

(i)

DIEL VARIATIONS IN MARINE PHYTOPLANKTON

by

ROBERT WARREN DRINNAN

B.Sc., University of Calgary, 1967

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biology

We accept this thesis as conforming
to the required standards

*Accepted for the
Faculty of Graduate Studies*

[Redacted]
Dean for Term
12 May, 1972.

[Redacted]
[Redacted]
[Redacted]
[Redacted]

© ROBERT WARREN DRINNAN, 1972

UNIVERSITY OF VICTORIA

April 1972

UNIVERSITY OF VICTORIA
LIBRARY
Victoria, B. C.

ABSTRACT

Supervisor: Dr. J.L. Littlepage

Diel variations in chlorophyll *a* concentration, photosynthetic potential and total particulate volume were followed in several marine environments. In an inshore location, all three measurements showed a diel variation at the surface, with maximum values during the day and minimum values in the dark period, but only the photosynthetic potential measurements continued to show a diel rhythm after correction for biomass changes. At 30 meters, there was no apparent diel variation in chlorophyll *a* concentration or total particulate volume but a slight rhythm, similar in phase to the surface rhythms, existed for photosynthetic potential. This rhythm continued when corrected for biomass changes, although the amplitude was much less than at the surface.

A similar diel rhythm for photosynthetic potential (with a maximum during the day and a minimum at night), was found to occur in two locations in the open ocean. Laboratory experiments on natural phytoplankton populations, showed identical rhythms in photosynthetic potential as measured *in situ*. The rhythms were found to continue during an extended dark period, and the timing of the maxima and minima could be altered by changing the light-dark cycle.

The rhythms in photosynthetic potential were not caused by changes in cellular chlorophyll *a*. In addition, temperature, salinity, nitrate concentration and the daily variations in light intensity were not believed to be directly responsible for the observed rhythms.

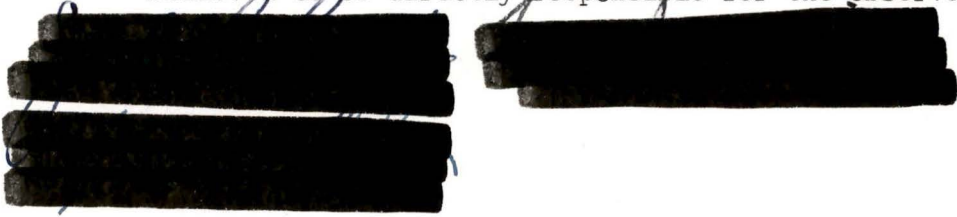


TABLE OF CONTENTS

	Page no.
ABSTRACT	(ii)
TABLE OF CONTENTS	(iii)
LIST OF TABLES	(vi)
LIST OF APPENDIX TABLES	(viii)
LIST OF FIGURES	(x)
ACKNOWLEDGEMENTS	(xvi)
INTRODUCTION	1
METHODS AND MATERIALS	11
Geographical Location	11
Sampling Procedure	11
Laboratory Experiments	14
Experiment A	15
Experiment B	15
Experiment C	16
Photosynthetic Uptake	16
Chlorophyll <i>a</i>	20
Particle Size Spectrum - Total Particulate Volume	21
pH - Alkalinity Measurements	22
Nitrates-Nitrites	22
Salinity	23

	Page no.
Light	23
Data Presentation	24
RESULTS	25
I. Inshore Waters - Station E-2	25
A. Surface Samples - Days IV-V	25
B. Surface Samples - Days VI-VII	31
C. Comparison of Day IV-VII - Surface Samples	36
D. 30 Meter Samples - Days IV-V	38
E. 30 Meter Samples - Days VI-VII	44
F. Comparison of Days IV-VII - 30 Meter Samples ..	48
II. Oceanic Waters - Station E-1	50
A. Surface Samples - Days I-III	50
B. 30 Meter Samples - Days I-III	55
III. Oceanic Waters - Ocean Station P	58
A. Total-Nanoplankton Series - Day A	60
B. Total-Nanoplankton Series - Day B	64
C. Surface-Depth Series - Day C	68
D. Surface-Depth Series - Day D	70
E. A Comparison of Surface Samples - Total Population	74

	Page no.
IV. Laboratory Experiments - Ocean Station P	76
A. Experiment A	76
B. Experiment C	81
C. Experiment B	84
DISCUSSION	87
I. Inshore Waters - Surface, Station E-2	87
II. Inshore Waters - 30 Meters, Station E-2	97
III. Oceanic Waters - Surface, Station E-1	113
IV. Oceanic Waters - 30 Meters, Station E-1	116
V. Oceanic Waters - Ocean Station P	121
VI. Lab Experiments	129
VII. The Possibility of Circadian Rhythms in Marine Phytoplankton	135
CONCLUSIONS	141
SUMMARY	144
LITERATURE CITED	147
APPENDIX	158

LIST OF TABLES

TABLE	Page no.
1. A Summary of Diel Variations Reported for Marine and Fresh Water Phytoplankton	7
2. Maximum and Minimum Values for Surface Chlorophyll α Concentration, Photosynthetic Potential and Total Particulate Volume, Stations E-1 and E-2	26
3. Maximum and Minimum Values for Surface Chlorophyll α per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Stations E-1 and E-2	29
4. Maximum and Minimum Values at 30 Meters for Chlorophyll α Concentration, Photosynthetic Potential and Total Particulate Volume, Stations E-1 and E-2 ..	39
5. Maximum and Minimum Values at 30 Meters for Chlorophyll α per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Stations E-1 and E-2	42
6. Maximum and Minimum Values for Chlorophyll α Concentration, Photosynthetic Potential and Assimilation Ratios for Day A and B (total and nano-plankton) and Day C and D (surface and 30 meters) at Ocean Station P	61

TABLE

Page no.

7. Maximum and Minimum Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Assimilation Ratios for Experiment A, B and C	77
--	----

APPENDIX TABLES

TABLE	Page no.
A1. Nitrate-Nitrite Concentration - Ocean Station E-1	159
A2. Nitrate-Nitrite Concentration - Station E-2, Saanich Inlet	160
A3. <i>In Situ</i> Temperature Measurements - Ocean Station E-1	161
A4. <i>In Situ</i> Temperature Measurements - Station E-2, Saanich Inlet	162
A5. Salinity Measurements - Ocean Station E-1	163
A6. Salinity Measurements - Station E-2, Saanich Inlet	163
A7. Nitrate-Nitrite Concentrations - Ocean Station P ...	164
A8. Nitrate-Nitrite Concentration - Laboratory Experiments	166
A9. <i>In Situ</i> Temperature Measurements - Ocean Station P .	167
A10. Subsurface Light Measurements - Ocean Station E-1, Station E-2, Saanich Inlet and Ocean Station P	168
A11. Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume Data for Endeavour Cruise, Stations E-1 and E-2	171

TABLE	Page no.
A12. Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios for Endeavour Cruise, Stations E-1 and E-2 ..	186
A13. Chlorophyll <i>a</i> Concentration and Photosynthetic Potential Values for Station P Cruise	201
A14. Assimilation Ratios for the Station P Cruise	216

LIST OF FIGURES

FIGURE	Page no.
1. Map showing the Geographical Locations of Sampling Stations	12
2. Diagramatic Drawing of Light Incubators	18
3. Surface Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume Day IV and V	27
4. Surface Values for Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume, and Assimilation Ratios, Day IV and V	30
5. Surface Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume, Day VI and VII	32
6. Surface Values for Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Day VI and VII	35
7. 30 Meter Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume, Day IV and V	40
8. 30 Meter Values for Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Day IV and V	43

FIGURE	Page No.
9. 30 Meter Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume, Day VI and VII	45
10. 30 Meter Values for Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Day VI and VII	47
11. Surface Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume, Days I-III	51
12. Surface Values for Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Days I-III	53
13. 30 Meter Values for Chlorophyll <i>a</i> Concentration, Photosynthetic Potential and Total Particulate Volume, Days I-III	56
14. 30 Meter Values for Chlorophyll <i>a</i> per Particulate Volume, Photosynthetic Potential per Particulate Volume and Assimilation Ratios, Days I-III	57
15. Surface Values for Chlorophyll <i>a</i> Concentrations in the Total Plankton and Nanoplankton Fraction on Day A, Station P	63

FIGURE

Page No.

16.	Surface Values for Chlorophyll <i>a</i> Concentrations in the Total Plankton and Nanoplankton Fraction, on Day B, Station P	63
17.	Surface Values for Photosynthetic Potential in the Total Plankton and Nanoplankton Fraction, on Day A, Station P	65
18.	Surface Values for Photosynthetic Potential in the Total Plankton and Nanoplankton Fraction, on Day B, Station P	65
19.	Surface Values for Assimilation Ratios in the Total Plankton and Nanoplankton Fraction, on Day A, Station P	67
20.	Surface Values for the Assimilation Ratios in the Total Plankton and Nanoplankton Fraction, on Day B, Station P	67
21.	Surface and 30 Meter Values for Chlorophyll <i>a</i> Concentration, on Day C, Station P	69
22.	Surface and 30 Meter Values for Chlorophyll <i>a</i> Concentration, on Day D, Station P	69
23.	Surface and 30 Meter Values for Photosynthetic Potential, on Day C, Station P	71

FIGURE	Page No.
24. Surface and 30 Meter Values for Photosynthetic Potential, on Day D, Station P	71
25. Surface and 30 Meter Values for Assimilation Ratios, on Day C, Station P	73
26. Surface and 30 Meter Values for Assimilation Ratios, on Day D, Station P	73
27. Chlorophyll <i>a</i> Concentration for the Lab and Control Cultures, Experiment A	78
28. Chlorophyll <i>a</i> Concentration for the Lab and Control Cultures, Experiment C	78
29. Photosynthetic Potential for the Lab and Control Cultures, Experiment A	80
30. Photosynthetic Potential for the Lab and Control Cultures, Experiment C	80
31. Assimilation Ratios for the Lab and Control Cultures, Experiment A	82
32. Assimilation Ratios for the Lab and Control Cultures, Experiment C	82
33. Chlorophyll <i>a</i> Concentration for the Lab and Control Cultures, Experiment B	85
34. Photosynthetic Potential for the Lab and Control Cultures, Experiment B	85

FIGURE	Page no.
35. Assimilation Ratios for the Lab and Control Cultures, Experiment B	85
36. Chlorophyll α per Particulate Volume for Surface Samples, Days IV-VII	96
37. Chlorophyll α per Particulate Volume at 30 Meters, Days IV-VII	96
38. Photosynthetic Potential per Particulate Volume for Surface Samples, Days IV-VII	98
39. Assimilation Ratios for Surface Samples, Days IV-VII	99
40. Photosynthetic Potential per Particulate Volume at 30 Meters, Days IV-VII	105
41. Assimilation Ratios at 30 Meters, Days IV-VII	106
42. Chlorophyll α per Particulate Volume at the Surface and 30 Meters, Day IV and V	108
43. Chlorophyll α per Particulate Volume at the Surface and 30 Meters, Day VI and VII	108
44. Photosynthetic Potential per Particulate Volume at the Surface and 30 Meters, Day IV and V	109
45. Photosynthetic Potential per Particulate Volume at the Surface and 30 Meters, Day VI and VII	110

FIGURE	Page no.
46. Assimilation Ratios at the Surface and 30 Meters, Days IV and V	111
47. Assimilation Ratios at the Surface and 30 Meters, Days VI and VII	112
48. Chlorophyll α per Particulate Volume at the Surface and 30 Meters, Days I and II	117
49. Photosynthetic Potential per Particulate Volume at the Surface and 30 Meters, Days I and II	119
50. Assimilation Ratios at the Surface and 30 Meters, Days I and II	120
51. Surface Values for Photosynthetic Potential, Days A-D	128
52. Surface Values for Assimilation Ratios, Days A-D ...	128

ACKNOWLEDGEMENTS

I would like to express my thanks and gratitude to Dr. J.L. Littlepage for his continual support and encouragement throughout the study. I would also like to thank Dr. L.A. Hobson and Dr. E.M. Hagmeier for their advice and useful criticism during the preparation of the manuscript.

I am especially grateful to Doug Hartley, Gordon Glova, Eric Marles and Marlene Roberge who helped during the sampling periods, and to the support of the captains and crew of the C.C.G.S. Quadra, and C.N.A.V. Endeavour. I would also like to thank Ron Norden for his work in drafting the many figures and Tom Gore for the reproduction of them.

Finally, I am indebted to my wife, Sophie, for the many hours spent in typing, and assembling the thesis, and for her patience and encouragement throughout the study.

The research was supported by a University of Victoria Faculty Research Grant and a National Research Council Grant awarded to Dr. J.L. Littlepage.

INTRODUCTION

The determination of plant production and standing crop has been a major goal of recent oceanographic investigations. Since 1957, however, it has become evident that some measurements of these parameters varied considerably, depending on the time of sampling (Table 1). Plant production, which is the amount of organic material produced by photosynthesis, was usually expressed as photosynthetic potential, the amount of photosynthesis occurring at a given light intensity. Standing crop, or biomass, has been defined by Strickland (1960) as "the instantaneous value of the amount of living plant material present in the water" and was normally expressed as chlorophyll content or cell numbers per unit volume of water.

The variations in the photosynthetic potential and standing crop were often diel in nature, occurring regularly every 24 hour period. Doty and Oguri (1957) were the first to report diel variations in photosynthetic potential. They found a 5-fold difference in tropical Pacific waters, between a morning maximum and a minimum during the evening, and attributed the variations to changes in the ability of phytoplankton cells to assimilate carbon, rather than to population changes. However, neither cell numbers or chlorophyll concentrations were measured.

Yentsch and Ryther (1957) and Shimada (1958) found that the chlorophyll *a* concentration in inshore waters, paralleled that of

the photosynthetic potential, with maxima during the morning and a minimum at night. Photo-oxidation of the plant chlorophyll was suggested by both groups as the cause of the variations. Cell numbers, however, were not monitored in either of these studies, and thus the effects of zooplankton grazing and/or physical transport of the water mass, could not be determined.

Diel variations in chlorophyll *a* concentration in inshore waters have also been reported by Ryther *et al* (1958) and Yentsch and Scagel (1958) with a maximum during the afternoon and minimum values in the dark period. Both groups reported that the variations in chlorophyll *a* were greater than could be attributed to changes in the phytoplankton population.

Ryther and co-workers felt that the changes in chlorophyll were due to decomposition and resynthesis of the pigment, the former being enhanced by high incident radiation. Yentsch and Scagel also felt that bleaching of chlorophyll by light and resynthesis were responsible for the variations measured, and concluded that fluxuations in photosynthetic potential reported in the literature, were due to changing chlorophyll content.

Wood and Corcoran (1966) and Glooschenko (1967) both found a diel variation in chlorophyll concentration in oceanic waters, but the former attributed the differences solely to changes in the phytoplankton population. Glooschenko, however, felt that the variations in

chlorophyll *a* and *c* were greater than could be accounted for by population changes, although cell numbers were not actually measured. He felt that these cellular variations in chlorophyll, regulated by incident light, would result in a constant photosynthetic rate.

Lorenzen (1963) in an inshore environment, and McAllister (1963) in oceanic waters, both found a parallel relationship between chlorophyll *a* concentration and photosynthetic potential, with maximum values near midday, decreasing to a minimum in the dark period. They also found a similar variation in assimilation ratios, defined as the amount of photosynthetic potential per unit of chlorophyll. McAllister concluded that daily changes in zooplankton grazing as well as some biological rhythm within the plant cell, would result in a diel variation in photosynthetic potential. Lorenzen suggested that there were diel changes in cellular concentrations of chlorophyll *a*, due to photo-oxidation and resynthesis of the pigment, but felt that there was also a variation in the photosynthetic efficiency (the amount of photosynthetic production per unit of chlorophyll) in the cell as well.

Newhouse *et al* (1967) found in inshore waters, a diel variation in the photosynthetic potential, similar to those reported by Lorenzen and McAllister. They concluded that the variations resulted from a combination of grazing effects, compounded by diel physiological variation (biological rhythm) in carbon assimilation.

A biological rhythm was also suggested by Eppley *et al* (1971a) for being at least partly responsible for variations in the photosynthetic potential. They measured changes in cultures of natural phytoplankton population, and found a diel variation in the time of cell division, but not in the synthesis of chlorophyll *a*. However, their data implied that the amount of chlorophyll *a* per cell, as well as the photosynthetic potential per unit of chlorophyll *a*, both underwent a diel variation.

In all of the variations in photosynthetic potential discussed so far, minimum values have occurred during the dark period. Ryther *et al* (1961), however, found that in the Sargasso Sea the chlorophyll *a* concentration, integrated over the euphotic zone, decreased during the night, but the total photosynthetic production (calculated from 24-hour *in situ* measurements) was greater for samples collected in the dark period. These data suggest an increase in photosynthetic efficiency during the dark period. However, cell counts were not made, and thus differences which might be caused by population changes cannot be determined.

Goldman *et al* (1963) also found higher rates of photosynthetic production during lower light intensities, in an investigation of Antarctic lake phytoplankton. He attributed the decrease during the higher light intensities to light inhibition, but because chlorophyll measurements were not made, it is not known whether the decrease is due to pigment

changes or to the inhibition of another segment of the photosynthetic mechanism.

It can be seen from the literature reviewed here, that diel variations in chlorophyll *a* concentration and photosynthetic potential exist, but the reasons given for these variations differ between some authors. In addition, the time of the maximum and minimum were not always the same. Changes in the phytoplankton population and/or cellular changes in pigments were suggested to explain the differences in chlorophyll *a* concentration. Variations in the photosynthetic potential have been attributed to changes in chlorophyll *a* (either through population changes or to a variation in cell pigments) or to some biological rhythm affecting the photosynthetic mechanism.

However, it is important to note that in none of the studies, were chlorophyll *a*, photosynthetic potential, and cell counts measured simultaneously. If ratios involving the photosynthetic potential per cell, chlorophyll *a* per cell, and photosynthetic potential per unit of chlorophyll *a* were followed, one would be able to determine whether the variations were caused by population changes, or were cellular in nature. For example, if a variation in photosynthetic potential was a result of changes in cellular chlorophyll, then one would expect a change in chlorophyll *a* per cell, but not necessarily in the amount of photosynthesis per unit of chlorophyll *a*.

However, if the diel variations in photosynthetic potential were endogeneous rhythms involving the photosynthetic mechanism, then

differences in the amount of carbon uptake per cell would occur, as well as variations in the photosynthetic potential per unit of chlorophyll a . A diel variation due to population changes alone, would not show any differences in the calculated ratios.

A study was therefore initiated to investigate the variations in chlorophyll a , photosynthetic potential and total particulate volume (used as a measurement of the phytoplankton population) in natural phytoplankton communities, and to determine whether the variations were intracellular or due to changes in biomass. Experiments were done over 24, 48 and 72-hour time periods to test whether any changes in the above parameters were diel in nature.

TABLE 1

A summary of diel variations in phytoplankton.

Location	Variation(s) Measured	Time of Maximum	Time of Minimum	Suggested Causes For Variations	Reference
Off-Shore Waters:					
Tropical Pacific	1) Photosynthetic Potential	- mid-day	start of dark	biological rhythm and/or changes in chlorophyll	Doty and Oguri (1957)
Tropical Pacific	1) Photosynthetic Potential 2) Chlorophyll Concentration	^ morning ^ morning	afternoon afternoon	variations in chlorophyll	Shimada, (1958)
Sargasso Sea	1) Chlorophyll Concentration (total euphotic zone) 2) Photosynthesis (24 hr - <i>in situ</i> , in total euphotic zone)	~ day v dark	dark day	1) effect of light 2) possible effect by nutrients	Rhyther, et al (1961)
N.E. Pacific	1) Chlorophyll α Concentration 2) Photosynthetic Potential 3) Assimilation Ratios	^ morning, dark (2000) ^ morning ^ morning	dark (1800, 0200) dark (2000) dark (2000)	1) grazing plus cellular changes 2) biological rhythms, chlorophyll changes plus grazing 3) biological rhythms, chlorophyll changes	McAllister, (1963)
Sargasso Sea	1) Photosynthetic Potential 2) Chlorophyll Concentration	morning (0600) v evening (1800)	dark dark	1) biological rhythms and cellular changes possibly influenced by nutrients 2) same as above	Goering, et al, (1964)
Tropical Atlantic	1) Cell Numbers 2) Chlorophyll Concentration (occasionally)	- day - varied	night varied	1) grazing 2) grazing	Wood and Corocran, (1966)

Table 1, cont'd.

Temperate Pacific	1) Chlorophyll Concentration	dark	day	1) influence of light	Glooshenko, (1967)
Tropical Pacific	1) Assimilation Ratio (* no dark period measured)	afternoon	mid-day*	light inhibition with influence by nutrients	Malone, (1971)
Inshore Waters:					
Woods Hole Harbor	1) Chlorophyll Concentration	morning - afternoon	noon-dark	1) influence of light	Yentsch and Ryther, (1957)
	2) Photosynthetic Potential	morning - afternoon	noon-dark	2) changes in chlorophyll	
Atlantic Estuary	1) Chlorophyll Concentration	afternoon	dark	1) light plus influence of nutrients	Ryther, et al, (1958)
Pacific Inlet (Washington)	1) Chlorophyll Concentration	dark	afternoon	1) influence of light and nutrients	Yentsch and Scagel, (1958)
	2) Chlorophyll Per Cell	dark - morning	mid-day	2) influence of light and nutrients	
Antarctic Fresh-Water	1) <i>In Situ</i> Photosynthesis (24 hr light cycle)	lowest light (midnight)	mid-day	1) light influence on chlorophyll	Goldman, et al, (1963)
Atlantic Estuary	1) Photosynthetic Potential	mid-day	dark	1) changes in chlorophyll	Lorenzen, (1963)
	2) Chlorophyll Concentration	mid-day	dark	2) influence of light	
	3) Assimilation Ratios	mid-day	dark	3) cellular changes in efficiency	
Weddell Sea	1) Photosynthetic Potential	midnight	mid-day	1) light inhibition	El-Sayed and Mandelli (1965)
	2) Chlorophyll	midnight	mid-day	2) influence of light	
	3) Assimilation Ratios (24 hr light cycle)	midnight	mid-day	3) possible biological rhythm	
Hawaii, Inshore	1) Photosynthetic Potential	afternoon	early morning	1) changes in biomass	Newhouse, et al, (1967)
	2) Photosynthetic Potential per unit biomass	afternoon	early morning	2) biological rhythm + excretion	

Table 1, cont'd.

Arctic Fresh-Water	1) <i>In Situ</i> Photosynthesis (24 hr light cycle)	evening	mid-day	1) light inhibition of chlorophyll	Kalff, (1969)
Cultures:					
<i>Euglena gracilis</i>	1) Chlorophyll Concentration	light	dark	-	Gibor and Meehan, (1961)
<i>Dunaliella tertiolecta</i>	1) Cell Division	start of dark	light	1) synchronous culture	Eppley and Coatsworth, (1966)
	2) Cell Pigment	light	dark	2) phasing of cellular activities to a light- dark cycle	
	3) Photosynthetic Potential	light	dark	3) phasing of cellular activities to a light- dark cycle	
	4) Assimilation Ratios	light	dark	4) biological rhythm	
<i>Skeletonema costatum</i>	1) Photosynthetic Potential per cell	mid-light	dark	1) biological rhythm	Jorgensen, (1966)
	2) Chlorophyll Per Cell	mid-light	dark	2) cyclic synthesis	
	3) Assimilation Ratios	mid-light	dark	3) biological rhythm	
	4) Cell Division	mid-light	dark	4) phasing with light- dark cycle	
<i>Ditylum brightwellii</i>	1) Cell Division	start of dark	end of dark	1) phasing with light- dark cycle	Eppley, et al, (1967)
	2) Chlorophyll Per Cell	start of dark	end of dark	2) phasing with light- dark cycles	
	3) Assimilation Ratios	end of light	mid-dark	3) light and/or biological rhythm	
<i>Coccolithus luxlegi</i>	1) Cell Division	dark	light	1) phasing of cellular activities to light- dark cycles	Paasche, (1967)
	2) Chlorophyll Per Cell (implied from data)	light	dark	2) phasing of cellular activities to light- dark cycles	

Table 1, cont'd.

<i>Ditylum brightwellii</i>	1) Cell Division	light	dark	1) phasing with light- dark cycles	Paasche, (1968)
	2) Chlorophyll Concentration	light (varied)	dark	2) variations in biomass	
	3) Photosynthetic Potential per cell	light	dark	3) variations in biomass	
<i>Gonyaulax polyedra</i>	1) Cell Division	end of dark	light	1) biological clock	Sweeney, (1969)
	2) Photosynthesis Per Cell	light	dark	2) biological clock	
Natural Populations	1) Cell Division	dark	light	1) phasing with light- dark cycles	Eppley, et al, (1971a)
	2) Photosynthetic Potential	mid-day	dark	2) biological rhythm	
	3) Chlorophyll Per Cell (implied from data)	mid-day	dark	3) biological rhythm	

METHODS AND MATERIALS

Geographical Location (Figure 1)

The oceanic environment was investigated at two locations in the N.E. Pacific Ocean. The first study was conducted during the summer (August - September) of 1969, at Ocean Station P, (145° W longitude, 50° N latitude) aboard the Department of Transport Weather Ship, C.C.G.S. Quadra. The station is located in the Sub-arctic North Pacific Current, which has a general eastward movement. Before reaching the North American coast, this current splits, with most of the movement deflecting south to form part of the California Current (Pickard, 1963). A second ocean station was located in this southward moving portion of the Sub-arctic Current, at a longitude $129^{\circ} 20'$ W, latitude $48^{\circ} 50'$ N. This cruise was carried out aboard the C.N.A.V. Endeavour, in May, 1970.

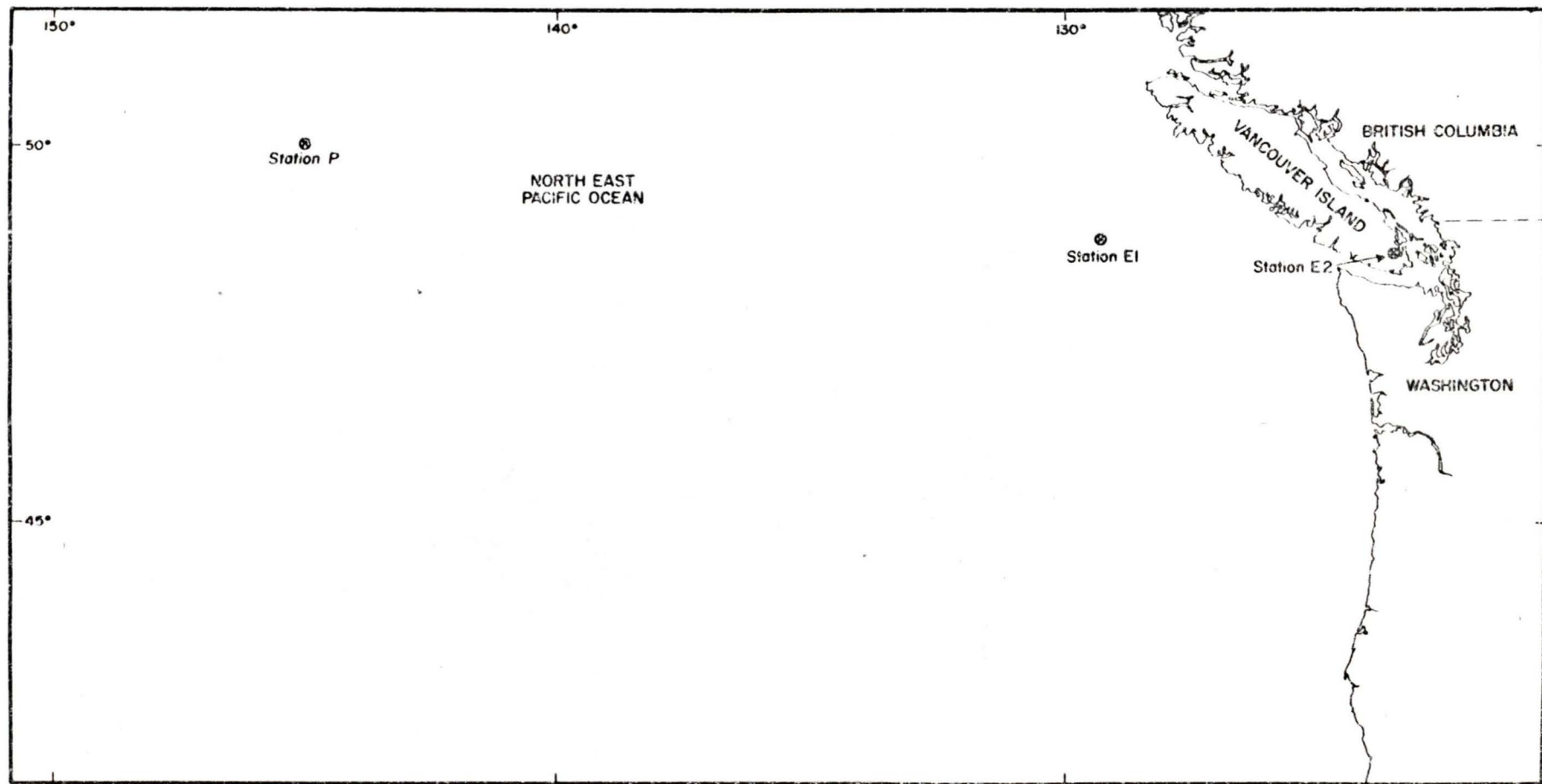
The inshore environment was studied in Saanich Inlet, Vancouver Island, the oceanography of which is described by Herlinveaux (1962). Samples at station E-2, longitude $123^{\circ} 29'$ W, latitude $48^{\circ} 40'$ N, were collected aboard the C.N.A.V. Endeavour in May 1970.

Sampling Procedures

At Station P a series of sampling procedures were set up to measure the variations in photosynthetic potential and chlorophyll a concentration over a 24-hour period. Differences between the total

FIGURE 1

Map Showing The Geographical
Location of Sampling Stations.



population and nanoplankton fraction were investigated, as well as differences between the surface and 30-meter populations. For the purposes of this study, nanoplankton was defined as those organisms passing through a 44-micron mesh net. Laboratory studies, using natural populations from the surface waters, were also done during this cruise.

Samples collected were placed in 20-litre carboys from which water for the various analyses was subsequently taken. For the total-nanoplankton study, surface water only was sampled, using a sea water supply located in the ship's laboratory. The line for this system was linked directly with the exterior, with the inlet port about $3\frac{1}{2}$ meters below the sea surface. During the time of the study, the water was flowing continuously.

For the surface-depth study, water was sampled using a submersible pump constructed at the Biological Laboratories in Nanaimo. Water for the laboratory experiments was collected using the laboratory sea water supply.

During the Endeavour cruise, all samples were obtained using a large volume sampler, similar to a Niskin sampler, which was built at the University of Victoria, or a seven-litre Van Dorn bottle.

All field investigations were initiated at 0900 local time, with a sampling period every two hours. At Station P, each study continued for 24 hours. Station E-1 was sampled continuously for 72 hours while at station E-2 two studies were done, each of 48 hours duration.

During sampling at Station P, the ship was drifting except for brief intervals (approximately 15 minutes) every four hours when steaming was necessary for the release of a weather balloon, or during rough weather when a constant position was maintained. At station E-1, a drogue was lowered into the water and followed, so as to remain in the same water mass. Due to weather conditions the buoy was removed during the last 36 hours and the ship maintained a constant position. At station E-2, the ship was anchored to a buoy located in Saanich Inlet.

Laboratory Experiments

Three sets of experiments were set up, which were designed to measure any changes in photosynthetic potential and chlorophyll *a* concentration brought about by altering the photoperiod on natural phytoplankton populations. Sea water from the laboratory sea water supply, was pumped through surgical tubing into wooden aquaria which had been painted with a non-toxic epoxy paint. Both aquaria were fitted with plexi-glass lids and placed in refrigerators. The temperature of each refrigerator was adjusted to equal that of the water at the time of collection.

Air was passed through a cotton wool plug into each aquarium to keep the culture circulating. Light was provided by three cool-white fluorescent bulbs fastened over the transparent covers, with an intensity of approximately 0.020 ly/min at the surface of the water.

Experiment A

Water was collected at 1800 (the beginning of the dark period) and the aquaria filled. The lights in both cabinets were turned off. The light period for both cultures was set for 12 hours, between 0600 and 1800, which best approximated the daily light cycle at the time of the experiment.

After the dark period of the third day, the lights in one aquarium were turned off, while the other culture was allowed to continue on the original cycle. The aquarium which was kept on the original light-dark cycle will be referred to as the control culture, while the other aquarium will be referred to as the lab culture. Sampling was started at 0900 the following day and continued every three hours for 24 hours.

Experiment B

Water was collected at 1800 hours and the procedure of Experiment A was followed, with the exception of the light-dark cycle in one of the aquaria. The light period was shifted 12 hours so that it was opposite to that of the control culture. The control culture had a light cycle between 0600 and 1800, while the lab culture had the light period between 1800 and 0600. At 0900 on the fourth day after the experiment was started, sampling was initiated, with collections every three hours for 24 hours.

Experiment C

This study was a repeat of Experiment A except that nitrate, phosphate and silicate were introduced at the beginning of the experiment, to prevent nutrient limitation. The compounds NaNO_3 , K_2HPO_4 , and $\text{NaSiO}_3 \cdot 9\text{H}_2\text{O}$ were added to make an additional concentration in the culture of 25 $\mu\text{g-at/l}$ NO_3 , 12.5 $\mu\text{g-at/l}$ PO_4 , and 25 $\mu\text{g-at/l}$ of SiO_3 .

Photosynthetic Uptake

To measure the photosynthetic potential of the phytoplankton population, the carbon-14 technique first described by Steemann-Nielsen (1952) was employed. In order to compare the populations throughout the twenty-four hour time period, the activity was recorded as the photosynthetic potential occurring near light saturation - the light intensity at which maximum photosynthesis occurs. During these studies, the light intensity of the incubators was kept less than the highest *in situ* light values so as to prevent any light inhibition.

250-ml glass stoppered bottles were filled with sea water at each time period. Duplicates were prepared for each depth. In the case of the total-nanoplankton experiment, four bottles were filled with surface water, with the nanoplankton fraction in two of the bottles separated after incubation. Duplicate dark bottles were prepared every four sampling periods, one for each depth.

Each sample bottle was inoculated immediately with 1 ml of $C^{14}HCO_3$, in distilled water, with an activity of 8.5 microcuries. The bottles were placed in the dark until all were inoculated, inverted several times, and placed in a light incubator.

For the investigations conducted at Station P, illumination was provided by two banks of two cool-white fluorescent bulbs each having an intensity of approximately .026 langleys per minute (Figure 2). Samples were placed in the center of the incubator to minimize differences in light intensity which may occur near the ends of the fluorescent bulbs. Surface seawater was used to cool the samples, the difference in temperature keeping within $1^{\circ}C$ of the surface water. Every hour, the bottles were inverted several times to prevent settling of the phytoplankton.

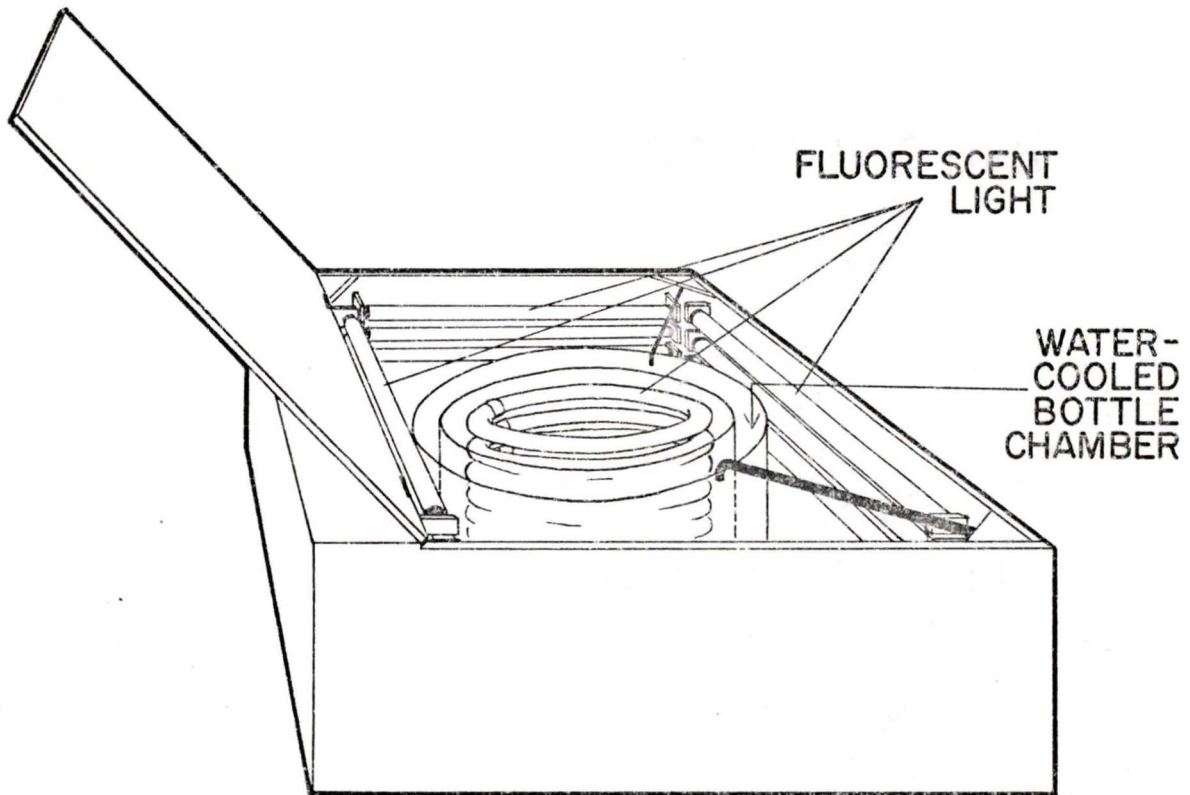
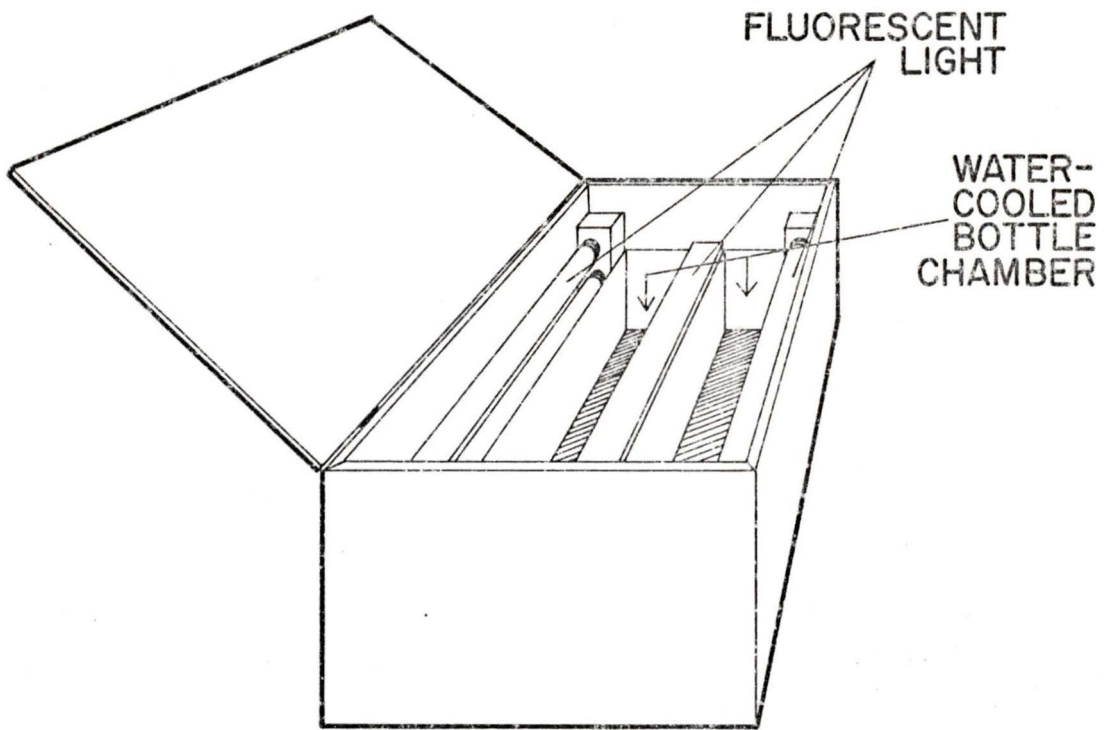
The incubator used during the C.N.A.V. Endeavour cruise is shown in Figure 2. Samples were automatically rotated around the lights to eliminate any variation in light intensity, which was approximately .052 ly/min. The incubator was placed in a dark constant temperature room held at $8^{\circ}C$. This temperature was essentially the same as found at 30 meters, while the surface water temperatures varied between 7.8 and 10.2 depending on the time of day.

After an incubation time of four hours, the organisms were preserved with 1 ml of 3% neutral formalin to stop photosynthesis, and filtered through 0.45-micron pore size membrane (Millipore[®]) filters. After several rinses with filtered sea water, the filters

FIGURE 2

Above: Diagramatic Drawing of the Light Incubator
Used During the Station P Cruise.

Below: Diagramatic Drawing of the Light Incubator
Used During the Endeavour Cruise.



were dried by vacuum and placed in scintillation vials containing a scintillation fluid of the following components: 4.0gPPO⁽¹⁾, 0.3gPOPOP⁽²⁾, and 220 ml Biosolv[®] per litre of toluene (Dr. G.C. Anderson, personal communication). The Biosolv was included to cause any aqueous material to become miscible in the toluene. The samples were then counted on a Beckman Model LS155 Liquid Scintillation Counter, as suggested by Wolfe and Schelske (1967).

In order to determine the efficiency of the counter, internal standards were made up. These consisted of filters through which varying volumes (0, 1/4, 1/2, 3/4, 1, 3, and 5, x 250 ml) of Saanich Inlet water was filtered. The filters were dried by vacuum, and added to a scintillation cocktail identical to the one used during the cruises. To each filter, was also added a known amount of C¹⁴ - labelled toluene which had a given activity of 4.36×10^5 d.p.m. The counting efficiency was found to be 90% and it is assumed that the data presented here was counted at the same efficiency.

The calculation of the photosynthetic potential (in mg C/m³/hr) was done using the equations of Steemann Nielsen (1952).

(1) 2,5-diphenyloxazole

(2) 1,4-Bis [2-(5-phenyloxazolyl)] - benzene

Chlorophyll α

Duplicate samples for chlorophyll α were measured with a graduated cylinder and filtered immediately through a 0.45-micron pore size Millipore[®] filter. To prevent the filter from becoming acidic, 1 ml of a solution of magnesium carbonate (1 g/100 ml) was added during the final stages of filtration. The filters were folded within a heavy Whatman filter paper and stored in a desiccator at -20°C .

Chlorophyll extractions were done at a later date, usually within one month of collection, and with the longest period of storage being $2\frac{1}{2}$ months. All chlorophyll samples collected on any particular 24-hour experiment, were done together, so that their storage time would be the same. It is assumed that the degradation effects within any one experiment would be constant.

The procedure for extraction followed that suggested by the SCOR/UNESCO Working Group on photosynthetic pigments (1966) with the following modifications. Samples were ground in a pestle-type homogenizer for $1\frac{1}{2}$ minutes with 5-6 ml of 90% acetone. The contents were transferred to centrifuge tubes and after two acetone washes of the pestle and homogenizer, were placed in the dark at room temperature for 15 minutes. They were then centrifuged for 20 minutes at 4500g. The contents were carefully pipetted into a graduated centrifuge tube, and brought to a volume of 10.0 ml. The extinction

of the acetone extract was measured in a 10.0 cm cell at wavelengths of 750, 663, 645, and 630 millimicrons with a Hitachi, Perkin-Elmer UV-Vis spectrophotometer, Model 139. The concentration of chlorophyll *a* was calculated using the trichromatic equations of the SCORE/UNESCO group.

Particle Size Spectrum - Total Particulate Volume

The particle size distribution and the total number and volume of particles were determined from sea water samples using a Model B Coulter Counter [®]. To obtain a particle size distribution, each sample was counted at discrete size ranges, adjusted so that a continuous spectrum was obtained. Several counts were made of the number of particles in a given size range, and averaged. Counts were taken during a specified time interval (20.0 seconds), which was converted to a volume measurement. All counts are expressed as numbers per ml of sample.

For the total particulate volume, the number of particles in a given size interval was multiplied by the mean volume of that range. The total volume of each interval was then summed to give the total particulate volume. Since the instrument measures the volume of a particle, independent of shape, particle diameters are those of spheres having an equivalent volume.

Calibration of the 100 μ tube was done using ragweed pollen, with an average diameter of 19.5 μ , following the procedure given by Strickland and Parsons (1968). The volume of liquid sampled during a specific

time interval was determined by counting the number of particles in a known volume, and the number of particles in the same solution, during a given time period.

pH-Alkalinity Measurements

The pH of a sample was measured on a Fisher Accumet pH meter, Model 220. The *in situ* pH was calculated using the temperature correction tables of Harvey, as modified and given in Strickland and Parsons (1968). The total alkalinity of the sea water was calculated using the method and tables of Anderson and Robinson, as given in Strickland and Parsons (1968).

Nitrates - Nitrites

Sea water samples were collected every four sampling periods (8 hr) during each experiment in polyethelene bottles or plastic sampling bags. These were frozen at -20°C for analysis at a later date.

For nitrate and nitrite determinations, the samples were thawed to room temperature and analyzed. Nitrate was done following the modified method of Morris and Riley, as given in Strickland and Parsons (1968). Nitrite was measured following the technique of Shinn, and Bendschneider and Robinson, as presented in Strickland and Parsons (1968).

Salinity

Sea water samples for salinity measurements were taken every four sampling periods (8 hr) and the conductivity of the sample determined on a Hytech Model 6 Laboratory Salinometer. Conductivity ratios were converted to salinity values (‰) using the tables supplied with the instrument.

Light

Light was measured during each sampling period using a Kahl Scientific Submarine Photometer, with a microamp meter readout, and calibrated with a G.E. Industrial Barrier Cell Photometer. The light intensities, in foot-candles, were converted to langley's per minute, using the conversion factors given in Strickland (1958). At the onset of each experiment, light measurements were made at several depths to obtain the extinction coefficient (k) of the water. These were calculated using the following equations given in Strickland (1958):

$$k = \frac{\log I_0 - \log I}{d}$$

where k is the extinction coefficient

I_0 is the initial illumination and

I is the illumination after passing through
a length (depth) of d

Data Presentation

The photosynthetic potential and chlorophyll α concentration are represented on the graphs by the range in duplicate measurements, with the lines drawn through the means. All values for photosynthetic potential and chlorophyll α in the text are the means of the duplicate measurements. Only one measurement was made of the total particulate volume, which is presented on the graphs and text, corrected to two decimal places.

The ratios of chlorophyll α per particulate volume were calculated by dividing each of the duplicate measurements for chlorophyll α by the total particulate volume measured for the same sample. The two values so obtained were plotted on the graphs with the line passing through the mean value. Photosynthetic potential per particulate volume was determined in a similar manner. Values for both photosynthetic potential and chlorophyll α per particulate volume given in the text, are the means corrected to two decimal places.

The assimilation ratios were determined by dividing each duplicate of the chlorophyll α concentration by each value for the photosynthetic potential, which resulted in four values. The data presented on the graphs are the extreme values (lowest and highest) with the line passing through the mean. Values in the text are the means, corrected to two decimal places.

The number placed beside some of the symbols refers to the number of values which that particular symbol consists. Questionable values are indicated on the graph by a question mark beside it.

RESULTS

I. Inshore Waters - Station E-2

A. Surface Samples - Days IV-V

Absolute Values Figure 3, Table 2, Table A11.

Generally, the chlorophyll *a* concentration was higher during the light period, decreasing to a minimum in the dark period with the overall range in concentration between 0.67 and 1.50 mg/m³.

Chlorophyll *a* maxima were found during the morning, at 1100 on Day IV (1.32 mg/m³) and at 0900 on Day V (1.49 mg/m³), with a second maximum on both days at the beginning of the dark period (2100 hours). The chlorophyll *a* concentration during the second maxima was 1.50 mg/m³ and 1.33 mg/m³ on Day IV and Day V respectively. Minimum values were measured during the dark period (at 0100 hours) with a concentration of 0.86 mg/m³ on Day IV and 0.67 mg/m³ on Day V.

A diel variation was found on both days for the photosynthetic potential measurements with maximum activity during the light period and the minima occurring at night. The maxima occurred at 1300 on Day IV (3.92 mg C/m³/hr) and 1100 on Day V (4.23 mg C/m³/hr), while minimum values were measured at 0100 on both days - 1.69 mg C/m³/hr on Day IV and 0.88 mg C/m³/hr on Day V.

Total particulate volume over the two day period showed a diel variation similar to, but not as great, as the chlorophyll *a* concentration or photosynthetic potential. Maximum values were

TABLE 2

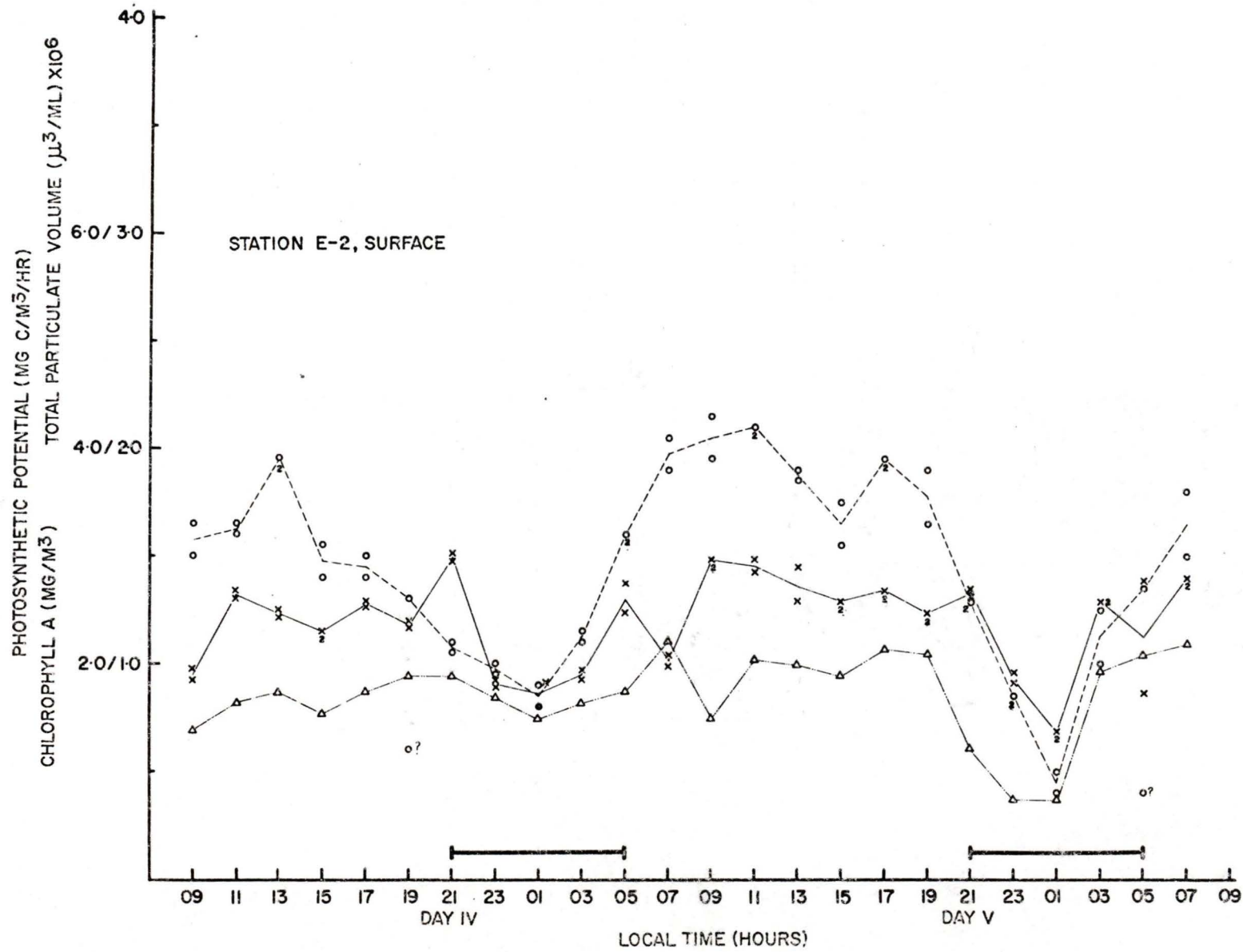
Maximum-minimum values for surface chlorophyll *a* concentration, photosynthetic potential and total particulate volume for Stations E-1 and E-2. Numbers in parentheses indicate the time of measurement.

Day	Chlorophyll <i>a</i> (mg/m ³)		Photosynthetic Potential (mg C/hr/m ³)		Total Particulate Volume (μ ³ /ml x 10 ⁶)	
	max.	min.	max.	min.	max.	min.
I	1.33 (1900)	0.77 (0100)	2.36 (1700)	0.57 (0900)	1.21 (1900)	0.63 (0100)
				1.11 (2100)		
II	1.30 (0700)	0.72 (1300)	3.36 (0700)	1.65 (2300)	1.29 (1500)	0.62 (2300)
III	0.97 (1100)	0.66 (1900)	3.52 (1100)	2.02 (0100)	N/A	N/A
IV	1.50 (2100)	0.86 (0100)	3.92 (1300)	1.69 (0100)	0.96 (2100)	0.77 (0100)
V	1.49 (0900)	0.67 (0100)	4.23 (1100)	0.88 (0100)	1.12 (0700)	0.38 (2300)
					1.08 (1700)	
VI	3.17 (1900)	1.42 (0900)	8.54 (1500)	4.58 (2100)	2.49 (1900)	1.40 (0100)
		2.48 (0900)				1.26 (1100)
VII	4.18 (2100)	2.40 (0500)	11.02 (1300)	5.43 (0100)	4.45 (2100)	2.19 (0500)
		2.94 (0900)				

FIGURE 3

Graph of Chlorophyll a Concentration in mg/m^3 (X — X), Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$ (O --- O), and total Particulate Volume, $\mu^3/\text{ml} \times 10^6$ (Δ --- Δ) for Surface Samples, Day IV and V. Chlorophyll a and Total Particulate Volume follow the Inner Scale; Photosynthetic Potential follows the Outer Scale.

Horizontal Dark Line Indicates the Period of No Measurable light.



reached towards the end of the light period with a total volume on Day IV, 1900, of $0.96 \times 10^6 \mu^3/\text{ml}$, and $1.08 \times 10^6 \mu^3/\text{ml}$ at 1700 on Day V. Values on both days decreased during the dark period, with a minimum concentration of $0.77 \times 10^6 \mu^3/\text{ml}$ at 0100 on Day IV, and $0.38 - 0.40 \times 10^6 \mu^3/\text{ml}$ between 2300 and 0100 on Day V.

Normalized Values Figure 4, Table 3, Table A12.

When chlorophyll *a* measurements were normalized for a constant cell population (defined here as the amount of chlorophyll per unit of particulate volume) there was no apparent diel variations as was found for the total chlorophyll *a* concentration. The range in values on Day IV were between 1.05 and $1.58 \times 10^{-12} \text{ mg chl-}a/\mu^3$. On Day V values were similar to Day IV, except for an increase near the start of the dark period. A maximum of $2.47 \times 10^{-12} \text{ mg chl-}a/\mu^3$ at 2300 was measured, but values decreased again to $1.06 \times 10^{-12} \text{ mg chl-}a/\mu^3$ by 0500.

Photosynthetic potential per particulate volume did, however, show a definite periodicity, with maximum values occurring in the morning, and decreasing to a minimum in the middle of the dark period. On Day IV, the maximum value of $4.44 \times 10^{-12} \text{ mg C/hr}/\mu^3$ occurred at 1300 while a maximum ratio of $5.41 \times 10^{-12} \text{ mg C/hr}/\mu^3$ was measured at 0900 on Day V. A secondary maximum on Day V, at 2100, had a value of $4.19 \times 10^{-12} \text{ mg C/hr}/\mu^3$. Minimum values

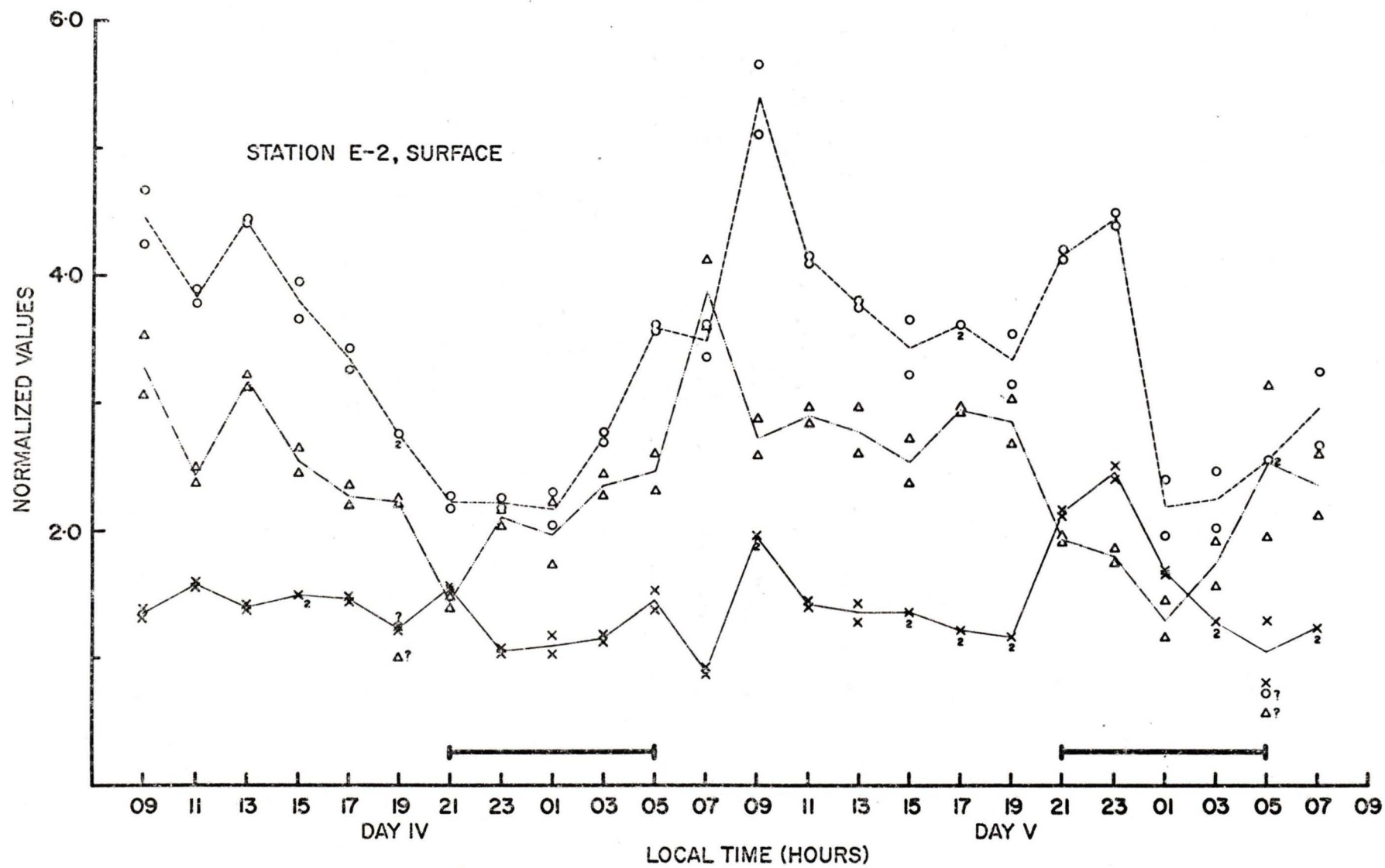
TABLE 3

Maximum-minimum values for surface chlorophyll *a* per particle volume, photosynthetic potential per particle volume and assimilation ratios, for Stations E-1 and E-2. Numbers in parentheses indicate the time of measurement.

Day	Chlorophyll <i>a</i> / Particle Volume (mg/ $\mu^3 \times 10^{-12}$)		Photosynthetic Potential/ Particle Volume (mg C/hr/ $\mu^3 \times 10^{-12}$)		Assimilation Ratios (mg C/hr/mg chl- <i>a</i>)	
	max.	min.	max.	min.	max.	min.
I	1.36 (0900)	0.91 (2300)	2.51 (1700)	0.59 (0900)	2.48 (1700)	0.45 (0900)
				1.12 (2100)		1.12 (2100)
II	1.23 (2300)	0.59 (1500)	4.36 (0900)	1.85 (0300)	4.13 (1300)	1.67 (2100)
III	N/A	N/A	N/A	N/A	3.95 (2100)	2.44 (0100)
						2.40 (1700)
IV	1.58 (1100)	1.05 (2300)	4.46 (0900)	2.18 (0100)	3.29 (0900)	1.43 (2100)
V	2.47 (2300)	0.90 (0700)	5.41 (0900)	2.20 (0100)	3.88 (0700)	1.30 (0100)
VI	1.95 (0100)	0.96 (1300)	5.48 (0900)	1.93 (2100)	5.23 (0900)	1.59 (1900)
VII	1.72 (0900)	0.94 (2100)	5.20 (0900)	1.57 (2100)	3.57 (1300)	1.60 (0100)
	1.42 (2300)					

FIGURE 4

Graph of Chlorophyll a Per Particulate Volume, $\text{mg}/\mu^3 \times 10^{-12}$ (X — X), Photosynthetic Potential Per Particulate Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$ (O --- O) and Assimilation Ratios, $\text{mg C/hr}/\text{mg chl-}a$ (Δ - - - Δ) for Surface Samples, Day IV and V. Horizontal Dark Line Indicates the Period of No Measurable Light.



occurred between 2300 and 0100 ($2.18 - 2.23 \times 10^{-12}$ mg C/hr/ μ^3) on Day IV, and between 0100 and 0300 ($2.20 - 2.26 \times 10^{-12}$ mg C/hr/ μ^3) on Day V.

The assimilation ratios (the amount of photosynthetic potential per unit of chlorophyll *a*) also showed diel variations, with maximum ratios measured during the light period and the minima found during the dark period. The maxima occurred earlier in the day than did the photosynthetic potential/volume ratio, with a value of 3.29 mg C/hr/mg chl-*a* measured at 0900 on Day IV, and 3.88 mg C/hr/mg chl-*a* at 0700 on Day V. The minimum assimilation ratio occurred at 2100 on Day IV, with a value of 1.42 mg C/hr/mg chl-*a*, and at 0100 on Day V (1.30 mg C/hr/mg chl-*a*).

B. Surface Samples - Day VI-VII

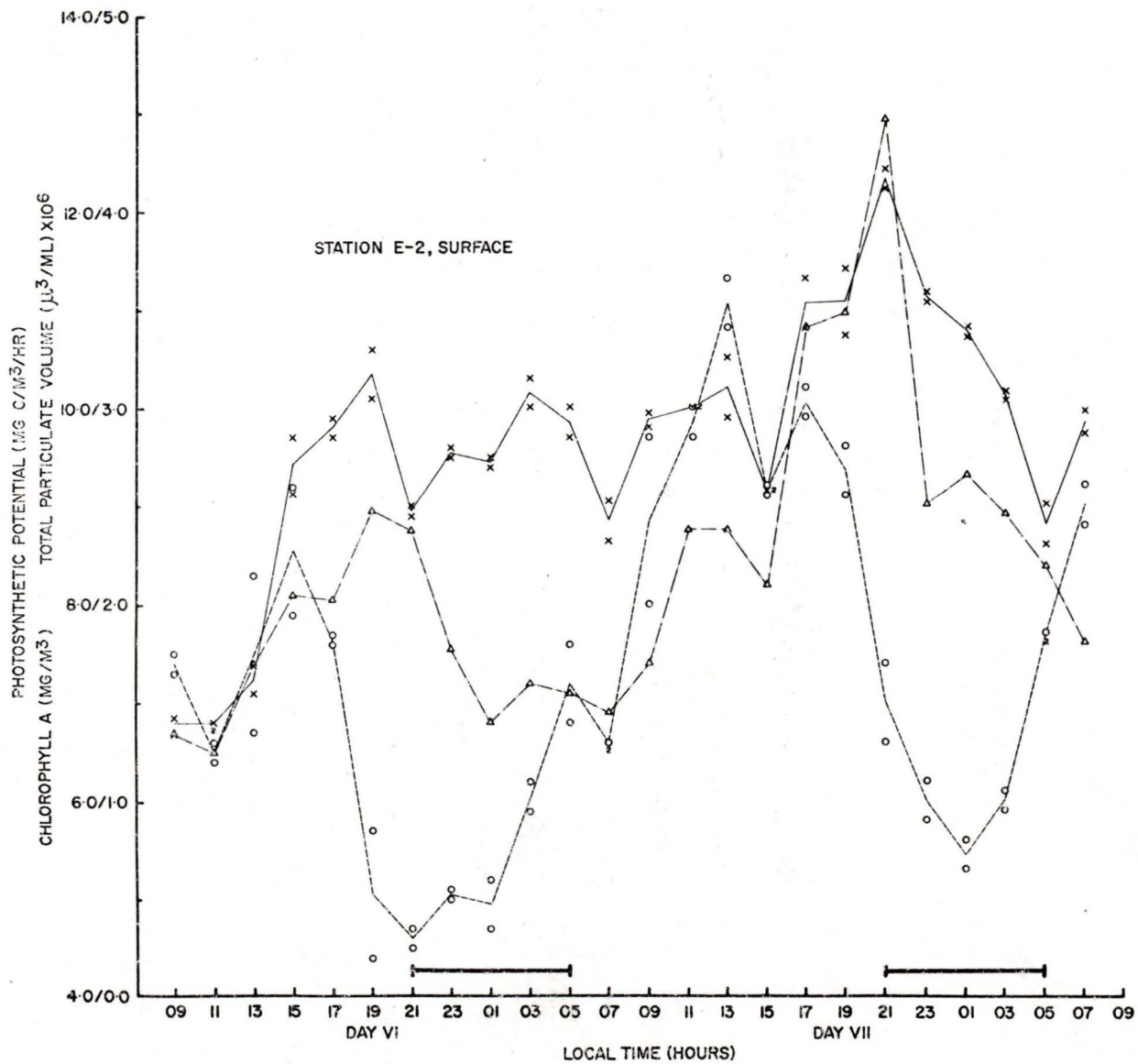
Absolute Values Figure 5, Table 2, Table A11.

The chlorophyll *a* concentration showed an incremental increase over the two day period, with the greatest change occurring between 1500 and 1900 on Day VI, and between 1500 and 2100 on Day VII. From an initial concentration of 1.42 mg/m³ at 0900, values increased during Day VI to 3.17 mg/m³ at 1900. There was little change in the chlorophyll *a* values during the light period on Day VII until 1500, when values increased to 4.18 mg/m³ by 2100. During the dark period on Day VI, there were no significant decreases in chlorophyll

FIGURE 5

Graph of Chlorophyll a Concentration, mg/m^3 (X — X), Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$ (O --- O) and Total Particulate Volume, $\mu^3/\text{ml} \times 10^6$ (Δ - - - Δ) for Surface Samples, Day VI and VII. Chlorophyll a and Total Particulate Volume follow the Inner Scale; Photosynthetic Potential follows the Outer Scale.

Horizontal Dark Line Indicates the Period of no Measurable Light.



concentration, but lower values were measured at 2100 (2.48 mg/m^3) and at 0700 in the next light period (2.44 mg/m^3). On Day VII, however, the chlorophyll *a* concentration decreased from the maximum at 2100 to a minimum value of 2.40 mg/m^3 at 0500.

Photosynthetic potential showed definite diel changes, with maximum values in the afternoon and the minima occurring during the dark periods. On Day VI, a maximum photosynthetic potential of $8.54 \text{ mg C/m}^3/\text{hr}$ was measured at 1500, while the Day VII maximum occurred at 1300, with a value of $11.02 \text{ mg C/m}^3/\text{hr}$. The minimum on Day VI occurred at 2100 ($4.58 \text{ mg C/m}^3/\text{hr}$) but remained low until 0100 ($5.03 \text{ mg C/m}^3/\text{hr}$). The photosynthetic potential on Day VII decreased to a minimum of $5.43 \text{ mg/m}^3/\text{hr}$, at 0100.

Total particulate volume also showed a diel variation although, like chlorophyll *a*, there was an overall increase during the two days. Maximum values were measured at the end of the light period, decreasing to a minimum near the start of the next light cycle. The values increased to a maximum concentration of $2.49 \times 10^6 \mu^3/\text{ml}$ at 1900 on Day VI, but the maximum occurred slightly later on Day VII (2100 hours), with a value of $4.45 \times 10^6 \mu^3/\text{ml}$. The particle concentration was at a minimum between 0100 and 0700 on Day VI, with a range in values of $1.40 - 1.47 \times 10^6 \mu^3/\text{ml}$, but on Day VII the concentration decreased steadily from the maximum, until sampling was terminated ($1.82 \times 10^6 \mu^3/\text{ml}$ at 0700).

Normalized Values Figure 6, Table 3, Table A12.

Chlorophyll α per particulate volume did not show a diel variation, although values did tend to increase during the dark period on both days. Values on Day VI ranged between 0.96 - 1.95×10^{-12} mg chl- α/μ^3 , and between 0.94 - 1.72×10^{-12} mg chl- α/μ^3 on Day VII. There was a gradual decrease from 0100, Day VI, (1.95×10^{-12} mg chl- α/μ^3) during the light period of Day VII, to a value of 0.94×10^{-12} mg chl- α/μ^3 at 2100. The chlorophyll/volume ratio then increased again to 1.42×10^{-12} mg chl- α/μ^3 at 2300.

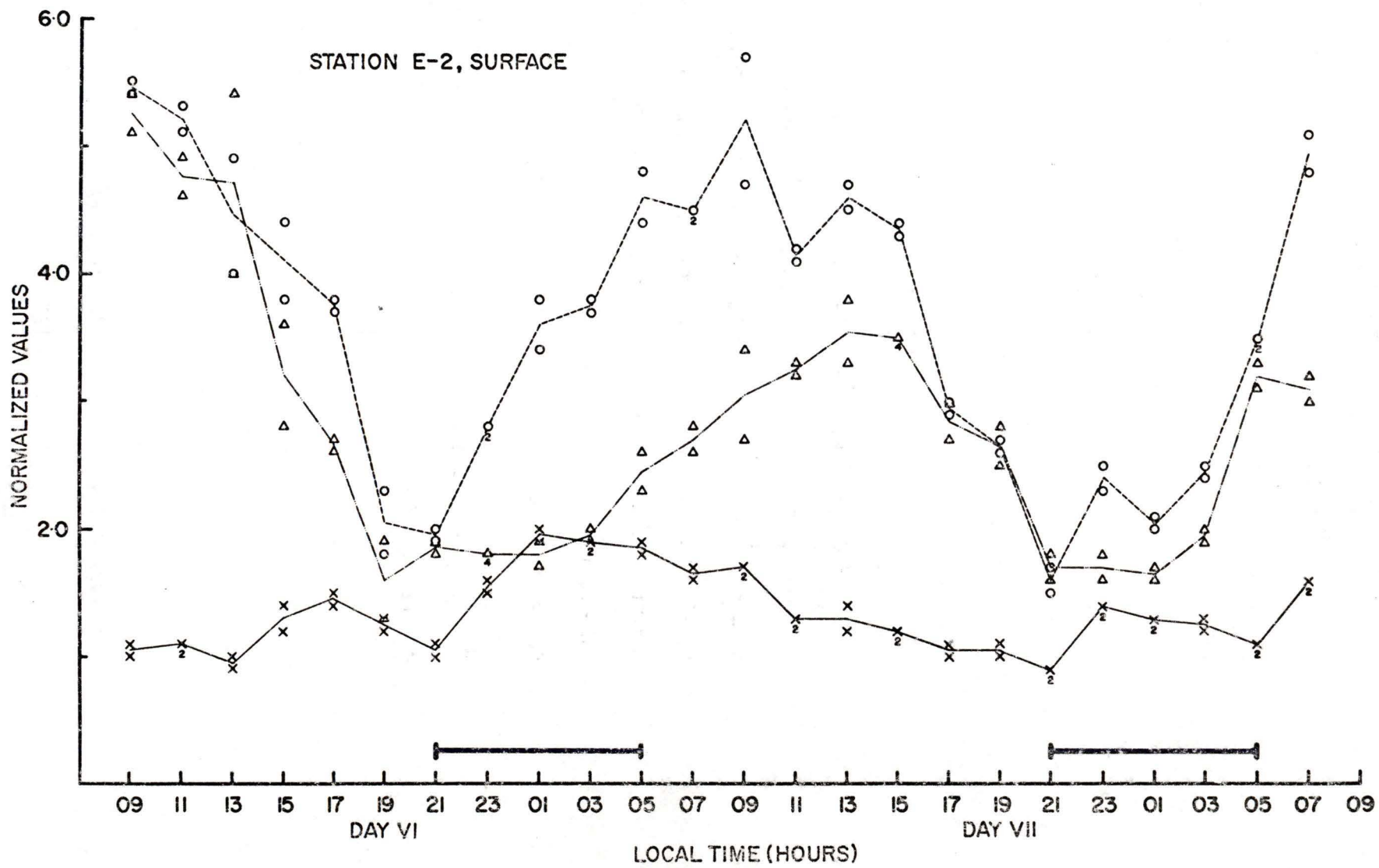
Photosynthetic potential per particulate volume showed a definite diel variation. Maximum values were reached in the morning, and decreased to a minimum during the dark period. Both maxima occurred at 0900, with a value of 5.48×10^{-12} mg C/hr/ μ^3 on Day VI and 5.20×10^{-12} mg C/hr/ μ^3 on Day VII. (By the time sampling was terminated, at 0700, the photosynthetic potential/volume had increased again to 4.95×10^{-12} mg C/hr/ μ^3 .) Both minima were measured at 2100, with a value of 1.93×10^{-12} mg C/hr/ μ^3 on Day VI and 1.57×10^{-12} mg C/hr/ μ^3 on Day VII.

The assimilation ratios also showed a diel periodicity with a maximum near midday, decreasing to a minimum in the dark period. The maximum on Day VI occurred at 0900, with a value of 5.23 mg C/hr/mg chl- α , while a value of 3.56 mg C/hr/mg chl- α was measured at 1300 on Day VII. The assimilation ratios on Day VI reached a

FIGURE 6

Graph of Chlorophyll *a* Per Particulate Volume, $\text{mg}/\mu^3 \times 10^{-12}$ (X —X), Photosynthetic Potential Per Particulate Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$ (O --- O), and Assimilation Ratios, $\text{mg C/hr/mg chl-}a$ (Δ - - - Δ) for Surface Samples, Day VI and VII. Photosynthetic Potential follows the Inner Scale; Chlorophyll *a* follows the Middle Scale; and Total Particulate Volume follows the Outer Scale.

The Horizontal Dark Line Indicates the Period of No Measurable Light.



minimum at 1900, with a value of 1.59 mg C/hr/mg chl-*a*, but remained low until 0100 (1.85 mg C/hr/mg chl-*a*). On Day VII, minimum values were recorded between 2100 and 0100, with a range of 1.60 - 1.67 mg C/hr/mg chl-*a*.

C. Comparison of Day IV-VII - Surface Samples

Absolute Values

During the three day interval between the initiation of the first series of measurements (Day IV-V) and the beginning of Days VI-VII, there was an overall increase in the phytoplankton concentration.

Chlorophyll *a* ranged from a low of 0.86 mg/m³ to a high of 1.50 mg/m³ for Day IV, and between 0.67 and 1.49 mg/m³ during Day V. By Day VI and VII, values had increased considerably, some twofold, with a range of 1.39 - 3.17 mg/m³ for Day VI and 2.40 - 4.18 mg/m³ for Day VII. On all four days, chlorophyll *a* increased during the light period, generally in the afternoon, while slower rates of increase or actual decreases in chlorophyll *a* concentration occurred during the dark period.

Photosynthetic potential also increased over the four days, with the Day VII maximum about three times that of Day IV. There were definite diel variations present, with maximum values occurring near midday, and decreasing to a minima in the dark period, generally near 0100. The range in values for Day IV was 1.69 - 3.92 mg C/m³/hr, while Day V was similar, varying between 0.88 - 4.23 mg C/m³/hr.

On Days VI and VII, however, the photosynthetic potential had increased, with a range of 4.58 to 8.54 mg C/m³/hr, and 5.43 - 11.02 mg C/m³/hr respectively, for the two days.

Total particulate volume showed a slight diel variation during the four days, with minima during the dark period and maxima in the light period. The highest concentration occurred near the end of the light period, while the lowest values were measured between 0100 and 0500. The total volume increased during the four days with nearly a four fold increase in values from Day IV to Day VII. The range for Day IV was 0.70 - 0.96 x 10⁶ μ³/ml, while Day V varied between 0.38 - 1.12 x 10⁶ μ³/ml. By Day VI and VII, the total particulate concentration had increased, with a range of 1.26 - 2.49 x 10⁶ μ³/ml on Day VI and 1.47 - 4.45 x 10⁶ μ³/ml on Day VII.

Normalized Values

During the four days, there was no apparent diel variation in chlorophyll *a* per particulate volume, although increases during the dark period were measured on Days V, VI and VII. During Day IV, values ranged between 1.05 and 1.58 x 10⁻¹² mg chl-*a*/μ³, while Day V was slightly higher, with a range of 0.90 to 2.47 x 10⁻¹² mg chl-*a*/μ³. The ratios calculated for Day VI and VII were similar, varying between 0.96 and 1.95 x 10⁻¹² and 0.94 to 1.72 x 10⁻¹² mg chl-*a*/μ³.

respectively for the two days.

Photosynthetic potential per particulate volume showed a definite diel periodicity during the four days, with similar maximum-minimum values measured on each day. All four days had a maxima in the morning, with minimum values occurring in the dark period. Days IV and V had a range of $2.18 - 4.44 \times 10^{-12}$ mg C/hr/ μ^3 and $2.20 - 5.41 \times 10^{-12}$ mg C/hr/ μ^3 respectively, while Day VI varied between 1.93 and 5.48×10^{-12} mg C/hr/ μ^3 , and Day VII between 1.57 and 5.20×10^{-12} mg C/hr/ μ^3 .

The assimilation ratios also showed a diel variation, with a maxima near midday, and decreasing to a minimum in the dark period. Values varied between 1.43 and 3.29 mg C/hr/mg chl-*a* on Day IV and 1.30 and 3.88 mg C/hr/mg chl-*a* on Day V. On Day VI the assimilation ratios were generally higher, ranging between $1.59 - 5.23$ mg C/hr/mg chl-*a* but Day VII was similar to Days IV and V, with a range of $1.60 - 3.56$ mg C/hr/mg chl-*a*.

D. 30 Meter Samples - Days IV-V

Absolute Values Figure 7, Table 4, Table A11.

The chlorophyll *a* concentration varied little over the two days, with a range of $0.47 - 0.57$ mg/m³ on Day IV, and $0.51 - 0.57$ mg/m³ on Day V.

Photosynthetic potential was similar to the chlorophyll *a* measurements, with no apparent diel variation. Values were between

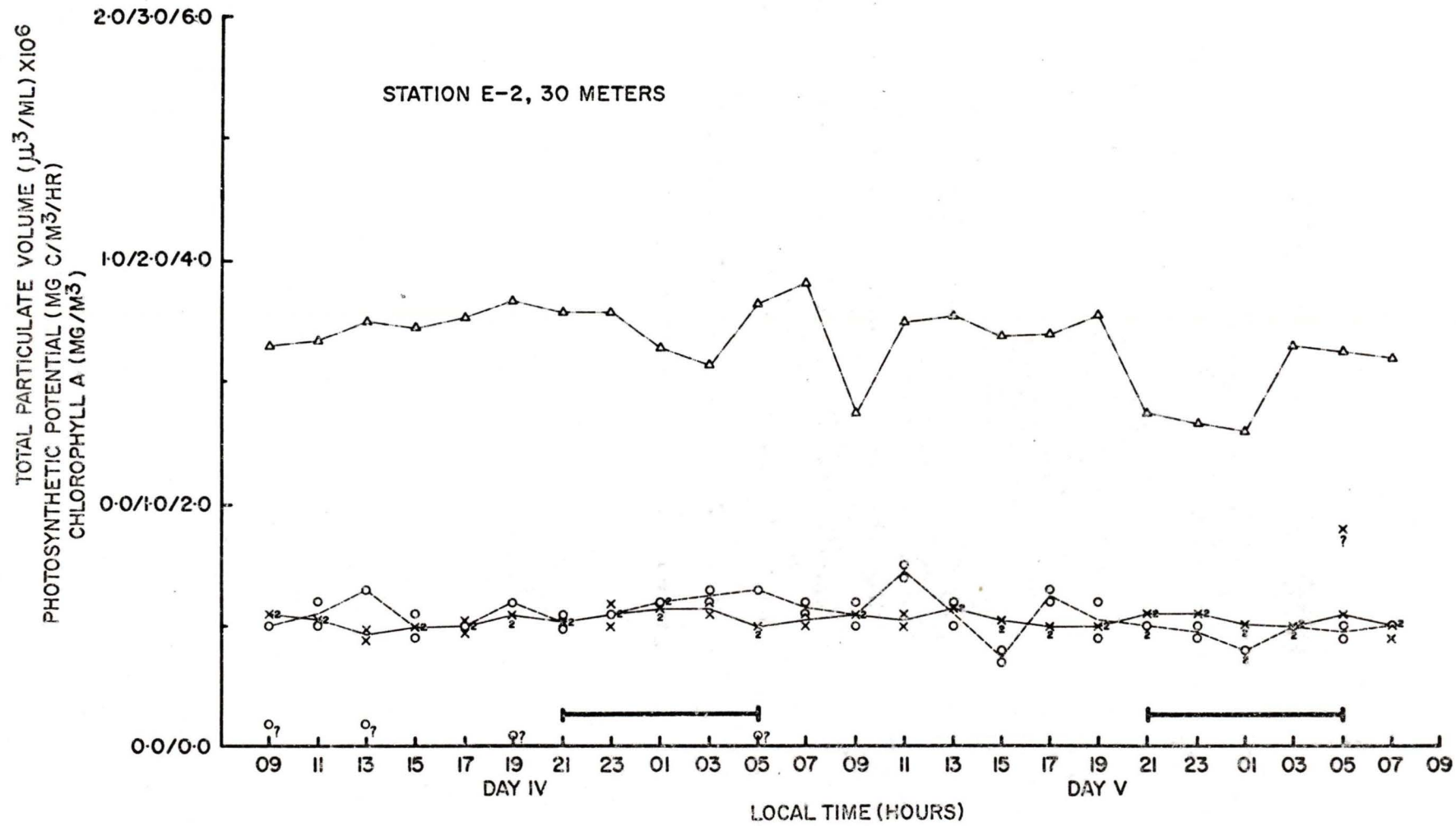
TABLE 4

Maximum-minimum values for chlorophyll *a* concentration, photosynthetic potential and total particulate volume for 30 meter samples, Stations E-1 and E-2. Numbers in parenthesis indicate the time of measurement.

Day	Chlorophyll <i>a</i> (mg/m ³)		Photosynthetic Potential (mg C/hr/m ³)		Total Particulate Volume (μ ³ /ml x 10 ⁶)	
	max	min.	max.	min.	max.	min.
I	1.24 (1300)	0.55 (0100)	2.06 (1500)	0.32 (1300)	0.91 (1300)	0.54 (0100)
				0.43 (2100)		
II	1.18 (0700)	0.62 (0900)	2.58 (1700)	1.37 (2300)	0.97 (0300)	0.44 (0900)
III	0.93 (1100)	0.63 (1900)	2.78 (1500)	0.72 (0100)	N/A	N/A
IV	0.56 (1900)	0.47 (1300)	1.28 (1300)	1.03 (1700)	0.84 (1900)	0.58 (0300)
V	0.57 (1300)	0.51 (1900)	1.46 (1100)	0.78 (1500)	0.93 (0700)	0.31 (0100)
VI	0.64 (1100)	0.50 (0300)	2.15 (1100)	0.25 (0100)	0.87 (1100)	0.62 (0100)
VII	0.73 (2100)	0.45 (1100)	1.32 (0900)	0.71 (1100)	0.80 (2300)	0.63 (0700)
				0.75 (2300)		

FIGURE 7

Graph of Chlorophyll a Concentration, mg/m^3 (X — X),
Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$ (O --- O), and
Total Particulate Volume, $\mu^3/\text{ml} \times 10^6$ (Δ - - - Δ) at
30 meters, Day IV and V. The Horizontal Dark Line
Indicates the Period of No Measurable Light.



1.00 and 1.28 mg C/m³/hr for Day IV, and 0.78 and 1.46 mg C/m³/hr on Day V.

There was not an apparent diel variation in total particulate volume, although lower values were recorded during the dark period on both days. Day IV varied between 0.58 - 0.84 x 10⁶ μ³/ml (with a minimum at 0300) while Day V had a range of 0.31 - 0.93 x 10⁶ μ³/ml with the minimum at 0100.

Normalized Values Figure 8, Table 5, Table A12.

The chlorophyll *a* per particulate volume showed a slight variation, in which values in the dark period were slightly higher than during the light period. The maximum occurred during the latter part of the dark period, with a value of 0.99 x 10⁻¹² mg chl-*a*/μ³ at 0300 on Day IV, and a value of 1.73 x 10⁻¹² mg chl-*a*/μ³ at 2300 on Day V. During the light period on Day IV and V the ratios were fairly consistent with a range of 0.63 - 0.82 x 10⁻¹² mg chl-*a*/μ³ and 0.57 - 0.78 mg chl-*a*/μ³ respectively for the two days.

Photosynthetic potential per particulate volume varied erratically, although there was a tendency towards higher values during the dark period. These maxima occurred at 0300 on Day IV, with a value of 2.22 x 10⁻¹² mg C/hr/μ³, and at 2300 on Day V (2.88 x 10⁻¹² mg C/hr/μ³). During the light period, Day IV varied between 1.38 - 1.71 x 10⁻¹² mg C/hr/μ³ while Day V had slightly higher values, ranging

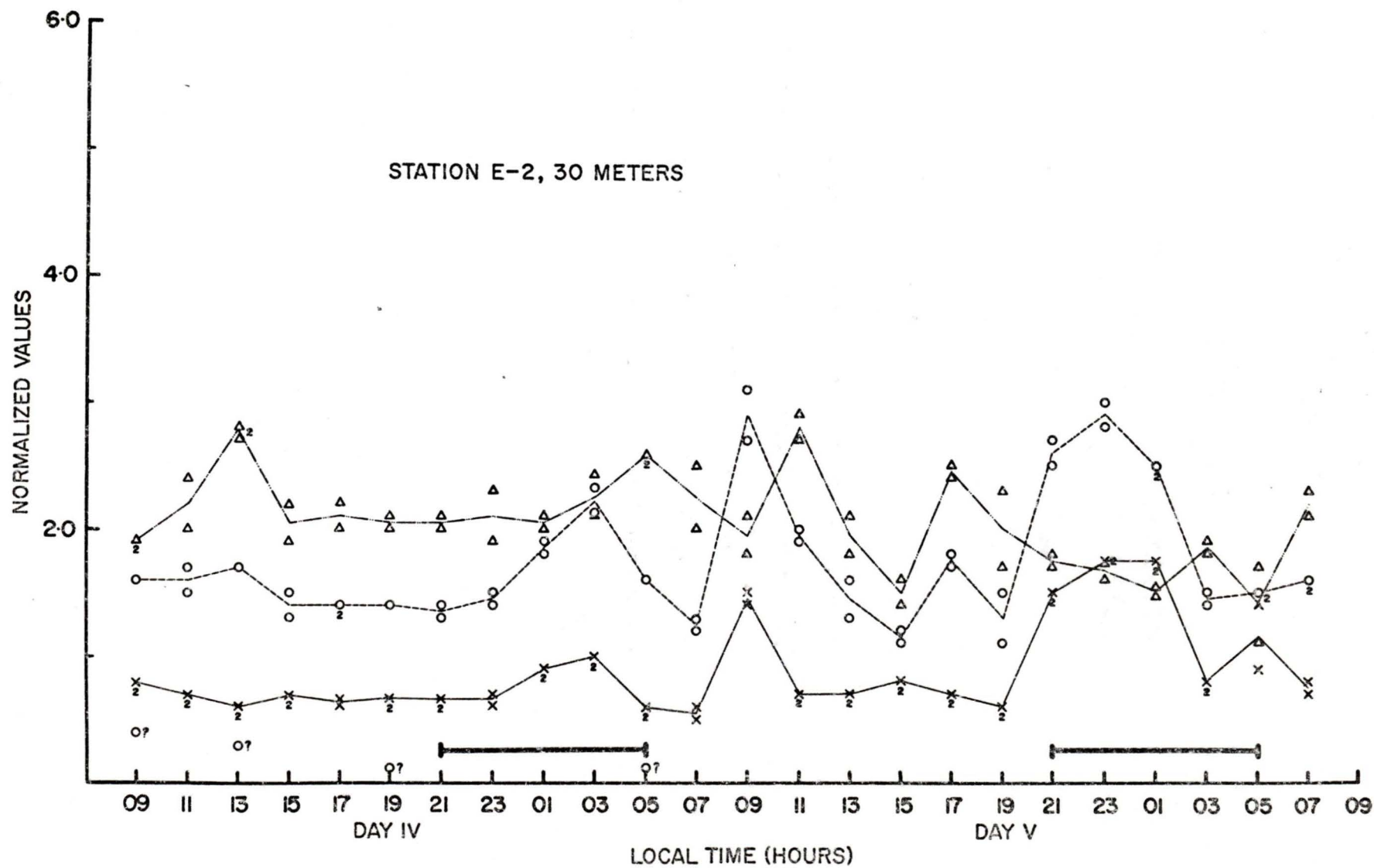
TABLE 5

Maximum-minimum values for chlorophyll α per particle volume, photosynthetic potential per particle volume and assimilation ratios for 30 meter samples, Stations E-1 and E-2. Numbers in parenthesis indicate the time of measurement.

Day	Chlorophyll α / Particle Volume ($\text{mg}/\mu^3 \times 10^{-12}$)		Photosynthetic Potential/ Particle Volume ($\text{mg C/hr}/\mu^3 \times 10^{-12}$)		Assimilation Ratios ($\text{mg C/hr}/\text{mg chl-}\alpha$)	
	max.	min.	max.	min.	max.	min.
I	1.82	0.94	2.86	0.35	1.80	0.26
	(1700)	(2300)	(1700)	(1300)	(1500)	(1300)
				0.28		0.43
				(2100)		(2100)
II	1.52	0.81	4.34	1.89	3.17	1.61
	(0700)	(0300)	(1100)	(2100)	(1100)	(2100)
III	N/A	N/A	N/A	N/A	3.24	1.01
					(1500)	(0100)
IV	0.99	0.63	2.22	1.37	2.73	1.18
	(0300)	(1300)	(0300)	(2100)	(1300)	(0900)
V	1.73	0.57	2.88	1.15	2.83	1.50
	(2300)	(0700)	(2300)	(1500)	(1100)	(0100)
VI	0.93	0.73	2.48	0.41	3.40	0.40
	(0100)	(0900)	(1100)	(0100)	(1100)	(0100)
VII	1.07	0.67	1.82	0.95	2.00	1.10
	(1900)	(1100)	(0900)	(2300)	(1300)	(0300)

FIGURE 8

Graph of Chlorophyll a Per Particulate Volume, $\text{mg}/\mu^3 \times 10^{-12}$ (X — X), Photosynthetic Potential Per Particulate Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$ (O --- O), and Assimilation Ratios, $\text{mg C/hr/mg chl-}a$ (Δ - - - Δ) at 30 meters, Day IV and V. Horizontal Dark Line Indicates the Period of No Measurable Light.



between $1.45 - 2.90 \times 10^{-12}$ mg C/hr/ μ^3 .

The assimilation ratios did not show any diel variation. The dark period on Day V had lower values, but this was not the case during Day IV. Values ranged between 1.18 and 2.59 mg C/hr/mg chl- α on Day IV, and between 1.47 and 2.83 mg C/hr/mg chl- α on Day V. A minimum on Day V occurred at 0100 with a value of 1.50 mg C/hr/mg chl- α .

E. 30 Meter Samples - Days VI-VII

Absolute Values Figure 9, Table 4, Table A11.

The chlorophyll α concentration did not show large variations, although values on Day VII were slightly higher towards the end of the light period and during the dark period. The maximum range encountered over Day VI was 0.50 - 0.64 mg/m³, with similar values, 0.45 - 0.73 mg/m³, measured during Day VII.

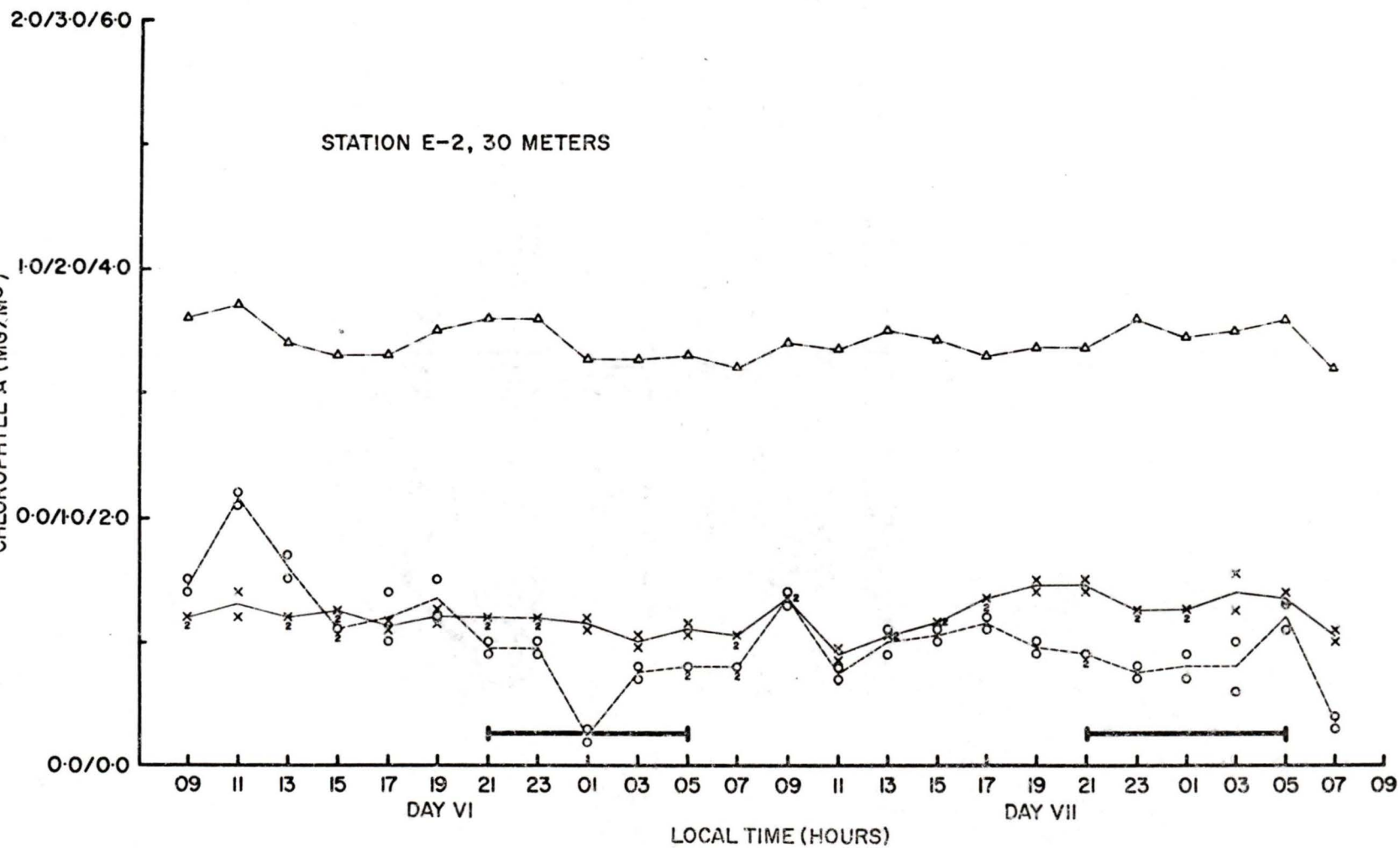
The photosynthetic potential showed a slight diel variation over the two days, with minimum values occurring during the dark period. Both days had two maxima, with the larger one occurring in the morning, and a smaller one in the late afternoon. The maxima on Day VI were at 1100 (2.15 mg C/m³/hr) and 1900 (1.39 mg C/m³/hr), while the maxima on Day VII were measured at 0900 (1.32 mg C/m³/hr) and 1700 (1.15 mg C/m³/hr). Minimum values for the photosynthetic potential were measured at 0100 on Day VI, with a value of

FIGURE 9

Graph of Chlorophyll *a* Concentration, mg/m^3 (X — X),
Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$ (O --- O) and Total
Particulate Volume, $\mu^3/\text{ml} \times 10^6$ (Δ --- Δ) at 30 meters,
Day VI and VII. Photosynthetic Potential follows the
Inner Scale; Chlorophyll *a* follows the Middle Scale; and
Total Particulate Volume follows the Outer Scale.

Horizontal Dark Line Indicates the Period of No
Measurable Light.

TOTAL PARTICULATE VOLUME ($\mu\text{L}^3/\text{ML}$) $\times 10^6$
PHOTOSYNTHETIC POTENTIAL ($\text{MG C}/\text{M}^3/\text{HR}$)
CHLOROPHYLL A (MG/M^3)



0.25 mg C/m³/hr, and at 2300 on Day VII, with a value of 0.75 mg C/m³/hr.

Total particulate volume did not show any diel variations, with similar concentrations throughout the two days. Values ranged between 0.62 - 0.87 x 10⁶ μ³/ml on Day VI, and between 0.63 - 0.80 x 10⁶ μ³/ml on Day VII.

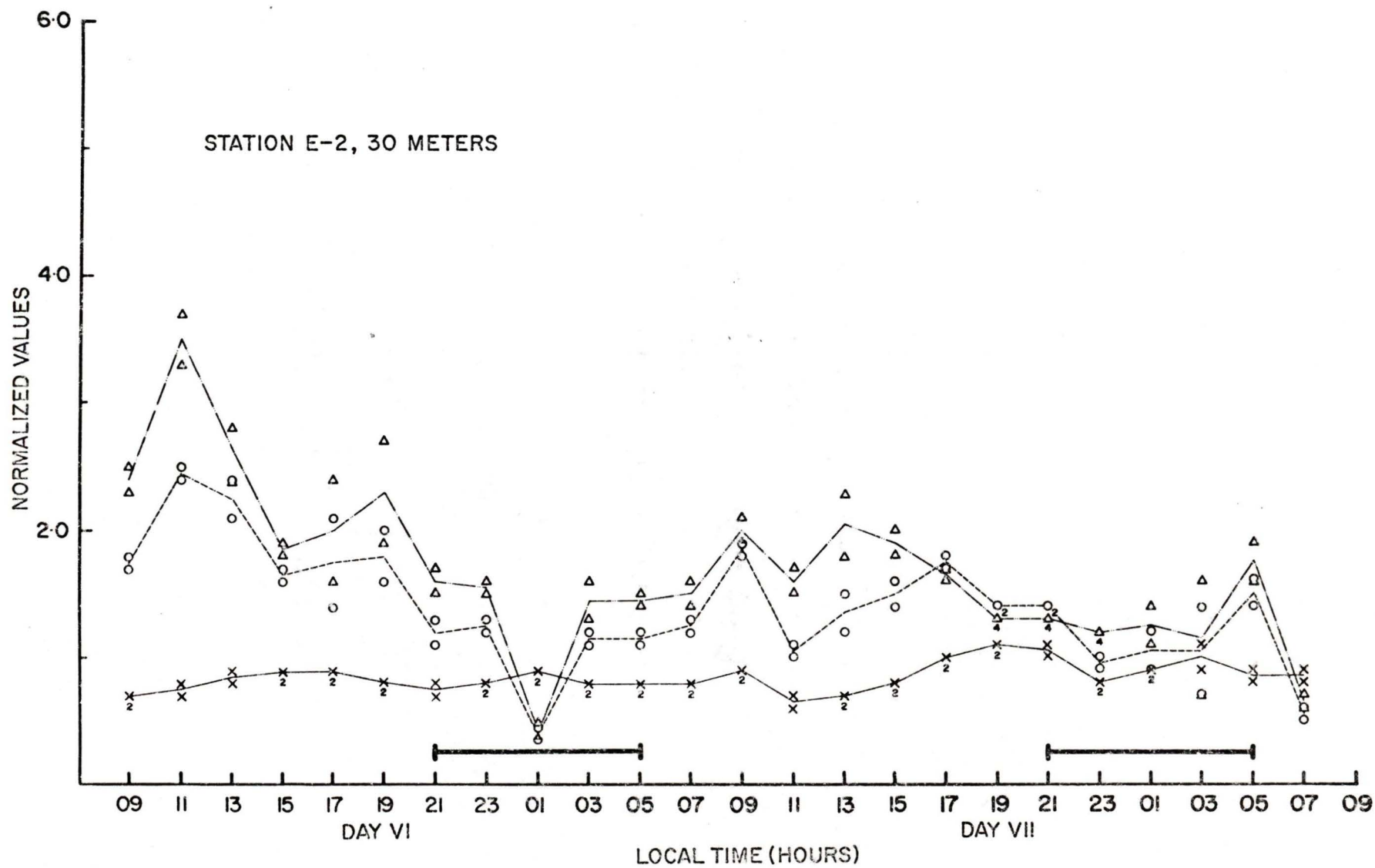
Normalized Values Figure 10, Table 5, Table A12.

The amount of chlorophyll *a* per particulate volume did not vary much, although there was a slight increase towards the end of the light period on Day VII. Day VI varied between 0.73 - 0.87 x 10⁻¹² mg chl-*a*/μ, while Day VII had a range of 0.66 - 1.07 x 10⁻¹² mg chl-*a*/μ³.

The photosynthetic potential per particulate volume showed a diel variation in which the maxima occurred in the morning and minimum values were measured during the dark period. The maximum on Day VI occurred at 1100, with a value of 2.48 x 10⁻¹² mg C/hr/μ³, while the highest value for Day VII, 1.82 x 10⁻¹² mg C/hr/μ³ was measured at 0900. A secondary maximum at 1700, Day VII, had a value of 1.73 x 10⁻¹² mg C/hr/μ³. Minimum values were measured at 0100 on Day VI (0.41 x 10⁻¹² mg C/hr/μ³) and at 2300 on Day VII (0.95 x 10⁻¹² mg C/hr/μ³).

FIGURE 10

Graph of Chlorophyll α Per Particulate Volume, $\text{mg}/\mu^3 \times 10^{-12}$ (X — X), Photosynthetic Potential Per Particulate Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$ (O --- O), and Assimilation Ratios, $\text{mg C/hr/mg chl-}\alpha$ (Δ - - - Δ) at 30 meters, Day VI and VII. Horizontal Dark Line Indicates the Period of No Measurable Light.



The assimilation ratios also showed a diel variation, similar to the photosynthetic potential/volume ratios. Maxima were measured near midday, with a value of 3.40 mg C/hr/mg chl- α at 1100 on Day VI, and 2.00 mg C/hr/mg chl- α at 1300 on Day VII.

Minimum assimilation ratios were recorded at 0100 on Day VI and 0300 on Day VII, with value of 0.44 and 1.10 mg C/hr/mg chl- α respectively for the two days.

F. Comparison of Days IV-VII - 30 Meter Samples

Absolute Values

During the four days there was no diel variation recorded for chlorophyll α . Values ranged between 0.47 and 0.58 mg/m³ during Days IV-V, and between 0.45 and 0.73 mg/m³ during Days VI and VII.

Photosynthetic potential did not show a diel periodicity during Days IV and V, but a slight variation, with maxima during the light period and minima in the dark period, was present on Days VI and VII. Day IV varied between 1.04 and 1.29 mg C/m³/hr, while Day V had a range of 0.78 - 1.46 mg C/m³/hr. Days VI and VII had a range of 0.26 - 2.16 mg C/m³/hr and 0.76 - 1.32 mg C/m³/hr respectively.

The data for the total particulate volume indicated a slight diel variation present during Days IV and V, with lower values during the dark period, but this was not the case for Days VI and VII.

Day IV varied between $0.58 - 0.82 \times 10^6 \mu^3/\text{ml}$, while Day V had a range of $0.31 - 0.79 \times 10^6 \mu^3/\text{ml}$. Days VI and VII had particle concentrations similar to the previous two days of measurements, with a range of $0.62 - 0.87 \times 10^6 \mu^3/\text{ml}$ for Day VI, and $0.63 - 0.80 \times 10^6 \mu^3/\text{ml}$ for Day VII.

Normalized Values

On Days IV and V, the chlorophyll *a* per particulate volume showed some variation, with higher values occurring during the dark period, but this trend was not found during Day VI and VII. Values for Day IV varied between 0.63 and $0.99 \times 10^{-12} \text{ mg chl-}a/\mu^3$, and between 0.57 and $1.73 \times 10^{-12} \text{ mg chl-}a/\mu^3$ on Day V. Although the range was less, the chlorophyll/volume ratios measured during Day VI and Day VII were similar to those of Days IV and V, with values between 0.73 and $0.93 \times 10^{-12} \text{ mg chl-}a/\mu^3$ on Day VI and between 0.66 and $1.07 \times 10^{-12} \text{ mg chl-}a/\mu^3$ during Day VII.

The photosynthetic potential per particulate volume varied erratically during the four days, with higher values during the dark period on Days IV and V, but occurring in the light period on Day VI and Day VII. The range on Day IV was $1.37 - 2.22 \times 10^{-12} \text{ mg C/hr}/\mu^3$, while Day V varied between 1.15 and $2.88 \times 10^{-12} \text{ mg C/hr}/\mu^3$. The photosynthetic potential/volume ratios on Days VI and VII varied between 0.41 and $2.48 \times 10^{-12} \text{ mg C/hr}/\mu^3$ during the former

and between 0.95 and 1.82×10^{-12} mg C/hr/ μ^3 during the latter.

The assimilation ratios showed a diel variation (with minimum values during the dark period) on Days V, VI and VII but not on Day IV. Overall, the highest values were recorded on Days V and VI. Day IV varied between 1.18 and 1.59 mg C/hr/mg chl-*a* while Day V had a range of $1.39 - 2.83$ mg C/hr/mg chl-*a*. Days VI and VII had ranges of $0.44 - 3.40$ mg C/hr/mg chl-*a* and $0.64 - 2.00$ mg C/hr/mg chl-*a* respectively.

II. Oceanic Waters - Station E-1

A. Surface Samples - Days I-III

Absolute Values Figure 11, Table 2, Table A11.

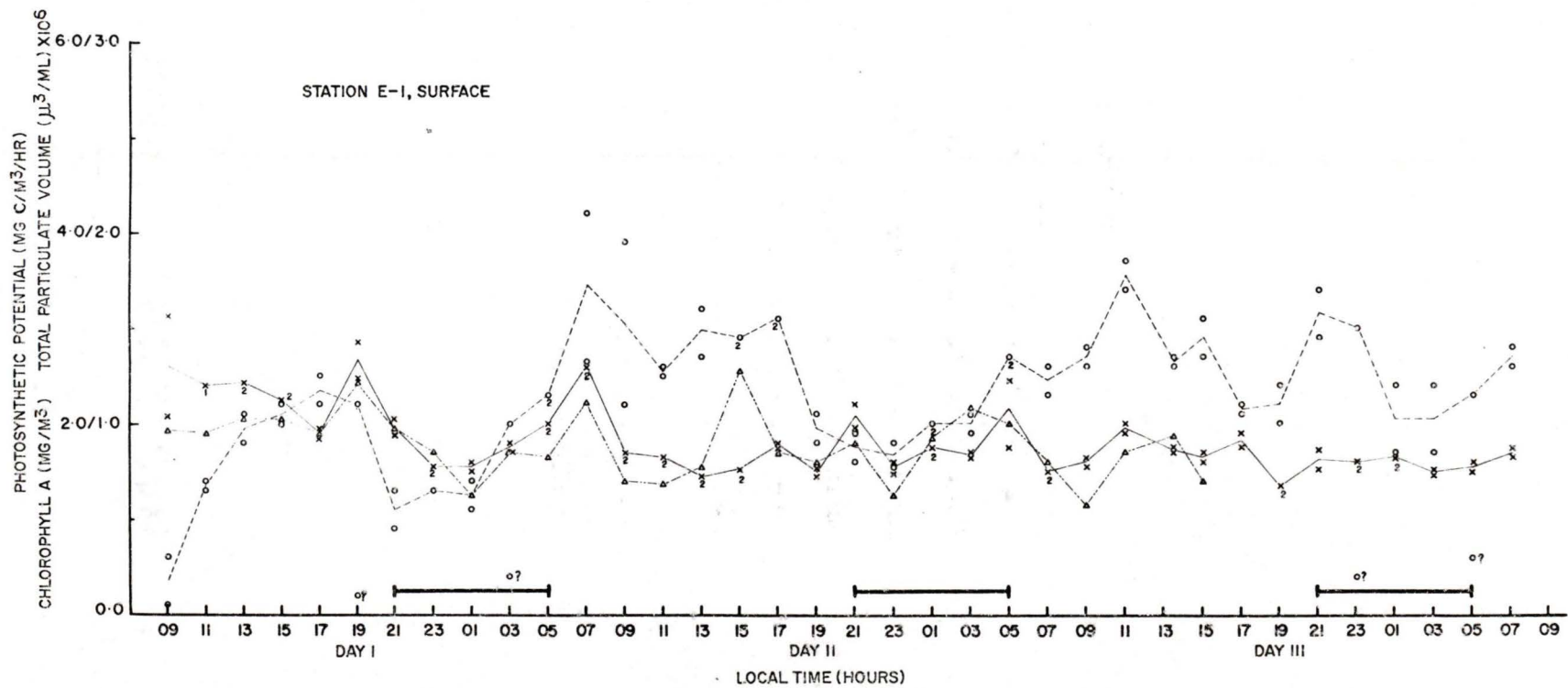
The amount of chlorophyll *a* present at the surface ranged between 0.66 and 1.33 mg/m³ during the three days, but there was no apparent diel variation. During Day I, there was a suggestion of lower values occurring in the dark period (with a maximum value of 0.77 mg/m³ at 0100), but this pattern was not present on Day II or Day III.

Photosynthetic potential, however, showed a rhythmical variation, with lower values occurring during the dark period, and a maximum during the day. Overall, values during Days II and III were greater than those measured during Day I. During Days I and II, the maxima appeared in the late afternoon (1700 hours) with a value of

FIGURE 11

Graph of Chlorophyll α Concentration mg/m^3 (X — X),
Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$ (O --- O), and
Total Particulate Volume, $\mu^3/\text{ml} \times 10^6$ (Δ - - - Δ) for
Surface Samples, Days I-III. Chlorophyll α and Total
Particulate Volume follow the Inner Scale; Photosynthetic
Potential follows the Outer Scale.

Horizontal Dark Line Indicates Period of No
Measurable Light.



2.36 mg C/m³/hr on Day I and 3.12 mg C/m³/hr on Day II. Two maxima, one at 1100 (3.52 mg C/m³/hr) and another at 2100 (3.18 mg C/m³/hr), were found on Day III. The minimum was measured at 2100 on Day I, with a value of 1.11 mg C/m³/hr, and at 2300 on Day II, with a value of 1.65 mg C/m³/hr. During Day III, the photosynthetic potential had minimum values between 1700 and 1900 (2.18 - 2.33 mg C/m³/hr) as well as between 0100 and 0300 (2.02 - 2.04 mg C/m³/hr).

Total particulate volume varied erratically, with a range of 0.62 - 1.29 x 10⁶ μ³/ml during the sampling period. (Due to instrument failure, volume measurements were not taken after 1500 on Day III). During Day I, the total volume decreased slightly during the dark period (with a minimum value of 0.63 x 10⁶ μ³/ml at 0100) but this was not found during Day II.

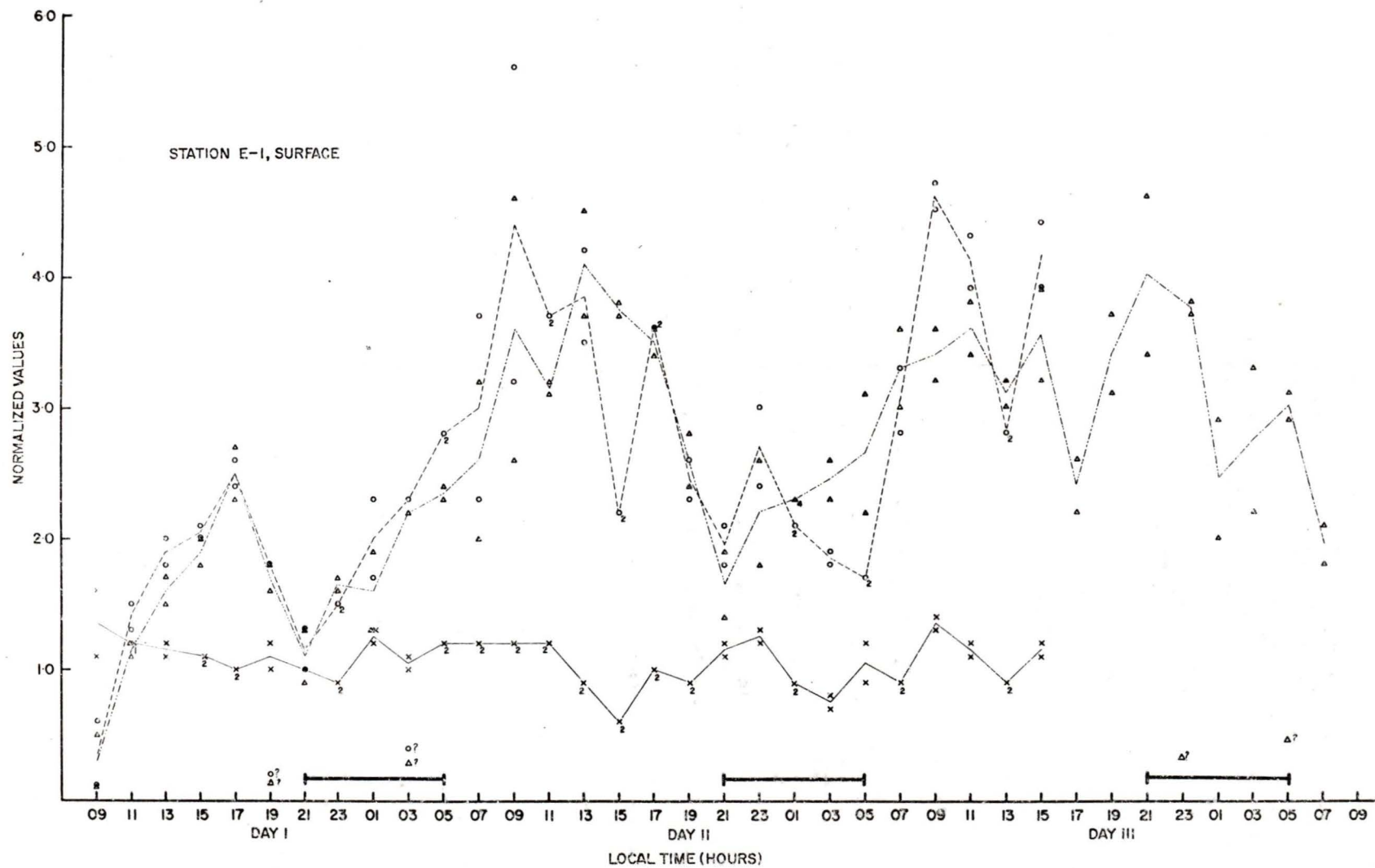
Normalized Values Figure 12, Table 3, Table A12.

Chlorophyll *a* per particulate volume did not show any diel rhythm, although there was an overall range of 0.59 - 1.36 x 10⁻¹² mg chl-*a*/μ³ for the three days. Values were fairly consistent up until 1100 on Day II, but were more erratic after that time.

Photosynthetic potential per particulate volume varied considerably, with apparent diel changes in which the minima occurred during the dark period and maximum values in the light period.

FIGURE 12

Graph of Chlorophyll *a* Per Particulate Volume, $\text{mg}/\mu^3 \times 10^{-12}$
(X — X), Photosynthetic Potential Per Particulate Volume,
 $\text{mg C/hr}/\mu^3 \times 10^{-12}$ (O --- O), and Assimilation Ratios,
 $\text{mg C/hr}/\text{mg chl-}a$ (Δ - - - Δ) for surface samples, Days I-III.
Horizontal Dark Line Indicates the Period of No Measurable
Light.



During Day I, the minimum was measured at 2100, with a value of 1.12×10^{-12} mg C/hr/ μ^3 , while the minimum on Day II occurred at 0300 (1.85×10^{-12} mg C/hr/ μ^3). Maximum values were measured during the afternoon on Day I (2.50×10^{-12} mg C/hr/ μ^3 at 1700) but were measured in the morning at 0900, on Day II, with a value of 4.36×10^{-12} mg C/hr/ μ^3 .

Like the chlorophyll *a*/volume ratios, the photosynthetic potential per particulate volume values varied erratically after 1100, Day II. When the two days were compared, Day II had higher values ($2.70 - 4.36 \times 10^{-12}$ mg C/hr/ μ^3) than were recorded for Day I ($1.12 - 2.50 \times 10^{-12}$ mg C/hr/ μ^3).

The assimilation ratios varied erratically, but also showed periodic variations, with values decreasing from maxima in the light period to minimum values during the dark period. As was found for the photosynthetic potential/volume ratios, values were generally higher during Day II and III, than on Day I.

The maxima were recorded during the afternoon, with a value of 2.48 mg C/hr/mg chl-*a* at 1700 on Day I, and 4.13 mg C/hr/mg chl-*a* on Day II, at 1300. The Day III maxima occurred later, at 2100, with a value of 3.96 mg C/hr/mg chl-*a*. The minima were found at 2100 for both Day I and Day II, with a value of 1.12 and 1.67 mg C/hr/mg chl-*a* respectively for the two days. During Day III, the minimum occurred at 0100, with a value of 2.44 mg C/hr/mg chl-*a*.

B. 30 Meter Samples - Days I-III

Absolute Values Figure 13, Table 4, Table A11.

The chlorophyll α concentration at 30 meters showed a diel variation on Day I, decreasing from a maximum value of 1.24 mg/m^3 at 1300, to a minimum of 0.55 mg/m^3 at 0100. During Days II and III, however, the concentration remained fairly constant, with most of the values between 0.60 and 0.80 mg/m^3 .

The photosynthetic potential varied erratically over the three days, although there is a suggestion of lower values during the dark period. Day I ranged between 0.32 and $2.06 \text{ mg C/m}^3/\text{hr}$, while somewhat higher values were measured on Days II and III, with a range of $1.37 - 2.61 \text{ mg C/m}^3/\text{hr}$ and $0.99 - 2.78 \text{ mg C/m}^3/\text{hr}$, respectively.

Total particulate volume did not show much variation during the three days, with most values between 0.5 and $1.0 \times 10^6 \mu^3/\text{ml}$.

Normalized Values Figure 14, Table 5, Table A12.

Chlorophyll α per particulate volume was fairly constant, with most values between $1.0 - 2.0 \times 10^{-12} \text{ mg chl-}\alpha/\mu^3$.

The photosynthetic potential per particulate volume varied considerably, but a diel rhythm was not obvious. There was a suggestion of higher values occurring during the day and decreasing during the dark period, but interpretation is difficult due to

FIGURE 13

Graph of Chlorophyll *a* Concentration, mg/m^3 (X — X),
Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$ (O --- O), and
Total Particulate Volume, $\mu^3/\text{ml} \times 10^6$ (Δ --- Δ at
30 meters, Days I-III. Photosynthetic Potential follows
the Inner Scale; Chlorophyll *a* follows the Middle Scale;
and total Particulate Volume follows the Outer Scale.

Horizontal Dark Line Indicates the Period of No
Measurable Light.

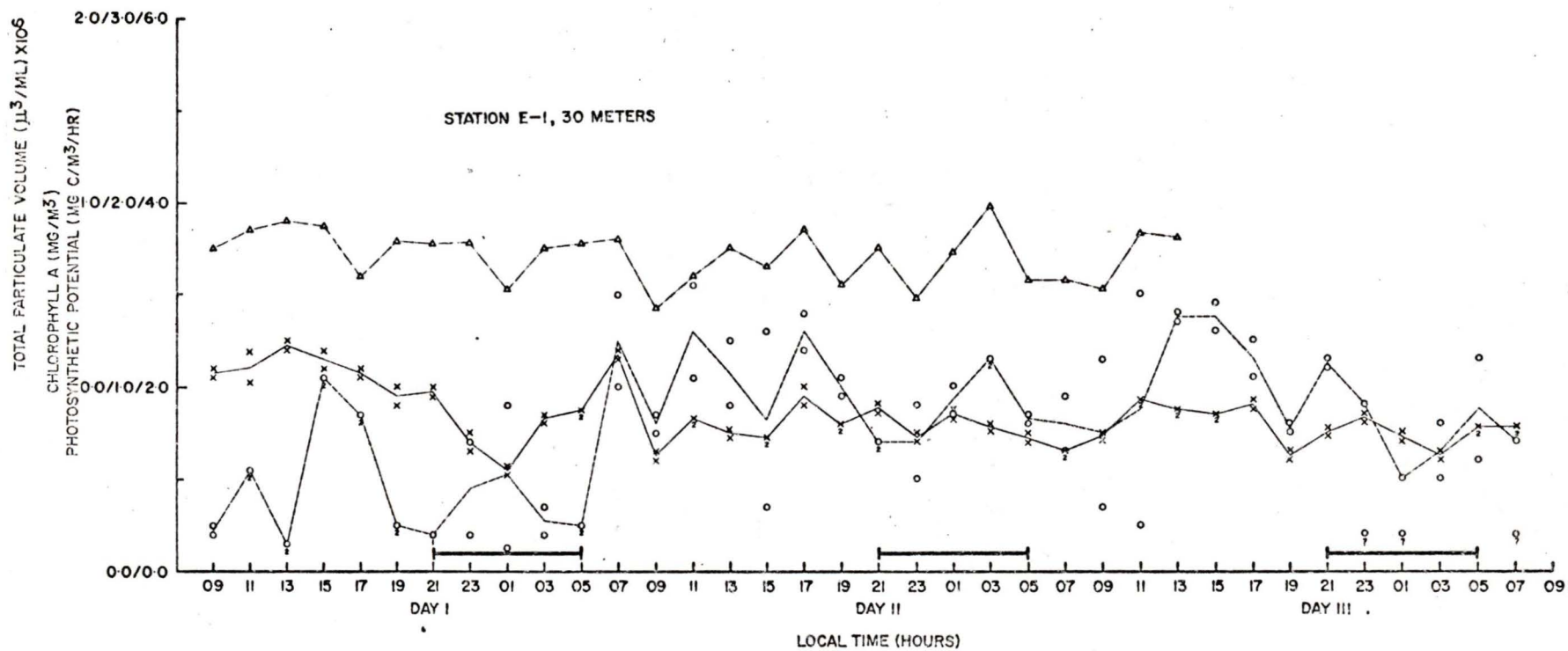
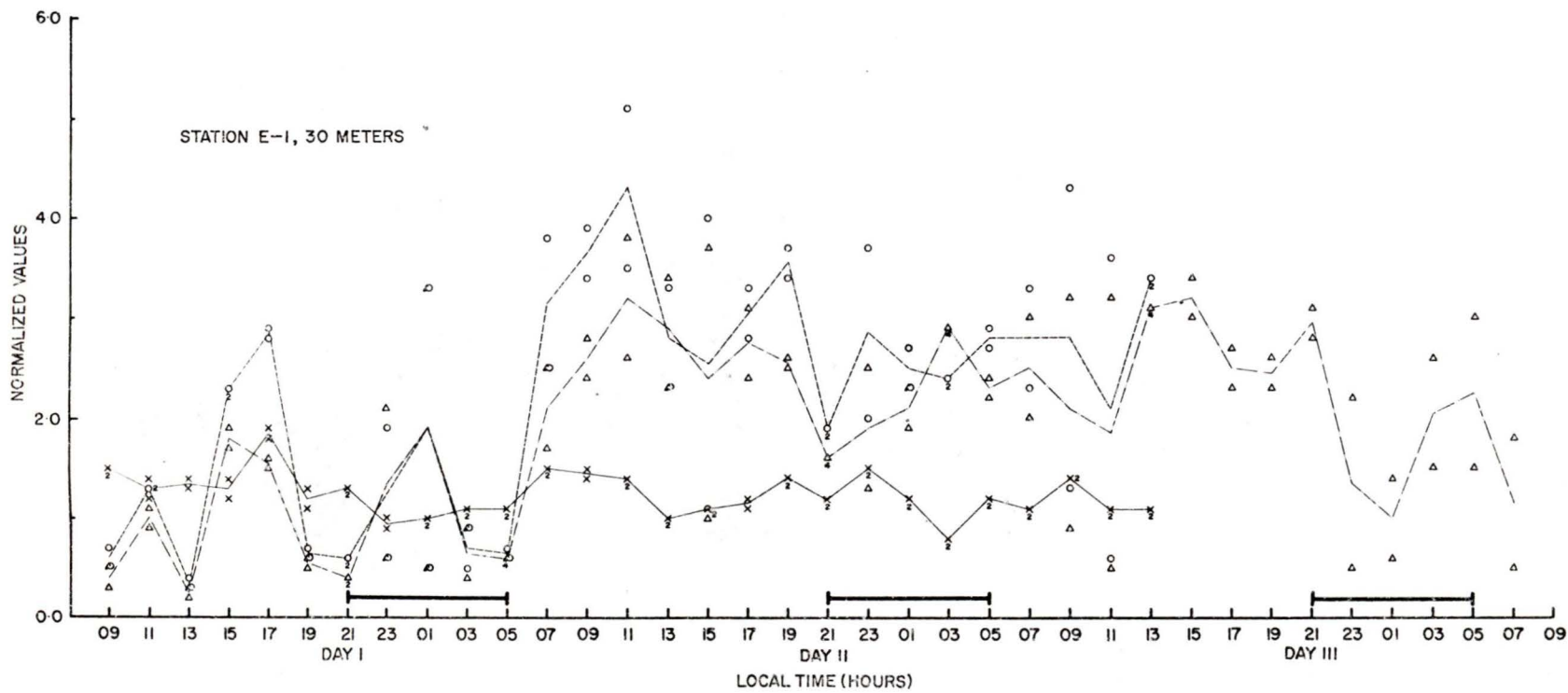


FIGURE 14

Graph of Chlorophyll *a* Per Particulate Volume, $\text{mg}/\mu^3 \times 10^{-12}$
(X — X), Photosynthetic Potential Per Particulate Volume,
 $\text{mg C/hr}/\mu^3 \times 10^{-12}$ (O --- O) and Assimilation Ratios,
 $\text{mg C/hr/mg chl-}a$ (Δ - - - Δ) at 30 meters, Days I-III.
Horizontal Dark Line Indicates the Period of No Measurable
Light.



poor replication. Values ranged between 0.35 and 2.86×10^{-12} mg C/hr/ μ^3 on Day I and between 1.89 and 4.34×10^{-12} mg C/hr/ μ^3 on Day II.

Assimilation ratios paralleled the photosynthetic potential/volume ratios, with maximum values during the day. However, the minima during the dark periods are not conclusive because of the poor replication. Maximum values were measured at 1500 on Day I, and 1100 on Day II, with a value of 1.80 and 3.17 mg C/hr/mg chl-*a* respectively. Day III was similar in value to Day II, with a maximum of 3.24 mg C/hr/mg chl-*a* at 1500. The minimum assimilation ratios all occurred during the dark period, at 2100 on Days I and II, and 0100 on Day III, with values of 1.12, 1.67 and 1.02 mg C/hr/mg chl-*a* respectively for the three days.

III. Oceanic Waters - Ocean Station P

The measurements taken during the Station P cruise were designed to test whether the variability which has been reported in the literature for photosynthetic potential and chlorophyll concentration, was a function of biomass changes, or caused by internal changes in the phytoplankton, or both. This work preceded that of the Endeavour cruise, but because of difficulties encountered, the data had to be interpreted using some conclusions formulated from the latter.

Lack of instrumentation for particle counts made it necessary to preserve water samples for later analysis. It was first thought that this would have little effect on the total particulate volume, but it became evident after analysis that there was a significant effect as data varied erratically. It was felt that the random breakdown of cells during preservation and the subsequent shaking (to obtain a homogeneous sample) resulted in a variable number of particles and hence a variable total particulate volume. Although information regarding total particulate volume or any calculation involving total volume, cannot be utilized, the chlorophyll and photosynthetic potential measurements remain valid, and thus interpretation on these data can be done.

It was also evident from the chlorophyll and photosynthetic potential data, that the period following the end of a 24 hour experiment could yield important information on the repeatability of any variation (i.e. to confirm whether it was a diel variation), and thus the Endeavour measurements were made to cover either 48 or 72 hours continuously, instead of the 24 hour sampling periods done on the Station P cruise.

The series of experiments at Station P were designed to test whether diel variation involving chlorophyll *a* and photosynthetic potential showed any differences between the total phytoplankton population and the nanoplankton fraction (defined as those organisms

passing through a 44 μ -mesh netting) as well as whether differences between surface waters and 30 meter samples existed. The total-nanoplankton set of experiments were done twice and will be referred to as Day A and Day B. Likewise, the surface-depth study was done twice; Day C and Day D.

Three laboratory experiments involving cultures of natural populations were also done, as described in the methods section, pages 15-16. The experiments will be referred to as Experiment A, Experiment B, and Experiment C (the data in Appendix however, refer to the Experiments A, B and C as Day E, Day F-G and Day H, respectively).

- A. Total Nanoplankton Series - Day A, Figures 15, 17, 19, Table 6, Tables A13, A14.

The chlorophyll *a* concentration (Figure 15) at the surface was found not to be significantly different between the total and nanoplankton groups, with values ranging between 0.25 - 0.50 mg/m³. No apparent diel variation was found during the sampling period.

Photosynthetic potential (Figure 17) measured for the nanoplankton fraction did not differ from the total population during the first six hours (0900 - 1500 hours) but was slightly less than measured for the whole population over the remainder of the experiment. These differences were slight, however, and it is not known whether the two groups, as defined, are distinct.

There was a definite diel variation in both groups, with a morning maxima, decreasing to minimum values by late afternoon, and

TABLE 6

Maximum-minimum values for chlorophyll *a* concentration, photosynthetic potential and assimilation ratios for Days A and B (total-nanoplankton) and Days C and D (surface - 30 meters) at ocean Station P. Numbers in parenthesis indicate the time of measurement.

Day	Chlorophyll <i>a</i> Concentration (mg/m ³)		Photosynthetic Potential (mg C/hr/m ³)		Assimilation Ratios (mg C/hr/mg chl- <i>a</i>)	
	max.	min.	max.	min.	max.	min.
A - Total	0.69 (0900)	0.36 (2300)	0.88 (0700)	0.38 (2100)	2.44 (0700)	0.68 (1300)
	0.77 (1300)		0.93 (1100)		2.28 (1100)	
A - Nano	0.63 (0900)	0.36 (0500)	0.71 (0700)	0.33 (2100)	2.09 (0300)	0.69 (1500)
		0.32 (2300)	0.88 (1100)		1.68 (1100)	
B - Total	0.56 (1300)	0.29 (0100)	1.72 (0700)	0.54 (2100- 2300)	3.26 (0700)	1.14 (2100)
		0.32 (1100)	1.26 (0900)		4.07 (1300)	
B - Nano	0.56 (1300)	0.28 (2300)	1.51 (0700)	0.53 (2300)	3.64 (0700)	1.22 (2100)
			1.16 (0900)		3.55 (1300)	
C - Surface	1.20 (1500)	0.60 (0100)	1.84 (0700)	0.77 (1900)	2.78 (0700)	0.96 (1900)
			1.83 (1100)		2.53 (0900)	
C - 30 Meters	0.70 (2300)	0.57 (1100)	1.03 (1100)	0.55 (1500)	1.81 (1100)	0.81 (1500)

..(cont'd)

TABLE 6, cont'd.

D - Surface	0.57 (0700)	0.36 (0500)	1.37 (0700)	0.85 (2100)	3.50 (0500)	1.97 (2100)
	0.52 (1500)	0.35 (1300)	1.94 (0900)		4.11 (1300)	
D - 30 Meters	0.61 (1900)	0.36 (0900)	1.25 (1300)	0.73 (2100)	2.76 (0900)	1.32 (0300)
		0.48 (2100)				

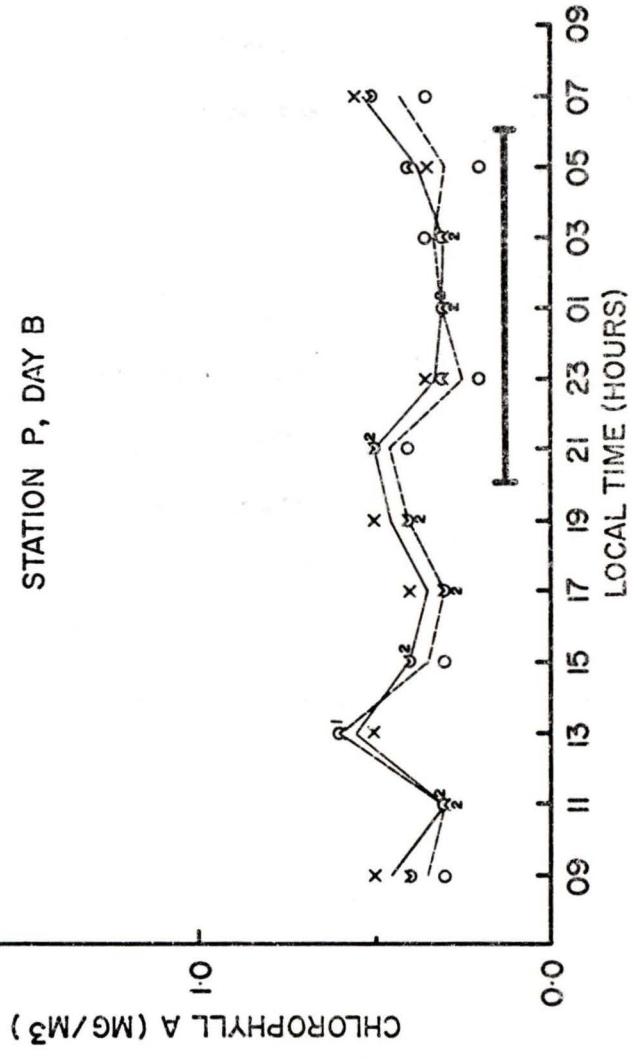
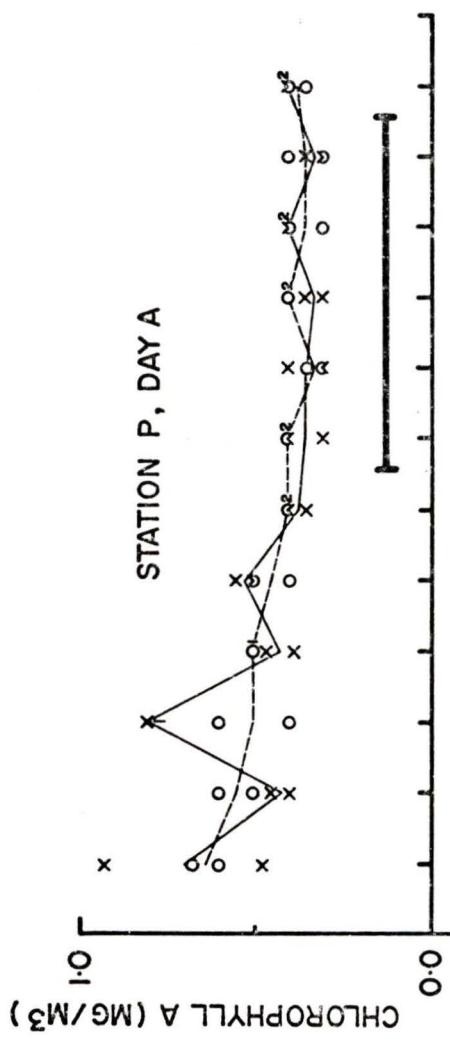
FIGURE 15

Graph of Surface Chlorophyll α Concentration mg/m^3 ,
for the Total Population (X — X) and Nanoplankton
Fraction (O --- O) for Day A.

FIGURE 16

Graph of Surface Chlorophyll α Concentration mg/m^3 ,
for the Total Population (X — X) and Nanoplankton
Fraction (O --- O) for Day B.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



increasing again at the onset of the dark period. The values obtained each morning (at the beginning and end of the experiment) were similar - 0.80 mg C/m³/hr at 0900, and 0.88 mg C/m³/hr at 0700. Low values were recorded between 1500 and 2100 (0.38 - 0.53 mg C/m³/hr) with the minimum occurring at 2100. (Values given are for the total population).

The assimilation ratios (Figure 19) also did not appear to differ between the total and nanoplankton fractions but a diel variation was evident. Data given here will be for the total population only. Values decreased from a morning maximum to a minimum during the afternoon, and remained low until the beginning of the dark period. They then gradually increased until 0700 when sampling was terminated. The maximum occurred at 1100 with a value of 2.28 mg C/hr/mg chl-*a*, but decreased to its lowest value, 0.68 mg C/hr/mg chl-*a* by 1300. The assimilation ratios remained low between 1300 and 2100, with a range of only 0.68 - 1.08 mg C/hr/mg chl-*a*. Values increased more rapidly after 2100, reaching 2.44 mg C/hr/mg chl-*a* by 0700.

B. Total Nanoplankton Series - Day B, Figures 16, 18, 20, Table A6, Tables A13, A14.

As with the previous experiment (Day A) there was no apparent difference in chlorophyll *a* concentration between the nanoplankton fraction and total population (Figure 16). There was also no

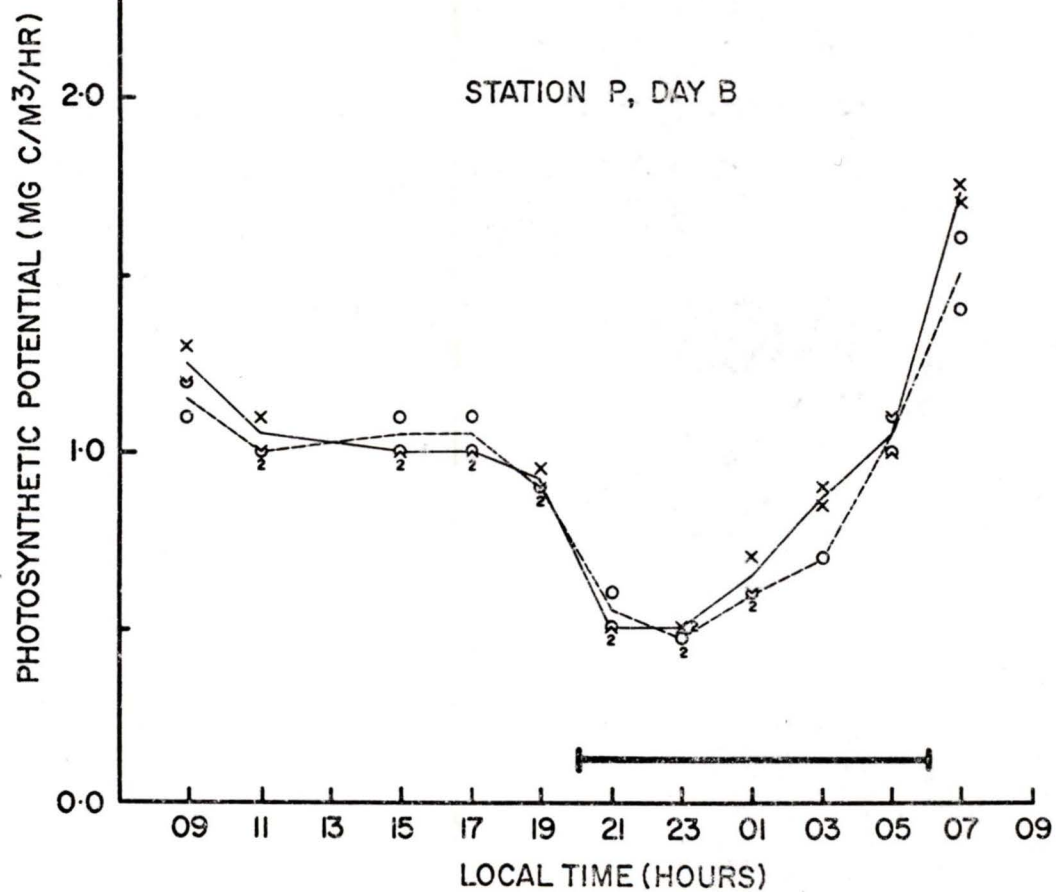
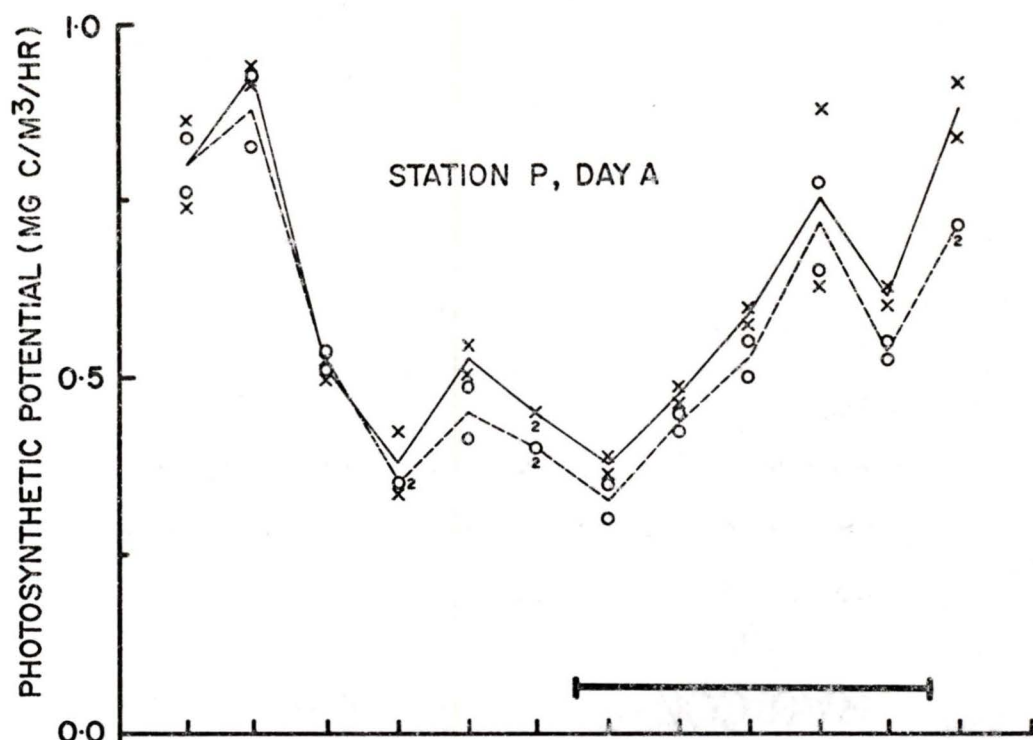
FIGURE 17

Graph of Surface Photosynthetic Potential, $\text{mg C/m}^3/\text{hr}$,
for the Total Population (X — X) and Nanoplankton
Fraction (O --- O), for Day A.

Figure 18

Graph of Surface Photosynthetic Potential, $\text{mg C/m}^3/\text{hr}$,
for the Total Population (X — X) and Nanoplankton
Fraction (O --- O) for Day B.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



indication of a diel variation in chlorophyll α , with most values within the range of 0.25 - 0.50 mg/m³.

Photosynthetic potential showed a diel variation, but there were no differences between the total population and nanoplankton fraction. From a morning maximum, the photosynthetic potential decreased to minimum values by 2300, with the greatest decrease after 1900. Values then increased steadily until sampling was terminated, at 0700 (Figure 18).

Maximum values for the total population were recorded at 0900 (1.26 mg C/m³/hr) and again at the end of the experiment at 0700 (1.72 mg C/m³/hr), (this does not include the very high value of 2.25 mg C/m³/hr at 1300). The minimum occurred at 2300, with a value of 0.52 mg C/m³/hr.

Assimilation ratios (Figure 20) also did not show any differences between the nanoplankton fraction and the total population. A diel variation was apparent, with values decreasing from the morning maximum to their lowest value at 2100. The ratios increased steadily after that time until the end of the experiment. Values (for the total population) were somewhat erratic between 0900 and 1700, but remained within the range of 2.70 - 4.07 mg C/hr/mg chl- α . After 1700, however, the decrease was significant, reaching its lowest value of 1.14 mg C/hr/mg chl- α at 2100. The maximum value of 3.26 mg C/hr/mg chl- α , reached by the end of the experiment was similar to the maximum measured the previous morning.

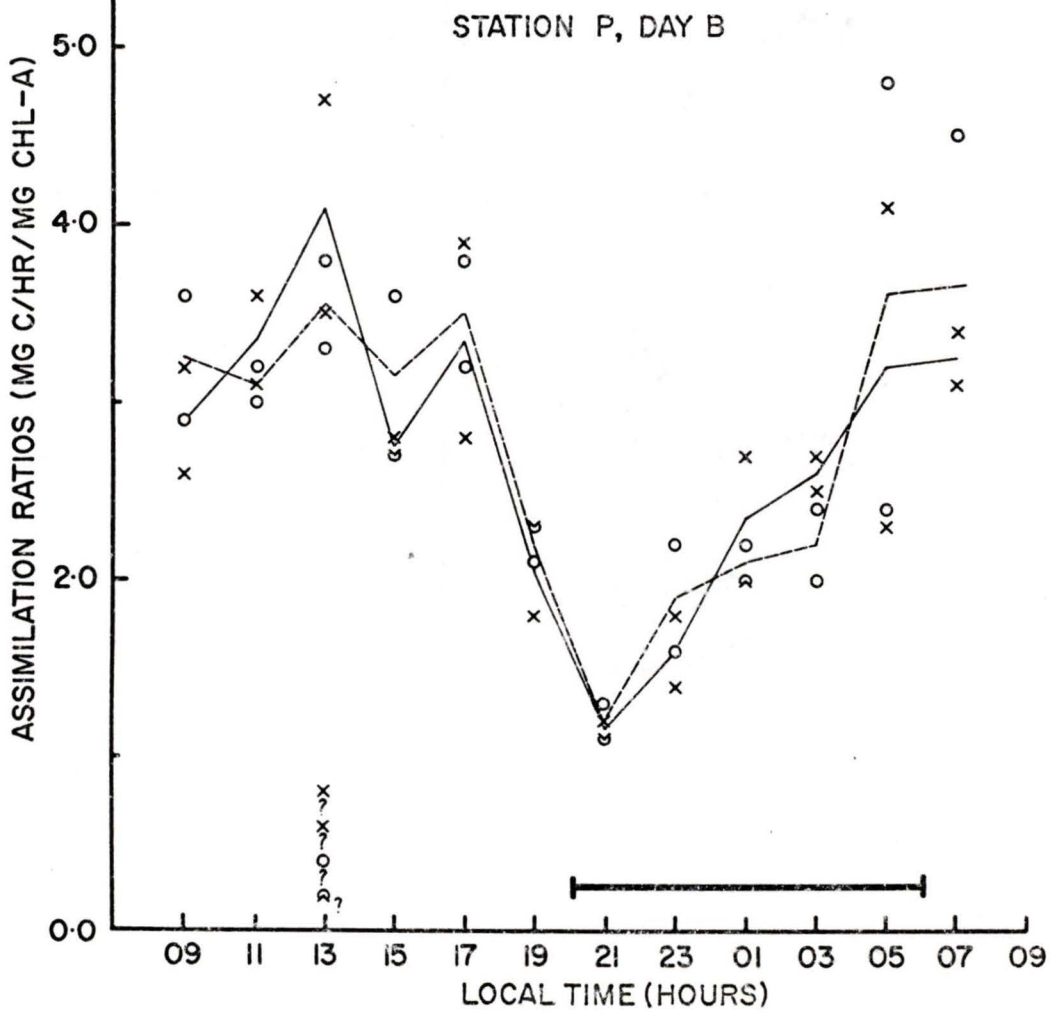
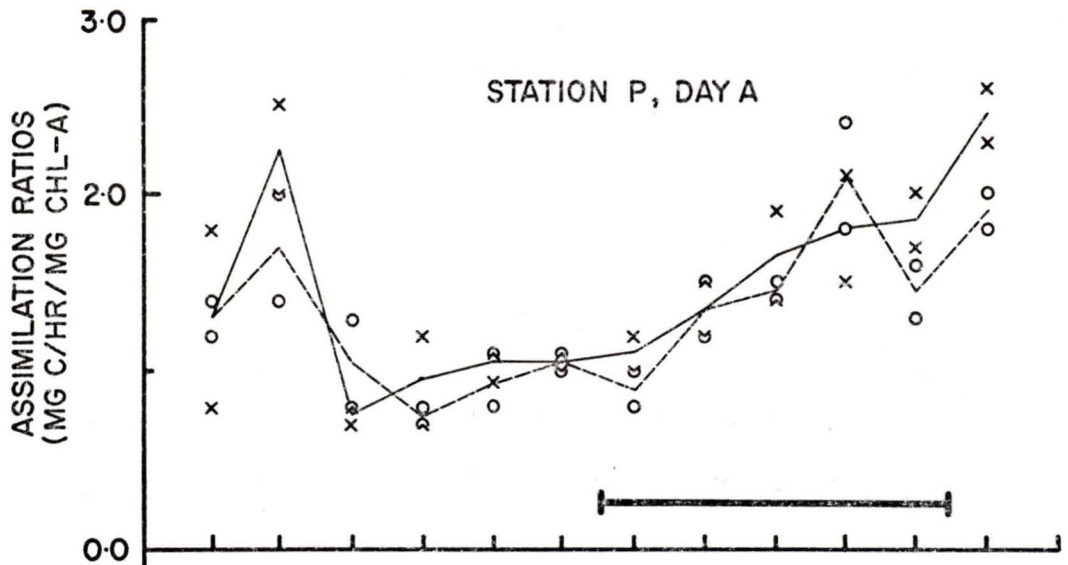
FIGURE 19

Graph of Surface Assimilation Ratios, mg C/hr/mg chl-*a*,
for the Total Population (X — X) and Nanoplankton
Fraction (O --- O) for Day A.

FIGURE 20

Graph of Surface Assimilation Ratios, mg C/hr/mg chl-*a*,
for the Total Population (X — X) and Nanoplankton
Fraction (O --- O) for Day A.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



C. Surface-Depth Series - Day C, Figures 21, 23, 25;
Table 6, Tables A13, A14.

The concentration of chlorophyll *a* at the surface showed little variation during the sampling period, with most values within the range of 0.50 - 0.75 mg/m³ (Figure 21). Due to weather conditions, sampling at 30 meters was terminated after 2300. Up to that time, however, the chlorophyll *a* at the lower depth was slightly less than found at the surface, with an overall range of 0.57 - 0.72 mg/m³. As with the surface samples, there was no indication of any rhythmical variation.

Photosynthetic potential (Figure 23) at the surface showed a definite diel pattern, with a significant decrease in values after 1500. The minimum occurred between 1900 and 0100, but increased steadily after 0100 until the end of the experiment. Values in the morning were fairly constant between 0900 and 1500 with a range of 1.71 - 1.83 mg C/m³/hr. Minimum values for the photosynthetic potential fell in the range 0.77 to 0.85 mg C/m³/hr, between 1900 and 0100.

The photosynthetic potential at 30 meters was more erratic, with no apparent diel variation. The decrease from the maximum at 1100 (1.03 mg C/m³/hr) may signify a decline, but this cannot be verified as sampling was terminated after 2300. The low values at

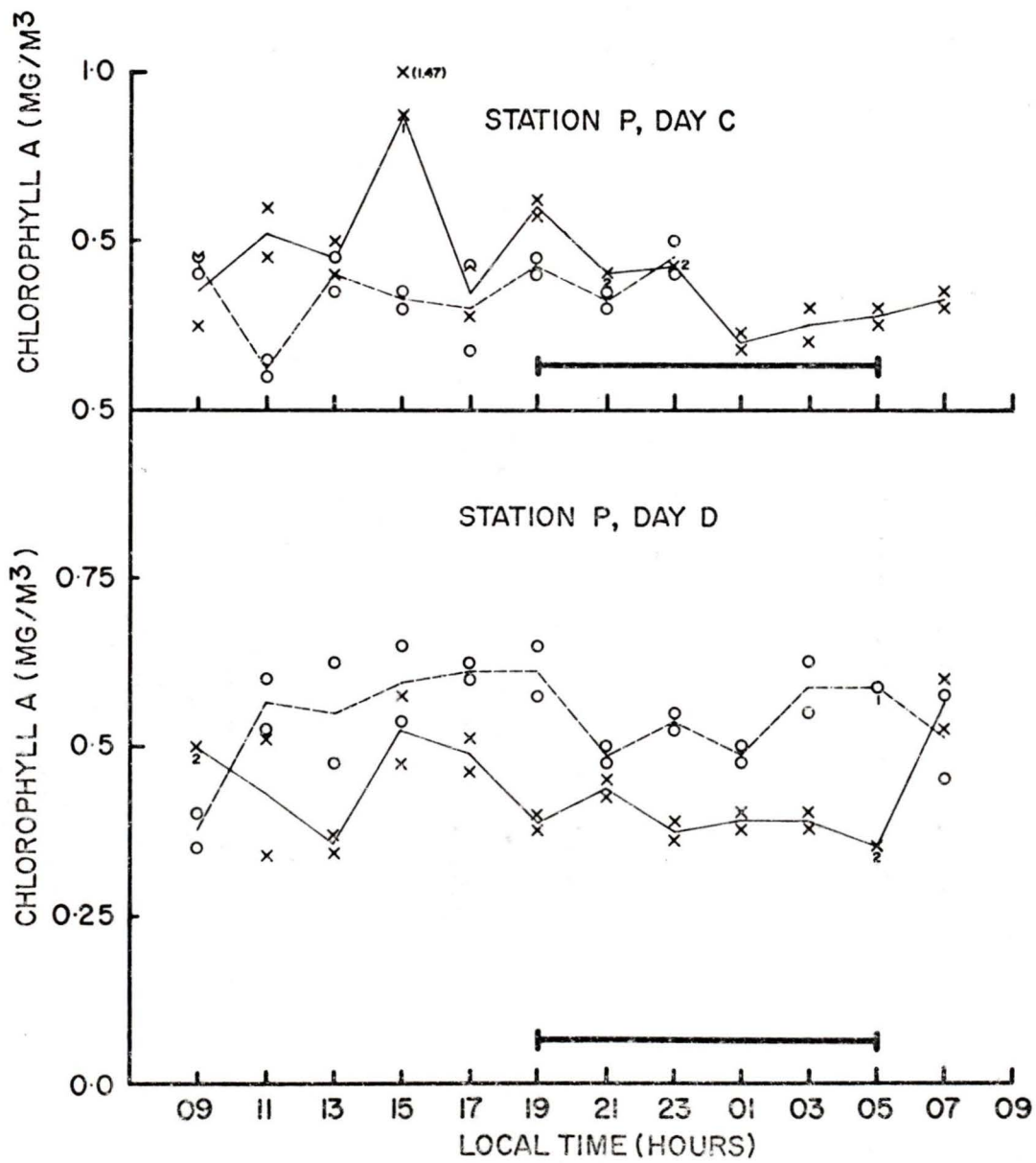
FIGURE 21

Graph of Chlorophyll a Concentration, mg/m^3 , for
Surface Samples (X — X) and 30 meters (O --- O),
Day C.

FIGURE 22

Graph of Chlorophyll a Concentration, mg/m^3 , for
Surface Samples (X — X) and 30 meters (O --- O),
Day D.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



30 meters were similar to the minima measured for the surface samples. Minimum values were measured between 1300 and 2300 with a range of 0.55 - 0.77 mg C/m³/hr.

The assimilation ratios at the surface, (Figure 25), also showed a diel variation. Values decreased from a morning maxima to a minimum during the late afternoon, and then increased until the end of the experiment. Values calculated for the morning (between 0900 and 1300 hours) varied between 2.39 and 2.53 mg C/hr/mg chl-*a*, which was similar to the ratio of 2.78 mg C/hr/mg chl-*a* obtained at 0700, at the end of the experiment. The minimum assimilation ratio occurred at 1900, with a value of 0.96 mg C/hr/mg chl-*a*.

A diel variation in the assimilation ratios at 30 meters was not apparent. Values decreased from a morning maximum to low values during the dark period, but did not show any subsequent increase. The maximum occurred at 1100 with a value of 1.81 mg C/hr/mg chl-*a*, but the remaining values were within the range of 0.81 - 1.17 mg C/hr/mg chl-*a*.

D. Surface-Depth Series - Day D, Figures 22, 24, 26;
Table 6, Tables A13, A14.

As was found during Day C, neither the surface or the 30 meter samples showed any diel variation in chlorophyll *a* concentration (Figure 22). Unlike Day C, however, the 30 meter samples had a slightly higher chlorophyll *a* concentration than found at the surface.

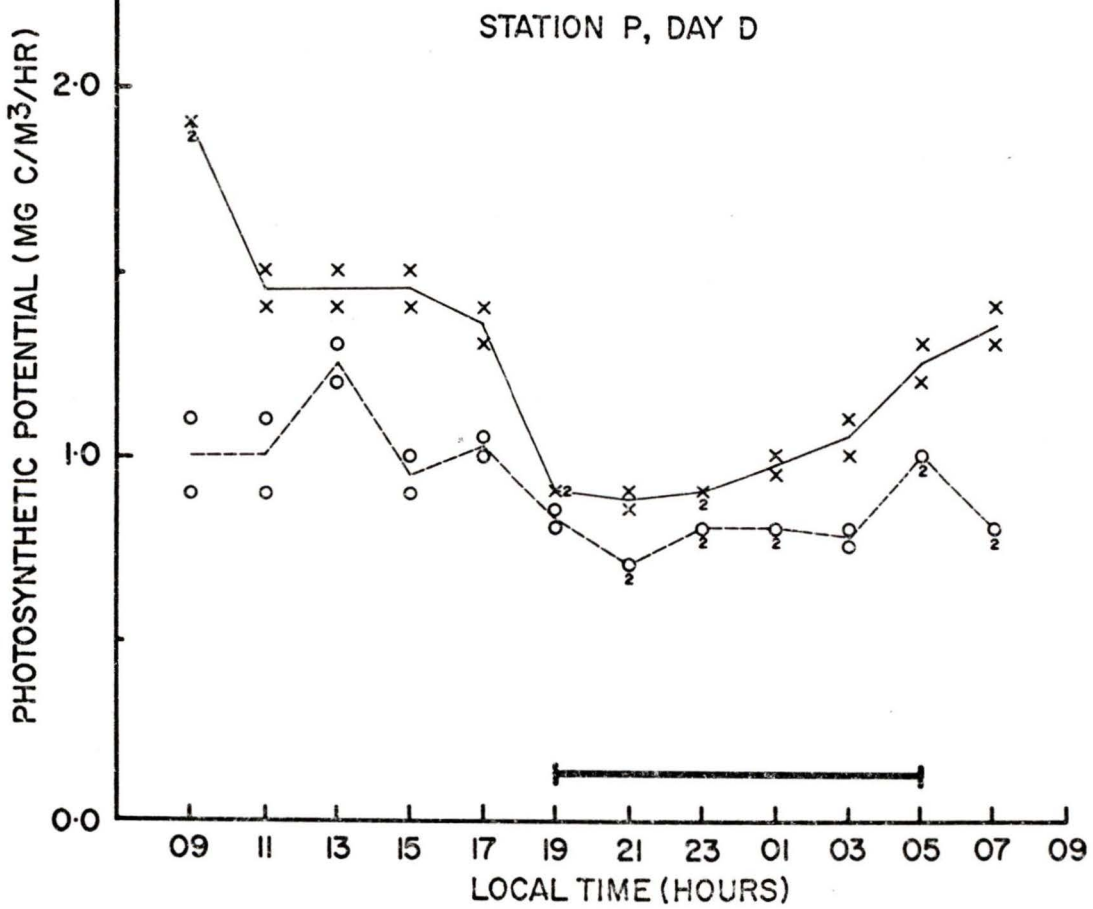
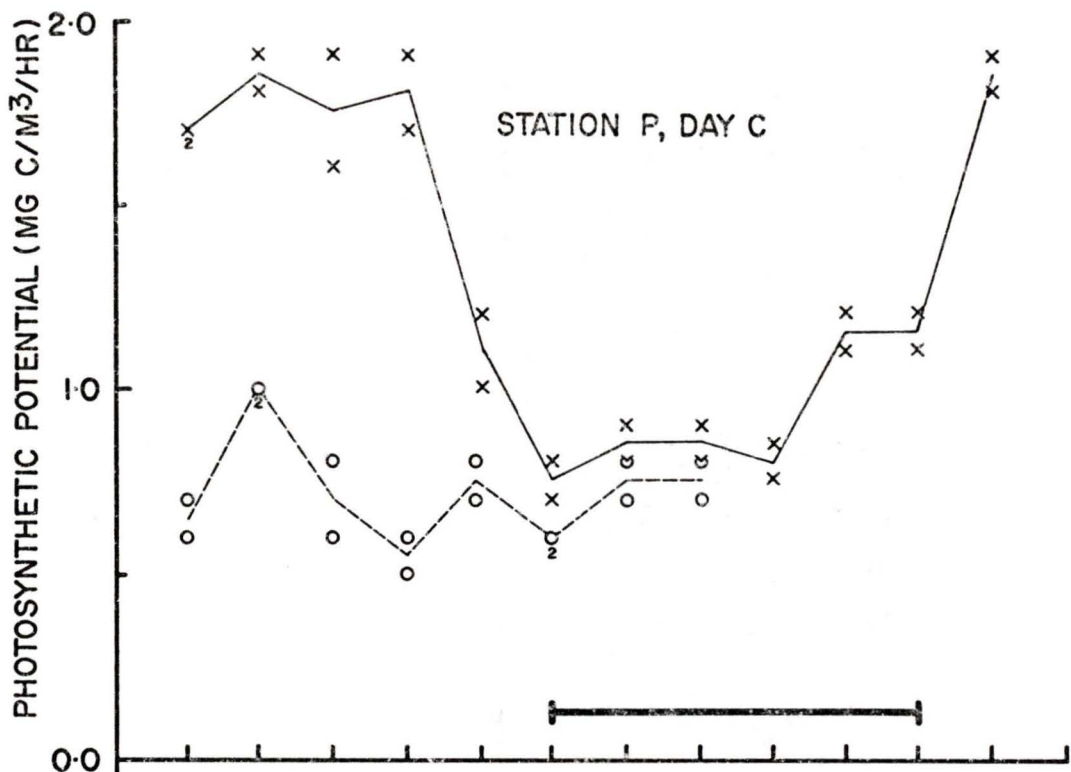
FIGURE 23

Graph of Photosynthetic Potential, mg C/m³/hr, for
Surface Samples (X — X) and 30 meters (O --- O),
Day C.

FIGURE 24

Graph of Photosynthetic Potential, mg C/m³/hr, for
Surface Samples (X — X) and 30 meters (O --- O),
Day D.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



The range in values at the surface was 0.35 - 0.57 mg/m³ while the 30 meter samples varied between 0.38 and 0.61 mg/m³.

The photosynthetic potential measurements at the surface showed a diel variation, decreasing from a midday maximum, to the lowest values near the onset of the dark period (Figure 24). From the minimum, the photosynthetic potential increased steadily until the end of the sampling period.

Except for a very high value at 0900 (1.94 mg C/m³/hr), the period from 1100 to 1700 hours had a fairly constant photosynthetic potential, with values between 1.37 and 1.42 mg C/m³/hr. After 1700 the photosynthetic potential decreased rapidly, to a minimum of 0.85 mg C/m³/hr at 2100. The values at 0700, 1.37 mg C/m³/hr was similar to values found during the previous morning.

Although a diel variation occurred at 30 meters, the magnitude of the variation was not as great as for the surface samples. The photosynthetic potential decreased from a morning maxima to its lowest value just prior to the dark period. However, because of a low value at 0700, it is not clear whether the photosynthetic potential was increasing again towards the end of the experiment.

The maximum occurred at 1300, with a value of 1.25 mg C/m³/hr. After 1700 the photosynthetic potential decreased to a minimum at 2100 of 0.73 mg C/m³/hr. Values remained low between 2100 and 0300 (range of 0.73 - 0.79 mg C/m³/hr) and then increased to 0.96 mg C/m³/hr by 0500.

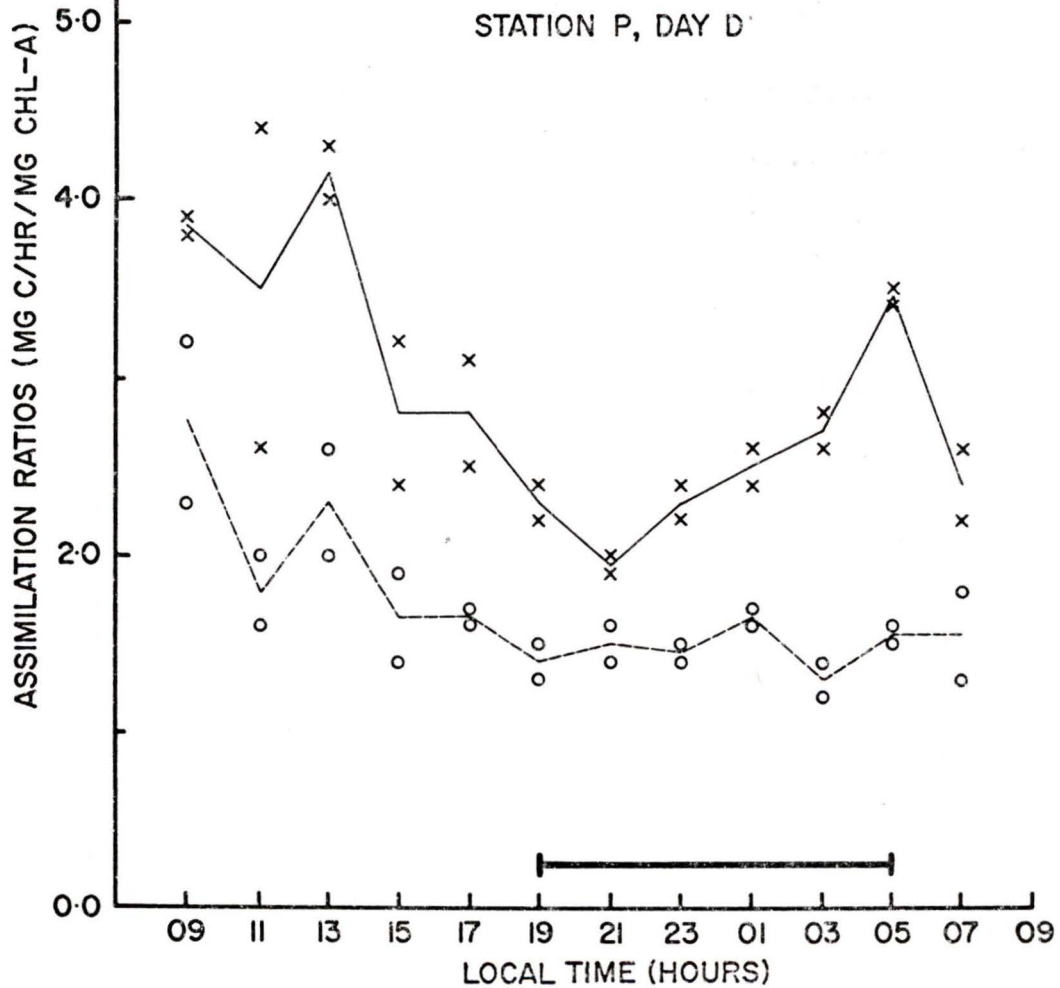
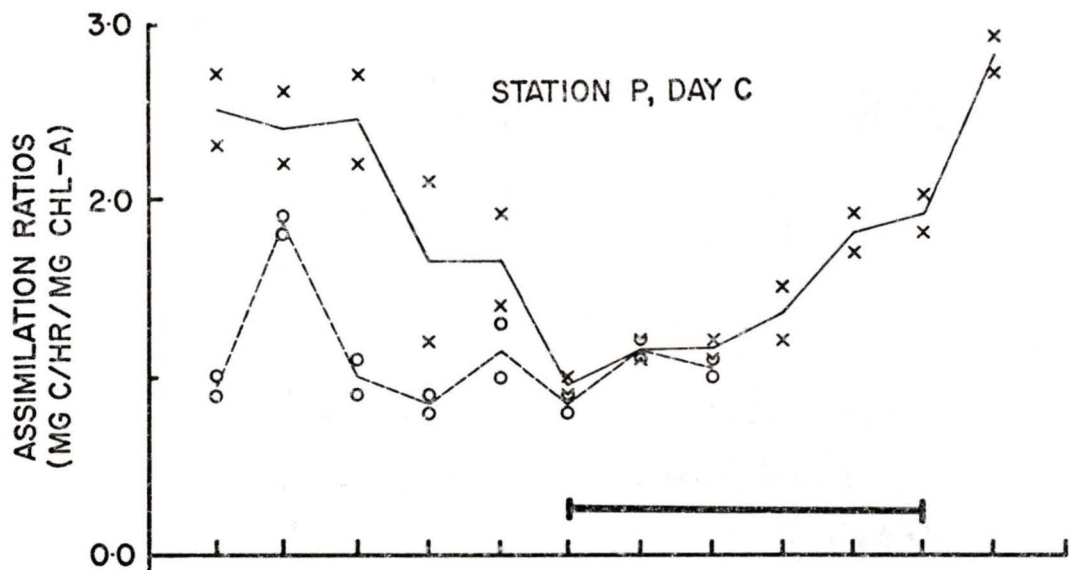
FIGURE 25

Graph of Assimilation Ratios, mg C/hr/mg chl-*a*,
for Surface Samples (X — X) and 30 meters
(O --- O), Day C.

FIGURE 26

Graph of Assimilation Ratios, mg C/hr/mg chl-*a*,
for Surface Samples (X — X) and 30 meters
(O --- O), Day D.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



The assimilation ratios (Figure 26) for the surface samples also showed a diel variation similar to that measured for the photosynthetic potential, decreasing after 1300 to a minimum just prior to the dark period. The ratios then increased until 0500 but decreased at 0700.

Maximum values ranged between 3.46 - 4.11 mg C/hr/mg chl-*a* (0900 - 1300 hours), while the minimum ratio of 1.97 mg C/hr/mg chl-*a* occurred at 2100. By 0500 the following day, the assimilation ratios had increased to a value of 3.50 mg C/hr/mg chl-*a*, which was similar to values measured the previous morning.

The assimilation ratios calculated for the 30 meter samples showed slightly lower values after 1300, but no diel variation was apparent. The maximum occurred at 0900 with a value of 2.76 mg C/hr/mg chl-*a*, but most of the values after 1300 were between 1.32 and 1.72 mg C/hr/mg chl-*a*. When compared with the surface samples the assimilation ratios at 30 meters were consistently lower, although the difference between the two was less during dark period.

E. A Comparison of Surface Samples - Total Population

Overall, four separate experiments were carried out dealing with the total population in surface waters.

As already mentioned, there were no diel variations in

chlorophyll α , although there were differences in concentration between days. Day A, B and D were all similar with most values between 0.3 and 0.8 mg/m³ while values on Day C were slightly higher, ranging between 0.6 and 1.2 mg/m³.

All four days showed a diel variation in the photosynthetic potential, decreasing from a midday maxima to minimum values just prior to the dark period. Generally, the photosynthetic potential increased during the dark period, with values at the end of the experiments, similar to those recorded the previous morning.

The lowest photosynthetic potential was recorded on Day A, which ranged between 0.38 and 0.93 mg C/m³/hr, while slightly larger values were found on Days B, C and D, with ranges of 0.54 - 1.72, 0.77 - 1.83 and 0.85 - 1.94 mg C/m³/hr respectively.

Assimilation ratios for all four days also showed diel changes, with a maxima during the morning, and decreasing to lower values at the end of the light period. During the dark period the ratios increased until sampling was terminated. On Day A the minimum was reached at midday, but values remained low until the beginning of the dark period.

The assimilation ratios on Days A and C had similar maxima (2.28 and 2.78 mg C/hr/mg chl- α respectively) but these were lower than values measured during Day B (4.07 mg C/hr/mg chl- α) on Day D (4.11 mg C/hr/mg chl- α). Minimum values for Day A, B and C

were similar, near 1.0 mg C/hr/mg chl- α , but Day D had a somewhat higher minimum, 1.97 mg C/hr/mg chl- α .

IV. Laboratory Experiments - Ocean Station P

Three sets of laboratory experiments were carried out to determine what effects the altering of light-dark cycles had on chlorophyll α , photosynthetic potential and total particulate volumes. The preservation of water samples made it necessary, as with other Station P samples, to interpret the data without the total particulate volume measurements. Therefore, only total chlorophyll, photosynthetic potential and assimilation ratios will be discussed.

The different laboratory experiments will be referred to as Experiment A, Experiment B and Experiment C. Two sets of conditions were set up in each experiment, and will be referred to as the control culture, (C), in which light-dark cycles were not altered and lab culture (L) which was subjected to different light-dark regimes.

- A. Lab Experiment A Figures 27, 29, 31;
Table 7, Tables A13, A14.

After allowing the populations to adjust to the new temperature and light regimes for three days, the lab culture was held in the dark during the fourth day and samples collected every three hours. The control

TABLE 7

Maximum-minimum values for chlorophyll *a* concentration, photosynthetic potential and assimilation ratios for laboratory experiments. Numbers in parenthesis indicate the time of measurement.

Day	Chlorophyll <i>a</i> (mg/m ³)		Photosynthetic Potential ₃ (mg C/hr/m ³)		Total Particulate Volume (μ ³ /ml x 10 ⁶)	
	max.	min.	max.	min.	max.	min.
Experiment A Lab Culture	1.77 (0600)	1.28 (1200)	3.97 (1200)	1.59 (0600)	3.12 (1200)	0.90 (0600)
			2.91 (1800)	1.24 (1500)	1.84 (1800)	0.95 (1500)
Control Culture	1.99 (0600)	1.40 (0900)	1.66 (0300)	0.87 (1500)	0.92 (0300)	0.54 (1500)
			1.96 (0900)		1.68 (1200)	
Experiment B Lab Culture	1.26 ₁ (0900 ¹)	1.13 (0300)	3.20 (2100)	1.17 ₂ (0900 ²)	2.89 (2100)	1.04 ₂ (0900 ²)
	1.24 (1800)	1.06 (1500)		1.47 (1200)		1.23 ₁ (0900 ¹)
Control Culture	1.14 ₁ (0900 ¹)	0.84 ₂ (0900 ²)	2.69 ₁ (0900 ¹)	0.58 (2400)	0.80 ₂ (0900 ²)	0.47 (2400)
	1.25 (1800)	1.05 (1200)			2.37 (1200)	
Experiment C Lab Culture	0.81 (0600)	0.70 (2400)	1.50 (0600)	0.70 (2100)	1.85 (0600)	0.86 (2100)
	0.96 (0900)		2.44 (0900)		2.61 (1200)	
Control Culture	0.95 (0600)	0.83 (1800)	1.79 (0600)	0.39 (2100)	1.88 (0600)	0.44 (2100)
			1.94 (0900)		2.30 (0900)	

¹ Initial measurement of the experiment. ² Final measurement of the experiment.

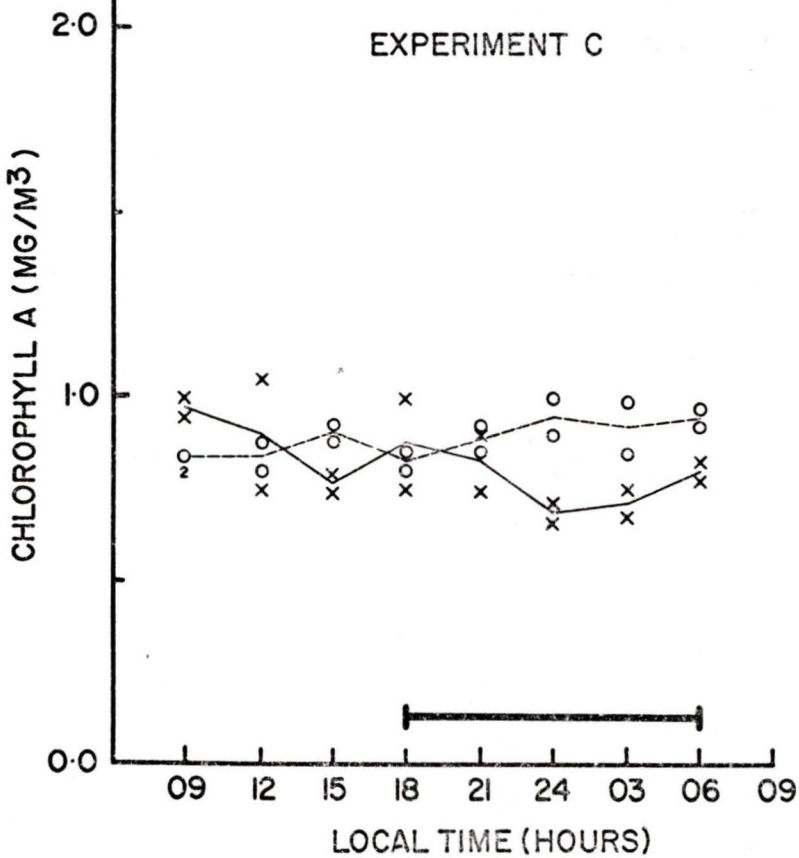
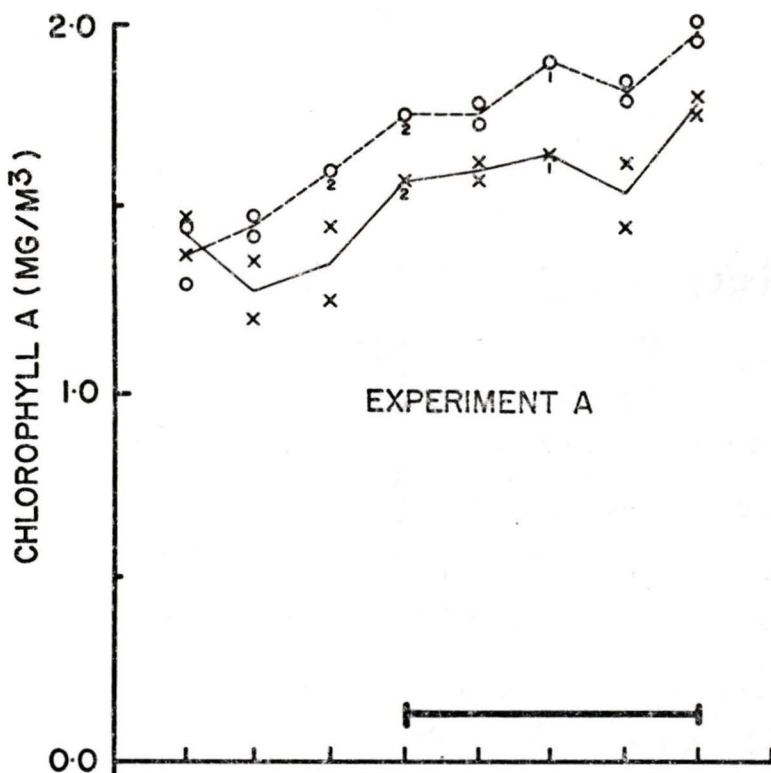
FIGURE 27

Graph of Chlorophyll *a* Concentration, mg/m^3 , for
Lab Cultures (X — X) and Control Cultures
(O --- O), Experiment A.

FIGURE 28

Graph of Chlorophyll *a* Concentration, mg/m^3 , for
Lab Cultures (X — X) and Control Cultures
(O --- O), Experiment C.

Horizontal Dark Lines Indicates the Period of No
Measurable Light.



remained on the same light-dark cycle, with the light period between 0600 and 1800.

Chlorophyll *a* concentration (Figure 27) increased considerably in both cultures during the experiment. The control increased steadily, from 1.40 mg/m³ to 1.99 mg/m³. The lab culture decreased during the first part of the experiment, but increased during the remaining period. The initial chlorophyll *a* concentration for the lab culture was 1.43 mg/m³, which decreased to 1.28 mg/m³ after 3 hours, but then increased to a final value of 1.77 mg/m³. At all times, except the initial measurement, the lab culture had less chlorophyll *a* than the control.

Photosynthetic potential (shown in Figure 29) for the control culture had decreased during the light period, but then increased slowly in the dark period during the remainder of the experiment. The maximum occurred at 0900 with a value of 2.56 mg C/m³/hr, and decreased to 0.87 mg C/m³/hr by 1500. By the end of the experiment values had increased to 1.61 mg C/m³/hr.

The photosynthetic potential in lab culture varied erratically, between a low of 1.24 mg C/m³/hr (1500 hours) and a high of 3.97 mg C/m³/hr (1200 hours). Values tended to decrease towards the end of the experiment, but at all sampling times they remained greater than values in the control culture.

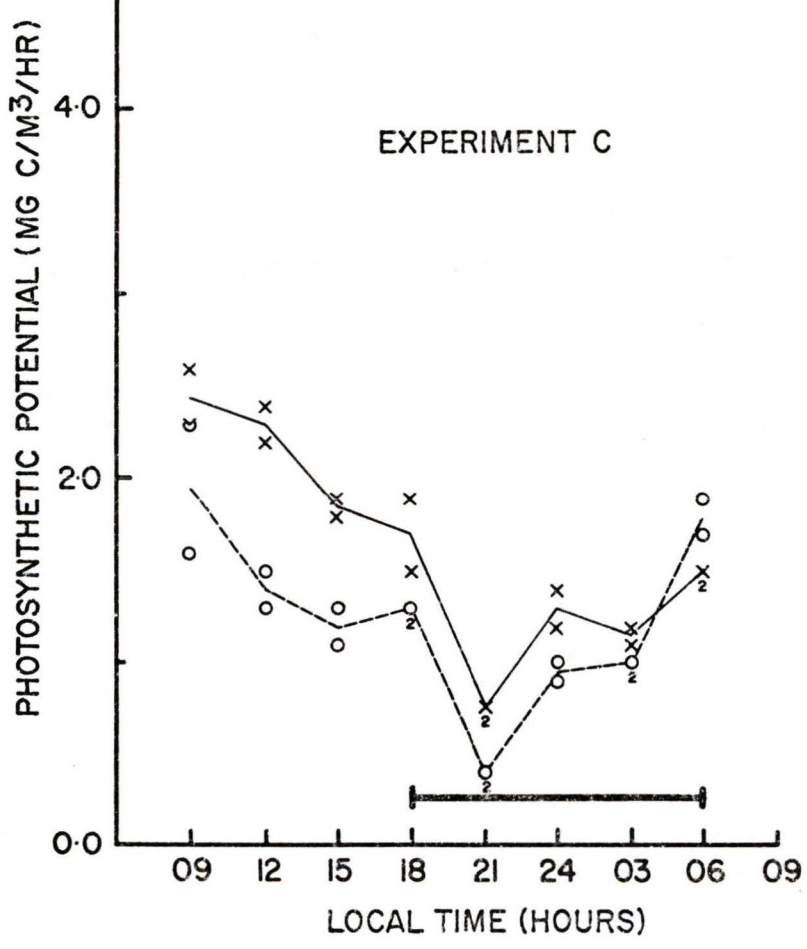
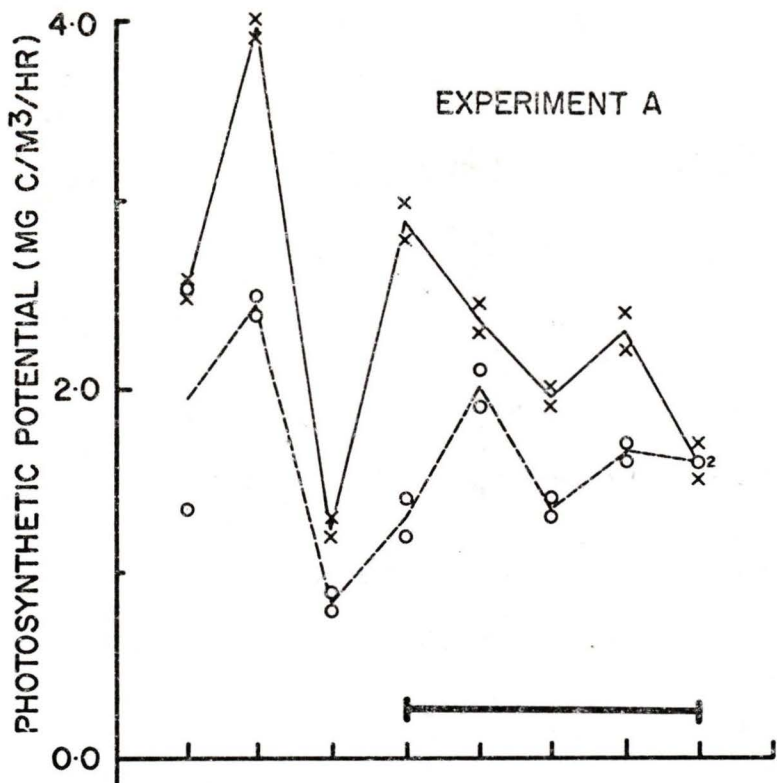
FIGURE 29

Graph of Photosynthetic Potential, $\text{mg C/m}^3/\text{hr}$, for
Lab Cultures (X — X) and Control Cultures
(O --- O), Experiment A.

FIGURE 30

Graph of Photosynthetic Potential, $\text{mg C/m}^3/\text{hr}$, for
Lab Cultures (X — X), and Control Cultures
(O --- O), Experiment C.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



Assimilation ratios (Figure 31) calculated for the control culture decreased from a maximum at 1200 (midway in the light period) to a minimum three hours later. Values remained low during the rest of the light period and first part of the dark period, with a slight increase three hours before the next light cycle. The maximum ratio was about 1.68 mg C/hr/mg chl- α , decreasing to a minimum of 0.54 mg C/hr/mg chl- α at 1500. From 0300 to 0600 the ratio ranged between 0.81 and 0.92 mg C/hr/mg chl- α .

The assimilation ratios calculated for the lab culture did not show any regular variation. Overall, values decreased during the study with a maximum value of 3.12 mg C/hr/mg chl- α at 1200 and a minimum at 0600 of 0.90 mg C/hr/mg chl- α .

B. Lab Experiment C - Figures 28, 30, 32;
Table 7, Tables A13, A14.

This experiment was identical to Experiment A, except for the addition of some inorganic nutrients. After pre-conditioning, the lab culture was kept in the dark during the sampling period, while the control culture retained the 12 hour light - 12 hour dark cycle. Lights were turned on at 0600 and off at 1800.

Chlorophyll α concentration (Figure 28) in the control culture did not change during the light period, but a slight increase was measured during the dark period. Values ranged between 0.83 and 0.95 mg/m³. Chlorophyll α in the lab culture decreased during the

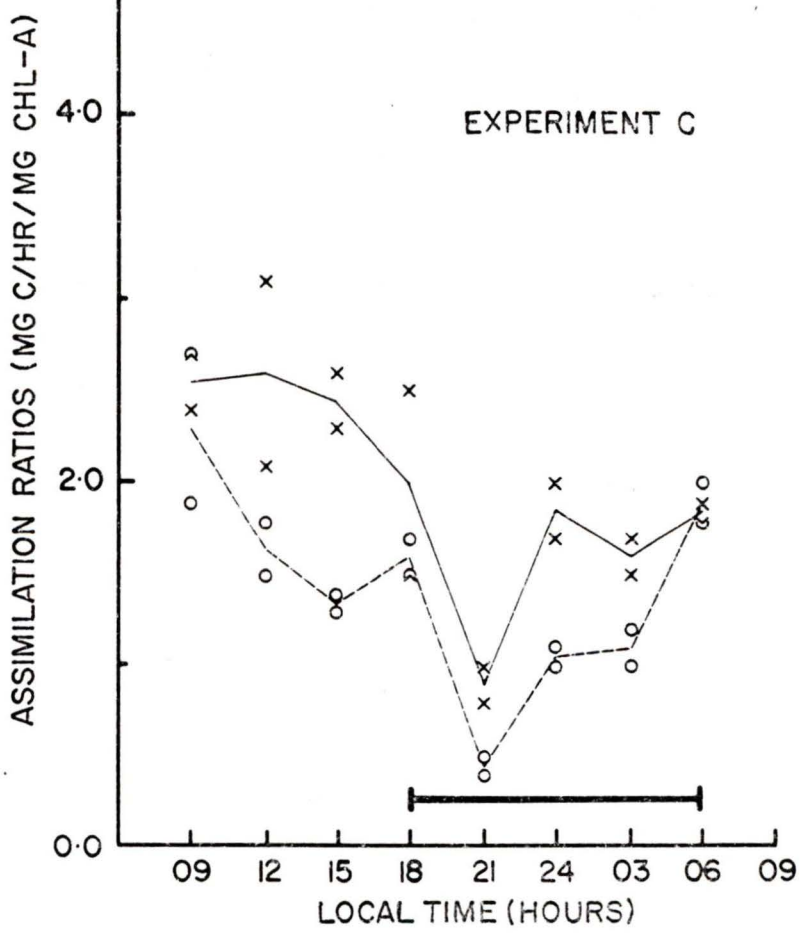
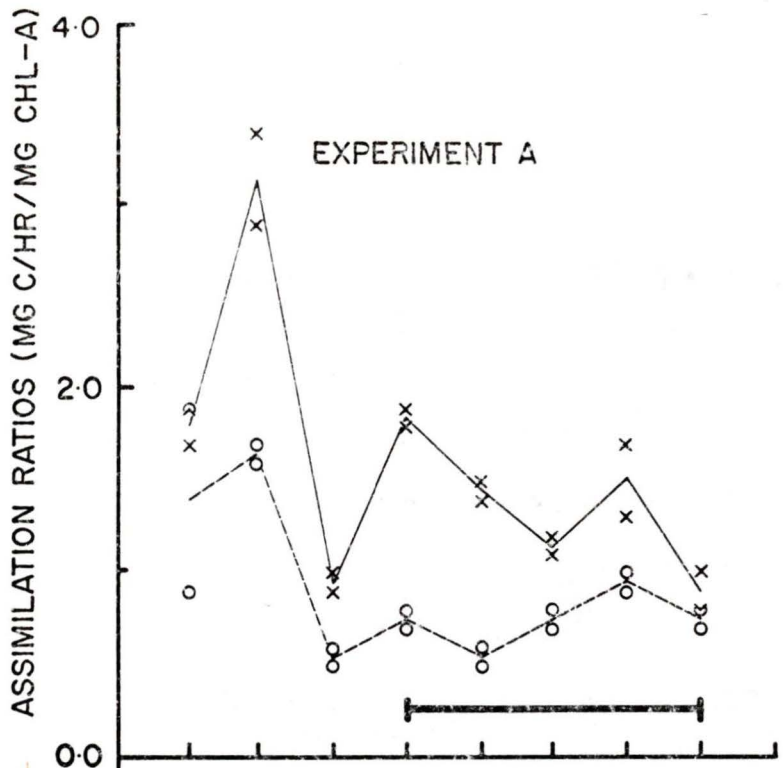
FIGURE 31

Graph of Assimilation Ratios, mg C/hr/mg chl-*a*,
for Lab Culture (X ——— X) and Control Culture
(O --- O), Experiment A.

FIGURE 32

Graph of Assimilation Ratios, mg C/hr/mg chl-*a*,
for Lab Culture (X ——— X) and Control Culture
(O --- O), Experiment C.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



first 15 hours of the experiment, but then increased slightly until the end. Up until 1800, the chlorophyll *a* concentration in the control culture was slightly less or about equal to the lab values, but after that time, the concentration in the lab culture decreased relative to the control. From an initial concentration of 0.70 mg/m^3 , the control culture increased to 0.96 mg/m^3 at 0600. The lab culture decreased from 0.96 mg/m^3 at 0900 to 0.70 mg/m^3 at 2400, but then increased to a final concentration of 0.81 mg/m^3 .

Photosynthetic potential (Figure 30) showed a diel variation in both the control and lab cultures, with a maximum at the beginning of the experiment, and a minimum three hours after the start of the dark period. The lab culture had higher values throughout the experiment, but the differences were less during the dark period.

The control culture decreased from a value of $1.93 \text{ mg C/m}^3/\text{hr}$ at 0900 to a minimum of $0.39 \text{ mg C/m}^3/\text{hr}$ at 2100, and then increased to $1.79 \text{ mg C/m}^3/\text{hr}$ at 0600, when sampling was ended. The lab culture showed a similar pattern, with a maximum photosynthetic potential of $2.44 \text{ mg C/m}^3/\text{hr}$ at 0900, a minimum of $0.70 \text{ mg C/m}^3/\text{hr}$ at 2100, and a final value of $1.50 \text{ mg C/m}^3/\text{hr}$.

Assimilation ratios (Figure 32) calculated for the lab and control cultures showed similar diel variations with values decreasing from an initial maximum at 0900 to minimum values in the dark period (2100 hours) and the increasing until the end of the experiment.

As was found for the photosynthetic potential measurements, the assimilation ratios for the lab culture were consistently higher than those for the control.

A maximum ratio of 2.30 mg C/hr/mg chl-*a* occurred at 0900 in the control culture, with the minimum of 0.44 mg C/m³/hr at 2100. Values at the end of the experiment (0600 hours) had increased to 1.88 mg C/hr/mg chl-*a*. In the lab culture, a maximum of 2.54 mg C/hr/mg chl-*a* occurred at 0900, with a minimum at 2100 of 0.86 mg C/hr/mg chl-*a*. The final value for the lab culture was 1.85 mg C/hr/mg chl-*a*.

C. Lab Experiment B - Figures 33, 34, 35;
Table 7, Tables A14, A15.

During this experiment, the two cultures were preconditioned as with Experiment A. The light-dark cycle in the lab culture, however, was opposite to that in the control culture, with the light period for the former between 1800 and 0600 while the light period for the control was between 0600 and 1800.

The chlorophyll *a* concentration of both cultures (Figure 33) varied little over the sampling period, with similar values ranging between 0.85 and 1.34 mg/m³.

Photosynthetic potential (Figure 34) showed a diel variation for both cultures, with maximum values occurring in the light period and a minimum during the dark period.

FIGURE 33

Graph of Chlorophyll α Concentration, mg/m^3 , for Lab Culture (X — X) and Control Culture (O --- O), Experiment B.

FIGURE 34

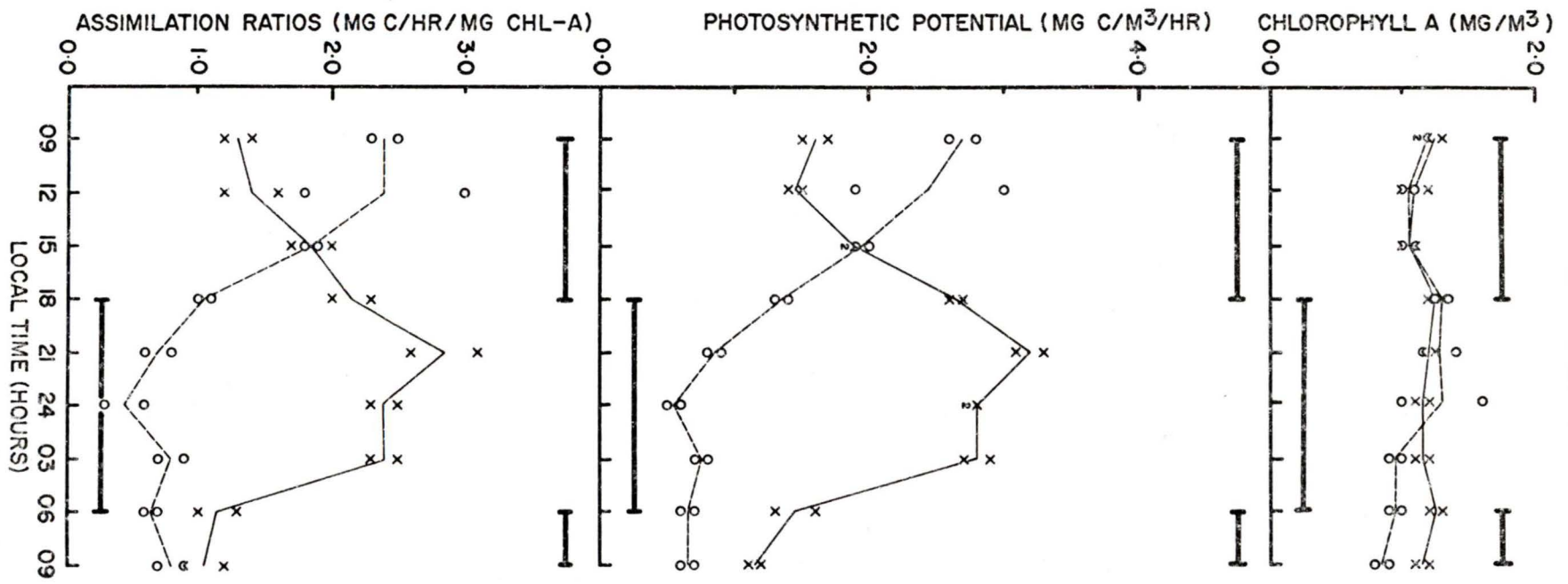
Graph of Photosynthetic Potential, $\text{mg C}/\text{m}^3/\text{hr}$, for Lab Culture (X — X) and Control Culture (O --- O), Experiment B.

FIGURE 35

Graph of Assimilation Ratios, $\text{mg C}/\text{hr}/\text{mg chl-}\alpha$, for Lab Culture (X — X) and Control Culture (O --- O), Experiment B.

Horizontal Dark Line Indicates the Period of No Measurable Light. The upper dark line refers to the lab culture, the lower one refers to the control culture.

EXPERIMENT B



In the control culture, a maximum of $2.69 \text{ mg C/m}^3/\text{hr}$ was measured at 0900, while the minimum occurred midway through the dark period, at 2400, with a value of $0.58 \text{ mg C/m}^3/\text{hr}$. There was little increase in the photosynthetic potential, however, during the remainder of the experiment ($0.77 \text{ mg C/m}^3/\text{hr}$ at 0900).

The lab culture reached a maximum value three hours after the start of the light period, with a value of $3.20 \text{ mg C/m}^3/\text{hr}$ at 2100. Minimum values occurred in the dark period, with a value of $1.47 \text{ mg C/m}^3/\text{hr}$ at the beginning of the experiment and $1.17 \text{ mg C/m}^3/\text{hr}$ at the end.

The assimilation ratios (Figure 35) for the two cultures showed a pattern similar to the photosynthetic potential, with a maximum during the light period and a minimum in the dark.

The control culture decreased from a maximum at 1200 of $2.37 \text{ mg C/hr/mg chl-}a$, to a minimum value midway through the dark period ($0.47 \text{ mg C/hr/mg chl-}a$ at 2400). There was a slight increase to the end of the experiment, with a value of $0.80 \text{ mg C/hr/mg chl-}a$ at 0900.

The assimilation ratios in the lab culture increased from a low value of $1.28 \text{ mg C/hr/mg chl-}a$ in the dark period (0900 hours), to a maximum three hours after the start of the light period ($2.89 \text{ mg C/hr/mg chl-}a$ at 2100 hours). Values then decreased until the next dark period to $1.04 \text{ mg C/hr/mg chl-}a$ at 0900.

DISCUSSION

Diel variations in phytoplankton have been reported in the literature for cell numbers, chlorophyll concentration and photosynthetic potential. Several theories have been given for these variations, and a summary is given in Table 1. Changes in phytoplankton populations (eg. as a result of grazing or water transport) changes in chlorophyll concentration within a cell, as well as an endogeneous mechanism controlling the photosynthetic uptake system, have all been suggested as reasons for the variations.

To date, however, there has been no work done in the field to isolate the cause of the variations, since phytoplankton biomass, chlorophyll concentration and photosynthetic potential, were never measured simultaneously. The data given in this discussion will attempt to clarify the factors responsible for the variations.

I. Inshore Waters - Surface, Station E-2

The total particulate volume, chlorophyll *a* concentration and photosynthetic potential at the surface all showed a diel variation, with maximum values during the day, decreasing to a minimum in the dark period (Figures 3 and 5). Of the three, however, only photosynthetic potential showed a regular, rhythmical variation. The time of the maximum and minimum values are summarized in Table 2.

During Days IV and V, both chlorophyll *a* and total particulate volume remained higher during the day, decreasing at the onset of the dark period. The time of the maximum had shifted on Days VI and VII, however, with the total volume and chlorophyll *a* increasing rapidly during the afternoon until the end of the light period. Values for the total particulate volume and chlorophyll *a* are similar to others reported for May and June in the same area (Parsons, 1969; Stephens *et al.*, 1969).

The change in the timing of the maxima for Days VI and VII, is undoubtedly due to the initiation of a phytoplankton bloom, which was not evident on Days IV and V. Cell division apparently took place around midday, increasing rapidly during the afternoon. Doubling times during these periods were short - in the order of six hours. This is faster than most reported cell division rates (Jitts *et al.*, 1964; Eppley and Sloan, 1965; 1966) but it is probable that this increase occurs only once every twenty-four or more hours. The data suggest a synchronized cell division time. Eppley *et al.* (1971a), reported periodic cell division in cultures of natural populations, but he had not found any report of synchronous division *in situ*, although he acknowledged its probable existence.

During the dark period both the total particulate volume and chlorophyll *a* concentration decreased. This night decrease is probably a result of zooplankton grazing, primarily by euphausiids.

Barraclough and Herlinveaux (1965) found that the deep-scattering layer in Saanich Inlet underwent diel variations existing near 100 meters during the day and rising to the surface at night. Their plankton samples indicated that the one of the principle zooplankton organisms associated with the layer was *Euphausia pacifica*. Hoos (1970) also found that *E. pacifica* was near the surface during the dark period (2400 hours).

E. pacifica has a well developed filter apparatus with many setae and barbs on the thoracic appendages and Nemoto (1967) has suggested that this is typical of a filter feeder. This conforms to personal observations of live euphausiids in the field, where many were seen with green gut contents. Parsons *et al* (1967) had found that *E. pacifica* in Saanich Inlet was able to feed on nanoplankton material in the size range 4-16 microns. This is similar to the size distribution of the particulate matter during this study (data not given) which was in the range 3-9 microns in diameter (this actually refers to particles having a volume equal to a sphere of those dimentions).

Unlike the biomass measurements of chlorophyll *a* and total particulate volume, the photosynthetic potential showed a more regular variation. The maximum values were always near midday (1100-1500 hours) while the minimum occurred at 0100 (Days IV, V, and VII) or between 2100 and 0100 (Day VI). The regularity of the

photosynthetic potential suggest mechanisms other than changes in biomass, and will be discussed subsequently.

A different pattern occurs if chlorophyll *a* and photosynthetic potential values are "normalized" for biomass changes. The times of the maxima and minima are summarized in Table 3. Although the total particulate volume includes all material in the water, including detritus, it has been assumed that the non-photosynthetic portion of the total would remain relatively constant during the sampling period. This method of measuring phytoplankton biomass has been used previously (Parsons *et al* 1967; Sheldon and Parson, 1967; Parsons, 1969; Evans and McGill, 1970) and the similarity between the chlorophyll *a* and the total volume curves, suggest that the variations are primarily due to phytoplankton.

It can be seen in Figures 4 and 6 that chlorophyll *a* per unit particulate volume did not vary greatly, and that the pattern was irregular. There is some suggestion that higher values are found during the dark period on Day V, VI and VII, but it cannot be stated whether the changes are significant.

Although chlorophyll synthesis is generally felt to occur in the light, Borograd (1962) has stated that dark synthesis can occur in several species of algae. This was suggested by the data of Yentsch and Scagel (1958) but most work with cultures of marine phytoplankton have shown chlorophyll synthesis to occur during the

light period (eg. Gibor and Meehan, 1961; Eppley and Coatsworth, 1966, Jorgensen, 1966 and Glooschenko, 1967).

The decrease during the light period may be due to photo-oxidation of the pigment as has been suggested by several authors (eg. Steemann Nielsen, 1949; 1962; Glooschenko, 1967).

A diel variation in total pigment per cell may account for variations in photosynthetic potential, but this possibility was not followed. However, changes in chlorophyll *a* has been shown to parallel chlorophyll *c*, (Glooschenko, 1967) or chlorophyll *c* and carotenoid pigments (Yentsch and Scagel, 1958; Jorgensen, 1966). Chlorophyll *a* is the only pigment which is able to transform light energy directly into chemical energy (Rabinovitch and Govindjee, 1969) which may be the reason that better correlation between C^{14} - uptake and chlorophyll *a* than with total pigments, has been reported (McAllister, *et al*, 1964; Anderson and Banse, 1965). It was thus assumed that the effect of the total plant pigment on the photosynthetic potential, would be reflected by the chlorophyll *a* measurements.

A rhythmical variation was found in the photosynthetic potential per particulate volume (Figures 4 and 6). Maximum values occurred in the morning, decreasing to a minimum at the beginning of the dark period, and increasing again before the next light period, (see Table 3). The secondary rise at the beginning of the dark period

on Day V cannot be explained. The curve, resembling a sine curve, is suggestive of some endogeneous rhythm, often found in nature (eg. Hastings, 1960; Pittendrigh, 1960; Bunning, 1964; Cumming and Wagner, 1968). Such a rhythm has been suggested for the variations found in photosynthetic potential for phytoplankton by Doty and Oguri (1957), Yentsch and Ryther (1957), Ryther *et al* (1958), Shimada (1958), Lorenzen (1963), McAllister (1963), and Newhouse *et al* (1967), although only Newhouse had accounted for changes in biomass. Diel rhythms in photosynthetic potential per cell have been reported in cultures of marine phytoplankton by Jorgensen (1966), Sweeney (1965), and Paasche (1968).

The actual mechanism for these rhythms has not been found but Jorgensen (1966) and Sweeney (1969) both found diel variations in photosynthetic enzymes which would affect the photosynthetic uptake of carbon. The low values during the dark period for photosynthetic potential suggest that some 'substance', such as an enzyme or enzyme-substrate was depleted during the previous light period and required a dark period for resynthesis.

One cause of the rhythms found in photosynthetic potential may be an endogeneous rhythm in chlorophyll content. This was found for an angiosperm (Mitrakos, 1963) and suggested by Steemann Nielsen and Jorgensen (1968). However, the chlorophyll α per particulate volume did not show a diel rhythm. In addition a diel variation in

the assimilation ratios, photosynthetic potential per unit of chlorophyll, was also found, (Figures 4 and 6), with a pattern similar to the photosynthetic potential/volume. The maxima occurred around midday, and the minima during the middle of the dark period (Table 3).

Similar rhythms in assimilation ratios (with day maxima and dark minima) have been reported by Shimada (1958), Lorenzen (1963), McAllister (1963), Newhouse *et al* (1967), Malone (1971), and Eppley *et al* (1971a). El-Sayed and Mandelli (1965) found the opposite relationship with higher assimilation ratios during the period of low light (a 24 hour day in the Weddell Sea) but attributed the decrease during the day to light injury of the cells.

It appears that the changes in photosynthetic potential are not a function of biomass changes or of the chlorophyll content of the cells.

It is also felt that these changes are not the direct result of nutrient, temperature, salinity, or light variations. During the study, nitrate values did not vary (Appendix I, Table A2), with concentrations well in excess. Because sampling was done early in the year (April), and since nitrate concentration was high, it is unlikely that the phytoplankton were nutrient limited.

There were not enough data points to indicate whether nitrate was assimilated in a diel fashion. However, in other studies with

natural populations, nitrate assimilation rates have been shown to vary (Goering *et al* 1964; Eppley *et al* 1970; Eppley *et al* 1971b), with an increase during the dark period. Eppley *et al* (1971b) suggested a subtle control mechanism such as an endogeneous rhythm, but no mention was made on whether this might be responsible for the variations in photosynthesis.

Temperature changes were not large over the period (Appendix I, Table A4) the greatest range occurring during Days VI and VII (8.3 - 10.2°C). In addition, the variations in temperature did not correspond to the variations in photosynthetic potential. Incubator temperature was kept constant at 8.0°C and the relatively small differences between the *in situ* temperature and incubator would probably not affect the organisms. The above suggests that temperature is neither the timing nor controlling factor in the photosynthetic rhythm. This is supported by the lab cultures where temperature was kept constant, and a rhythm persisted (see Section V of the Discussion). Sweeney (1969) showed that with *Gonyaulax polyedra*, the rhythms in photosynthetic potential were temperature independent.

Although salinity values varied (Appendix I, Table A5), these were random due to increased precipitation during part of the sampling period, and consequently not felt to be a factor in the photosynthetic rhythms. The lab cultures, kept at a constant

salinity (Section V) also showed a diel rhythm.

Incident light varies periodically and many authors feel that this may be the timing mechanism to which the photosynthetic potential rhythms are set (Hastings and Keynan, 1965). Light, however, is not the direct cause of the rhythm in this instance, as photosynthesis was measured at a constant light intensity. Furthermore, the changes in photosynthetic potential did not parallel the variation in light suggesting a more subtle mechanism involved. This rhythm was also found to persist in constant dim light in *Gonyaulax* (Hastings *et al* 1961), and in constant dark conditions during a laboratory experiment done at Station P (Section V).

The light intensity of the incubator was not felt to have affected the measurement of photosynthesis as it was less than maximum values for incident light. The long incubation period would offset any inhibition effect on samples collected during the dark period.

Excretion of dissolved organic matter has been reported by several authors (Nalewajko, 1966; Anderson and Zeutschel, 1970; Samuel *et al*, 1971; Thomas 1971) and probably occurred during the measurement of photosynthetic potential. Thomas (1971) however, suggested that the time of day would affect the particulate carbon retained more than the release of dissolved organic carbon. Furthermore, the above authors have suggested that the most important factor affecting excretion

FIGURE 36

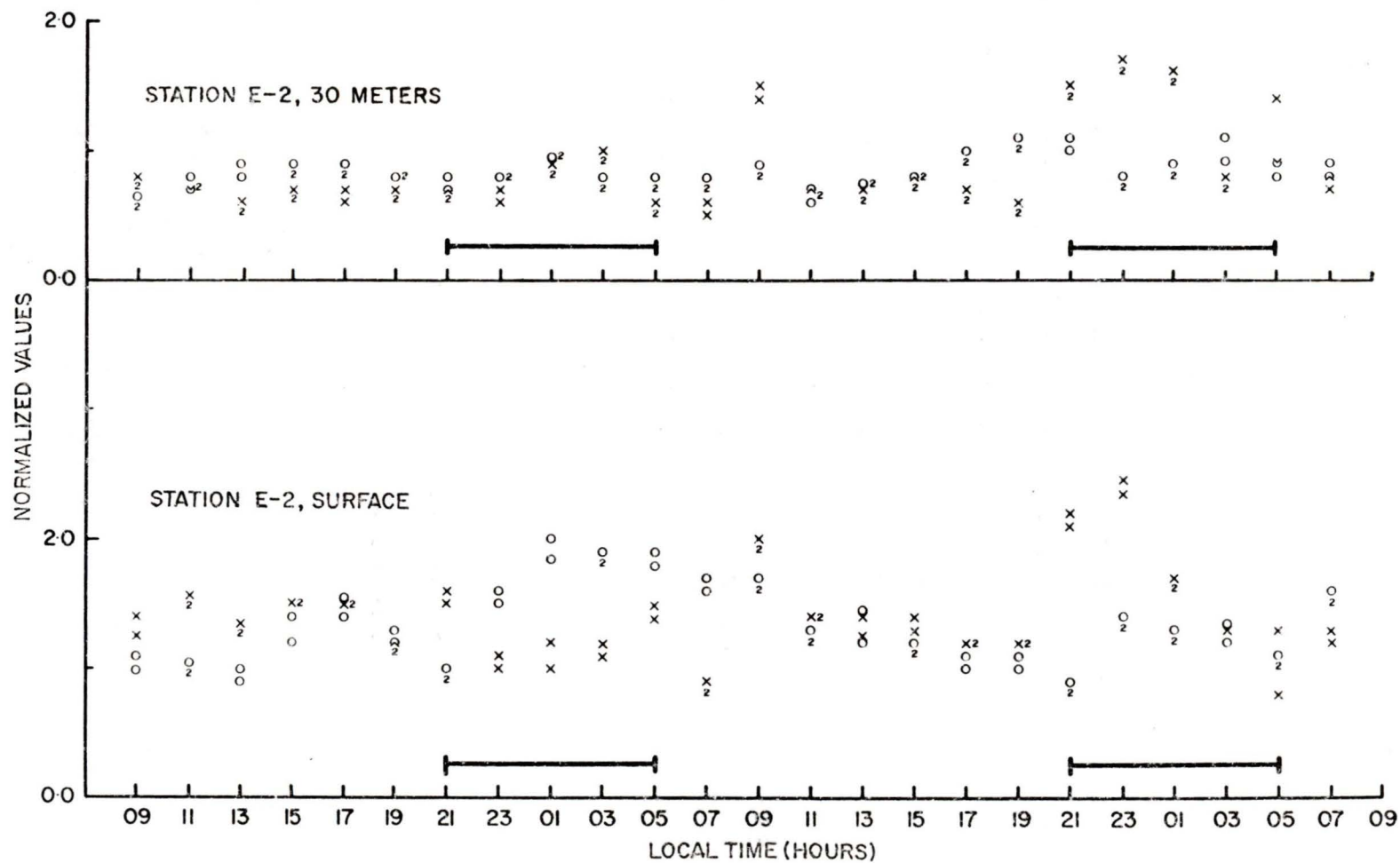
Below: Graph of Chlorophyll *a* Per Particulate
 Volume, $\text{mg}/\mu^3 \times 10^{-12}$, for Surface
 Samples, Days IV-VII. Day IV-V — X
 Day VI-VII - 0

FIGURE 37

Above: Graph of Chlorophyll *a* Per Particulate
 Volume, $\text{mg}/\mu^3 \times 10^{-12}$, at 30 meters,
 Days IV-VII. Day IV-V — X
 Day VI-VII - 0

Horizontal Dark Line Indicates the Period of No
 Measurable Light.

CHLOROPHYLL A RATIOS, DAYS IV-VII



was the physiological stress on the organisms. However, during the measurement of photosynthetic potential in this study, stress effects due to temperature, light intensity and nutrients, were felt to be minimal. It is assumed that although excretion is probably present, it is either constant or its variation is less than the variation in particulate carbon retained.

Although it was not possible to collect large numbers of replicate samples, it is felt that this can be compensated for by a replicate experiment in time. If similar patterns appear during these repeated trials, it lends credibility to any conclusions. In all, four, twenty-four hour time studies were done (Day IV to VII).

It can be seen that the changes in chlorophyll a per particulate volume (Figure 36) are small with no apparent diel rhythm. The photosynthetic potential per particulate volume (Figure 38) and assimilation ratios (Figure 39), however, both show similar diel rhythms on all four days, with maximum values during the day, decreasing to a minimum in the dark period, and increasing again before the next light period. This similarity is taken as evidence that the observed differences are real.

II. Inshore Waters - 30 Meters, Station E-2

The pronounced changes found at the surface in chlorophyll a , photosynthetic potential and total particulate volume, were not

FIGURE 38

Graph of Photosynthetic Potential Per Particulate Volume,
mg C/hr/ $\mu^3 \times 10^{-12}$, for Surface Samples, Days IV-VII.

Day IV - V — X
Day V - VII - 0

Horizontal Dark Line Indicates the Period of No Measurable
Light.

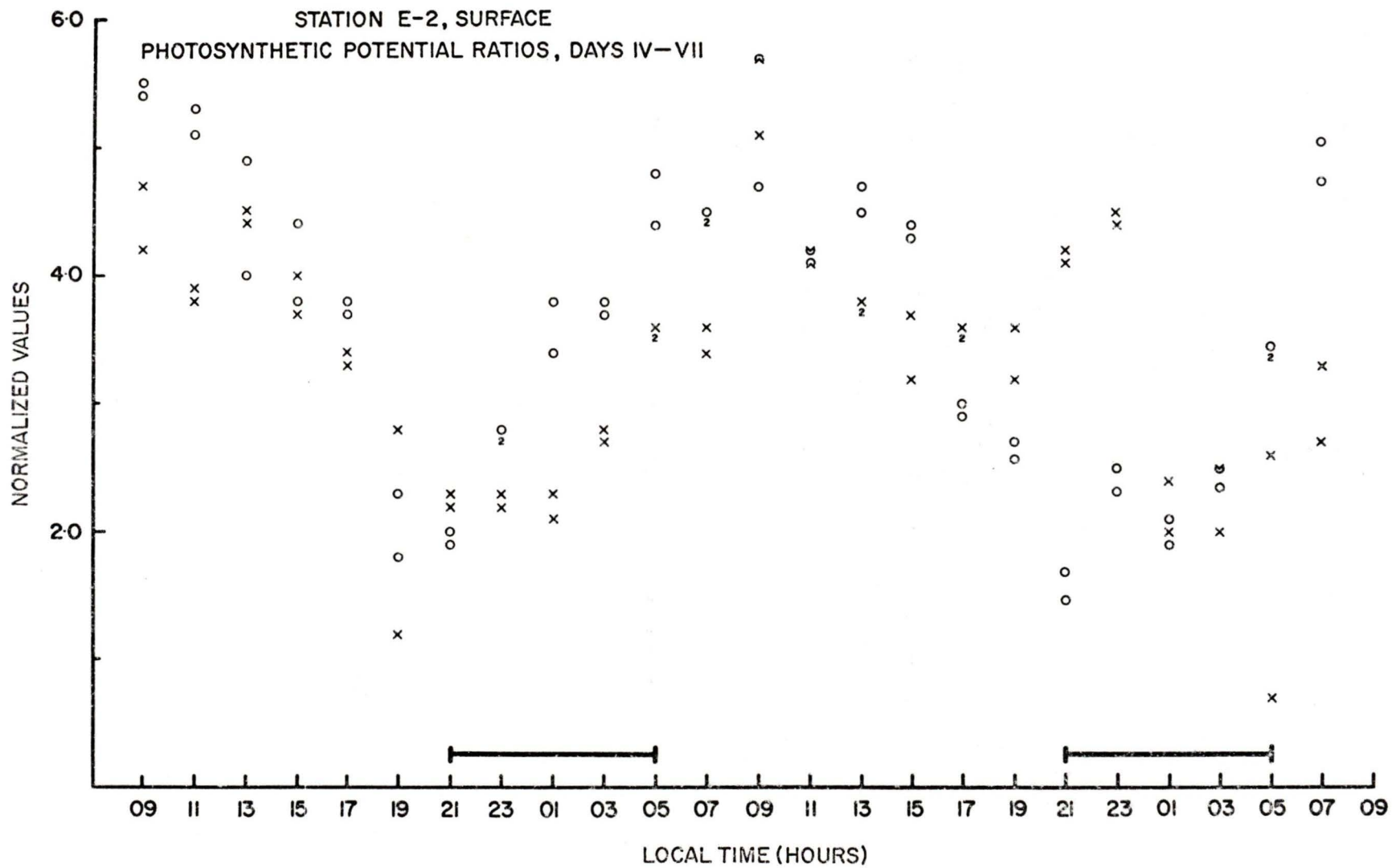
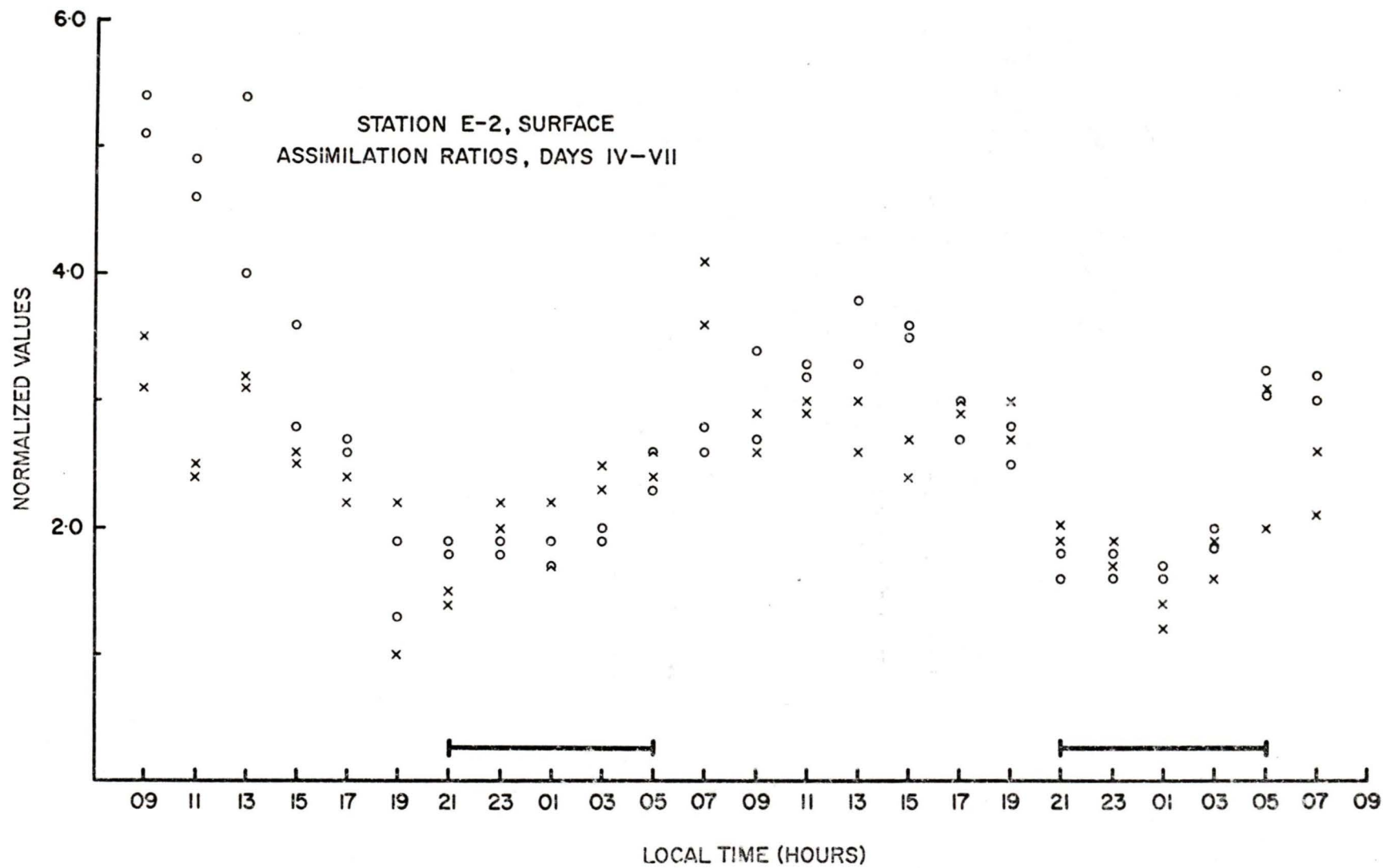


FIGURE 39

Graph of Assimilation Ratios, mg C/hr/mg chl- α ,
for Surface Samples, Days IV-VII.

Day IV - V — X
Day VI - VII - O

Horizontal Dark Line Indicates the Period of No
Measurable Light.



apparent at 30 meters (Figures 7 and 9; Table 4).

Chlorophyll *a* concentrations remained essentially unchanged during Days IV to VI, with only a slight increase occurring during Day VII. Although values were lower than at the surface, they were measurable, and comparable to other data collected in June for Saanich Inlet and surrounding waters (Stephens *et al* 1969).

Photosynthetic potential also showed little variation during Days IV and V, but there is an indication of a slight rhythm during Days VI and VII, with minimum values occurring during the night.

Total particulate volume did not show any periodic variation, and except for a decrease during the dark period on Day V, values were fairly constant. Like the surface population, the organisms fall into the nanoplankton category of Dussard, reported by Shelden and Parsons (1967), with most of the population between 4 and 16 microns in diameter. The total particulate volume at 30 meters is similar to the May nanoplankton concentrations at 10 meters, given in Parsons (1969).

Overall, the 30-meter measurements were considerably less than found at the surface, with differences between the two depths increasing during Days VI and VII as a result of the nanoplankton bloom. It was noted however, that the differences were less during the dark period, when grazing factors reduced the surface biomass.

The smaller population at 30 meters could be due to either minimal or constant 24-hour grazing, with the deeper zooplankton migrating through this region to the surface at night. Unfortunately, the variations in the zooplankton population at 30 meters are not known. However, the data of Hoos (1971) shows a considerable population of *Euphausia pacifica* at 25 meters at midnight, but not at 50 meters, while Barraclough and Herlinveaux (1965) found that the deep-scattering layer generally rose to near the surface during the dark.

The light intensity at 30 meters was estimated from subsurface light measurements, which were done on Day IV and Day VI (see Appendix I, Table A10). The extinction coefficients for the two days were 0.203 and 0.204 respectively.

Light may be a limiting factor for phytoplankton growth at this depth, which could explain the lower biomass measurements. The euphotic zone is often thought to be down to the depth of 1% of the surface light, near the compensation depth (Strickland, 1965). The compensation depth during these sampling periods was estimated at 23-25 meters, with the 30 meter sample receiving about 0.2% of the surface light (between .0005 and .001 ly/min). Although viable phytoplankton have been found at depths greater than 0.1% light, associated with the chlorophyll maximum layer (Anderson, 1969), it

is not known whether the low biomass at 30 meters is a direct result of the low light values.

When the chlorophyll *a* and photosynthetic uptake values were normalized for biomass changes, there were some periodic variations found in the photosynthetic potential and assimilation ratios, but not for chlorophyll *a* (Figures 8 and 10; Table 5).

Chlorophyll *a* per particulate volume did not show much change except for an increase during the dark period on Day V. This dark increase is also suggested for curves during Day IV and VII, but not for Day VI. If these increases are real, it would reflect chlorophyll synthesis as mentioned previously for the surface samples (page 90). However, the decrease in values during the day cannot be explained, as photo-oxidation is unlikely to occur at that depth. Some endogeneous rhythm in chlorophyll *a* concentration may be responsible, although the phase is opposite to that expected (ie. higher values during the day).

Diel changes in chlorophyll per cell for low light intensities (.0001 - .0004 ly/min) were reported by Glooschenko (1967) for *Skeletonema costatum*. Although the light intensities are similar to those at 30 meters during Days IV-VII, his results were reversed, with increased chlorophyll per cell during the day. He had also found increases *in situ* in chlorophyll *a* and *c*, at 50 meters, at several oceanic stations, and although his measurements were not

corrected for biomass changes, he suggested the variations were largely intracellular. Yentsch and Scagel (1958), however, found no variations in pigment per cell in samples collected at 25 meters.

Photosynthetic potential per particulate volume variations were not clear at 30 meters, particularly during Days IV and V where an increase occurred during the dark period. Values for Days VI and VII showed similar variations as found at the surface but the magnitude of the changes at 30 meters, were much less (see Figures 8 and 10; Table 4).

There has been no literature found in which diel changes in photosynthetic potential were followed at lower depths. Many authors have hypothesized that phytoplankton living near the bottom of the euphotic zone had increased chlorophyll content per cell, as a mechanism for increasing photosynthesis (eg. Steemann Nielsen and Hansen, 1959; Yentsch and Lee, 1966; Steemann Nielsen and Jorgensen, 1968; Anderson, 1969), but this was for over long periods of time and no mention was made of daily variations.

Assimilation ratios (Figures 8 and 10) did not show any consistent variation during Days IV and V, although there is a possibility of a decrease during the dark period on Day V. The data for Days VI and VII were similar to photosynthetic potential/volume ratios, with maximum values during the day, and decreasing during the dark period (Table 4). The variations were not as great as

those found in the surface samples. Curl and Small (1965) on the other hand found little change in assimilation ratios at depths near the 1% light level.

When the data for both studies, Days IV and V and Days VI and VII are plotted, it can be seen in Figure 37 that there was no pattern to the variations in chlorophyll a per particulate volume. However, there was an indication of a rhythm in photosynthetic potential (Figure 40) and assimilation ratios (Figure 41), with maxima during the day and minima in the dark period. This rhythm is similar to the pattern found in the surface samples but the amplitude at 30 meters was considerably less. The lack of a rhythm in chlorophyll a /volume plus the similarity between the photosynthetic potential/volume and assimilation ratios, indicates that the rhythm exhibited by the photosynthetic potential is independent of chlorophyll a .

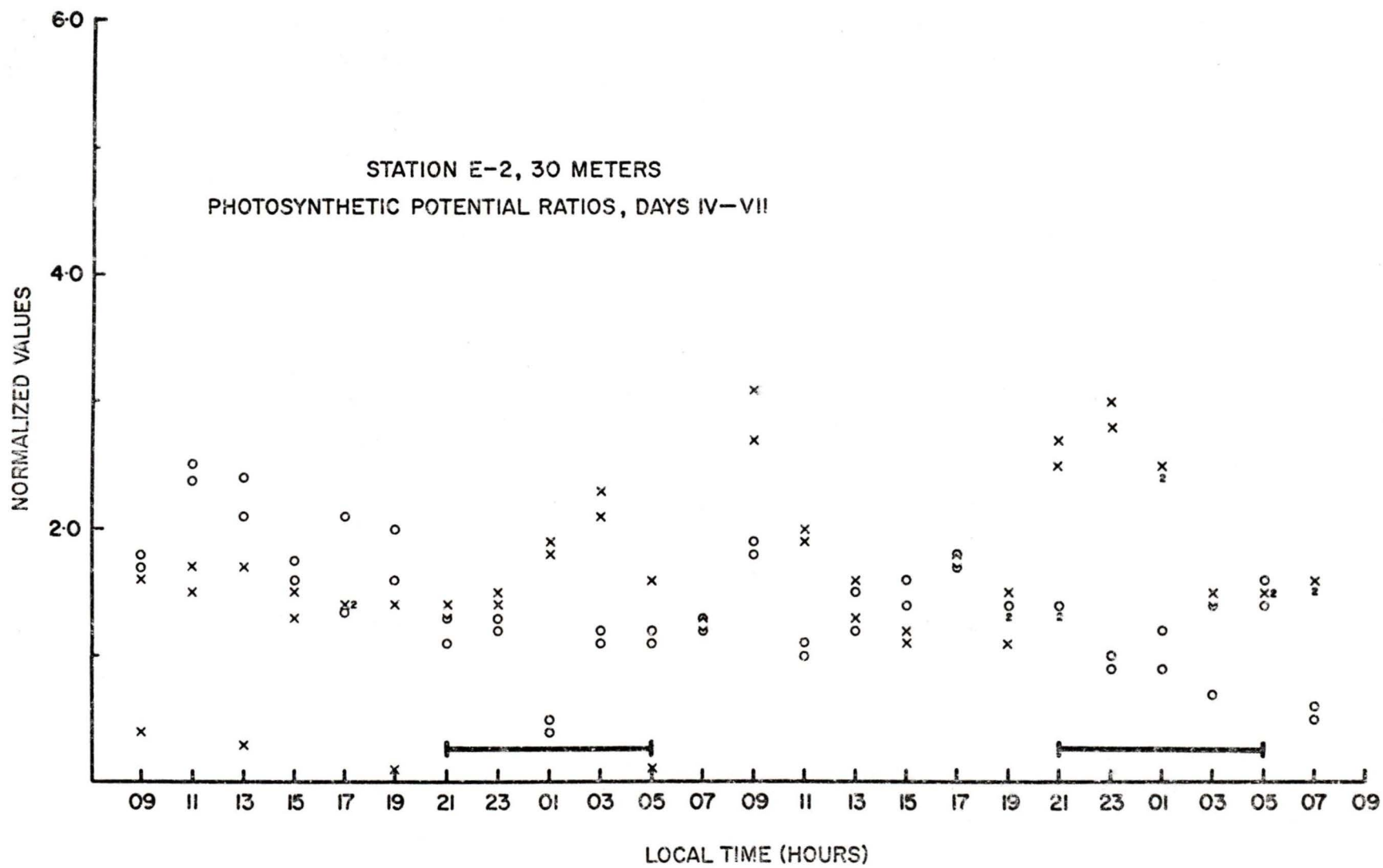
Temperature, salinity, or nutrient concentration, are also not believed to be the cause of the variations in photosynthetic potential. Temperature of the incubator was kept at 8^oC, which was the same temperature as found at 30 meters (Table A4), while constant values for salinity (Table A6) indicated that the same water mass was sampled each time. Nitrates (Table A2) also did not show any diel periodicity, with concentrations remaining quite high throughout the sample period. Light was not felt to be directly causing the

FIGURE 40

Graph of Photosynthetic Potential Per Particulate
Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$, at 30 meters, Days IV-VII.

Day IV - V — X
Day VI - VII - 0

Horizontal Dark Line Indicates Periods of No Measurable
Light.



light-dark cycle, (Sweeney, 1960; Hastings *et al* 1961; McMurray and Hastings, 1972).

Sweeney (1965) also showed that these changes were not due to periodic changes in the photosystem II and suggested that it did not occur in the photosystem I (see Rabinowitch and Govindjee, 1969). Jorgensen (1966) suggested that the variations in photosynthetic potential were due to changes in photosynthetic enzymes, although he did not state which one(s). In a later paper, Sweeney (1969) showed that the activity of ribulose diphosphate carboxylase (the first enzyme involved in the dark reaction uptake of CO₂) underwent periodic variations similar in both phase and magnitude of change, to the photosynthetic capacity. Furthermore, it was a change in enzyme activity which was responsible for the observed differences, and not changes in substrate concentration (ribulose diphosphate) or to bicarbonate concentration.

A variation in the enzyme activity was also found in luciferase (Bode, as was reported by Sweeney, 1969), which presumably regulates the diel periodicity in luminescence, found in *Gonyaulax* (Sweeney and Hastings, 1962). Diel variations in nitrate and nitrite uptake rates have also been shown to be regulated by changes in enzyme activity (Eppley *et al* 1971b).

Hastings and Keynan (1965) summarized work on the possible mechanism involved in photosynthetic uptake rhythms in *Gonyaulax*,

Salinity was not the cause of the observed rhythms, since values either remained constant, or underwent random changes due to precipitation. In the lab experiments, salinity was constant, while variations in photosynthetic potential were still present.

Nutrients were also not responsible for the variations in photosynthetic potential. Diel variations in nutrient concentrations have been recorded (Ryther *et al*, 1961) but were not found during this study. The lab experiments showed a steady decrease in nitrate, with a rhythm in the photosynthetic potential still present. Uptake rates of nitrate, nitrite and phosphate has been shown to undergo diel variations (Goering *et al* 1964; Eppley *et al* 1970; Eppley *et al* 1971b) and to have the same phase relationships as photosynthetic potential. Uptake rates were not followed in this study and consequently it is not known whether variations in photosynthetic potential were a result of changes in nutrient assimilation, or whether both are expressions of some common "biological clock". The latter, however, is suspected.

In *Gonyaulax polyedra*, the mechanisms involved in the rhythm of photosynthetic potential have been studied by B.M. Sweeney, J.W. Hastings, and co-workers. It has been shown by them that the rhythmicity in photosynthetic potential is persistent for several days in dim continuous light, is relatively temperature independent, and that the rhythm pattern can be shifted by changes in the

to show this rhythm when normalized for changes in biomass or chlorophyll *a* concentration. Furthermore, this rhythm was observed in all the environments studied - inshore waters at the surface and at 30 meters (although the rhythm amplitude is dampened at the lower depth), on two different occasions in time and space for surface open ocean waters (Station E-1 and Station P) and in cultures of natural populations of oceanic phytoplankton. This rhythm was also shown, in these cultures, to continue under conditions of constant dark. In addition, the timing of the photosynthetic potential rhythms, could be shifted by a change in the light-dark cycle.

The rhythms were not the result of daily temperature changes. *In situ* temperature variations were slight (at 30 meters they did not change at all) and the magnitude was always less than 4°C. Furthermore, changes in photosynthetic potential occurred when there was no corresponding change in temperature. In addition, a rhythm was found at 30 meters, although the temperature was constant. In the laboratory experiments, where temperature was kept constant, a definite rhythm in photosynthetic potential remained. This agrees with the work of Sweeney (1960), in which the periodic variations in photosynthetic variation were found to be relatively independent of temperature.

continuous dim light, cell division, photosynthetic potential and luminescence all had a diel rhythm persisting for several days. These rhythms were found to also be shifted in timing, by the exposure to a six hour dark period (McMurray and Hastings, 1972).

VII. The Possibility of Circadian Rhythms

In Marine Phytoplankton

It has been found during the course of this study, that the measurements of chlorophyll a concentration and total particulate volume may or may not show a diel periodicity. Variations were most noticeable in a confined, inshore environment, where the mixing processes were slight, and where there is a very definite migration of zooplankton to the surface at night. These variations were less apparent at 30 meters in the inshore location, and at both surface and 30 meters in the open ocean.

The variation in chlorophyll a concentration was attributed to changes in the biomass (thought to be primarily due to grazing) as seen when the chlorophyll a per particulate volume is calculated. This value remained fairly constant during most of the investigations, except for a slight increase during the dark period found on several occasions. Chlorophyll a synthesis during the dark was suggested for the cause of the increases.

On the other hand, photosynthetic potential, while showing a definite diel periodicity in population measurements, also continued

decreasing to a minimum near the initiation of the dark period, and increasing again during the dark. The failure of the photosynthetic potential and assimilation ratios values to reach the level of the previous light period for Experiment A and B, may be a result of nutrient depletion as measurable nitrate decreased to near zero during the study (Appendix I, Table A7). Experiment C, which had nutrients added, had photosynthetic potential values at the end of the experiment similar to initial values. Unfortunately, it is not known what the limiting nutrient might be.

A diel variation in nitrate was not found and thus is not felt to be the regulating mechanism of the rhythms in photosynthetic potential. During all experiments, the temperature was kept constant, as was the light intensity (except during the dark) and consequently these factors were not thought to cause the variations.

Experiments A and C were designed to show the continuation of the photosynthetic rhythm in a continuous dark period. This was only apparent in Experiment C, although the maximum and minimum values of photosynthetic potential and assimilation ratios for Experiment A occurred at the same time.

During Experiment B, after 3 days of preconditioning, the rhythm of the photosynthetic potential was switched to correspond to a new light-dark regime. This has also been found in studies with *Gonyaulax polyedra* (Sweeney, 1969). She showed that in cultures with

During Experiment B, the light cycle was set so that the lab culture had a light-dark cycle exactly opposite to the control culture.

There was no change in the chlorophyll *a* concentration throughout the experiment, with both cultures showing similar values (Figure 33).

Photosynthetic potential (Figure 34; Table 7) had a definite diel variation in both the lab and control cultures, with maximum values in the first part of the light period, and a minimum during the dark period. The control culture, however, did not show much increase during the dark period.

Assimilation ratios were similar (Figure 35; Table 7). Both cultures had maximum values during the light period, decreasing in the latter part of the light period to a minimum during the dark period. There was some increase again in the ratios during the dark period, but this was less in the control culture.

The changes in photosynthetic potential and assimilation ratios found during the laboratory experiments suggest periodic changes in the photosynthetic mechanism. The chlorophyll *a* concentration did not vary in any periodic manner, and the changes in assimilation ratios suggest that the photosynthetic rhythm found, was independent of variations in the chlorophyll *a* concentration within a cell.

The timing of the rhythm found in the experiments was similar to those found *in situ* at Station P, with morning or midday maxima,

A diel variation in assimilation ratios was found in the control culture for both Experiment A and C, with maxima at the beginning of the light cycle, and minima just prior to the dark period (Figures 31 and 32; Table 7). Both experiments showed a subsequent increase during the dark period. The lab culture in Experiment A was erratic, but maximum and minimum values corresponded to those in the control culture. During Experiment C, the assimilation ratios for the lab culture paralleled values for the control culture. On both occasions, however, the lab values were greater than found for the control culture.

The higher photosynthetic potential measured in the lab cultures is surprising, since in both experiments the chlorophyll α concentration for the control cultures were equal to, or greater than in the lab culture. The higher assimilation ratios indicate a greater efficiency in the photosynthetic uptake per unit of chlorophyll α . Yentsch and Reichert (1963) found that oxygen evolution per unit of chlorophyll α at light saturation increased during the dark period reaching a maximum after 24 hours of darkness.

It has been previously suggested (page 92) that some prerequisite or 'substance', required for the photosynthetic uptake of carbon, may be built up during the dark. The lab culture, kept in continuous dark, would then have relatively more of this unknown element than the control culture.

decrease in chlorophyll relative to the control culture. However, this does not explain the increases in the dark which occurred in both cultures. Dark synthesis of chlorophyll *a* has been suggested earlier in the thesis (page 90), and may be occurring here as well. More likely, the increases during the experiments are a result of cell division, while grazing by microzooplankton, not removed by the plankton netting (100 - micron mesh), could account for the decreases observed.

The control cultures of Experiment A and C both showed a diel variation in photosynthetic potential (Figures 29 and 30; Table 7). These values decreased during the light period to a minimum either just prior to the dark period (Experiment A) or just after its initiation (Experiment C). An increase during the dark period was found in both studies, but only Experiment C values reached a level comparable to the start of the sampling.

The lab culture for Experiment A did not show any regular variation, except that the maximum occurred in the first part of the light period, and the minimum corresponded to the minimum of the control culture. The results from Experiment C were different, with the lab culture having a rhythm in photosynthetic potential identical to the control culture. In both experiments, the lab cultures had higher photosynthetic potential than in the control.

diel variations in photosynthetic potential remained during a continuous dark period, and whether the phase of the rhythm could be shifted by a change in the light-dark cycle.

In Experiments A and C, both control and lab cultures were pre-conditioned for three days on a 12:12-hour light-dark cycle. After the dark period of the third day, the lights in the lab culture were kept off.

During Experiment A, the chlorophyll *a* concentration increased continuously throughout the sampling period with the control culture showing consistently higher values (Figures 27). However, the increase in chlorophyll *a* was not as great during Experiment C. During that experiment, values for the lab and control culture were similar until midway through the sampling period, after which the control culture showed a higher concentration of chlorophyll *a* (Figure 28). There was no indication of a diel variation in either experiment.

It is not known whether these changes were a result of population changes, or whether chlorophyll *a* per cell was changing as well. Chlorophyll *a* is said to require light for synthesis from protochlorophyll *a* (Virgin, 1958; 1964) and the continuous dark treatment of lab cultures could have resulted in a

Nitrate values (Appendix I, Table A8) were always high, suggesting, as was concluded by McAllister *et al* (1960) for the same location, that nutrients were not limiting. There was no rhythmical variation in nitrate values. Light, as was explained for Stations E-1 and E-2, in the previous sections, was felt not to be the direct cause of the rhythm.

The diel variations in chlorophyll *a* and photosynthetic potential may be caused by changes in biomass, such as grazing or water transport. This has been suggested as a partial cause at Station P by McAllister (1963). However, it has been shown for the oceanic waters at Station E-1, and for the samples collected in Saanich Inlet, Station E-2, (Sections I-III), that chlorophyll *a* per particulate volume varied to a much lower degree than did the photosynthetic potential per particulate volume. This fact, plus the similarity in pattern between the photosynthetic potential and assimilation ratios at Station P, support the conclusion that the variations are independent of biomass changes and of chlorophyll variations within a cell, and are part of some diel rhythm, such as a biological clock, affecting the photosynthetic mechanism.

VI. Lab Experiments

The lab experiments were conducted on natural populations collected at Ocean Station P, and were designed to determine whether

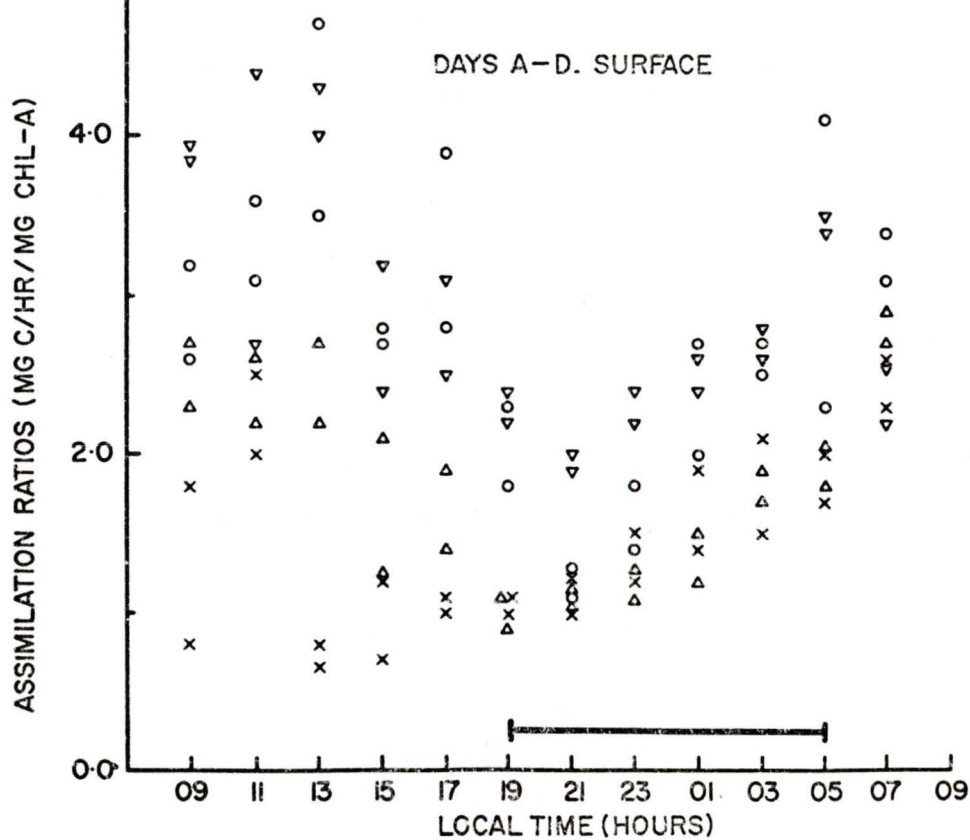
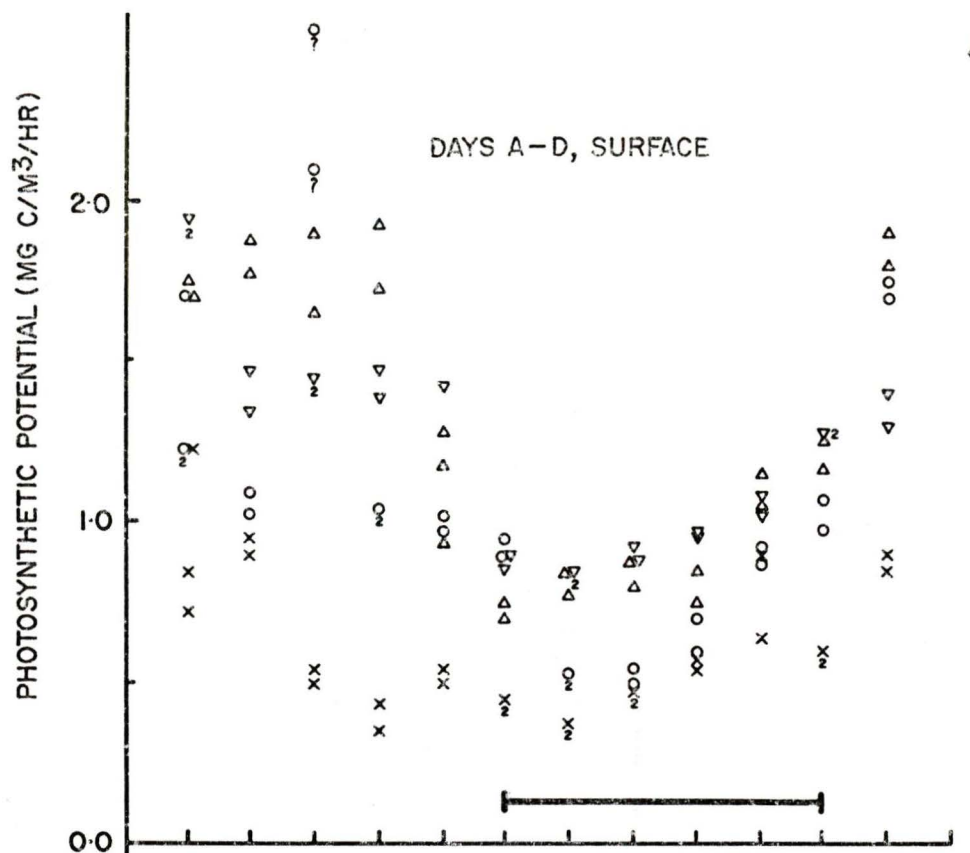


FIGURE 51

Graph of Photosynthetic Potential, $\text{mg C/m}^3/\text{hr}$,
for Surface Samples, Days A-D.

Day A - X
Day B - O
Day C - Δ
Day D - ∇

FIGURE 52

Graph of Assimilation Ratios, $\text{mg C/hr/mg chl-}a$,
for Surface Samples, Days A-D.

Day A - X
Day B - O
Day C - Δ
Day D - ∇

Horizontal Dark Line Indicates the Period of No
Measurable Light.

light intensities, over a 24-hour period. Steemann Nielsen and Hansen (1959) however, have suggested a greater efficiency for surface plankton relative to deeper samples on the basis of increased enzymes for the surface population.

The photosynthetic potential for the surface samples were measured on four different occasions (Days A-D) and are shown in Figure 51. A similar rhythm was found on all four days, with maximum values during the morning and a minimum just prior to the dark period (2100 hours). All days showed a subsequent increase during the dark period to a value near that measured the previous morning. The assimilation ratios (Figure 52) showed a similar pattern.

The diel rhythms found for the photosynthetic potential and assimilation ratios are nearly identical to those reported by McAllister (1963). He found at the same station, a maximum at 1000 and a minimum at 2200. The repeatability of the results with respect to the different days, suggests that the phenomenon is real, particularly when McAllister's data, collected in the summer of 1961, is compared to those collected during this study, in the summer of 1969.

Temperature, salinity and nutrients were not felt to be the cause of the observed variations. Temperature varied little (Appendix I, Table A9) and while salinity was not measured during the study it was noted that day to day salinity changes were slight.

the two depths at Station E-1 is attributed to the mixed nature of the water column).

The lower efficiency in the photosynthetic uptake mechanism during the dark period may be due to the depletion of some 'substance' such as an enzyme or enzyme substrate, or enzyme activity, which is depleted during the course of the light period, requiring resynthesis during the dark period.

Because the efficiency at the surface during the dark period was close to the efficiency at 30 meters there is a possibility that the amount of light available to the organism during its past history in some way affects the photosynthetic mechanism. The 30-meter samples, because of the low light available, would be unable to produce as much of the above mentioned 'substance' as would the surface samples, and hence the lower photosynthetic potential per unit of chlorophyll a . During the dark period, the surface efficiency decreases due to the depletion of the 'substance' but because of the past history of the cell (ie. exposed to higher light intensities) it is able to resynthesize more of this unknown. The synthesis of this substance may be regulated by some biological clock mechanism, and is discussed more completely in Section VII of the discussion.

Unfortunately, there has been no literature found for the measurement of assimilation ratios in phytoplankton grown at different

The differences in assimilation ratios between the surface and 30 meters are similar to those found for photosynthetic potential. Values measured during the surface minima were closer to the 30 meter values than at other times of the sampling period.

There is the possibility of light inhibition from the incubator in the 30 meter samples during the photosynthetic uptake measurement. Light at 30 meters was near 1% of the surface light (a maximum of 0.002 ly/min) for Day C and 6% on Day D (a maximum of 0.008 ly/min), compared to the incubator light of 0.026 ly/min (see Appendix I; Table A10). However, it was concluded that inhibition over the four hour incubation period was minimal in studies done in Saanich Inlet (Section II of the discussion), and it is felt that the relatively low light of the incubator (less than the observed maxima for incident light) would not affect the photosynthetic uptake to any large degree.

The efficiency of the photosynthetic mechanism, as reflected by the assimilation ratios, has been shown to be greater at the surface than at 30 meters, but the differences between the two depths were less during the time of the surface minima. A similar phenomena was found in Saanich Inlet (Station E-2) during Day VI and VII, with a suggestion of it occurring on Days IV and V as well (see Section II of the discussion). (The similarity between

the opposite, with the 30-meter samples having higher values (Figure 22).

For the surface samples, both Days C and D showed a higher chlorophyll *a* concentration in the afternoon, followed by a slight decrease towards the dark period (Table 6). This is similar to Days A and B but again caution is required due to the low chlorophyll concentrations. As was suggested previously, grazing effects plus possible chlorophyll synthesis could account for the patterns found.

Photosynthetic potential showed a definite diel variation at the surface for both Days C and D (Figures 23 and 24; Table 6) with maximum values measured in the morning. Values decreased during the late afternoon to a minimum by the start of the dark period, with subsequent increases during the night. At 30 meters, the photosynthetic potential was much lower, but during Day D, there is a suggestion of a variation similar to the surface samples, although the amplitude of the rhythm was much smaller. Differences between the surface and 30-meter samples were found to be less during the dark period.

The assimilation ratios also showed a diel variation (Figures 25 and 26; Table 6). Maximum values were measured near midday decreasing to a minimum at the end of the light period (1900 hours - Day C) or beginning of the dark period (2100 hours - Day D). Values then increased again during the dark period.

It is not known what factors were affecting the chlorophyll *a* concentration in this study. Earlier in this thesis, the chlorophyll *a* per particulate volume was shown to be relatively constant, and that changes in chlorophyll *a* concentration were due mostly to changes in biomass.

Photosynthetic potential showed a diel variation, although the pattern was not exactly symmetrical between the two days (Table 6). Maximum values were found in the morning, and decreased to the minimum either in the late afternoon (Day A) or at the beginning of the light period (Day B). On both days, however, subsequent increases did not occur until the dark period.

Assimilation ratios also showed a diel variation (Figures 19 and 20; Table 6) similar to but not symmetrical with, photosynthetic potential. Lowest values on Day A were reached in the afternoon, after a morning maximum but did not show any increase until the dark period. Day B decreased from a midday maximum to a minimum in the dark period, and then increased again. On both days the dark period increase in assimilation ratios occurred at 2100 hours.

Samples for both the surface and 30 meters were collected on Days C and D. During Day C, the 30-meter sampling was terminated at 2300 hours, but the data obtained indicated only slightly higher chlorophyll concentrations at the surface (Figure 21). Day D, showed

groups for either chlorophyll *a* concentration (Figures 15 and 16) or in photosynthetic potential (Figures 17 and 18). This is not unexpected as the pore size of the netting used for separation (44 microns) was quite large, and would allow the bulk of the particles to pass through. The small size of the phytoplankton has been reported before, for the same location (McAllister, *et al* 1960). The plankton classification of Dussard (given in Sheldon and Parsons, 1967) places nanoplankton between 4 and 20 microns. In an inshore location such as Saanich Inlet, the 44-micron netting, on occasion, would separate out many organisms, particularly chain diatoms such as *Skeletonema* sp. and *Chaetoceros* sp. However, microscopic examination of samples at Station P showed only single celled diatoms such as *Coscinodiscus* sp. and *Nitzschia* sp. plus unidentified flagellates - all less than 20 microns in diameter or length.

Chlorophyll *a* concentration did not vary much during Day A, but on Day B, a maximum in the morning and afternoon followed by a decrease in the dark period, was noted (Table 6). This same pattern was also found by McAllister (1963) at the same location, but as he pointed out, the changes are close to the limit of precision of the analytical procedure. McAllister's suggestion was that grazing could account for the decrease at night, while pigment synthesis (or cell division) could account for the increases in the afternoon and morning.

an endogeneous rhythm affecting the photosynthetic mechanism, but not caused by changes in chlorophyll α . As was found for the inshore waters and the surface oceanic waters, temperature, salinity and nutrients (Appendix I, Tables A3, A5 and A1, respectively) did not show any pattern which could be the cause of the variations measured.

The amount of light available at 30 meters (0.001 - 0.002 ly/min) was calculated to be 0.8% of the surface light which was considerably less than in the incubator (.052 ly/min) (see Appendix I, Table A10). However, it is felt that light inhibition during the measurement of the photosynthetic uptake was not significant, as the phytoplankton would normally be exposed to a wide range of light intensities because of water mixing.

Although incident light shows a general daily variation, the changes in the light intensity at 30 meters were varied and slight. Because changes in photosynthetic potential occurred at times when the incident light was not changing, it is believed that the rhythms report are not directly caused by variations in light. This is similar to conclusions made for inshore and surface oceanic waters (Sections I-III).

V. Oceanic Waters - Ocean Station P

During the studies of total and nanoplankton populations at the surface, there were no measurable differences between the two

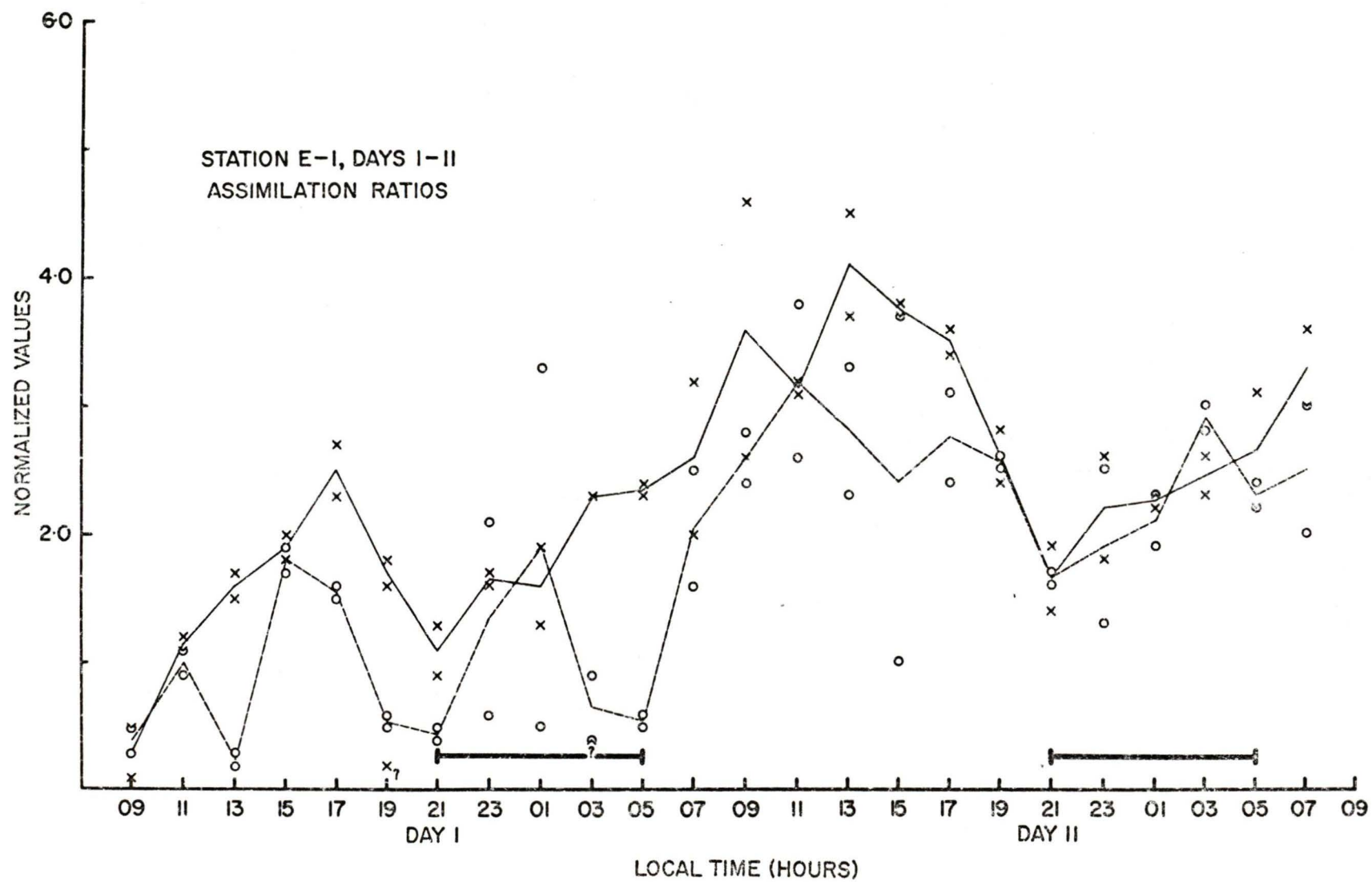


FIGURE 50

Graph of Assimilation Ratios, mg C/hr/mg chl-*a*,
at the Surface (X — X) and at 30 meters
(O --- O), Days I and II.

Horizontal Dark Line Indicates the Period of
No Measurable Light.

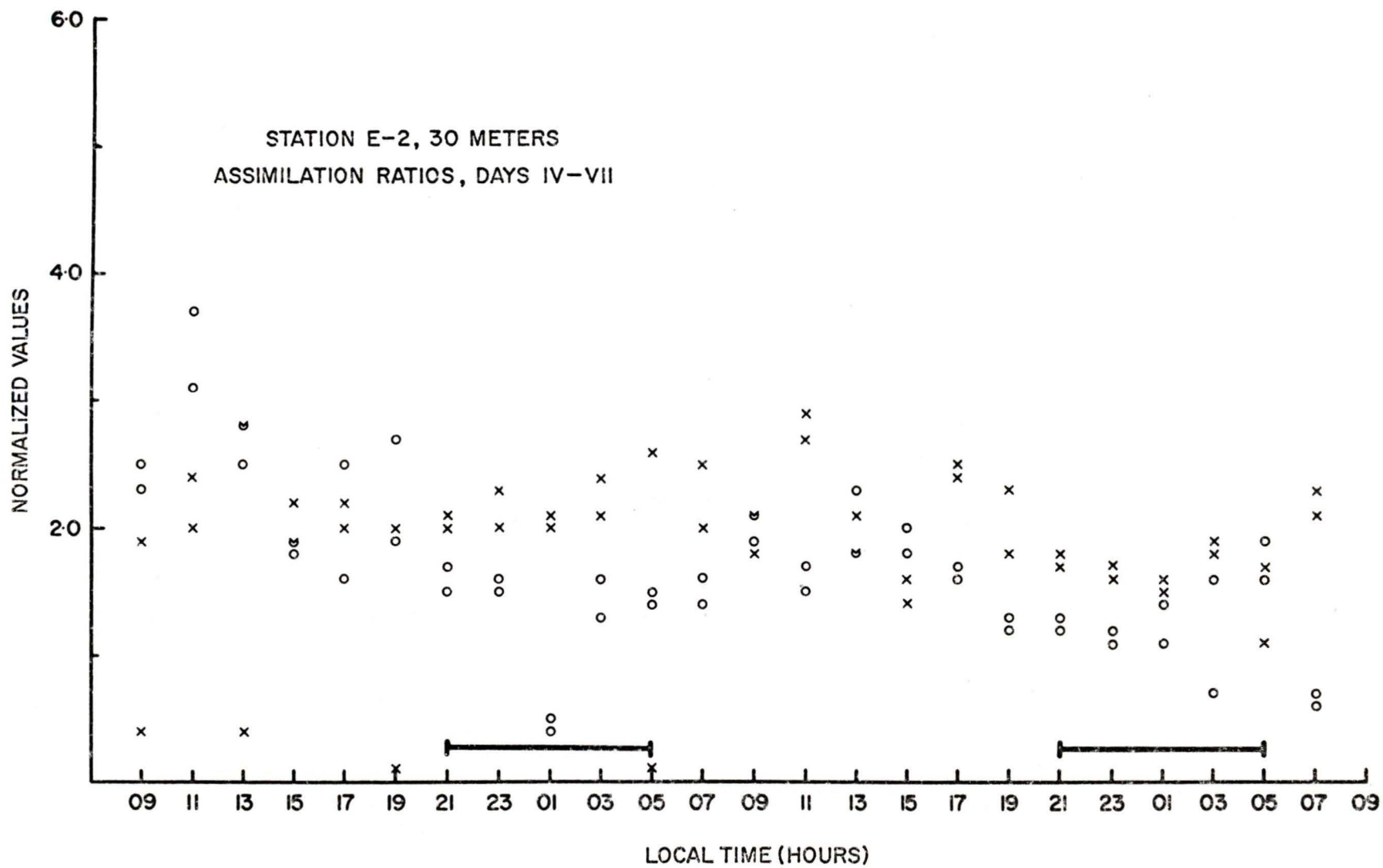
FIGURE 41

Graph of Assimilation Ratios, mg C/hr/mg chl- α ,
at 30 meters for Days IV-VII.

Day IV - V — X
Day VI - VII - O

Horizontal Dark Line Indicates the Period of No
Measurable Light.

STATION E-2, 30 METERS
ASSIMILATION RATIOS, DAYS IV-VII



rhythms that were found, as changes in intensity at 30 meters were slight, and the variations were not in phase with the photosynthetic rhythm. These conclusions are the same as found for the surface samples (Section I).

When the chlorophyll a per particulate volume at the surface and 30 meters were compared (Figures 42 and 43), it was found that the latter was consistently lower in value. This may be an artifact caused by an increase in detritus at that depth, which would be included in the measurement of total particulate volume. As already mentioned (page 90) the opposite has been suggested by several authors. Similarly, the photosynthetic potential per particulate volume was lower at 30 meters (Figures 44 and 45) which also may be due to increased detritus.

A comparison of the assimilation ratios (Figures 46 and 47) indicate that the differences between the higher surface values and 30 meter samples are less than that with either chlorophyll a /volume or photosynthetic potential/volume. There is also a suggestion that the surface assimilation ratios, measured during the time of the minimum, are closer in value to the 30 meter samples, than at other times in the day. This finding is discussed more fully in Section V.

The data of the assimilation ratios support the theory that the lower values for chlorophyll a /volume and photosynthetic

FIGURE 42

Below: Graph of Chlorophyll *a* Per Particulate
Volume, $\text{mg}/\mu^3 \times 10^{-12}$, at the Surface
(X — X) and 30 meters (O --- O),
Day IV-V.

FIGURE 43

Above: Graph of Chlorophyll *a* Per Particulate
Volume, $\text{mg}/\mu^3 \times 10^{-12}$, at the Surface
(X — X) and 30 meters (O --- O),
Day VI-VII.

Horizontal Dark Line Indicates the Period of No
Measurable Light.

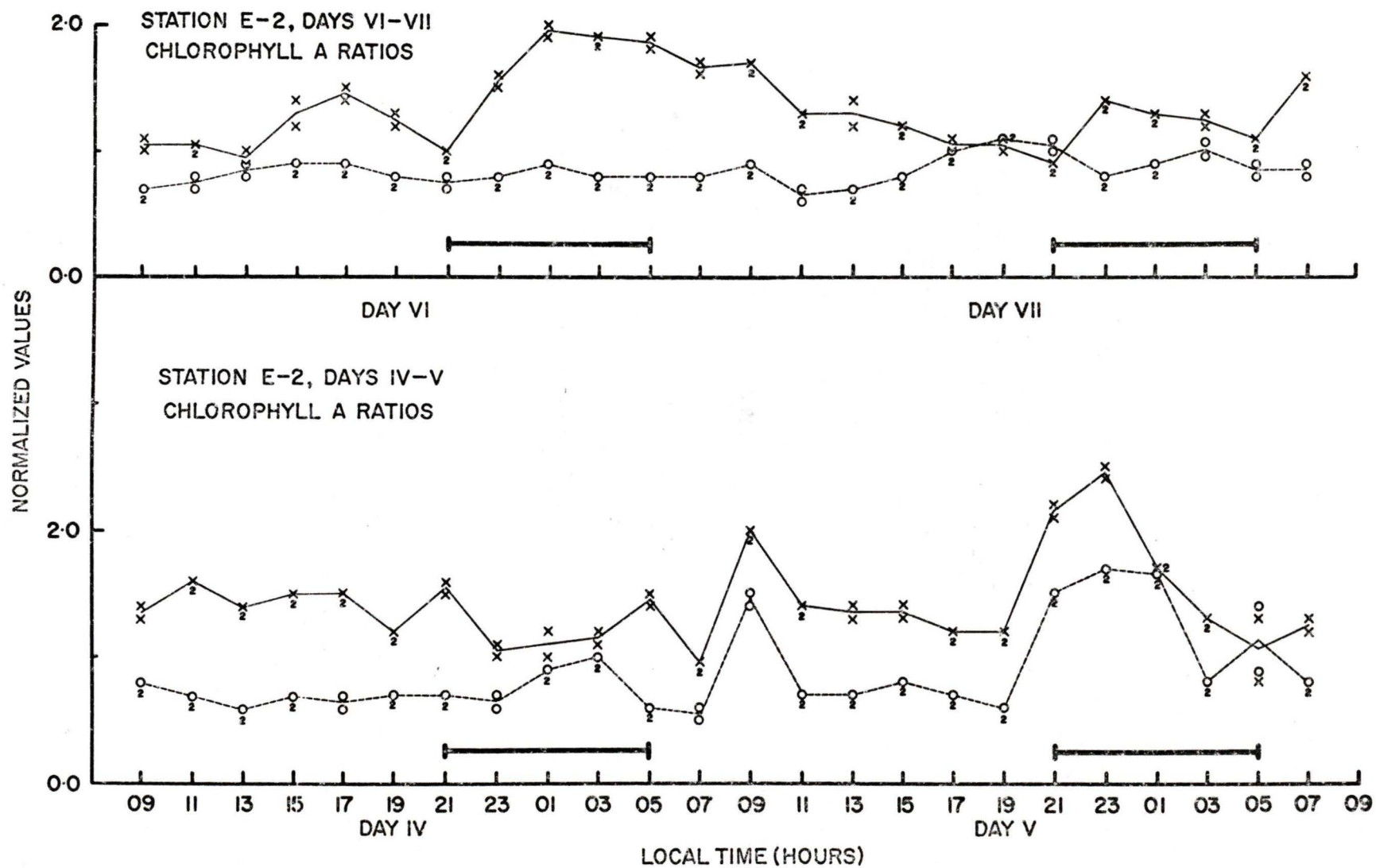


FIGURE 44

Graph of Photosynthetic Potential Per Particulate
Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$, at the Surface (X — X)
and 30 meters (O --- O), Days IV-V.

Horizontal Dark Line Indicates the Period of No
Measurable Light.

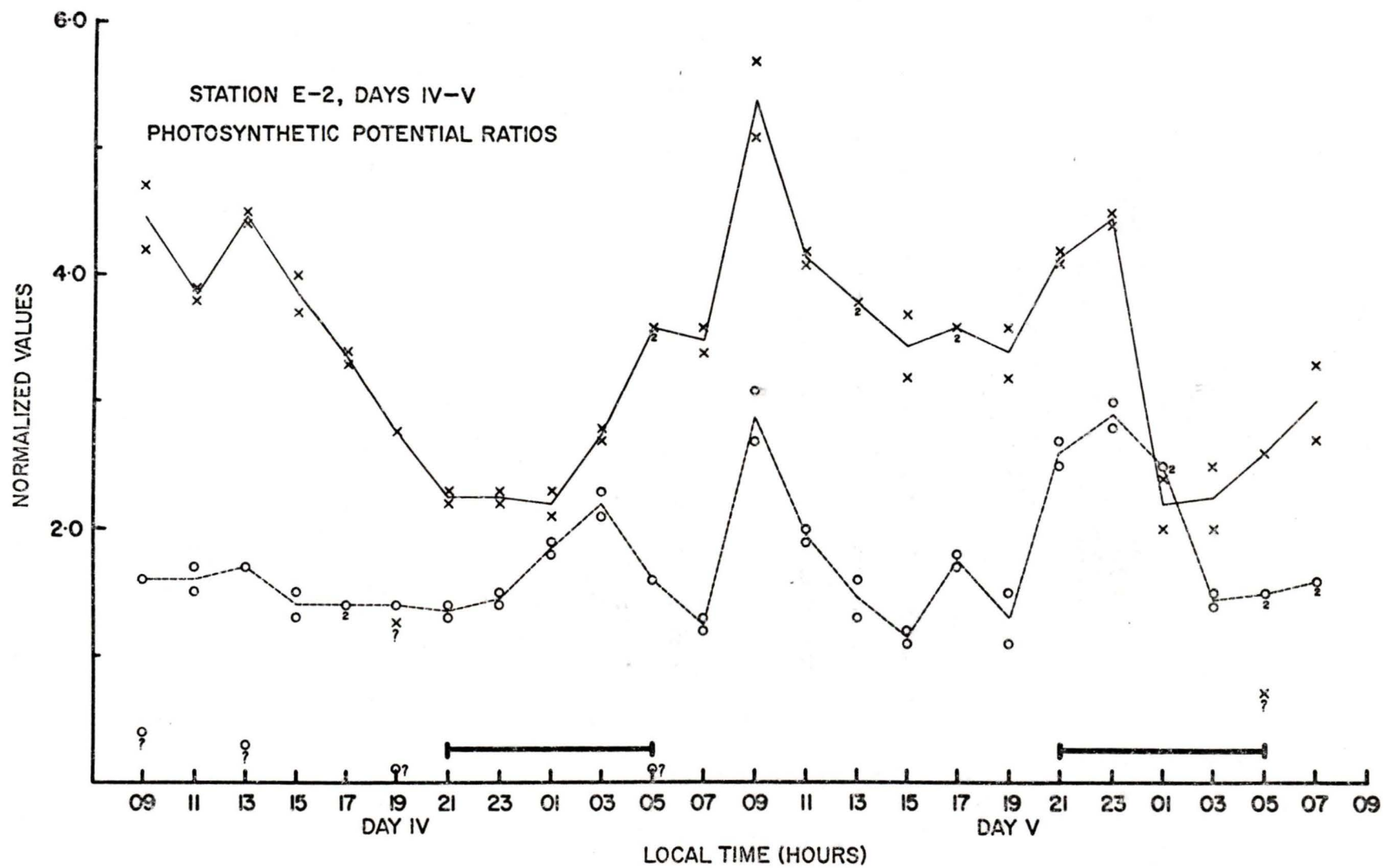


FIGURE 45

Graph of Photosynthetic Potential Per Particulate
Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$, at the Surface (X — X)
and at 30 meters (O --- O), Days VI and VII.

Horizontal Dark Line Indicates the Period of No
Measurable Light.

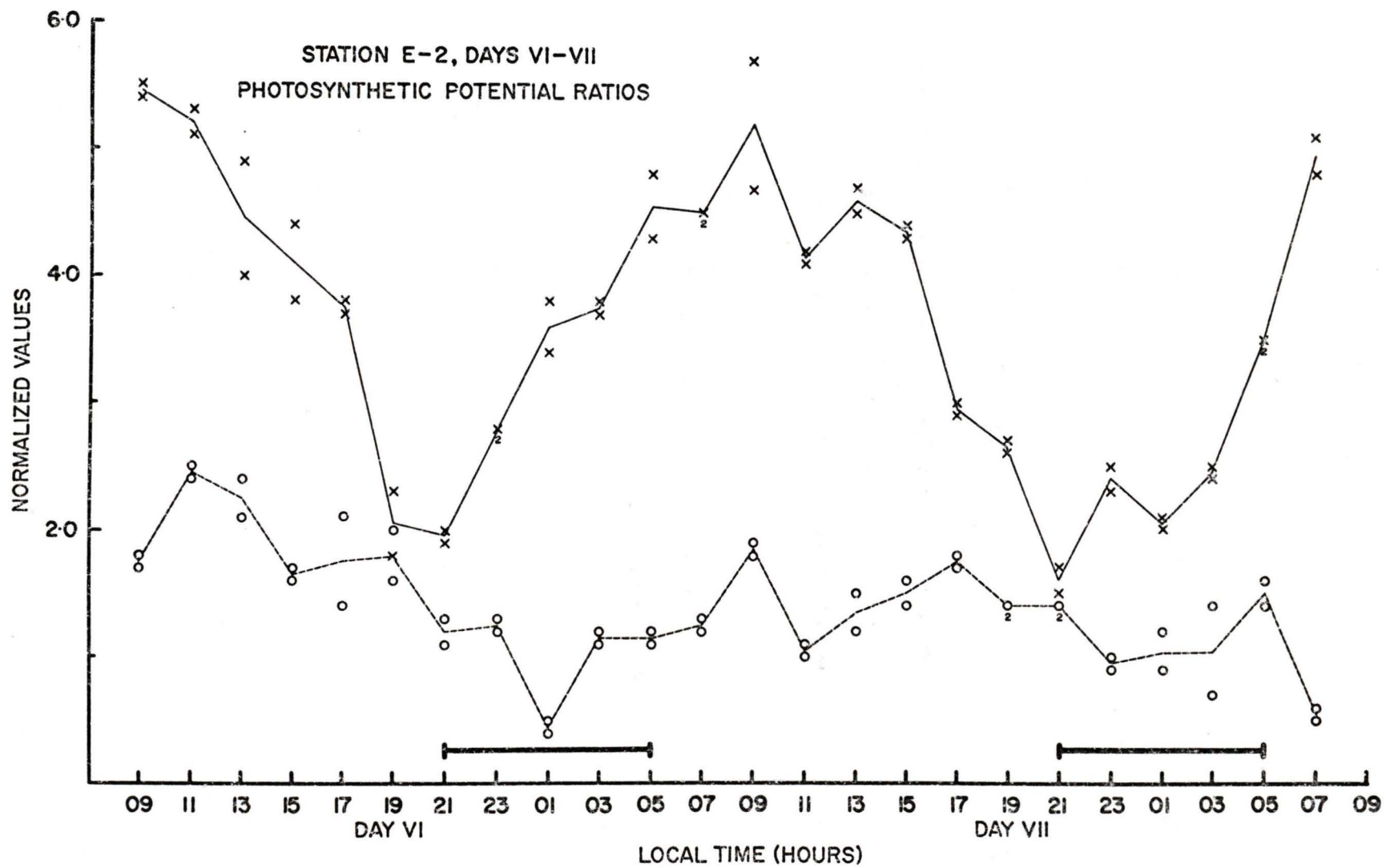


FIGURE 46

Graph of Assimilation Ratios, mg C/hr/mg chl-*a*,
at the Surface (X — X) and 30 meters (O --- O),
Days IV and V.

Horizontal Dark Line Indicates the Period of No
Measurable Light.

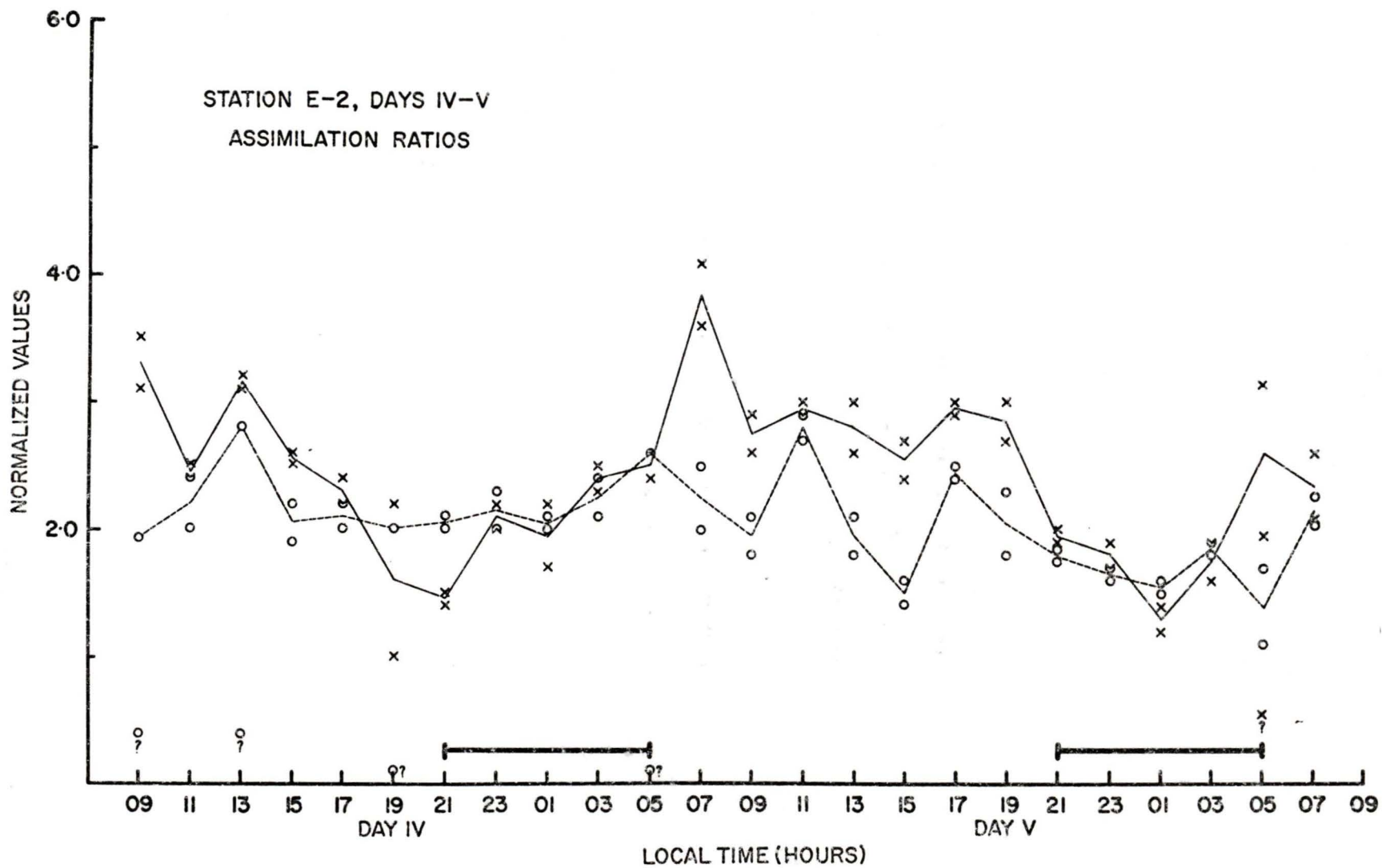
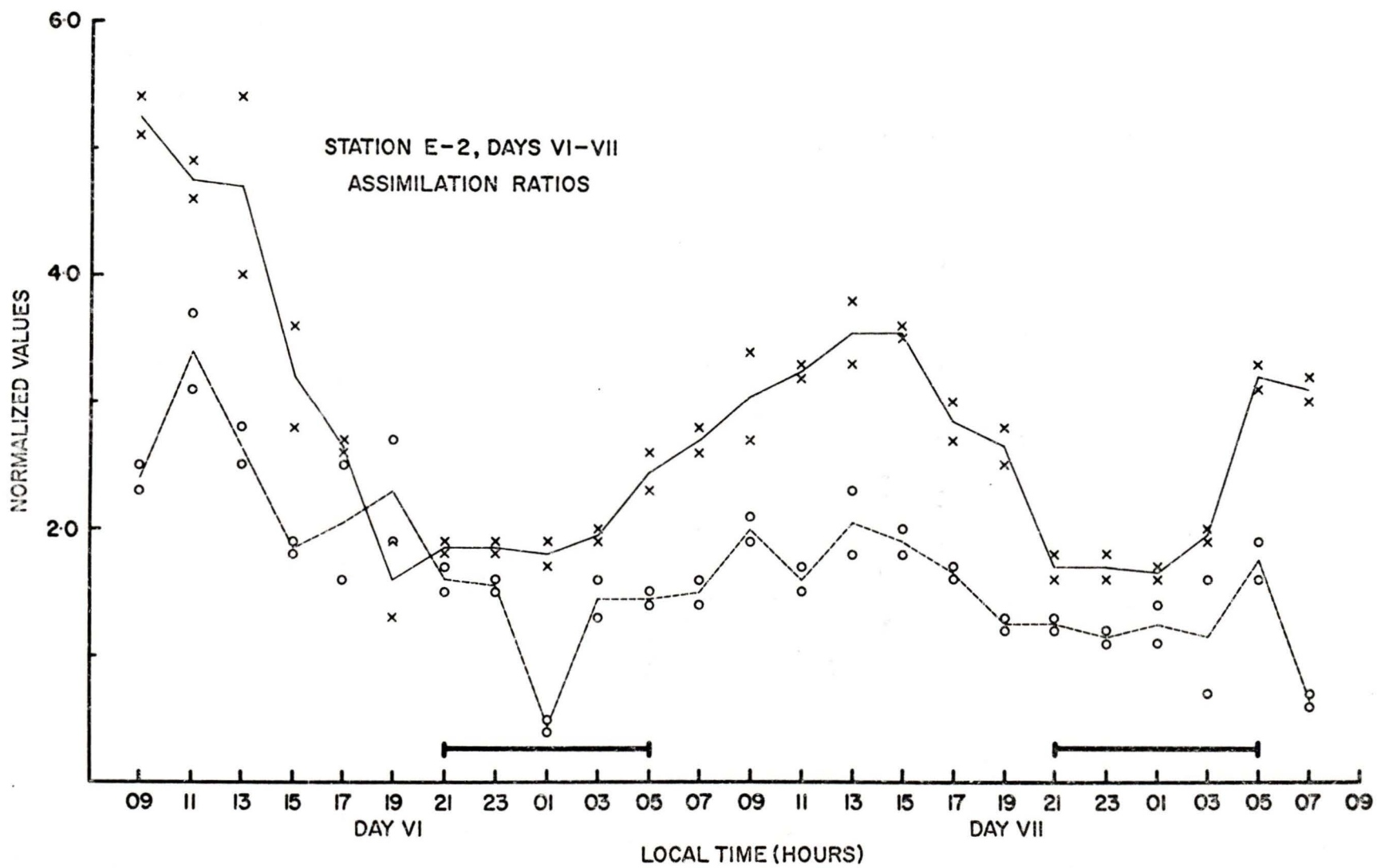


FIGURE 47

Graph of Assimilation Ratios, mg C/hr/mg chl- α ,
at the Surface (X — X) and 30 meters (O --- O),
Days VI-VII.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



potential/volume at 30 meters, can be partly explained by the increase in detritus. Sheldon and Parsons (1967) state that both particle size and concentration may increase with depth because of settling.

It is also possible that there is some light injury of cells in the 30 meter samples, due to the relatively higher light intensities in the incubator compared to *in situ* values. This would lead to an underestimate of both photosynthetic potential/volume and assimilation ratios. Unfortunately, this possibility was not followed. It should be noted, however, that photosynthesis at 30 meters was not completely (if at all) inhibited, and that during Days VI and VII at least, there is some indication of a diel variation. The similarity of the assimilation ratios values between the surface samples and 30 meters, also suggests that there is little light inhibition at the lower depth.

III. Oceanic Waters - Surface, Station E-1

During the first day and a half of sampling, chlorophyll *a*, photosynthetic potential, and total particulate volume (shown in Figure 11, and summarized in Table 2) decreased from a maximum in the afternoon to a minimum in the dark period, increasing again before the start of the next light period. However, both chlorophyll *a* and total volume decreased again during the morning of Day II.

Neither chlorophyll *a* nor total particulate volume showed any pattern to the variations after about 1700 hours on Day II. This was probably a result of storm conditions which had developed, with seas reaching a height of 25-30 feet.

Photosynthetic potential, however, increased during Day II to a maximum in the afternoon and decreased again into the next dark period. The maximum on Day III was near midday, but the afternoon decrease was followed by a rise in values during the third dark period.

The low values for chlorophyll *a* and total particulate volume during the dark period of Day I may be due to grazing, as has been suggested by Ryther *et al* (1961), McAllister (1963), and Wood and Corcoran (1966). After Day I, storm conditions would probably obscure grazing effects, by continuously mixing and by possibly affecting the zooplankton.

The normalized values for photosynthetic potential, chlorophyll *a*, and assimilation ratios, are given in Figure 12 with the maxima and minima summarized in Table 3. Chlorophyll *a* per particulate volume did not show a regular pattern over Day I and II, and fluctuated very little. Conversely, photosynthetic potential/volume showed a definite diel variation with the maximum occurring in the afternoon (Day I) or morning (Day II). Minimum values on both days were measured at the beginning of the dark period. Assimilation

ratios paralleled photosynthesis except that the maximum of Day II was shifted to the afternoon.

Both photosynthetic potential per particulate volume, and assimilation ratios were higher during Day II, than in Day I. This was not found in the inshore samples, and the reason for its occurrence here is not clear. The increase in wind and sea activity may be one explanation, with increased agitation stimulating carbon uptake by the organisms. It had been noticed on previous cruises that plankton filtered through netting tended to have a higher uptake of carbon-14, than samples that were not filtered.

The data for the chlorophyll *a* per total particulate volume are not in agreement with Glooschenko (1967). He suggested that the changes in chlorophyll in the N.E. Pacific were too great to be accounted for by grazing. Wood and Corcoran (1966) however, felt that variation in chlorophyll *a* were due to changes in cell numbers.

The diel variations in photosynthetic potential reported here are similar to those of Doty and Oguri (1957), Ryther *et al* (1958), Shimada (1958), McAllister (1963) Goering *et al* (1964) and Eppley *et al* (1971a, for cultures of natural populations), although the time of the maxima varied between the morning and afternoon. None of the above studies, however, were actually corrected for changes in biomass.

The diel variations in assimilation ratios agrees with McAllister (1963) and Eppley *et al* (1971a) but not with Shimada (1958) or Malone (1971). Malone, however, only tested morning and afternoon changes and not during the dark period.

These data indicate that an endogeneous rhythm affecting the photosynthetic uptake mechanism but independent of chlorophyll *a*, is present, similar to that already discussed for the inshore waters in Sections I and II of the discussion.

Nitrates, temperature and salinity measurements (Appendix I, Tables A1, A3, A5, respectively) showed little variation during the study and are not felt to be the mechanism in controlling the variations in photosynthetic potential. Although incident light varied during the day, the fact that the photosynthetic potential per particulate volume increased in value during the dark period, suggests a more subtle mechanism than the direct influence of light.

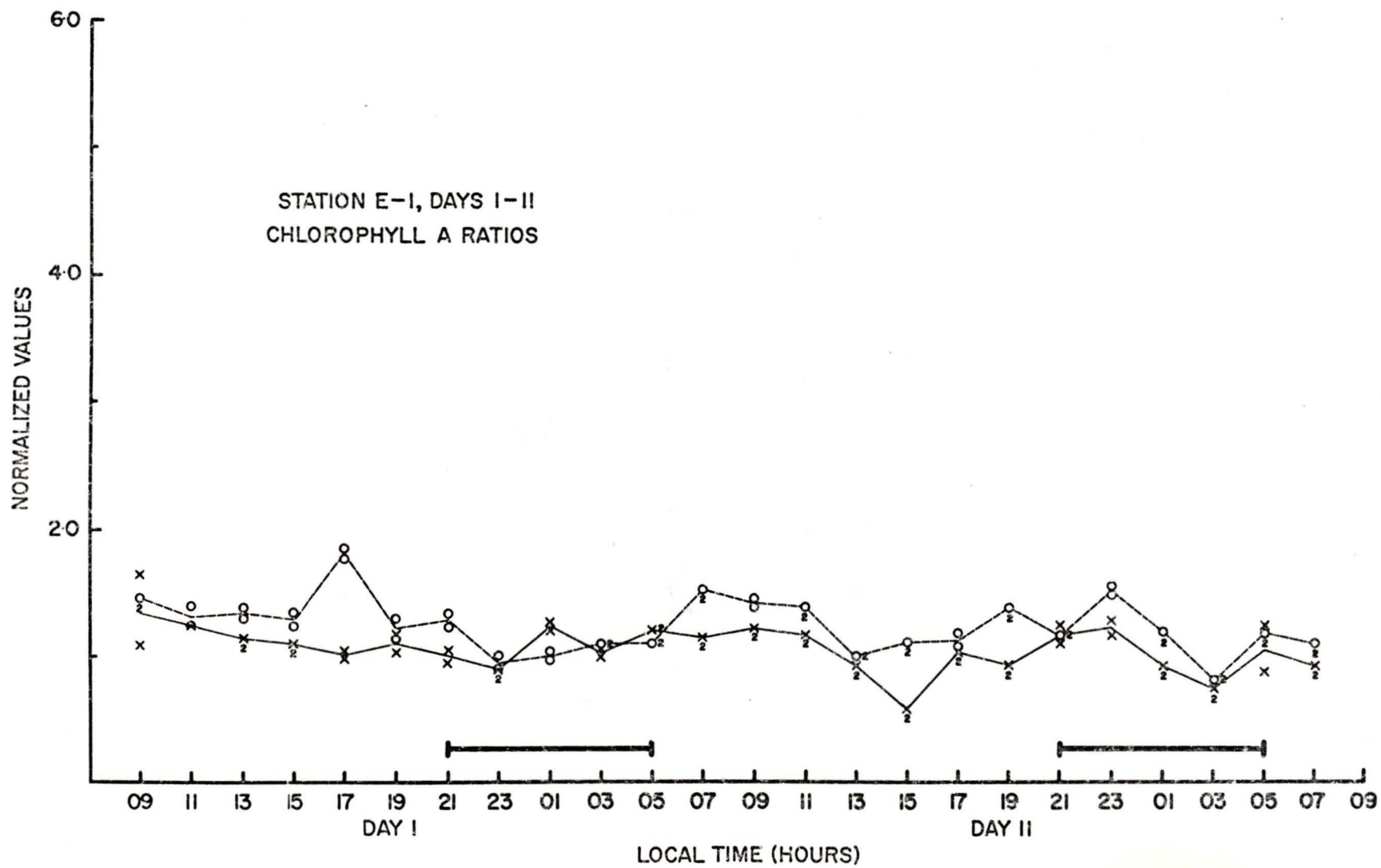
IV. Oceanic Waters - 30 Meters, Station E-1

The data from 30 meters is very erratic (Figure 13, Table 4). Only during Day I is any variation noted for chlorophyll *a* concentration or photosynthetic potential, with a decrease in values during the dark period. No variation was found for total particulate volume. The random variability of the data is more apparent after

FIGURE 48

Graph of Chlorophyll *a* Per Particulate Volume,
 $\text{mg}/\mu^3 \times 10^{-12}$, at the Surface (X — X) and
30 meters (O --- O), Days I and II.

Horizontal Dark Line Indicates the Period of
No Measurable Light.



the middle of Day II, suggesting influences by the storm as was found at the surface.

The normalized data is shown in Figure 14, with the times of the maxima and minima summarized in Table 5. Chlorophyll *a* per particulate volume did not show regular or large variations during Day I and II. However, with both photosynthetic potential per unit volume, and assimilation ratios, there is a suggestion of a diel rhythm. The maxima occurred during the day, decreasing into the dark period, although the time of the minimum was variable. (The increase shown for the dark period, Day I, is probably not real due to the spread in replicate values). Much higher values for photosynthetic potential per volume and assimilation ratios were found during Day II, which may be the result of increased agitation as suggested for surface samples.

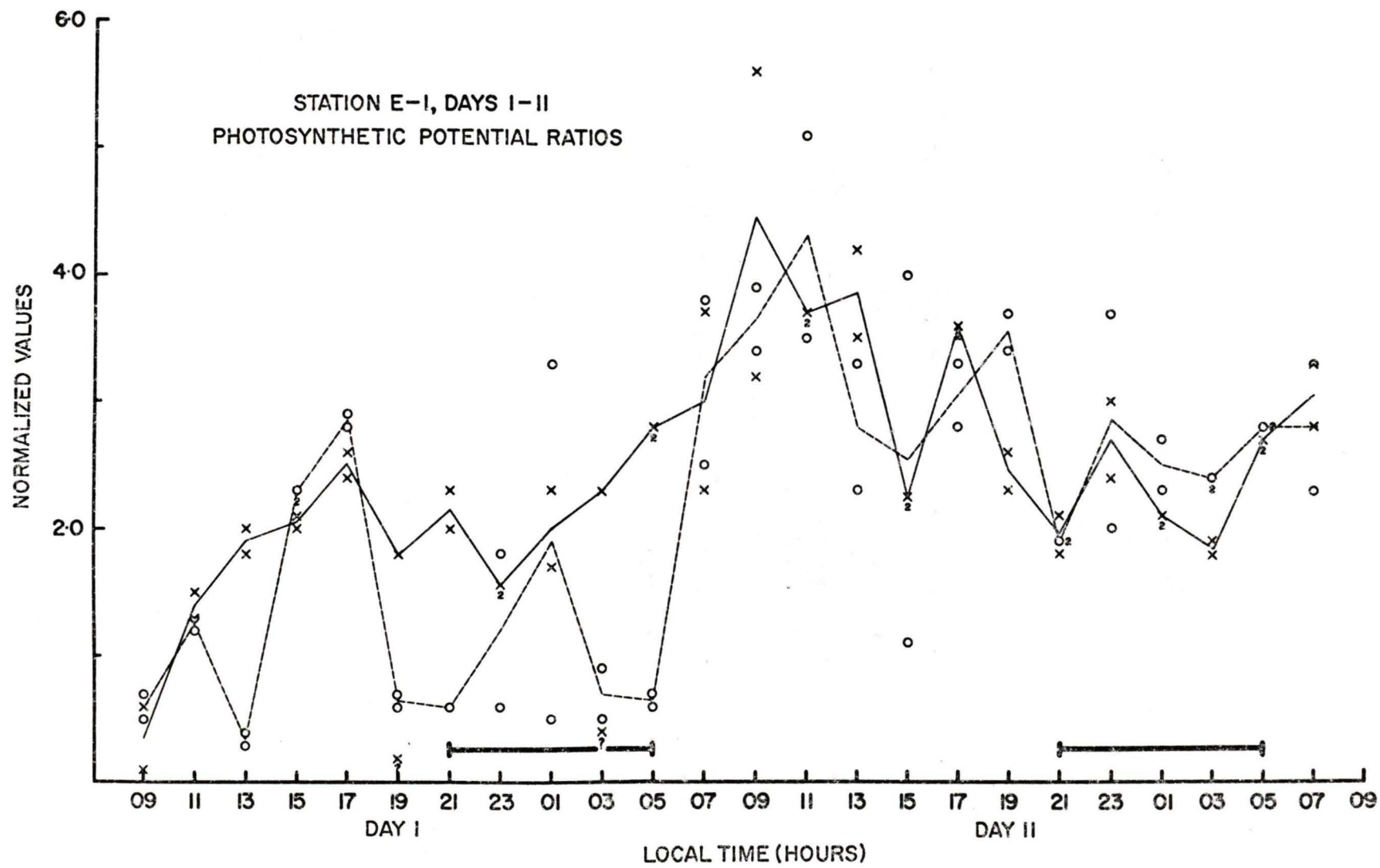
A comparison of chlorophyll *a* per particulate volume between surface and 30 meter samples (Figure 48) showed little differences between the two depths. This was also the case for photosynthetic potential per volume (Figure 49) and assimilation ratios (Figure 50). This would indicate a similarity in the plankton populations which could result from a homogeneous water column, and is supported by the temperature and salinity data. This mixed layer is not uncommon for an oceanic environment, (Pickard, 1963).

The diel nature of the variations in photosynthetic potential, and the parallel pattern shown for the assimilation ratios, suggest

FIGURE 49

Graph of Photosynthetic Potential Per Particulate
Volume, $\text{mg C/hr}/\mu^3 \times 10^{-12}$, at the Surface (X — X)
and at 30 meters (O --- O), Days I and II.

Horizontal Dark Line Indicates the Period of No
Measurable Light.



based on biochemical inhibitors of various reactions or compounds. They speculated that "rhythmicity is in some way dependent upon the cells normal ability to synthesize a specific RNA. The action of this RNA does not seem to be mediated simply through the effect upon *de nova* protein synthesis, and its synthesis occurs many hours before its activity is expressed". Further postulation by Sweeney (1969) suggested that permeability changes in membranes are controlled by the "biological clock" and that these in turn control the enzymes involved in the rhythms observed.

It has been noticed during this study that the efficiency of the photosynthetic mechanism (as reflected by the assimilation ratios) was greater during the day, than in the dark period, but that differences between the surface and 30 meters in assimilation ratios was less during the period of the surface minima. It was suggested by the author that some 'substance' was depleted during the day which required resynthesis during the dark period. Because of the similarity of the efficiency between the surface and 30 meters during the dark period, it was felt that the deeper samples did not have the same amount of this substance, as present in the surface samples during the day.

This 'substance' has been suggested in this thesis to be under the control of some biological clock regulating its synthesis or activity. Since light energy and/or light quality are two of the obvious differences between the surface and 30 meters,

it is possible that these may influence the biological clock. Light quality has been shown to affect photosynthetic pigments and production rates in marine algae (Wallen and Geen, 1971 a, b) while light intensity has been shown to influence algae as well (Steemann Nielsen and Hansen, 1959; Yentsch and Lee, 1966; Steemann Nielsen and Jorgensen, 1968). However, it has been concluded in this thesis that photoperiod also affects the photosynthetic mechanism, by being able to alter the timing of the rhythm. Further work into the effects of light on the regulating mechanism of the diel rhythms in photosynthetic potential, is beyond the scope of this thesis.

It can be concluded that the rhythmical variations found for the photosynthetic potential appear to be the result of an endogeneous rhythm, regulating photosynthetic uptake mechanism of a cell. These rhythms are independent of small environmental changes as well as from changes in incident light. Photoperiodism, however, is probably responsible for the timing of the rhythm. It is felt by the author that the results discussed here concerning the photosynthetic potential, follow the definition of a circadian rhythm - eg. a twenty-four hour periodic variation which is repeatable in time and space, and controlled by some internal cellular mechanism.

CONCLUSIONS

Several marine environments were investigated to determine the nature of reported diel variations in chlorophyll a , photosynthetic potential and cell populations.

It was concluded that measurement of chlorophyll a or total particulate volume would reveal a diel rhythm only under certain conditions. These were found to be enhanced by water stability and periodic zooplankton migration, in which the increase in zooplankton at the surface resulted in a decrease in the phytoplankton population. In areas where this grazing effect was less, or with greater turbulence, the presence of a diel variation was reduced or absent. No variation was found at 30 meters in the inshore environment.

When chlorophyll a and photosynthetic potential were normalized for biomass changes, it was found that chlorophyll a per particulate volume varied very little when compared to the changes in photosynthetic potential per particulate volume. Slight increases in chlorophyll a /volume were found during the dark period, suggesting some chlorophyll a synthesis.

Diel rhythms in photosynthetic potential existed at the surface at all stations sampled, and were attributed to variations of some internal mechanism, rather than to changes in biomass, or to the variations of chlorophyll a within a cell.

Variations in photosynthetic potential at 30 meters were not as large as at the surface, although it was present. Again, an internal mechanism was thought to be the cause of the rhythms. It was suggested that the efficiency of the photosynthetic uptake was in some way related to the light history of the cells, with phytoplankton normally exposed to higher light intensities having a higher photosynthetic uptake per unit of chlorophyll *a* than those living at lower light intensities.

Studies with cultures of natural phytoplankton populations showed that the rhythm in photosynthetic potential persisted under conditions of continuous dark. The variations were not due to variations in cellular concentrations of chlorophyll *a*. In addition, it was found that the timing of the rhythm could be altered by changing the light-dark cycle.

The diel rhythms in photosynthetic potential were not the direct result of changes in temperature, nitrate concentration, salinity or light. However, light (or photoperiod) was found to be a factor involved in the timing of the rhythm. It was suggested by the author that some 'substance', such as an enzyme or enzyme substrate, was depleted during the light period, which required resynthesis during the dark period. The rhythmical pattern of the changes, plus the results of the laboratory experiment, indicated that some 'biological clock' regulated the variations in photosynthetic potential. This hypothesis was supported by work reported

in the literature.

This study is the only one known in which the diel variation in photosynthetic potential in natural phytoplankton communities, has been shown to be independent of both biomass and chlorophyll *a* changes. Because the rhythms were found in all environments examined in the study, as well as being documented in the literature for natural populations over wide geographical range, and in various laboratory investigations, it is felt that a diel variation in photosynthetic potential is ubiquitous among marine phytoplankton.

SUMMARY

1. Measurements of chlorophyll *a*, photosynthetic potential and total particulate volume were made every two hours for 24, 48 or 72-hour time periods. The stations were located in both inshore and oceanic environments.
2. Diel variations in the three measurements were found to occur in inshore waters at the surface but not at 30 meters (compensation depth). These variations were attributed to zooplankton grazing during the dark period.
3. When corrected for biomass changes only photosynthetic potential showed a diel rhythm, with maximum values during the day and a minimum at night. This was found to occur at the surface, but was not as apparent at 30 meters. Assimilation ratios (photosynthetic potential per unit chlorophyll *a*) showed a similar diel variation, indicating that the changes in photosynthetic potential were not due to changes in chlorophyll *a*. Chlorophyll *a* per particulate volume remained fairly constant except for a slight increase in the dark period, which was felt to be a result of pigment synthesis.
4. In surface oceanic waters (Station E-2), photosynthetic potential showed a diel variation, but this was not always apparent for

measurements of chlorophyll *a* concentration or total particulate volume. When adjusted for biomass changes, only photosynthetic potential and the assimilation ratios exhibited a diel variation. These had similar patterns as found in the inshore waters, with a maximum during the day and a minimum at night. Agitation by storm waves appeared to disrupt the rhythm. Samples at 30 meters showed similar results, both with the absolute values as well as with the normalized values. Mixing of the water column was thought to be the cause of the similarity between depths.

5. Samples at Station P indicated that all of the phytoplankton population was smaller than 44 microns in diameter. At the surface chlorophyll *a* concentration showed little variation at the surface or at 30 meters, but a diel rhythm in photosynthetic potential was present at both depths. The rhythm was shown to be independent of chlorophyll *a* changes, and was not directly a function of temperature, salinity, nitrate concentration or variations in light intensity.
6. Cultures of natural phytoplankton, under constant conditions, did not show a diel variation in chlorophyll *a*. A rhythm was found in the photosynthetic potential measurements, which was independent of the chlorophyll *a* concentration. The timing of

the rhythms were similar to the *in situ* variations measured in the same area. The diel rhythm in photosynthetic potential remained when cultures were kept in continuous dark, and the timing of the rhythm could be shifted by altering the light-dark cycle.

7. It was suggested that the variations in photosynthetic potential were a result of changes in some 'substance', which in turn was regulated by some 'biological clock' mechanism. Furthermore, the light history of the phytoplankton cells, such as light intensity and/or light quality were suggested to have an effect on the magnitude of the photosynthetic rhythm.
8. It was concluded that the diel rhythms in photosynthetic potential reflected a circadian rhythm in marine phytoplankton, independent of temperature, nutrients, salinity and light intensity, but in some manner set by the light-dark cycle.

LITERATURE CITED

- Anderson, G.C. 1969. Subsurface chlorophyll maximum in the Northeast Pacific Ocean. *Limnol. & Oceanogr.* 14: 386-391.
- , and K. Banse. 1965. Chlorophylls in marine phytoplankton: Correlation with carbon uptake. *Deep-Sea Res.* 12: 531-533.
- , and R.P. Zeutschel. 1970. Release of dissolved organic matter by marine phytoplankton in coastal and offshore areas of the Northeast Pacific Ocean. *Limnol. & Oceanogr.* 15: 402-407.
- Antia, N.J., C.D. McAllister, T.R. Parsons, K. Stephens, and J.D.H. Strickland. 1963. Further measurements of primary production using a large-volume plastic sphere. *Limnol. & Oceanogr.* 8: 166-183.
- Barraclough, W.E., and R.H. Herlinveaux. 1965. Exploratory studies of the echo scattering layers in Saanich Inlet and the Strait of Georgia, British Columbia. *Fish. Res. Bd. Can.* Manuscript Report No. 199.
- Boragrad, L. 1962. Chlorophylls. In: *Physiology and Biochemistry of plant pigments*. Editor, Ralph A. Lewen. Academic Press, New York and London. pp. 385-408.
- Bunning, Erwin. 1964. *The physiological clock. Endogenous diurnal rhythms and biological chronometry*. Academic Press, New York. 145 pp.

- Cumming, B.C., and Edgar Wagner. 1968. Rhythmic processes in plants. *Ann. Rev. Plant Physio.* 19: 381-416.
- Curl, Herbert Jr., and Lawrence F. Small. 1965. Variations in photosynthetic assimilation ratios in natural, marine phytoplankton communities. *Limnol. & Oceanogr. Supp.* 10: R 67-R 73.
- Doty, M.S., and M. Oguri. 1957. Evidence for a photosynthetic daily periodicity. *Limnol. & Oceanogr.* 2: 37-40.
- El-Sayed, Z. Sayed, and Enrique F. Mandelli. 1965. Primary production and standing crop of phytoplankton in the Weddell Sea and Drake Passage. In: *Biology of the Antarctic Seas. II. Antarctic Research Series, Vol. 5.* Editor, G.A. Llano.
- Eppley, R.W., and Phillip R. Sloan. 1965. Carbon balance experiments with marine phytoplankton. *J. Fish. Res. Bd. Can.* 22: 1083-1097.
- ., and J.L. Coatsworth. 1966. Culture of the marine phytoplankton, *Dunaliella tertiolecta*, with light dark cycles. *Arch. Mikrobiol.* 55: 66-80.
- ., and Phillip R. Sloan. 1966. Growth rates of marine phytoplankton: Correlation with light absorption by cell chlorophyll *a*. *Physiol. Plant.* 19: 47-59.

- Eppley, R.W., R.W. Holmes, and E. Paasche. 1967. Periodicity in cell division and physiological behaviour of *Ditylum brightwellii*, a marine planktonic diatom, during growth on light-dark cycles. Arch. Mikrobiol. 56: 305-323.
- ., T.T. Packard, and J.J. MacIsaac. 1970. Nitrate reductase in Peru current phytoplankton. Mar. Biol. 6: 195-199.
- ., A.F. Carlucci, O. Holm-Hansen, D. Kiefer, J.J. McCarthy, Elizabeth Venrick, and P.M. Williams. 1971a. Phytoplankton growth and composition in shipboard cultures supplied with nitrate, ammonium, or urea as the nitrogen source. Limnol. & Oceanogr. 16: 741-751.
- ., J.N. Rogers, J.J. McCarthy, and A. Sournia. 1971b. Light/dark periodicity in nitrogen assimilation of the marine phytoplankters *Skeletonema costatum* and *Coccolithus huxleyi* in N-limited chemostat culture. J. Phycol. 7: 150-154.
- Evans, J.H., and S.M. McGill. 1970. An investigation of the Coulter Counter in "biomass" determinations of natural freshwater phytoplankton populations. Hydrobiologia. 35: 401-419.
- Gibor, Ahron, and William R. Meehan. 1961. Diurnal variations in chlorophyll α content of some freshwater algae. Ecology 42: 156-157.
- Glooschenko, Walter Arthur. 1967. The ecological significance of the diel periodicity of photosynthetic pigments in marine phytoplankton. Ph.D. Thesis, Oregon State University. 155 pp.

- Goering, J.J., R.C. Dugdale, and D.W. Menzel. 1964. Cyclic diurnal variations in the uptake of ammonia, and nitrate by photosynthetic organisms in the Sargasso Sea. *Limnol. & Oceanogr.* 9: 448-451.
- Goldman, Charles R., David T. Mason, and Brian J.B. Wood. 1963. Light injury and inhibition in Antarctic freshwater phytoplankton. *Limnol. & Oceanogr.* 8: 313-322.
- Hastings, J. Woodland. 1960. Biochemical aspects of rhythms: Phase shifting by chemicals. In: Cold Springs Harbor Symposia on Quantitative Biology. Biological Clocks. Vol. 25. pp. 131-143.
- , Lazarus Astrachan, and Beatrice M. Sweeney. 1961. A persistent daily rhythm in photosynthesis. *J. Gen. Physiol.* 45: 69-76.
- , and Alex Keynan. 1965. Molecular aspects of circadian systems. In: Circadian Clocks. Editor, Jurgen Ashoff. North-Holland Publishing Co., Amsterdam. pp. 167-175.
- Herlinveaux, R.H. 1962. Oceanography of Saanich Inlet in Vancouver Island, British Columbia. *J. Fish. Res. Bd. Can.* 19: 1-37.
- Hoos, Richard Alan. 1970. Distribution and physiology of zooplankton in an oxygen minimum layer. M.Sc. Thesis, University of Victoria. 113 pp.

- Jitts, H.R., C.D. McAllister, K. Stephens, and J.D.H. Strickland. 1964. The cell division rates of some marine phytoplankters as a function of light and temperature. J. Fish. Res. Bd. Can. 21: 139-157.
- Jorgensen, E.G. 1966. Photosynthetic activity during the life cycle of synchronous *Skeletonema* cells. Physiol. Plant. 19: 789-799.
- Kalff, J. 1966. A diel periodicity in the optimum light intensity for maximum photosynthesis in natural phytoplankton populations. J. Fish. Res. Bd. Can. 26: 463-468.
- Lorenzen, Carl J. 1963. Diurnal variation in photosynthetic activity of natural phytoplankton populations. Limnol. & Oceanogr. 8: 56-62.
- Malone, T.C. 1971. Diurnal rhythms in net plankton and nano-plankton assimilation ratios. Mar. Biol. 10: 285-289.
- McAllister, C.D., T.R. Parsons, and J.D.H. Strickland. 1960. Primary productivity at Station "P", in the Northeast Pacific Ocean. J. Cons. Int. Explor. Mer. 25: 240-259.
- , 1963. Measurements of diurnal variations in productivity at ocean Station "P". Limnol. & Oceanogr. 8: 289-292.
- , N. Shah, and J.D.H. Strickland. 1964. Marine phytoplankton photosynthesis as a function of light intensity: A comparison of methods. J. Fish. Res. Bd. Can. 21: 159-181.

- McMurray, Laura, and J.W. Hastings. 1972. No desynchronization among four circadian rhythms in the unicellular alga, *Gonyaulax polyedra*. *Science*. 175: 1137-1139.
- Mitrakos, Konstantinos. 1963. Relationship to chlorophyll metabolism and its photoperiodism, endogeneous daily rhythm and red, far-red reaction system. *Photochem. & Photobiol.* 2: 223-231.
- Morris, Ian, Clarice M. Yentsch, and Charles S. Yentsch. 1971. Relationship between light carbon dioxide fixation and dark carbon dioxide fixation by marine algae. *Limnol. & Oceanogr.* 16: 854-858.
- Nalewajko, C. 1966. Photosynthesis and excretion in various planktonic algae. *Limnol. & Oceanogr.* 11: 1-10.
- Nemoto, Takahisa. 1967. Feeding pattern of euphausiids and differentiations in their body characters. *Information Bull. on Planktology in Japan*.
- Newhouse, Jan, S. Doty Maxwell, and Roy T. Tsuda. 1967. Some diurnal features of a neritic surface plankton population. *Limnol. & Oceanogr.* 12: 207-212.
- Paasche, E. 1967. Marine plankton algae grown with light-dark cycles. I. *Coccolithus huxleyi*. *Physiol. Plant.* 20: 946-956.

- Paasche, E. 1968. Marine plankton algae grown with light-dark cycles. II. *Ditylum brightwellii* and *Nitzschia turgidula*. *Physiol. Plant.* 21: 66-77.
- Parsons, T.R. 1969. The use of particle size spectra in determining the structure of a plankton community. *J. Oceanog. Soc. Japan.* 25: 172-181.
- ., R.J. Le Brasseur, and J.D. Fulton. 1967. Some observations on the dependence of zooplankton grazing on the cell size and concentration of phytoplankton blooms. *J. Oceanog. Soc. Japan.* 23: 10-17.
- Pickard, G.L. 1963. Descriptive physical oceanography. Pergamon Press Oxford. 200 pp.
- Pirson, A., and H. Lorenzen. 1966. Synchronized dividing algae. *Annu. Rev. Plant Physiol.* 17: 439-458.
- Pittendrigh, Colin S. 1960. Perspectives in the study of biological clocks. In: *Perspectives in Marine Biology*. Editor, A.A. Buzzato-Traverse. University of California, Berkeley and Los Angeles. pp. 239-268.
- Rabinowitch, Eugene, and Gouindjee. 1969. Photosynthesis. John Wiley and Sons Inc., New York. 273 pp.
- Ryther, J.H., C.S. Yentsch, E.M. Hulburt, and R.F. Vaccaro. 1958. The dynamics of a diatom bloom. *Biol. Bull.* 115: 257-268.

- Ryther, J.H., D.W. Menzel, and R.F. Vaccaro. 1961. Diurnal variations in some chemical and biological properties of the Sargasso Sea. *Limnol. & Oceanogr.* 6: 149-153.
- Samuel, S., N.M. Shah, and G.E. Fogg. 1971. Liberation of extracellular products of photosynthesis by tropical phytoplankton. *J. Mar. Biol. Assoc. U.K.* 51: 793-798.
- SCOR/UNESCO. 1966. Determination of photosynthetic pigments in sea water. Monographs on oceanographic methodology A 1. Published by UNESCO, Imprimerie Rolland, Paris, France.
- Sheldon, R.W., and T.R. Parsons. 1967. A continuous size spectrum for particulate matter in the sea. *J. Fish. Res. Bd. Can.* 24: 909-915.
- Shimada, B.M. 1958. Diurnal fluctuation in photosynthetic rate and chlorophyll *a* content of phytoplankton from Eastern Pacific waters. *Limnol. & Oceanogr.* 3: 336-339.
- Steemann Nielsen, E. 1949. A reversible inactivation of chlorophyll *in vivo*. *Physiol. Plant.* 2: 247-265.
- , 1952. The use of radioactive carbon (C^{14}) for measuring organic production in the sea. *J. Cons. Internat. Explor. Mer.* 18: 117-140.

- Steemann Nielsen, E. 1962. Inactivation of the photochemical mechanism in photosynthesis as a means to protect the cells against too high light intensities. *Physiol. Plant.* 15: 161-171.
- ., and Vagn Kr. Hansen. 1959. Light adaptation in marine phytoplankton populations and its interrelation with temperature. *Physiol. Plant.* 12: 353-370.
- ., and E.G. Jorgensen. 1968. The adaptation of plankton algae III. With special considerations of the importance in nature. *Physiol. Plant.* 21: 647-654.
- Stephens, K., J.D. Fulton and O.D. Kennedy. 1969. Summary of biological oceanographic observations in the Strait of Georgia, 1965-1968. *Fish. Res. Bd. Can. Tech. Report No.* 110.
- Strickland, J.D.H. 1958. Solar radiation penetrating the ocean. A review of requirements, data, and method of measurement, with particular reference to photosynthetic productivity. *J. Fish. Res. Bd. Can.* 15: 453-493.
- .. 1960. Measuring the production of marine phytoplankton. *Bull. Fish. Res. Bd. Can.* 122: 1-172.
- .. 1965. Production of organic matter in the primary stages of the marine food chain. In: *Chemical Oceanography*. Editor, J.P. Riley. Academic Press, London, & New York. pp. 478-610.

- Strickland, J.D.H., and T.R. Parsons. 1968. A practical handbook of seawater analysis. Bull. Fish. Res. Bd. Can. 167. 311 pp.
- Sweeney, Beatrice M. 1960. The photosynthetic rhythm in single cells of *Gonyaulax polyedra*. In: Cold Springs Harbor Symposia on Quantitative Biology. Biological Clocks. Vol. 25, pp. 145-148.
- , 1965. Rhythmicity in the biochemistry of photosynthesis in *Gonyaulax*. In: Circadian clocks. Ed. Jurgen Aschoff. North-Holland Publ. Co. Amsterdam. pp. 190-194.
- , 1969. Transducing mechanisms between circadian clock and overt rhythms in *Gonyaulax*. Can. J. Bot. 47: 299-308.
- , and J.W. Hastings. 1962. Rhythms In: Physiology and Biochemistry of Algae. Ed. R.A. Lewin, Academic Press, New York. pp. 687-700.
- , -----, 1958. A rhythmic cell division in populations of *Gonyaulax polyedra*. J. Protozool. 5: 217-224.
- Thomas, J.P. 1971. Release of dissolved organic matter from natural populations of marine phytoplankton. Mar. Biol. (Berlin). 11: 311-323.
- Virgin, H.I. 1958. Studies on the formation of protochlorophyll and chlorophyll α under varying light treatments. Physiol. Plant. 11: 347-362.
- , 1964. Some effects of light on chloroplasts and plant protoplasm. In: Photophysiology. I. General Principles: Action of light on plants. Ed. A.C. Giese. Academic Press, New York. pp. 273-303.

- Wallen, D.G., and G.H. Geen. 1971a. Light quality in relation to growth, photosynthetic rates and carbon metabolism in two species of marine plankton algae. *Mar. Biol.* 10: 34-43.
- , 1971b. Light quality and concentration of proteins, RNA, DNA, and photosynthetic pigments in two species of marine plankton algae. *Mar. Biol.* 10: 44-51.
- Wolfe, Douglas A., and Claire L. Schelske. 1967. Liquid scintillation and geigar counting efficiencies for Carbon-14 incorporated by marine phytoplankton in productivity measurements. *J. Cons. Perm.Int. Explor. Mer.* 31: 31-37.
- Wood, E.J. Ferguson, and Eugene F. Corcoran. 1966. Diurnal variation in phytoplankton. *Bull. Mar. Science.* 16: 383-403.
- Yentsch, C.S., and R.W. Lee. 1966. A study of photosynthetic light reactions, and a new interpretation of sun and shade phytoplankton. *J. Mar. Res.* 24: 319-337.
- ., and J.H. Ryther. 1957. Short-term variations in phytoplankton chlorophyll and their significance. *Limnol. & Oceanogr.* 2: 140-142.
- ., and Robert F. Scagel. 1958. Diurnal study of phytoplankton pigments an *in situ* study in East Sound, Washington, *J. Mar. Res.* 17: 567-583.
- ., and Carol A. Reichert. 1963. The effects of prolonged darkness on photosynthesis, respiration, and chlorophyll in the marine flagellate, *Dunaliella euchlora*. *Limnol. & Oceanogr.* 8: 338-342.

APPENDIX

TABLE A1.

NITRITE-NITRATE CONCENTRATIONS - OCEAN STATION E-1

Day/Time	Surface		30 Meters	
	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)
I - 0900	0.08	2.92	0.07	3.51
1500	0.07	2.88	0.06	4.85
2300	0.06	2.58	0.07	4.64
0700	0.07	2.88	0.09	3.47
II - 1500	0.06	2.96	0.07	2.53
2300	0.07	2.37	0.11	3.54
0700	0.05	2.52	0.04	4.34
III - 1500	0.08	1.48	0.07	2.31
2300	0.06	2.58	0.06	2.43
0700	0.09	2.84	0.07	3.02

TABLE A2.

NITRITE-NITRATE CONCENTRATIONS - STATION E-2: SAANICH INLET.

Day/Time	Surface		30 meters	
	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)
IV - 0900	0.09	16.55	0.12	18.50
1500	0.15	16.83	0.10	17.61
2100	0.08	16.74	0.14	17.74
0300	0.15	17.61	0.11	17.87
V - 0900	0.19	18.60	0.18	19.45
1500	0.12	18.08	0.14	19.06
2100	0.10	16.26	0.11	24.59
0300	0.07	16.38	0.17	20.19
0700	0.02	18.50	0.13	18.72
VI - 0900	0.07	18.04	0.10	23.97
1500	0.07	14.83	0.08	19.34
2100	0.08	12.64	0.10	20.50
0300	0.09	13.33	0.17	18.22
VII- 0900	0.09	14.47	0.09	18.18
1500	0.07	11.63	0.06	20.20
2100	0.05	12.40	0.07	20.20
0300	0.08	13.30	0.06	22.03
0700	0.07	12.81	0.03	21.00

TABLE A3.

IN SITU TEMPERATURE MEASUREMENTS ($^{\circ}$ C) - OCEAN STATION E-1

Day/Time	Surface	30 Meters	Day/Time	Surface	30 Meters
I - 0900	7.9	7.8	III - 0900	8.0	8.0
1100	8.0	8.0	1100	8.0	8.0
1300	7.9	7.8	1300	8.0	8.0
1500	8.0	8.0	1500	8.0	8.0
1700	8.6	8.3	1700	8.0	8.0
1900	8.0	8.1	1900	8.2	8.0
2100	8.0	8.0	2100	8.2	8.1
2300	8.2	8.2	2300	8.0	8.0
0100	8.2	8.2	0100	8.0	8.0
0300	8.2	8.2	0300	8.1	8.0
0500	8.0	8.0	0500	8.1	8.1
0700	8.1	8.0	0700	8.4	8.4
II - 0900	8.0	8.0			
1100	8.2	8.2			
1300	8.2	8.1			
1500	8.2	8.2			
1700	8.0	8.0			
1900	8.0	8.0			
2100	8.0	8.0			
2300	8.0	8.0			
0100	8.5	8.5			
0300	8.0	8.3			
0500	8.0	8.0			
0700	8.0	8.0			

TABLE A4.

IN SITU TEMPERATURE MEASUREMENTS (°C) - STATION E-2: SAANICH INLET

Day/Time	Surface	30 Meters	Day/Time	Surface	30 Meters
IV - 0900	7.8	8.0	VII- 0900	9.0	8.0
1100	8.2	8.0	1100	9.4	8.0
1300	8.8	8.0	1300	10.0	8.4
1500	8.5	8.0	1500	9.5	8.0
1700	8.9	8.0	1700	10.2	8.0
1900	9.3	8.0	1900	10.2	8.0
2100	9.2	8.0	2100	10.0	8.0
2300	8.5	8.0	2300	9.5	8.0
0100	8.5	8.0	0100	9.5	8.1
0300	8.5	8.0	0300	9.2	8.0
0500	8.0	8.0	0500	9.2	8.0
0700	8.0	8.1	0700	9.1	8.0
V - 0900	8.0	8.0			
1100	9.0	8.0			
1300	9.0	8.0			
1500	9.4	8.0			
1700	9.2	8.1			
1900	9.2	8.2			
2100	9.0	8.2			
2300	9.0	8.1			
0100	8.8	8.0			
0300	8.4	8.0			
0500	7.8	8.0			
0700	7.9	8.0			
VI - 0900	9.0	7.5			
1100	9.2	7.6			
1300	9.0	8.0			
1500	9.5	8.0			
1700	9.2	8.2			
1900	9.3	8.2			
2100	9.4	8.5			
2300	9.3	8.4			
0100	9.0	8.1			
0300	8.7	7.9			
0500	8.4	7.9			
0700	8.3	8.0			

TABLE A5.
SALINITY MEASUREMENTS (‰): OCEAN STATION E-1

Day/Time	Surface	30 Meters
I - 0900	32.15	32.18
1500	32.15	32.16
2300	32.01	32.08
0700	32.14	32.15
II - 1500	32.21	32.21
2300	32.21	32.24
0700	32.18	32.19
III- 1500	32.18	32.18
2300	32.12	32.12
0700	32.07	32.08

TABLE A6.
SALINITY MEASUREMENTS (‰) - STATION E-2: SAANICH INLET

Day/Time	Surface	30 Meters
IV - 0900	29.39	29.82
1700	29.40	29.80
0300	28.06	29.79
V - 0900	28.44	29.81
1700	29.06	29.80
0100	28.44	29.82
VI - 0900	28.12	29.45
1700	28.66	29.86
0100	27.40	29.47
VII- 0900	28.59	29.80
1700	28.57	29.82
0100	28.66	29.84

TABLE A7.

NITRITE-NITRATE CONCENTRATIONS - OCEAN STATION P

Day/Time	Surface		30 Meters	
	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)
A 0900	0.38	6.76	--	--
1100	0.26	5.64	--	--
1300	0.23	6.16	--	--
1500	0.17	5.29	--	--
1700	0.21	5.87	--	--
1900	0.21	5.27	--	--
2100	0.19	4.94	--	--
2300	0.23	4.73	--	--
0100	0.30	5.74	--	--
0300	0.32	5.56	--	--
0500	0.26	5.08	--	--
0700	0.21	4.94	--	--
B 0900	0.38	6.49	--	--
1100	0.21	4.71	--	--
1300	0.19	4.28	--	--
1500	0.19	4.25	--	--
1700	0.23	5.45	--	--
1900	0.19	4.80	--	--
2100	0.19	4.52	--	--
2300	0.19	5.04	--	--
0100	0.19	5.06	--	--
0300	0.19	5.48	--	--
0500	0.21	6.66	--	--
0700	0.36	4.77	--	--
C 0900	0.47	6.83	0.37	7.53
1100	0.33	5.74	0.31	5.71
1300	0.30	5.19	N/A	N/A
1500	0.31	5.86	0.30	4.16
1700	0.33	4.79	0.30	4.73
1900	0.35	5.71	0.30	4.96
2100	0.32	5.27	0.34	6.83
2300	0.29	6.41	0.27	7.00
0100	0.28	5.80	N/A	N/A
0300	0.31	4.47	N/A	N/A
0500	0.29	5.13	N/A	N/A
0700	0.30	5.52	N/A	N/A

..(cont'd)

TABLE A7 (cont'd)

Day/Time	Surface		30 Meters	
	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)
D 0900	0.23	5.26	0.19	3.98
1100	0.15	4.84	0.13	4.86
1300	0.17	5.07	0.19	8.00
1500	0.19	5.99	0.15	6.30
1700	0.23	7.05	0.15	5.89
1900	0.21	6.02	0.13	5.48
2100	0.23	6.66	0.13	6.44
2300	0.15	6.08	0.17	6.60
0100	0.17	5.60	0.17	6.28
0300	0.15	6.19	0.17	5.92
0500	0.15	6.42	0.15	7.13
0700	0.13	5.89	0.13	6.48

TABLE A8.

NITRITE-NITRATE CONCENTRATIONS- LAB EXPERIMENTS

Day/Time	Lab Culture		Control Culture	
	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)	Nitrite ($\mu\text{g-at/l}$)	Nitrate ($\mu\text{g-at/l}$)
Experiment A				
0900	0.08	2.82	0.28	0.95
1200	0.19	0.14	0.15	4.18
1500	0.13	0.06	0.13	2.19
1800	0.11	0.20	0.13	1.87
2100	0.15	0.50	0.04	0.60
2400	0.02	0.03	0.06	0.05
0300	0.0	0.02	0.11	0.63
0600	0.08	N/A	0.08	0.42
Experiment B				
0900	0.36	1.10	0.15	0.04
1200	0.17	1.00	0.08	0.0
1500	0.08	1.02	0.08	0.03
1800	0.08	0.97	0.08	0.0
2100	0.08	0.72	0.11	0.0
2400	0.11	0.31	0.06	0.0
0300	0.11	0.40	0.06	0.21
0600	0.04	0.12	0.06	0.53
0900	0.04	0.58	0.0	0.09
Experiment C				
0900	0.13	20.40	0.28	20.22
1200	0.11	19.37	0.15	20.80
1500	0.15	17.39	0.11	19.24
1800	0.08	19.87	0.11	17.04
2100	0.17	15.52	0.26	18.09
2400	0.11	20.84	0.11	17.38
0300	0.11	18.53	0.11	18.89
0600	0.06	20.44	0.11	17.91

TABLE A9.

IN SITU TEMPERATURE MEASUREMENTS - OCEAN STATION P.

Day/Time	Surface	30 Meters	Day/Time	Surface	30 Meters
Day A			Day C		
0900	11.3	--	0900	12.0	12.0
1100	11.3	--	1100	12.1	12.0
1300	11.3	--	1300	12.2	12.0
1500	11.3	--	1500	12.2	12.1
1700	11.3	--	1700	12.2	12.0
1900	11.4	--	1900	12.1	12.0
2100	11.4	--	2100	12.0	12.0
2300	11.4	--	2300	12.0	12.0
0100	11.4	--	0100	12.2	N/A
0300	11.3	--	0300	11.9	N/A
0500	11.3	--	0500	11.8	N/A
0700	11.3	--	0700	11.9	N/A
Day B			Day D		
0900	11.7	--	0900	12.5	12.0
1100	12.3	--	1100	12.6	12.1
1300	12.5	--	1300	12.6	13.0
1500	12.5	--	1500	13.0	13.0
1700	12.5	--	1700	13.1	12.8
1900	12.2	--	1900	12.8	12.8
2100	12.0	--	2100	12.8	12.9
2300	11.8	--	2300	12.7	12.6
0100	11.6	--	0100	12.2	12.6
0300	11.6	--	0300	12.7	12.7
0500	11.5	--	0500	12.7	12.7
0700	11.6	--	0700	12.6	12.6

TABLE A10

Subsurface light measurements used for calculations of extinction coefficient.

Day	Depth (M)	Light Intensity (ly/min)
I	0.5	0.118
(Ocean Station E-1)	5	0.055
	10	0.023
	25	0.006

Mean extinction coefficient for top 25 meters = 0.160

Depth of the 1% surface light = 28.5 M

Light intensity at 30 meters = 0.001 ly/min

IV	0.5	0.418
(Saanich Inlet, Station E-2)	5	0.138
	10	0.040
	15	0.020
	20	0.006

Mean extinction coefficient for top 25 meters = 0.203

Depth of the 1% surface light = 23 M

Light intensity at 30 meters = 0.0009 ly/min

.. cont'd.

Table A10, cont'd.

VI	0.5	0.070
(Saanich Inlet, Station E-2)	3	0.033
	5	0.010
	10	0.006
	15	0.002
	20	0.0008
	25	0.0004

Mean extinction coefficient for top 25 meters = 0.204

Depth of the 1% surface light = 23 M

Light intensity at 30 meters = 0.0001 ly/min

C	0.5	.153
(Ocean Station P)	2	.138
	3	.118
	4	.098
	5	.089
	7	.060

Mean extinction coefficient for top 7 meters = 0.15

Depth of the 1% surface light = 30 M

Light intensity at 30 meters = 0.002 ly/min

.. cont'd.

Table A10, cont'd.

D	1	.086
(Ocean Station P)	2	.079
	5	.065
	10	.045
	15	.024

Mean extinction coefficient for top 15 meters = 0.145

Depth of the 1% light = 55 M

Light intensity at 30 meters = 0.008 ly/min

TABLE A11

(pages 171-185)

Chlorophyll α concentration (mg/m^3), photosynthetic potential ($\text{mg C}/\text{m}^3/\text{hr}$) and total particulate volume ($\mu^3/\text{ml} \times 10^6$) data for Endeavour cruise, Stations E-1 and E-2.

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU. MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU. M)	PHOTOSYNTHETIC POTENTIAL (MG/CU. M/HR)
I	00.	0900	962526.	1.579 1.043	0.097 0.570
I	30.	0900	746594.	1.095 1.089	0.536 0.381
I	00.	1100	948663.	-0.001 1.181	1.409 1.270
I	30.	1100	848271.	1.026 1.196	1.130 1.085
I	00.	1300	1032700.	1.193 1.183	2.051 1.819
I	30.	1300	914303.	1.219 1.261	0.341 0.303
I	00.	1500	1025171.	1.130 1.129	2.033 2.203
I	30.	1500	887028.	1.204 1.089	2.074 2.050
I	00.	1700	942801.	0.985 0.924	2.236 2.488
I	30.	1700	595112.	1.109 1.061	1.660 1.741
I	00.	1900	1208885.	1.418 1.244	0.243 2.216
I	30.	1900	785151.	0.897 1.007	0.485 0.523

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
I	00.	2100	992915.	1.034 0.944	0.948 1.267
I	30.	2100	766434.	1.021 0.961	-0.012 0.430
I	00.	2300	854270.	0.788 0.775	1.285 1.269
I	30.	2300	758116.	0.764 0.663	0.434 1.403
I	00.	0100	632816.	0.799 0.747	1.431 1.050
I	30.	0100	541160.	0.564 0.541	1.775 0.273
I	00.	0300	857172.	0.907 0.862	0.377 2.013
I	30.	0300	759700.	0.838 0.811	0.718 0.376
I	00.	0500	830907.	1.004 0.986	2.338 2.332
I	30.	0500	772792.	0.863 0.871	0.509 0.492
I	00.	0700	1121638.	1.297 1.307	2.550 4.175
I	30.	0700	776652.	1.174 1.189	2.957 1.963

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU. MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU. M)	PHOTOSYNTHETIC POTENTIAL (MG/CU. M/HR)
II	00.	0900	699350.	0.849 0.860	3.885 2.219
II	30.	0900	436433.	0.635 0.611	1.721 1.499
II	00.	1100	690668.	0.810 0.807	2.538 2.571
II	30.	1100	600939.	0.827 0.820	2.121 3.093
II	00.	1300	770900.	0.724 0.715	2.703 3.237
II	30.	1300	755751.	0.761 0.740	2.518 1.760
II	00.	1500	1288424.	0.770 0.761	2.886 2.850
II	30.	1500	653381.	0.726 0.713	0.730 2.630
II	00.	1700	869902.	0.904 0.879	3.113 3.129
II	30.	1700	852412.	0.997 0.903	2.369 2.781
II	00.	1900	802857.	0.760 0.741	2.088 1.847
II	30.	1900	566257.	0.786 0.787	2.069 1.940

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
II	00.	2100	886322.	1.098 0.978	1.872 1.575
II	30.	2100	754963.	0.896 0.884	1.442 1.417
II	00.	2300	615590.	0.715 0.796	1.845 1.464
II	30.	2300	479927.	0.733 0.714	1.791 0.951
II	00.	0100	939460.	0.873 0.864	1.969 1.977
II	30.	0100	724326.	0.847 0.877	1.964 1.679
II	00.	0300	1082125.	0.801 0.821	1.911 2.101
II	30.	0300	972617.	0.772 0.800	2.299 2.286
II	00.	0500	1002379.	0.875 1.238	2.676 2.744
II	30.	0500	577396.	0.705 0.677	1.576 1.651
II	00.	0700	806830.	0.754 0.741	2.649 2.278
II	30.	0700	573161.	0.637 0.635	1.296 1.884

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
III	00.	0900	590675.	0.773 0.815	2.637 2.798
III	30.	0900	528093.	0.743 0.723	2.279 0.701
III	00.	1100	854995.	0.959 0.988	3.681 3.365
III	30.	1100	820639.	0.930 0.933	2.969 0.486
III	00.	1300	944404.	0.848 0.870	2.601 2.686
III	30.	1300	810495.	0.878 0.887	2.723 2.769
III	00.	1500	693869.	0.793 0.845	2.673 3.079
III	30.	1500	NO DATA AVAILABLE	0.854 0.863	2.945 2.613
III	00.	1700	NO DATA AVAILABLE	0.957 0.869	2.244 2.120
III	30.	1700	NO DATA AVAILABLE	0.894 0.915	2.079 2.452
III	00.	1900	NO DATA AVAILABLE	0.658 0.671	2.440 2.020
III	30.	1900	NO DATA AVAILABLE	0.615 0.653	1.620 1.521

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
III	00.	2100	NO DATA AVAILABLE	0.872 0.746	2.938 3.422
III	30.	2100	NO DATA AVAILABLE	0.774 0.730	2.171 2.295
III	00.	2300	NO DATA AVAILABLE	0.814 0.804	0.385 3.015
III	30.	2300	NO DATA AVAILABLE	0.813 0.826	0.418 1.782
III	00.	0100	NO DATA AVAILABLE	0.826 0.833	2.374 1.666
III	30.	0100	NO DATA AVAILABLE	0.737 0.687	0.994 0.449
III	00.	0300	NO DATA AVAILABLE	0.761 0.727	1.709 2.375
III	30.	0300	NO DATA AVAILABLE	0.657 0.611	1.600 1.001
III	00.	0500	NO DATA AVAILABLE	0.799 0.744	0.587 2.326
III	30.	0500	NO DATA AVAILABLE	0.792 0.778	2.338 1.172
III	00.	0700	NO DATA AVAILABLE	0.875 0.830	1.574 1.753
III	30.	0700	NO DATA AVAILABLE	0.786 0.782	0.408 1.387

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
IV	00.	0900	701766.	0.975 0.929	3.276 2.979
IV	30.	0900	651129.	0.533 0.534	1.031 0.232
IV	00.	1100	835363.	1.337 1.300	3.255 3.168
IV	30.	1100	686725.	0.506 0.515	1.200 1.047
IV	00.	1300	881770.	1.220 1.253	3.928 3.907
IV	30.	1300	752728.	0.481 0.461	0.208 1.285
IV	00.	1500	770917.	1.153 1.153	2.830 3.051
IV	30.	1500	725709.	0.503 0.494	0.934 1.074
IV	00.	1700	867826.	1.294 1.264	2.841 2.983
IV	30.	1700	764081.	0.508 0.473	1.039 1.037
IV	00.	1900	959297.	1.198 1.176	1.198 2.644
IV	30.	1900	844608.	0.571 0.558	0.069 1.163

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU. MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU. M)	PHOTOSYNTHETIC POTENTIAL (MG/CU. M/HR)
IV	00.	2100	957228.	1.507 1.483	2.091 2.174
IV	30.	2100	787470.	0.517 0.528	1.047 1.107
IV	00.	2300	868451.	0.897 0.933	1.966 1.902
IV	30.	2300	782159.	0.575 0.500	1.099 1.148
IV	00.	0100	774861.	0.796 0.915	1.787 1.590
IV	30.	0100	635650.	0.570 0.566	1.194 1.143
IV	00.	0300	829741.	0.984 0.940	2.243 2.307
IV	30.	0300	575836.	0.553 0.584	1.224 1.338
IV	00.	0500	885546.	1.227 1.366	3.217 3.171
IV	30.	0500	824874.	0.494 0.503	0.059 1.288
IV	00.	0700	1121169.	1.041 0.987	3.781 4.085
IV	30.	0700	928464.	0.498 0.555	1.100 1.238

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
V	00.	0900	754265.	1.492 1.483	3.875 4.290
V	30.	0900	369856.	0.536 0.553	0.994 1.152
V	00.	1100	1019275.	1.474 1.425	4.247 4.204
V	30.	1100	752639.	0.502 0.523	1.471 1.440
V	00.	1300	995788.	1.436 1.282	3.811 3.742
V	30.	1300	779385.	0.568 0.577	1.219 1.032
V	00.	1500	949058.	1.289 1.278	3.073 3.484
V	30.	1500	682641.	0.542 0.526	0.737 0.831
V	00.	1700	1082799.	1.326 1.336	3.925 3.942
V	30.	1700	697014.	0.503 0.512	1.213 1.260
V	00.	1900	1056659.	1.237 1.243	3.759 3.339
V	30.	1900	791939.	0.499 0.512	0.892 1.169

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
V	00.	2100	619362.	1.347 1.321	2.568 2.618
V	30.	2100	383599.	0.571 0.569	0.960 1.036
V	00.	2300	381188.	0.961 0.923	1.681 1.724
V	30.	2300	326434.	0.563 0.568	0.972 0.911
V	00.	0100	399084.	0.680 0.665	0.791 0.963
V	30.	0100	307563.	0.509 0.514	0.754 0.782
V	00.	0300	989871.	1.278 1.288	2.022 2.461
V	30.	0300	659373.	0.520 0.512	0.979 0.956
V	00.	0500	1056093.	1.386 0.862	2.711 0.773
V	30.	0500	632914.	0.555 0.889	0.955 0.945
V	00.	0700	1112062.	1.404 1.388	2.997 3.625
V	30.	0700	611664.	0.444 0.483	1.007 0.993

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
VI	00.	0900	1349616.	1.442 1.389	7.485 7.309
VI	30.	0900	805759.	0.585 0.595	1.483 1.397
VI	00.	1100	1262566.	1.402 1.387	6.468 6.731
VI	30.	1100	870506.	0.676 0.597	2.210 2.099
VI	00.	1300	1682419.	1.548 1.677	8.288 6.704
VI	30.	1300	697138.	0.590 0.596	1.652 1.494
VI	00.	1500	2071091.	2.585 2.843	9.197 7.886
VI	30.	1500	664129.	0.617 0.612	1.084 1.148
VI	00.	1700	2016726.	2.959 2.852	7.673 7.554
VI	30.	1700	661638.	0.582 0.563	1.415 0.959
VI	00.	1900	2492683.	3.283 3.060	5.662 4.388
VI	30.	1900	757963.	0.575 0.642	1.536 1.235

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
VI	00.	2100	2378945.	2.499 2.461	4.661 4.507
VI	30.	2100	792261.	0.591 0.596	1.027 0.870
VI	00.	2300	1790864.	2.804 2.764	4.976 5.050
VI	30.	2300	775614.	0.624 0.617	0.976 0.945
VI	00.	0100	1396572.	2.739 2.711	4.742 5.238
VI	30.	0100	622106.	0.589 0.569	0.280 0.228
VI	00.	0300	1618716.	3.115 3.017	5.940 6.173
VI	30.	0300	618101.	0.476 0.515	0.658 0.761
VI	00.	0500	1570595.	2.996 2.878	7.553 6.847
VI	30.	0500	661204.	0.555 0.539	0.806 0.760
VI	00.	0700	1470704.	2.532 2.338	6.628 6.609
VI	30.	0700	628502.	0.517 0.528	0.754 0.811

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
VII	00.	0900	1708482.	2.897 2.974	8.016 9.740
VII	30.	0900	724714.	0.662 0.634	1.359 1.286
VII	00.	1100	2382996.	3.030 3.011	10.039 9.717
VII	30.	1100	675701.	0.462 0.437	0.756 0.670
VII	00.	1300	2381019.	3.261 2.936	10.777 11.255
VII	30.	1300	764166.	0.506 0.514	1.141 0.900
VII	00.	1500	2114618.	2.587 2.620	9.218 9.072
VII	30.	1500	717327.	0.581 0.565	1.142 1.029
VII	00.	1700	3391164.	3.385 3.653	9.921 10.160
VII	30.	1700	663939.	0.689 0.692	1.162 1.136
VII	00.	1900	3477066.	3.695 3.374	9.556 9.141
VII	30.	1900	677551.	0.719 0.735	0.950 0.937

DAY	DEPTH	TIME	TOTAL PARTICULATE VOLUME (CU.MICRONS/ML)	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
VII	00.	2100	4451559.	4.135 4.222	7.375 6.590
VII	30.	2100	688816.	0.737 0.720	0.942 0.941
VII	00.	2300	2511997.	3.583 3.543	6.239 5.768
VII	30.	2300	796091.	0.637 0.627	0.763 0.746
VII	00.	0100	2652962.	3.423 3.352	5.312 5.556
VII	30.	0100	729464.	0.647 0.651	0.875 0.686
VII	00.	0300	2451226.	3.074 3.027	5.876 6.091
VII	30.	0300	747250.	0.653 0.805	0.551 1.034
VII	00.	0500	2189945.	2.305 2.493	7.688 7.678
VII	30.	0500	800289.	0.646 0.717	1.255 1.121
VII	00.	0700	1822175.	2.982 2.865	9.247 8.797
VII	30.	0700	604070.	0.502 0.519	0.296 0.357

TABLE A12

(pages 187-200)

Chlorophyll *a* per particulate volume ($\text{mg}/\mu^3 \times 10^{-12}$),
photosynthetic potential per particulate volume
($\text{mg C/hr}/\mu^3 \times 10^{-12}$) and assimilation ratios (mg C/hr/mg
chl-a) for Endeavour Cruise, Stations E-1 and E-2.

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
I	00.	0900	1.640	1.084	0.101	0.592	0.061	0.093	0.361	0.547
		MEAN V&LUES	1.362		0.346		0.265			
I	30.	0900	1.467	1.459	0.718	0.510	0.489	0.492	0.348	0.350
		MEAN V&LUES	1.463		0.614		0.420			
I	00.	1100	-0.001	1.245	1.485	1.339	*****	1.193	*****	1.075
		MEAN V&LUES	0.622		1.412		*****			
I	30.	1100	1.210	1.410	1.332	1.279	1.101	0.945	1.058	0.907
		MEAN V&LUES	1.310		1.306		1.003			
I	00.	1300	1.155	1.146	1.986	1.761	1.719	1.734	1.525	1.538
		MEAN V&LUES	1.150		1.874		1.629			
I	30.	1300	1.333	1.379	0.373	0.331	0.280	0.270	0.249	0.240
		MEAN V&LUES	1.356		0.352		0.260			
I	00.	1500	1.102	1.101	1.983	2.149	1.799	1.801	1.950	1.951
		MEAN V&LUES	1.102		2.066		1.875			
I	30.	1500	1.357	1.228	2.338	2.311	1.723	1.904	1.703	1.882
		MEAN V&LUES	1.293		2.325		1.803			
I	00.	1700	1.045	0.980	1.372	2.639	2.270	2.420	2.526	2.693
		MEAN V&LUES	1.012		2.505		2.477			
I	30.	1700	1.864	1.783	2.789	2.925	1.497	1.565	1.570	1.641
		MEAN V&LUES	1.823		2.857		1.568			
I	00.	1900	1.173	1.029	0.201	1.833	0.171	0.195	1.563	1.781
		MEAN V&LUES	1.101		1.017		0.928			
I	30.	1900	1.142	1.283	0.618	0.666	0.541	0.482	0.583	0.519
		MEAN V&LUES	1.213		0.642		0.531			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)				
I	00.	2100	1.041	0.951	0.955	1.276	0.917	1.004	1.225	1.342	
		MEAN VALUES	0.996		1.115		1.122				
I	30.	2100	1.332	1.254	-0.016	0.561	-0.012	-0.012	0.421	0.447	
		MEAN VALUES	1.293		0.273		0.211				
I	00.	2300	0.922	0.907	1.504	1.485	1.631	1.658	1.610	1.637	
		MEAN VALUES	0.915		1.495		1.634				
I	30.	2300	1.008	0.875	0.572	1.851	0.568	0.655	1.836	2.116	
		MEAN VALUES	0.941		1.212		1.294				
I	00.	0100	1.263	1.180	2.261	1.659	1.791	1.916	1.314	1.406	
		MEAN VALUES	1.222		1.960		1.607				
I	30.	0100	1.042	1.000	3.280	0.504	3.147	3.281	0.484	0.505	100
		MEAN VALUES	1.021		1.892		1.854				
I	00.	0300	1.058	1.006	0.440	2.348	0.416	0.437	2.219	2.335	
		MEAN VALUES	1.032		1.394		1.352				
I	30.	0300	1.103	1.068	0.945	0.495	0.857	0.885	0.449	0.464	
		MEAN VALUES	1.085		0.720		0.664				
I	00.	0500	1.208	1.187	2.814	2.807	2.329	2.371	2.323	2.365	
		MEAN VALUES	1.197		2.810		2.347				
I	30.	0500	1.117	1.127	0.659	0.637	0.590	0.584	0.570	0.565	
		MEAN VALUES	1.122		0.648		0.577				
I	00.	0700	1.156	1.165	2.273	3.722	1.966	1.951	3.219	3.194	
		MEAN VALUES	1.161		2.998		2.583				
I	30.	0700	1.512	1.531	3.807	2.528	2.519	2.487	1.672	1.651	
		MEAN VALUES	1.521		3.167		2.082				

DAY	DEPTH	TIME	CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
II	00.	0900	1.214	1.230	5.555	3.173	4.576	4.517	2.614	2.580
		MEAN V&LUES	1.222		4.364		3.572			
II	30.	0900	1.455	1.400	3.943	3.435	2.710	2.817	2.361	2.453
		MEAN V&LUES	1.427		3.689		2.585			
II	00.	1100	1.173	1.168	3.675	3.722	3.133	3.145	3.174	3.186
		MEAN V&LUES	1.171		3.699		3.160			
II	30.	1100	1.376	1.365	3.529	5.147	2.565	2.587	3.740	3.772
		MEAN V&LUES	1.370		4.338		3.166			
II	00.	1300	0.939	0.927	3.506	4.199	3.733	3.780	4.471	4.527
		MEAN V&LUES	0.933		3.853		4.128			
II	30.	1300	1.007	0.979	3.332	2.329	3.309	3.403	2.313	2.378
		MEAN V&LUES	0.993		2.830		2.851			
II	00.	1500	0.598	0.591	2.240	2.212	3.748	3.792	3.701	3.745
		MEAN V&LUES	0.594		2.226		3.747			
II	30.	1500	1.111	1.091	1.117	4.025	1.006	1.024	3.623	3.689
		MEAN V&LUES	1.101		2.571		2.335			
II	00.	1700	1.039	1.010	3.579	3.597	3.444	3.542	3.461	3.560
		MEAN V&LUES	1.025		3.588		3.502			
II	30.	1700	1.170	1.059	2.779	3.263	2.376	2.623	2.789	3.080
		MEAN V&LUES	1.114		3.021		2.717			
II	00.	1900	0.947	0.923	2.501	2.301	2.747	2.818	2.430	2.493
		MEAN V&LUES	0.935		2.451		2.622			
II	30.	1900	1.388	1.390	3.654	3.426	2.632	2.629	2.468	2.465
		MEAN V&LUES	1.389		3.540		2.549			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
II	00.	2100	1.239	1.103	2.112	1.777	1.705	1.914	1.434	1.610
		MEAN V&LUES	1.171		1.945		1.666			
II	30.	2100	1.187	1.171	1.910	1.877	1.609	1.631	1.581	1.603
		MEAN V&LUES	1.179		1.893		1.606			
II	00.	2300	1.161	1.293	2.997	2.378	2.580	2.318	2.048	1.839
		MEAN V&LUES	1.227		2.688		2.196			
II	30.	2300	1.527	1.488	3.732	1.982	2.443	2.508	1.297	1.332
		MEAN V&LUES	1.508		2.857		1.895			
II	00.	0100	0.929	0.920	2.096	2.104	2.255	2.279	2.265	2.288
		MEAN V&LUES	0.924		2.100		2.272			
II	30.	0100	1.169	1.211	2.711	2.318	2.319	2.239	1.982	1.914
		MEAN V&LUES	1.190		2.515		2.114			
II	00.	0300	0.740	0.759	1.766	1.942	2.386	2.328	2.623	2.559
		MEAN V&LUES	0.749		1.854		2.474			
II	30.	0300	0.794	0.823	2.364	2.350	2.978	2.874	2.961	2.857
		MEAN V&LUES	0.808		2.357		2.918			
II	00.	0500	0.873	1.235	2.670	2.737	3.058	2.162	3.136	2.216
		MEAN V&LUES	1.054		2.704		2.643			
II	30.	0500	1.221	1.173	2.729	2.859	2.235	2.328	2.342	2.439
		MEAN V&LUES	1.197		2.794		2.336			
II	00.	0700	0.935	0.918	3.283	2.823	3.513	3.575	3.021	3.074
		MEAN V&LUES	0.926		3.053		3.296			
II	30.	0700	1.111	1.108	2.261	3.287	2.035	2.041	2.958	2.967
		MEAN V&LUES	1.110		2.774		2.500			

DAY	DEPTH	TIME	CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
III	00.	0900	1.309	1.380	4.464	4.737	3.411	3.236	3.620	3.433
		MEAN VALUES	1.344		4.601		3.425			
III	30.	0900	1.407	1.369	4.316	1.327	3.067	3.152	0.943	0.970
		MEAN VALUES	1.388		2.821		2.033			
III	00.	1100	1.122	1.156	4.305	3.936	3.838	3.726	3.509	3.406
		MEAN VALUES	1.139		4.120		3.620			
III	30.	1100	1.133	1.137	3.618	0.592	3.192	3.182	0.523	0.521
		MEAN VALUES	1.135		2.105		1.855			
III	00.	1300	0.898	0.921	2.754	2.844	3.067	2.990	3.167	3.087
		MEAN VALUES	0.910		2.799		3.078			
III	30.	1300	1.083	1.094	3.360	3.416	3.101	3.070	3.154	3.122
		MEAN VALUES	1.089		3.388		3.112			
III	00.	1500	1.143	1.218	3.852	4.437	3.371	3.163	3.883	3.644
		MEAN VALUES	1.180		4.145		3.515			
III	30.	1500	NO DATA		NO DATA		3.448	3.413	3.060	3.028
		MEAN VALUE					3.237			
III	00.	1700	NO DATA		NO DATA		2.345	2.582	2.215	2.440
		MEAN VALUE					2.395			
III	30.	1700	NO DATA		NO DATA		2.326	2.272	2.743	2.680
		MEAN VALUE					2.505			
III	00.	1900	NO DATA		NO DATA		3.708	3.636	3.070	3.010
		MEAN VALUE					3.356			
III	30.	1900	NO DATA		NO DATA		2.634	2.481	2.473	2.329
		MEAN VALUE					2.479			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)	PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR./CU. MICRON) (X 10E-12)	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
III	00.	2100	NO DATA	NO DATA	3.369	3.938	3.924	4.587
		MEAN VALUE				3.955		
III	30.	2100	NO DATA	NO DATA	2.805	2.974	2.965	3.144
		MEAN VALUE				2.972		
III	00.	2300	NO DATA	NO DATA	0.473	0.479	3.704	3.750
		MEAN VALUE				2.101		
III	30.	2300	NO DATA	NO DATA	0.514	0.506	2.192	2.157
		MEAN VALUE				1.342		
III	00.	0100	NO DATA	NO DATA	2.874	2.850	2.017	2.000
		MEAN VALUE				2.435		
III	30.	0100	NO DATA	NO DATA	1.349	1.447	0.609	0.654
		MEAN VALUE				1.015		
III	00.	0300	NO DATA	NO DATA	2.246	2.351	3.121	3.267
		MEAN VALUE				2.746		
III	30.	0300	NO DATA	NO DATA	2.435	2.619	1.524	1.638
		MEAN VALUE				2.054		
III	00.	0500	NO DATA	NO DATA	0.735	0.789	2.911	3.126
		MEAN VALUE				1.890		
III	30.	0500	NO DATA	NO DATA	2.952	3.005	1.480	1.506
		MEAN VALUE				2.236		
III	00.	0700	NO DATA	NO DATA	1.799	1.896	2.003	2.112
		MEAN VALUE				1.953		
III	30.	0700	NO DATA	NO DATA	0.519	0.522	1.765	1.774
		MEAN VALUE				1.145		

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG./HR./CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR./MG. CHL A)			
IV	00.	0900	1.389	1.324	4.668	4.245	3.360	3.526	3.055	3.207
		MEAN V&LUES	1.357		4.457		3.287			
IV	30.	0900	0.819	0.820	1.583	0.356	1.934	1.931	0.435	0.434
		MEAN V&LUES	0.819		0.970		1.184			
IV	00.	1100	1.601	1.556	3.897	3.792	2.435	2.504	2.369	2.437
		MEAN V&LUES	1.578		3.844		2.436			
IV	30.	1100	0.737	0.750	1.747	1.525	2.372	2.330	2.069	2.033
		MEAN V&LUES	0.743		1.636		2.201			
IV	00.	1300	1.384	1.421	4.455	4.431	3.220	3.135	3.202	3.118
		MEAN V&LUES	1.402		4.443		3.169			
IV	30.	1300	0.639	0.612	0.276	1.707	0.432	0.451	2.677	2.787
		MEAN V&LUES	0.626		0.992		1.586			
IV	00.	1500	1.496	1.496	3.671	3.958	2.454	2.454	2.646	2.646
		MEAN V&LUES	1.496		3.814		2.550			
IV	30.	1500	0.693	0.681	1.287	1.480	1.857	1.891	2.135	2.174
		MEAN V&LUES	0.687		1.383		2.014			
IV	00.	1700	1.491	1.457	3.274	3.437	2.196	2.248	2.305	2.360
		MEAN V&LUES	1.474		3.356		2.277			
IV	30.	1700	0.665	0.619	1.260	1.357	2.045	2.197	2.041	2.192
		MEAN V&LUES	0.642		1.358		2.119			
IV	00.	1900	1.249	1.226	1.249	2.756	1.000	1.019	2.207	2.248
		MEAN V&LUES	1.237		2.003		1.619			
IV	30.	1900	0.676	0.661	0.082	1.377	0.121	0.124	2.037	2.084
		MEAN V&LUES	0.668		0.729		1.091			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
IV	00.	2100	1.574	1.549	2.134	2.271	1.388	1.410	1.443	1.466
		MEAN V&LUES	1.562		2.228		1.427			
IV	30.	2100	0.657	0.671	1.330	1.406	2.025	1.983	2.141	2.097
		MEAN V&LUES	0.664		1.368		2.061			
IV	00.	2300	1.033	1.074	2.264	2.190	2.192	2.107	2.120	2.039
		MEAN V&LUES	1.054		2.227		2.114			
IV	30.	2300	0.735	0.639	1.405	1.468	1.911	2.198	1.997	2.296
		MEAN V&LUES	0.687		1.436		2.100			
IV	00.	0100	1.027	1.181	2.306	2.052	2.245	1.953	1.997	1.738
		MEAN V&LUES	1.104		2.179		1.983			
IV	30.	0100	0.897	0.890	1.878	1.798	2.095	2.110	2.005	2.019
		MEAN V&LUES	0.894		1.838		2.057			
IV	00.	0300	1.186	1.133	2.703	2.780	2.279	2.386	2.345	2.454
		MEAN V&LUES	1.159		2.742		2.366			
IV	30.	0300	0.960	1.014	2.126	2.324	2.213	2.096	2.420	2.291
		MEAN V&LUES	0.987		2.225		2.255			
IV	00.	0500	1.386	1.543	3.633	3.581	2.622	2.355	2.584	2.321
		MEAN V&LUES	1.464		3.607		2.471			
IV	30.	0500	0.599	0.610	0.072	1.561	0.119	0.117	2.607	2.561
		MEAN V&LUES	0.604		0.816		1.351			
IV	00.	0700	0.928	0.880	3.372	3.644	3.632	3.831	3.924	4.139
		MEAN V&LUES	0.904		3.508		3.881			
IV	30.	0700	0.536	0.598	1.135	1.333	2.209	1.982	2.486	2.231
		MEAN V&LUES	0.567		1.259		2.227			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)				
V	00.	0900	1.978	1.966	5.137	5.688	2.597	2.613	2.875	2.893	
		MEAN V&LUES	1.972		5.413		2.745				
V	30.	0900	1.449	1.495	2.688	3.115	1.854	1.797	2.149	2.083	
		MEAN V&LUES	1.472		2.901		1.971				
V	00.	1100	1.446	1.398	4.167	4.125	2.881	2.980	2.852	2.950	
		MEAN V&LUES	1.422		4.146		2.916				
V	30.	1100	0.667	0.702	1.954	1.913	2.930	2.786	2.869	2.727	
		MEAN V&LUES	0.684		1.934		2.828				
V	00.	1300	1.442	1.287	3.827	3.758	2.654	2.973	2.606	2.919	
		MEAN V&LUES	1.365		3.792		2.788				
V	30.	1300	0.729	0.740	1.564	1.324	2.146	2.113	1.817	1.789	105
		MEAN V&LUES	0.735		1.444		1.966				
V	00.	1500	1.358	1.347	3.238	3.671	2.384	2.405	2.703	2.726	
		MEAN V&LUES	1.352		3.454		2.554				
V	30.	1500	0.794	0.771	1.080	1.217	1.360	1.401	1.533	1.580	
		MEAN V&LUES	0.782		1.148		1.468				
V	00.	1700	1.225	1.234	3.625	3.641	2.960	2.938	2.973	2.951	
		MEAN V&LUES	1.229		3.633		2.955				
V	30.	1700	0.722	0.735	1.740	1.808	2.412	2.369	2.505	2.461	
		MEAN V&LUES	0.728		1.774		2.437				
V	00.	1900	1.171	1.176	3.557	3.160	3.039	3.024	2.699	2.686	
		MEAN V&LUES	1.174		3.359		2.862				
V	30.	1900	0.630	0.647	1.126	1.476	1.788	1.742	2.343	2.283	
		MEAN V&LUES	0.638		1.301		2.039				

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
V	00.	2100	2.175	2.133	4.146	4.227	1.906	1.944	1.944	1.982
		MEAN VALUES	2.154		4.187		1.944			
V	30.	2100	1.489	1.483	2.503	2.701	1.681	1.687	1.814	1.821
		MEAN VALUES	1.486		2.602		1.751			
V	00.	2300	2.521	2.421	4.410	4.523	1.749	1.821	1.794	1.868
		MEAN VALUES	2.471		4.466		1.808			
V	30.	2300	1.725	1.740	2.978	2.791	1.726	1.711	1.618	1.604
		MEAN VALUES	1.732		2.884		1.665			
V	00.	0100	1.704	1.666	1.982	2.413	1.163	1.189	1.416	1.448
		MEAN VALUES	1.685		2.198		1.304			
V	30.	0100	1.655	1.671	2.452	2.543	1.481	1.467	1.536	1.521
		MEAN VALUES	1.663		2.497		1.502			
V	00.	0300	1.291	1.301	2.043	2.486	1.582	1.570	1.926	1.911
		MEAN VALUES	1.296		2.264		1.747			
V	30.	0300	0.789	0.776	1.485	1.450	1.883	1.912	1.838	1.867
		MEAN VALUES	0.783		1.467		1.875			
V	00.	0500	1.312	0.816	2.567	0.732	1.956	3.145	0.558	0.897
		MEAN VALUES	1.064		1.649		1.639			
V	30.	0500	0.877	1.405	1.509	1.493	1.721	1.074	1.703	1.063
		MEAN VALUES	1.141		1.501		1.390			
V	00.	0700	1.263	1.248	2.695	3.260	2.135	2.159	2.582	2.612
		MEAN VALUES	1.255		2.977		2.372			
V	30.	0700	0.726	0.790	1.646	1.623	2.268	2.085	2.236	2.056
		MEAN VALUES	0.758		1.635		2.161			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)				
VI	00.	0900	1.068	1.029	5.546	5.416	5.191	5.389	5.069	5.262	
		MEAN VALUES	1.049		5.481		5.228				
VI	30.	0900	0.726	0.738	1.840	1.734	2.535	2.492	2.388	2.348	
		MEAN VALUES	0.732		1.787		2.441				
VI	00.	1100	1.110	1.099	5.123	5.331	4.613	4.663	4.801	4.853	
		MEAN VALUES	1.104		5.227		4.733				
VI	30.	1100	0.777	0.686	2.539	2.411	3.269	3.702	3.105	3.516	
		MEAN VALUES	0.731		2.475		3.398				
VI	00.	1300	0.920	0.997	4.926	3.985	5.354	4.942	4.331	3.998	
		MEAN VALUES	0.958		4.455		4.656				
VI	30.	1300	0.846	0.855	2.370	2.143	2.800	2.772	2.532	2.507	197
		MEAN VALUES	0.851		2.256		2.653				
VI	00.	1500	1.248	1.373	4.441	3.808	3.558	3.235	3.051	2.774	
		MEAN VALUES	1.310		4.124		3.154				
VI	30.	1500	0.929	0.922	1.632	1.729	1.757	1.771	1.861	1.876	
		MEAN VALUES	0.925		1.680		1.816				
VI	00.	1700	1.467	1.414	3.805	3.746	2.593	2.690	2.553	2.649	
		MEAN VALUES	1.441		3.775		2.621				
VI	30.	1700	0.880	0.851	2.139	1.449	2.431	2.513	1.648	1.703	
		MEAN VALUES	0.865		1.794		2.074				
VI	00.	1900	1.317	1.228	2.271	1.760	1.725	1.850	1.337	1.434	
		MEAN VALUES	1.272		2.016		1.586				
VI	30.	1900	0.759	0.847	2.026	1.629	2.671	2.393	2.148	1.924	
		MEAN VALUES	0.803		1.828		2.284				

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)				
VI	00.	2100	1.050	1.034	1.959	1.895	1.865	1.894	1.804	1.831	
		MEAN V&LUES	1.042		1.927		1.848				
VI	30.	2100	0.746	0.752	1.296	1.098	1.738	1.723	1.472	1.460	
		MEAN V&LUES	0.749		1.197		1.598				
VI	00.	2300	1.566	1.543	2.779	2.820	1.775	1.800	1.801	1.827	
		MEAN V&LUES	1.555		2.799		1.801				
VI	30.	2300	0.805	0.795	1.258	1.218	1.564	1.582	1.514	1.532	
		MEAN V&LUES	0.800		1.238		1.548				
VI	00.	0100	1.961	1.941	3.395	3.751	1.731	1.749	1.912	1.932	
		MEAN V&LUES	1.951		3.573		1.831				
VI	30.	0100	0.947	0.915	0.450	0.366	0.475	0.492	0.387	0.401	198
		MEAN V&LUES	0.931		0.408		0.439				
VI	00.	0300	1.924	1.864	3.670	3.814	1.907	1.969	1.982	2.046	
		MEAN V&LUES	1.894		3.742		1.976				
VI	30.	0300	0.770	0.833	1.065	1.231	1.382	1.278	1.599	1.478	
		MEAN V&LUES	0.802		1.148		1.434				
VI	00.	0500	1.908	1.832	4.809	4.359	2.521	2.624	2.285	2.379	
		MEAN V&LUES	1.870		4.584		2.452				
VI	30.	0500	0.839	0.815	1.219	1.149	1.452	1.495	1.369	1.410	
		MEAN V&LUES	0.827		1.184		1.432				
VI	00.	0700	1.722	1.590	4.507	4.494	2.618	2.835	2.610	2.827	
		MEAN V&LUES	1.656		4.500		2.722				
VI	30.	0700	0.823	0.840	1.200	1.290	1.458	1.428	1.569	1.536	
		MEAN V&LUES	0.831		1.245		1.498				

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
VII	00.	0900	1.696	1.741	4.692	5.701	2.767	2.695	3.362	3.275
		MEAN VALUES	1.718		5.196		3.025			
VII	30.	0900	0.913	0.875	1.875	1.774	2.053	2.144	1.943	2.028
		MEAN VALUES	0.894		1.825		2.042			
VII	00.	1100	1.272	1.264	4.213	4.078	3.313	3.334	3.207	3.227
		MEAN VALUES	1.268		4.145		3.270			
VII	30.	1100	0.684	0.647	1.119	0.992	1.636	1.730	1.450	1.533
		MEAN VALUES	0.665		1.055		1.587			
VII	00.	1300	1.370	1.233	4.526	4.727	3.305	3.671	3.451	3.833
		MEAN VALUES	1.301		4.627		3.565			
VII	30.	1300	0.662	0.673	1.493	1.178	2.255	2.220	1.779	1.751
		MEAN VALUES	0.667		1.335		2.001			
VII	00.	1500	1.223	1.239	4.359	4.290	3.563	3.518	3.507	3.463
		MEAN VALUES	1.231		4.325		3.513			
VII	30.	1500	0.810	0.788	1.592	1.434	1.966	2.021	1.771	1.821
		MEAN VALUES	0.799		1.513		1.895			
VII	00.	1700	0.998	1.077	2.926	2.996	2.931	2.716	3.001	2.781
		MEAN VALUES	1.038		2.961		2.857			
VII	30.	1700	1.038	1.042	1.750	1.711	1.687	1.679	1.649	1.642
		MEAN VALUES	1.040		1.731		1.664			
VII	00.	1900	1.063	0.970	2.748	2.629	2.586	2.832	2.474	2.709
		MEAN VALUES	1.017		2.689		2.650			
VII	30.	1900	1.061	1.085	1.402	1.383	1.321	1.293	1.303	1.275
		MEAN VALUES	1.073		1.393		1.298			

DAY DEPTH TIME			CHLOROPHYLL PER PARTICLE VOLUME (MG./CU. MICRON) (X 10E-12)		PHOTOSYNTHETIC POTENTIAL PER PARTICLE VOLUME (MG/HR/CU. MICRON) (X 10E-12)		ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)				
VII	00.	2100	0.929	0.948	1.657	1.480	1.784	1.747	1.594	1.561	
		MEAN V&LUES	0.939		1.569		1.671				
VII	30.	2100	1.070	1.045	1.368	1.366	1.278	1.308	1.277	1.307	
		MEAN V&LUES	1.058		1.367		1.293				
VII	00.	2300	1.426	1.410	2.484	2.296	1.741	1.761	1.610	1.628	
		MEAN V&LUES	1.418		2.390		1.685				
VII	30.	2300	0.800	0.788	0.958	0.937	1.198	1.217	1.171	1.190	
		MEAN V&LUES	0.794		0.948		1.194				
VII	00.	0100	1.290	1.263	2.002	2.094	1.552	1.585	1.623	1.658	
		MEAN V&LUES	1.277		2.048		1.604				
VII	30.	0100	0.887	0.892	1.200	0.940	1.352	1.344	1.060	1.054	200
		MEAN V&LUES	0.890		1.070		1.203				
VII	00.	0300	1.254	1.235	2.397	2.485	1.912	1.941	1.981	2.012	
		MEAN V&LUES	1.244		2.441		1.962				
VII	30.	0300	0.874	1.077	0.737	1.384	0.844	0.684	1.583	1.284	
		MEAN V&LUES	0.976		1.061		1.099				
VII	00.	0500	1.053	1.138	3.511	3.506	3.335	3.084	3.331	3.080	
		MEAN V&LUES	1.095		3.508		3.208				
VII	30.	0500	0.807	0.896	1.558	1.401	1.943	1.750	1.735	1.563	
		MEAN V&LUES	0.852		1.484		1.748				
VII	00.	0700	1.637	1.572	5.075	4.828	3.101	3.228	2.950	3.071	
		MEAN V&LUES	1.604		4.951		3.087				
VII	30.	0700	0.831	0.859	0.490	0.591	0.590	0.570	0.711	0.688	
		MEAN V&LUES	0.845		0.541		0.640				

TABLE A13

(pages 202-215)

Chlorophyll *a* concentration (mg/m^3) photosynthetic potential ($\text{mg C}/\text{m}^3/\text{hr}$) for Station P cruise, Days A-D and Experiments A-C.

Note: Experiment A is referred to as Day E,
Experiment B as Day F and G and
Experiment C as Day H.

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
A - T	00	0900	0.906 0.466	0.736 0.856
A - N	00	0900	0.662 0.591	0.857 0.762
A - T	00	1100	0.459 0.369	0.939 0.923
A - N	00	1100	0.477 0.584	0.830 0.930
A - T	00	1300	0.0 0.774	0.514 0.534
A - N	00	1300	0.616 0.414	0.541 0.523
A - T	00	1500	0.462 0.356	0.421 0.333
A - N	00	1500	0.520 0.0	0.361 0.355
A - T	00	1700	0.530 0.513	0.513 0.540
A - N	00	1700	0.499 0.447	0.482 0.413
A - T	00	1900	0.430 0.436	0.450 0.446
A - N	00	1900	0.377 0.376	0.410 0.414

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
A - T	00	2100	0.371 0.324	0.373 0.377
A - N	00	2100	0.357 0.375	0.313 0.347
A - T	00	2300	0.323 0.405	0.474 0.482
A - N	00	2300	0.355 0.286	0.434 0.441
A - T	00	0100	0.317 0.392	0.566 0.596
A - N	00	0100	0.356 0.355	0.499 0.542
A - T	00	0300	0.437 0.428	0.883 0.640
A - N	00	0300	0.325 0.367	0.771 0.672
A - T	00	0500	0.318 0.363	0.613 0.632
A - N	00	0500	0.387 0.340	0.517 0.545
A - T	00	0700	0.355 0.367	0.843 0.919
A - N	00	0700	0.385 0.352	0.710 0.712

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
B -BT	00	0900	0.395 0.483	1.278 1.232
B -BN	00	0900	0.382 0.334	1.196 1.122
B -BT	00	1100	0.331 0.306	1.030 1.090
B -BN	00	1100	0.320 0.331	1.033 0.988
B -BT	00	1300	0.513 0.600	2.405 2.097
B -BN	00	1300	0.569 0.655	2.139 2.184
B -BT	00	1500	0.382 0.388	1.033 1.042
B -BN	00	1500	0.308 0.382	1.032 1.099
B -BT	00	1700	0.358 0.261	1.024 0.997
B -BN	00	1700	0.298 0.284	0.969 1.070
B -BT	00	1900	0.412 0.508	0.915 0.953
B -BN	00	1900	0.429 0.412	0.900 0.935

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
B -BT	00	2100	0.474 0.473	0.541 0.540
B -BN	00	2100	0.425 0.458	0.554 0.520
B -BT	00	2300	0.350 0.304	0.533 0.507
B -BN	00	2300	0.234 0.330	0.524 0.527
B -BT	00	0100	0.307 0.266	0.708 0.613
B -BN	00	0100	0.298 0.289	0.647 0.606
B -BT	00	0300	0.341 0.340	0.850 0.915
B -BN	00	0300	0.344 0.284	1.751 0.688
B -BT	00	0500	0.264 0.416	0.576 1.075
B -BN	00	0500	0.414 0.225	1.069 1.014
B -BT	00	0700	0.546 0.509	1.747 1.686
B -BN	00	0700	0.349 0.513	1.441 1.587

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
C - S	00	0900	0.630 0.726	1.688 1.725
C - D	30	0900	0.729 0.695	0.632 0.685
C - S	00	1100	0.811 0.728	1.877 1.786
C - D	30	1100	0.561 0.580	1.038 1.029
C - S	00	1300	0.750 0.699	1.903 1.646
C - D	30	1300	0.736 0.668	0.648 0.759
C - S	00	1500	0.936 1.474	1.736 1.931
C - D	30	1500	0.659 0.684	0.560 0.532
C - S	00	1700	0.636 0.708	1.186 0.981
C - D	30	1700	0.588 0.712	0.765 0.742
C - S	00	1900	0.812 0.788	0.732 0.805
C - D	30	1900	0.701 0.730	0.578 0.603

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
C - S	00	2100	0.703 0.700	0.788 0.857
C - D	30	2100	0.655 0.670	0.748 0.787
C - S	00	2300	0.716 0.720	0.887 0.822
C - D	30	2300	0.748 0.697	0.725 0.752
C - S	00	0100	0.584 0.619	0.858 0.764
C - D	30	0100	NO DATA OBTAINED DUE 30 FT SEAS	
C - S	00	0300	0.605 0.646	1.158 1.066
C - D	30	0300	NO DATA OBTAINED DUE 30 FT SEAS	
C - S	00	0500	0.638 0.630	1.236 1.139
C - D	30	0500	NO DATA OBTAINED DUE 30 FT SEAS	
C - S	00	0700	0.668 0.657	1.895 1.783
C - D	30	0700	NO DATA OBTAINED DUE 30 FT SEAS	

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
D -BS	00	0900	0.513 0.505	1.948 1.937
D -RD	30	0900	0.407 0.345	1.124 0.937
D -BS	00	1100	0.518 0.338	1.475 1.354
D -BC	30	1100	0.596 0.525	1.065 0.936
D -BS	00	1300	0.365 0.340	1.456 1.440
D -BC	30	1300	0.619 0.489	1.208 1.289
D -BS	00	1500	0.579 0.468	1.378 1.488
D -BD	30	1500	0.541 0.654	1.026 0.931
D -BS	00	1700	0.524 0.466	1.443 1.293
D -BD	30	1700	0.605 0.597	1.025 1.036
D -BS	00	1900	0.374 0.401	0.881 0.899
D -BD	30	1900	0.647 0.571	0.810 0.846

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
D -BS	00	2100	0.426 0.441	0.858 0.848
D -BD	30	2100	0.468 0.500	0.733 0.725
D -BS	00	2300	0.385 0.371	0.869 0.899
D -BD	30	2300	0.541 0.528	0.755 0.777
D -BS	00	0100	0.375 0.387	0.970 0.949
D -BD	30	0100	0.482 0.496	0.774 0.797
D -BS	00	0300	0.398 0.382	1.068 1.036
D -BD	30	0300	0.617 0.559	0.798 0.755
D -BS	00	0500	0.355 0.356	1.251 1.237
D -BD	30	0500	0.591 0.0	0.961 0.964
D -BS	00	0700	0.528 0.608	1.338 1.397
D -BD	30	0700	0.571 0.446	0.790 0.767

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
E - L	00	0900	1.488 1.389	2.582 2.494
E - C	00	0900	1.462 1.335	1.371 2.555
E - L	00	1200	1.362 1.195	4.012 3.935
E - C	00	1200	1.469 1.439	2.466 2.428
E - L	00	1500	1.397 1.240	1.273 1.214
E - C	00	1500	1.596 1.605	0.885 0.857
E - L	00	1800	1.582 1.573	3.041 2.772
E - C	00	1800	1.655 1.674	1.400 1.203
E - L	00	2100	1.578 1.628	2.353 2.409
E - C	00	2100	1.758 1.736	0.928 1.082
E - L	00	2400	1.628 0.0	1.988 1.869
E - C	00	2400	1.879 0.0	1.355 1.409

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
E - L	00	0300.	1.633 1.447	2.203 2.389
E - C	00	0300	1.779 1.837	1.608 1.702
E - L	00	0600	1.782 1.766	1.691 1.497
E - C	00	0600	2.010 1.963	1.603 1.615

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
F -BL	00	0900	1.200 1.313	1.686 1.524
F -BC	00	0900	1.137 1.141	2.797 2.592
F -BL	00	1200	1.189 0.952	1.401 1.532
F -BC	00	1200	1.084 1.011	3.022 1.936
F -BL	00	1500	1.131 0.996	1.940 1.945
F -BC	00	1500	1.036 1.047	1.901 2.003
F -BL	00	1800	1.300 1.172	2.742 2.587
F -BC	00	1800	1.257 1.252	1.344 1.291
F -BL	00	2100	1.040 1.185	3.261 3.148
F -BC	00	2100	1.096 1.351	0.839 0.757
F -BL	00	2400	1.110 1.215	2.788 2.796
F -BC	00	2400	1.612 0.978	0.551 0.604

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
F -BL	00	0300	1.134 1.129	2.660 2.865
F -BC	00	0300	0.965 0.913	0.720 0.823
F -BL	00	0600	1.285 1.211	1.269 1.560
F -BC	00	0600	0.877 1.008	0.600 0.646
G -BL	00	0900	1.215 1.043	1.238 1.103
G -BC	00	0900	0.836 0.867	0.643 0.726

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
H -CL	00	0900	0.937 0.988	2.566 2.323
H -CC	00	0900	0.845 0.838	1.581 2.295
H -CL	00	1200	1.056 0.759	2.387 2.228
H -CC	00	1200	0.802 0.869	1.337 1.481
H -CL	00	1500	0.804 0.730	1.801 1.869
H -CC	00	1500	0.897 0.906	1.292 1.135
H -CL	00	1800	0.747 1.000	1.851 1.457
H -CC	00	1800	0.803 0.862	1.347 1.319
H -CL	00	2100	0.889 0.740	0.706 0.684
H -CC	00	2100	0.848 0.918	0.364 0.416
H -CL	00	2400	0.698 0.692	1.355 1.209
H -CC	00	2400	0.903 0.985	0.942 1.027

DAY	DEPTH	TIME	CHLOROPHYLL A CONCENTRATION (MG/CU.M)	PHOTOSYNTHETIC POTENTIAL (MG/CU.M/HR)
H -CL	00	0300	0.678 0.763	1.185 1.143
H -CC	00	0300	0.975 0.871	1.045 0.957
H -CL	00	0600	0.831 0.789	1.509 1.488
H -CC	00	0600	0.934 0.965	1.860 1.711

TABLE A14

(pages 217-230)

Assimilation ratios (mg C/hr/mg chl-*a*) for Station P
cruise, Days A-D and Experiments A-C.

Note: Experiment A is referred to as Day E,
Experiment B as Day F and G, and
Experiment C as Day H.

DAY DEPTH TIME

ASSIMILATION RATIO-
(PHOTOSYNTHETIC POTENTIAL/CHL A)
(MG.CARBON/HR/MG.CHL A)

A - T	00	0900	0.812	1.579	0.945	1.837
		MEAN VALUE		1.293		
A - N	00	0900	1.295	1.450	1.151	1.289
		MEAN VALUE		1.296		
A - T	00	1100	2.046	2.545	2.011	2.501
		MEAN VALUE		2.276		
A - N	00	1100	1.740	1.421	1.950	1.592
		MEAN VALUE		1.676		
A - T	00	1300	0.0	0.664	0.0	0.690
		MEAN VALUE		0.677		
A - N	00	1300	0.878	1.307	0.849	1.263
		MEAN VALUE		1.074		
A - T	00	1500	0.911	1.183	0.721	0.935
		MEAN VALUE		0.938		
A - N	00	1500	0.694	0.0	0.683	0.0
		MEAN VALUE		0.688		
A - T	00	1700	0.968	1.000	1.019	1.053
		MEAN VALUE		1.010		
A - N	00	1700	0.966	1.078	0.828	0.924
		MEAN VALUE		0.949		
A - T	00	1900	1.047	1.032	1.037	1.023
		MEAN VALUE		1.035		
A - N	00	1900	1.088	1.090	1.098	1.101
		MEAN VALUE		1.094		

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
A - T	00	2100	1.005	1.151	1.016	1.164
		MEAN VALUE		1.084		
A - N	00	2100	0.877	0.835	0.972	0.925
		MEAN VALUE		0.902		
A - T	00	2300	1.467	1.170	1.492	1.190
		MEAN VALUE		1.330		
A - N	00	2300	1.223	1.517	1.242	1.542
		MEAN VALUE		1.381		
A - T	00	0100	1.785	1.444	1.880	1.520
		MEAN VALUE		1.657		
A - N	00	0100	1.402	1.406	1.522	1.527
		MEAN VALUE		1.464		
A - T	00	0300	2.021	2.063	1.465	1.495
		MEAN VALUE		1.761		
A - N	00	0300	2.372	2.101	2.068	1.831
		MEAN VALUE		2.093		
A - T	00	0500	1.928	1.689	1.987	1.741
		MEAN VALUE		1.836		
A - N	00	0500	1.336	1.521	1.408	1.603
		MEAN VALUE		1.467		
A - T	00	0700	2.375	2.297	2.589	2.504
		MEAN VALUE		2.441		
A - N	00	0700	1.844	2.017	1.849	2.023
		MEAN VALUE		1.933		

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
B -BT	00	0900	3.235	2.646	3.119	2.551
		MEAN VALUE		2.888		
B -BN	00	0900	3.131	3.581	2.937	3.359
		MEAN VALUE		3.252		
B -BT	00	1100	3.112	3.366	3.293	3.562
		MEAN VALUE		3.333		
B -BN	00	1100	3.228	3.121	3.087	2.985
		MEAN VALUE		3.105		
B -BT	00	1300	4.688	4.008	4.088	3.495
		MEAN VALUE		4.070		
B -BN	00	1300	3.759	3.266	3.838	3.334
		MEAN VALUE		3.549		
B -BT	00	1500	2.704	2.662	2.728	2.686
		MEAN VALUE		2.695		
B -BN	00	1500	3.351	2.702	3.568	2.877
		MEAN VALUE		3.124		
B -BT	00	1700	2.860	3.923	2.785	3.820
		MEAN VALUE		3.347		
B -BN	00	1700	3.252	3.412	3.591	3.768
		MEAN VALUE		3.505		
B -BT	00	1900	2.221	1.801	2.313	1.876
		MEAN VALUE		2.053		
B -BN	00	1900	2.098	2.184	2.179	2.269
		MEAN VALUE		2.183		

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
B -BT	00	2100	1.141	1.144	1.139	1.142
		MEAN VALUE	1.141			
B -BN	00	2100	1.304	1.210	1.224	1.135
		MEAN VALUE	1.218			
B -BT	00	2300	1.523	1.753	1.449	1.668
		MEAN VALUE	1.598			
B -BN	00	2300	2.239	1.588	2.252	1.597
		MEAN VALUE	1.919			
B -BT	00	0100	2.306	2.662	1.997	2.305
		MEAN VALUE	2.317			
B -BN	00	0100	2.171	2.239	2.034	2.097
		MEAN VALUE	2.135			
B -BT	00	0300	2.493	2.500	2.683	2.691
		MEAN VALUE	2.592			
B -BN	00	0300	5.090	6.165	2.000	2.423
		MEAN VALUE	3.920			
B -BT	00	0500	3.697	2.346	4.072	2.584
		MEAN VALUE	3.175			
B -BN	00	0500	2.582	4.751	2.449	4.507
		MEAN VALUE	3.572			
B -BT	00	0700	3.200	3.432	3.088	3.312
		MEAN VALUE	3.258			
B -BN	00	0700	4.129	2.809	4.547	3.094
		MEAN VALUE	3.645			

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
C - S	00	0900	2.679	2.325	2.738	2.376
		MEAN VALUE	2.530			
C - D	30	0900	0.867	0.909	0.940	0.986
		MEAN VALUE	0.925			
C - S	00	1100	2.314	2.578	2.202	2.453
		MEAN VALUE	2.387			
C - D	30	1100	1.850	1.790	1.834	1.774
		MEAN VALUE	1.812			
C - S	00	1300	2.537	2.722	2.195	2.355
		MEAN VALUE	2.452			
C - D	30	1300	0.880	0.970	1.031	1.136
		MEAN VALUE	1.004			
C - S	00	1500	1.855	1.178	2.063	1.310
		MEAN VALUE	1.601			
C - D	30	1500	0.850	0.819	0.807	0.778
		MEAN VALUE	0.813			
C - S	00	1700	1.865	1.675	1.542	1.386
		MEAN VALUE	1.617			
C - D	30	1700	1.301	1.074	1.262	1.042
		MEAN VALUE	1.170			
C - S	00	1900	0.901	0.929	0.991	1.022
		MEAN VALUE	0.961			
C - D	30	1900	0.825	0.792	0.860	0.826
		MEAN VALUE	0.826			

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
C - S	00	2100	1.121	1.126	1.219	1.224
		MEAN VALUE	1.172			
C - D	30	2100	1.142	1.116	1.202	1.175
		MEAN VALUE	1.159			
C - S	00	2300	1.239	1.232	1.148	1.142
		MEAN VALUE	1.190			
C - D	30	2300	0.969	1.040	1.005	1.079
		MEAN VALUE	1.023			
C - S	00	0100	1.469	1.386	1.308	1.234
		MEAN VALUE	1.349			
C - D	30	0100	NO DATA OBTAINED DUE TO 30 FT SEAS			
C - S	00	0300	1.914	1.793	1.762	1.650
		MEAN VALUE	1.780			
C - D	30	0300	NO DATA OBTAINED DUE TO 30 FT SEAS			
C - S	00	0500	1.937	1.962	1.785	1.808
		MEAN VALUE	1.873			
C - D	30	0500	NO DATA OBTAINED DUE TO 30 FT SEAS			
C - S	00	0700	2.837	2.884	2.669	2.714
		MEAN VALUE	2.776			
C - D	30	0700	NO DATA OBTAINED DUE TO 30 FT SEAS			

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
D -BS	00	0900	3.797	3.857	3.776	3.836
		MEAN VALUE		3.817		
D -BD	30	0900	2.762	3.258	2.302	2.716
		MEAN VALUE		2.759		
D -BS	00	1100	2.847	4.364	2.614	4.006
		MEAN VALUE		3.458		
D -BD	30	1100	1.787	2.029	1.570	1.783
		MEAN VALUE		1.792		
D -BS	00	1300	3.989	4.282	3.945	4.235
		MEAN VALUE		4.113		
D -BD	30	1300	1.952	2.470	2.082	2.636
		MEAN VALUE		2.285		
D -BS	00	1500	2.380	2.944	2.570	3.179
		MEAN VALUE		2.768		
D -BD	30	1500	1.896	1.569	1.721	1.424
		MEAN VALUE		1.652		
D -BS	00	1700	2.754	3.097	2.468	2.775
		MEAN VALUE		2.773		
D -BD	30	1700	1.694	1.717	1.712	1.735
		MEAN VALUE		1.715		
D -BS	00	1900	2.356	2.197	2.404	2.242
		MEAN VALUE		2.300		
D -BD	30	1900	1.252	1.419	1.308	1.482
		MEAN VALUE		1.365		

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG. CARBON/HR/MG. CHL A)			
D -BS	00	2100	2.014	1.946	1.991	1.923
		MEAN VALUE		1.968		
D -BD	30	2100	1.566	1.466	1.549	1.450
		MEAN VALUE		1.508		
D -BS	00	2300	2.257	2.342	2.335	2.423
		MEAN VALUE		2.339		
D -BD	30	2300	1.396	1.430	1.436	1.472
		MEAN VALUE		1.433		
D -BS	00	0100	2.587	2.506	2.531	2.452
		MEAN VALUE		2.519		
D -BD	30	0100	1.606	1.560	1.654	1.607
		MEAN VALUE		1.607		
D -BS	00	0300	2.683	2.796	2.603	2.712
		MEAN VALUE		2.699		
D -BD	30	0300	1.293	1.428	1.224	1.351
		MEAN VALUE		1.324		
D -BS	00	0500	3.524	3.514	3.485	3.475
		MEAN VALUE		3.499		
D -BD	30	0500	1.626	0.0	1.631	0.0
		MEAN VALUE		1.629		
D -BS	00	0700	2.534	2.201	2.646	2.298
		MEAN VALUE		2.420		
D -BD	30	0700	1.384	1.771	1.343	1.720
		MEAN VALUE		1.554		

ASSIMILATION RATIO-
(PHOTOSYNTHETIC POTENTIAL/CHL A)
(MG.CARBON/HR/MG.CHL A)

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
E - L	00	0900	1.735	1.859	1.676	1.796
		MEAN VALUE	1.766			
E - C	00	0900	0.938	1.027	1.748	1.914
		MEAN VALUE	1.407			
E - L	00	1200	2.946	3.357	2.889	3.293
		MEAN VALUE	3.121			
E - C	00	1200	1.679	1.714	1.653	1.687
		MEAN VALUE	1.683			
E - L	00	1500	0.911	1.027	0.869	0.979
		MEAN VALUE	0.946			
E - C	00	1500	0.555	0.551	0.537	0.534
		MEAN VALUE	0.544			
E - L	00	1800	1.922	1.933	1.752	1.762
		MEAN VALUE	1.842			
E - C	00	1800	0.846	0.836	0.727	0.719
		MEAN VALUE	0.782			
E - L	00	2100	1.491	1.445	1.527	1.480
		MEAN VALUE	1.486			
E - C	00	2100	0.528	0.535	0.615	0.623
		MEAN VALUE	0.575			
E - L	00	2400	1.221	0.0	1.148	0.0
		MEAN VALUE	1.185			
E - C	00	2400	0.721	0.0	0.750	0.0
		MEAN VALUE	0.735			

DAY DEPTH TIME

ASSIMILATION RATIO-
(PHOTOSYNTHETIC POTENTIAL/CHL A)
(MG. CARBON/HR/MG. CHL A)

E - L	00	0300	1.349	1.522	1.463	1.651
		MEAN VALUE		1.496		
E - C	00	0300	0.904	0.875	0.957	0.927
		MEAN VALUE		0.916		
E - L	00	0600	0.949	0.958	0.840	0.848
		MEAN VALUE		0.899		
E - C	00	0600	0.798	0.817	0.803	0.823
		MEAN VALUE		0.810		

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
F-BL	00	0900	1.405	1.284	1.270	1.161
		MEAN VALUE		1.280		
F-BC	00	0900	2.460	2.451	2.280	2.272
		MEAN VALUE		2.366		
F-BL	00	1200	1.178	1.472	1.288	1.609
		MEAN VALUE		1.387		
F-BC	00	1200	2.788	2.989	1.786	1.915
		MEAN VALUE		2.369		
F-BL	00	1500	1.715	1.948	1.720	1.953
		MEAN VALUE		1.834		
F-BC	00	1500	1.835	1.816	1.933	1.913
		MEAN VALUE		1.874		
F-BL	00	1800	2.109	2.340	1.990	2.207
		MEAN VALUE		2.162		
F-BC	00	1800	1.069	1.073	1.027	1.031
		MEAN VALUE		1.050		
F-BL	00	2100	3.136	2.752	3.027	2.657
		MEAN VALUE		2.893		
F-BC	00	2100	0.766	0.621	0.691	0.560
		MEAN VALUE		0.659		
F-BL	00	2400	2.512	2.295	2.519	2.301
		MEAN VALUE		2.407		
F-BC	00	2400	0.342	0.563	0.375	0.618
		MEAN VALUE		0.474		

DAY DEPTH TIME

ASSIMILATION RATIO-
(PHOTOSYNTHETIC POTENTIAL/CHL A)
(MG.CARBON/HR/MG.CHL A)

F	-BL	00	0300	2.346	2.356	2.526	2.538
			MEAN VALUE		2.441		
F	-BC	00	0300	0.746	0.789	0.853	0.901
			MEAN VALUE		0.822		
F	-BL	00	0600	0.988	1.048	1.214	1.288
			MEAN VALUE		1.134		
F	-BC	00	0600	0.684	0.595	0.737	0.641
			MEAN VALUE		0.664		
G	-BL	00	0900	1.019	1.187	0.908	1.058
			MEAN VALUE		1.043		
G	-BC	00	0900	0.769	0.742	0.868	0.837
			MEAN VALUE		0.804		

DAY	DEPTH	TIME	ASSIMILATION RATIO- (PHOTOSYNTHETIC POTENTIAL/CHL A) (MG.CARBON/HR/MG.CHL A)			
H-CL	00	0900	2.739	2.597	2.479	2.351
		MEAN VALUE	2.542			
H-CC	00	0900	1.871	1.887	2.716	2.739
		MEAN VALUE	2.303			
H-CL	00	1200	2.260	3.145	2.110	2.935
		MEAN VALUE	2.613			
H-CC	00	1200	1.667	1.539	1.847	1.704
		MEAN VALUE	1.689			
H-CL	00	1500	2.240	2.467	2.325	2.560
		MEAN VALUE	2.398			
H-CC	00	1500	1.440	1.426	1.265	1.253
		MEAN VALUE	1.346			
H-CL	00	1800	2.478	1.851	1.950	1.457
		MEAN VALUE	1.934			
H-CC	00	1800	1.677	1.563	1.643	1.530
		MEAN VALUE	1.603			
H-CL	00	2100	0.794	0.954	0.769	0.924
		MEAN VALUE	0.860			
H-CC	00	2100	0.429	0.397	0.491	0.453
		MEAN VALUE	0.442			
H-CL	00	2400	1.941	1.958	1.732	1.747
		MEAN VALUE	1.845			
H-CC	00	2400	1.043	0.956	1.137	1.043
		MEAN VALUE	1.045			

DAY DEPTH TIME

ASSIMILATION RATIO-
(PHOTOSYNTHETIC POTENTIAL/CHL A)
(MG.CARBON/HR/MG.CHL A)

H -CL	00	0300	1.748	1.553	1.686	1.498
		MEAN VALUE		1.621		
H -CC	00	0300	1.072	1.200	0.982	1.099
		MEAN VALUE		1.088		
H -CL	00	0600	1.816	1.913	1.791	1.886
		MEAN VALUE		1.851		
H -CC	00	0600	1.991	1.927	1.832	1.773
		MEAN VALUE		1.881		

VITA

Surname: DRINNAN Given Names: ROBERT WARREN

Place of Birth: VICTORIA, B.C. Date of Birth: January 16, 1946

Educational Institutions Attended, with Dates of Entering and Leaving:

UNIVERSITY OF CALGARY, CALGARY 1964-1967

Degrees, Diplomas, Etc., Awarded, with Dates and Names of Institutions:

B.Sc. 1967 University of Calgary

Honors and Awards:

Province of Alberta, Department of Education Grant, 1969

Publications:

Drinnan, R.W., D.V. Ellis, and J.L. Littlepage. 1971. Finnerty Cove Outfall. Report on marine biology and water quality. A report submitted to the Greater Victoria Capital Regional District of British Columbia. 180 pp.

-----, *et al.* 1971. Macaulay Point Outfall Monitoring Program. 5th quarterly data report. Submitted to the Greater Victoria Capital Regional District of British Columbia. 115 pp.

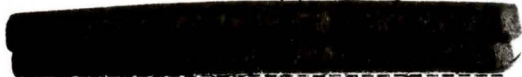
Ellis, D.V., J.L. Littlepage, and R.W. Drinnan. 1971. The Macaulay Point Outfall Monitoring Program Annual Report, 1970-71. Pre-discharge environmental and biological data. Submitted to the Greater Victoria Capital Regional District of British Columbia. 157 pp.

Littlepage, J.L., D.V. Ellis, and R.W. Drinnan. 1972. Distribution of mine and mill tailings in a marine inlet and a comparison of methods and measurements. Presented at Public Inquiry into Mining, Mine-milling and Smelting Industries.

THE UNIVERSITY OF VICTORIA LIBRARY
MANUSCRIPT THESIS AUTHORITY TO
DISTRIBUTE

AUTHOR: This thesis may be lent or microfilm copies made available:

(a) Without restriction



(b) With the restriction that,
for a period of five years

(until _____) the

written approval of the
following is required:

(1) The Chairman, School
of Graduate Studies

(2) The Author

(3) both the Chairman,
School of Graduate
Studies, and the Author

BORROWERS: The borrower undertakes, by signing below, to give proper credit for any use made of the dissertation, and to obtain the consent of the author if it is proposed to make extensive quotations, or to reproduce the dissertation in whole or in part.

Signature of Borrower

Address

Date

