AN ABSTRACT OF THE THESIS OF

John Higgins Lyford, Jr.   for the   Ph. D.   in   Botany
_____(Name)_____   (Degree)   (Major)

Date thesis is presented   *6 May 1966*

Title PRIMARY PRODUCTIVITY AND COMMUNITY STRUCTURE

OF AN ESTUARINE IMPOUNDMENT

Abstract approved   Redacted for Privacy
                         (Major professor)

An impounded estuary was employed to study primary pro-
ductivity, community respiration, and community structure as they
related to seasonal and temporal succession, salinity, and water
temperature. Plankton metabolism was studied by means of the
light- and dark-bottle technique. Benthic community metabolism
was determined by using the "diurnal oxygen curve" method.

Four different physical environments developed due to water
control procedures required in the management of the impoundment.
One environment was saline, two were brackish water, and one was
freshwater. Distinct benthic plant communities developed in each
of these environments, and these communities were named according
to the dominant plants. The Enteromorpha-Melosira Community de-
veloped in the saline environment and accounted for the highest meta-
bolic rates of the entire study. A P/R of 1.36 resulted in the develop-
ment of a large standing crop which dramatically became senescent

during late fall and formed organic ooze on the bottom as well as dissolved and suspended organic matter in the water. The Melosira-Enteromorpha Community developed in brackish water and maintained a P/R of 0. 76. The Melosira-Spirogyra Community developed in the freshwater environment and maintained a P/R of 0. 78, and the Rhizoclonium-Melosira-Synedra Community which developed in brackish water maintained a P/R of 0. 77. The plankton flora was characteristically tychoplankton and the magnitude of plankton metabolic rates was less than that of the benthic communities.

The impoundment maintained a mean P/R of 1. 02 over the entire study period, and was essentially autotrophic, primarily due to the large standing crop developed by the Enteromorpha-Melosira Community. Little exogenous organic material was thought to have been imported into the ecosystem.

PRIMARY PRODUCTIVITY AND COMMUNITY STRUCTURE
OF AN ESTUARINE IMPOUNDMENT

by

JOHN HIGGINS LYFORD, JR.

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1966

APPROVED:

Redacted for Privacy

~~Professor~~ of Botany

In Charge of Major

Redacted for Privacy

Acting Chairman of Department of Botany

Redacted for Privacy

Dean of Graduate School

Date thesis is presented *6 May 1966*

Typed by Marion F. Palmateer

ACKNOWLEDGMENTS

TABLE OF CONTENTS

LIST OF FIGURES

PRIMARY PRODUCTIVITY AND COMMUNITY STRUCTURE
OF AN ESTUARINE IMPOUNDMENT

INTRODUCTION

One of the major objectives to which any science directs itself

is the development of a concept which can be applied broadly through-

out that discipline. The ecosystem, first named by Tansley (1935),

is such a concept for the science of ecology and provides unity be-

tween the study of the individual organisms, the populations and the

community. Lindeman (1942) added a most important facet to the

concept of the ecosystem when he first described the trophic-dynamic

aspect of ecology, in which he emphasized the energy relationships

between members of the communities.

If an ecologist is to study the energy relationships between

members of a community, he needs basic information about the only

organisms that can transform radiant energy into organic compounds

that in turn are available to successive organisms. This fundamental

energy resource is, of course, the autotrophic plant segment of the

community, and the energy which they fix in organic compounds

available to other organisms is referred to as the primary produc-

tivity of the ecosystem. The study of primary production has thus

assumed importance, and the relationship between primary production

and primary and secondary consumers has been studied with some

determination, especially since Odum (1953) described and popu-

larized the subject in his textbook and emphasized the trophic dynamic

approach to ecology. The understanding of primary production in

any ecosystem is essential to the understanding of the nature of that

system, and the subject of primary production has been studied under

many different environmental conditions. Some of these studies are:

in fertilized salt water (Edmondson 1947), in lakes (Jackson and

McFadden 1954, Verduin 1956), in coral reefs (Kohn and Helfrich

1957, Odum 1955), in rivers (McConnell and Sigler 1959, Odum 1956),

in freshwater bays (McQuate 1956), in springs (Odum 1957), in es-

tuaries (Odum 1958, 1963, Park 1958), in salt marshes (Pomeroy

1959), in the open ocean (Nielsen 1957, 1960, Ryther 1954), in tropi-

cal freshwater (Talling 1957), in cold springs (Teal 1957), in artificial

streams (McIntire 1964), and in a tidal creek (Ryther 1958).

The present study examines a unique aquatic ecosystem in the

form of an impoundment that has been constructed from a natural

tidal estuary, and in which water control structures made it possible

to at least greatly influence the salinities present if not to control

them exactly. The impoundment was constructed for the purpose of

raising anadromous fish to smolting size so that eventually upon their

return for spawning the sports fishery of the river and estuary system

would be increased. Since no energy in the form of food or other

organic matter was to be introduced into the impoundment, the rela-

tionship of primary productivity to temperature and salinity, and the

nature of the developing plant communities, assumed utmost impor-

tance. A study of these factors is the subject of this thesis.

DESCRIPTION OF THE STUDY AREA

The impoundment is located in the town of Waldport, Lincoln County, Oregon. Water of a natural tidal estuary, tributary to Alsea Bay and referred to locally as Lint Slough, was impounded by two earthen dams. The main dam (Structure 1) across the mouth of the estuary was designed to control the entrance of sea water by means of two 120 cm tubes extending through the dam. It was possible to exclude all tidal waters from entrance into the impoundment by lowering control doors located on the outside entrance of the tubes. The inside openings were equipped with hinged doors which functioned to permit tidal waters to enter, but would not allow water in the impoundment to flow out. These hinged doors could be lifted, however, so that the entire impoundment could be drained during a series of low tides.

The second earth dam was constructed approximately 1.4 km upstream and blocked the entrance of freshwater of Lint Creek from entering the impoundment. A concrete water control structure (Structure 3) which permitted discretionary entrance of the freshwater into the impoundment was part of this dam. The normal runoff of water from Lint Creek has been diverted around the impoundment by the construction of an earth dike which created a canal running parallel to the length of the impoundment. Freshwater from

Lint Creek, thus, could either be admitted to the impoundment or be diverted and emptied into Alsea Bay outside the main dam.

Approximately midway in the dike a third concrete water control structure (Structure 2) was built. This was designed with two tubes 120 cm in length extending from the impoundment to the canal and with the opening on the under surface so that the more dense seawater entering at the main dam could be siphoned off the bottom and returned via the canal to the salt water bay outside the main dam. Structure 2 could also function in allowing seawater entering the canal at high tide to enter the impoundment. Both uses created a gentle circulation of saline water. The finished impoundment was a narrow body of water approximately 1. 4 km long with a smoothly sloping bottom varying from 1. 5 meters to 0. 6 meters in depth, oriented in a north-south direction, and impounding appoximately 14 hectares of water surface (Figure 1).

Three sampling stations were chosen on the basis of the depth of the water and proximity to the water control structures (Figure 1). Station 1, just inside the main dam, was usually 1. 3 meters in depth and was the first station affected by the entrance of seawater through the main dam. However, this local effect was usually temporary due to the circulation of water caused by wind action and the flow through the water control structures. Frequently, more dense saltwater could be located in depressions on the bottom in the area of this

Figure 1. An aerial photograph of Lint Slough with control facilities drawn in. Numbers indicate sampling stations. The town is Waldport, Oregon.

station, particularly in the old stream channel. Station 2, located approximately 200 meters north of water control Structure 2, was characterized by water 1. 3 meters in depth but was affected less by surface agitation caused by wind than Station 1, and generally tended to support a larger, more stable plant community. Station 3, located 400 meters north of structure 3 was generally maintained at a depth of approximately 0. 6 meters. The bottom was exposed to light at this station more than at Stations 1 or 2 due to clarity and shallowness of the water. Trees at this station afforded protection from prevailing winds so that the water generally was calm.

METHODS

Primary productivity and community respiration of the plankton were measured by the light- and dark-bottle method introduced by Gaarder and Gran (1927), and since used extensively in both fresh-water and marine aquatic environments. A 19 liter polyethylene carboy was filled with water from the impoundment and gently swirled for several minutes in order to distribute evenly the dissolved oxygen present in the water. Water was then siphoned into two initial 300 ml Biochemical Oxygen Demand (BOD) bottles to which immediately were added chemicals to fix the dissolved oxygen for later Winkler analysis. Then, two clear 300 ml BOD, and two darkened 300 ml BOD bottles were filled. The light and dark bottles were suspended at 45 cm on a line supported by a buoy and incubated for 24 hours. All samples from July to October 1964 were analyzed for dissolved oxygen by the Alsterberg modification of the Winkler method, and afterwards, be-cause of the presence of additional organic matter in the water from November 1964 to November 1965, by the Pomeroy-Kirschman-Alsterberg modification of the Winkler method (APHA 1960). Gross primary productivity was calculated by multiplying the difference in dissolved oxygen content between the light and dark bottles by the water depth to get the grams of oxygen produced per square meter per day. Community respiration, likewise, was calculated from the

difference in dissolved oxygen between the initial bottle and the dark

bottle, and then by multiplying by the water depth, arriving at a value

in grams of oxygen per square meter of surface per day. A sample

calculation for the 23-24 September 1964 sampling period follows.

Duplicate light- and dark-bottle samples were taken and their means

are in parentheses.

Initial Bottle	Light Bottle	Dark Bottle
9. 80	9. 14	9. 04
9. 72	9. 14	9. 06
(9. 76)	(9. 14)	(9. 05)

LB - DB = Gross production of 0.09 g $0_2/m^3/day$

$$(0. 09) \times (. 66) = 0. 06 \text{ g } 0_2/m^2/day$$

IB - DB = Community respiration of 0. 71 g $0_2/m^3/day$

$$(0. 71) \times (. 66) = 0. 47 \text{ g } 0_2/m^2/day$$

Structure of the plankton community was determined from sam-

ples prepared by siphoning a sample of water from the 19 liter

carboy into a polyethylene container and fixing the sample with for-

malin. This sample was later either centrifuged with a Forst con-

tinuous flow centrifuge, or filtered onto an AAWG 0. 8 μ 47 mm

Millipore filter (MFC 1966). Plankton organisms thus concentrated

were examined microscopically to determine species present and

permit estimation of their relative abundance. Net tows were made

with a plankton net of #20 mesh silk bolting cloth, and these samples

were examined alive so that the presence of forms quickly destroyed by fixation, such as small flagellates, could be determined.

Benthic primary production and community respiration were determined graphically by use of the "diurnal oxygen curve" described in detail by Odum and Hoskin (1958). Duplicate water samples were collected at a depth of 45 cm at each of the three sampling stations every three hours for a 24 hour period. These water samples were fixed chemically in the field and later analyzed for dissolved oxygen by the modifications of the Winkler method mentioned above. At the same time temperature and salinity were determined at 30 cm intervals from the bottom to the surface using an Industrial Instruments Salinometer Model RS-5. Salinities remained consistent, but temperatures were plotted throughout the 24 hour sampling period (Figure 2A). Observations of wind direction and force, surface action of the water, and density of cloud formation were recorded. The means of the concentrations of dissolved oxygen of the duplicate samples taken each three hours were plotted on millimeter graph paper below the temperature curve (Figure 2C). The percentage saturation of the water by dissolved oxygen was determined by dividing the actual dissolved oxygen concentration in the water sample by the amount water could hold at that particular temperature and salinity. These saturation values were obtained from a nomogram developed by Truesdale (1955). A percentage saturation curve was
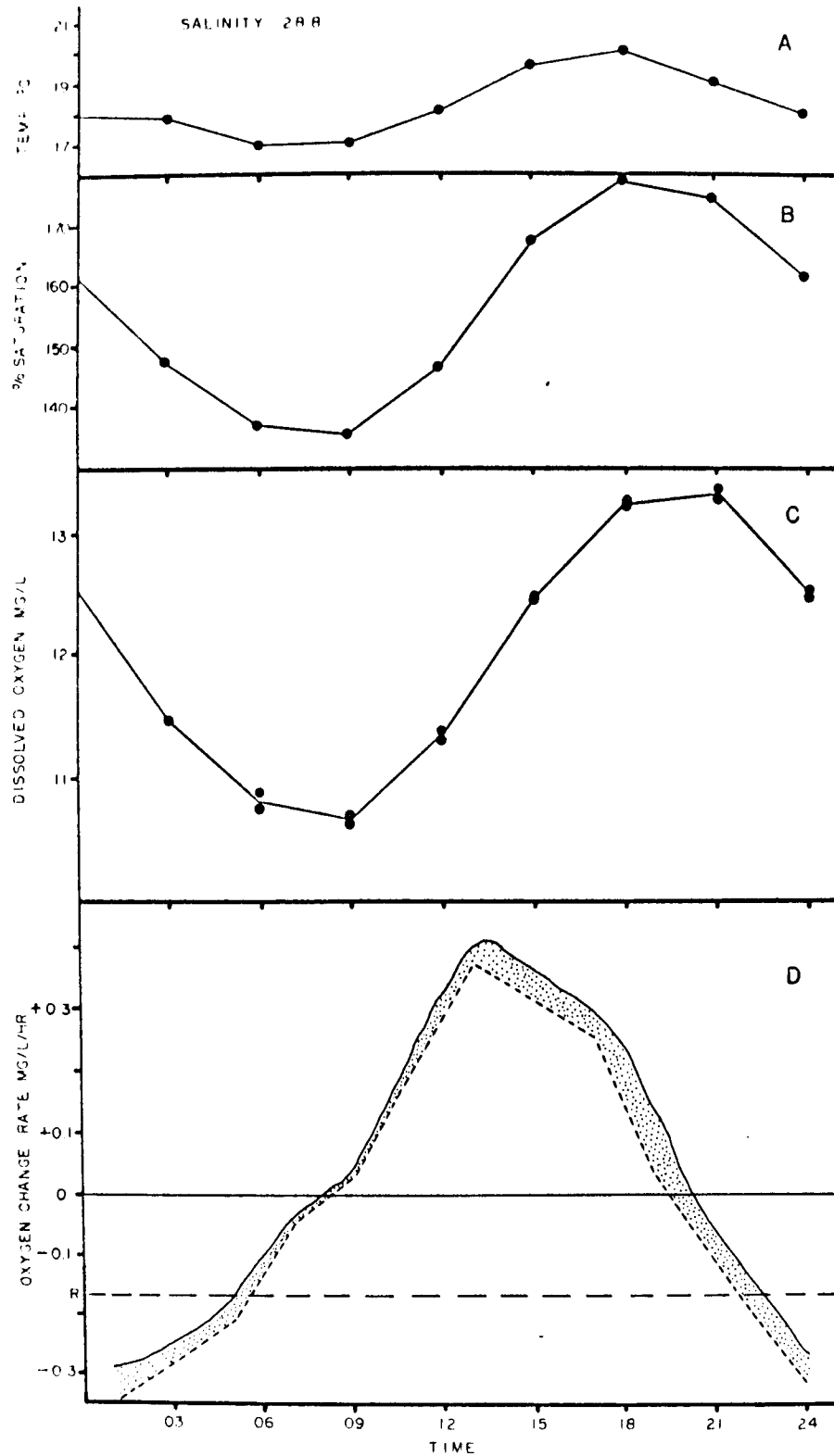
Figure 2. Temperature, percentage saturation with oxygen,
dissolved oxygen in mg/l, and the rate of change of oxygen
in mg/l/hr for the 23-24 September 1964 sampling period.

drawn with the temperature and oxygen curves (Figure 2B). A rate

of change curve for the dissolved oxygen content of the water in

mg/l/hr was then constructed (Figure 2D).

The rate of change of dissolved oxygen within the water column

was affected by one physical and two biological factors, i. e. photo-

synthesis, respiration, and molecular diffusion. Primary produc-

tivity was estimated from the amount of oxygen released into the

water by plants in the process of photosynthesis. Community res-

piration was estimated as the amount of oxygen removed from the

water and presumed utilized by the living community in the process

of respiration. However, oxygen was also lost from the system

through diffusion if the water was supersaturated and gained by the

system if there was a saturation deficit. The amount of this dif-

fusion was determined by use of a mathematical expression derived

as follows. The oxygen rate of change during hours of darkness

when photosynthesis did not occur, was related to a volume-based

diffusion constant at 100 percent saturation and the actual percentage

saturation of the water at that same time, minus whatever oxygen

was utilized by community respiration. So that,

$$Q_m = kS_m - r \qquad Q_e = kS_e - r$$

where

Q_m = the oxygen rate of change at a specific time before dawn

k = a volume diffusion constant

Sm = the actual percentage saturation or saturation deficit at the same time as Qm

r = community respiration

Qe = the oxygen rate of change at a specific time after sunset

Se = the actual percentage saturation or saturation deficit at the same time as Qe

The relationship

$$Qm - Qe = kSm - r - kSe + r$$ follows.

If the values for community respiration (r) are equal, i. e. community

respiration was constant during the hours of darkness, then the r

factors cancel out and the equation

$$k = \frac{Qm - Qe}{Sm - Se}$$

can be established.   The value k represents the volume based dif-

fusion constant at zero saturation deficit (100 percent saturation),

and the actual diffusion for any chosen time during the sampling

period could be determined by multiplying k by the actual percent-

age saturation or saturation deficit (which ever applies).   This

amount of change in oxygen is then either added to the oxygen rate

of change curve or subtracted from it depending upon whether the

water was supersaturated or maintained a saturation deficit, and thus

lost or gained dissolved oxygen through the process of diffusion

(Figure 2D). The k value obtained for the example given (Figure 2) was only 0.07 mg/l/hr, a small constant due to the very calm water at Station 3. In this case, because respiration accounted for most of the oxygen lost from the water column during the night, the constant was small and calculated diffusion change was not great.

A line representing the average of the night time rates of change taken from the curve corrected for diffusion was drawn on the graph and extended through the daytime period. The average of the night time rate of change multiplied by the water depth and the number of hours (24) was used as an estimate of community respiration in g O_2/m^2/day (Figure 2D).

Likewise, the number of squares in the area beneath the corrected curve and above respiration in the daytime hump multiplied by the value of each square in mg/l and by the water depth in meters was then used as an estimate of gross primary production in g O_2/m^2/day (Figure 2D).

The diurnal curve method yielded estimates of the metabolism resulting in changes in oxygen concentration in the free water and included the metabolism of plankton and benthic communities. The plankton metabolism determined by the light- and dark-bottle method was then subtracted from the free water measurements of metabolism to arrive at the metabolism for the benthic community.

Structure of the benthic community was determined by direct

observation of the plants growing on the bottom of the pond, combined

with collection and identification of the species present. The entire

impoundment was examined visually during each collection period

and conditions and changes were recorded in field notes.

WATER CONTROL

The impoundment was constructed for the purpose of fish management and the period of confinement varied according to species of fish and season. Control of the water was in accordance with such requirements and was not designed to promote the development of a particular plant community. A brief chronological history of this control is necessary to the understanding of the community development that occurred in the impoundment (Figure 3).

Construction of the impoundment was completed and water admitted in the middle of March 1964. This water was initially freshwater, but through the introduction of seawater, it was gradually increased in salinity to 20 parts per thousand (0/00). The impoundment was emptied for the release of fish during June. After a brief, dry period during which time water from various sources prevented complete dessication of the community, water was readmitted from Lint Creek during the middle of June. This was essentially fresh water, varying in salinity from 4 to 5 0/00. The sampling program of the present study was started at this time. During early July salt water was admitted and circulated so that by the middle of July the salinity was 24 0/00 (varying from station to station and at different depths between 23-27 0/00). Salinity varying between this low and a high of 30 0/00 was maintained from July through November, until

AVERAGE SALINITY 3 STATIONS

A

AVERAGE TEMPERATURE 3 STATIONS

B
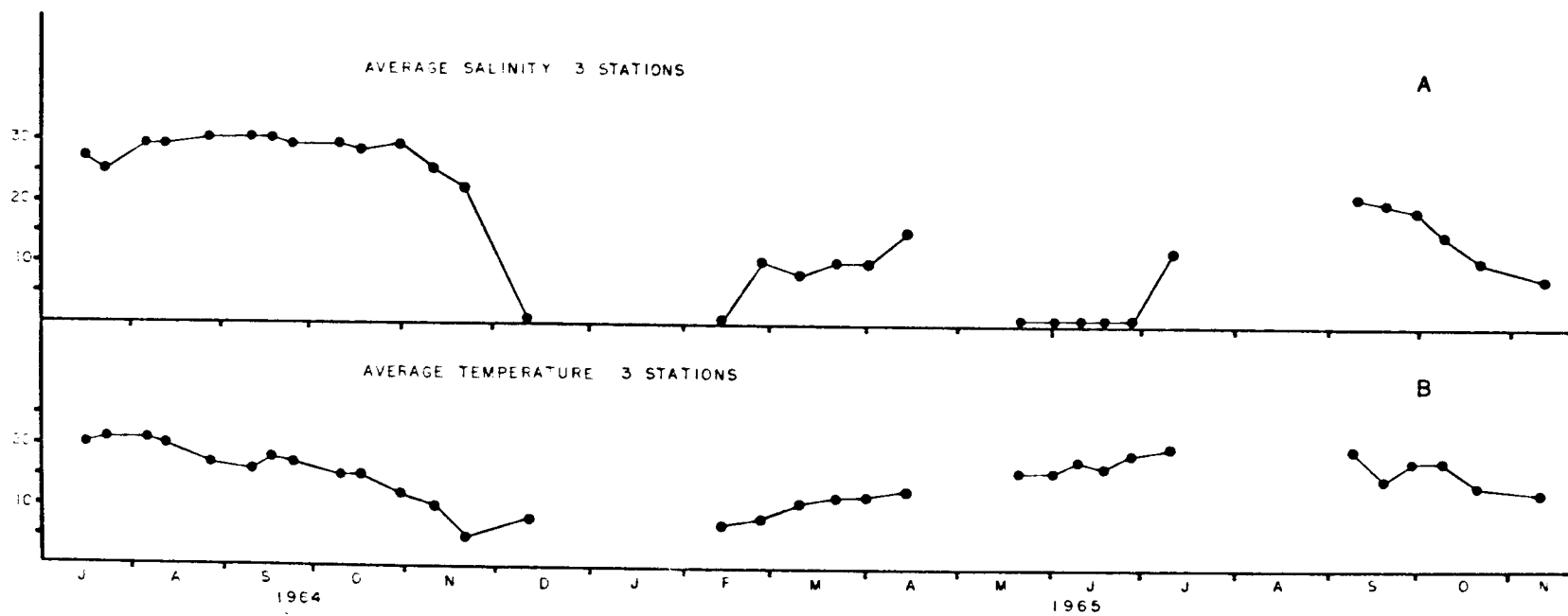
Figure 3.   Temperature and salinities on sampling dates averaged for the three stations.

heavy rains and flooding conditions rapidly decreased the salinity and created a freshwater system in early December.

Flooding conditions continued through January 1965 and the impoundment remained freshwater entirely until middle February when seawater was circulated. The system remained somewhat stratified with respect to salinity during late February with a low of 5 0/00 in the top two feet increasing from there to a high of 22 0/00 near the bottom. During March, wind circulation mixed the water thoroughly with a resulting salinity of between 9-12 0/00. Just prior to the water level being lowered for release of fish, sea-water was again introduced and a layered system was evident during early April, varying from 10-27 0/00. The impoundment was empty for a period of approximately three weeks, and was again filled with freshwater during the middle of May. Freshwater was maintained through June, until just prior to release of fish when seawater was admitted during the first week in July. During this short period of seawater circulation a somewhat layered system occurred varying between 5-25 0/00, the high salinity water forming a shallow layer near the bottom. The impoundment was then emptied and remained dry until the last of August. The plant community that had developed was completely dessicated. The impoundment was then filled with a well mixed combination of freshwater from Lint Creek and seawater from the bay to a salinity of 21 0/00. This salinity was maintained

with slow decrease to 19 0/00, until early October when accretion of pluvial water resulted in recordings of 16 0/00. Gradual decrease due to rain occurred through November when the salinity was 9 0/00.

During periods when seawater was admitted, Stations 1 and 2 were first affected by a saltwater wedge near the bottom because of their proximity to the main dam and water control structure. Station 3, however, being shallower and farther from the seawater source, sometimes did not become saline for several days. The dense salt water layer was eventually pushed up through the water control structure at the upper end of the impoundment by tidal waters entering the lower end.

In recapitulation, there were four major environmental conditions that existed during 1964-1965 (Figure 4, Column 1). The July through December 1964 period (Period 1) was characterized by saline water in the impoundment, but 1965 could conveniently be divided into three periods. The first of these (Period 2), from February through April was basically a brackish water environment. The second (Period 3) from the middle of May to early July was a freshwater environment, and the third (Period 4) from August through November was characterized by brackish water conditions somewhat more saline than Period 2.

Figure 4. Community Structure

Period	Benthic Community	Plankton Community
1 July-December 1964	Enteromorpha-Melosira Zostera Rhizoclonium Ruppia	Melosira Naviculoid pennates Nitzschia closterium Gyrosigma Euglena Chaetocerous Rhizosolenia Gymnodinium
2 February-April 1965	Melosira-Enteromorpha Corophium	Melosira Naviculoid pennates Flagellates Fragillaria Gyrosigma Oscillatoria Rotifers
3 May-July 1965	Melosira-Spirogyra Corophium	Naviculoid pennates Melosira Oscillatoria Fragillaria Spirogyra Synedra Rotifers
4 August-November 1965	Rhizoclonium-Melosira- Synedra Enteromorpha Cordylophora Corophium	Melosira Naviculoid pennates Gyrosigma Synedra Nitzschia closterium Flagellates Polydora Acartia

COMMUNITY STRUCTURE

Benthic Community

The term "benthic community" is used in this study to include the periphyton, i.e. organisms attached to substrates extending above the bottom.

The composite Cotula coronopifolia, typically found near brackish water on sand and mud areas, was a conspicuous flowering plant near the edge of the impoundment and formed floating mats out into the water. It also grew as a submerged aquatic, particularly when it started during periods when the impoundment bottom was partially dry. Typha latifolia was found in one small area near shore close to Station 1, and a species of Scirpus was found along the eastern edge of the impoundment, but most noticable in the proximity of Station 3. These plants were somewhat salt tolerant, but continued high salinities resulted in their death. Zostera marina was collected near Station 1 during 1964 when the impoundment was saline, and two clumps of Ruppia maritima approximately three meters in diameter were observed, one near Station 3 and another south of Station 2. These plants, as well as submerged rocks, float-ing and fixed branches, and logs, formed substrates on which a dense growth of Melosira moniliformis formed. Water movement frequently

caused segments of <u>Melosira</u> to become loosened from the substrate
and it was found as a major component of the plankton. During July
1964, a gradually increasing population of <u>Enteromorpha</u> <u>tubulosa</u>
was observed. This growth began along the rocky edges and shallow
bottom of the west edge of the impoundment, and intermittently spaced
clumps from 1 to 15 meters apart began to form on the bottom in
deeper water. Growth first began in the vicinity of Station 1 and
within a few weeks was observed along the entire length of the im-
poundment. The clumps gradually increased in size until the bottom
and every available vertical substrate were covered with either
<u>Enteromorpha</u> <u>tubulosa</u> or <u>Melosira</u> <u>moniliformis</u> or a combination of
both species. This community was designated as the <u>Enteromorpha-</u>
<u>Melosira</u> Community and it continued through the Fall of 1964. Col-
lections made in October revealed the <u>Enteromorpha</u> to be less vig-
orous and the matted clumps, particularly those floating on or near
the surface, were more easily pulled apart, giving an impression of
early senescence. The community remained intact, however, until
a period between October 30th and November 9th, during which time
the algae degenerated almost completely and bacterial action reduced
the plants to loose organic material on the bottom that retained slight
morphological integrity. In addition, there was obvious suspended
and dissolved organic matter in the water that resulted in a deep
brown opalescence. The transformation over a short period of time

was dramatic.

During February 1965, Melosira again became noticable, particularly along the east bank of the impoundment, where the bank provided a vertical substrate on which the algae could attach. This growth continued and gradually became evident on most available substrates. The April 12th observations and collections revealed a growth on the bottom that resembled the growth of Enteromorpha of 1964. Clumps of Enteromorpha tubulosa were observed beginning to form between Stations 1 and 2 and the water had lost much of its brownish coloration. This community was designated as the Melosira-Enteromorpha Community.

The impoundment was lowered for approximately four weeks, during which time the bottom was intermittently allowed to dry and the plant community was alternately dessicated and partially flooded. Freshwater was admitted from Lint Creek in early May. Melosira was observed gradually developing on the bottom and growing along the margins during June and early July. At Station 3 a large patch of Ruppia maritima was observed in the same location as in 1964. On June 25th the collections revealed no growth of green filamentous forms of algae, but on July 8th the edges of the impoundment and all floating and attached submerged substrates were covered with a species of Spirogyra. This community was designated as the Spirogyra-Melosira Community.

The impoundment was emptied and allowed to completely dry between July 12th and August 20th. It was filled with a combination of freshwater and seawater so that a well-mixed system was stabilized at 21 0/00. Sampling was resumed on September 7th at which time a species of Ulva was observed growing on the cement anchor at Station 2, but no noticable growth of filamentous algae was evident except at Station 3 where Melosira was observed. In the middle of September, a loose reticulate mat of Rhizoclonium riparum appeared in all areas of the impoundment closely associated with the bottom organic material, with Melosira, and with the epiphytic pennate diatom Synedra. Enteromorpha was observed on the anchors at Stations 1 and 2 and growth was observed until November, but it never attained any consequence as in its past development. This plant growth was designated as the Rhizoclonium-Melosira-Synedra Community.

Plankton Community

The phytoplankton that developed within the impoundment was characteristically tychoplankton, i. e. consisted of organisms generally growing as part of the benthic community but due to disruption and mixing by currents may become planktonic. The filamentous diatom Melosira moniliformis was the most consistent member of the plankton, being found in all four periods and nearly all collections. The naviculoid pennate diatoms were also consistently found. The

only "bloom" that occurred during the entire study period occurred

locally at Station 3 during the middle of August 1964 and consisted

of the dinoflagellate Gymnodinium. A peak of plankton productivity

also occurred at this time at Station 1, but the major part of this

production was due to the presence of the tychoplankter Melosira.

During the periods of greatest salinity (Periods 1 and 4), the

diatoms Nitzschia closterium and Gyrosigma were present, while the

less saline and freshwater environments (Periods 2 and 3) supported

the diatom Fragillaria and the filamentous blue-green Oscillatoria.

Synedra was also present as an adventive plankter during Period 4

when it occurred as an epiphyte on the benthic organisms. One col-

lection on October 9, 1964 contained species of the marine centric

diatoms Chaetocerous and Rhizosolenia, but only at Station 1 near the

saltwater inlet . Euglena was also present during the Fall of 1964

at salinities ranging up to 30 0/00.

Plankton collected in the net tows and examined alive generally

exhibited the same forms as plankton preserved with formalin. The

major exception to this was during Periods 2 and 4 when minute

green flagellates were found present in the live plankton. They were

not identified.

Period 1 was characterized by a lack of zooplankton until early

October when occasional nauplii and adult stages of the copepod

Acartia clausii were present and continued to be present until the

impoundment was flooded by freshwater in December. During Periods 2 and 3, the plankton community included a bloom of rotifers and during Period 4 the planktonic larva of the polychete worm _Poly-dora_ were observed with their gut cavities filled with a greenish material. During September and October 1965 these larval forms were very abundant and along with the copepod _Acartia clausii_ made up the majority of the animal plankton.

RESULTS OF METABOLIC STUDIES

For convenience of discussion, the metabolic studies will be divided into the four plant communities described previously. Primary productivity and community respiration for each community will be discussed by comparison of the benthic and plankton communities, a comparison of the three sampling stations, high and low values obtained, and by suggestion of reasons for some apparent fluctuations in the curves shown in Figures 5, 6, and 7. All metabolic rates will be given in grams of oxygen per square meter per day.

Enteromorpha-Melosira Community
July - December 1964

Figures 5, 6, and 7 clearly indicate that the magnitude of the primary production and community respiration for the benthic community was much greater than that of the plankton. At Station 1 (Figure 5), the benthic community reached a high primary production of 11.13 g $O_2/m^2/day$ on August 6th, with high rates at Stations 2 and 3 being 7.57 on September 17th and 6.05 on August 27th respectively, while corresponding rates for the plankton were 2.33 and 0.69 on August 27th, and 1.47 on August 12th. Low rates of production for the benthic community of 0.17 on October 17th, 0.40 on August 6th, and 0.91 on July 16th, were recorded for Stations 1, 2 and 3 -

PRIMARY PRODUCTION STATION 1
● BENTHIC COMMUNITY
▲ PLANKTON

GMO₂/M²/DAY

COMMUNITY RESPIRATION

1964   1965
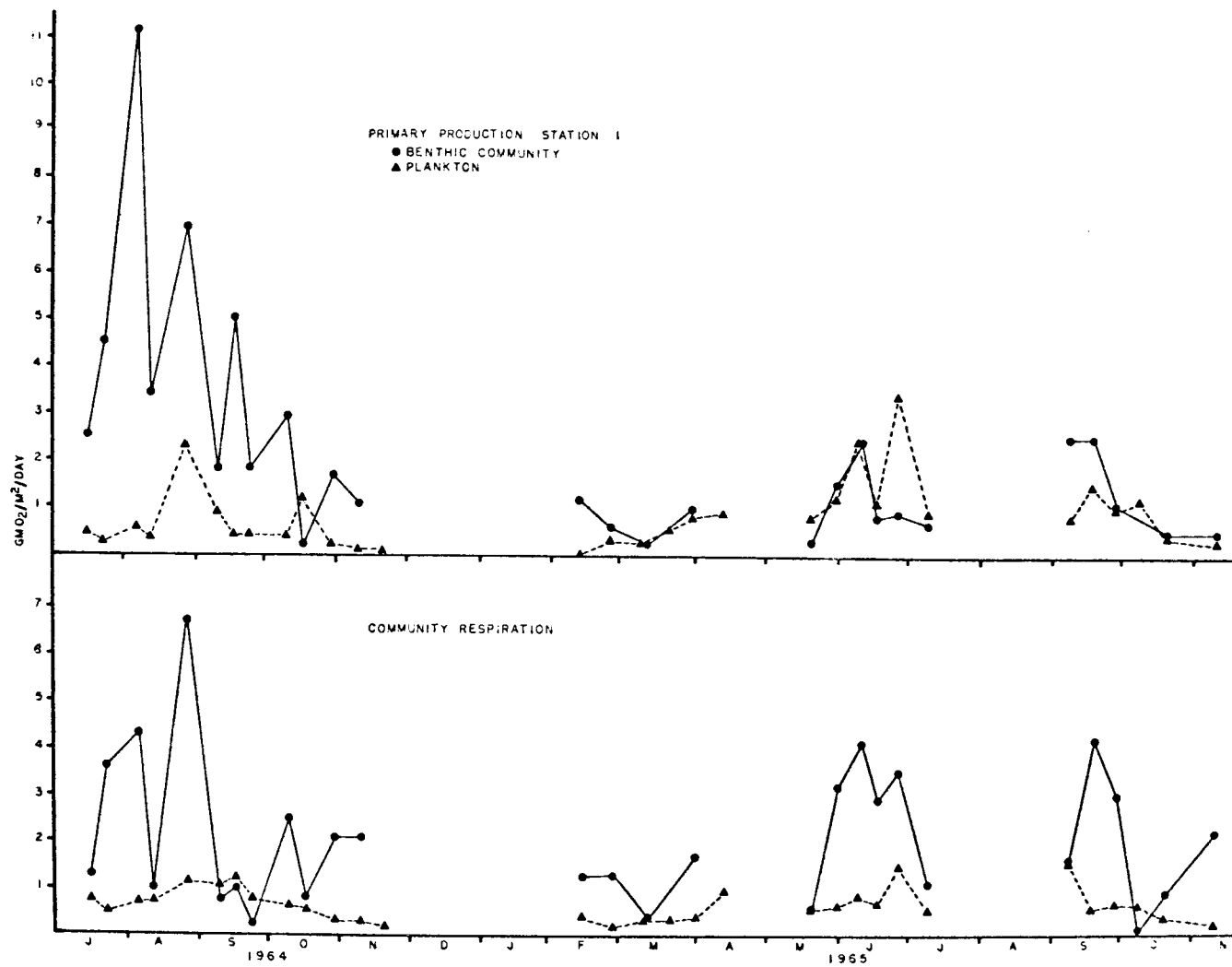
Figure 5. Station 1 gross primary production and community respiration

28
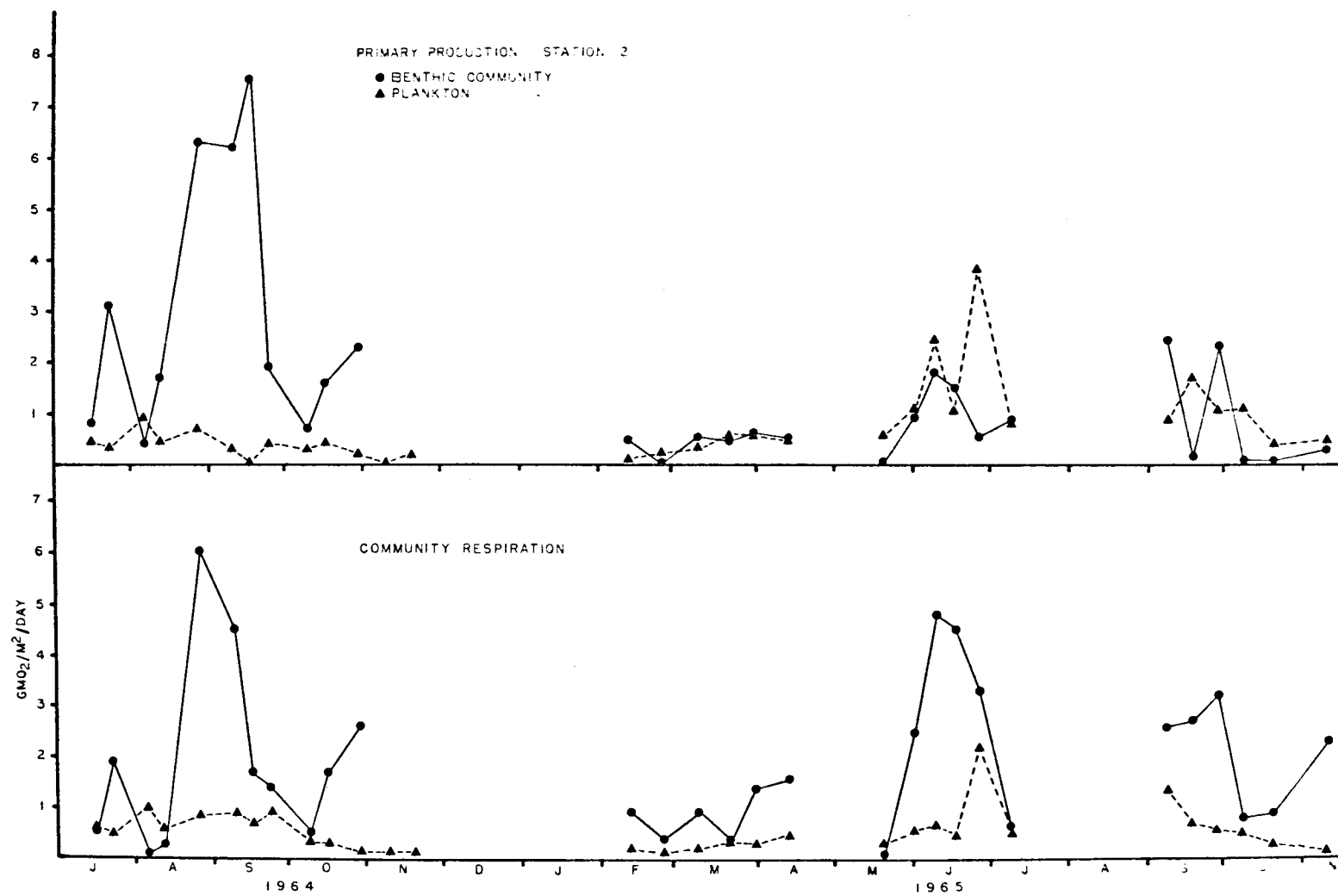
Figure 6. Station 2 gross primary production and community respiration.
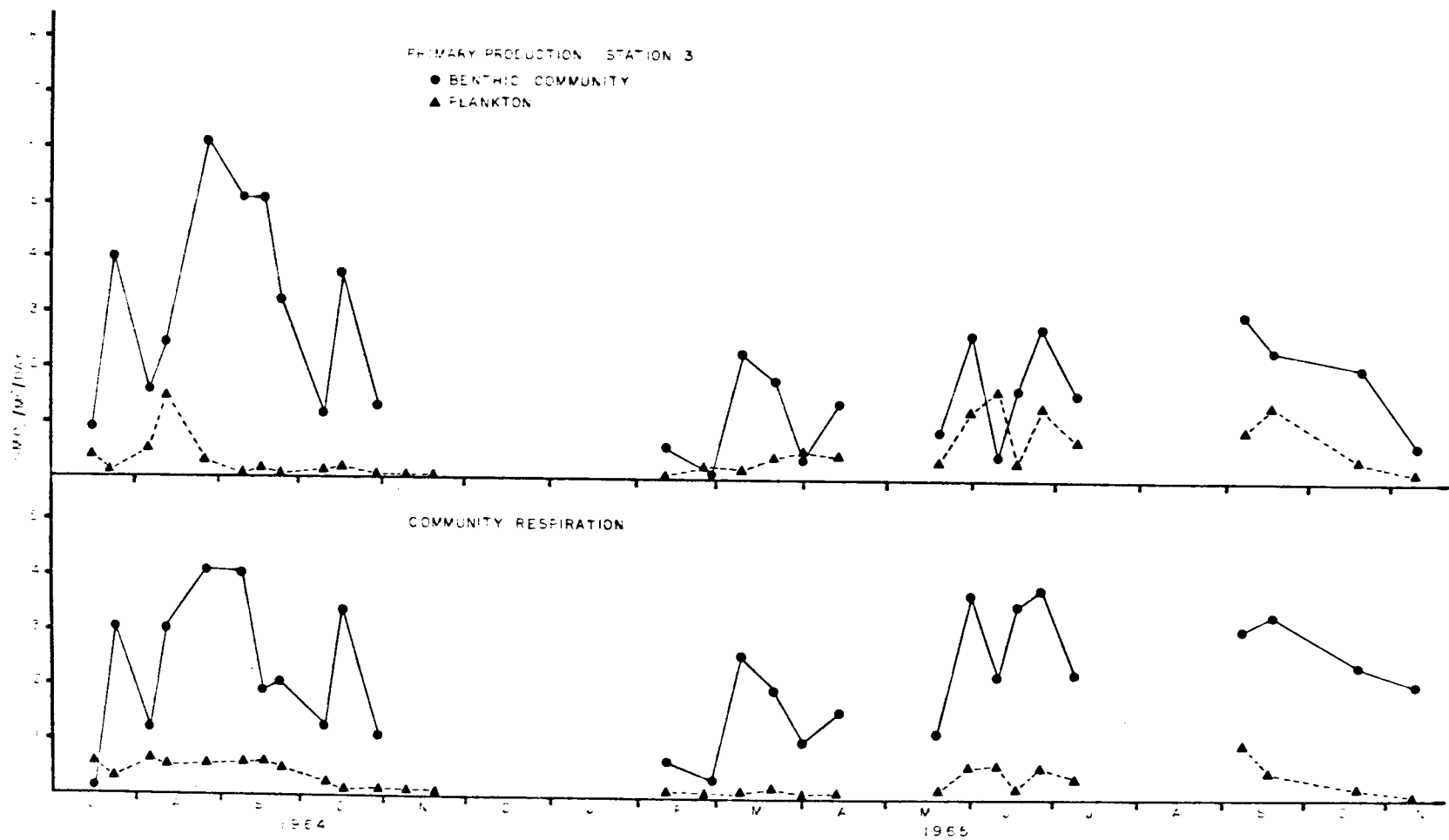
Figure 7. Station 3 gross primary production and community respiration.

30

respectively, while low rates of production by plankton for the same stations were 0.12 on November 20th, 0.07 on November 10th, and 0.05 on November 20th.

In general community respiration rates for the benthic and planktonic communities paralleled the production rates closely at all three stations. High benthic community respiration rates of 6.68 g $O_2/m^2/day$ at Station 1, 6.00 at Station 2, and 4.21 at Station 3 were all recorded on August 27th, while high rates of plankton respiration of 1.18 on September 17th, and 0.99 and 0.70 on August 6th were recorded for Stations 1, 2, and 3 respectively. Low rates of benthic community respiration of 0.19 on September 24th, 0.10 on August 6th and 0.11 on July 16th for Stations 1, 2, and 3 respectively, compared with low rates of plankton respiration of 0.14 on November 20th, 0.16 and 0.05 both on October 30th for the same stations.

There was an increase in both production and respiration rates at all three stations from July to September. This was due to the maximum photoperiod which occurred during this period, and to the increasing plant biomass as mentioned in a previous section of this paper.

The reasons for the fluctuating rates of primary production at Station 1 compared to the similarity of the productivity curves for Stations 2 and 3 are not readily apparent and can be understood only with the knowledge of the nature of the situation at Station 1 in

comparison with Stations 2 and 3. The diurnal oxygen curve method of measuring primary production depends on a water column evenly mixed by gentle currents. The extent to which this is not accomplished results in some error. The Enteromorpha-Melosira Community developed first in the vicinity of Station 1, but remained clumped as was described earlier. It was possible that the plant material, being generally unattached, drifted some with the currents between sampling periods, and since primary production was estimated by a measurement of the dissolved oxygen in the water column, if the plants were not homogeneously arranged, dissolved oxygen might have been unevenly distributed, especially if mixing by currents was at a minimum. At Stations 2 and 3, however, the clumped plants developed into a continuous bottom cover which, although somewhat irregular, did lend continuity to the community and probably promoted a more even distribution of the dissolved oxygen even under conditions of little water movement.

The general decline in production at all three stations during the fall months was attributed to the decrease in daylight hours and the decrease in water temperature, both of which probably contributed to gradual community senescence. The low rates of production on October 17th were attributed to heavy clouds during that entire sampling period with bright or cloudy-bright conditions prevailing during succeeding periods.

The Enteromorpha-Melosira Community at Stations 2 and 3

abruptly became senescent early in November as described earlier.

Attempts were made to measure the metabolic rates of the benthic

community during November and December 1964, but the death of

most of the plant community resulted in large amounts of organic

sediments, opalescent water, and concurrently, a high bacterial

population. Under these conditions, diurnal oxygen curves such as

in Figure 8 were obtained, where oxygen values were erratic and

duplicate samples showed great variation. Because of this, the last

measurements of benthic productivity and respiration were made at

Stations 2 and 3 on October 29th and 30th. The plant community at

Station 1 had not developed to such a high degree and senescence

was delayed so that metabolic measurements were possible at that

station until November 10th, after which erratic oxygen data were

no longer useful in determining metabolic rates.

The only phytoplankton bloom that occurred during the two year

study was observed at Station 3 on August 12th, when production

rates of 1.47 g O_2/m^2/day were recorded. Examination of the con-

centrated water sample revealed an abundance of the dinoflagellate

Gymnodinium. The corresponding peak in production rate occurring

at Station 1 was attributed to Melosira moniliformis, a tychoplanker.
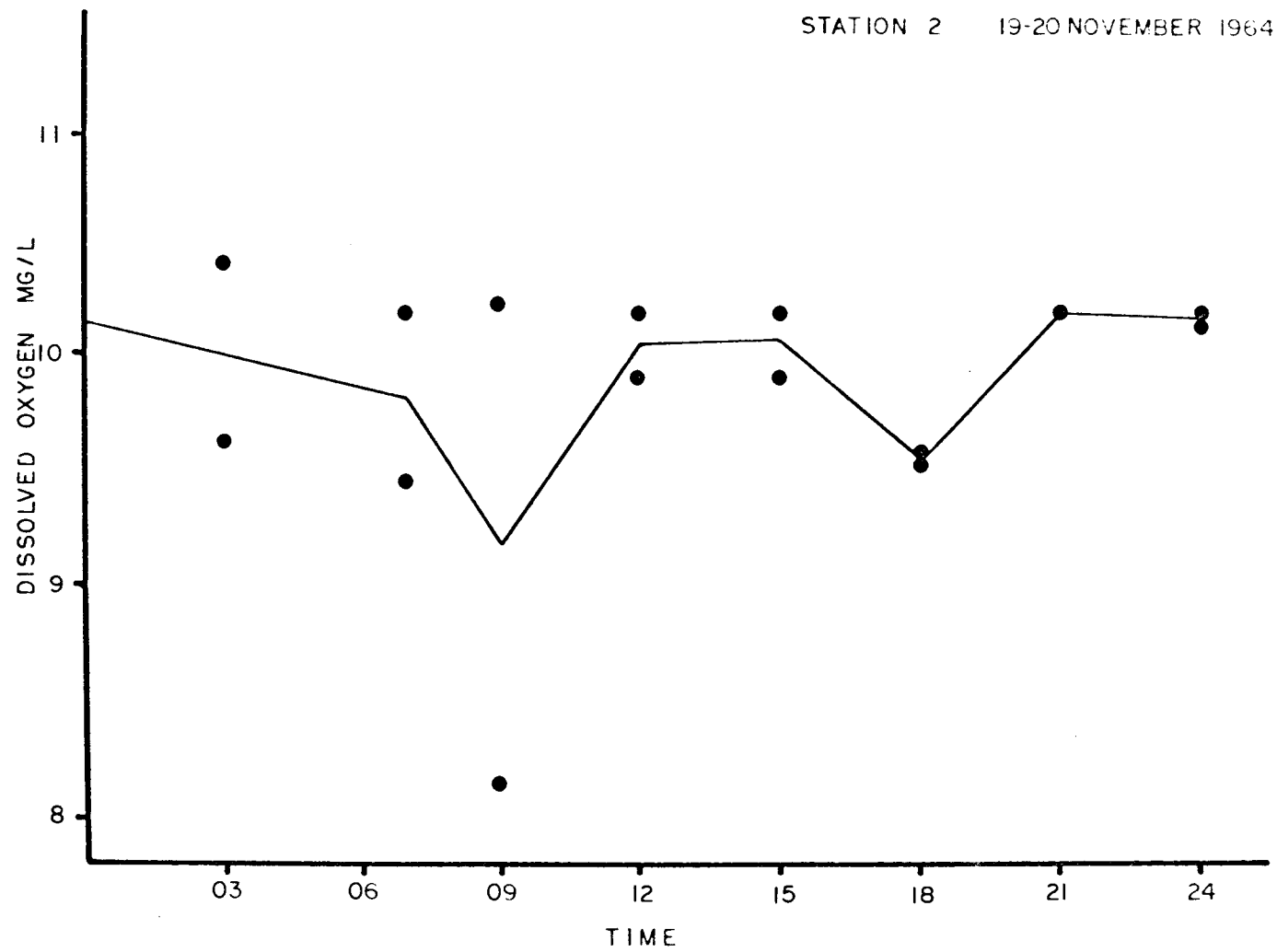
Figure 8. Dissolved oxygen values for Station 2, 19-20 November 1964.

Melosira-Enteromorpha Community
February - April 1965

Primary production and community respiration of both the

benthic community and the plankton were of a lower magnitude at all

three stations than for the preceding period (see Figures 5, 6, and

7). The benthic community exceeded the plankton in both production

and respiration rates. High rates of benthic productivity of 1.18 g

$O_2/m^2/day$ on February 11th at Station 1, 0.59 on April 1st at

Station 2, and 2.30 on March 9th at Station 3 were recorded as com-

pared to 0.91 on April 13th, and 0.59 and 0.47 on April 1st at Sta-

tions 2 and 3 for the plankton. Low rates of production showed the

same relationship. Low rates of benthic production of 0.25 on March

9th and 0.06 and 0.08 both on February 25th were recorded for Sta-

tions 1, 2, and 3 respectively.

Respiration rates indicated a similar relationship, but with the

respiration of the benthic community being relatively higher than the

plankton respiration as compared with production rates of the same

communities. High values for benthic respiration of 1.70 and 1.89 g

$O_2/m^2/day$ were recorded for Stations 1 and 2 on April 1st, and 2.57

was recorded at Station 3 on March 9th, while high rates for plankton

respiration at the same stations were 0.96, 0.51, and 0.25, all re-

corded on April 13th. Low rates for benthic respiration recorded

for the three stations were 0.41 on March 9th and 0.41 and 0.27 both

recorded on February 25th, while low rates of plankton respiration

for the same stations were 0. 16, 0. 16, and 0. 11 all recorded on

February 25th.

At all three stations, primary production showed an early de-

cline in rates for the benthic Melosira community, and a gradual in-

crease for the plankton, until early March when production by the

benthic community gradually increased at Stations 1 and 2, and

sharply increased at Station 3. The reason for this is somewhat

speculative, but an interpretation that is most plausible and fits

nicely with the field observations of the developing community would

be as follows. The early Melosira development on the bottom and

other available substrates was subjected to water currents which

fragmented the easily broken diatom filaments, so that much of it

became tychoplanktonic and, as a component of the plankton, in-

creased the production measurements made with the light- and dark-

bottles. The production rates of the plankton show this gradual in-

crease, and examination of the plankton samples showed the presence

of Melosira. In addition to the rapid development of the Melosira,

there was a gradual build-up of Enteromorpha tubulosa, resulting in

an increase in production rates particularly at Station 3 where, be-

cause of the shallower water, light reached the bottom with greater

intensity. The rapid increase in salinity (Figure 3) during February

might have affected the production values through physiological shock,

although Melosira proved to be euryhaline throughout the study. The

sharp decline at Station 3 on April 1st was attributed to a heavy over-

cast sky with some precipitation, which affected bottom production at

the shallow Station 3 more than at the deeper Stations 1 and 2. The

plankton production, measured in suspended bottles, was not affected

as much by the decreased light.

Due to a water column partially layered with respect to salinity,

erratic oxygen values were recorded at Station 1 on April 13th and

no data could be used in estimating metabolic rates of the benthic

community.

Respiration rates for both the benthic community and the plank-

ton were generally greater than the rates of production. This re-

flected the presence of two dominant animal species, one planktonic

and the other benthic. An abundance of an unidentified rotifer was

found in the plankton collections, gradually increasing throughout the

period, and a growth of the amphipod Corophium, a mud-tube builder,

paralleled the plant community development.

Melosira-Spirogyra Community
May - July 1965

Melosira rapidly became the dominant plant of the benthic com-

munity in this freshwater environment as it had in the more saline

conditions of the previous communities. Rates of benthic production

at Stations 1 and 2 were generally somewhat less than that of the plankton, but the reverse was true at Station 3, reflecting again the shallow water at Station 3 which was more suitable for growth on the bottom.

Maximum productivity for the benthic community at Stations 1, 2, and 3 respectively were 2. 36 and 1. 84 g $O_2/m^2/day$ both recorded on June 9th, and 2. 81 recorded on June 26th. The highest rates of plankton production for the entire study were recorded during this period. Values for the three stations were 3. 35 and 3. 78, both recorded on July 26th, and 1. 64 recorded on June 9th. Plankton net tows revealed the presence of some green flagellates during June and July, but at Stations 1 and 2 rotifers, that had green material concentrated in the gut, were present in abundance. It was suspected that a bloom of autotrophic flagellates had occurred, but that due to heavy grazing by the zooplankton no large standing crop was observed. Minimum production values for the benthic community were 0. 32 and 0. 00 g $O_2/m^2/day$ on May 21st and 0. 41 on June 9th for Stations 1, 2, and 3 respectively. Low production rates of plankton for the same stations were generally less than the benthic low values, being 0. 80, 0. 58, and 0. 34 all recorded on May 21st.

Rates of oxygen consumption by the benthic community were greater than either the production rates of that community or the plankton respiration rates. It is thought that the rates of benthic

respiration reflected the abundance of <u>Corophium</u>, which, because of the protection afforded by the mud-tubes, were able to survive the period of dryness when the impoundment was lowered for release of fish. The rates of plankton respiration show peaks during late June at Stations 1 and 2. These corresponded to the peak abundance of the rotifers and of the nauplii and adult stages of the copepod <u>Acartia clausii</u>.

High rates of benthic respiration were 4. 05 and 4. 79 g O_2/m^2/day recorded on June 9th at Stations 1 and 2, and 3. 83 recorded on June 26th at Station 3. High respiration rates for the plankton were 1. 35, 2. 24, and 0. 66 all recorded on June 26th. These values are considerably lower than the benthic rates, but the 2. 24 at Station 2 was the highest plankton respiration recorded throughout the study. Low benthic respiration rates, all recorded on May 21st were 0. 55, 0. 09, and 1. 13 for the three stations, while the low plankton respiration values were 0. 49 on July 9th and 0. 32 and 0. 17 recorded on May 21st.

<u>Rhizoclonium-Melosira-Synedra</u> Community
August - November 1965

The production rates of the benthic community generally were greater than the rates of plankton production, especially at Station 3, and showed a gradual decline similar to the decline of the

Enteromorpha-Melosira Community during the fall of 1964. This

was attributed to the shortening photoperiod. High rates of benthic

production were 2.52, 2.37, and 3.09 g O_2/m^2/day, all recorded

on September 8th for the three stations, while high rates of plankton

production were 1.45, 1.66, and 1.41 g O_2/m^2/day all recorded on

September 18th. Low production rates of the benthic community

were 0.06 and 0.11 on October 8th and 0.71 on November 10th at

Stations 1, 2, and 3, respectively. Low plankton production was

0.33 on November 10th, 0.43 on October 20th, and 0.21 on November

10th for the three stations.

Rates of benthic respiration were consistently much higher

than those obtained for the plankton, and both benthic and planktonic

respiration generally paralleled the production rates at Station 3.

At Stations 1 and 2 benthic respiration increased sharply, most

probably due to the decline of the plant community and the consequent

increase in bacterial respiration. However, respiration rates were

probably increased also by the development of the colonial hydroid

Cordylophora which was observed growing on every available sub-

strate near the surface, such as buoy lines, floats, and concrete

water control structures. Although Cordylophora was not observed

at Station 3 and respiration rates did not increase sharply at that

station, it was felt that the greatest influence in increasing the rates

of respiration at the other stations was the decline of the plant

community with resultant increased bacterial respiration.

High values for benthic respiration of 4. 17 g $O_2/m^2/$day on September 18th at Station 1, 3. 23 on September 28th at Station 2, and 3. 33 on September 18th at Station 3 were obtained, as compared to high rates of plankton respiration of 1. 47, 1. 35, and 0. 98, all recorded on September 8th. The respiratory rates of the plankton at Stations 1 and 3 were the highest recorded during the study. Minimum benthic respiration rates of 0. 10 and 0. 83 were recorded on October 8th for Stations 1 and 2, and 2. 06 on November 10th for Station 3. The low rates of plankton respiration were 0. 18, 0. 17, and 0. 10 g $O_2/m^2/$day all on November 10th. The values at Stations 1 and 3 were the lowest recorded during the study.

The general high rates of plankton respiration were attributed to the planktonic larvae of the worm Polydora, which were found in great abundance during September, but gradually declined in numbers through October and November. These larval forms and Acartia clausii formed the dominant plankton fauna.

DISCUSSION

Since Gaarder and Gran (1927) first described the light- and
dark-bottle technique for measurement of productivity and community
respiration in plankton, there has accumulated an abundant literature
on this subject. Most studies have described production in oceanic
and deep lake ecosystems where the plankton unquestionably is the
most important producer. Among others, Calvert (1932, 1933) in-
vestigated variations in the oxygen content of river waters and re-
corded dissolved oxygen data that indicated a diurnal fluctuation.
The amount of dissolved oxygen in a water column was used as a pol-
lution index (Purdy, 1935) but no method of determining metabolic
rates from these data was developed.

As mentioned by Strickland (1960), investigations of shallow
waters where the euphotic zone included the bottom revealed dis-
crepancies between the amount of material produced in an area and
the productivity rates as measured by the isotope C^{14} in light- and
dark-bottles. Most notable of these investigations is the work of
Sargent and Austin (1949), who earlier investigated production by
plankton in the neighborhood of an atoll and found that the amount of
plankton swept across the coral reefs was not sufficient to support
the animals living on the reefs. This knowledge led to their analysis
of the change in dissolved oxygen between two stations in the free

water surrounding sections of the reef. Diurnal oxygen curves were constructed and estimates of the total oxygen produced and consumed by the ecosystem were obtained. They found by using this new "flow method" approach that the reef was dependent on organic material synthesized by the benthic plants.

Odum and Odum (1955) elaborated on the flow method of estimating metabolic rates of a coral reef. Using two stations, one upstream from the other, they measured the oxygen content simultaneously. Oxygen increase between the stations during the day represented net photosynthetic production. Oxygen decrease between stations during the night represented community respiration, and the net production plus the community respiration gave the total production for the coral ecosystem. No consideration was given in these studies, however, to the loss or gain of oxygen from the system through the process of molecular diffusion.

Odum (1956), using the data of Haney (1954) and others, first proposed an equation by which a diffusion constant could be mathematically derived for water at zero percentage saturation deficit, and then by knowledge of the percentage saturation of the water with oxygen at any particular time, absolute diffusion estimates could be ascertained. Since 1956, this "diurnal oxygen curve" method of measuring metabolic rates within an entire aquatic ecosystem has been used by several workers. Kohn and Helfrich (1957), using

Odum's diffusion correction equation, determined metabolic rates

on an Hawaiian coral reef, and Odum (1957a, 1957b) published two

papers which described trophic relationships in Silver Springs,

Florida.   A comparative study of marine bays was conducted by Odum

and Hoskin (1958) and marine turtle grass communities were studied

in two geographical areas, Texas bays (Odum 1963) and Puerto Rico

bays (Odum, et al. 1959).   All of these studies have shown without

question that within a stabilized shallow water ecosystem, the amount

of energy fixed in primary productivity is primarily due to the con-

tribution made by the benthic community.   The present study rein-

forces that supposition.

The question of determining the amount of oxygen that is lost

or gained by a natural aquatic community through diffusion still lacks

an adequate answer.   Ryther, et al. (1958), in their study of a diatom

bloom in a small tidal creek on Long Island, New York, assumed

that night time oxygen changes were due entirely to respiration.   The

diffusion equation proposed by Odum (1956) and discussed in the

methods section of this paper, is dependent on selecting "typical"

oxygen rate of change times, one after sunset and one before dawn.

The choice of times is subjective and depends upon adequate field

observations as to environmental conditions, such as a sudden wind,

which would tend to make diffusion rates greater than normally ex-

pected, and metabolic rates would consequently be in error.   If the

water were supersaturated metabolic rates would be under estimated, and if the water had a saturation deficit then metabolic rates would be over estimated.

The diffusion equation proposed by Odum also assumes constant respiration rates for the selected times, and if the diffusion constant is to be used during daylight hours, a constant respiration rate for the entire 24 hour sampling period. Odum recognizes that this is probably not true, but the extent of the variation of respiration rates is not known. Jackson and McFadden (1954) found an increase in respiration during the day in their study of lake phytoplankton. Gessner and Pannier (1958), concerned with the assumption that respiration is much the same in the light- and dark-bottles, found through experiments that the respiration rates were affected by both light and photosynthesis, so that the net photosynthesis values obtained by Winkler titration are somewhat too low. McIntire (1967) found that rates of respiration in periphyton communities decreased rapidly when the dissolved oxygen concentration was reduced below air-saturation, and respiration was enhanced by increasing oxygen tensions above air-saturation under controlled environmental conditions. The water column in the impoundment, particularly during 1964 when the community was well developed, characteristically showed greater amounts of dissolved oxygen in the water after sunset than just prior to dawn. Usually, however, the water was

supersaturated with oxygen at both times.

Odum and Wilson (1962) made further studies on the relationship between reaeration and metabolism in Texas bays. Because systematic trends in community respiration had not been worked out, they felt that the simple diffusion equation continued to be the best method for estimating a diffusion constant. They suggested that an ultimate solution to the problem would be a separate physical determination of a diffusion constant, so that daytime net photosynthesis and night-time respiration could be determined after correction for diffusion determined independently. Copeland and Duffer (1964) have applied themselves to just such a study. Utilizing a clear plastic dome which enclosed a portion of the body of water under study, they simultaneously measured oxygen concentrations and temperatures in the free water and in the completely filled plastic dome. They hoped to arrive at values for two factors, the magnitude of the diffusion constant and the variation of that constant through a 24 hour period. The magnitude (0.00 - 0.5 for still water) of the k value was very close to that of Odum's work, and also agrees closely with the k values as presented in this paper (see appendix). However, since a greenhouse effect interfered with accurate measurements during the daytime, all measurements were made at night. If observations of wind and other environmental conditions showed a difference between nighttime and daytime (as was generally the case),

then measurements taken at night were matched to similar conditions

observed during the day and these were used to estimate the daytime

diffusion constants. They concluded that these independently deter-

mined k values were in agreement with previous work as far as

magnitude was concerned, but that the difference between the methods

was in the variation of the k values through a 24 hour period.

Since they were not able to use data obtained during the day, it is

difficult to accept their assumption that all measurements were an

accurate estimation of the actual natural diffusion occurring within

the ecosystem.

An attempt was made in the present study to measure diffusion

rates independently. A child's plastic swimming pool approximately

1. 3 meters in diameter was inflated and filled with water from the

impoundment so that the water in the pool was nearly level with that

of the impoundment. The pool was anchored at Station 1 so that it

was subjected to the same wind and water motions as the water at

the station, with the possible exception of large scale water currents

that tended to turn the water column over in a gentle mixing motion.

Formaldehyde was introduced so that an approximate three to four

percent formalin solution resulted. The filled pool held approximately

380 liters. Water samples were taken periodically and examined for

living organisms and none were found. Dead organisms accumulated

on the bottom during the first few days and remained there in a

preserved condition, so it was assumed that no living material was present. Bacterial examinations were not made.

Prior to starting the sampling for the "diurnal curve" measurements, compressed nitrogen gas was bubbled through the pool and as a result the dissolved oxygen content of the water was lowered to well below saturation levels. Each time water samples and temperature measurements were taken at Station 1, duplicate samples and measurements were taken from the pool with extreme care not to disturb the water in the pool. Theoretically, the water in the pool should have yielded values of oxygen change not affected by either respiration or photosynthesis, and thus have given independent diffusion rates. However, the data have not been used in this paper because of difficulty met in the interference by the formalin with Winkler titrations. An accurate end point could not be determined, and the variation between duplicate samples was frequently larger than the variation between sampling periods. It was apparent, however, that diffusion rates were generally low and that those rates determined by Odum's equation and used in this paper are probably maximum.

In light of the fact that, as yet, no good field technique has been adequately worked out to measure molecular diffusion rates between the atmosphere and an aquatic medium, it seemed best to utilize the equation as proposed by Odum.

In temperate regions, annual curves of gross primary produc-
tivity and community respiration of aquatic communities character-
istically show a gradual buildup during the early spring and summer
with maximum rates usually during late June, July, and August, and
a gradual decline during the fall months (Odum and Wilson 1962 and
Figures 5, 6, 7). This decline is due to reduction in total light
energy received primarily as a result of shortening of the photoperiod.
Superimposed upon the annual curve are irregularities from day to
day and from week to week. These result from fluctuations in light
intensity, community structure, water temperature, salinity, and
undoubtedly other environmental and biological factors which are not
completely understood. Fluctuations also occur during a 24 hour
cycle. Two examples are given in Figures 9A and 9B.

Figure 9A shows an oxygen rate of change curve of a hetero-
trophic community which clearly shows the effects of cloud cover as
a "noon dip". The 24 hour sampling program in this case began at
1500 after a morning of heavy cloud cover and presumably lower
production rates. During the afternoon and next morning, however,
bright sun prevailed which supported higher production rates. In the
coastal region where this study was conducted, such daily and hourly
fluctuations in light intensity were common so a curve such as illus-
trated is not atypical. Figure 9B shows a rate of change of oxygen
curve for a heterotrophic community where the rate was affected by
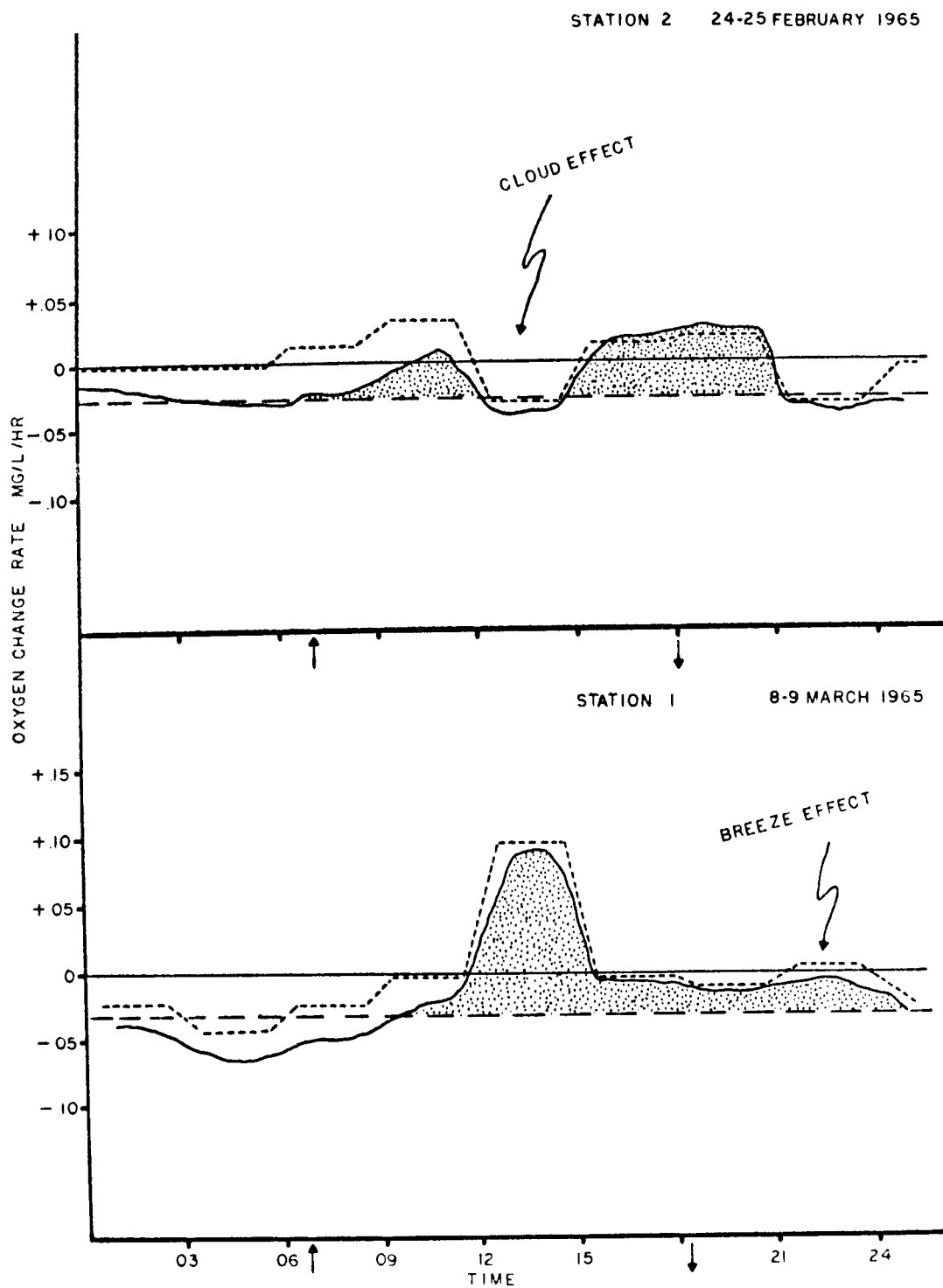
Figure 9. Rate of change of oxygen for Station 2, 24-25 February 1965 and for Station 1, 8-9 March 1965

a sudden brisk breeze after sunset. The amount of dissolved oxygen

would not increase after photosynthesis had ceased during darkness,

but the uncorrected curve indicates such an increase in the amount of

dissolved oxygen in the water. The increase was caused by more

rapid diffusion of oxygen from the air into an unsaturated water

column aided by rapid mixing by the sudden breeze. The corrected

curve is stippled. The area under the corrected curve above the

respiration line, represents the gross primary production. Con-

versely, a sudden breeze over a supersaturated water column

usually resulted in a loss of oxygen from the water.

Weekly variations in oxygen curves are the result of the additive

effects of such daily fluctuations as well as other environmental

changes. It is felt that over an extended period of time such fluctua-

tions generally were typical of the natural processes. The biggest

criticism of a field study under natural conditions is the fact that

there are many simultaneous variables. This, however, is the way

the physical and biological environments act upon the ecosystem,

and the strict control in the laboratory of all but one variable changes

the system from a natural one to an artificial one.

Odum (1959) has compiled a range of values for gross primary

productivity in grams of oxygen per square meter per day for various

types of ecosystems, some of which are as follows. Values from a

lotic environment (Reese, 1966) and this study have been added.

Deserts and semi-arid grasslands	less than	0. 5
Open oceans, deep lakes	less than	0. 5
Continental shelf, shallow lakes, average forests, moist grass- lands, ordinary agriculture		0. 5 - 5. 0
Coral reefs, estuaries, ever- green forests, intensive agriculture		5. 0 - 20. 0
Maximum rates which may be maintained for short periods		up to 60. 0
Berry Creek Experimental Streams Benton County, Oregon (Reese, 1966)		0. 08 - 5. 16
Lint Slough Impoundment		0. 30 - 11. 70

The impounded estuary in which this study was made fits well into the over-all pattern which the above figures suggest, and reinforces the idea that estuarine and other shallow marine ecosystems are among the most productive in the world. Gross productivity values, however, can be misleading if community respiration is not known.

All ecosystems are in a sense "open" systems, since they require a continued source of energy that originally comes from sunlight. This radiant energy is fixed photosynthetically by autotrophic plants into various organic compounds which then enter the "food-chain" and are either utilized directly by the autotrophic plants or by primary and secondary heterotrophic grazing organisms. If the primary source of energy within an ecosystem is produced by auto-trophic plants then such a system is called autotrophic. If on the other hand, the primary source of energy is exogenous fixed carbon, then the system is classed as heterotrophic. The relationship

between autotrophy and heterotrophy then, is the relationship be-
tween productivity and respiration, and an index can be established
in the form of a P/R ratio.

Figure 10 illustrates clearly the P/R relationship of the im-
poundment during the period of this study. For this purpose the
three stations have been averaged and metabolic figures are given
for the entire water column which included the plankton as well as
the benthic community. The Enteromorpha-Melosira Community of
1964 was autotrophic the entire period up to the end of October when
respiration rates exceeded production rates. The community over-
all had a P/R of 1. 36. A large standing crop developed because
more organic matter was produced than utilized in respiration.
When this community became senescent in the late fall of 1964, the
organic matter settled to the bottom or through bacterial action was
returned to the water in the form of suspended colloidal and dis-
solved materials.

During 1965 water control requirements did not permit the
plant communities to develop as extensively as in 1964 and production
rates rarely exceeded community respiration rates. The P/R was
0. 76 for the Melosira-Enteromorpha Community, 0. 78 for the
Melosira-Spirogyra Community, and 0. 77 for the Rhizoclonium-
Melosira-Synedra Community. Whatever organic material might
have been introduced into the impoundment during filling is not
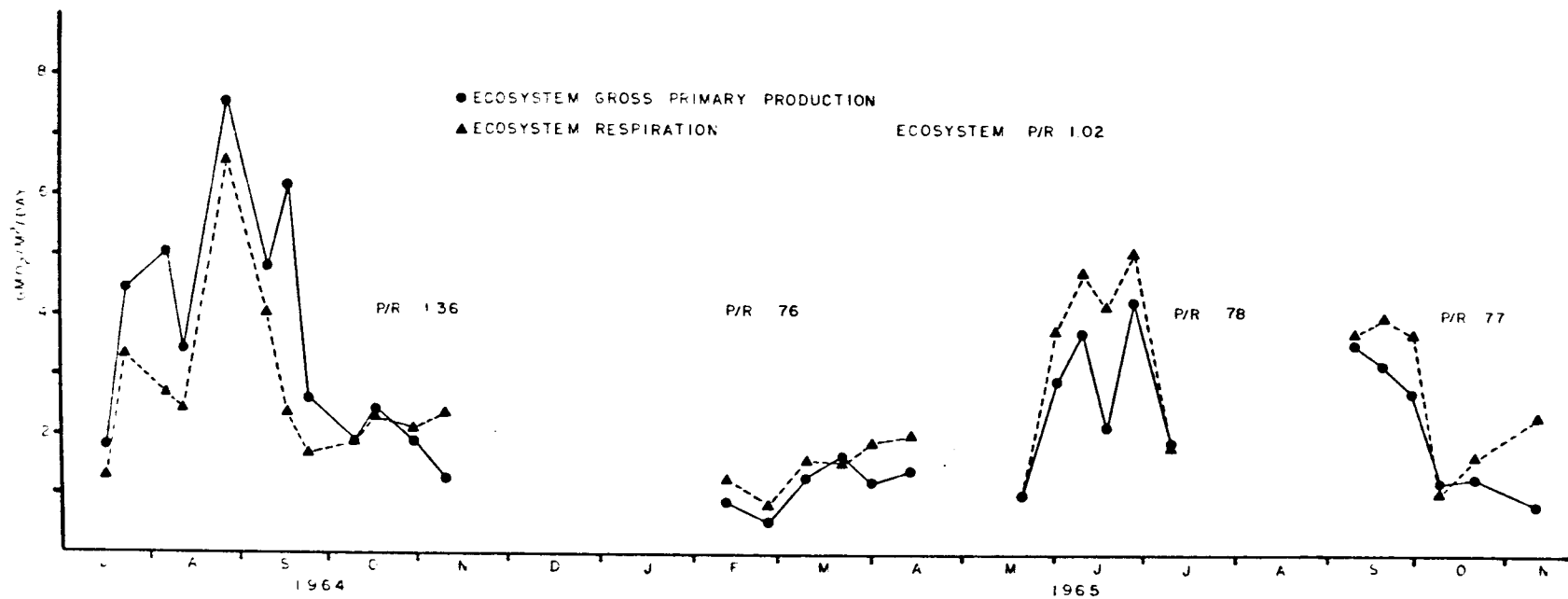
Figure 10. Average community metabolism for three stations

known, but because of the nature of the water admitted it is assumed

probable that very little organic matter was imported. A large

faunal population was supported by the ecosystem during a period

when the average P/R did not exceed 0.78. Since the average P/R

for the impoundment over the entire study period was 1.02, it became

obvious that the autotrophic community during 1964 had produced suf-

ficient standing crop to support the heterotrophic communities that

developed during 1965, and that over-all production rates exceeded

respiration rates by a small amount.

SUMMARY AND CONCLUSIONS

1. An impounded estuary was employed to study primary productivity, community respiration, and community structure as they related to seasonal and temporal succession, salinity, and water temperature.

2. Plankton metabolism was studied by means of the light- and dark-bottle technique, and plankton community structure was analyzed from samples concentrated by either centrifugation or filtration.

3. Benthic community metabolism was determined by using the "diurnal oxygen curve" method for free water metabolism and then subtracting the values for metabolism of the plankton. Benthic community structure was determined by field observations and from collections.

4. Four different physical environments developed due to water control procedures required in the management of the impoundment. One was saline, two were brackish water, and one was a freshwater environment.

5. Four distinct benthic plant communities were observed and were named according to the dominant plants as follows: Enteromorpha-Melosira, Melosira-Enteromorpha, Melosira-Spirogyra, and Rhizoclonium-Melosira-Synedra. The plankton that

developed simultaneously was included under the same terminology as the benthic community.

6. The plankton flora was characteristically tychoplankton, with only one "bloom" occurring. This occurred at only one station and the organism was identified as a species of Gymnodinium.

7. The magnitude of the primary production and community respiration for the benthic Enteromorpha-Melosira Community was much greater than for the plankton. The highest metabolic rates of the entire study were recorded for this community. A P/R of 1.36 resulted in the development of a large standing crop which dramatically became senescent during early November and formed organic ooze on the bottom as well as dissolved and suspended organic matter in the water.

8. In the Melosira-Enteromorpha Community the benthic community exceeded the plankton in both rates of production and respiration, but at a lower magnitude. This community had a P/R of 0.76.

9. Benthic production rates for the Melosira-Spirogyra Community were generally less than the plankton rates, but respiration rates were greater. The community had a P/R of 0.78.

10. The benthic community generally had greater production rates than the plankton in the Rhizoclonium-Melosira-Synedra Community, and the benthic respiration rates were consistently much higher than for the plankton. This community maintained a P/R of

0. 77.

11.   A brief resume of the history of free water measurements of metabolic rates was given, and difficulties encountered with this type of study were discussed.

12.   The impoundment over the entire study period maintained a P/R of 1. 02, and was essentially "self-supporting", primarily due to the large standing crop developed during 1964.   Little exogenous organic material was thought to have been imported into the eco-system.

BIBLIOGRAPHY

American Public Health Association. 1960. Standard methods for
the examination of water. 11th ed. New York. 626 p.

Calvert, C. K. 1932. The hourly variation of Indianapolis sewage.
Sewage Works Journal 4:815-820.

_____. 1933. Effects of sunlight on dissolved oxygen
in White River. Sewage Works Journal 5:685-694.

Copeland, B. J. and W. R. Duffer. 1964. Use of a clear plastic
dome to measure gaseous diffusion rates in natural waters.
Limnology and Oceanography 9:494-499.

Edmondson, W. T. and Y. H. Edmondson. 1947. Measurements of
production in fertilized salt water. Journal of Marine Research
6:228-245.

Gaarder, T. and H. H. Gran. 1927. Investigations of the production
of plankton in the Oslo Fjord. Rapports et Procès-Verbaux
Réunions Conseil Permanent International pour L'Exploration
de la Mer 42:1-48.

Gessner, G. and F. Pannier. 1958. Influence of oxygen tension on
respiration of phytoplankton. Limnology and Oceanography
3:478-480.

Haney, Paul D. 1954. Theoretical principles of aereation. Journal
of the American Water Works Association 46:353-376.

Jackson, D. F. and J. McFadden. 1954. Phytoplankton photo-
synthesis in Sanctuary Lake, Pymatuning Reservoir. Ecology
35:1-4.

Kohn, A. J. and P. Helfrich. 1957. Primary organic productivity
of a Hawaiian coral reef. Limnology and Oceanography
2:241-252.

Lindeman, Raymond L. 1942. The trophic dynamic aspect of
ecology. Ecology 23:399-418.

McConnell, W. J. and W. F. Sigler. 1959. Chlorophyll and pro-
ductivity in a mountain river. Limnology and Oceanography
4:335-351.

McIntire, C. David. 1967. Some factors affecting respiration of
periphyton communities in lotic environments. Ecology.
(In press)

McIntire, C. David et al. 1964. Primary production in laboratory
streams. Limnology and Oceanography 9:92-102.

McQuate, A. G. 1956. Photosynthesis and respiration of the phyto-
plankton in Sandusky Bay. Ecology 37:834-839.

Millipore Filter Corporation. 1966. Techniques for microbiological
analysis. Rev. ed. Bedford, Massachusetts. 37 p. (ADM 40).

Nielsen, E. Steemann. 1960. Productivity of the oceans. Annual
Review of Plant Physiology 11:341-362.

Nielsen, E. Steemann and A. Jensen. 1957. Primary oceanic pro-
duction. The autotrophic production of organic matter in the
ocean. Galathea Report 1:49-136.

Odum, Eugene P. 1953. Fundamentals of ecology. Philadelphia,
W. B. Saunders. 384 p.

_____. 1959. Fundamentals of ecology. Philadelphia,
W. B. Saunders. 546 p.

Odum, Howard T. 1956. Primary production in flowing waters.
Limnology and Oceanography 1:102-117.

_____. 1957a. Primary production measurements in
eleven Florida springs and a marine turtle grass community.
Limnology and Oceanography 2:85-97.

_____. 1957b. Trophic structure and productivity of
Silver Springs, Florida. Ecological Monographs 27:55-112.

_____. 1963. Productivity measurements in Texas
turtle grass and the effects of dredging an intracoastal channel.
Publications of the Institute of Marine Science, Texas 9:48-58.

Odum, Howard T. and Charles M. Hoskin. 1958. Comparative studies on the metabolism of marine waters. Publications of the Institute of Marine Science, Texas 5:16-46.

Odum, Howard T. and Eugene P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecological Monographs 25:291-320.

Odum, Howard T. and Ronald F. Wilson. 1962. Further studies on reaeration and metabolism of Texas bays, 1958-1960. Publications of the Institute of Marine Science, Texas 8:23-55.

Odum, Howard T. et al. 1959. Measurements of productivity of turtle grass flats, reefs, and the Bahia Fosforescente of southern Puerto Rico. Publications of the Institute of Marine Science, Texas 6:159-170.

Oliver, J. H. 1957. Production of carbon in the sea. Nature 180:617.

Park, Kilho, D. W. Hood and Howard T. Odum. 1958. Diurnal pH variation in Texas bays and its application to primary production estimation. Publications of the Institute for Marine Science, Texas 5:47-64.

Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. Limnology and Oceanography 4:386-397.

Purdy, W. C. 1935. Results of algal activity, some familiar, some obscure. Journal of the American Water Works Association 27:1120-1133.

Reese, W. Harold. 1966. Physiological ecology and structure of benthic communities in a woodland stream. PhD. thesis. Corvallis, Oregon State University. (In press)

Ryther, John H. 1954. The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. Deep Sea Research 2:134-139.

Ryther, John H. et al. 1958. The dynamics of a diatom bloom. Biological Bulletin 115:257-268.

Sargent, Marston C. and T. S. Austin. 1949. Organic productivity
of an atoll. Transactions of the American Geophysical Union
30:245-249.

Strickland, J. D. H. 1960. Measuring the production of marine
phytoplankton. Ottawa Fisheries Research Board of Canada.
172 p. (Bulletin 122).

Talling, J. F. 1957. Diurnal changes of stratification and photo-
synthesis in some tropical African waters. Proceedings of
the Royal Society, Ser. B 147:57-83.

Tansley, A. G. 1935. The use and abuse of vegetational concepts
and terms. Ecology 16:284-307.

Teal, John M. 1957. Community metabolism in a temperate cold
spring. Ecological Monographs 27:283-302.

Truesdale, G. A., A. L. Downing and G. F. Lowden. 1955. The
solubility of oxygen in pure water and seawater. Journal of
Applied Chemistry 5:53-62.

Verduin, J. 1956. Primary production in lakes. Limnology and
Oceanography 1:85-91.

APPENDIX

Symbols:

S	Station		Pb	Gross productivity of the benthos
k	Volume based diffusion constant		Rb	Community respiration of the benthos
Z	Water depth in meters		P/Rfw	P/R for the ecosystem (free water)
Pp	Gross productivity of the plankton		P/Rp	P/R for the plankton
Rp	Community respiration of the plankton		P/Rb	P/R for the benthos
Pfw	Ecosystem productivity (free water)		T	Average temperature in degrees centigrade
Rfw	Ecosystem respiration (free water)		o/oo	Average salinity

All metabolic rates are given in gO2/m2/day

Sampling Dates	S	k	Z	Pp	Rp	Pfw	Rfw	Pb	Rb	P/Rfw	P/Rp	P/Rb	T	o/oo
	1	.38	1.3	.43	.69	2.93	2.03	2.50	1.34	1.44	.62	1.87	19	25
15-16 July 1964	2	0	1.3	.42	.65	1.20	1.19	.78	.54	1.01	.65	1.44	20	25
	3			.39	.54	1.30	.65	.91	.11	2.17	.72	8.27	21	27
	1	.39	1.0	.28	.46	5.80	4.08	4.52	3.62	1.42	.61	1.25	21	25
22-23 July 1964	2	.30	1.0	.34	.51	3.45	2.40	3.11	1.89	1.44	.67	1.65	21	25
	3	.18	.66	.13	.32	4.09	3.42	3.96	3.10	1.20	.41	1.28	22	24
	1	.05	1.3	.57	.66	11.70	4.91	11.13	4.25	2.38	.86	2.62	19	29
5-6 August 1964	2		1.3	.90	.99	1.30	1.09	.40	.10	1.19	.91	4.00	20	29
	3	.25	1.0	.53	.70	2.10	1.99	1.57	1.29	1.06	.76	1.22	22	29
	1	.04	1.3	.34	.72	3.77	1.75	3.43	1.03	2.15	.47	3.33	19	29
11-12 August 1964	2	.14	1.3	.44	.56	2.13	.84	1.69	.28	2.54	.79	6.04	19	29
	3	.27	1.0	1.47	.49	4.35	4.60	2.88	3.11	.95	3.00	.93	21	29
	1	.10	1.3	2.33	1.12	9.23	7.80	6.90	6.68	1.18	2.08	1.03	16	30
26-27 August 1964	2		1.3	.69	.86	7.02	6.86	6.33	6.00	1.02	.80	1.06	17	30
	3	.09	1.0	.35	.68	6.30	4.89	6.05	4.21	1.31	.51	1.44	19	30

APPENDIX

Sampling Dates	S	k	Z	Pp	Rp	Pfw	Rfw	Pb	Rb	P/Rfw	P/Rp	P/Rb	T	o/oo
	1	0	1.3	.92	1.09	2.73	1.84	1.81	.75	1.48	.84	2.41	16	30
9-10 September 1964	2	.08	1.3	.30	.88	6.50	5.43	6.20	4.55	1.20	.34	1.36	16	30
	3	.02	1.0	.02	.59	5.10	4.70	5.08	4.11	1.09	.03	1.24	17	30
	1	.19	1.3	.43	1.18	5.46	2.18	5.03	1.00	2.50	.36	5.03	18	30
16-17 September 1964	2	.28	1.3	.10	.70	7.67	2.43	7.57	1.73	3.16	.14	4.38	18	30
	3	.20	1.0	.16	.65	5.20	2.40	5.04	1.75	2.17	.25	2.88	20	31
	1	.32	1.3	.42	.75	2.21	.94	1.79	.19	3.18	.56	9.42	17	29
23-24 September 1964	2	0	1.3	.40	.95	2.34	1.43	1.94	1.43	1.64	.42	4.04	17	29
	3	.07	.66	.06	.47	3.23	2.60	3.17	2.13	1.24	.13	1.49	19	29
	1	.11	1.3	.39	.61	3.25	3.12	2.86	2.51	1.04	.64	1.14	14	29
9-10 October 1964	2	.06	1.3	.30	.34	1.03	.90	.73	.56	1.14	.88	1.30	15	29
	3		1.0	.15	.21	1.35	1.53	1.20	1.32	.88	.71	.91	17	29
	1	.16	1.2	1.15	.48	1.32	1.29	.17	.81	1.02	2.40	.14	14	28
16-17 October 1964	2	.18	1.2	.40	.31	2.04	2.02	1.64	1.71	1.00	1.29	.96	15	29
	3		.75	.14	.12	3.86	3.47	3.72	3.35	1.11	1.17	1.11	15	28
	1	.15	1.0	.22	.31	1.90	2.40	1.68	2.09	.79	.71	.80	12	29
29-30 October 1964	2	.06	1.0	.20	.16	2.45	2.73	2.25	2.57	.90	1.25	.88	12	29
	3	.05	.60	.04	.05	1.29	1.12	1.25	1.07	1.15	.80	1.17	13	28
	1	.22	1.3	.13	.26	1.26	2.34	1.13	2.08	.54	.50	.54	10	24-30
9-10 November 1964	2		1.3	.07	.17						.40		10	24-30
	3		1.0	.09	.14						.64		11	25

Sampling Dates	S	k	Z	Pp	Rp	Pfw	Rfw	Pb	Rb	P/Rfw	P/Rp	P/Rb	T	o/oo
	1			.12	.14							.82	4-11	17-27
19-20 November 1964	2			.20	.14							1.36	4-11	17-27
	3			.05	.14							.36	4-11	18-25
	1												8	0
10-11 December 1964	2												8	0
	3													
	1		1.2	.05	.35	1.23	1.68	1.18	1.33	.73	.14	.89	7	0
10-11 February 1965	2	.28	1.3	.13	.23	.65	1.18	.52	.95	.55	.57	.55	7	0
	3	.22	1.0	.08	.14	.70	.86	.62	.72	.81	.57	.86	7	0
	1	.58	1.2	.30	.16	.93	1.44	.63	1.29	.65	2.00	.49	8	4-21
24-25 February 1965	2	.66	1.0	.27	.16	.33	.57	.06	.41	.58	1.69	.15	9	
	3	.14	.75	.22	.11	.30	.38	.08	.27	.79	2.00	.30	9	4-10
	1	.31	1.0	.28	.31	.53	.72	.25	.41	.74	.90	.61	11	5-10
8-9 March 1965	2	.46	1.1	.33	.28	.87	1.26	.54	.98	.69	1.18	.55	12	5-9
	3	.46	.75	.10	.11	2.40	2.68	2.30	2.57	.90	.91	.89	11	5
	1			.56	.32						1.77		12	8-13
20-21 March 1965	2		1.3	.62	.38	1.07	.81	.45	.43	1.32	1.63	1.05	12	8-15
	3	1.14	1.0	.41	.15	2.20	2.18	1.79	2.03	1.01	2.73	.88	13	8-10
	1	.48	1.3	.81	.38	1.82	2.06	1.01	1.70	.88	2.25	.59	12	7-13
31 March - 1 April 1965	2	.49	1.3	.59	.35	1.17	2.24	.59	1.89	.52	1.65	.31	12	5-15
	3	.33	1.0	.47	.22	.85	1.32	.38	1.10	.64	2.13	.35	13	4-9

Sampling Dates	S	k	Z	Pp	Rp	Pfw	Rfw	Pb	Rb	P/Rfw	P/Rp	P/Rb	T	o/oo
	1			.91	.96						.95			15-27
12-13 April 1965	2	1.59	1.3	.53	.51	.98	2.12	.45	1.61	.46	1.04	.28	13	9-27
	3	.28	1.0	.43	.25	1.80	1.80	1.37	1.55	1.00	1.72	.88	14	12-25
	1	.10	1.0	.80	.53	1.12	1.08	.32	.55	1.04	1.51	.58	16	0
20-21 May 1965	2	.26	1.0	.58	.32	.58	.41	0	.09	1.41	1.81	0	16	0
	3	0	.66	.34	.17	1.24	1.30	.91	1.13	.95	1.94	.81	16	0
	1	.31	1.3	1.17	.61	2.73	3.81	1.56	3.20	.72	1.92	.49	16	0
31 May - 1 June 1965	2	.32	1.3	1.13	.57	2.05	3.03	.92	2.46	.68	1.98	.37	16	0
	3	.18	1.0	1.22	.65	3.85	4.30	2.63	3.65	.90	1.88	.72	17	0
	1	.22	1.3	2.39	.78	4.75	5.83	2.36	4.05	.81	3.06	.58	18	0
8-9 June 1965	2	.20	1.3	2.39	.68	4.23	5.47	1.84	4.79	.77	3.51	.38	18	0
	3	.12	1.0	1.64	.57	2.05	2.71	.41	2.14	.76	2.87	.19	18	0
	1	.19	1.3	1.11	.64	1.92	3.49	.81	2.85	.55	1.73	.28	17	0
16-17 June 1965	2	.27	1.3	1.03	.47	2.54	4.99	1.51	4.52	.51	2.19	.33	17	0
	3	.27	1.0	.34	.24	1.90	3.82	1.56	3.58	.50	1.42	.44	17	0
	1	.24	1.3	3.35	1.35	4.23	5.02	.88	3.67	.84	2.49	.24	19	0
25-26 June 1965	2	.38	1.3	3.78	2.24	4.29	5.55	.51	3.31	.77	1.69	.15	19	0
	3	.11	1.0	1.34	.66	4.15	4.49	2.81	3.83	.92	2.03	.73	20	0
	1	.21	1.3	.91	.49	1.59	1.56	.68	1.07	1.02	1.86	.64	20	6-16
8-9 July 1965	2	.47	1.3	.77	.49	1.62	1.12	.85	.63	1.45	1.57	1.35	20	4-25
	3	.38	1.0	.74	.40	2.35	2.66	1.61	2.26	.88	1.85	.71	21	3-6

APPENDIX

Sampling Dates	S	k	Z	Pp	Rp	Pfw	Rfw	Pb	Rb	P/Rfw	P/Rp	P/Rb	T	o/oo
7-8 September 1965	1	.34	1.0	.78	1.47	3.30	3.12	2.52	1.65	1.06	.53	1.53	19	21
	2	.26	1.0	.88	1.35	3.25	3.98	2.37	2.63	.82	.65	.90	20	21
	3	.22	.66	.94	.98	4.03	4.13	3.09	3.15	.98	.96	.98	20	20
17-18 September 1965	1	.41	1.0	1.45	.53	3.90	4.70	2.45	4.17	.83	2.74	.59	15	20
	2	.30	1.0	1.66	.69	1.80	3.36	.14	2.67	.54	2.40	.05	15	20
	3	.10	.66	1.41	.55	3.82	3.88	2.41	3.33	.98	2.56	.72	17	19
27-28 September 1965	1	.60	.84	1.04	.60	2.18	3.63	1.14	3.03	.60	1.73	.38	17	19
	2	.10	1.0	1.06	.56	3.30	3.79	2.34	3.23	.87	1.89	.72	18	19
	3													
7-8 October 1965	1	.38	1.0	1.19	.62	1.25	.72	.06	.10	1.74	1.92	.60	17	13-16
	2	.45	1.0	1.11	.51	1.22	1.34	.11	.83	.91	2.17	.13	18	13-16
	3													
19-20 October 1965	1	.34	1.0	.36	.26	.88	1.20	.52	.94	.73	1.38	.55	13	10
	2	.34	1.0	.43	.31	.55	1.20	.12	.89	.46	1.39	.13	14	10-12
	3	.56	.77	.41	.25	2.46	2.59	2.05	2.34	.95	1.64	.88	15	10-12
9-10 November 1965	1	.43	1.0	.33	.18	.83	2.40	.50	2.22	.35	1.83	.23	12	8
	2	.30	1.0	.49	.17	.78	2.45	.29	2.28	.32	2.88	.13	13	8
	3	.39	.60	.21	.10	.93	2.16	.71	2.06	.43	2.20	.34	13	8