summer.

3. In the back bays receiving runoff, respiration often exceeded photosynthesis. Such conditions existed in low salinity bays and also in hypersaline bays after rains.

4. In bays where P and R were equal total metabolism was often greater than where P and R were not in balance and where one or the other part of the nutrient cycle between P and R may have been limiting. Metabolism and phosphorus levels were higher in hypersaline bays in which there was little flushing out by rivers.

5. The reaeration constant as computed from diurnal graphs were related to depth and wind velocity. The area-based reaeration constant K increased with water depth from about 0.1 gm/m^2/hr at 10 cm depth to 5 gm/m^2/hr/100% deficit in bays 4 m deep. The volume based reaeration constant k was fairly constant with depth, about

1.0 gm/1/hr/100% deficit. Reaeration was surprisingly unimportant in the shallowest film communities measured.

6. The volume based reaeration constant increases with wind velocity by a factor of at least 2.

7. Several refinements in the diurnal graphic analyses were introduced to increase accuracy and avoid recurring artifacts. A photosynthetic bulge after sunset was found on many rate graphs of diurnal analysis and identified as an artifact due to seabreeze effects, easily recognizable from data on wind velocities and a convex shape of the post-sunset oxygen graph.

8. Inferences were drawn from studies of particular case histories. Dredging produced a condition in which R exceeded P during dredging. After the shading of the turbidity disappeared, P was equal or higher than before. Respiration was also increased when strong winds stirred the bottom in a tropical storm.

9. The small shallow sloughs and pools isolated from the main bays contained tremendous ranges of diurnal temperature and oxygen content, but on an area basis only one receiving pollutants was as productive and metabolic as the best developed, larger, grassy bays. Film communities went anaerobic at night and developed blue-green algal mats.

10. Some of the graphs indicated a greater respiratory metabolism of oxygen just after dark than before dawn, suggesting diurnal rhythm of respiration related to the photosynthetic output. Efficiency of photosynthesis was slightly greater just after dawn than just before sunset suggesting the stimulatory effect of nighttime R on P.

11. Hexadecanol on two sloughs was temporary in effect and did not greatly affect the diffusion constant or metabolism.

12. A boat basin with active operations of small boats retained apparently near-normal photosynthetic and respiratory metabolism without going anaerobic at any time of night.

13. One sequence of diurnal data from the turbid, low salinity bayous in Louisiana marsh lands indicated a relatively low photosynthesis and respiration in April.

14. An enclosure with fiberglass walls placed over a turtle grass bed for experimental purposes did not immediately disrupt photosynthesis and respiratory metabolism.

15. In representative Texas bays the light of visible wave lengths suitable for photosynthesis penetrating to the bottom averaged about 36% of surface intensity. Turbidities as indicated by extinction coefficients per meter for a visible range photometer without filters ranged from 7.7 per m in turbid back bays to 0.33 in the lower Laguna Madre at Brownsville and 0.11 on the Gulf shelf off Port Aransas. In most bays the critical depth for phytoplankton growth was not often exceeded.

16. A close hour by hour correlation of photosynthesis with light intensity was observed in the daily measurements during passage of fronts, or in comparisons of successive clear and cloudy days. Turbid bays contained much less photosynthesis than some clear bays at similar light intensity.

17. The graph of photosynthesis versus light intensity was without a light saturation point. High efficiency was found at low light intensity, but maximum gross production was found at maximum light intensity.

18. Maximum efficiencies, productivities, and sustained respiration were found in natural, high salinity, grass flat systems with values equal to those in artificial sewage ponds. Values were as great as in tropical reefs with photosynthetic efficiencies as high as other aquatic communities of maximum fertility on earth.

19. To produce maximum total photosynthesis in all of the waters of Texas, measures for management should include: reducing turbidity, eliminating irregular flushing of flood waters, developing grass bottoms, retaining wind driven circulation, and adjusting water depths of shallow and deep areas towards an average depth of 0.5 m.

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