THE PRODUCTION OF PLANKTONIC HERBIVOROUS FOOD CHAINS IN LARGE-SCALE CONTINUOUS CULTURES

by

PENELOPE STEVENSON BROWN
B.Sc., University of Victoria, 1971

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

in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology, Institute of Oceanography)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

August, 1979

© Penelope Stevenson Brown, 1979

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date October 10th, 1979

ABSTRACT

Research Supervisor: Prof. T.R. Parsons

The production of planktonic herbivorous food chains was examined in large scale continuous cultures using a deep nutrient-rich source of seawater to promote high productivity rates. Both turbulent and non-turbulent upwelling systems were investigated in one-stage culture experiments with flushing rates ranging from 0.25/day to 0.75/day. The systems were analyzed in terms of the dynamics of the primary community and their suitability for the growth and survival of two bivalve molluscs, oysters (Crassostrea gigas) and scallops (Chlamys hastata hericia). The results indicated that a high flushing rate of the continuous culture system (0.75/day) was required for the growth of the scallops under natural forcing conditions. Maximum rates of 16.8% per month were achieved at a depth of one metre, due to a reduced light intensity and temperature at this depth compared with surface conditons. In contrast, the one-stage culture system with a flushing rate of 0.25/day provided suitable environmental conditions for the growth of oysters, although an experimental comparison of two stocking densities indicated that the phytoplankton concentration limited the growth of Crassostrea gigas at densities below commercial levels.

In the two-stage culture experiments, the dynamics of the of the primary communities were monitored at constant and variable flushing rates, ranging from 0.10/day to 1.00/day, in turbulent upwelling systems with natural forcing conditions. The dynamics of the primary community were predicted with reasonable

accuracy using a numerical simulation model with experimentally determined parameters and values of the forcing variables. The growth of the oysters was also examined as a function of their size, their density and various primary communities as a food source. The results indicated that a primary system with a flushing rate of 1.0/day provided the most suitable environmental conditions for the production of oysters. The maximum growth rates attained during the experiment (18%/week) were greater than rates measured in an 'optimal' field location in British Columbia.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENT

I would like to acknowledge, with thanks, the support and assistance of many people, who contributed to the completion of this study. I would also like to acknowledge the National Research Council of Canada for providing financial support with Post-Graduate Scholarships.

I would first like to thank my supervisor, Dr. T.R. Parsons, for his inspiration in the initiation of this research, criticism of its design and financial support for the experimental operations, including the invaluable assistance of Bill Li during the one-stage culture experiments, and Angela Norton and Carole Bawden of the Institute of Oceanography, U.B.C., for analysis of nutrient samples. Many other people at the Institute were also most helpful.

I would also like to acknowledge the co-operation of the Fisheries and Marine Service, Department of the Environment, for providing experimental facilities at the Pacific Environment Institute, West Vancouver, and in particular, thank the many scientists and technicians who provided valued scientific and moral support while the experiments were being conducted.

I am also most grateful to Dr. J.W.C. Tomlinson, Faculty of Commerce and Business Administration, U.B.C., for helpful discussions on systems research, and to C.S.C. Willie for her expert advice in the design of a computer data base and in the analysis of the data.

Finally, I would like to thank my committee for helpful discussions during this study: Dr. T.R. Parsons, Dr. A.G. Lewis, and Dr. F.J.R. Taylor of the Institute of Oceanography; Dr. T.H. Carefoot of the Department of Zoology; and Dr. D.M. Farmer of the Institute of Ocean Sciences, Patricia Bay, British Columbia.

CHAPTER 1. INTRODUCTION

Maximizing organic production in aquatic ecosystems is an essential component of effective fisheries management (Paloheimo and Dickie, 1970; Saila, 1971), aquaculture development (Pillay, 1970), and eutrophication control (Di Toro et al., 1975; Bierman et al., 1974). Observations of highly productive ecosystems, such as areas of upwelling (Cushing, 1971) and estuarine environments (Teal, 1962; Odum and Schleske, 1961; Ryther, 1969), indicate the importance of time and space variables in determining both the production and organization of primary, secondary, and tertiary communities. Extensive studies of these ecosystems using field experiments and explanatory multidimensional models have described with varying complexity the production and organization of that particular food chain or web, exemplified by Walsh and Dugdale (1971), Wiegert et al. (1973) and Caperon (1973) respectively. However at this complex level of interactions, with inherent non-linearities, ecosystem responses to natural or artificial perturbations are less predictable, particularly if parameter values for the original model are estimated or borrowed from the literature (Saila, 1973).

Two complementary research approaches to improve this situation are, first, to reduce the complexity and connectivity of the natural ecosystem by initially 'subsystemizing' on a trophic basis, and secondly, to investigate controlled ecosystems, with known forcing conditions using time and space as control parameters. In the first case for example, analysis

of phytoplanktonic subsystems include studies of naturally eutrophic environments which emphasize production (Patten and Van Dyne, 1968; Winter et al., 1975; Smayda, 1973) and organization (Platt and Subba Rao, 1970; McAllister et al., 1972), some relating specifically to time, expressed as the flushing rate of the system (Dickman, 1969; Cassin and McLaughlin, 1971), or to space (Platt, 1972). In the second case, controlled experiments of organic production have varied in operational scale, number of trophic levels, and operational control in terms of time and space, as outlined later in this chapter.

Conditions for maximizing production at the primary level have been proposed by Steele and Menzel (1962), Steeman Nielsen (1962), and Takahashi and Parsons (1972) by focusing on the importance of spatial considerations such as turbulent mixing and the depth of the water column. In addition to these field and controlled experiments, more theoretical approaches to production and organization of planktonic systems have been considered by Bella (1970), Grenney et al. (1973a), Grenney et al. (1973b), Ross (1973), Platt et al. (1977) for phytoplankton and by Phillips (1974), Steele (1974), and Steele and Mullin (1977) for higher trophic levels.

The importance of the flushing rate and of spatial considerations in determining the production and structure of marine ecosystems, provided the basis for the present research strategy to examine production in planktonic systems. The hypothesis was that production in bivalve food chains could be enhanced by using a deep nutrient-rich source of seawater and an

optimal flushing rate and spatial structure of the ecosystem to maximize productivity. In order to test this hypothesis, duplicate controlled ecosystems were designed with the following operational capabilities:

1. a large continuous culture tank system in which the flushing rate could be varied and controlled, and the seawater either upwelled with a minimum of turbulence or artificially mixed.
2. a deep nutrient-rich source of seawater to enhance primary productivity.
3. a relatively shallow water column (about 1 metre) to minimize light limitation of the primary community.
4. a choice between controlled, constant forcing conditions of light and temperature to simplify the system response, or, naturally fluctuating environmental conditions to simulate production in the field.
5. utilization of the production system as a one-stage culture by placing the herbivores in situ , or expansion to a two-stage culture system, with the primary production tank feeding into a set of herbivore tanks.

Using this controlled system, the objectives of the research were essentially two-fold. The first objective was to examine the production and organization of a natural phytoplanktonic community at various flushing rates in turbulent upwelling systems for a significant period of time (greater than one month), and to analyze numerically the ecosystem responses with a deterministic mathematical model using simulation techniques. The flushing rates ranged from 0.10 day-1 to 1.0

day-1 during the experiments since the growth of phytoplankton is enhanced at these rates (Brown and Parsons, 1972) and they represent attainable flows for small mariculture impoundments.

The second objective was to examine the resulting growth of the herbivore populations in both one-stage and two-stage cultures. Populations of oysters (Crassostrea gigas), in the form of commercial cultch [1] , and scallops (Chlamys hastata hericia) which were confined in net cages, were positioned at specific substations and depths in the primary production tanks. Their growth and effect on the primary community was monitored during the one-stage culture experiments. Bivalves were chosen as the experimental herbivores since they produce a commercially harvestable resource at a low, ecologically efficient level in the food chain. Furthermore, the spatial heterogeneity of the herbivores could be experimentally controlled. In the two-stage culture experiment, growth of juvenile Crassostrea gigas were examined using artificially constructed cultch (with eight oysters per cultch), designed to simulate the cultch used in commercial production. The production of young oysters could then be determined as a function of the following factors: size of the oysters, density of the oysters, and flushing rate of the system. The dynamics of the temperature, standing stock of phytoplankton, oxygen, ammonia and urea in the herbivore tanks, were analyzed as covariates.

Examples of studies pertinent to this research, which

---

[1] A large oyster half-shell with oyster spat attached to it, for stringing from rafts.

basically includes productive marine planktonic ecosystems, are categorized in Table I with the following observations.

First, there have been few marine ecosystems which have been experimentally controlled at a large-scale field level. One example, however, is the 750 acre tidal impoundment of the Lummi Indian Tribal Enterprise. This mariculture system relies on the natural surface plankton as the food supply for rearing molluscs and a supplement to the commercial diets for raising salmonids. A marine impoundment utilizing deep nutrient-rich seawater (Shiels and Hood, 1970) could be even more beneficial by enhancing productivity, and reducing high surface temperatures and bacterial levels.

Secondly, nine large scale experiments are notable in their variability of trophic analysis and operational control in time and space. Of the four continuous culture studies, two (Baab et al., 1973; Malone et al., 1975) utilized nutrient-rich seawater from depth and were conducted in a semi-tropical environment, with average experimental temperatures greater than ca. 25 °C. The Malone study is of limited value with only a four day experimental duration and a phytoplankton population (Chaetoceros) which is probably a sub-optimal herbivore diet due to its morphology. The Baab study, which concentrated on the mollusc populations, determined that their controlled ecosystem favoured the growth of Ostrea edulis rather than Crassostrea species. A preliminary experiment to the present research (Brown and Parsons, 1972) examined simulated upwelling at various flushing rates of nutrient-rich seawater and the effect on the maximization and stability of primary communities.

Thirdly, an organic source of nutrients, diluted sewage, has been used in a series of medium-scale continuous cultures investigated by Dunstan and Tenore, and provides a useful specialized system for eutrophication control and mariculture production.

Fourthly, five small-scale continuous culture studies are included as examples of controlled experiments which provide insights into maximizing production [1], although they are limited in scale for applications to mass culture production in hatcheries. In plankton research, continuous culture techniques have been applied mostly on a small-scale to elucidate physiological principles of nutrient, temperature and light limitation, either in a turbidostat (Eppley and Dyer, 1965; Maddux and Jones, 1964) or in a chemostat (Caperon, 1967; Eppley et al., , 1971; Caperon and Myer, 1972; Davis et al., , 1973; Harrison et al., , 1976; Davis, 1976; Conway, 1977). Finally, two of the small-scale studies in Table I have utilized a raceway for operational control (Walker and Zahradnik, 1976; Kirby-Smith and Barber, 1974), although in terms of optimization, this system has the disadvantage of providing only areal or two-dimensional production.

Table I is not intended as a complete listing of field or laboratory studies on the growth of marine phytoplankton or bivalve molluscs, the herbivores used in this research. What Table I represents is a sample of studies which have

---

[1] For a discussion of the continuous culture technique, see Taylor (1960) and Oppenheimer (1966).

experimentally acknowledged the significance of either the scale of operation, trophic level or time and space as control parameters, or more usually, a combination of these factors, in the organization and production of phytoplankton and planktonic herbivores. Other investigations to improve production of bivalves have ranged from breeding and collection of seed (Loosanoff and Davis, 1963; Imai, 1967), to rearing bivalves using rafts (Quayle, 1969,1971) and trays (Parsons, 1974) to increase production in the natural environment. Some have concentrated on physiological factors which affect the growth of bivalves, including studies by Walne (1972), Shra and Baggaley (1976), and feeding experiments by Tenore and Dunstan (1973b,c) and Walne (1970) which indicate the importance of the type of the phytoplankters, as well as the relationship between the uptake rate at various concentrations of phytoplankton.

The research presented in this dissertation has been structured to provide comparisons between non-turbulent and turbulent continuous cultures in either a one-stage or two-stage system, at various flushing rates of the system. Five continuous culture experiments, ranging from three to ten weeks duration, were conducted during this study. The forcing conditions of light, temperature and nutrients were essentially constant during Experiment 1. Experiments 2 to 5 were conducted in outdoor continuous culture systems in order to examine the effect of more natural conditions of light and temperature on production in 'planktonic' [1] food chains.

[1] The term planktonic is used throughout this study to incorporate the fact that the experimental bivalves were suspended in the water column and fed on the phytoplankton.

In Experiment 1 (Chapter 3), duplicate non-turbulent upwelling systems were used to examine the dynamics of a natural phytoplankton community and the resulting growth of an *in situ* population of scallops, at a flushing rate of 0.5 day^{-1}. In Experiment's 2 and 3 (Chapter 4), the one-stage production of both oyster and scallop food chains was examined in a turbulent upwelling system. Chapter 5 presents the results and discussion of Experiment 4, an analysis of the dynamics of primary communities at two comparative flushing rates (0.50 day^{-1} and 1.00 day^{-1}). The experimental design was expanded in Experiment 5 to include an examination of variable flushing rates of the primary system during the experimental period (Chapter 6), and the suitability of the resulting phytoplankton communities as a food source for the two-stage culture of oysters (Chapter 7). An analysis of the dynamics of the primary community, using a simulation model, is presented in Chapter 8. Chapter 9 provides a comparative discussion of the results of the five experiments, and the conclusions from the study are summarized in Chapter 10.

CHAPTER 2. EXPERIMENTAL FACILITIES AND METHODOLOGY

Experimental Facilities

All continuous culture experiments were conducted using large tank facilities at the Pacific Environment Institute, West Vancouver, B.C. The incoming seawater for the experimental system was pumped from a depth of ca. 60 feet in English Bay, passed through a 5 micron filter and provided a source of cool, nutrient-rich seawater (11 °C , 20 uM nitrate l^{-1}) to the production system resevoir. The flow rate from the seawater resevoir to the experimental tanks was expressed as the flushing rate (FR), determined by the flow rate required to replace the total volume of the experimental tank in one day; that is

$$FR(\ day^{-1}\ ) = v\ V^{-1}$$

where v=flow rate (l day^{-1}) and V=tank volume (l). The flushing rate remained relatively constant during the experiments by using a gravity-feed method from the resevoir, with the flow controlled by in-line valves. Flushing rates up to 1.0 day^{-1} could be attained using this method. All materials used in the system were 'inert' , including the fibreglass resevoirs and experimental tanks, 1/2 " PVC& [1] piping and fittings, and plexiglass and tygon samplers.

---

[1] & denotes a registered trademark.

One-stage Culture Experiment with Constant Forcing Conditions

The indoor facilities for Experiment 1 are illustrated in Figure 1, including surface and side views of the experimental tanks. These duplicate production tanks had a volume of 720 litres and the depth of the water column was 0.8 metres. The upwelling rate of 0.4 m/day was constant over the whole area of the tank by using a rectangular-shaped inflow pipe with small holes every 5 cm apart. In-situ samplers were located in both tanks at the surface, mid and bottom depths at half the distance from the end of the tank to the centrally located levelling pipe.

One-stage Culture Experiments with Natural Forcing Conditions

As illustrated in Figures 2 and 3, duplicate tank systems (A an B) were set up on an outdoor platform for Experiments 2 and 3. Each consisted of a covered seawater resevoir (3200 l volume) which gravity-fed to a large production tank (3.0 m diameter, ca. 7500 l volume). The inflow pipe near the bottom of the production tank was angled towards the centre of the tank, and the water flow was directed perpendicularly upward at half the distance (0.75 m) to the sampling tube, as shown in Figure 3 for Tank A. The inflowing seawater to the production tank was sampled from the resevoir outflow using a tygon-tubing siphon. In situ samplers [1] were located at three 'stations' in

---

[1] Three long pieces of blackened tygon tubing were inserted into a PVC standpipe and used as siphons.

the center of the production tank: surface (0.05m), mid (0.5m) and bottom (1.0m). The total depth of the water column was 1.1 m. The seawater outflow from the surface of the production tank was sampled using a T-joint with a reduced tygon fitting. The production tanks were covered with a thin (1/8") sheet of plexiglass to reduce aerial contamination and photo-inhibition.

Twelve substations were established in each production tank for location of the herbivores during Experiment 2 and 3, as illustrated in Figure 2 for Tank B. Tank A was used to examine the growth of the Pacific oyster, Crassostrea gigas , and commercial cultch were strung at surface, mid and bottom depths per substation. The other experimental herbivores, Chlamys hastata hericia (scallops), were confined to rectangular net cages, constructed with a plexiglass frame (ca. 30cm X 20cm X4cm) and herring seine net. These cages were suspended horizontally at the surface, mid or bottom depths in Tank B during Experiments 2 and 3.

Two-stage Culture Experiments with Natural Forcing Conditions

The experimental facilities for Experiments 4 and 5 are illustrated in Figures 4 and 5. The primary production tanks were identical to the one-stage culture system, except there were no herbivores in situ and turbulent diffusion was actively produced in both Tanks A and B by using submersible pumps. Outflow from either primary tank could be fed into the smaller herbivore tanks (170 litres), shown in Plate I. Two were used for acclimation and the other four as experimental tanks to examine three densities of oysters (16, 32 and 48 oysters per

tank respectively), plus a control (no oysters). All tanks had *in situ* circulating pumps to keep the system homogenous.

Throughout the text, A and B are included in the identification of experiments as a reference to the appropriate tank system.

Methodology

The same sampling procedures were followed for all experiments. Water samples (4 litres) were taken from the five 'stations' in the production system (inflow(I), surface(S), mid(M), bottom(B) and outflow(O)) between 0800 and 0900 hours (PST) for the measurement of physical, chemical and biological parameters. The samples were analyzed in the laboratory according to the methods outlined below. Measurements on the experimental animals were made in the aquarium wet-lab to minimize handling. A description and derivation of the variables and parameters which pertained to the primary systems are summarized in Appendix 1.

Physical Parameters: Light, Temperature and Salinity

During Experiment 1, continuous artificial radiation was provided by Vitalite® fluorescent tubes, which simulated solar radiation in spectral composition in the range of photosynthetically available radiation (PAR) from *ca.* 400-700 nm. There was no difference in the radiation intensities of 0.10 langley min^{-1} between the duplicate culture tanks, and a 5% decrease in PAR at the periphery of each tank was not considered

a significant reduction.

During the experiments conducted outdoors, measurement of the incident solar radiation (SR) was continually recorded under the plexiglass sheet covering the experimental tanks, using a solarimeter (5% precision) with a calibrated YSI& recording millivoltmeter (chart speed= 2" per hour). The plexiglass reduced the incident solar radiation by 10%. The light curves were integrated for four hour intervals, including the period of the primary productivity experiments, and then summed for daily radiation estimates (langley day^{-1}). Estimation of the photosynthetically active radiation (PAR) was based on Suckling (1974) who determined experimentally that the PAR was not a function of cloud cover, and:

$$PAR = 0.50\ SR + 0.0 \quad (r^2=0.98)$$

Similar results were previously found by Szeicz (1966). A submarine photometer (Maddux, 1966) was placed in the experimental tank to determine the solar radiation at depth (PARZ) by measuring the extinction coefficient (EXTK). However, continual problems with seawater leakage into the photocell produced unreliable measurements; consequently, estimates of EXTK were based on Riley's empirical relation between the extinction coefficient and the chlorophyll a concentration:

$$EXTK = .04 + (.0088*CHLA) + (.054*(CHLA**.66667))$$

which proved reliable for a range of chlorophyll a values when other particulate matter was minimal (Riley, 1956).

Temperatures were measured to 0.1 °C using a thermometer inserted into the seawater sample. During the first half of Experiment 1, *in situ* thermistors connected to a 2-channel

Rustrak®, recorded temperatures at the surface and bottom of the two productivity tanks, primarily to detect any evidence of thermal instability. Temperature fluctuations of ca. 0.2 °C occurred in the tanks only during the ten minute sampling period each day.

Salinity samples were collected daily in salinity bottles from the inflow and analyzed using a Beckman® salinometer.

Nutrient Parameters

Nitrate, ammonia, urea, reactive phosphorous and silicate nutrients were determined using the methods outlined in Strickland and Parsons (1972). Daily samples for nitrate determinations were analyzed using the cadmium-copper reduction column method, either manually in Experiments 1 to 3, or with a Technicon® Auto-analyzer in Experiments 4 and 5. The samples were stored at 2 °C in the dark and usually analyzed within a few days of collection; however, there was no significant change ($P<.01$) in concentrations of nitrate with a storage duration of eight days. The precision of the method was 2%, measured over the range of *in situ* concentrations (0 - 25 uM N l^{-1}) and differences between the manual and automated methods were not significant since the columns were replaced at the first sign of deterioration in either case (Hager *et al.*, 1972).

Ammonia concentrations were determined manually using the phenol-hypochlorite method. Although care was taken to reduce contamination of samples by acid cleaning glassware, covering flasks and using double deionized distilled water, the precision of the method (S.E.= 0.26 uM N l^{-1} ; n=3) was poor relative to

the low *in situ* concentrations (< 2.0 uM N l^{-1}). Urea analysis was based on the urease method with the inherent problems of the ammonia analysis. Since ammonia and urea samples were frozen for a few weeks before analysis, variabilities in the concentrations of these nutrients may have increased (Degobbis, 1973). Only occasional measurements of phosphorous and silicate were taken since nitrogen appeared to be the primary nutrient limiting phytoplankton productivity, like many coastal ecosystems.

Primary Parameters: Standing Stock, Primary Productivity, and Community Structure

The standing stock of phytoplankton was usually measured every day at all four *in situ* stations as the concentration of chlorophyll *a* (CHLA), as outlined in Strickland and Parsons (1972). Water samples were filtered through 0.8 micron Millipore® AA filters and the pigments extracted immediately in 10.0 ml of spectrophotometric grade acetone. The tubes were stored in a freezer for two to seven days before chlorophyll, carotenoid and phaeopigments were determined using a Beckman Acta II® spectrophotometer. Calculations of pigment concentrations were based on the Parsons and Strickland (P.S.) equations, although there was no difference between these and the SCOR/UNESCO (S/U) equations for CHLA:

$$CHLA(P.S.) = 1.0 * CHLA(S/U) \quad (r^2=1.0;\ n=41)$$

The precision of the method at the 30 ug Chl *a* l^{-1} level was an average standard error of 0.5 ug Chl *a* l^{-1} , based on eight duplicate determinations.

To estimate the phytobenthic standing stock, plexiglass plates were suspended in the primary tanks, each with four 2 cm x 6 cm glass slide attached by plastic clips. Algae was scraped from both sides of the slide (20 cm^2) onto a preweighed GFC filter, and duplicate chlorophyll *a* and biomass estimates were determined.

Primary productivity was estimated approximately every three days as net carbon fixed per litre per hour using the method outlined in Strickland and Parsons (1972). A 100 ml water sample was placed in a small (112 ml) BOD bottle and one ampoule of 5 uC radioactive sodium bicarbonate (in 3% NaCl solution) added to this. This production bottle and a corresponding dark bottle were suspended horizontally in the experimental tank using plexiglass holders, and incubated for 4.0 hours from *ca.* 0900 - 1300 hours (PST). After incubation, the samples were immediately filtered through 0.45 micron HA Millipore® filters, then placed in scintillation vials containing 15 ml of Aquasol® scintillation fluid. Samples were counted twice, each for ten minutes, using a Packard Tri-Carb LSC® . The determination of carbonate carbon required to calculate the rate of carbon fixation was based on the pH method. Precision estimates for ^{14}C productivity between duplicate bottles ranged from a coefficient of variation of 11% for values < 10 ug C l^{-1} hr^{-1} to 9% for productivities > 75 ug C l^{-1} hr^{-1} .

Exudation of organic carbon was determined once a week using a modification of the methodology outlined in Anderson and Zeutschel (1970). 5 ml of filtrate from the ^{14}C productivity

samples were acidified with phosphoric acid tc a pH of 3.0 and then bubbled with nitrogen gas fcr 20 minutes to remove any inorganic radioactive carbon. 2 ml aliquots were transferred to scintillation vials containing 10 ml of Aquasol& scintillation fluid and the prepared samples ccunted for 10 minutes.

Oxygen samples were taken on a daily basis in 300 ml BOD bottles, except in Experiment 1. They were fixed immediately and stored in the dark for analysis within a day or two. An analysis of variance during Experiment 3 indicated that there was no significant difference in oxygen ccncentration between bottles stored in this manner. Primary productivity and respiration were also estimated using the light and dark bottle oxygen technique (Strickland and Parsons, 1972). Light and dark BOD bottles were suspended horizontally by plexiglass holders during the same period as the radioactive carbon experiments. A photosynthetic quotient of 1.2 and a respiratory quotient of 1.0 were used in the conversicn to carbon units. The precision of the method based on duplicates was a coefficient of variation of 0.8% at the 325 mg oxygen l^{-1} hr^{-1} level, 1.0% at the 300 mg oxygen l^{-1} hr^{-1} and 7.5% at the 250 mg oxygen l^{-1} hr^{-1} level.

Water samples (250 ml) were also collected semi-weekly for phytoplankton species compositicn and size determination. A 10 ml subsample was fixed with Lugol sclution and examined in a 5 cc sedimentation chamber with a Zeiss inverted microscope. The remaining sample was stored at 2 °C in the dark until it could be counted cn a Model B Coulter Counter& as outlined in Sheldon and Parsons (1967). The analysis employed a flow-through rate

of 0.044 ml sec^{-1} using a 100 micron aperature. Eleven particle diameters ranging from 2.82 to 28.5 microns were counted in triplicate and then averaged.

Secondary Productivity

Experiment 1

Scallops (*Chlamys hastata hericia*) were collected at *ca.* 20 metres by divers near Victoria, British Columbia two weeks before the start of Experiment 1 (EXP1). They were put into holding tanks and provided with a constant supply of seawater from the resevoir tank (Figure 1). Ten litres of surface seawater from English Bay were added to the tanks every couple of days. 50 healthy scallops were selected as experimental animals [1] and a few were cleaned of encrusting sponges (*Myxilla incrustans* , *Mycale adhaerens*). The scallops were tagged, weighed and measured, and added to the benthos of Tank A on Day 45. After one month, the *Chlamys* were re-measured and weighed to determine their growth.

Experiment 2A

Crassostrea gigas cultch were obtained from a commercial grower near Victoria on April 25 and kept in a 3000 litre holding tank with unfiltered running seawater (*ca.* 29 ppt, 13

[1] The larger scallops with the boring sponge *Cliona celata* were rejected.

°C). 10 litres of phytoplankton stock were added to the holding tank every couple of days. Twelve cultch were tagged for identification and transferred at the beginning of EXP2A to smaller tanks receiving the outflow from Tank A. The total weight, weight in water and number of oysters per cultch were measured before their addition to the one-stage continuous culture experiment on Day 6. Four strings, with cultch at the surface (0.1 m), mid (0.5 m) and bottom (0.9m) depths, were located at substations 1 to 4 (Figure 2). The oysters were grown for five weeks before the final measurements were made of the growth variables.

Experiment 2B

At the beginning of EXP2B, six dozen scallops were collected at the same location in Victoria and 64 were selected as experimental animals. They were ordered by length and weight into four groups of increasing size, and within each group of 16 scallops, one-half were randomly selected for a cage to be located at mid depth and the other half for a cage to be located at the bottom station. The same procedure was adopted for the three larger size groups. The scallops were acclimated for four days in small covered tanks fed by the outflow from Tank B. After the scallops were weighed and measured, the cages were transferred on Day 10 of EXP2B to their designated substation. The four cages at the mid depth were located at substation's 1 to 4, while the four cages at the bottom depth were located at substation's 5,8,9 and 12 (Figure 2). One month later, final measurements were made of the growth variables.

Experiment 3A

The 24 oyster cultch selected for EXP3A were tagged and transferred during EXP2A to the small holding tanks fed by the outflow from Tank A. The growth variables were measured on Day 6 of EXP3A, and 8 strings with cultch at the surface, mid and bottom depths, were located at substations 1 to 8 in Tank A. Final measurements were taken after two weeks of growth.

Experiment 3B

Another nine dozen scallops were collected at the same Victoria location on Day 7 of EXP3B. The same procedure used in EXP2B was adopted for the selection of the 96 experimental animals and grouping them into four classes of increasing size. In this experiment (EXP3B), there were enough scallops to string four cages (containing 8 scallops per cage) at the surface depth (SUBSTN's 6,7,10 and 11) as well as the mid and bottom stations. The scallops were acclimated for three days as in EXP2B, and after they were weighed and measured, the cages were transferred on Day 11 to the appropriate SUBSTN in Tank B. The final measurements were made of the growth variables after one month.

Experiment 5

Juvenile Crassostrea gigas were obtained from a commercial oyster grower near Victoria, British Columbia and held in a 3000 litre tank outdoors until the start of the hervivore experiments. Unfiltered running seawater (29 ppt, 13 °C) was constantly supplied to the holding tank and 10 litres of

phytoplankton stock were added to the tank every couple of days. A small hole (1/32") was drilled in the umbo of the shell for wiring the oysters to small square plexiglass boxes designed to simulate cultch (Plate II), so growth variability between and within size groups could be assessed.

Details of the design of the two-stage continuous culture experiments are presented in Chapter 7. The linear dimensions (length, width and depth), weight in air (± 0.1 g), weight in water and whole volume of the individual oysters were measured as growth variables.

A description and the derivation of the variables pertinent to the herbivore growth experiments are summarized in Appendix 2.

CHAPTER 3. ONE-STAGE CONTINUOUS CULTURES IN NON-TURBULENT UPWELLING SYSTEMS WITH CONSTANT FORCING CONDITIONS

The initial experiment was designed and conducted to examine physical and biological variables in duplicate non-turbulent upwelling systems with a flushing rate of 0.5 day^{-1}. The experimental system, described in Chapter 2, permitted the examination of the phytoplankton dynamics under controlled, constant forcing conditions. This experiment (EXP1) was conducted for ten weeks, beginning on October 1. After the tanks were filled with filtered inflowing seawater and initial samples taken, each tank was seeded with 10 litres of phytoplankton stock which had been collected from the surface of English Bay and passed through a small diameter (54u) wire screen to remove any zooplankton. The benthic herbivores, Chlamys hastata hericia , were introduced into Tank A on Day 45 to determine the suitability of this continuous culture system for the survival and growth of a local scallop population.

Dynamics of the Primary Communities

The flushing rate remained relatively constant at 0.5 day^{-1} throughout the experiment, although on a few days the rate decreased to as low as 0.45 day^{-1}. However on Day 31 the water level in Tank A increased by 2 inches due to clogging of the in situ levelling pipe by a filamentous Navicula mat which had been growing on the overflow pipe since Day 13. The same problem occurred in Tank B on Day 43 although the situation was

more severe since the tank overflowed for about half an hour. In each case, the Navicula around the pipe were removed.

Physical Environment

The continuous source of photosynthetically available radiation of 0.10 langley min^{-1} represented a daily radiation flux of 144 langley day^{-1}. The resulting in situ temperatures were significantly different between depths but essentially constant between tanks and within depths for the first eight weeks of the experiment, averaging 14.5 °C (± .1 °C) at the surface, 12.0 °C (± .1 °C) at the mid station and 10.5 °C (± .1 °C) at the bottom station. During the last two weeks, the average temperature decreased ca. 3 °C at the surface of the tanks and ca. 1.5 °C at the mid and bottom stations. The temperature and salinity of the inflowing seawater was constant at 10.0 °C (± .1 °C) and 29.2 ppt (± 0.6 ppt) during EXP1.

Nutrient Conditions

The concentrations of the nutrients important in phytoplankton productivity were measured at various times during the experiment. Samples of the inflowing seawater were analyzed before the start of EXP1, with the resulting average concentrations: nitrate (NO3) = 17.8 uM N l^{-1}, ammonia (NH3) = 0.88 uM N l^{-1}, phosphate (PO4) = 1.75 uM P l^{-1}, silicate (SIO3) = 71.3 uM Si l^{-1}. The ratios of these nutrient concentrations suggested that the experimental system would

probably be nitrogen-limited [1].

The concentration of nitrate during EXP1 is illustrated in Figures 6 and 7. The high inflow NO3 was relatively constant, averaging 23.6 uM N l^{-1} (SE = 0.39 uM N l^{-1} ;n=35) during the first five weeks. The pattern of damped oscillations for the *in situ* nitrate concentration was similar between tanks for the first three weeks, with an NO3 minimum of <2 uM N l^{-1} by Day 10, recovery to levels of *ca.* 15 uM N l^{-1} by Day 15, and then a decrease to nitrate concentrations of 2-5 uM N l^{-1}. Throughout the experiment, the NO3 at the bottom station was significantly greater than the surface concentration. During the fourth and fifth weeks, the average nitrate levels in Tank B were about twice as high as in Tank A. There was a high negative correlation between NO3 at the surface and bottom stations for the duration of EXP1A. The same trend was not apparent in Tank B, although this may have been partly due to the tank overflowing on Day 43.

The average weekly inflow concentration of phosphate was 2.43 uM P l^{-1} to both tanks. As in the case of NO3, the PO4 at the bottom station was greater than the phosphate concentration at the surface and outflow stations. Phosphate levels were never less than 0.5 uM P l^{-1}, even when NO3 values were *ca.* 2 uM N l^{-1}, indicating that PO4 did not limit primary productivity.

After the introduction of the scallops to the system, the difference between the net concentration of ammonia at the

[1] Results from Antia *et al.* (1963) indicated that a similar primary community had a N/P ratio greater than 12, whereas the N/P ratio of the seawater source was only 10.

bottom station was significantly higher in Tank A (1.50 uM N l^{-1}) than Tank B (0.10 uM N l^{-1}).

Phytoplankton Dynamics

Standing Stock

The phytoplankton stock was measured as the chlorophyll *a* concentration (CHLA) every two to three days for the first five weeks of EXP1. During this time, the phytoplankton stock generally followed a pattern of damped oscillations in both tanks, with the initial bloom on Days 8 and 9, a reduced secondary maximum approximately two weeks later and a third increase at the end of the five week period (Figures 8 and 9). The stock levels increased significantly with depth throughout EXP1. The magnitude of the bloom was the same in both tanks, averaging 52.9 ug Chl *a* l^{-1} and 54.5 ug Chl *a* l^{-1} in Tanks A and B respectively, although the secondary phytoplankton maximum was not as large in Tank B. This probably resulted from the fact that the benthic diatom, *Navicula sp.*, which was more prevalent in Tank B, further reduced the PAR at depth in a system which was already light-limited. A comparison of CHLA between tanks A and B during the post-bloom period (t>10), produced averages of 18.8 ug Chl *a* l^{-1} (SD=5.19) and 7.4 ug Chl *a* l^{-1} (SD=6.49) at the surface, 21.2 ug Chl *a* l^{-1} (SD=9.17) and 16.1 ug Chl *a* l^{-1} (SD=9.88) at the mid depth, and 29.1 ug Chl *a* l^{-1} (SD=18.57) and 27.0 ug Chl *a* l^{-1} (SD=16.74) at the bottom depth.

After the scallops were added to Tank A on Day 45, the phytoplankton stock was reduced to less than 5 ug Chl *a* l^{-1} at the bottom station, which was less than the surface and mid stations and *ca.* 40 ug Chl *a* l^{-1} less than the corresponding value for Tank B. During the initial bloom, estimates were made in both tanks of the phytoplankton stock which sank to the benthos [1]. The phytobenthos was measured on Days 9, 10 and 14 as 180 ug Chl *a* l^{-1} (± 5 ug Chl *a* l^{-1}), 256 ug Chl *a* l^{-1} (± 11 ug Chl *a* l^{-1}) and 343 ug Chl *a* l^{-1} (± 11 ug Chl *a* l^{-1}), which represented an average value of 23.4 ug Chl *a* l^{-1} day^{-1}. On average, the phytobenthos concentration was approximately 2.5 times the phytoplankton concentration in the water column, representing an average net sinking rate of 1.0 m/day or 1.4 m/day with respect to the water column.

Primary Productivity

Primary productivity rates on hourly basis were low in both tanks during the experiments (Figures 10 and 11). Values were less than 30 ug C l^{-1} hr^{-1}, except on Day 49 at the bottom station. When standardized on a standing stock basis, primary productivities (ASS) ranged from 0.0 ug C (ug Chla)$^{-1}$ hr^{-1} at the bottom station to a value of 5.1 ug C (ug Chla)$^{-1}$ hr^{-1} on Day 19 as illustrated in Figure 12. The values of ASS were similar between tanks but decreased significantly with depth.

[1] Circular plexiglass collectors were constructed and placed at known locations on the bottom of the tank before the start of EXP1. These collectors were retrieved by placing a covering plate (with an O-ring on the inside surface) attached to an inflexible 1 metre rod, over the benthos collector and bringing it to the surface.

Excluding Day 19, the standardized productivity rates during th experiment averaged 0.96 ug C (ug Chla)$^{-1}$ hr^{-1} (av SD=.40), 0.76 ug C (ug Chla)$^{-1}$ hr^{-1} (av SD=.21) and 0.40 ug C (ug Chla)$^{-1}$ hr^{-1} (av SD=.26) at the surface, mid and bottom stations respectively.

Phytoplankton Stock Composition

During the initial bloom, Skeletonema costatum was the dominant phytoplankter, although several other species of diatoms (Nitzschia spp. , Thalassiosira spp. , Navicula sp. , Chaetoceros sp.) were also present. Increased numbers and diversity of nano-flagellates [1] were apparent at the surface station during the third and fourth weeks. By the end of the sixth week, Skeletonema costatum was not present in the surface samples. Three dinoflagellates (Peridinium sp. , Gymnodinium sp. , Dinophysis sp.), a green flagellate, and the filamentous Navicula sp. were the dominant phytoplankters. The dominance of Skeletonema costatum at the mid and bottom stations was replaced by Nitzschia spp. , Thalassiosira sp. , and Rhizosolenia sp. . After the scallops were added to Tank A, Chaetoceros sp. became the dominant phytoplankter at the bottom station compared with Thalassiosira sp. in Tank B.

[1] Flagellates in the 2-20 micron size range (See Parsons and Takahashi (1973a), p.6).

Growth and Survival of the Scallop Population

The results of Experiment 1 indicated that the non-turbulent upwelling system with a moderate exchange rate (0.5 day^{-1}) provided a suitable environment for the growth of *Chlamys hastata hericia*. After the scallops were introduced to the benthos of Tank A on Day 45, the amount of detritus and phytoplankton at the bottom station was reduced and the scallops were often observed swimming in the ventral direction, indicating their need for removal of pseudofeces.

The 50 scallops ranged in length from 3.0 cm to 6.6 cm and weighed 5.0g to 51.7g initially. The frequency distribution of the experimental population based on length (L) indicated that 30 of the 50 *Chlamys* were in the 4.0-4.9 cm range, averaging 4.5 cm (SD=.25). The 8 scallops in the 3.0-3.9 cm range averaged 3.5 cm (SD=.29) in length. Of the remaining 12 scallops, 7 were in the 5.0-5.9 cm range (av L= 5.4cm; SD=.22) and 5 were longer than 6.0 cm (av L= 6.2cm; SD=.33). The corresponding total weight per scallop at t(0) averaged 6.2g (SD=.33), 12.6g (SD=2.77), 24.5g (SD=3.35) and 37.0g (SD=10.28) for the four size groups.

After the four week growth experiment, most of the *Chlamys* had laid down a thin, darkly pigmented band of new shell. The average increase in length (NETL) and width (NETW) of the scallop population was 0.09 cm (SD=.096) and 0.05 cm (SD=.085), which represented growth rates of 2.0% and 1.2% respectively during the month. However, NETL was also a function of the size of the scallops, and the net length as a percent increase from

the initial length (PERL), ranged from 5.1% for the small size group to 2.0%, 1.8% and 0.0% for the three larger size classes respectively. The average increase in total weight (NETWT) was 2.7%, although NETWT was also a function of the size of the scallops. The smallest Chlamys had the highest growth rates of 6.9%, compared with rates of 2.9%, 1.3% and 2.7% for the larger size classes.

The 60' depth of the seawater intake at the Institute was similar to the depth from which the scallop population was collected, suggesting that their endemic physical environment of temperature and salinity was probably fairly similar to the experimental conditions. Although the light intensity was higher than the natural environment, the Chlamys did not seem bothered by this, and were observed actively feeding on the phytobenthos and occasionally swimming around the tank. The most significant difference between the natural and experimental environments was the phytobenthic concentration, and the results of this experiment indicated that this type of upwelling system enhanced secondary productivity in the scallop food chain.

CHAPTER 4. ONE-STAGE CONTINUOUS CULTURES IN NON-TURBULENT UPWELLING SYSTEMS WITH NATURAL FORCING CONDTIONS

Turbulent upwelling systems at various flushing rates were examined as growth environments for the sessile planktonic herbivores. To evaluate the culture system under more natural forcing condtions of solar radiation and temperature, two sets of controlled experiments (designated as Experiments 2 and 3) were conducted outdoors in duplicate tank systems at low and high flushing rates.

In Experiment 2, the dynamics of the primary communities and the growth of two different herbivore populations were examined in one-stage continuous cultures at flushing rates of 0.25 day^{-1}. In earlier experiments, this flushing rate had promoted a mixed diatom/phytoflagellate community and resulted in environmental conditions potentially suitable for the growth of oysters. In EXP2, survival and growth of oysters (Crassostrea gigas) and scallops (Chlamys hastata hericia) were examined in Tank A and Tank B respectively, to obtain a first approximation of the factors limiting secondary productivity and to compare changes in the primary community caused by different herbivore populations.

Based in part on the results of EXP2, a similar one-stage continuous culture system was re-examined in Experiment 3 with the following modifications:

1. Tank A was stocked with twice the density of herbivores (oyster cultch at eight substations) while using the same flushing rate (0.25 day^{-1}) since optimal temperatures and

suitable phytoplankton stocks were produced in this system.

2. Tank B was stocked with scallops at the surface, mid and bottom depths but the flushing rate was increased three-fold to 0.75 day^{-1} to promote a suitable growth environment for these herbivores primarily by lowering the *in situ* temperature.

Comparison of Two Herbivorous Food Chains at a Low Flushing Rate

Both production tanks A and B were filled with filtered seawater on June 18, the flushing rates adjusted to 0.25 day^{-1} and the initial physical and chemical conditions monitored at 0900 hr (PST). Surface seawater from English Bay was collected and filtered through a 54u netting to remove zooplankton. 20 litres of this natural phytoplankton community were added to the surface of each production tank at 1100 hr. This seed community consisted mainly of diatom chains, predominantly *Skeletonema costatum* and *Thalassiosira sp.*, as well as *Nitzschia spp.*, *Navicula sp.*, and a few nano-flagellates. The flushing rates remained relatively constant at 0.25 day^{-1} in both tanks during the experiment. In the oyster tank, the 5% coefficient of variation (CV) for the flushing rate was primarily due to growth of the filamentous benthic diatom, *Navicula sp.*, around the inflow pipe, reducing the flow rate into the tank. This was not apparent until Day 33 at which time the algal mat was removed. The total duration of Experiment 2 was 6 weeks in Tank A (EXP2A) and 5 weeks in Tank B (EXP2B). The *Crassostrea gigas* population

was added to Tank A on Day 6. The cages containing the Chlamys were strung at the appropriate substations on Day 10, as outlined in Chapter 2.

Dynamics of the Primary Communities

The dynamics of the physical, chemical and primary productivity variables for both Tank A and Tank B are illustrated in Figures 13 to 25. Descriptive statistics for both the forcing (incoming) and in situ values of the primary variables are summarized in Tables 2 and 3 for EXP2A and EXP2B respectively. Where appropriate, a breakdown into the pre-grazing and grazing periods are included for the measurements.

Physical Environment

Solar radiation at the surface of the tanks (SR) ranged considerably during the experiments, from 110 langley day^{-1} on Days 6 and 7 to 550 langley day^{-1} for an extended period during the fourth week (Figure 13) [1]. The large CV of 35% based on an average SR of 410 langley day^{-1} indicated the lack of an ideally constant solar radiation level. There was no significant difference between the inflow temperature of 10.9 °C to the two tanks and during the experimental period, in situ temperatures (TEMP) fluctuated in response to the variability in SR (Figures 14 and 15). The thermal structure between the tanks was similar, including a significant decrease in TEMP with depth

[1] The values in the plot are for incident SR, which was 10% higher than SR just above the surface of the water, as mentioned in Chapter 2. This was also true for the other graphs of SR during Experiments 2 and 3.

(Tables 2 and 3). The difference in temperature between the surface and bottom depths was ca. 5 °C during the extended period of high SR. At sampling time during the experiments, maximum in situ temperatures were ca. 21.0 °C , although an examination of the diel temperature variation on two sunny days showed that 15.0 °C temperatures at sampling time increased by ca. 5 °C at the surface and outflow stations, and 2-3 °C at the mid and bottom stations by late afternoon. The salinity averaged 28.3 ppt and was essentially constant during the experiments (CV=2.2%).

Nutrient Conditions

Initial phosphate concentrations averaged 2.15 uM P l^{-1} and the relatively constant N:P atomic ratio of 8.5 for the inflowing seawater indicated that nitrogen was the limiting nutrient for the primary formation of particulate organic matter.

The greatest source of nitrogen was in the form of nitrate, with inflow concentrations averaging 18.5 uM N l^{-1} within an 11-27 uM N l^{-1} range (CV=19%). There was no significant difference in inflow NO3 between tanks except during the first week when nitrate levels increased in the inflow to Tank B for some reason. However, the fluctuations in the inflow NO3 with time were real and the general decreasing trend could be attributed to a decreasing tidal height at sampling time [1] during the first

[1] The intake pipe for the Institute's seawater system is higher in the water column at low tidal heights and since NO3 increased with depth, the inflow contained lower nitrate concentrations.

part of the experiment and also to an influx of a surface water mass (high temperatures and oxygen levels with low nitrate concentrations), probably due to unstable conditions in English Bay during the last week of the experiment. The high initial *in situ* nitrate concentrations (22.5 uM N l^{-1}) were depleted at all stations by Day 6, averaging less than 1 uM N l^{-1} during both experiments (Figures 16 and 17). There was a minor recovery to non-limiting nitrate concentrations at the end of the second and fourth weeks.

Inflow ammonia concentrations were low (max=1.85 uM N l^{-1}), and with an average concentration of 0.74 uM N l^{-1} (SD=0.42) contributed little to the source of nitrogen for the system. In both production tanks, NH3 remained at low steady state levels (*ca.* 0.4 - 0.7 uM N l^{-1}) indicating that any excreted NH3 by the oysters or scallops was taken up immediately by the phytoplankters.

Phytoplankton Dynamics

The dynamics of the resultant primary communities, including the phytoplankton standing stock (CHLA), primary productivity (PROD) and the primary productivity rate standardized per unit of standing stock (ASS), are illustrated in Figures 18 to 25.

Standing Stock

In the oyster tank (A), a subsurface maximum of phytoplankton (ca. 46 ug Chl a l^{-1}) developed by Day 5, followed by a surface maximum of only half this concentration on Day 6 (Figure 18). This indicated that sinking of the phytoplankton through the water column was a significant factor in determining the spatial distribution of the primary community and at times was greater than the upwelling rate of 0.25 m/day. During the grazing period (t>6), CHLA decreased to average values of 3.3 ug Chl a l^{-1} at the surface, 4.2 ug Chl a l^{-1} at the mid depth, and 6.8 ug Chl a l^{-1} at the bottom station. Except at the bottom station, the phytoplankton stock assumed a quasi steady-state with biweekly periodic oscillations of ca. 1-5 ug Chl a l^{-1}. A secondary chlorophyll maximum occurred at the bottom station at the end of four weeks in response to the significant increase in the inflow NO3 concentration.

In the scallop tank (B), the initial bloom occurred at the same time (Day 6) and was similar in magnitude to the oyster tank, However, the post-bloom dynamics varied to some extent (Figure 19). The duration of the bloom was two days longer in Tank B in the absence of any grazing pressure. The standing stock during the grazing period in Tank B (t>10) averaged 5.7 ug Chl a l^{-1}, 1.6 ug Chl a l^{-1} more than the value during the corresponding period in EXP2A. This was primarily due to the significant increase in CHLA to levels of ca. 13 ug Chl a l^{-1} subsequent to the period of high inflow NO3 at the end of the fourth week, and, as mentioned later, to the removal of floating algal clumps at the surface of the tank.

Oxygen Levels

The oxygen concentration (OXY) in the inflow to both production systems was relatively constant (CV=6%) during the experiment, averaging 7.5 mg l^{-1} with an average saturation level of 82%. Within the oyster tank, a positive net production of oxygen (OXYN) was maintained and Figure 20 illustrates the effective damping of the oxygen levels after the initial bloom of *Ca.* 17 mg l^{-1}. Significant differences in OXY occurred between depths, coincident with the periods of thermal stability, although for the total experimental period, the mean concentrations and variances were similar between depths (Table 2), averaging *ca.* 11.6 mg l^{-1} with a CV=24%. The tank was supersaturated during most of the experiment, reaching a maximum of *ca.* 210% during the initial phytoplankton bloom and averaging approximately 140% at all depths.

The oxygen curves exhibited a similar pattern in the scallop tank, but average OXY concentrations at depth were lower, and larger variances occurred with time (Figure 21). At the end of the fourth week, oxygen levels at the bottom station were reduced temporarily below inflowing concentrations, probably due to high respiration rates of the scallops as a result of the high *in situ* temperatures. A similar oxygen stress was not evident at the mid station, but as noted later, one-half of the scallops died during EXP2B at this depth.

Primary Productivity

The primary productivity curves for Tank A followed a similar pattern to the standing stocks, and the maximum values ranged from 110 to 170 ug C l^{-1} hr^{-1} from the surface to bottom during the initial bloom (Figure 22).

A similar pattern of primary productivity was evident in Tank B (Figure 23), but the rates were ca. 35% greater, partially as a result of the higher standing stock concentrations. A significant difference in PROD occurred between tanks and stations on Day 10 as a result of the high nitrate concentration (26 uM N l^{-1}) in the inflow to the scallop tank on the previous day; this suggested that the phytoplankton productivity was already nutrient-limited by this time.

The standardized primary productivity (ASS) fluctuated considerably at all stations during EXP2A (Figure 24), ranging from 1-9 ug C (ug Chla)$^{-1}$ hr^{-1} . During the grazing period, the damping of the oscillations was minimal, with a decrease in the range (2.5-7.5 ug C (ug Chla)$^{-1}$ hr^{-1}) and an increase in the period (to two weeks). The variability in ASS between stations was also greater at this time. The maximum value of ca. 9.0 ug C (ug Chla)$^{-1}$ hr^{-1} at the end of the initial bloom indicated that although in situ nitrate concentrations were depleted , intracellular nitrogen levels were not limiting primary productivity on Day 8. The significant increase in ASS on Day 15 at all stations was unpredictable, since at this time, there was a lower influx of NO3 (plus a temporary increase in the in situ nitrate levels) and SR and TEMP were less than on Day

12. This indicated that perhaps some micro-nutrient, such as a vitamin, was limiting primary productivity. During the fifth week, there was evidence of light limitation of primary productivity in Tank A, with ASS greatest at the surface and least at the bottom, attributable to the low level of incoming solar radiation. During most of the post-bloom period the highest standardized productivity rates were at the mid station; this seems reasonable since compared to the bottom station, phytoplankton at the mid depth would have a higher productivity as a function of SR, while compared to the surface which was relatively isolated physically, phytoplankton would have a higher productivity rate as a function of the limiting nutrient(s).

The standardized productivity rate in the scallop tank was unstable, as illustrated in Figure 25. The curves exhibited undamped oscillations of a large amplitude and considerably out of phase between depths. The high value at the bottom station on Day 10 confirmed that the high inflow NO_3 on the previous day reduced the level of nutrient limitation. The average value of ASS during the EXP2B was ca. 5.6 ug C (ug Chla)$^{-1}$ hr^{-1} for all depths; the averages between tanks were similar despite the high variances.

Composition of the Phytoplankton Community

The bloom in both tanks was dominated by *Skeletonema costatum* (ca. 60% by numbers) and *Thalassiosira spp.* (20%) with other diatoms (*Chaetoceros spp.* , *Navicula spp.* And *Nitzschia spp.*) and nano-flagellates contributing

approximately 10% each. After the addition of the oysters to Tank A, Chaetoceros sp. became the dominant phytoplankter. During the fifth week, a thick mat of the filamentous benthic Navicula sp. was removed from the inflow pipe. However there was no significant recovery of the phytoplankton stock.

Navicula sp. was also a problem in Tank B. During the third week, flocculent clumps of the algae, which also contained scallop feces, floated on the surface of the tank. The problem worsened and on Day 28, the clumps of Navicula were removed from the surface of Tank B. As illustrated in Figure 19, there was an immediate recovery of the phytoplankton stock.

Growth of the Herbivores, Crassostrea gigas, during EXP2A

The results of the oyster growth during EXP2A are summarized in Table 4, which includes the net increase in the three weight variables - total weight (NETWT), meat weight (NETWM) and shell weight (NETWS). Only the percent increase in meat weight (PERWM) could be calculated since there was no way of estimating the proportion of live shell in the cultch. The calculation of NETWM and NETWS per oyster per week was based on the number of oysters greater than 2.0 cm. It was impossible to get accurate measurements of the linear dimensions of the oysters. However there was a considerable range in size within and between the cultch. A few cultch had oysters with lengths of ca. 5 cm. The NETWM:NETWS ratio was also calculated.

There was significant growth of all the cultch during EXP2A. The percent increase in meat weight ranged from 10.9% to 36.6%. The highest average rate for the four substations was

25% at the mid depth, although this mean could not be considered significantly greater than the other two depths in view of the variability between SUBSTN. The average increase in meat weight per oyster per week was 0.24 g (SD=.051 g). The corresponding value for shell weight was 0.83 g/zoo/wk, which ranged from 0.5 g/zoo/wk to 1.17 g/zoo/wk. There was also a large range in the NETWM:NETWS ratio from 0.16 to 0.40. The highest average ratio and least variability was 0.32 (SD=.037) at the bottom station. However, since this ratio is a function of the size and number of oysters per cultch, a large variance is not unexpected.

Growth of the Herbivores, Chlamys hastata hericia, during EXP2B

The results of the survival (NSURV) and growth of the scallop population during EXP2B are summarized in Table 5. Less than half of the 32 scallops at the four mid substations survived; of the scallops that did survive, most lost weight, except in Cage 2 which had a 1.1% increase in total weight (WGTT). The smallest scallops in Cage 1 had the largest average percent increase in length (0.5%) and in width (2.0%). In comparison, all of the scallops in the four cages at the bottom depth survived. However most scallops decreased in total weight and the average percent loss ranged from 5.0% for Cage 9 to 10.5% for Cage 12 (which contained the largest scallops).

As mentioned earlier, the average temperatures during the grazing period were 15.6 °C at the bottom depth and 17.2 °C at the mid depth. However, during periods of high SR, the difference increased to ca. 5 °C. The solar radiation also

decreased significantly with depth. Therefcre, high values of SR or TEMP, or more likely a combination of both variables, were probably responsible for the low survival and growth rates.

Further Investigation of the Oyster Food Chain at an Increased Herbivore Density

EXP3A was initiated and conducted in the same manner as EXP2A, except that the *in situ* herbivore density was doubled to 24 oyster cultch, using 8 substations. The tank became contaminated with zooplankton after a couple of weeks and EXP3A was restarted on August 20 and conducted for only three weeks because of the delay. The oyster cultch were added to the tank on Day 6 at the appropriate substations, as outlined in Chapter 2.

Dynamics of the Primary Community

The flushing rate remained constant at 0.25 day^{-1} during the experiment (CV=1%). The results for the physical, chemical and primary variables are illustrated in Figures 26 to 32 and summarized in Table 6.

Physical Environment

Although the weather was better during EXP3A than EXP2A, the average incident solar radiation was 11% less due to the shorter daylength (Figure 26). However, in terms of the temperature, there was no significant difference in TEMP between

experiments. The reduction in solar radiation was compensated for by an increase in the temperature of the inflow to maintain the 16.2 °C average. As shown in Figure 27, the tank was considerably better mixed during EXP3A, even during the afternoon.

Nutrient Regime

Nitrate concentrations were continually monitored during the first twelve days of the experiment. Inflow levels averaged 21.0 uM N l^{-1} (SD=2.05) which was not significantly different from the EXP2A average of 21.8 uM N l^{-1} (SD=3.62) for the same period. The inflow NO3 was probably low during the last week of the experiment, as evidenced by the high inflow temperatures from Day 14 on, and the subsequent low inflow concentration of 12.9 uM N l^{-1} on Day 20. In-situ nitrate concentrations were depleted to values less than 1 uM N l^{-1} after the bloom (Figure 28), although by the end of the experiment, high in situ levels were recorded at all stations unlike EXP2A. Low inflow ammonia concentrations averaging 0.50 uM N l^{-1} contributed little to the nitrogen source for the production system. The in situ NH3 concentration at any depth was not significantly different from the inflow value at any time during the experiment.

Phytoplankton Dynamics

Standing Stock

The dynamics of the phytoplankton community during EXP3A

are illustrated in Figure 29. Both the standing stock and primary productivity curves exhibited damped oscillations with approximately a one week period. The bloom occurred on Day 4, and during the pre-grazing period, CHLA was 36% higher compared with EXP2A, and the difference in CHLA between depths was less, ranging from 13.9 to 16.2 ug Chl *a* l^{-1} . During the grazing period (t>6), the phytoplankton stock averaged 7.3 ug Chl *a* l^{-1} compared with 5.2 ug Chl *a* l^{-1} for the corresponding period in EXP2A, in spite of the increased grazing pressure. However, the phytoplankton stock was primarily *Chaetoceros sp.* , which was apparently rejected by the oysters as a suitable food source.

Oxygen Levels

The lack of constancy in the inflow seawater conditions was also apparent in the oxygen concentration (Figure 30), which averaged only 7.04 mg l^{-1} with a CV of 10.2%. Although *in situ* oxygen levels followed a similar pattern of damped oscillations as EXP2A, the maximum OXY concentration of 14.1 mg l^{-1} was *ca.* 3.0 mg l^{-1} lower and the period was approximately a week, one-half the duration in EXP2A. There was no significant difference in oxygen levels between depths, and a high positive correlation was apparent between the production of oxygen and CHLA from two days previously. The average value of OXY during the experiment was 9.92 mg l^{-1} which represented a 50% decrease in the production of oxygen (OXYN) compared with the first three weeks of EXP2A.

Primary Productivity

The primary productivity rates were similar between depths throughout the experiment (Figure 31), averaging 27.2 ug C l^{-1} hr^{-1}, and were also positively correlated with the phytoplankton stock. The standardized primary productivity (ASS) exhibited undamped oscillations (Figure 32), ranging from 1.2 during the pre-grazing period to 8.8 at the end of the experiment. During the grazing period, ASS was greatest at the bottom station indicating that the system was not light-limited. However, the high *in situ* nitrate concentration at the end of the experiment also suggested that another nutrient, perhaps vitamin B12, was limiting primary productivity in this experiment, as well as Experiment 2. The pattern of ASS between EXP3A and EXP2A was very different. The initial maximum occurred on Day 3 in EXP3A, and the average value of 2.4 during the pre-grazing period was 25% less than in EXP2A. During the grazing period, the standardized productivity rate averaged 4.3 ug C (ug Chla)$^{-1}$ hr^{-1}, which was also 25% less than the mean for the corresponding time period in EXP2A.

Composition of the Phytoplankton Community

The composition of the phytoplankton community during EXP3A was similar to EXP2A, with *Skeletonema costatum* dominating the bloom and *Chaetoceros sp.* the dominant phytoplankter during the grazing period. Large numbers of nano-flagellates were not found in either EXP2A or EXP3A in contrast to a similar culture system (FR=0.25 day^{-1}) with no *in situ* herbivore population

(Brown and Parsons, 1972). The biomass of Navicula sp. on the inflow pipe was less in EXP3A although there was some growth on the oyster cultch. By the end of the experiment, Tank A was very clear and large amounts of fecal material were apparent on the bottom of the tank.

Growth of the Oysters at a Higher Stocking Density

The results of the oyster growth during EXP3A, in which the stocking density was doubled from EXP2A, are summarized in Table 7. The average change in NETWM per oyster per week was 0.16 g/zoo/wk (SD=.159) compared with 0.24 g/zoo/wk (SD=.051) for EXP2A. However, the large variability within substations removed the chance of any significant probability that the growth during EXP3A was less due to the increased stocking density. The variability was also high between depths and the maximum average values at the bottom station of 0.23 g/zoo/wk (SD=.178) for NETWM and 0.60 g/zoo/wk (SD=.376) for NETWS were not significantly greater than the surface or mid substations.

The same problem with variability existed for the NETWM:NETWS ratio, which ranged from .03 to 1.00 and averaged .37 (SD=.285) for the 24 cultch. This value was higher than the average ratio of 0.29 (SD=0.70) during EXP2A. The higher temperatures during the fourth and fifth week of EXP2A may have promoted an increased growth in shell weight, particularly at the surface depth which had a NETWM:NETWS ratio of 0.26.

Further Investigation of the Scallop Food Chain at an Increased Flushing Rate of the System

The flushing rate was set at 0.75 day^{-1} for Experiment 3B and the tank seeded at 1500 hours on July 28, in the same manner as EXP2B. As outlined in Chapter 2, the scallop cages were introduced into Tank B on Day 11 for one month.

Dynamics of the Primary Community

During the experiment, the flushing rate did not remain constant at 0.75 day^{-1} (CV=9.4%) due to problems with the seawater system and high sediment loads reducing the flow rate through the filter to the resevoir. The flushing rates sometimes decreased to 0.6 day^{-1} but were readjusted to 0.75 day^{-1} at sampling time. The results of EXP3B are illustrated in Figures 33 to 39 and statistically summarized in Table 8.

Physical Environment

Although the solar radiation was 8% less than in EXP2B due to decreasing daylength, the variablility in SR during EXP3B was less (CV=28%), especially at the beginning of the experiment (Figure 33). During the bloom period (Days 1-6), the solar radiation was 15% greater for EXP3B than the same period in EXP2B. Because of the increased flushing rate, the average *in situ* temperature was lowered to 14.8 °C at all depths, which represented a net thermal increase of 3.4 °C for this production system (Figure 34). The net increase in EXP2B was 5.5 °C

indicating that tripling the flushing rate caused a 2.0 °C decrease in the *in situ* temperature at sampling time. The diurnal increase was less than 2.5 °C.

Nutrient Regime

Inflow nitrate concentrations averaged 19.3 uM N l^{-1}, which was not significantly higher than EXP2B, and the variance was less (CV=10%). *In-situ* concentrations of nitrate were again depleted by Day 6 and averaged 0.3 uM N l^{-1} in the tank with no significant recovery from limiting concentrations during the experiment (Figure 35). The average inflow ammonia concentration was only 0.42 uM N l^{-1}. There was no significant *in situ* change in NH3, indicating that a steady-state existed between the uptake of NH3 by the phytoplankton and excretion of NH3 by the scallops.

Phytoplankton Dynamics

Standing Stock

The standing stock, measured as the chlorophyll *a* concentration, is illustrated in Figure 36. The initial bloom peaked on Day 6 coincident with the depletion of *in situ* NO3. However, a larger secondary maximum of *ca.* 40 ug C l^{-1} hr^{-1} occurred on Day 10 in response to an increase in the inflow nitrate concentration. During the grazing period, the phytoplankton stock displayed a series of damped oscillations and maintained a quasi steady-state level at *ca.* 30 ug Chl *a* l

$^{-1}$, and there was no significant difference between depths. The dynamics of the phytoplankton stock at this higher flushing rate of 0.75 day^{-1} were considerably different than CHLA during EXP2B (FR=0.25 day^{-1}). The phytoplankton stock averaged 23.7 ug Chl *a* l^{-1} for the total experimental period, approximately three times the average CHLA value during EXP2B and directly proportional to the difference in flushing rates. During the grazing period, the ratio increased to 5:1 indicating that the effect of the increased FR in this experiment dominated the system. The grazing pressure did not cause a decrease in CHLA, and in fact, the excretion of NH3 by the scallops may have enhanced the primary productivity rate.

Oxygen Levels

The oxygen curves for EXP3B (Figure 37) showed a completely different pattern from the previous results in EXP2B, supported by the reproducibility between depths. The average OXY concentration was 11.45 mg l^{-1} during EXP3B and there was no difference between stations. There were three major differences in the oxygen concentration during EXP3B compared with EXP2B: first, the initial OXY maximum during the bloom was 70% less; second, a steady-state level of oxygen was maintained for the duration of EXP3B, exemplified by the low average CV of 6.7% during the grazing period and a standard deviation which approached the value for the inflow; third, the net oxygen concentration (OXYN) was 25% less during the pre-grazing period and 50% greater during the grazing period.

Primary Productivity

The primary productivity rate reached a maximum value of ca. 80 ug C l^{-1} hr^{-1} on Day 6 and decreased in a series of damped oscillations to steady-state rates (Figure 38). During the experiment, PROD averaged 38.3 ug C l^{-1} hr^{-1} and there was no significant difference between depths. The maximum standardized primary productivity rate occurred three days before the phytoplankton bloom in EXP2B, and in contrast to EXP3B, ASS was less during the grazing period due to the high CHLA concentrations. The values of ASS were relatively constant at a low rate of 1.1 ug C (ug Chla)$^{-1}$ hr^{-1} during the grazing period in contrast to the higher average value (6.0 ug C (ug Chla)$^{-1}$ hr^{-1}) and greater variability during EXP2B (Figure 39).

Composition of the Phytoplankton Community

In contrast to EXP2B, Skeletonema costatum remained the dominant phytoplankter during the experiment. Other diatoms in significant numbers were Nitzschia spp., Navicula sp. and Thalassiosira sp., and only a few flagellates were noticeable. More significantly, there were no clumps of the filamentous Navicula sp. floating on the surface of the tank at any time during the EXP3B.

Growth of the Scallops at a Higher Flushing Rate

The results of the survival and growth of the scallop population during EXP3B are summarized in Table 9. In spite of the increased flushing in this experiment, all of the scallops

died at the surface substations, approximately one-half died at the mid depth and only one Chlamys died at the bottom depth. Only the scallops at the bottom station showed any appreciable growth during EXP3B. The maximum percent increase in total weight was the greatest in Cage 9, averaging 16.8% above the initial average weight of 16.9 g. However, the largest scallops in Cage 12 increased by only 1.2% at the bottom depth. The smallest scallops at the bottom (Cage 8) had the largest percent increase of 1.8% in length with a corresponding increase of 0.5% in width.

As pointed out earlier, the temperature during the grazing period averaged 14.5 °C and there was no significant difference in TEMP between depths. Therefore it appears that the increased light intensity was the primary cause of the 100% mortality at the surface. Approximately one-half of these scallops were dead within a week. Secondly, the environmental conditions resulting from the increased flushing rate provided a favourable environment for the growth of Chlamys at a depth of 1 metre.

CHAPTER 5. TWO-STAGE CONTINUOUS CULTURES IN TURBULENT UPWELLING SYSTEMS: DYNAMICS OF THE PRIMARY COMMUNITY AT TWO COMPARATIVE FLUSHING RATES

The dynamics of natural phytoplankton communities in turbulent systems with no grazing pressure were first investigated in a set of experiments which compared two constant flushing rates of the primary system. The flushing rates in the duplicate primary systems were controlled at 0.5 day^{-1} during EXP4A and 1.00 day^{-1} during EXP4B in this set of experiments. During the five week experimental period, the rates remained relatively constant at 0.49 day^{-1} (SD=.019) and 1.00 day^{-1} (SD=.001). However, as a result of outside interference with the experimental facilities on Day 12, the central sampling tube in Tank A became angled toward the inflow pipe in the tank. Consequently, the apparent significant differences in the variable measurements between the bottom station and the other stations (surface, mid and outflow) in this tank can be explained as sampling incompletely mixed inflowing seawater.

After each primary tank was filled with the filtered inflowing seawater and the flushing rates set, initial samples were taken from both tanks. Then each tank was seeded with 10 litres of phytoplankton stock which had been collected from the surface of English Bay and passed through a small diameter wire screen to remove any zooplankton. The experiments were terminated on Day 35 due to problems with the seawater system intake at the Institute.

Dynamics of the Primary Communities at Two Comparative Flushing Rates

Experimental results for the two primary tanks (EXP4A and EXP4B) are graphically illustrated in Figures 40 to 56 and the data statistically summarized in Tables 10 to 15. In the statistical analyses, 'a' and 't' refer to the factors station and time respectively, and the term 'significant' indicates a statistical probability level of 0.05 unless otherwise stated. Variables and parameters are sometimes referred to by their computer names, and Appendix 1 contains a summary of their description and derivation.

Physical Environment

Incident solar radiation (SR) oscillated considerably from 110-560 langley day^{-1}, averaging *ca.* 380 langley day^{-1} (SD=150) during the experiments (Figure 40). There was no sustained period of high solar radiation levels and in fact, the significance of the serial correlation coefficients for SR indicated a strong forcing periodicity to both primary systems A and B (Table 10). The resulting *in situ* temperatures (TEMP) varied significantly with time in both tanks (Figure 41) and the high average correlations of $r(A)=.748$ and $r(B)=.804$ between the solar radiation and the net temperature increase (TEMPN) persisted at a significant level for at least one day in both tanks, particularly in Tank A with the lower flushing rate. The multiple correlation for TEMP and TEMPN with station and time was >0.99, and the temperature in Tank A averaged 14.6 °C

(av SD=1.28), a net increase of 4.2 °C from the inflow temperature. A pattern of weekly periodic oscillations in temperature and a high correlation between stations were similarly apparent in Tank B, but at this higher flushing rate of 1.0 day^{-1}, the average temperature and amplitude were reduced to 13.0 °C (av SD=0.77), a net increase of 2.6 °C . Although the average solar radiation decreased slightly during the nutrient-depleted period of the experiments, there was no significant reduction in the *in situ* temperatures in either tank. It should also be noted that during the experiment the temperature and salinity of the inflowing seawater were relatively constant to both tanks at 10.4 °C (av SD=0.40) and 27.3 ppt (SD=0.79) and there was no significant correlation of either variable with incident solar radiation (Table 10).

Nutrient Regime

Inflow nitrate concentrations (NO3) to both tanks were more variable with time, averaging 18.8 uM N l^{-1} (CV=14.5%), due in part to the correlation between NO3 and the varying tidal height at sampling time, as mentioned in Chapter 4. However, although the tidal height at sampling time was high during the first two weeks of the experiments, the nitrate concentration was lower than average due to the presence of a surface water mass in the vicinity of the seawater intake. This was also detected by the higher inflow temperatures and oxygen levels during this period, and the high correlations between these three variables are verified in Table 10. The inflow NO3 was also significantly correlated with the solar radiation from two days previously.

Although there was no significant difference in the inflow nitrate between tanks, nutrient depletion was apparent by Day 6 at the 0.5 day^{-1} flushing rate in Tank A with a two day time lag at the 1.0 day^{-1} flushing rate in Tank B (Figure 42). During the post-bloom period, the inflow NO3 remained at the average level of ca. 19 uM N l^{-1}, but there was no *in situ* nitrate in Tank B and the presence of sporadic high concentrations of nitrate in Tank A are attributed to the incomplete mixing. The concentration of nitrate utilized by the primary community was calculated (NO3N) and included in the statistical summaries.

The contribution of ammonia and urea as nitrogen sources for the primary systems was minimal. There was no significant uptake of these nutrients in either tank due to the low average inflow concentration of ammonia (0.44 uM N l^{-1}) and urea (0.86 uM N l^{-1}) and to the large variances within and between stations during the experiment.

Phytoplankton Dynamics

Standing Stock

The phytoplankton standing stock was estimated each day as chlorophyll a. In Tank A, the initial bloom was coincident with nutrient depletion on Day 6 (Figure 43) and for the duration of the experiment (t=29), the standing stock averaged 18.3 ug Chl *a* l^{-1} including the higher value of 20.5 ug Chl *a* l^{-1} at the bottom station. Although there was a significant variance in CHLA with time at all four stations (av CV=32%), the correlation was poor between the bottom station and the other *in situ*

stations for CHLA, as well as TEMP, NO3 and OXY, after Day 12. However the standing stock at the other stations oscillated fairly regularly with a one week period, with maxima occurring on Days 17, 24 and 31 and the minima on Days 21 and 28.

The dynamics of the phytoplankton bloom exhibited several major differences in Tank B. First, the initial bloom was produced subsequent to the depletion of *in situ* nitrate on Day 8, due to the low influxes of solar radiation and nitrate at this time. The CHLA maximum did not occur until Day 15 except at the bottom station, which had a significantly higher standing stock from Day 9 to Day 12 due to a problem maintaining the artificial turbulence at this time. Secondly, the standing stock during the nitrate-depleted period (t=27) averaged 40.6 ug Chl *a* l^{-1} and there was a significant ($P>.01$) but small increase with depth. For the total experimental period, the average standing stock in Tank B (1.0 day^{-1} FR) was 32.6 ug Chl *a* l^{-1}, exactly 2.0 times the chlorophyll *a* concentration in Tank A (0.5 day^{-1} FR). Thirdly, although the dynamics of the phytoplankton standing stock were considerably different between tanks in the first few weeks, the timing of the maxima and minima during the last two weeks were similar. However, the standing stock in Tank B exhibited a pattern of damped oscillations after the initial bloom compared with the more unstable pattern of oscillations in Tank A. This was exemplified statistically by the similarities in the variances between tanks for CHLA although the standing stock was twice as large in Tank B.

Pigment Ratios

The concentrations of chlorophyll b (CHLB), chlorophyll c (CHLC) and carotenoids (CT) and the pigment ratios are summarized in Table 11 and Table 12, including the ratios of the pigments in the seed population. The chlorophyll b:chlorophyll a ratio (BA) and carotenoid:chlorophyll a ratio (CTA) during the experiments are also illustrated in Figure 44 and Figure 45. During the nitrate-depleted period (t=29), all pigments ratios in both tanks were significantly different with time, but not between stations. Average pigment ratios for this period indicated a decrease in the BA ratio from 0.105 in the seed population to 0.086 and 0.042 in Tanks A and B respectively, as well as large decreases in the CA ratio. The average CTA ratios of 1.28 and 1.12 in the tanks showed little change from the 1.12 ratio for the initial population. The multiple correlation between the pigment ratios and both the independent factors TIME and STATION was >0.90 for both tanks, except for the C:A and C:CT ratios which probably reflects the poor precision of the chlorophyll c measurements (see Strickland and Parsons, 1972, p.187).

Oxygen Levels

The oxygen concentration (OXY), a forcing variable as well as a state-determined variable, averaged 7.56 mg l^{-1} (av SD=.675) in the inflow to both tanks during the experimental period. In Tank A, the OXY maximum and the maximum net increase in oxygen (OXYN) were not coincident with the initial depletion

of nitrate and bloom of phytoplankton (Figure 46), but occurred on Day 19 (OXY(19)=13.35 mg l^{-1} ,a=3; OXYN(19)=6.47 mg l^{-1} ;a=3) as a result of the high inflow nitrate concentrations and solar radiation from Days 18 to 20. Excluding the bottom station, the average oxygen level during the post-bloom period (t=29) was 11.18 mg l^{-1} , which represents a 3.71 mg l^{-1} net increase in oxygen in Tank A. The variance in OXY and OXYN was highly significant with time but not between stations. However, in Tank B, there was a significant difference in OXY and OXYN between stations, with small positive deviations from the grand mean for the surface and mid stations and small negative deviations for the bottom and outflow stations. The multiple correlation coefficient for OXY and OXYN with both factors remained high at >0.94 (Table 14).

A large increase in oxygen did occur in Tank B subsequent to the initial depletion of nitrate on Day 8 (OXYN(12)=5.65 mg l^{-1} ;a=4), although two larger maxima of 5.91 mg l^{-1} and 6.35 mg l^{-1} occurred on Days 26 and 34 respectively (Figure 46). The net increase in oxygen in Tank B was 20% larger than in Tank A for the comparable time period (t>6), averaging 4.44 mg l^{-1} (av SD=0.193). Oxygen saturation (SAT) increased in both tanks from about 79% to supersaturated levels averaging greater than 130% during the post-bloom period and the analysis of variance pattern was similar to the OXY and OXYN results for both tanks.

Primary Productivity

Primary productivity, including an analysis of the components, was measured using the radiocarbon technique for estimates of net particulate carbon fixation (PROD) and exudation of organic carbon (EXC), plus the oxygen method for measurements of gross productivity (PGO), respiration (RES) and the resultant net productivity (PNO), which were converted to carbon units using a photosynthetic quotient (P.Q.) of 1.2 and a respiratory quotient (R.Q.) of 1.0.

The gross productivity rates (PGO) were high in both Tanks A and B, averaging 220 ug C l^{-1} hr^{-1} and 340 ug C l^{-1} hr^{-1} respectively, for the surface, mid and bottom stations for the ten TIMES (every third day starting on Day 6). Although there was no significant difference in PGO between stations, there was a significant variance in these productivity rates with time, particularly in Tank B in which the phytoplankton maximum did not occur until Day 15 (Figure 47). The multiple correlation for PGO with TIME and STATION was relatively poor in Tank A ($r=.78$) compared with Tank B ($r=.96$) due to the deviant bottom station in Tank A. After the first three weeks there was a higher correlation between tanks.

The repiration rate (RES) averaged 40 ug C l^{-1} hr^{-1} and 47 ug C l^{-1} hr^{-1} during EXP4A and EXP4B, and the patterns were similar with particularly high rates on Day 12 (Figure 48). The average 'net productivity', based on the oxygen method (PNO), was 82% and 86% of the gross productivity in Tanks A and B respectively. However, the net productivity rate determined by the carbon-14 method (PROD), was only a small fraction of PGO

(0.21 in Tank A and 0.17 in Tank B), indicating that there was a large average discrepancy between the two methods of estimating 'net productivity'. As also suggested by other studies (McAllister et al., 1964; Eppley and Sloan, 1965), PROD appears to represent the net fixation of particulate carbon, taking into account the losses of cellular carbon due to exudation (EXC) as well as respiration. The ^{14}C productivity rate was relatively constant during both experiments (Figure 49) although there was a significant difference between stations in Tank A due to the higher values at the bottom station.

Daily estimates of PROD were calculated (PCDY) to normalize any differences in solar radiation between days during the incubation period. The rate of productivity was multiplied by the ratio of the total solar radiation during the day to the solar radiation during the incubation period (see Appendix 1). The rationale for this conversion factor was that since PROD is a hyperbolic function of SR (Chapter 8) and the productivity rates were measured during the period of maximum SR, daily productivity estimates could be expected to be proportional to the lower light levels during the remaining early morning and late afternoon periods. The resulting estimated fixation of particulate carbon averaged 0.35 mg C l^{-1} dy^{-1} and 0.46 mg C l^{-1} dy^{-1} in Tanks A and B, and there were no major changes in the ^{14} C productivity with time (Figure 50). In terms of daily gross productivity, PGODY values averaged 2.11 mg C l^{-1} dy^{-1} and 3.17 mg C l^{-1} dy^{-1} during the experiments, with a maximum value (a=3) of 4.21 mg C l^{-1} dy^{-1} on Day 12 in Tank B (Figure 51).

Values for the productivity component variables were also

standardized on a standing stock basis (ug C (ug Chla)$^{-1}$ hr^{-1}) represented by PGOST, PNOST, RESST, ASS and EXCST. The standardized gross productivity (PGOST) oscillated during the experiments, although there was a decreasing trend with time, particularly in Tank A (Figure 52). As indicated in Table 13 and Table 14, the average and maximum values of PGOST were higher in in Tank A and there was more variability compared with Tank B.

All the component variables of PGOST were also greater in magnitude in Tank A, with average values of 2.4 for RESST, 2.0 for ASS and 6.5 for EXCST, compared with RESSI=1.5, ASS=1.7 and EXCST=6.0 for Tank B. The highest assimilation rates (ASS=7.2 ug C (ug Chla)$^{-1}$ hr^{-1}) occurred in both tanks three days before each system reached its maximum standing stock levels during the initial bloom period (Figure 53). During the post-bloom period, the standardized net primary productivity remained constant between both STATION and TIME. Althcugh there were only five measurement times for the exudation rate, EXCST generally decreased in both tanks with time and the values were significantly lower at the bottom station in Tank A. The standardized respiration rate during EXP4A and EXP4B was similar to RES, with maximum values occurring on Day 12. However, in EXP4B, the highest RESST values were apparent on Day 6 (Figure 54).

Estimation of Parameters for a Primary Productivity Model

Since the exudation rate was only measured every second productivity time, a productivity component analysis was based on t=5, a=3 to evaluate the parameters in the following productivity sub-model:

Gross Productivity = Assimilation + Respiration + Exudation

or $1 = ASS/PGOST + RESST/PGOST + EXCST/PGOST$

The results are shown in Table 15. First, this additive model seems a good approximation of the experimental results. The estimated gross productivity (ESTPGO) is close to 1.00 in both tanks and there was no significant differences in ESTPGO with TIME or STATION. Second, the estimate of the parameters for the component variables are similar between tanks in spite of the difference in flushing rates, with assimilation representing about 20% of the gross productivity and losses of ca. 20% to respiration and ca. 60% to exudation. When the respiration and assimilation components were calculated for t=10 and a=3, the values were similar, indicating that these parametric estimates based on t=5 are reasonable. The assimilation fraction increased during the fourth and fifth weeks of the experiments, particularly in Tank A, suggesting that APGO increased in response to high inflow concentrations. Also the exudation fraction of gross productivity (EPGO) was lowest when the NO3/CHLA ratio was highest.

Parametric estimates were also calculated for the initial slope, ALPHAC (ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$) in the

hyperbolic productivity versus light (PAR) relationship. Since the measurements of the extinction coefficient (EXTK) were of questionable accuracy due to faulty equipment, the solar radiation at depth (PARZC) used in the calculation of ALPHAC, was estimated using Riley's formulation of EXTK (See Chapter 2) in the following equation:

$$PARZ\ (\text{langley min}^{-1}) = (PARZC/240.) * EXP(-EXTK*Z)$$

The average value for ALPHAC, 11.0 ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$, was predictably much lower than for ALPHAG. Maximum ALPHAC values of 30.0 occurred in both tanks on Day 30 (Figure 55), at which time SR and TEMP were below average and NO3(IN) above average. Although the standing stock and nutrient flux in Tank B were double the levels in Tank A, the standing stock per unit of nitrate was equal. Therefore it seems reasonable that there were no significant differences in ALPHAC between tanks since both systems had predominantly diatom communities. The initial slope based on gross productivity (ALPHAG) was very similar for both tanks, averaging 64.3 ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$, although in both cases there was a significant increase in ALPHAG with depth due to the decrease in PARZO (Figure 56). The significant variability in ALPHAG with time was not surprising since both ASS and PARZ varied significantly with time. A similar analysis of variance was obtained for ALPHAC.

Composition of the Phytoplankton Community

The size composition of the phytoplankton community was monitored during both experiments using the Coulter Counter. The numbers of particles were converted into volume concentrations (microns per ml), as outlined in Sheldon and Parsons (1967), and plotted as a function of the particle size, measured as the diameter (microns). Figures 57 to 61 are representative of the results during both the bloom and post-bloom periods of EXP4A. The first point to note is the similarity in the shape of the volume versus size curves over time. The unimodal trend with the maximum volume at 18.4 microns during the bloom (Figures 57 and 58) persisted throughout the experiment (Figures 22 to 25) with little variation in the magnitude over time. Secondly, the size composition was similar between stations, and the correlation between the Coulter counts and chlorophyll *a* was generally good except for a time lag in the particle volumes during the initial bloom.

The results for EXP4B were similar to EXP4A in most respects, except for two features. The particle volumes during the initial bloom were higher on Day 12 than Day 9, and secondly, the magnitude of the maximum volume per ml in EXP4B was about twice as large as EXP4A.

Throughout the experiments, the dominant phytoplankter was *Skeletonema costatum* in both systems. In EXP4B, the other few species present were mostly diatoms, including *Chaetoceros decipens* (?), *Thalassiosira aestivalis* (?) and *Nitzschia spp.* A filamentous benthic diatom (*Navicula sp.*) was apparent on

the sides of the primary production tank, but the standing stock was low compared with the phytoplankton stock. In comparison, the previous experiments indicated that production of benthic diatoms was significant in non-turbulent systems. In EXP4A, there was a greater diversity of phytoplankters and a few flagellate species were noticable during the the post-bloom period, including *Gymnodinium sp.* , a *Prorocentrum* species and some cryptomonads. There was also less *Navicula* on the sides of Tank A than Tank B.

These findings are consistent with previous laboratory and field results which indicated that systems with lower nutrient fluxes tend to have more phytoplankton diversity, and an increase in the nutrient concentration causes an increase in the dominance of diatoms. At high flushing rates of 2.0 day^{-1} , most of the phytoplankton community was washed out of the system and the primary community became dominated by benthic diatoms such as the *Navicula sp.* (Brown and Parsons, 1972).

CHAPTER 6. TWO-STAGE CONTINUOUS CULTURES OF PLANKTONIC HERVIVOROUS FOOD CHAINS: DYNAMICS OF THE PRIMARY COMMUNITY AT VARIABLE FLUSHING RATES

A set of two-stage continuous culture experiments were investigated in the two production systems . In this case, the dynamics of the primary communities were examined using controlled, but variable, flushing rates of the system. In production Tank A, the initial flushing rate (FR) was set at 0.25 day^{-1} for two weeks duration. On Days 14 and 28 the flushing rates were altered to 0.50 day^{-1} and 0.10 day^{-1}, respectively. The experiment in this tank ended after 6 weeks due to contamination of the primary system by two herbivorous protozoans, one a holotrich ciliate (Dileptus sp?) and the other a hypotrich. The experiment in production Tank B was continued to Day 49, with the flushing rate reset from the initial rate of 1.00 day^{-1} to 0.50 day^{-1} on Day 41. In the second stage of the production system, the outflow from either Tank A or B was fed at different rates into the four herbivore tanks containing the three densities of oysters plus one control. This provided four unique experimental conditions (Experiments I to IV) and the experimental design for the investigation of the two-stage continuous cultures is summarized in Table 16. The results are presented in Chapter 7.

During the experimental period, two related aspects of primary productivity were investigated. A series of productivity versus light experiments were conducted as a function of the temperature and the nutrient status of the phytoplankton, to estimate the effects of these three variables

on the primary productivity of the system. The procedure and results are presented in Chapter 8. The primary productivity was also analyzed in a series of enrichment experiments to verify that some micro-nutrient was not limiting the system. The procedure was similar to the other radiocarbon uptake measurements except that the samples from Tank B were enriched with either Guillard's F medium, or a vitamin mix (with no B12) or vitamin B12 only. The latter two enrichments were made at the same concentration as the addition of the F medium (Table 17). Experiments were conducted on two days of varying light intensity, one at a light-limiting level and the other at a light-saturating level. The results indicated that only the B12 enrichment at the high light intensity produced a significant increase in the primary productivity rate in comparison to the control. However, there was no significant increase in primary productivity on either day with the F enrichment which contained the same concentration of vitamin B12. Therefore is seems probable that NO3 was the primary limiting nutrient during these experiments.

Dynamics of the Primary Communities at Variable Flushing Rates during the Experimental Period

After each primary tank was filled with the filtered inflowing seawater and the flushing rates set, initial samples from each tank were taken. In this set of experiments, each tank was seeded with 10 litres of phytoplankton stock from EXP4B so that both experiments would have similar initial primary

communities, composed mainly of Skeletonema costatum plus a few other diatoms and flagellates [1]. Results of the experiments (EXP5A,EXP5B) are illustrated in Figures 62 to 90, with statistical summaries in Tables 18 to 23. In the following discussion of EXP5A, Period's 1, 2 and 3 refer to the 0.25 day^{-1}, 0.50 day^{-1}, and 0.10 day^{-1} flushing rates respectively.

Physical Environment

During the first six weeks, which includes the total experimental period for Tank A and the 1.0 day^{-1} flushing rate period in Tank B, the incident solar radiation averaged 400 langley day^{-1} (SD=106). As illustrated in Figure 62, the means and variances for SR were very different between the three periods of variable flushing rates in EXP5A, averaging 500 langley day^{-1} (SD=15) during Period 1, 340 langley day^{-1} (SD=132) for the second period and 380 langley day^{-1} (SD=49) during the third period (Table 18). The combination of the variability in solar radiation and flushing rate resulted in average net temperature increases (TEMPN) of 6.7 °C, 3.8 °C, and 8.8°C during the three two-week periods in EXP5A. The large variability in TEMP during the experiment in Tank A (Figure 63) was due to the coincidence of a reinforcing effect of SR with the alteration in flow rate, particularly during Period 2, when the FR was increased to 0.50 day^{-1} (with a subsequent decrease in TEMP) and SR was lower than average. Temperatures reached a

---

[1] EXP4B was terminated two days before the start of Experiment 5

maximum of 21.9 °C during the 0.10 day^{-1} FR and averaged 19.8 °C , compared with 18.7 °C at the 0.25 day^{-1} FR and 16.0 day^{-1} at the 0.50 day^{-1} FR. The temperature averaged 18.1 °C during EXP5A, and although the correlation between the four in situ stations was high (r=.994), there was a statistically significant but small (0.6 °C) decrease in TEMP with depth (Table 20). The temperature in Tank B during the same period (t=1,41) averaged 15.0 °C , with less variability with time (CV=6.1%), although there was also a significant decrease of 0.3 °C in TEMP with depth. The temperature during the last week of EXP5B (FR=0.50 day^{-1}) remained at the average value. The salinity was essentially constant at 27.2 ppt (SD=0.92) during both experiments.

Nutrient Regime

Inflow nitrate to both systems was similar but extremely variable with time, averaging 16.5 uM N l^{-1} (av SD=8.80). As illustrated in Figure 64 , there was a decreasing trend in the inflow nitrate concentration for the first three weeks, increasing to levels greater than 20 uM N l^{-1} during the remaining period. The inflow NO3 concentrations during the three periods of EXP5A averaged 14.3 uM N l^{-1} (SD=2.91), 14.1 uM N l^{-1} (SD=7.70) and 21.9 uM N l^{-1} (SD=1.24) respectively. The low inflow concentrations during the third week could be partly attributed to the fact that the sampling time coincided with low tide. As described in Chapter 5, this caused an underestimation in the inflow concentration on a daily basis. An algorithm was designed to partially compensate for the discrepancy. A tidal

ratio was calculated based on the amount of time during the day that the tidal height was above the height at sampling time to the amount of time per day that the tidal height was below the height at sampling time; this factor was then applied to the nitrate concentration at sampling time to estimate a revised daily inflow nitrate concentration, TNO3(IN). The results indicated that the inflow nitrate value of 16.6 uM N l^{-1} averaged for t=1,41 increased to 19.0 uM N l^{-1} for the same time period when the temporal effect of the tide upon sampling was taken into account. However, no factor was included to account for the increase in nitrate concentration with tidal height, since the tidal amplitude and rate of change in NO3 with tidal height varied during the experimental period. So the revised estimates of TNO3 probably still underestimated the actual average inflow nitrate concentration.

In Tank A, the depletion of nitrate occurred by Day 5 at the 0.25 day^{-1} flushing rate, and there was no in <u>in situ</u> recovery of significant NO3 for the remainder of the experiment. The net uptake of nitrate (NO3N) by the primary community increased during the experiment, averaging 9.3 uM N l^{-1} , 14.1 uM N l^{-1} and 21.9 uM N l^{-1} for the three periods; the corresponding values based on the tidal correction factor, TNO3N, were 12.0 uM N l^{-1} , 16.3 uM N l^{-1} and 24.1 uM N l^{-1} . Nitrate depletion did not occur until Day 7 in Tank B (FR=1.0 day^{-1}) and significant concentrations (>2 uM N l^{-1}) of nitrate were apparent on Days 12 and 13. The tank was very clear at this time and much of the phytoplankton stock had sunk to the benthos, in spite of the <u>in situ</u> circulating pumps. However

Skeletonema costatum was still the dominant phytoplankter. As in Experiment 4, inflow ammonia and urea concentrations were low (<1 uM N l^{-1}) during the experiments.

Phytoplankton Dynamics

Standing Stock

The initial phytoplankton blooms were coincident with nutrient depletion in both Tanks A and B (Figure 65) and were of a similar magnitude (35-40 ug Chl *a* l^{-1}). The characteristic minimum in CHLA following nutrient depletion was apparent by Day 9 in Tank A and by Day 12 in Tank B. In Tank A, the CHLA level stabilized at *ca.* 8.9 ug Chl *a* l^{-1} during the last three days of the 0.25 day^{-1} FR period. After the flushing rate was doubled to 0.5 day^{-1} on Day 14, the phytoplankton increased to *ca.* 21 ug Chl *a* l^{-1} and restabilized at 17.1 ug Chl *a* l^{-1} from Days 19 to 22. This was approximately double the steady-state value during the first period. The large increase in the phytoplankton stock during the remaining 6 days of the second period (FR=0.50 day^{-1}) was significantly correlated with the large positive trend in the inflow nitrate concentration from Day 21 to Day 28 and the high incident solar radiation from Days 21 to 23. The results indicated that there was a 2 day lag between the more favourable forcing conditions for productivity and the resultant increase in phytoplankton stock, and by the end of the second period in Tank A, the stock levels had reached 45 ug Chl *a* l^{-1} . After the FR was lowered to 0.10 day^{-1} on Day 28, the phytoplankton stock decreased to concentrations between

15-20 ug Chl *a* l^{-1} , before approaching near-zero values at the end of the experiment due to the contamination of the primary tank by protozoans.

During the nutrient-depleted period in Tank B (t>6), the phytoplankton stock reached a steady-state value from Days 19-22 which was similar to Tank A, although the FR was twice as high as Tank A. However, after the increase in incoming NO3 and SR at this time, the phytoplankton stock doubled by Day 23 and reached maximum levels of *ca.* 60 ug Chl *a* l^{-1} , except at the outflow station which was significantly lower for some reason. The phytoplankton stock displayed a series of damped oscillations following this bloom, decreasing to a level of *ca.* 30 ug Chl *a* l^{-1} at the end of the 1.0 day^{-1} FR period. The standing stock remained at a similar concentration in Tank B during the 0.5 day^{-1} FR (t=42,49). There was a small significant increase in CHLA with depth in both tanks (Table 20 and Table 21).

Pigment Ratios

The concentration of CHLB, CHLC, and carotenoid (CT) pigments are summarized in Tables 18 and 19. All the accessory pigments and the calculated pigment ratios were significantly variable with time although generally not different between stations. In Tank A, after nutrient-depletion had occurred during the 0.25 day^{-1} FR period, there was a significant increase in the BA ratio (Figure 66). However, by the end of the second period, CHLB concentrations were reduced to zero at this higher FR. CHLB again increased during Period 3,

contributing to an exponential increase in the BA ratio. The CTA ratio is illustrated in Figure 67 and the correlation between the CTA and BA ratio was high for both tanks. During the first six weeks of EXP5B (FR=1.00 day^{-1}), there was an exponential decrease in the BA ratio, except for an increase to ca. 0.1 from Day 16 to 22, which was coincident with the low inflow nitrate concentrations.

Oxygen levels

Inflow oxygen concentrations (OXY) averaged 7.26 mg l^{-1} (av SD=.835) for both tanks during the first six weeks. The changes in *in situ* oxygen levels during the experiments are illustrated in Figure 68. In both tanks, OXY maxima were coincident with the initial phytoplankton bloom, and in Tank A, the 13.63 mg l^{-1} average on Day 5 was the maximum value during the experiment. There was also a significant difference in oxygen between stations in both tanks. In Tank A, this was particularly evident during the 0.10 day^{-1} FR period. To compensate for the variability in the inflow oxygen concentration, the net oxygen increase (OXYN) was calculated for each *in situ* station. The correlation between OXYN and CHLA was high (r=.830), particularly with a one day time lag for CHLA (r=.888). Excluding the bottom station which was significantly lower, OXYN reached an average maximum of 6.99 mg l^{-1} on Day 29, which represented an oxygen concentration of 13.21 mg l^{-1} and an oxygen saturation level of 160%. In Tank B, the average value of OXY was only 1.00 mg l^{-1} higher for t=1,41 and the maximum on Day 32 was not much larger than for Tank A. The correlation

between OXYN and CHLA for the same time period was also high in Tank B (r=.812), but with no time lag. Oxygen saturation levels were similar to Tank A.

Primary Productivity

Results from the primary productivity measurements are summarized in Tables 20 and 21. The number of TIMES (days) used in the analysis was eleven, represented by every third day from Day 6 as in EXP4A and EXP4B [1].

The gross productivity rates in Tanks A and B are illustrated in Figure 69. In both cases there was a significant variability in gross productivity with time since PGO is a function of CHLA. However, in Tank A, the maximum rate occurred on Day 4, one day before the CHLA maximum, while in Tank B the initial PGO maximum was coincident with the CHLA maximum on Day 7. A large secondary maximum of 460 ug C l^{-1} hr^{-1} also occurred in Tank B on Day 33, with an estimated daily value (PGODY) of 3.83 mg C l^{-1} dy^{-1}. There were no significant differences between stations for any of the productivity variables and the average gross productivity during EXP5A and EXP5B was 160 ug C l^{-1} hr^{-1} and 304 ug C l^{-1} hr^{-1} respectively. The pattern between PGO and PGODY was similar during the experiments (r(A)=.96; r(B)=.98), except the gross productivity on a daily basis decreased during the secondary bloom (Figure 70). The respiration rate (RES) was relatively constant during both

---

[1] The data for Day 15 is missing for all productivity variables in Experiment 5.

experiments, averaging ca. 42 ug C l^{-1} hr^{-1}, and only in Tank B was there a marginal significant difference in RES with time (Figure 71). The net productivity based on the oxygen method (PNO) was highly correlated with PGO in both tanks (r>.97) and the rate based on the radiocarbon method (PROD) was also significantly correlated with PGO and PNO (Figure 72). The correlation was greater in Tank A (av r(A)=.65) than for Tank B (av r(B)=.47). The average PROD rates during the experiments were 61 ug C l^{-1} hr^{-1} and 101 ug C l^{-1} hr^{-1} in the two tanks, which represented daily net productivity rates of 0.51 mg C l^{-1} dy^{-1} and 0.84 mg C l^{-1} dy^{-1}. The changes in PCDY with time are illustrated in Figure 73.

The effect of the variable flushing rates on primary productivity was analyzed by comparing the productivity variables standardized per unit of CHLA. The resulting PGOST, RESST and ASS curves are illustrated in Figures 74 to 76. Maximum standardized gross productivity rates of at least 20.7 ug C (ug Chla)$^{-1}$ hr^{-1} were attained in Tank A subsequent to the initial phytoplankton bloom, and secondary maxima were also apparent on Day 21 during Period 2 (FR=0.50 day^{-1}) and on Day 39 during Period 3 (FR=0.10 day^{-1}) when the standing stock level approached zero. The pattern for PGOST in Tank B was somewhat different. During the first two weeks, the standardized gross productivity was relatively constant, ranging from ca. 10-15 ug C (ug Chla)$^{-1}$ hr^{-1}. Only during the second two-week period was the correlation high between the two tanks for PGOST, although the variability with time was again less in Tank B. During the third two-week period, PGOST significantly

increased to a maximum of ca. 20 ug C (ug Chla)$^{-1}$ hr^{-1} in Tank B, while the average values remained at ca. 8 ug C (ug Chla)$^{-1}$ hr^{-1} in Tank A until the increase on Day 39. These maximum values in both tanks are greater than the high Pmax's found in Tokyo Bay, also during a Skeletonema costatum bloom (see Parsons and Takahashi, 1973a).

The standardized respiration rate (RESST) was more variable during EXP5A (Figure 75), especially during the bloom period when ca. 45% of the gross productivity was lost to respiration compared with ca. 13% for Tank B (Table 22). During the second period of EXP5A, RESST decreased to a low rate of 1.5 ug C (ug Chla)$^{-1}$ hr^{-1}, the same value for EXP5B during the corresponding time period. After the FR was reduced to 0.1 day^{-1} in Tank A, RESST increased by 75% while the standardized respiration rate increased by only 20% during Period 3 in Tank B.

The standardized net productivity rate (ASS) was characterized by damped oscillations during Period 1 in EXP5A (Figure 76), averaging 6.0 ug C (ug Chla)$^{-1}$ hr^{-1}. The variability in Tank B was less even even though the magnitude was greater at 6.5 ug C (ug Chla)$^{-1}$ hr^{-1}. The assimilation rates were the the lowest (2.5 ug C (ug Chla)$^{-1}$ hr^{-1}) during Period 2 in both tanks. The rate increased in Tank B on Day 27 in response to the large increase in the inflow nitrate concentration. The rate also increased in Tank A during Period 3 in spite of the five-fold decrease in FR. A close examination of ASS as a function of STATION in Tank B (Figure 76) suggested two interesting features. The linear increase in inflow NO3 from ca. 3 uM N l^{-1} on Day 20 to ca. 20 uM N l^{-1} by Day 24

failed to alleviate the nutrient-limited state of the phytoplankton by Day 24. However, the system had become light-limited by Day 27, indicated by the high assimilation rate at the surface compared with the bottom station. By Day 33, the phytoplankton stock appeared to become nitrate-limited again.

Estimation of Parameters for a Primary Productivity Model

A productivity component analysis similar to the one outlined in Chapter 5 was used to evaluate the proportion of gross productivity represented by assimilation, respiration and exudation. The results are shown in Table 23. The estimated gross productivity (ESTPGO) was 6% higher than 1.00 in Tank A and 16% lower than expected in Tank B. In the case of EXP5B, the ratio of exudation to gross productivity (EPGO) was suspect. The estimates of RPGO (respiration:gross productivity) and APGO (assimilation:gross productivity) were 0.15 and 0.36 respectively, regardless of whether the estimates were based on the productivity data for the total experimental period (t=11) or only the times when EXC was measured (t=5). Therefore EPGO was probably closer to 0.50. On the other hand, if the values for RPGO and APGO were based on the total experiment in EXP5A, then ESTPGO closely approximated the expected value of 1.00. Summarizing, in EXP5A respiration and exudation each represented ca. 30% of the gross productivity with ca. 40% attributed to assimilation; in EXP5B, the largest proportion of gross productivity was channeled through exudation (ca. 50%), the assimilation component decreased slightly to ca. 35% and the respiration fraction was 15%, about half the value in EXP5A.

Values for ALPHAC (ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$), the initial slope in the ^{14}C productivity versus light (PAR) relationship, were also estimated from the ASS and PARZC data as in Chapter 5. In EXP5A, ALPHAC reached a maximum of ca. 60 ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$ at the bottom station and decreased to an average value of 11.7 ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$ during Period 3 (Figure 77). The average value for EXP5A was 14.0 ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$ compared with 15.7 ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$ for EXP5B. The lowest estimates of ALPHAC occurred on Day 21 in both tanks when the inflowing NO3 was very low and SE was high. The corresponding estimates of the initial slope based on the gross productivity (ALPHAG) are illustrated in Figure 78.

Composition of the Phytoplankton Community

The evolution of the phytoplankton communities in terms of size composition are illustrated in Figures 79 to 84 for EXP5A and Figures 85 to 90 for EXP5B. The six times or days were representative of the structure of the primary community approximately one week after each change in the flushing rate in EXP5A. The corresponding results from Tank B were also included as a comparison of a system with a high constant flushing rate.

During the initial bloom period in EXP5A (Figures 79 and 80), the maximum volume of 'particles' was found at the 22.6 micron size on Day 6; with the onset of nutrient-depletion, the decreased maximum volume shifted to the 14.3 u diameter size by Day 12. By comparison, the maximum volume in Tank B was evident

at the same diameter of 22.6 u on Days 6, 9 and 12 (Figures 85 and 86). The later timing of the maximum particle volume on Day 9 followed the same trend as the phytoplankton stock measured as CHLA.

During Period 2 (Days 15-28), the size composition in Tank A shifted to a bimodal distribution with maximum volumes at the 9.0 u and 18.5 u sizes (Figures 81 and 82). However, the phytoplankton in EXP5B retained a unimodal size distribution, although the diameter of the maximum volume had shifted to 11.3 u by Day 24 (Figures 87 and 88). The cell diameter of the maximum volume increased again to 14.3 u by Day 39 (Figures 89 and 90). During Period 3 in EXP5A, the phytoplankton volume concentration returned to a unimodal size distribution with the maximum volume at 11.3u, although the magnitude had decreased significantly by Day 39 (Figures 46 and 47).

Skeletonema costatum was the dominant phytoplankter for the duration of EXP5B even on Day 12 when the system was initially depleted of nutrients and the phytoplankton stock was at a minimum. The other two main diatom species in Tank B were Chaetoceros decipens (?) and Nitzschia closterium (?), although some Rhizosolenia were also apparent at the end of the 1.0 day^{-1} FR. The phytoplankton composition during EXP5A was quite different from EXP5B. Although present in significant numbers, Skeletonema costatum was not the dominant phytoplankter. A Chaetoceros species (compressum?) was the dominant phytoplankter after the initial bloom and Thalassiothrix and Nitzschia were also present in significant numbers. Throughout the experiment, Tank A had a much higher diversity, with more species of diatoms

and a variety of nano-flagellates. By the end of EXP5A, the species list also included *Rhizosolenia delicatula*, a unicellular *Chaetoceros*, cryptomomads (*Cryptomonas sp.*,) and (*Oxhyrris sp.*). It should be noted that the species composition, as well as cell numbers, in Tank A would have been affected by the presence of the predatory ciliates which 'contaminated' the primary system during the last week of the experiment.

CHAPTER 7. TWO-STAGE CONTINUOUS CULTURES OF PLANKTONIC HERBIVOROUS FOOD CHAINS: GROWTH OF THE HERBIVORES

Experimental Design

Growth of the sessile 'planktonic' herbivore, Crassostrea gigas , was investigated in a two-stage culture system (Figure 5) using the outflow from either primary tank A or B as a continuous source of phytoplankton and oxygen to the four herbivore tanks. Four oyster experiments (EXPI to EXPIV) of one week duration were conducted from Days 18 to 50 during the post-bloom period of the primary tanks. The four experiments differed in the source of the inflow (Tank A or B) and in the flushing rate of the herbivore tanks (FR= 1.0 day^{-1} or 2.0 day^{-1}) to compare various types of phytoplankton communities (flagellate, diatom, or mixed) and various concentrations of phytoplankton and other growth variables. The experimental design is shown in Table 16.

As described in Chapter 2, Tank 4 was the control with no oysters and Tanks 1, 2 and 3 were stocked with 2, 4 and 8 cultch respectively, with 8 oysters per artificial cultch. 96 healthy juvenile oysters were selected and then divided into four size groups: very small (35-45 mm), small (45-55 mm), large (55-65 mm) and very large (65-75 mm). The 8 'very small' oysters were attached to Cultch #1, while the 32 oysters in the 45-55 mm range were randomly chosen for placement on one of the four 'small' cultch (#2 to #5). A similar procedure was used to

produce the four 'large' cultch (#6 to #9) and the three 'very large' cultch (#10 to #12), giving the required twelve cultch.

Therefore the production of oysters could be examined to some extent as a function of their density and size in each of the experiments. Before each herbivore experiment, the cultch were held in the outflow from the appropriate primary tank for ca. 24 hours. Initial measurements were taken for the oyster growth variables (length, width, depth, total weight, meat weight and shell weight) and the oyster experiments conducted for one week periods. The temperature, oxygen level, chlorophyll a concentration, urea and ammonia were monitored once a day at ca. 1200 hours PST. At the end of each experiment, the oysters were again weighed and measured and the feces and pseudofeces collected from the herbivore tanks.

Experimental Results

Results for the oyster experiments are summarized in Figures 91 to 95 and Tables 24 to 26. Appendix 2 contains the description and derivation of additional variables pertinent to the production of herbivores.

Environmental Conditions during the Oyster Growth Experiments

The in situ temperatures during the oyster growth experiments are illustrated in Figure 91. Although there was no significant difference in temperature between tanks in any of the four experiments, there was a significant difference ($P=.001$) in TEMP between experiments (Table 24). In Experiment

3, the temperature during the week averaged the highest value (23.3 °C), resulting from two factors. The temperature of the source inflow from Tank A was significantly higher than from Tank B (the source inflow for the other three experiments) and the flushing rate of the herbivore tanks in Experiment 3 was only 1.0 day^{-1} . The 18.5 °C average temperature in Experiment 1 was the lowest and most variable during the one week period. The temperatures in Experiments 2 and 4 averaged 20.2 °C and 19.5 °C respectively.

As illustrated in Figure 92, the inflow phytoplankton concentrations varied considerably within and between experiments. The low inflow CHLA during the latter part of the Experiment 3 was coincident with the contamination of the primary Tank A by protozoans, as mentioned in Chapter 6. In all four experiments, the phytoplankton concentration in the control tank (4) was significantly lower than the inflow concentration, indicating a proportion of the stock was lost to the benthos in spite of the use of in situ circulating pumps. The loss averaged 30% in Experiments 2 and 4 at the 2.0 day^{-1} flushing rate and increased to 58% at the 1.0 day^{-1} flushing rate in Experiments 1 and 3. Since there were no herbivores in the control tank, these percentage losses of phytoplankton due to sinking would be higher compared to the other herbivore tanks which had a significant but variable grazing rate depending on the number of oysters per tank.

In view of the lack of direct measurements of phytoplankton sinking rates within each herbivore tank, the uptake of phytoplankton (STKUP) was estimated as the difference between

the inflow and *in situ* phytoplankton stcck and provides a maximum estimate. The *in situ* phytoplankton standing stock decreased expcnentially in Tanks 1 to 3 during the one week period in all four experiments, and the uptake of phytoplankton remained fairly constant in EXPII and EXPIV. In EXPI, the *in situ* phytoplankton stock levels remained low in all three herbivore tanks in spite of the increased inflow concentration during the last half of the experiment.

Excluding the control tank, there was a significant difference (P=.000) in STKUP between the four experiments, with values averaging 22.3 ug Chl *a* l^{-1} , 24.5 ug Chl *a* l^{-1} , 7.8 ug Chl *a* l^{-1} and 24.8 ug Chl *a* l^{-1} in Experiments 1 to 4 (Table 24); although if EXPIII is excluded, since it was the only growth experiment with the flagellate ccmmunity as a food source, there were no differences in STKUP between experiments (P=.738). However, the flushing rates in Experiments 2 and 4 were twice as high as in Experiment 1, and when the phytoplankton source was expressed as an uptake rate (STKUPR) , Experiments 2 and 4 had similar average values of 8.4 mg Chl *a* dy^{-1} , more than double the uptake rate in Experiment 1. Since the stock concentration in Experiments 1 and 3 were grazed to a level approaching zero in the three oyster tanks, only in Experiments 2 and 4 was there a significant difference in STKUP between tanks. The phytoplankton stock levels in Tank 3 with the highest density of oysters were less than 2 ug Chl *a* l^{-1} in both EXPII and EXPIV.

The ratio of chlorophyll *b* to chlorophyll *a* (BA) is also summarized in Table 24, since it gives some indication of the

species composition of the phytoplankton stock. In all experiments, the BA of the phytoplankton in the herbivore tanks were significantly higher than the control which retained a similar value to the inflow. The oysters appear to preferentially graze the large diatoms, leaving an environment conducive to the growth of nano-flagellates (i.e. a high light and temperature, low nutrient system). A similar trend was also apparent between the herbivore tanks from the low to high densities, particularly in EXPI and EXPIV.

Oxygen concentrations for the four oyster experiments are illustrated in Figure 93. As with the phytoplankton stock, the inflow oxygen levels varied between experiments and the net oxygen uptake was calculated as the difference between the inflow and *in situ* concentrations. The average uptake of oxygen (OXYUP) in Experiments 1 to 4, excluding the control tank, was 3.77 mg l^{-1} , 5.45 mg l^{-1} , 3.85 mg l^{-1} and 5.23 mg l^{-1} respectively. During Experiment 3, the oxygen concentration in the three oyster tanks increased during the last half of the experiment to levels above the inflow concentration. Furthermore, the uptake in Tank 3 was the least although this tank contained the highest density of oysters. This is in contrast to the other three experiments, in which there was a significant increase ($p=.006$) in OXYUP between Tanks 1 to 3. When the uptake of oxygen was expressed as a rate, OXYUPR was least in EXPI (640 mg dy^{-1}) and greatest in EXPII (1852 mg dy^{-1}) in contrast to the results for STKUPR. By comparing the OXYUPR:STKUPR ratio, it is apparent that this ratio was least for EXPI (0.17), with values of 0.22 for EXPII and EXPIV and a

large maximum ratio of 0.49 for EXPIII. Furthermore, these results are positively correlated with temperature.

Ammonia, the primary excretory product of oysters, did not increase significantly in any of the experiments, with production rates of 1.9 uM NH3 l^{-1} , 0.8 uM NH3 l^{-1} , 1.4 uM NH3 l^{-1} and 0.6 uM NH3 l^{-1} . There was no significant difference between tanks either, and the results indicate that a steady state existed between NH3 uptake by phytoplankton and NH3 excretion by the herbivores. There was no significant increase in UREA concentrations either.

Oyster Growth as a Function of the Experimental Factors

Results of the oyster growth in terms of the three experimental factors, experiment (EXP), density (DENS) and size (SIZE)) are summarized in Table 25 and Table 26 and illustrated in Figures 94 and 95.

The means and standard deviations for the six growth variables (length, width, depth, total weight, meat weight and shell weight) were calculated for each of the twelve oyster cultch (n=8) at the beginning of each herbivore experiment (Table 25). The initial dimensions and weights, averaged for the total population of oysters (N=96), were: length(L)= 5.7 cm; width(W)= 3.2 cm; depth(D)= 1.7 cm; total weight (WGTT)= 12.8 g; meat weight (WGTM)= 4.0 g; shell weight (WGTS)- 8.8 g. At the end of all four experiments, the average length had increased by 0.4 cm (7%), the width by 0.6 cm (18%) and the depth by 0.2 (12%). The total weight increased by 50% to 19.2 g, with WGTM representing 32% of the total weight, which was the same

proportion as the initial measurements.

The net and percent increases during each experiment were calculated for all six growth variables for each oyster and the averages summarized in Table 26. Average net increases for all three dimensional measurements of growth (NETL, NETW and NETD) were significantly different (P>.001) between experiments. Maximum average increases of 0.17 cm, 0.24 cm and 0.08 cm were attained during EXPII for NETL, NETW and NETD respectively; these values represent more than 40% of the total increase for the entire experimental period (four weeks) for all three variables. In terms of percent increases [1] this represents values of 3.2% $week^{-1}$ for PERL, 7.5% $week^{-1}$ for PERW and 4.7 % $week^{-1}$ for PERD. The lowest average net increases in the linear dimensions of the oyster population occurred in EXPIV, with growth rates of less than 1.2% per week.

There were also significant differences between experiments in the net increases in the growth variables which were measured in terms of weight. The largest net increases occurred in EXPIV, with averages of 2.1 g/oyster for NETWT, 0.7 g for NETWM and 1.4 g for NETWS. Large net increases in the total weight, meat weight and shell weight also occurred in EXPII , which on the basis of % increase in growth, were the largest average values for total weight (PERWT=13.5% $week^{-1}$), meat weight (PERWM=15.4%) and shell weight (PERWS=12.6%). A similar pattern of growth was apparent in EXPIV and EXPI, with slightly lower

---

[1] The % growth rate was calculated for each oyster as the net increase during the experimental period divided by the value at the beginning of that experiment.

percentage increases. During EXPIII, there was only an 8.1% increase in the total weight and the ratio of NETWM:NETWT dropped to ca. 0.17 from the 0.37 during EXPI and EXPII. It was low compared with the original WGTM:WGTT ratio of 0.32, but by the end of EXPIV, the ratio had returned to 0.34. Finally, the smallest increase in shell weight occurred in EXPIV.

The net and percent increases in growth are illustrated as a function of the factors density (DENS) and size (SIZE) for all six dependent variables. In Figure 94, the oyster growth in each experiment is broken down by density, with DENS=1 corresponding to the lowest density in Tank 1, DENS=2 to the medium density in Tank 2 and DENS=3 to the highest density in Tank 3. There was generally a decrease in the average net linear dimensions with an increasing density of oysters, particularly in EXPI and EXPII. However the differences in the linear dimensions between DENS were not significant on a net or percentage basis, except in the case of depth for EXPI and EXPII. The results for EXPIII and EXPIV did not follow a similar definite pattern. The highest linear growth rates in EXPIII were found in the high density tank, while in EXPIV, the medium density tank (2) had the lowest rates.

In terms of the weight variables, there was generally a significant decrease in total weight, meat weight and shell weight with an increasing density of oysters. However in EXPII, oysters in the medium density tank grew more than those in the low density tank, although on a percentage basis, this trend persisted only in the case of NETWM. When considering the growth in weight on a percentage basis, the significance levels

were less and there was no significant increase in PERWM with DENS in any of the experiments. It appears that the combination of a low FR of the secondary system and low inflow concentration of phytoplankton was limiting an increase in growth in EXPIII; by doubling the flow rate in the oyster tanks in EXPII, only the oysters in the high density tank (DENS=3) were limited in growth. However, in EXPIV there was a significant difference in growth between DENS although the FR and values of the covariates (STKUP, OXYUP and TEMP) were similar to EXPII. In fact the only difference between EXPII and EXPIV was the type of phytoplankton community. Within experiments, the pattern between shell weight and total weight as a function of DENS, were similar.

The effect of SIZE upon growth rates of oysters differed more between experiments depending on the variables under consideration (Figure 95). In terms of linear dimensions, there was generally a decrease in NETL and PERL with increasing size, particularly in EXPI and EXPII. On the other hand, although there were significant differences in width between the size of oysters in some experiments, there was no significant linear effect (Table 26). This was also true of NETD and PERD. In terms of the weight variables, the larger size 3 and 4 oysters had the highest net growth rates in all experiments, although on a percentage basis, the trend was reversed. There was a significant linear effect of size upon PERWT and PERWS in all four experiments. Growth in meat weight was not a function of SIZE in EXPIII.

CHAPTER 8. ANALYSIS OF THE RESULTS USING A SIMULATION MODEL

Estimation of the Physiological Parameters during the Continuous Cultures

In order to estimate appropriate parametric values for a primary productivity model of this ecosystem, a short series of experiments on photosynthetic productivity as a function of light, temperature and nutrients (nitrate) were conducted simultaneously with EXP5. Phytoplankton samples were taken from the surface of Tank B (F.R.= 1.0 day^{-1}) on four consecutive days during the initial bloom period (Days 3 to 7), and on each day, productivity versus light intensity (PAR) was examined at one of the four experimental temperatures (14 °C , 16 °C , 18 °C or 20 °C). This process was repeated for the three highest temperatures during the initial period of nutrient depletion in the primary tank (Days 10 to 12).

Primary productivity for the phytoplankton samples was measured by the uptake of radioactive carbon in a specially constructed water-cooled incubator, at eight levels of natural irradiance using neutral density filters. All the experiments were carried out during clear, bright days and there was no significant difference in SR between days during the incubation period from 1030 to 1430 hours P.S.T. The total radiation in each compartment of the incubator was measured with the sclarimeter and the PAR was calculated as 0.50 of this value as outlined in Chapter 2. The techniques for the measurement of

primary productivity and standing stock are also described there.

The results of the 'P versus I' experiments are illustrated in Figure 96. All values of primary productivity were normalized in terms of CHLA, and as expected, the curves do not pass through the origin since the radiocarbon method approximates net particulate productivity (McAllister et al., 1964; Eppley and Sloan, 1965). The curves indicated a hyperbolic relation between P^B and PAR for both sets of nutrient conditions, and the asymptote increased with temperature. During the bloom period, photo-inhibition was apparent at the highest experimental light intensity for all four experimental temperatures; these data points were not included in the estimation of the parameters of the various mathematical functions tested.

The two common parameters in the mathematical relationship between primary productivity and light, namely the initial slope ALPHA (ug C (ug Chla)$^{-1}$ hr^{-1} (ly/min)$^{-1}$) of the linear portion of the light saturation curve, and PMAX (ug C (ug Chla)$^{-1}$ hr^{-1}), the asymptote or photosynthetic rate at optimal irradiation, were estimated for the seven 'P versus I' experiments. Two hyperbolic models were used to describe the data: the hyperbolic tangent

$$P^B(I) = PMAX * TANH(ALPHA*X(I)/PMAX) - R^B$$

and Smith's function (Smith, 1936)

$$P^B(I) = PMAX*ALPHA*X(I)/(SQRT((PMAX**2)+(ALPHA*X(I))**2)) - R^B$$

using a non-linear least squares fit (LSF) procedure outlined in Bevington (1969). The parametric estimates for ALPHA and R^B, the respiration term or negative intercept at zero irradiance, were first calculated using linear regression as advised by Jassby and Platt (1976). The resulting estimates for these parameters were then used in the estimation of the gross PMAX.

The mathematical results for both models are summarized in Table 19, including input and output values and parameters. The PMAX values reported are based on net productivities (ug C (ug Chla)$^{-1}$ hr^{-1}).

The least squares fit was evaluated by calculating the reduced chi-square using a grid search technique. In all cases, the fits were excellent with P>.90 that the actual and fitted data were the same. Furthermore, there was little difference between the fit of the two models, although the standard deviations of PMAX, SIGMAA, were much less using the TANH model in all 7 cases. The values of ALPHA were also similar between bloom and post-bloom conditions at any given temperature. The data in Figure 96 indicated that the PMAX's were less during the post-bloom period. A t-test of the hypothesis that the PMAX's for bloom and post-bloom conditions (for a given temperature) are equal, indicated that this parameter was not significantly different (P>.10) between the bloom and post-bloom conditions for 16 ^{o}C , 18 ^{o}C or 20 ^{o}C . The variability in the forcing conditions (SR,TEMP,NO3) during Experiment 5 made it difficult to confirm this hypothesis. Furthermore, the cell size and self-shading of the phytoplankton may have an important effect on the light saturation curve (Platt and Jassby, 1976) as well

as the temperature and nutrient status of the cells.

Simulation of the Phytoplankton Dynamics

Description of the Model

In order to test the validity of the productivity model using the experimentally determined parameters, a series of simulations were run using SIMCON, a simulation control command language [1], with the model programmed in FORTRAN.

The primary purpose of the simulations was to predict the phytoplankton stock over time from the primary productivity model and compare it with the actual experimental results. The operational procedure of the simulation allowed the daily values of the forcing conditions, solar radiation (SR), temperature (TEMP) and nitrate (NO3), and the seed phytoplankton concentration to be read in initially. The increase in the phytoplankton stock was then calculated based on the productivity model and this derivative added to the initial value in order to estimate the phytoplankton stock after that day. This 'final' value was then used as the initial phytoplankton stock for the following day. The number of iterations of this procedure was specified interactively in SIMCON and was determined by the number of days in the

---

[1] Documentation for this procedure is available from the UBC Computing Centre file IARE:SIMCON.W

experiment. It should be noted that in the following discussion, PHYTO and P represent the simulation variables for the phytoplankton stock and assimilation rate, and correspond to the experimental variables CHLA and ASS. PHAV represents the CHLA data averaged for all four in situ stations.

The basic structure of the model included calculation of the extinction coefficient (EXTK) using Riley's equation in which EXTK is a function of PHYTO (see Chapter 2). The photosynthetically available radiation was calculated as an average for the tank (since the system was turbulently mixed) using the equation:

$$PARAV = 0.5*SR/(EXTK*Z) * (1-EXP(-EXTK*Z))$$

with the appropriate conversion factor to transform the variable into langley min^{-1}. The growth rate, GROWR (t^{-1}), was then estimated using the following equations determined from the results of the 'P versus I' experiments:

$$GROWR = P / CCHLA$$

where $$P = PMAX*TANH(ALPHAI*PARAV/PMAX)$$

$$PMAX = PTMAX*TANH(ALPHAT*TEMP/PTMAX)$$

and CCHLA is the CARBON:CHLA ratio.

The estimates of ALPHAI were taken directly from Table 19. However, because of the limited number of data points in the 'P versus TEMP' curves, the estimates of the corresponding parameters, ALPHAT (the initial slope) and PTMAX (the maximum productivity at the optimal SR and TEMP for the given nutrient conditions), were more difficult to predict. A survey of the literature suggested that PMAX approaches a maximum at temperatures only marginally higher than 20 °C for a Skeletonema

costatum population. So by extrapolation of the data in this experiment (Figure 96, Table 27), values from 10.0 to 15.0 seemed reasonable first approximations for PTMAX. No direct measurements of the carbon:chlorophyll *a* parameter (CCHLA) were possible. However, other experiments have indicated that CCHLA is a function of the phytoplankton dynamics, with values of *ca.* 30 during bloom conditions for a similar phytoplankton community, increasing to values of *ca.* 60 in a nutrient-depleted system (see Parsons and Takahashi, 1973a). These CCHLA values were used in the simulations during the appropriate periods as indicated by the experimental results. An intermediate CCHLA value of 45 was also used during periods of relatively steady-state phytoplankton concentrations.

After the calculation of the growth rate of the phytoplankton, the derivative was calculated as:

$$d(PHYTO)/dt = (GROWR*PHYTO)-(FR*PHYTO)-(SINK*PHYTO)$$

The sinking rate of the phytoplankton, SINK (t^{-1}), was introduced into the equation as well as the flushing rate. Even though the system was continually mixed, some loss of phytoplankton to the benthos was apparent, particularly after the initial depletion of nitrate. Sinking rates of 0.10 day^{-1} to 0.30 day^{-1} were tested in the simulation runs based on some experimental estimates.

Simulation Results

The results of some of the simulation runs for Experiment 5 are illustrated in Figures 97 to 100 for EXP5B and Figures 101 and 102 for EXP5A. The simulation analysis was first applied to the data from EXP5B, the experiment with the constant flushing rate for six weeks. During the simulations, the FR was set at 1.0 day^{-1}, and on Day 41, was decreased to 0.5 day^{-1} as in the experiment. The sinking rate was initially set at 0.0 day^{-1}; after the bloom, SINK was altered to 0.3 day^{-1} for four days (since the tank was very clear during this period), and then held constant at 0.1 day^{-1} for the remainder of the experiment. The CCHL ratio was set at 30, increased to 60 during the post-bloom period, and reset to an intermediate value of 45 during the third week when the actual phytoplankton stock concentration was fairly stable. During the fourth week, CCHL was altered to 30 in view of the large increase in the inflow nitrate concentration (Figure 74). CCHL was then increased to 45 until the end of the 1.0 day^{-1} FR period and reset to 60 when FR was altered to 0.5 day^{-1} .

As illustrated in Figure 97, using these parameters plus those derived from the 'P versus I' data, a reasonable approximation of the actual phytoplankton stock (PHAV) was estimated by the simulation model (PHYTO). The magnitude and timing of the maxima were similar although the simulated data had a one day time lag during the first two weeks compared with PHAV. The sensitivity of the system was tested by altering the parameters in the model. By increasing SINK from 0.3 day^{-1} to 0.4 day^{-1} after the initial bloom, the recovery of the

phytoplankton stock in the middle of the third week was reduced by ca. 50%, although the PHYTO(max) for the simulation was then closer to the experimental value of 54.2 ug Chl *a* l^{-1} (Figure 98). On the other hand, by maintaining a constant SINK of 0.1 day^{-1} after the initial bloom, the post-bloom oscillations in phytoplankton stock are not as closely approximated (Figure 99).

A significant feature of the plots was how the simulation model points out the periods in which SR or NO3 were the predominant forcing conditions. The actual and simulated damped oscillations after the initial bloom and depletion of NO3 indicated that the variability in SR had a significant effect on the standing stock. However, during the fourth week, the variability in the simulated phytoplankton stock was not apparent in the experimental results indicating that the system was not light-limited. The growth was then a function of the nitrate concentration and the model could be adjusted so that GROWR was a function of the uptake and assimilation of NO3, often described by Michaelis-Menten kinetics. The original estimate of 10.0 ug C (ug Chla)$^{-1}$ hr^{-1} for the productivity parameter PTMAX used in the calculation of PHYTO (Figure 97) provided a closer prediction of the experimental standing stock compared with PTMAX=12.0 (Figure 100) or higher values of PTMAX.

The conditions and results of EXP5A were more difficult to simulate accurately because of the changes in FR and the use of lower FR's (0.1 day^{-1} to 0.5 day^{-1}) which would alter the magnitude and frequency of the parameters in the system. Simulation runs using a constant value of 10.0 for PTMAX, with the appropriate flushing rates and reasonable estimates of the

sinking rates (0.25 day^{-1} for Period 1; 0.1 day^{-1} for Period 2; 0.5 day^{-1} for Period 3), resulted in a PHYTO(max) which was about twice as large as PHAV(max). Since PTMAX decreases with the nutrient concentration of the system, PTMAX was decreased to 5.0 ug C (ug Chla)$^{-1}$ hr^{-1} after the initial bloom and was reset to 8.0 ug C (ug Chla)$^{-1}$ hr^{-1} during Period 2 and to 5.0 ug C (ug Chla)$^{-1}$ hr^{-1} during Period 3. Similarly a value of 60 was assigned to CCHL during Period 2 and CCHL=75 for the 0.10 day^{-1} FR period. As illustrated in Figure 101, the resulting simulated phytoplankton stock (PHYTO) did not show a significant post-bloom decrease and recovery (PHAV). If SINK was increased to 0.6 day^{-1}, the simulation pattern and magnitude more closely approximated PHAV. As might be expected, the system was less sensitive to changes in SR compared to the combination of the changes in FR and low inflow concentrations of NO3.

A grazing term (GRAZE) of 0.5 day^{-1} was introduced into the model starting on Day 27 after the phytoplankton stock reached levels of *ca.* 50 ug Chl *a* l^{-1} in response to the high inflow concentration of NO3. As illustrated in Figure 103, there was a significant recovery of the phytoplankton stock even with the additional grazing pressure. This resulted from the negative feedback effect of the consequent reduction in the extinction coefficient, coupled with the high NO3 concentration. When the grazing rate was increased to 1.0 day^{-1}, the primary system 'crashed' during the simulation run. This scenario corresponded to an overall phytoplankton loss rate of 2.0 day^{-1}. A similar effect was obtained experimentally by Brown and Parsons (1972) when a large tank was flushed at a rate of 2.0 day^{-1} and the

phytoplankton stock was reduced to zero.

CHAPTER 9. COMPARATIVE DISCUSSION OF THE EXPERIMENTAL RESULTS

The experimental results of this study have indicated the importance of the flushing rate and turbulence of the system in determining the dynamics of herbivorous food chains. The various flushing rates provided a difference in the inflow concentrations of nutrients and temperature, with subsequent proportional changes in phytoplankton stock and the available radiation for primary productivity, as well as changes in the composition of the phytoplankton communities. The primary productivity at all the experimental flushing rates (0.25 day^{-1} to 1.00 day^{-1}) was enhanced by using a deep nutrient-rich source of seawater which averaged ca. 20 uM N l^{-1} during the experiments, except Experiment 1 which was conducted in the autumn (av NO3 = 24 uM N l^{-1}).

The interaction between the flushing rate (0.5 day^{-1}) and a constant upwelling rate in a stratified water column determined the dynamics of the primary community in the one-stage culture with constant forcing conditions (EXP1). Unlike the other experiments, this system was light-limited due to the restrictions on the light intensity which could be achieved by an artificial source. The reproducibility of the dynamics of the primary system was excellent between the the duplicate experimental tanks during the six-week pre-grazing period, particularly in the first three weeks . The differential sinking rate of the phytoplankton, relative to the constant upwelling rate, contributed to the significant increase in CHLA with depth and variability over time. Within each depth, the

phytoplankton stock displayed a series of damped oscillations and reached a steady-state after one month, averaging approximately 30 ug Chl *a* l^{-1} for the water column. The stratification of the system also promoted a change in the composition of the primary community as a function of depth in response to the decrease in PAR and TEMP. Micro-flagellates were dominant at the surface compared with diatoms at the bottom station. The dynamics of the phytoplankton community were complicated by a wall effect, the growth of a filamentous Navicula species at the surface of the tanks. This diatom developed into large flocculent mats, supported by oxygen 'vacuoles', and further reduced the light intensity at depth, particularly in Tank B.

In contrast, the culture experiments in both the non-turbulent and turbulent systems with natural forcing conditions of solar radiation and temperature were nutrient-limited most of the time, and there was an indication that some micro-nutrient (such as vitamin B12) may have replaced nitrate as the limiting nutrient in some of the experiments. The low flushing rate of 0.25 day^{-1} , combined with the lack of artificial mixing, allowed a large degree of thermal stratification to develop, particularly during periods of high solar radiation. The stratification was almost totally eliminated during Experiments 4 and 5 by introducing artificial turbulence. Despite the variability in SR, TEMP and NO3 between the experiments, the phytoplankton bloom occurred on Day 5 in all the experiments with an initial FR=0.25 day^{-1} ; in contrast, the CHLA in the experiments at 1.0 day^{-1} did not reach a maximum until Day 8.

In all cases, the bloom was coincident with the depletion of in-situ nitrate concentrations. The magnitude of the bloom was a function of the flushing rate (and the associated NO3 concentration) and the timing and magnitude of SR, but in spite of this, generally ranged between 30 to 40 ug Chl *a* l^{-1} in all of the experiments. In the primary cultures with no grazing pressure (Experiments 4 and 5), there was a high correlation between the oxygen production and phytoplankton stock. In the one-stage culture with *in situ* herbivores, the correlation was reduced as a result of the uptake of oxygen by the herbivores and the decrease in CHLA by grazing. The standardized primary productivity rates (ASS) were also much greater in magnitude and variability during these experiments (Experiments 2 and 3), probably as a result of the lower flushing rate as well as the grazing pressure.

The results in Experiment 4 indicated that for the same forcing conditions of SR, TEMP and NO3, the phytoplankton stock doubled when the flushing rate was doubled from 0.5 day^{-1} to 1.0 day^{-1}, provided that the system was turbulently mixed to minimize the loss of phytoplankton to the benthos. At flushing rates greater than 0.5 day^{-1}, the primary community was mainly composed of diatoms. The pigment ratios and Coulter counts provided supporting evidence that there was little change in the composition of the primary community at constant, high (>0.5 day^{-1}) flushing rates, although the proportion of nano-flagellates increased during periods of low inflow NO3.

A component analysis of gross primary productivity during Experiments 4 and 5 indicated that at flushing rates of 0.5 day

-1 or greater, a large proportion (50% to 60%) of the primary productivity was 'lost' by exudation, compared with 30% at lower flushing rates (0.1 day^{-1} and 0.25 day^{-1}). The respiration fraction in the systems with high flushing rates was 15%, approximately one-half the value for the lower flushing rates, probably as a result of the lower *in situ* temperatures. The assimilation fraction was more variable and ranged from 20% to 35% at flushing rates of at least 0.5 day^{-1} .

The 'P versus I' experiments attempted to obtain direct estimates of parameters for a given culture system, as a function of the temperature and two conditions of the nutrient status - before nitrate-depletion of the system and three days after the system had become nitrate-limited. Although the results indicated a significant difference in the standardized productivity rates between temperatures, the difference between the two nutrient conditions was not statistically significant. Ideally one would like 'P versus I' data at various concentrations of nitrate; however, the variability in the inflow NO3 concentration to the experimental system, combined with the natural variability in SR and TEMP, did not provide conditions for controlled factoral experiments. However, the estimates of the parameters predicted from a non-linear least squares fit of a TANH model, were used in a phytoplankton simulation model with success, particularly in the case of EXP5B (the experiment for which the estimates of PMAX, PTMAX and ALPHAC were based). The model predicted the dynamics and magnitude of the phytoplankton stock and illustrated the experimental time periods when the productivity was independent

of SR. The best fit for the simulation runs for EXP5B was obtained using a constant value of 10.0 for PTMAX, which was determined from the 'P versus I' data and agreed with the maximum *in situ* values of ASS calculated for the primary tank. Although the parameter CCHL was important in determining the growth rate (t^{-1}), only three representative values were were used in the simulation in lieu of direct measurements: 30 for bloom conditions with nutrient sufficiency, 60 during the initial post-bloom period with nutrient depletion, and 45 during a steady-state period. These parametric estimates were sufficiently sensitive to provide a close prediction of the phytoplankton stock.

Even in the turbulent systems, the sinking rate was a significant factor for about four days after the system became nutrient-limited. At the lower flushing rate and in the non-turbulent one-stage cultures, SINK was more significant in determining the spatial heterogeneity of the phytoplankton. Consequently, the simulation runs for EXP5A, with the variable flushing rate, did not predict the oscillations and magnitude of the phytoplankton stock as accurately. However, the other parameters in the model were also a function of FR, and estimates of their magnitude and variability were more difficult to predict.

The results of the herbivore growth and survival during the experiments indicated two main features. First, the growth of the scallops was enhanced in both turbulent and non-turbulent systems with high flushing rates (> 0.5 day^{-1}), provided that the herbivores were located at a depth of 1.0 m to avoid high

light intensities. A comparison of EXP1 and EXP3B indicated that the growth was probably limited by temperature during EXP1 (av TEMP=9.5 °C). The growth rate of the scallops reached a maximum of 16.8% at in situ temperatures of 14.5 °C during EXP3B (FR=0.75 day^{-1}). The growth environment even at 1.0 m was poor during EXP2B (FR=0.25 day^{-1}) as a result of the increased temperature (15.6 day^{-1}), increased SR at depth and decreased phytoplankton stock in this culture system.

In contrast, the culture systems with a flushing rate of 0.25 day^{-1} provided a suitable environment for the growth of Crassostrea gigas with a maximum growth rate of 1.18 g/zoo/week for oysters ranging in size from 2.0 cm to 5.0 cm. It was impossible to estimate the significance of excreted ammonia in alleviating the nitrogen-limitation of primary productivity. However, the oyster growth during the one-stage cultures appeared to be limited by the phytoplankton stock.

During the two-stage culture of oysters (Experiments I to IV), the growth rate of Crassostrea gigas was a function of their density, their size, and the type of phytoplankton provided as the food source (which was determined by the flushing rate of the primary tank). The highest rates were apparent in the low density tank, which received ca. 20.0 l/day per oyster during EXPII and EXPIV. These potential filtration rates were low compared with other feeding experiments for Crassostrea (Walne, 1972; Tenore and Dunstan, 1973b). Walne determined that the average filtration rate for 5.5 cm Crassostrea gigas was about 6.5 l/hr in a system with a FR=5.0 day^{-1} . However, in the oyster experiments in this study (EXPI

to EXPIV), the flushing rate of the herbivore tanks was limited by the flow rate from the primary tank. In order to increase this feeding rate in a two-stage culture, the volume of the primary tank would have to be increased, since an increase in FR to levels of 2.0 day^{-1} only causes a 'wash-out' of the primary system. In terms of size, the highest growth rates were found in the smallest size class, particularly in Experiment II, when the oysters increased in weight by ca. 21% in one week.

A comparison between the four herbivore experiments during EXP5 indicated two major features. First, the growth rate of the oysters was significant but least during Experiment III (8.1% per week). The herbivore tanks were fed at a rate of 1.0 day^{-1} with a nano-flagellate community which was promoted by a flushing rate of 0.10 day^{-1} in the primary tank. This primary system provided a suitable qualitative food source, but the concentration of phytoplankton and maximum attainable flow rate of the herbivore tanks limited the growth of the oysters. Furthermore, the high resultant temperature (>23 °C) in the herbivore tanks during this experiment was probably a significant factor in the reduction of the meat to shell weight ratio.

Secondly, the oyster growth in the other three experiments averaged greater than 10%/week. In each of these experiments, the phytoplankton community was composed of diatoms, indicating that either a 0.5 day^{-1} or 1.00 day^{-1} flushing rate of the primary tank provided an excellent food source for the oysters. The highest average growth rates of 13.5%/week were attained in the two-stage culture during Experiment II. During this

experiment, the Crassostrea gigas were fed at a flushing rate of 2.0 day^{-1} from primary tank B (FB=1.0 day^{-1}), which contained the highest concentration of CHLA dominated by Skeletonema costatum . The temperature averaged 20.1 °C , which according to Quayle (1969) is optimal for the growth of Crassostrea gigas , and the in situ oxygen levels were sufficient for respiration. However, the growth of oysters in the high density tank appeared to be limited by the phytoplankton concentration. The data indicated that 25 ug CHLA/day/g oyster was required so that growth was not limited by the food concentration. At these feeding levels, growth rates of 17.7%/week could be achieved. An extrapolation of the results, incorporating the fact that the growth rate decreased with increasing size, indicated that the experimental oysters would be a marketable size of ca. 60 g after another 3.5 months using the Experiment II culture system.

The growth rates in this culture system were 15% greater than the maximum field rates measured by Quayle (1971) at Ladysmith Harbour, the best oyster growing area of the sixteen locations tested in British Columbia. Marketable oysters were obtained after two years, instead of three or four years at the other sites. However, although the growth rates of Crassostrea gigas were high in the continuous culture system, approximately four tanks (6m diameter X 1m deep) would be required to achieve the same production as one of Quayle's rafts. Therefore the economic feasibility of growing oysters in a controlled culture system should be assessed carefully.

CHAPTER 10. SUMMARY AND CONCLUSIONS

Five continuous culture experiments were conducted to test the hypothesis that production in bivalve food chains could be enhanced by using a deep nutrient-rich source of seawater and an optimal flushing rate and spatial structure of the ecosystem to maximize productivity. The results indicated that:

1. The optimal flushing rate to maximize productivity in a turbulent system was 1.0/day. The system was nitrate-limited, and with natural forcing conditions of solar radiation and temperature, a maximum phytoplankton stock of 60 ug Chl *a* l^{-1} was attained in the one metre water column at inflow nitrate concentrations of 25 uM N l^{-1}. Based on a compensation light intensity of 1%, the compensation depth for the system was *ca.* 3.0 metres indicating that at this level of inflow nitrate, the flushing rate could be reduced to 0.33/day in a 3.0 metre impoundment to maintain the same phytoplankton concentration.

2. The chain diatom *Skeletonema costatum* dominated the ecosystem at the 1.0/day flushing rate and was selectively grazed when fed to the commercial oyster *Crassostrea gigas*. The maximum growth rates of the juvenile oysters were achieved when the herbivore tanks were flushed at a rate of 2.0/day with the outflow from the primary tank (FR=1.0/day). The temperature was optimal for the growth of *Crassostrea gigas* (20.1 °C) and oxygen levels were sufficient for respiration requirements. The growth rate of the oysters was

a function of their size, with the smallest size group having the maximum percent increase in weight, and an average of 25 ug Chl *a* dy^{-1} per gram oyster was required to achieve maximum growth rates of 18%/week.

3. In terms of the application of the results to oyster mariculture, the growth rates in the optimal continuous culture system were *ca.* 15% greater than the rates in an 'optimal' field location in British Columbia. A system of this size (7500 litres) could support 250 oysters/ m^3 of a 10 gram size, and provide a marketable crop at the end of the first growing season (when the oysters are *ca.* 1.5 years old).

4. At lower flushing rates (0.25/day), there was a decrease in the standing stock of phytoplankton in direct proportion to the decrease in flushing rate. Although the *in situ* conditions, such as temperature, were favourable at this flushing rate, the growth of the oysters was limited by the lower phytoplankton stock levels and a change in the composition of the community from *Skeletonema costatum* to *Chaetoceros sp.*

5. Higher flushing rates also enhanced the production of the scallop food chain, provided that the *Chlamys hastata hericia* were grown at a depth of 1.0 metre to avoid high surface light intensities. Maximum growth rates of 16.8% in total weight per month were attained at a flushing rate of 0.75/day

when the *in situ* temperature was 14.5 °C and the phytoplankton concentration (29 ug Chl *a* l^{-1}) was not limiting growth. However, under these conditions, a faster growing species such as *Patinopecten yessoensis* would be preferable for mariculture production.

6. At very high flushing rates of the primary system (2.0/day), the phytoplankton stock was washed out of the tank and attached species, such as *Navicula* , dominated the system. The productivity of *Navicula* also increased in two other situations in response to higher light levels: when the system was stratified and a significant proportion of the phytoplankton stock sank to the benthos, and secondly, when the grazing pressure of the *in situ* herbivores reduced the phytoplankton stock to low levels.

In conclusion, the large-scale continuous culture system provided a useful experimental tool for examining the dynamics of natural phytoplankton communities. A simulation model, incorporating experimentally determined parameters for primary productivity and measured values for the forcing conditions, predicted with reasonable accuracy the pattern and magnitude of the phytoplankton stock, and could be used to examine ecosystems with various flushing rates, sinking rates and grazing rates.

Table 1. Relevant culture studies of marine organic production in terms of their experimental design and control (*)

STUDY	SCALE OF OPERATION	TROPHIC SCOPE	OPERAT. TIME	CONTROL SPACE	COMMENTS
Haynes, 1973	Field	Natural food web	none	A.T.	Lake system
Gross et al., 1950	Field	Natural food web	batch inorg		Scottish loch
I.I.T.E., 1970	Field	Oys Salmon	semi-c natural		750 ac. tidal impoundment
Takahashi et al., 1975	LSC	Natural food web	batch inorg		2.5X10m plastic cylinder
Baab et al, 1973	LSC	P. Comm Oys	cont inorg		Two-stage Cult. 45,000l P.tank
McAllister et al., 1961	LSC	P. Comm	none	none	Plastic sphere (121 cu m)
Antia et al., 1963	LSC	P. Comm	none	A.T.	Plastic sphere (121 cu m)
Brown and Parsons, 1972	LSC	P. Comm	cont inorg	UPW	1800 l tank
Goldman et al., 1975	LSC	P. Comm	cont inorg	A.T.	2000 l tank
Malone et al., 1975	LSC	P. Pop	cont inorg	A.T.	2000 l tank 4 day exps.
Strickland et al., 1969	LSC	P. Pop	batch inorg	A.T.	3m x 10m tank
Ansell et al., 1963	LSC	P. Pop	batch inorg	A.T.	1000 l tank
Tenore et al., 1973	MSC	Oys, Scall	cont p. comm		760 l tank 17 - 23 Deg C.
Dunstan and Tenore, 1972	MSC	P. Comm	semi-c org	A.T.	400 l tank 20 - 28 Deg C.
Dunstan and Tenore, 1974	MSC	P. Comm	semi-c org		400 l tank
Tenore and Dunstan, 1973a	SSC	Oys, Scall	cont p. comm		9 l trays
Epifanc and Mootz, 1976	SSC	Oys	cont p. pops		100 l tank (recirculat.)
Walker and Zahradnik, 1976	SSC	Oys	cont nat.comm		10 l raceway (.1x.1x1.0 m)
Kirby-Smith & Barber, 1974	SSC	Scall	cont nat.comm		3 l raceway (.3X.2X.05 m)
Ketchum et al., 1949	SSC	P. Pops	semi-c inorg	A.T.	8 l flask

*
SCALE OF OPERATION: LSC (large scale culture- >1000 l);MSC (medium scale culture- 100-1000 l); SSC (small scale culture- <100 l)
TROPHIC SCOPE: P.(primary); Pop(population); Comm(community); Oys (Oyster); Scall(Scallops)
TIME(Rate of addition): batch;semi-c(semi-continuous);cont(contin)
TIME(Form of nutrient): inorg(inorganic);org(organic);P.(phytopl.)
SPACE: A.T.(artificial turbulence);UPW(upwelling);blank(not spec.)

Table 2. Descriptive statistics summary of selected variables for EXP2A, including a breakdown into the pre-grazing and grazing period. Day 37 and 40 measurements for CHLA, PROD and ASS have been excluded from the statistics for a direct comparison with EXP2B. The statistics for CHLA and ASS are also given for the grazing period corresponding to EXP3A.

		TOTAL EXPERIMENT (t=1,41)			PRE-GRAZING (t=1,6)			GRAZING PERIOD (t=7,41)		
VAR	STN	N	MEAN	S.D.	N	MEAN	S.D.	N	MEAN	S.D.
SR	I	41	410.	144.	6	380.	165.	35	410.	142.
SAL	I	41	28.3	0.61						
TEMP	I	41	11.0	0.87	6	9.6	0.50	35	11.2	0.68
	S	41	17.0	2.60	6	14.4	3.47	35	17.5	2.17
	M	41	16.2	2.26	6	13.3	2.79	35	16.7	1.76
	B	41	15.4	1.62	6	13.2	2.68	35	15.8	1.02
	O	41	17.0	2.61	6	14.7	3.88	35	17.4	2.17
NO3	I	41	18.2	3.62	6	23.3	1.72	35	17.3	3.08
	S				6	15.4	10.08	35	0.5	0.59
	M				6	15.0	10.49	35	0.4	0.34
	B				6	15.4	9.78	35	0.4	0.55
	O				6	15.0	10.04	35	0.3	0.36
NH3	I	41	0.77	0.43						
	S	41	0.50	0.42						
	M	41	0.42	0.32						
	B	41	0.64	0.48						
	O	41	0.47	0.31						
OXY	I	41	7.50	0.39	6	7.09	0.17	35	7.57	0.06
	S	41	11.41	2.60	6	9.37	3.57	35	11.76	2.28
	M	41	11.76	2.82	6	9.22	4.01	35	12.19	2.38
	B	41	11.72	2.76	6	9.08	3.95	35	12.17	2.28
	O	41	11.26	2.24	6	9.72	3.29	35	11.52	1.96
SAT	I	41	82.	5.1						
	S	41	141.	33.2						
	M	41	143.	35.9						
	B	41	140.	34.1						
CHLA	S	18	5.2	6.42	6	8.8	10.12	12	3.3	2.48
	M	18	7.2	10.83	6	13.2	17.60	12	4.2	3.35
	B	18	9.5	11.88	6	14.9	19.71	12	6.8	4.21
	O	18	5.6	6.50	6	8.5	10.06	12	4.1	3.46
	S							7	4.3	2.55
	M							7	5.4	3.81
	B							7	6.2	3.94
	O							7	5.1	3.86
PROD	S	14	20.2							
	M	14	28.6							
	B	14	32.1							
ASS	S	14	4.9	2.35	3	3.5	2.27	11	5.3	
	M	14	5.2	1.88	3	3.3	1.67	11	5.7	
	B	14	4.1	2.15	3	2.7	1.27	11	4.5	
	S							6	5.7	2.76
	M							6	5.8	1.91
	B							6	5.0	2.91

Table 3. Descriptive statistics summary of selected variables for EXP2B, including a breakdown into the pre-grazing and grazing period. See Appendix 1 for a definition of the variable names. The statistics for CHLA and ASS are given for the corresponding time periods in EXP2A.

		TOTAL EXPERIMENT (t=1,34)			PRE-GRAZING (t=1,10)			GRAZING PERIOD (t=11,34)		
VAR	STN	N	MEAN	S.D.	N	MEAN	S.D.	N	MEAN	S.D.
SR	I	34	420.	147.	10	390.	172.	24	420.	139.
SAL	I	34	28.3	0.67	10					
TEMP	I	34	10.8	0.86	10	9.9	0.61	24	11.2	0.64
	S	34	17.2	2.77	10	15.4	3.11	24	17.9	2.29
	M	34	16.4	2.58	10	14.3	2.59	24	17.2	2.09
	B	34	15.1	1.68	10	14.0	2.30	24	15.6	1.11
	O	34	17.0	2.72	10	15.3	3.19	24	17.7	2.20
NO3	I	34	18.8	3.58	10	22.6	2.09	24	17.2	2.78
	S							24	0.5	0.45
	M							24	0.4	0.40
	B							24	1.1	1.54
	O							24	0.4	0.43
NH3	I	34	0.71	0.42						
	S	34	0.58	0.49						
	M	34	0.67	0.44						
	B	34	0.50	0.31						
	O	34	0.65	0.61						
OXY	I	34	7.52	0.52	10	7.19	0.29	24	7.65	0.54
	S	34	11.45	2.79	10	12.03	4.29	24	11.21	1.93
	M	34	11.57	2.94	10	12.11	4.31	24	11.35	2.23
	B	34	10.51	3.10	10	12.07	4.33	24	9.86	2.22
	O	34	11.39	2.43	10	11.69	3.72	24	11.27	1.73
SAT	I	34	81.	6.5						
	S	34	141.	34.6						
	M	34	140.	35.9						
	B	34	125.	37.2						
CHLA	S	18	6.8	9.69	9	9.0	13.00	9	4.8	4.40
	M	18	9.7	10.95	9	13.7	14.04	9	5.6	4.59
	B	18	10.3	10.83	9	14.0	13.65	9	6.6	3.39
	O	18	8.8	9.82	9	12.1	12.45	9	5.9	4.64
CHLA	S				6	10.6	16.05	12	4.9	4.03
	M				6	11.7	16.08	12	8.6	8.03
	B				6	12.0	15.72	12	9.4	7.20
	O				6	11.1	15.33	12	7.6	6.15
PROD	S	14	27.1							
	M	14	32.3							
	B	14	44.4							
ASS	S	14	5.3	2.39	5	4.4	2.36	9	5.8	2.41
	M	14	5.3	3.13	5	4.0	1.95	9	6.1	3.52
	B	14	6.2	4.65	5	5.9	5.66	9	6.3	4.37
ASS	S				3	4.6	3.17	11	5.5	2.29
	M				3	4.1	2.42	11	5.7	3.32
	B				3	4.0	2.65	11	6.8	1.51

Table 4. Results of the oyster growth during Experiment 2A. GRWM and GRWS refer to the growth rate of the meat and shell weights per oyster per week for a comparison with EXP3A and EXP5. MSRATIO is the ratio between NETWM and NETWS.

SURFACE DEPTH

SUBSTN	NETWT	NETWM	PERWM	GRWM	NETWS	GRWS	MSRATIO
1	81.0	11.0	17.3	0.16	70.0	1.00	.162
2	88.5	19.5	26.0	0.24	69.0	0.86	.283
3	55.5	14.0	22.4	0.23	41.0	0.68	.341
4	65.8	14.0	25.9	0.28	51.5	1.03	.272

MID DEPTH

SUBSTN	NETWT	NETWM	PERWM	GRWM	NETWS	GRWS	MSRATIO
1	68.5	11.5	11.6	0.16	57.0	0.81	.202
2	88.0	23.5	36.4	0.28	64.5	0.76	.364
3	78.0	22.5	36.6	0.30	55.5	0.74	.405
4	81.5	16.0	15.2	0.25	65.5	0.80	.244

BOTTOM DEPTH

SUBSTN	NETWT	NETWM	PERWM	GRWM	NETWS	GRWS	MSRATIO
1	52.5	12.5	14.1	0.23	40.0	0.73	.313
2	111.5	23.5	25.1	0.31	88.0	1.17	.267
3	98.0	24.0	23.3	0.28	74.0	0.87	.324
4	40.0	10.5	10.9	0.19	29.5	0.54	.356

Table 5. Growth of the scallops during Experiment 2B. See Appendix 2 for an explanation of the variables.

MID STATION

SUBSTN	NSURV	L	SD	PERL	W	SD	PERW	WGTT	SD	PERWT
1	4/8	5.0	.58	0.5	4.4	.58	2.0	16.1	4.36	-0.2
2	4/8	5.6	.19	-1.0	5.1	.20	0.1	23.5	0.51	1.1
3	3/8	6.1	.35	-0.1	5.4	.32	1.7	29.8	3.33	-0.6
4	3/8	6.8	.38	-0.2	6.2	.44	-0.5	43.8	6.62	-1.7

BOTTOM STATION

SUBSTN	NSURV	L	SD	PERL	W	SD	PERW	WGTT	SD	PERWT
5	8/8	4.7	.59	0.3	4.2	.62	0.7	13.8	4.11	-9.6
8	8/8	5.6	.27	0.1	4.9	.25	0.3	22.0	3.10	-6.9
9	8/8	6.1	.22	0.0	5.6	.21	0.3	32.5	3.77	-5.0
12	8/8	6.7	.35	-0.3	6.1	.43	0.0	44.3	6.76	-10.5

Table 6. Descriptive statistics summary of selected variables for EXP3A, including a breakdown into the pre-grazing and grazing period. See Appendix 1 for a definition of the variable names.

		TOTAL EXPERIMENT (t=1,21)			PRE-GRAZING (t=1,6)			GRAZING PERIOD (t=7,21)		
VAR	STN	N	MEAN	SD	N	MEAN	SD	N	MEAN	SD
SR	I	21	330.	104.	6	400.	55.	15	300.	108.
TEMP	I	21	11.6	1.36	6	11.1	0.17	15	11.8	1.58
	S	21	16.3	0.96	6	15.9	0.49	15	16.4	1.08
	M	21	16.2	0.92	6	15.8	0.54	15	16.4	1.00
	B	21	16.2	0.89	6	15.8	0.49	15	16.3	0.98
	O	21	16.2	0.98	6	15.8	0.46	15	16.4	1.09
NO3	I	21	21.0	2.05	6	20.4	1.35		N/A	
NH3	I	21	0.50	0.28						
	S	6	0.40	0.29						
	M	6	0.34	0.31						
	B	6	0.27	0.17						
	O	21	0.50	0.50						
OXY	I	21	7.04	0.72	6	6.73	0.43	15	7.16	0.78
	S	21	9.91	1.89	6	10.50	2.84	15	9.68	1.41
	M	21	9.88	1.91	6	10.56	2.88	15	9.60	1.40
	B	21	9.97	2.51	6	10.54	2.84	15	9.74	1.75
	O	21	9.92	1.69	6	10.36	2.62	15	9.74	1.23
CHLA	S	13	10.4	9.74	6	13.9	12.70	7	7.3	5.69
	M	13	11.1	11.20	6	15.8	14.80	7	7.2	5.34
	B	13	11.5	11.42	6	16.2	14.99	7	7.5	5.78
	O	13	11.2	11.50	6	16.0	15.10	7	7.1	5.64
PROD	S	9	25.0	19.09						
	M	9	29.3	21.94						
	B	9	27.2	16.83						
ASS	S	9	3.4	1.98	3	2.3	0.95	6	4.0	2.18
	M	9	3.8	2.33	3	2.8	1.80	6	4.3	2.55
	B	9	3.9	2.71	3	2.2	1.23	6	4.7	2.94

Table 7. Results of the oyster growth during Experiment 3A. GRWM and GRWS refer to the growth rate of the meat and shell weights per oyster per week for a comparison with EXP2A and EXP5. MSRATIO is the ratio between NETWM and NETWS.

SURFACE DEPTH

SUBSTN	NETWT	NETWM	PERWM	GRWM	NETWS	GRWS	MSRATIO
1	18.5	4.8	4.4	0.12	14.5	0.45	.276
2	9.5	2.0	1.4	0.06	7.5	0.25	.267
3	8.0	2.0	1.9	0.08	6.0	0.25	.333
4	16.5	2.5	3.8	0.13	14.0	0.70	.179
5	16.5	0.5	0.8	0.02	16.0	0.53	.031
6	6.5	1.0	2.6	0.03	5.5	0.20	.182
7	24.5	11.0	11.2	0.61	13.5	0.75	.815
8	28.0	5.0	4.3	0.21	23.0	0.96	.217

MID DEPTH

SUBSTN	NETWT	NETWM	PERWM	GRWM	NETWS	GRWS	MSRATIO
1	6.5	2.0	3.5	0.10	4.0	0.20	.500
2	19.5	2.5	1.8	0.08	17.0	0.50	.147
3	12.0	2.0	3.3	0.09	10.0	0.46	.200
4	2.0	1.0	2.4	0.05	1.0	0.05	1.000
5	11.5	4.5	7.2	0.18	7.0	0.27	.643
6	8.0	0.5	0.8	0.03	7.5	0.47	.067
7	9.5	2.0	2.9	0.08	7.5	0.31	.267
8	7.5	1.0	1.5	0.04	6.5	0.27	.154

BOTTOM STATION

SUBSTN	NETWT	NETWM	PERWM	GRWM	NETWS	GRWS	MSRATIO
1	31.0	5.2	4.4	0.18	25.8	0.92	.202
2	9.5	4.0	6.5	0.12	5.5	0.17	.727
3	18.5	2.0	3.5	0.08	16.5	0.69	.121
4	30.0	7.0	10.9	0.23	23.0	0.77	.304
5	27.0	5.5	7.1	0.30	21.5	1.19	.256
6	4.0	2.0	2.2	0.06	2.0	0.06	1.000
7	24.5	7.5	4.8	0.22	17.0	0.50	.441
8	25.0	10.0	10.6	0.62	15.0	0.47	.667

Table 8. Descriptive statistics summary of selected variables for EXP3B, including a breakdown into the pre-grazing and grazing period. See Appendix 1 for a definition of the variable names.

		TOTAL EXPERIMENT (t=1,34)			PRE-GRAZING (t=1,11)			GRAZING PERIOD (t=12,34)		
VAR	STN	N	MEAN	SD	N	MEAN	SD	N	MEAN	SD
SR	I	34	380.	105.	11	410.	102.	23	366.	106.
TEMP	I	34	11.4	0.52	11	11.5	0.32	23	11.4	0.59
	S	34	14.9	1.05	11	15.5	0.78	23	14.5	1.02
	M	34	14.8	1.04	11	15.5	0.76	23	14.5	1.02
	B	34	14.8	1.04	11	15.5	0.74	23	14.5	1.01
	O	34	14.8	1.10	11	15.5	0.83	23	14.5	1.06
NO3	I	34	19.3	2.02	11	18.9	1.26	23	19.6	2.29
	S							23	0.3	0.37
	M							23	0.3	0.34
	B							23	0.3	0.38
	O							23	0.2	0.32
NH3	I	34	0.42	0.29						
	S	11	0.59	0.47						
	M	11	0.61	0.35						
	B	11	0.60	0.31						
	O	34	0.48	0.18						
OXY	I	34	6.98	0.54	11	6.93	0.21	23	7.01	0.65
	S	34	11.49	1.59	11	10.39	2.14	23	12.01	0.90
	M	34	11.52	1.58	11	10.44	2.18	23	12.03	0.84
	B	34	11.46	1.54	11	10.42	2.16	23	11.96	0.79
	O	34	11.31	1.40	11	10.41	2.05	23	11.74	0.66
CHLA	S	18	22.1	12.37	9	14.9	13.70	9	29.2	4.87
	M	18	22.8	12.54	9	15.8	14.48	9	29.7	4.08
	B	18	22.6	12.55	9	15.2	14.14	9	29.9	3.56
	O	18	23.0	12.78	9	16.2	15.06	9	29.7	4.20
PROD	S	14	38.3	13.86						
	M	14	36.9	14.98						
	B	14	39.8	19.79						
ASS	S	14	2.4	2.11	5	4.4	2.51	9	1.2	0.28
	M	14	2.2	2.13	5	4.3	2.59	9	1.1	0.10
	B	14	2.3	2.13	5	4.4	2.33	9	1.0	0.26

Table 9. Growth of the scallops during Experiment 3E. See Appendix 2 for an explanation of the variables.

SURFACE STATION

SUBSTN	NSURV	L	SD	PERL	W	SD	PERW	WGTT	SD	PERWT
6	0/8	3.6	.23	N/A	3.1	.19	N/A	6.0	1.08	N/A
7	0/8	4.3	.39	N/A	3.8	.41	N/A	10.6	2.89	N/A
10	0/8	5.4	.19	N/A	4.8	.17	N/A	19.4	1.27	N/A
11	0/8	5.8	.44	N/A	5.2	.42	N/A	26.3	4.83	N/A

MID STATION

SUBSTN	NSURV	L	SD	PERL	W	SD	PERW	WGTT	SD	PERWT
1	3/8	3.6	.22	0.3	3.1	.19	-0.1	6.2	1.12	-0.4
2	4/8	4.2	.29	0.0	3.7	.19	0.1	9.8	1.35	-1.9
3	6/8	5.2	.31	0.3	4.7	.32	1.6	18.3	2.48	1.6
4	5/8	5.9	.53	0.2	5.3	.51	0.2	26.6	6.92	0.8

BOTTOM STATION

SUBSTN	NSURV	L	SD	PERL	W	SD	PERW	WGTT	SD	PERWT
8	7/8	3.8	.45	1.8	3.3	.42	0.5	6.3	1.82	11.7
5	8/8	4.5	.27	1.0	4.0	.26	1.0	11.4	1.11	14.4
9	8/8	5.1	.15	0.4	4.6	.20	0.3	16.9	2.87	16.8
12	8/8	5.7	.31	0.4	5.1	.34	0.5	25.4	4.23	1.2

Table 10. Pearson correlation coefficients between the forcing variables during Experiment 4 for both Tank A (upper right) and Tank E (lower left). The variables include: incident solar radiation, SR (ly/day); inflow temperature, TEMP (deg-C.);, inflow nitrate concentration, NO3 (uM/litre); and inflow oxygen concentration, OXY (mg/litre). As the prefix A in the variable name indicates, the variables were 'first averaged', so that AVAR = 0.5*(VARt + VARt+1), for a comparison with the daily integrated solar radiation, SR. SR has been lagged one to three days (SR1 to SR3) to examine the serial correlation for solar radiation.

EXP4A X	SR	ATEMP	ANO3	AOXY	SR1	SR2	SR3
E 4 E	SR	.118 t=33 S=.512	.085 t=33 S=.640	.345 t=33 S=.050	.422 t=32 S=.016	-.118 t=31 S=.528	-.433 t=30 S=.016
ATEMP	.080 t=33 S=.660		-.769 t=33 S=.002	.678 t=33 S=.002			
ANO3	.008 t=33 S=.964	-.844 t=33 S=.002		-.598 t=33 S=.002	-.137 t=32 S=.456	-.364 t=31 S=.044	-.365 t=30 S=.048
AOXY	.356 t=33 S=.042	.662 t=33 S=.002	-.657 t=33 S=.002				
SR1	.422 t=32 S=.016		-.137 t=32 S=.254				
SR2	-.118 t=31 S=.528		-.332 t=31 S=.068				
SR3	-.433 t=30 S=.016		-.307 t=30 S=.098				

Table 11. Descriptive statistics of selected variables for EXP4A, including statistics for the nitrate-depleted period (t=29). See Appendix 1 for the definition of the variable names.

VAR	STN	T	MEAN	S.D.	S.E.	C.V.	RANGE	MAX
SR	I	34	378.	149.7	25.7	39.6	453.	564.
SAL	I	34	27.3	0.79	0.14	2.9	3.0	28.5
TEMP	I	34	10.4	0.41	0.07	3.9	1.3	11.1
	S	34	14.7	1.29	0.22	8.8	4.4	16.6
	M	34	14.6	1.26	0.22	8.6	4.1	16.3
	B	34	13.1	1.54	0.26	11.8	5.1	16.1
	O	34	14.6	1.30	0.22	8.9	4.4	16.5
TEMPN	S	34	4.3	1.32	0.23	30.7	4.9	6.1
	M	34	4.2	1.28	0.22	30.5	4.9	6.1
	B	34	2.7	1.41	0.24	52.2	4.9	5.3
	O	34	4.2	1.32	0.23	31.4	5.0	6.1
NO3	I	34	18.8	2.56	0.44	13.6	9.5	22.2
OXY	I	34	7.58	0.682	0.117	9.0	3.23	9.97
	S	34	10.85	1.364	0.234	12.5	5.04	13.26
	M	34	10.90	1.406	0.241	12.9	5.20	13.69
	B	34	8.98	1.163	0.199	12.9	5.03	11.01
	O	34	10.69	1.479	0.254	13.8	5.95	13.28
OXYN	S	34	3.26	1.824	0.313	56.0	6.40	6.21
	M	34	3.32	1.822	0.312	54.9	6.73	6.81
	B	34	1.39	1.062	0.182	76.4	4.34	2.91
	O	34	3.11	1.891	0.324	60.8	6.53	6.40
SAT	I	34	81.	7.6	1.3	9.4	35.	107.
	S	34	126.	17.7	3.0	14.0	65.	160.
	M	34	127.	18.1	3.1	14.3	66.	163.
	B	34	102.	15.2	2.6	14.9	68.	131.
	O	34	125.	18.8	3.2	15.0	74.	160.
CHLA	S	34	15.4	7.20	1.23	46.8	28.8	28.9
	M	34	15.4	7.09	1.22	46.0	25.3	25.4
	B	34	18.2	8.82	1.51	48.5	33.1	33.2
	O	34	16.3	7.82	1.34	48.0	30.7	30.8
SR	I	29	358.	149.0	27.7	41.6	445.	556.
TEMP	I	29	10.4	0.39	0.07	3.8	1.3	11.1
	S	29	14.7	1.27	0.24	8.6	4.0	16.6
	M	29	14.6	1.23	0.23	8.4	3.7	16.3
	B	29	12.8	1.39	0.26	10.9	5.1	16.1
	O	29	14.6	1.27	0.24	8.7	3.9	16.5
TEMPN	S	29	4.3	1.28	0.24	29.8	4.1	6.1
	M	29	4.2	1.24	0.23	29.5	4.1	6.1
	B	29	2.4	1.30	0.24	54.2	4.9	5.3
	O	29	4.3	1.28	0.24	29.8	4.1	6.1
NO3	I	29	19.0	2.65	0.49	13.9	9.5	22.2
NO3N	S	29	18.7	3.06	0.57	16.4	10.5	22.2
	M	29	18.9	2.81	0.52	14.9	10.6	22.2
	B	29	15.3	5.56	1.03	36.3	24.5	22.1
	O	29	18.1	2.98	0.55	16.5	13.1	22.2
OXY	I	29	7.47	0.669	0.124	9.0	3.23	9.97
	S	29	11.20	1.142	0.212	10.2	3.76	13.26
	M	29	11.30	1.112	0.207	9.8	4.08	13.69

	B	29	8.99	1.251	0.232	13.9	5.03	11.01
	O	29	11.04	1.306	0.243	11.8	5.95	13.28
OXYN	S	29	3.73	1.533	0.285	41.1	6.40	6.21
	M	29	3.83	1.439	0.267	37.6	5.69	6.81
	B	29	1.53	1.080	0.201	70.6	4.34	2.91
	O	29	3.58	1.632	0.303	45.6	6.53	6.40
SAT	I	29	79.	7.4	1.4	9.3	35.	107.
	S	29	131.	15.6	2.9	11.9	52.	160.
	M	29	132.	15.3	2.8	11.6	55.	163.
	B	29	101.	16.2	3.0	16.0	68.	131.
	O	29	129.	17.2	3.2	13.3	74.	160.
CHLA	S	29	17.2	5.37	1.00	31.2	22.1	28.9
	M	29	17.2	5.16	0.96	30.0	16.9	25.4
	B	29	20.5	6.74	1.25	32.9	23.6	33.2
	O	29	18.3	5.90	1.10	32.2	22.6	30.8
CHLB	S	29	1.4	0.70	0.13	50.0	2.6	2.7
	M	29	1.4	0.80	0.15	57.1	3.2	3.2
	B	29	2.3	1.18	0.22	51.3	4.6	5.2
	O	29	1.4	0.80	0.15	57.1	3.2	3.4
CHLC	S	29	11.0	2.93	0.54	26.6	12.4	18.2
	M	29	12.2	3.49	0.65	28.6	14.4	20.7
	B	29	12.1	4.01	0.74	33.1	13.6	18.0
	O	29	11.1	2.97	0.55	26.8	12.1	17.2
CT	S	29	21.8	6.76	1.26	31.0	24.8	35.8
	M	29	21.6	6.00	1.11	27.8	19.9	31.6
	B	29	23.2	7.08	1.32	30.5	29.8	42.5
	O	29	23.2	7.26	1.35	31.3	27.2	37.0
EA	I	1	.105					
	S	29	.092	.049	.009	53.3	.188	.194
	M	29	.086	.051	.010	59.3	.202	.202
	B	29	.119	.074	.014	62.2	.395	.400
	O	29	.081	.046	.009	56.8	.201	.210
CA	I	1	1.153					
	S	29	.660	.105	.020	15.9	.358	.852
	M	29	.634	.115	.021	18.1	.405	.893
	B	29	.598	.103	.019	17.2	.402	.788
	O	29	.624	.097	.018	15.5	.481	.943
CTA	I	1	1.123					
	S	29	1.283	.209	.039	16.3	.768	1.727
	M	29	1.277	.196	.036	15.3	.677	1.609
	B	29	1.153	.152	.028	13.2	.599	1.507
	O	29	1.274	.159	.030	12.5	.573	1.590
EC	I	1	.091					
	S	29	.136	.065	.012	47.8	.257	.267
	M	29	.132	.073	.014	55.3	.259	.259
	B	29	.200	.112	.021	56.0	.553	.561
	O	29	.127	.065	.012	51.2	.207	.223
ECT	I	1	.093					
	S	29	.073	.038	.007	52.1	.135	.140
	M	29	.068	.038	.007	55.9	.135	.135
	B	29	.102	.055	.010	53.9	.288	.293
	O	29	.065	.037	.007	56.9	.161	.168
CCT	I	1	1.027					
	S	29	.526	.110	.021	20.9	.454	.779
	M	29	.510	.128	.024	25.1	.559	.882
	B	29	.521	.072	.013	13.8	.301	.646
	O	29	.496	.097	.018	19.6	.459	.754

Table 12. Descriptive statistics of selected variables for EXP4B, including statistics for the nitrate-depleted period (t=27). See Appendix 1 for the definition of the variable names.

VAR	STN	T	MEAN	S.D.	S.E.	C.V.	RANGE	MAX
SR	I	34	378.	149.7	25.7	39.6	453.	564.
SAL	I	34	27.3	0.79	0.14	2.9	3.0	28.5
TEMP	I	34	10.4	0.39	0.07	3.8	1.3	11.1
	S	34	13.0	0.78	0.13	6.0	2.4	14.2
	M	34	13.0	0.76	0.13	5.8	2.4	14.2
	B	34	13.0	0.76	0.13	5.8	2.5	14.2
	O	34	13.0	0.78	0.13	6.0	2.5	14.3
TEMPN	S	34	2.7	0.76	0.13	28.1	2.7	3.7
	M	34	2.6	0.74	0.13	28.5	2.6	3.6
	B	34	2.6	0.76	0.13	29.2	2.6	3.6
	O	34	2.6	0.76	0.13	29.2	2.6	3.8
NO3	I	34	18.7	2.87	0.46	15.3	11.3	22.7
OXY	I	34	7.55	0.670	0.115	8.9	3.23	9.97
	S	34	11.58	1.645	0.282	14.2	5.64	14.13
	M	34	11.48	1.653	0.284	14.4	5.41	13.96
	B	34	11.26	1.679	0.288	14.9	5.72	14.30
	O	34	11.27	1.487	0.255	13.2	5.20	13.75
OXYN	S	34	4.03	1.904	0.327	47.2	6.79	6.87
	M	34	3.93	1.903	0.326	48.4	6.60	6.74
	B	34	3.70	1.835	0.315	49.6	5.92	6.02
	O	34	3.71	1.711	0.293	46.1	5.86	6.00
SAT	I	34	80.	7.4	1.3	9.2	36.	107.
	S	34	131.	18.9	3.2	14.4	67.	164.
	M	34	130.	19.0	3.3	14.6	70.	165.
	B	34	127.	19.0	3.2	15.0	61.	158.
	O	34	127.	17.2	2.9	13.5	67.	165.
CHLA	S	34	31.5	15.93	2.73	50.6	51.6	51.7
	M	34	33.1	16.84	2.89	50.9	54.3	54.4
	B	34	34.0	17.09	2.93	50.3	54.1	54.2
	O	34	33.1	16.97	2.91	51.3	52.4	52.6
SR	I	27	345.	146.4	28.2	42.4	445.	556.
TEMP	I	27	10.3	0.40	0.08	3.9	1.3	11.1
	S	27	12.9	0.76	0.15	5.9	2.4	14.2
	M	27	12.9	0.74	0.14	5.7	2.4	14.2
	B	27	12.9	0.76	0.14	5.9	2.5	14.4
	O	27	12.8	0.75	0.14	5.9	2.4	14.2
TEMPN	S	27	2.6	0.76	0.15	28.5	2.6	3.6
	M	27	2.5	0.75	0.14	30.0	2.6	3.6
	B	27	2.5	0.78	0.15	31.2	2.6	3.6
	O	27	2.5	0.75	0.14	30.0	2.5	3.5
NO3	I	27	19.1	2.82	0.54	14.8	11.3	22.7
NO3N	S	27	19.1	2.81	0.54	14.7	11.3	22.7
	M	27	19.1	2.82	0.54	14.8	11.3	22.7
	B	27	19.1	2.81	0.54	14.7	11.3	22.7
	O	27	19.1	2.79	0.54	14.6	11.3	22.7
OXY	I	27	7.39	0.644	0.124	8.7	3.23	9.97
	S	27	12.26	1.022	0.197	8.3	3.87	14.13
	M	27	12.13	1.121	0.216	9.2	4.24	13.96

	B	27	11.84	1.336	0.257	11.3	4.99	14.30
	O	27	11.86	0.970	0.187	8.2	3.93	13.75
OXYN	S	27	4.87	0.935	0.180	19.2	3.43	6.87
	M	27	4.74	1.045	0.201	22.0	4.22	6.74
	B	27	4.45	1.141	0.220	25.6	3.79	6.02
	O	27	4.47	0.806	0.155	18.0	3.00	6.00
SAT	I	27	79.	7.1	1.4	9.1	36.	107.
	S	27	138.	13.0	2.5	9.4	50.	164.
	M	27	137.	13.9	2.7	10.1	57.	165.
	B	27	133.	15.8	3.0	11.9	55.	158.
	O	27	134.	12.4	2.4	9.3	56.	165.
CHLA	S	27	38.8	7.08	1.36	18.2	27.2	51.7
	M	27	40.8	7.57	1.46	18.6	25.0	54.4
	B	27	41.8	7.46	1.44	17.8	26.6	54.2
	O	27	40.8	7.73	1.49	18.9	30.4	52.6
CHLB	S	27	1.7	1.50	0.29	88.2	5.9	5.9
	M	27	1.5	1.11	0.21	74.0	4.4	4.4
	B	27	1.6	1.28	0.25	80.0	5.4	5.4
	O	27	1.6	1.46	0.28	91.3	4.9	4.9
CHLC	S	27	20.2	3.19	0.62	15.8	13.4	26.5
	M	27	20.0	3.02	0.58	15.1	11.3	24.6
	B	27	20.8	3.49	0.67	16.8	13.8	25.9
	O	27	20.8	3.15	0.61	15.1	11.2	25.6
CT	S	27	43.0	7.70	1.48	17.9	34.4	56.1
	M	27	45.2	7.84	1.51	17.3	31.3	56.9
	B	27	45.7	6.94	1.34	15.2	27.6	59.5
	O	27	46.0	7.78	1.50	16.9	35.8	55.8
EA	I	1	.105					
	S	27	.047	.044	.008	93.6	.179	.179
	M	27	.039	.035	.007	89.7	.148	.148
	B	27	.040	.033	.006	82.5	.148	.148
	O	27	.041	.043	.008	104.	.136	.136
CA	I	1	1.153					
	S	27	.528	.066	.013	12.5	.275	.681
	M	27	.497	.065	.012	13.1	.284	.689
	B	27	.503	.066	.013	13.1	.290	.689
	O	27	.519	.073	.014	14.1	.289	.707
CTA	I	1	1.123					
	S	27	1.120	.168	.032	15.0	.706	1.544
	M	27	1.118	.161	.030	14.4	.659	1.528
	B	27	1.104	.133	.026	12.0	.569	1.509
	O	27	1.138	.145	.028	12.7	.654	1.562
EC	I	1	.091					
	S	27	.086	.078	.015	90.7	.333	.333
	M	27	.075	.063	.012	84.0	.291	.291
	B	27	.078	.065	.012	83.3	.285	.285
	O	27	.074	.070	.014	94.6	.255	.255
BCT	I	1	.093					
	S	27	.045	.046	.009	102.	.186	.186
	M	27	.037	.036	.007	97.3	.147	.147
	B	27	.037	.032	.006	100.	.140	.140
	O	27	.036	.038	.007	106.	.131	.131
CCT	I	1	1.027					
	S	27	.481	.087	.017	18.1	.399	.708
	M	27	.453	.093	.018	20.5	.437	.739
	B	27	.459	.064	.012	13.9	.273	.589
	O	27	.461	.076	.015	16.5	.377	.719

Table 13. Results of the analysis of variance and multiple classification analysis for selected variables for EXP4A as a function of the independent factors TIME and STATION. F values and significance levels in the ANOVA are presented for the nitrate-depleted period only, since the significance values for the total experiment (t=34) are similar. The ten sampling times for the productivity variables include every third day from Day 6. Data from the bottom station has been excluded (N/I) in the analyses of the other variables (TEMP to CCT). MULT R is the multiple correlation between the dependent variable and both independent variables TIME and STATION. The MCA table indicates the effect of each category of STATION, expressed as a deviation from the grand mean, and shows the time of the minimum and maximum deviations during the nitrate-depleted period.

VAR NAME	ANALYSIS OF VARIANCE BY TIME T	F	SIG.	BY STATION A	F	SIG.	MULT R	GRAND MEAN	MULTIPLE CLASSIFICATION ANALYSIS DEV'N BY STATION SUR	MID	BOT	OUT	DEV'N BY TIME MIN.	DAY	MAX.	DAY
TEMP	29	***	.000	3	8.5	.001	.998	14.6	.05	-.06	N/I	.01	-2.03	24	1.84	34
TEMPN	29	***	.000	3	8.5	.001	.998	4.3	.05	-.06	N/I	.01	-2.27	31	1.83	19,20
OXY	29	16.	.000	3	1.9	.161	.942	11.18	.02	.12	N/I	-.13	-1.49	30,31	2.17	19
OXYN	29	27.	.000	3	1.9	.161	.965	3.71	.02	.12	N/I	-.13	-3.45	13	2.76	20
SAT	29	22.	.000	3	1.7	.185	.957	130.	.3	1.2	N/I	-1.5	-22.6	30	29.6	19
CHLA	29	16.	.000	3	2.4	.096	.942	17.6	-.38	-.38	N/I	.76	-8.87	13	9.70	24
CHLB	29	14.	.000	3	0.6	.567	.937	1.4	.05	-.04	N/I	.00	-1.23	20	1.41	6
CHLC	29	18.	.000	3	0.8	.447	.949	11.0	.06	-.23	N/I	.16	-4.39	14	6.87	6
CT	29	8.1	.000	3	1.8	.178	.897	22.2	-0.4	-0.6	N/I	1.0	-10.9	28	9.1	7
BA	29	16.	.000	3	2.2	.119	.942	.09	.01	.00	N/I	-.01	-0.08	20,25	.10	34
CA	29	3.3	.000	3	1.5	.224	.793	.64	.02	.00	N/I	-.02	-0.13	25	.19	28
CTA	29	12.	.000	3	0.1	.929	.928	1.28	.00	.00	N/I	.00	-0.25	29	.31	19
BC	29	16.	.000	3	0.8	.479	.944	0.13	.00	.00	N/I	.00	-0.11	20,25	.12	34
BCT	29	17.	.000	3	2.2	.115	.947	0.07	.00	.00	N/I	.00	-0.06	20,25	.06	28,34
CCT	29	3.6	.000	3	0.9	.409	.803	0.51	.02	.00	N/I	-.01	-0.16	20	.15	9
PGO	10	2.8	.030	3	1.4	.274	.780	220.	-11.	-18.	29.	N/A	-115.	30	86.	6,21
PNO	10	2.7	.036	3	1.3	.287	.773	181.	-12.	-17.	29	N/A	- 93.	30	102.	6
RES	10	5.6	.001	3	0.0	.984	.859	40.	1.	0.	-1.	N/A	-22.	30	65.	12
PROD	10	2.1	.092	3	5.4	.014	.787	38.	-6.	-5.	11.	N/A	-14.	9	20.	27
PGODY	10	3.6	.011	3	1.2	.338	.810	2.11	-.09	-.16	.25	N/A	-1.01	30	1.11	6
PCDY	10	2.2	.079	3	5.1	.018	.788	0.35	-.05	-.04	1.00	N/A	-0.15	9	0.16	6
PGOST	10	5.0	.002	3	2.1	.153	.856	11.6	0.9	0.1	-1.1	N/A	- 4.3	30	4.3	12
PNOST	10	2.7	.034	3	0.5	.600	.766	9.2	0.6	0.0	-0.6	N/A	- 3.3	30	4.1	21
RESST	10	5.0	.002	3	0.9	.435	.850	2.4	0.4	0.1	-0.5	N/A	- 1.3	24	5.4	12
ASS	10	4.0	.006	3	0.6	.588	.821	2.0	-0.1	-0.1	0.1	N/A	- 0.6	24	1.0	34
EXCST	5	6.8	.011	3	7.3	.015	.916	6.5	0.4	1.5	-2.0	N/A	- 3.6	30	1.7	5
ALPHAG	10	13.	.000	3	5.6	.013	.935	63.2	-10.0	-1.6	11.6	N/A	-28.6	15,18	48.1	21
ALPHAC	10	24.	.000	3	16.	.000	.966	11.6	- 2.8	-0.7	3.5	N/A	- 7.0	12	17.5	30

Table 14. Results of the analysis of variance and multiple classification analysis for selected variables for EXP4B as a function of the independent factors TIME and STATION. F values and significance levels in the ANOVA are presented for the nitrate-depleted period only, since the significance values for the total experiment (t=34) are similar. The ten sampling times for the productivity variables include every third day from Day 6. Data from the bottom station has been excluded (N/I) in the analyses of the other variables (TEMP to CCT). MULT R is the multiple correlation between the dependent variable and both independent variables TIME and STATION. The MCA table indicates the effect of each category of STATION expressed as a deviation from the grand mean, and shows the time of the minimum and maximum deviations during the nitrate-depleted period.

VAR NAME	ANALYSIS OF VARIANCE BY TIME T	F	SIG.	BY STATION A	F	SIG.	MULT R	GRAND MEAN	MULTIPLE CLASSIFICATION ANALYSIS DEV'N BY STATION SUR	MID	BOT	OUT	DEV'N BY TIME MIN.	DAY	MAX.	DAY
TEMP	27	***	.000	4	3.2	.028	.998	12.9	.02	.01	-.01	-.02	-1.07	24	1.33	13,34
TEMPN	27	***	.000	4	3.2	.029	.998	2.5	.02	.01	-.01	-.02	-1.54	31	1.04	20
NO3N	27	***	.000	4	0.5	.677	.999	19.1	.00	.03	-.01	-.02	-7.67	8	3.53	27
OXY	27	29.	.000	4	7.2	.000	.953	12.02	0.23	.11	-.18	-.16	-2.25	23	1.91	12
OXYN	27	22.	.000	4	7.2	.000	.940	4.63	0.23	.11	-.18	-.16	-1.68	23	1.71	33,34
SAT	27	37.	.000	4	8.3	.000	.962	135.	2.8	1.3	-2.3	-1.8	-26.9	23	27.7	13
CHLA	27	18.	.000	4	4.1	.009	.926	40.6	-1.8	0.2	1.3	0.3	-12.7	9	11.6	15
CHLB	27	20.	.000	4	0.9	.442	.933	1.6	.13	-.11	.03	-.04	-1.60	20,21	3.54	8
CHLC	27	24.	.000	4	3.3	.026	.944	20.5	-.24	-.48	.37	.36	-7.23	19	4.31	24
CT	27	***	.000	4	2.7	.052	.876	45.0	-2.0	0.2	0.7	1.0	-20.2	9	9.6	15
BA	27	20.	.000	4	1.4	.264	.933	.04	.01	.00	.00	.00	- .04	19-21	.11	8
CA	27	5.6	.000	4	2.7	.053	.815	.51	.02	-.01	-.01	.01	- .09	19,22	.09	29,33
CTA	27	26.	.000	4	1.6	.209	.947	1.12	.00	.00	-.02	.02	- .23	9	.34	26
BC	27	29.	.000	4	1.4	.252	.953	.08	.01	.00	.00	.00	- .08	20,21	.21	8
BCT	27	31.	.000	4	2.4	.071	.956	.04	.01	.00	.00	.00	- .04	19-21	.11	8
CCT	27	9.3	.000	4	1.8	.160	.870	.46	.02	-.01	.00	.00	- .14	19	.18	9
PGO	10	25.	.000	3	2.6	.103	.963	341.	20.	-13.	- 7.	N/A	-249.	6	108.	12
PNO	10	18.	.000	3	3.0	.076	.951	294.	23.	-13.	-10.	N/A	-231.	6	79.	12
RES	10	1.8	.150	3	.23	.786	.688	47.	- 3.	- 0.	- 4.	N/A	- 24.	9	29.	12
PROD	10	1.7	.163	3	.92	.318	.697	51.	3.	- 4.	2.	N/A	- 16.	6	18.	34
PGODY	10	21.	.000	3	2.4	.117	.957	3.17	19.	-13.	-06.	N/A	-2.26	6	1.04	12
PCDY	10	1.4	.247	3	0.9	.428	.670	0.46	25.	-37.	.12	N/A	- .13	6	.13	34
PGOST	10	9.8	.000	3	3.8	.022	.919	9.5	1.0	-0.4	-0.6	N/A	- 3.0	30	4.6	6
PNOST	10	5.1	.002	3	5.8	.011	.873	8.0	1.1	-0.5	-0.6	N/A	- 2.8	30	2.1	18
RESST	10	7.7	.000	3	0.3	.735	.892	1.5	-0.1	0.1	0.0	N/A	- 0.8	24	3.0	6
ASS	10	38.	.000	3	1.9	.176	.980	1.7	0.1	-0.1	0.0	N/A	- 0.7	21	3.7	6
EXCST	5	9.9	.003	3	2.6	.134	.921	6.0	0.8	-0.2	-0.6	N/A	- 2.8	30	1.8	18
ALPHAG	10	4.6	.003	3	10.	.001	.880	65.4	-21.4	-9.5	-30.9	N/A	-29.2	6	78.8	30
ALPHAC	10	9.8	.000	3	18.	.000	.934	10.4	- 3.2	-1.5	4.4	N/A	- 6.4	18	10.5	30

Table 15. Productivity component analysis for EXP4. RPGO,APGO and EPGO represent the proportion of gross productivity due to respiration, assimilation and exudation. ESTPGO is the estimated gross productivity based on the model: ESTPGO=RPGO + APGO + EPGO . See the text for an explanation of the results.

EXP4 - TANK A

VAR	GRAND MEAN	MULT R	ANALYSIS OF VARIANCE BY STN A	SIG	BY TIME T	SIG	TOTAL N	SIG
RPGO	0.21	.805	3	.988	5	.055	15	.119
APGO	0.18	.857	3	.271	5	.029	15	.046
EPGO	0.59	.951	3	.002	5	.002	15	.001
ESTPGO	0.98	.697	3	.231	5	.461	15	.372
RPGO	0.20	.745	3	.946	10	.048	30	.087
APGO	0.19	.876	3	.039	10	.001	30	.001

EXP4 - TANK B

VAR	GRAND MEAN	MULT R	ANALYSIS OF VARIANCE BY STN A	SIG	BY TIME T	SIG	TOTAL N	SIG
RPGO	0.18	.844	3	.387	5	.035	15	.061
APGO	0.19	.953	3	.893	5	.000	15	.001
EPGO	0.63	.768	3	.526	5	.122	15	.193
ESTPGO	0.99	.762	3	.872	5	.108	15	.207
RPGO	0.15	.807	3	.434	10	.011	30	.018
APGO	0.17	.921	3	.581	10	.000	30	.000

Table 16. Experimental design for the investigation of two-stage continuous cultures of planktonic herbivorous food chains, with variable flushing rates in both the primary production tank experiments (EXP5A,EXP5B) and the secondary production tanks (EXP1 to EXP4). Results for the secondary production systems are discussed in Chapter 7.

	TIME PERIOD (Days)	EXP5A F.R. (/day)	EXP5B F.R. (/day)
PRIMARY PRODUCTION SYSTEMS	t=1,14	0.25	1.00
	t=15,28	0.50	1.00
	t=29,41	0.10	1.00
	t=42,49	N/A	0.50

	EXP	TIME PERIOD (days)	F.R. (/day)	SOURCE OF INFLOW	PRIMARY COMMUNITY
SECONDARY PRODUCTION SYSTEMS	I	t=18,25	1.00	Tank B (F.R.=1.0)	Diatoms
	II	t=26,33	2.00	Tank B (F.R.=1.0)	Diatoms
	III	t=35,42	1.00	Tank A (F.R.=0.1)	Flagellate
	IV	t=43,50	2.00	Tank E (F.R.=0.5)	Mixed

Table 17. Results of the nutrient enrichment experiments at low (0.13 ly/min) and high (0.40 ly/min) intensities of photosynthetically available radiation during EXP5. The productivity was measured by the uptake of radioactive carbon (ug C/l/hr). The 'Vitamin mix' and 'Vitamin B12' additions were made at the same concentration (*) or at 10x the concentration (**) as in the 'F Medium' addition.

EXPERIMENT 1 (low PAR)		EXPERIMENT 2 (high PAR)	
Enrichment	Productivity	Enrichment	Productivity
Control	101.	Control	104.
F Medium (10.0 ml)	117.	F Medium (10.0 ml)	114.
(1.0 ml)	110.	(1.0 ml)	108.
Vitamin Mix (**)	93.	Vitamin Mix (**)	103.
		(*)	83.
Vitamin B12 (**)	112.	Vitamin B12 (**)	136.
		(*)	123.

Table 18. Descriptive statistics for selected variables for EXP5A, including a breakdown into the three periods of variable flushing rates: F.R.=.25/day for t=1,14; F.R.=.50/day for t=15,28; and F.R.=.10/day for t=29,41. N represents the total number of data points, incorporating both the factors TIME and STATION.

		TOTAL EXPERIMENT					F.R.=.25/DAY			F.R.=.50/DAY			F.R.=.10/DAY		
VAR	STN	N	MEAN	S.D.	RANGE	MAX	N	MEAN	S.D.	N	MEAN	S.D.	N	MEAN	S.D.
SR	1	41	404.	105.6	371.	519.	14	495.	14.9	14	337.	131.7	13	378.	49.0
SAL	1	41	27.2	0.92	3.1	28.9									
TEMP	1	41	11.8	1.08	4.2	14.3	14	12.0	0.76	14	12.2	1.49	13	11.1	0.34
	2-5	164	18.1	2.38	8.5	21.9	56	18.7	2.16	56	16.0	1.39	52	19.8	1.61
TEMPN	2-5	164	6.4	2.45	5.7	8.4	56	6.7	1.55	56	3.8	1.26	52	8.8	1.38
NO3	1	41	16.7	5.97	22.0	25.1	14	14.3	2.91	14	14.1	7.70	13	21.9	1.24
	2-5	164	1.7	5.54	21.7	21.7	56	5.0	8.60	56	0.0	0.08	52	0.0	0.13
NO3N	2-5	164	14.9	7.68	28.5	25.1	56	9.3	6.19	56	14.1	7.48	52	21.9	1.20
TNO3N	2-5	164	17.3	7.07	27.1	27.1	56	12.0	6.12	56	16.3	5.72	52	24.1	1.98
OXY	1	41	7.24	.787	2.88	8.89	14	7.65	.473	14	7.46	.973	13	6.55	.160
	2-5	164	9.93	1.629	6.84	13.83	56	9.40	1.822	56	10.64	.813	52	9.73	1.812
OXYN	2-5	164	2.69	1.834	7.74	7.05	56	1.74	1.658	56	3.18	1.584	52	3.18	1.896
TOXYN	2-5	164	2.95	1.849	7.61	7.05	56	1.98	1.794	56	3.71	1.405	52	3.18	1.896
SAT	1	41	80.	10.0	38.	102.	14	84.	6.1	14	83.	12.7	13	71.	2.0
	2-5	164	124.	19.3	85.	177.	56	119.	24.5	56	127.	8.4	52	125.	20.4
CHLA	2-5	164	17.7	12.95	54.0	54.1	56	9.7	10.67	56	26.6	12.34	52	16.8	9.52
CHLB	2-5	164	0.5	0.81	3.6	3.6	56	0.9	1.10	56	0.3	0.63	52	0.3	0.37
CHLC	2-5	164	9.6	6.96	39.6	39.6	56	4.4	4.50	56	14.5	7.01	52	10.0	4.87
CT	2-5	164	26.0	16.32	65.8	66.0	56	12.6	11.45	56	34.0	13.72	52	31.8	14.31
BA	2-5	164	0.083	0.157	0.833	0.833	56	0.143	0.172	56	0.017	0.031	52	0.090	0.192
CA	2-5	164	0.632	0.389	2.667	2.667	56	0.586	0.424	56	0.549	0.081	52	0.772	0.503
CTA	2-5	164	1.779	0.996	6.829	7.800	56	1.558	0.464	56	1.322	0.159	52	2.511	1.443
BC	2-5	164	0.100	0.148	1.000	1.000	56	0.201	0.189	56	0.029	0.051	52	0.068	0.103
BCT	2-5	164	0.040	0.059	0.294	0.294	56	0.085	0.075	56	0.012	0.020	52	0.021	0.033
CCT	2-5	164	0.368	0.123	0.714	0.714	56	0.370	0.179	56	0.419	0.066	52	0.310	0.054

Table 19. Descriptive statistics for selected variables for EXP5B, including a breakdown into the two periods of variable flushing rates: F.R.=1.00/day for t=1,41 and F.R.=.50/day for t=42,49. Note that the first period (F.R.=1.00/day) corresponds to the total experimental period for EXP5A. N represents the total number of data points, incorporating both the factors TIME and STATION.

		F.R.=1.00 PER DAY					F.R.=0.50 PER DAY				
VAR	STN	N	MEAN	S.D.	RANGE	MAX	N	MEAN	S.D.	RANGE	MAX
SR	1	41	404.	105.6	371.	519.	8	298.	89.0	259.	380.
SAL	1	41	27.2	0.92	3.1	28.9	8				
TEMP	1	41	11.9	1.10	4.2	14.3	8	10.6	0.46	1.4	11.5
	2-5	164	15.0	.925	3.8	16.5	32	15.0	0.57	1.8	16.0
TEMPN	2-5	164	3.1	0.87	4.3	4.9	32	4.4	0.83	2.5	5.6
NO3	1	41	16.4	6.18	22.4	24.9	8	22.9	1.86	5.0	25.4
	2-5	164	2.8	6.48	21.9	21.9	32	0.0	0.0	0.0	0.0
NO3N	2-5	164	13.5	8.92	29.8	24.9	32	22.9	1.76	5.0	25.4
TNO3N	2-5	164	15.9	8.06	27.1	27.2	32	23.4	1.89	5.6	26.6
OXY	1	41	7.29	.884	3.08	8.96	8	6.14	0.387	1.00	6.76
	2-5	164	10.92	1.612	6.44	14.12	32	11.05	0.981	4.44	12.61
OXYN	2-5	164	3.62	1.999	8.08	7.89	32	4.90	0.908	3.86	6.27
TOXYN	2-5	164	3.87	1.882	7.49	7.89	32	4.90	0.908	3.86	6.27
SAT	1	41	80.	11.1	38.	101.	8	66.	4.62	12.	74.
	2-5	164	128.	19.4	74.	88.	32	130.	11.6	51.	148.
CHLA	2-5	164	25.8	15.78	61.4	61.5	32	32.7	3.96	15.9	41.0
CHLB	2-5	164	0.6	0.88	3.3	3.3	32	0.7	1.52	7.0	7.0
CHLC	2-5	164	15.0	9.76	39.1	39.1	32	20.1	2.95	14.5	30.3
CT	2-5	164	30.0	17.67	69.3	69.5	32	38.3	5.14	22.5	48.0
BA	2-5	164	0.081	0.172	0.943	0.943	32	0.023	0.049	0.227	0.227
CA	2-5	164	0.659	0.392	2.285	2.285	32	0.616	0.084	0.418	0.959
CTA	2-5	164	1.275	0.396	2.359	3.201	32	1.169	0.073	0.341	1.338
BC	2-5	164	0.093	0.133	0.545	0.545	32	0.036	0.077	0.370	0.370
BCT	2-5	164	0.049	0.075	0.318	0.318	32	0.020	0.041	0.189	0.189
CCT	2-5	164	0.500	0.156	1.013	1.013	32	0.528	0.076	0.379	0.828

Table 20. Results of the analysis of variance and multiple classification analysis for selected variables as a function of the independent factors TIME and STN for EXP5A. Statistics are based on data from the nitrate-depleted period (T>4). *** indicates F-values greater than 99. The eleven 'TIMES' for the productivity variables include every third day from Day 6, except Day 15 when the data was missing. The MCA indicates the effect of each category of STATION, expressed as a deviation from the grand mean, and shows the maximum and minimum deviations during the nitrate-depleted period. MULT R is the multiple correlation between the dependent variable and both independent variables TIME and STN. Significance values in the ANOVA are based on t-1 df for TIME and a-1 df for STATION.

VAR NAME	ANALYSIS OF VARIANCE BY TIME T	F	SIG.	BY STATION A	F	SIG.	MULT R	GRAND MEAN	MULTIPLE CLASSIFICATION ANALYSIS DEV'N BY STATION SUR	MID	BOT	OUT	DEV'N BY TIME MIN.	DAY	MAX.	DAY
TEMP	37	***	.000	4	41.	.000	.994	18.4	0.15	0.09	-.45	0.20	-4.5	27	2.9	37
TEMPN	37	***	.000	4	41.	.000	.995	6.6	0.15	0.10	-.45	0.20	-5.1	20	3.6	36
NO3	37	2.5	.061	4	1.0	.482	.536	0.0	-.01	-.01	.03	-.01	0.0	MANY	0.2	33
NO3N	37	***	.000	4	2.8	.042	1.000	16.5	0.01	0.01	-.03	0.01	-13.4	20	8.6	27
TNO3N	37	***	.000	4	2.7	.051	1.000	18.8	0.01	0.01	-.04	0.01	-9.2	20	8.4	34
OXY	37	***	.000	4	12.	.000	.991	10.05	0.13	0.04	-.21	0.04	-3.02	41	3.58	5
OXYN	37	***	.000	4	12.	.000	.993	2.83	0.13	0.04	-.21	0.04	-3.35	10	3.91	29
TOXYN	37	***	.000	4	12.	.000	.993	3.09	0.13	0.04	-.21	0.04	-3.47	10	3.65	29
SAT	37	***	.000	4	18.	.000	.987	126.	2.0	0.8	-3.6	0.9	-34.	41	48.	5
CHLA	37	***	.000	4	4.9	.003	.991	18.8	-0.6	-0.5	-1.0	0.1	-18.0	41	26.8	26
CHLB	37	7.3	.000	4	1.2	.311	.851	0.4	0.0	0.0	0.1	-0.1	-0.4	23-31	3.0	5
CHLC	37	43.	.000	4	3.2	.025	.969	10.2	-0.3	-0.2	0.9	-0.4	-9.5	11	16.6	26
CT	37	90.	.000	4	2.3	.078	.985	27.9	-0.6	-0.8	0.5	0.9	-23.5	41	28.7	26
BA	37	8.6	.000	4	.79	.500	.862	0.07	0.01	0.01	0.00	-.02	-0.07	MANY	0.55	41
CA	37	6.1	.000	4	1.5	.213	.829	0.61	0.04	0.02	0.02	-.07	-0.47	11	1.58	41
CTA	37	26.	.000	4	.62	.606	.951	1.81	0.01	0.05	-.06	0.00	-0.68	5	4.30	41
BC	37	5.2	.000	4	.42	.737	.798	0.08	-.01	0.01	0.00	0.00	-0.08	23-31	0.41	8
BCT	37	6.3	.000	4	.36	.782	.824	0.03	0.00	0.00	0.00	0.00	-0.03	23-31	0.11	9
CCT	37	4.0	.000	4	3.0	.033	.769	0.35	0.01	0.00	0.03	-.03	-0.26	11	0.14	24
PGO	11	18.	.000	3	1.3	.284	.949	160.	4.	9.	-13.	N/A	-104.	9	109.	21
PNO	11	18.	.000	3	0.7	.523	.948	119.	-3.	9.	-6.	N/A	-107.	9	125.	21
RES	11	1.7	.153	3	1.4	.267	.705	41.	6.6	0.2	-6.8	N/A	-20.9	39	21.4	27
PROD	11	34.	.000	3	1.7	.208	.972	61.	-2.4	4.2	-1.7	N/A	-46.9	9	50.1	24
PGODY	11	14.	.000	3	1.4	.261	.938	1.39	.04	.08	-.12	N/A	-.89	9,39	1.03	21
PCDY	11	26.	.000	3	1.8	.197	.983	0.50	-.25	.34	-.09	N/A	-.38	9	.36	6
PGOST	11	3.4	.010	3	1.1	.353	.801	10.6	2.1	-0.4	-1.8	N/A	-6.0	18	17.4	9
PNOST	11	12.	.000	3	1.4	.267	.929	6.5	-0.1	0.6	-0.5	N/A	-3.6	18	7.2	21
RESST	11	4.3	.003	3	1.4	.259	.834	4.1	2.2	-0.9	-1.2	N/A	-2.8	24	18.5	9
ASS	11	3.7	.006	3	0.5	.626	.811	3.8	0.3	0.0	-0.3	N/A	-2.1	18	3.0	9
EXCST	5	8.3	.006	3	1.8	.234	.906	2.2	-0.2	0.3	-0.1	N/A	-0.7	18	1.3	12
ALPHAG	11	2.4	.043	3	0.2	.813	.744	39.8	-1.6	-1.3	2.9	N/A	-17.9	36	29.2	6
ALPHAC	11	2.6	.032	3	3.1	.068	.786	14.0	-2.5	-0.2	2.7	N/A	-6.4	27	8.9	24
BPGO	11	7.1	.000	3	1.9	.170	.888	0.32	0.06	-.03	-.03	N/A	-.22	21	0.47	9
APGO	11	3.2	.012	3	1.5	.238	.799	0.40	-.04	-.02	.05	N/A	-.18	21	.29	6

Table 21. Results of the analysis of variance and multiple classification analysis for selected variables as a function of the independent factors TIME and STN for EXP5B. Statistics are based on data from the nitrate-depleted period (T>6). F-values greater than 99. are denoted by ***. The eleven 'TIMES' for the productivity variables include every third day from Day 6, except Day 15 when the data was missing. The MCA indicates the effect of each category of STATION, expressed as a deviation from the grand mean, and shows the maximum and minimum deviations during the nitrate-depleted period. MULT R is the multiple correlation between the dependent variable and both independent variables TIME and STN. Significance values in the ANOVA are based on t-1 df for TIME and a-1 df for STATION.

VAR NAME	ANALYSIS OF VARIANCE BY TIME T	F	SIG.	BY STATION A	F	SIG.	MULT R	GRAND MEAN	MULTIPLE CLASSIFICATION ANALYSIS DEV'N BY STATION SUR	MID	BOT	OUT	DEV'N BY TIME MIN.	DAY	MAX.	DAY
TEMP	35	***	.000	4	25.	.000	.986	15.1	0.12	-.02	-.21	0.10	-2.1	26	1.3	9
TEMPN	35	***	.000	4	25.	.000	.986	3.2	0.12	-.02	-.21	0.10	-2.6	20	1.4	41
NO3	35	37.	.000	4	1.7	.168	.962	0.3	0.0	0.0	0.1	0.0	-0.3	MANY	4.0	13
NO3N	35	***	.000	4	1.7	.163	.999	16.2	0.0	0.0	-0.1	0.0	-13.7	20	8.5	27
TNO3N	35	***	.000	4	1.7	.164	.999	18.3	0.0	0.0	-0.1	0.0	-9.3	20	8.9	34
OXY	35	16.	.000	4	11.	.000	.921	11.38	0.24	0.21	-.44	-.01	-2.80	12	1.95	32
OXYN	35	30.	.000	4	11.	.000	.955	4.17	0.24	0.21	-.44	-.01	-2.84	20	2.96	32
TOXYN	35	***	.000	4	11.	.000	.947	4.41	0.24	0.21	-.44	-.01	-2.92	12	2.72	32
SAT	35	15.	.000	4	12.	.000	.920	134.	3.2	2.4	-5.7	0.2	-32.	12	25.	8
CHLA	35	50.	.000	4	3.7	.015	.971	29.6	-0.6	-0.4	1.8	-0.9	-23.3	12	24.6	27
CHLB	35	47.	.000	4	.38	.768	.970	0.6	0.0	0.0	0.0	0.0	-0.6	MANY	2.3	7
CHLC	35	68.	.000	4	1.2	.304	.979	17.1	0.0	0.1	0.4	-0.5	-15.0	11	15.2	26
CT	35	42.	.000	4	1.1	.352	.966	34.3	0.0	-0.5	1.1	-0.7	-26.8	12	26.8	27
BA	35	21.	.000	4	.28	.843	.934	0.03	0.00	0.00	0.00	0.00	-0.03	MANY	0.07	8
CA	35	24.	.000	4	.98	.403	.943	0.57	0.01	0.01	-.01	0.0	-0.34	11	0.31	21
CTA	35	21.	.000	4	1.3	.265	.935	1.18	0.02	-.01	-.01	0.01	-0.25	7	0.36	36
BC	35	19.	.000	4	.41	.748	.928	0.06	0.00	0.00	0.00	-.01	-0.06	MANY	0.27	8
BCT	35	17.	.000	4	.35	.789	.922	0.02	0.00	0.00	0.00	0.00	-0.02	MANY	0.08	8
CCT	35	16.	.000	4	.57	.637	.919	0.48	0.00	0.01	0.00	-.01	-0.25	11	0.19	18
PGO	11	83.	.000	3	0.8	.465	.988	304.	7.	0.	-7.	N/A	-225.	12	155.	33
PNO	11	65.	.000	3	0.4	.666	.985	263.	-4.	-1.	5.	N/A	-200.	12	148.	33
RES	11	3.2	.012	3	1.6	.235	.800	44.	8.5	-2.1	-6.4	N/A	-37.2	6	25.2	36
PROD	11	9.6	.000	3	0.5	.607	.911	101.	-5.	-3.	8.	N/A	-64.	12	139.	27
PGODY	11	68.	.000	3	0.8	.473	.986	2.56	.06	.00	-.06	N/A	-1.85	12	1.27	33
PCDY	11	8.9	.000	3	0.5	.610	.905	0.84	-.46	-.23	.70	N/A	-.52	12	1.12	27
PGOST	11	15.	.000	3	2.1	.151	.941	11.0	0.2	0.6	-0.8	N/A	-5.9	18	6.1	36
PNOST	11	21.	.000	3	0.7	.507	.956	9.5	0.0	0.3	-0.3	N/A	-5.3	18	4.9	36
RESST	11	2.7	.029	3	0.2	.842	.759	1.7	0.0	0.1	-0.1	N/A	-1.3	6	1.4	21
ASS	11	8.8	.000	3	1.0	.403	.904	3.8	-0.4	0.2	0.2	N/A	-2.0	27	4.0	6
EXCST	5	59.	.000	3	0.1	.939	.984	4.0	0.0	-0.1	0.1	N/A	-2.6	12	4.2	36
ALPHAG	11	8.0	.000	3	37.	.000	.941	48.1	-15.4	-1.7	17.1	N/A	-19.7	21	17.9	30
ALPHAC	11	3.1	.015	3	22.	.000	.888	15.7	-6.3	-0.6	7.0	N/A	-8.2	21	6.2	9

Table 22. Results for the productivity variables, averaged for the three periods of variable flushing rates in EXP5A, with EXP5B results during the same time period as a comparison. Sampling times include Days 6,9 and 12 for Period 1 (F.R.=.25/day), Days 18,21,24,27 for Period 2 (F.R.=.50/day) and Days 30,33,36,39 for Period 3 (F.R.=.10/day). Means for the total time period are found in Table 20 and Table 21.

EXP5A

VAR	STN	F.R.=.25/DAY N	MEAN	S.D.	F.R.=.50/DAY N	MEAN	S.D.	F.R.=.10/DAY N	MEAN	S.D.
PGO	2-4	9	111.	46.3	12	224.	88.4	12	132.	62.0
PGO	2-4	9	69.	45.1	12	182.	85.8	12	93.	54.9
RES	2-4	9	42.	20.6	12	42.	21.3	12	40.	22.1
PROD	2-4	9	56.	40.2	12	70.	30.8	12	55.	23.6
PGOST	2-4	9	16.6	13.28	12	8.4	4.40	12	8.2	2.25
PNOST	2-4	9	7.1	3.06	12	7.0	4.42	12	5.5	1.79
RESST	2-4	9	9.5	13.1	12	1.5	0.70	12	2.6	1.30
ASS	2-4	9	6.0	2.3	12	2.5	0.94	12	3.3	0.70
PGODY	2-4	9	1.00	.414	12	1.96	.592	12	1.11	.513
PCDY	2-4	9	0.47	.322	12	0.58	.173	12	0.45	.195
ALPHAG	2-4	9	43.3	31.39	12	47.7	17.72	12	29.3	11.12
ALPHAC	2-4	9	15.3	5.68	12	15.4	8.61	12	11.7	3.45
APGO	2-4	9	0.45	.203	12	0.34	.145	12	0.43	.135
RPGC	2-4	9	0.45	.276	12	0.21	.148	12	0.32	.142

EXP5B

PGO	2-4	9	206.	105.6	12	262.	134.2	12	420.	56.1
PGO	2-4	9	179.	89.9	12	225.	116.8	12	366.	44.2
RES	2-4	9	27.	26.8	12	46.	26.6	12	55.	22.4
PROD	2-4	9	110.	68.7	12	105.	88.2	12	91.	26.3
PGOST	2-4	9	12.6	1.70	12	7.1	1.89	12	13.7	2.77
PNOST	2-4	9	10.9	1.91	12	6.1	1.74	12	11.9	2.09
RESST	2-4	9	1.7	1.41	12	1.5	1.07	12	1.8	0.86
ASS	2-4	9	6.5	1.90	12	2.6	1.12	12	2.9	0.52
PGODY	2-4	9	1.78	.913	12	2.20	.874	12	3.50	.467
PCDY	2-4	9	0.93	.597	12	0.87	.704	12	0.75	.218
ALPHAG	2-4	9	35.5	10.68	12	48.1	24.42	12	57.7	18.56
ALPHAC	2-4	9	18.7	9.67	12	16.4	8.26	12	12.7	6.22
APGC	2-4	9	0.52	.047	12	0.38	.156	12	0.22	.064
RPGO	2-4	9	0.13	.106	12	0.20	.105	12	0.13	.045

Table 23. Productivity component analysis for EXP5. RPGO, APGO and EPGO represent the proportion of gross productivity due to respiration, assimilation and exudation. ESTPGO is the estimated gross productivity based on the sub-model: ESTPGO=RPGO + APGO + EPGO . See the text for an explanation of the results.

EXP5 - TANK A

VAR	GRAND MEAN	MULT R	ANALYSIS OF VARIANCE BY STN A	SIG	BY TIME T	SIG	TOTAL N	SIG
RPGO	0.29	.798	3	.062	5	.287	15	.131
APGO	0.48	.791	3	.489	5	.089	15	.145
EPGO	0.29	.657	3	.549	5	.383	15	.479
ESTPGO	1.06	.825	3	.724	5	.042	15	.086
RPGO	0.32	.888	3	.170	11	.000	33	.000
APGO	0.40	.799	3	.238	11	.012	33	.016

EXP5 - TANK B

VAR	GRAND MEAN	MULT R	ANALYSIS OF VARIANCE BY STN A	SIG	BY TIME T	SIG	TOTAL N	SIG
RPGO	0.14	.856	3	.063	5	.063	15	.048
APGO	0.36	.951	3	.352	5	.000	15	.000
EPGO	0.34	.985	3	.081	5	.000	15	.000
ESTPGO	0.84	.781	3	.353	5	.122	15	.165
RPGO	0.15	.764	3	.986	11	.024	33	.045
APGO	0.36	.890	3	.427	11	.000	33	.000

Table 24. Two-stage continuous culture of herbivores. Statistical summary of environmental variables during each oyster experiment (t=8) for the four tanks (Tank 4= Control). ANOVA's are for Tanks 1,2 and 3 only. See Appendices 1 and 2 for a description of the variables.

		EXP. I		EXP. II		EXP. III		EXP. IV		ANOVA BY EXP	ANOVA BY TANK
VAR	TANK	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	SIG.	SIG.
TEMP	1	18.4	2.44	20.1	1.17	23.3	2.29	19.5	1.51		
	2	18.5	2.40	20.1	1.12	23.3	2.31	19.4	1.53	.000	.793
	3	18.4	2.36	20.4	1.16	23.5	1.86	19.8	1.67		
	4	18.4	2.38	20.0	1.16	23.1	1.96	19.4	1.48		
STKUP	1	21.2	14.79	17.7	8.80	7.2	6.25	18.5	6.71		
	2	22.6	14.88	25.4	11.60	8.1	6.86	26.2	7.69	.000	.050
	3	23.1	15.47	30.4	14.49	8.1	6.92	29.7	9.60		
	4	15.3	10.40	12.1	7.00	5.8	4.96	10.3	5.73		
BA	1	.195	.1947	.031	.0468	.400	.4416	.019	.0202		
	2	.269	.1306	.062	.0744	.668	.4514	.068	.0557	.000	.186
	3	.326	.1569	.056	.0579	.463	.3044	.157	.1274		
	4	.070	.0833	.000	.0000	.229	.2440	.014	.0223		
OXYUP	1	3.39	1.375	4.47	1.198	3.97	1.112	4.77	0.793		
	2	3.84	1.180	5.57	1.570	4.16	1.662	5.18	0.664	.000	.055
	3	4.07	1.258	6.31	1.699	3.43	1.231	5.74	0.566		
	4	1.87	1.276	4.37	1.065	3.74	0.898	4.24	0.757		
CTA	1	1.35	.120	1.50	.219	3.80	2.461	1.48	.056		
	2	1.49	.326	1.55	.199	3.72	1.038	1.45	.091	.000	.970
	3	1.55	.285	1.47	.220	3.76	0.755	1.57	.188		
	4	1.56	.256	1.54	.181	4.92	2.060	1.52	.152		

Table 25. Descriptive statistics for the six growth variables for each cultch at the start of each of the four herbivore experiments; TIME=4 summarizes the final measurements.

		LENGTH		WIDTH		DEPTH		TOTAL WGT		MEAT WGT		SHELL WGT		
	I.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	N
TIME=0														
CULTCH	ALL	5.7	0.97	3.2	0.61	1.7	0.30	12.8	4.70	4.0	1.51	8.8	3.27	96
CULTCH	1	4.0	0.39	2.8	0.40	1.4	0.21	5.7	0.97	1.8	0.38	3.9	0.68	8
CULTCH	2	5.1	0.27	3.4	0.35	1.7	0.15	10.5	1.66	3.6	0.76	7.0	0.98	8
CULTCH	3	5.1	0.40	2.8	0.62	1.7	0.24	9.7	3.59	3.1	1.26	6.6	2.37	8
CULTCH	4	4.9	0.19	3.1	0.53	1.5	0.20	8.9	2.01	2.8	0.91	6.1	1.18	8
CULTCH	5	5.2	0.39	2.9	0.50	1.7	0.36	10.2	2.38	3.2	0.75	6.9	1.72	8
CULTCH	6	6.0	0.19	3.6	0.34	1.6	0.31	14.4	2.88	4.7	1.10	9.7	1.88	8
CULTCH	7	5.8	0.26	3.2	0.45	1.7	0.23	12.8	2.37	4.0	0.94	8.8	1.52	8
CULTCH	8	5.8	0.43	3.1	0.83	1.9	0.24	14.1	3.50	4.3	1.16	9.8	2.48	8
CULTCH	9	5.8	0.16	3.1	0.42	1.6	0.31	13.2	2.85	4.1	1.05	9.1	1.80	8
CULTCH	10	6.9	0.36	3.9	0.73	1.9	0.31	18.3	3.84	5.6	1.41	12.7	2.46	8
CULTCH	11	7.2	0.26	3.6	0.70	1.9	0.29	18.3	2.29	5.5	1.17	12.8	1.50	8
CULTCH	12	7.1	0.37	3.2	0.39	1.9	0.24	18.1	3.60	5.4	1.20	12.7	2.55	8
TIME=1														
CULTCH	ALL	5.8	0.95	3.4	0.61	1.8	0.28	14.1	4.87	4.5	1.56	9.6	3.37	96
CULTCH	1	4.1	0.38	2.9	0.40	1.5	0.18	6.7	1.11	2.1	0.41	4.6	0.78	8
CULTCH	2	5.3	0.35	3.5	0.55	1.8	0.12	12.0	1.74	4.1	0.73	8.0	1.06	8
CULTCH	3	5.1	0.39	2.9	0.59	1.7	0.24	10.6	3.77	3.6	1.29	7.1	2.45	8
CULTCH	4	5.0	0.21	3.1	0.47	1.6	0.19	10.0	2.06	3.3	0.87	6.8	1.26	8
CULTCH	5	5.3	0.42	3.0	0.44	1.7	0.36	11.2	2.37	3.5	0.80	7.6	1.81	8
CULTCH	6	6.1	0.30	3.8	0.31	1.7	0.26	15.7	2.74	5.2	1.05	10.5	1.80	8
CULTCH	7	6.0	0.29	3.5	0.53	1.8	0.23	14.4	2.70	4.6	0.98	9.8	1.78	8
CULTCH	8	5.8	0.39	3.2	0.84	1.9	0.23	15.1	3.61	4.6	1.22	10.4	2.52	8
CULTCH	9	6.0	0.20	3.5	0.39	1.7	0.28	15.2	2.87	4.9	1.01	10.3	1.89	8
CULTCH	10	6.9	0.37	3.9	0.74	2.0	0.28	19.7	4.11	6.1	1.49	13.7	2.66	8
CULTCH	11	7.3	0.29	3.7	0.67	1.9	0.26	19.7	2.64	6.1	1.25	13.6	1.68	8
CULTCH	12	7.1	0.42	3.4	0.37	1.9	0.23	19.1	3.99	5.9	1.28	13.3	2.82	8

		LENGTH		WIDTH		DEPTH		TOTAL WGT		MEAT WGT		SHELL WGT		
	I.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	MEAN	S.D.	N
TIME=2														
CULTCH	ALL	6.0	0.93	3.6	0.67	1.8	0.25	15.9	5.27	5.1	1.71	10.8	3.63	96
CULTCH	1	4.4	0.50	3.2	0.55	1.6	0.16	8.1	1.36	2.6	0.46	5.6	0.97	8
CULTCH	2	5.6	0.52	3.9	0.62	1.9	0.12	14.3	2.10	4.8	0.69	9.4	1.48	8
CULTCH	3	5.3	0.38	3.0	0.54	1.7	0.18	11.7	4.11	4.0	1.57	7.7	2.58	8
CULTCH	4	5.3	0.37	3.3	0.41	1.6	0.23	12.1	2.04	4.1	0.83	8.1	1.35	8
CULTCH	5	5.4	0.47	3.1	0.40	1.8	0.33	12.3	2.48	3.9	0.86	8.4	1.73	8
CULTCH	6	6.4	0.45	4.1	0.38	1.8	0.22	17.4	2.76	5.9	1.03	11.5	1.90	8
CULTCH	7	6.2	0.33	3.8	0.69	1.9	0.24	16.2	3.18	5.2	1.06	11.0	2.15	8
CULTCH	8	5.9	0.40	3.4	0.90	1.9	0.24	16.7	3.98	5.2	1.39	11.5	2.70	8
CULTCH	9	6.1	0.28	3.8	0.50	1.9	0.24	16.9	3.02	5.5	1.03	11.4	2.05	8
CULTCH	10	6.9	0.36	4.1	0.72	2.0	0.26	22.6	4.72	6.9	1.69	15.6	3.08	8
CULTCH	11	7.4	0.35	3.9	0.74	2.0	0.25	21.6	3.19	6.8	1.36	14.7	2.04	8
CULTCH	12	7.2	0.50	3.7	0.45	2.0	0.21	21.1	4.75	6.7	1.49	14.4	3.36	8
TIME=3														
CULTCH	ALL	6.1	0.93	3.8	0.71	1.9	0.27	17.2	5.66	5.4	1.78	11.8	3.96	96
CULTCH	1	4.5	0.45	3.6	0.61	1.6	0.21	9.3	1.53	2.8	0.58	6.5	1.16	8
CULTCH	2	5.6	0.51	4.1	0.70	2.0	0.23	15.5	2.40	5.2	0.82	10.3	1.70	8
CULTCH	3	5.5	0.43	3.3	0.59	1.7	0.20	12.7	4.19	4.2	1.53	8.6	2.69	8
CULTCH	4	5.3	0.34	3.3	0.40	1.7	0.21	12.7	2.87	4.1	1.11	8.6	1.85	8
CULTCH	5	5.4	0.51	3.2	0.48	1.9	0.36	13.2	2.75	4.0	0.95	9.3	1.94	8
CULTCH	6	6.4	0.43	4.2	0.51	1.8	0.21	18.4	3.17	5.8	1.23	12.6	2.11	8
CULTCH	7	6.2	0.33	3.9	0.72	1.9	0.20	17.4	3.46	5.4	1.11	12.0	2.38	8
CULTCH	8	6.1	0.46	3.6	1.03	2.0	0.18	18.0	4.37	5.4	1.40	12.6	3.04	8
CULTCH	9	6.2	0.38	4.0	0.60	1.9	0.33	18.7	3.37	6.0	1.08	12.7	2.35	8
CULTCH	10	7.1	0.28	4.3	0.77	2.1	0.26	24.8	5.09	7.4	1.60	17.4	3.57	8
CULTCH	11	7.3	0.37	3.9	0.74	2.0	0.26	22.9	3.65	7.1	1.44	15.9	2.40	8
CULTCH	12	7.3	0.48	3.9	0.50	2.0	0.22	22.1	5.13	6.9	1.51	15.3	3.73	8

	I.D.	LENGTH MEAN	LENGTH S.D.	WIDTH MEAN	WIDTH S.D.	DEPTH MEAN	DEPTH S.D.	TOTAL WGT MEAN	TOTAL WGT S.D.	MEAT WGT MEAN	MEAT WGT S.D.	SHELL WGT MEAN	SHELL WGT S.D.	N
TIME=4														
CULTCH	ALL	6.1	0.91	3.8	0.74	1.9	0.27	19.2	6.15	6.1	1.97	13.2	4.27	96
CULTCH	1	4.6	0.43	3.7	0.71	1.7	0.21	10.5	1.77	3.2	0.57	7.4	1.30	8
CULTCH	2	5.6	0.41	4.1	0.64	2.0	0.22	18.1	2.94	5.8	0.72	12.3	2.44	8
CULTCH	3	5.5	0.41	3.2	0.85	1.8	0.20	14.5	4.51	4.9	1.69	9.7	2.85	8
CULTCH	4	5.3	0.31	3.3	0.41	1.7	0.25	14.6	2.96	4.7	1.24	9.9	1.78	8
CULTCH	5	5.4	0.43	3.2	0.46	1.8	0.33	14.6	3.19	4.5	1.13	10.1	2.23	8
CULTCH	6	6.5	0.41	4.3	0.47	1.9	0.22	20.8	3.21	6.7	1.21	14.1	2.26	8
CULTCH	7	6.2	0.33	3.9	0.69	1.9	0.21	19.7	4.29	6.3	1.34	13.4	3.00	8
CULTCH	8	6.1	0.49	3.6	1.04	2.1	0.20	19.5	4.97	6.1	1.57	13.4	3.46	8
CULTCH	9	6.3	0.35	4.0	0.51	1.9	0.32	21.6	3.58	6.7	0.98	14.8	2.81	8
CULTCH	10	7.1	0.23	4.3	0.79	2.1	0.22	27.0	5.42	8.4	1.73	18.5	3.77	8
CULTCH	11	7.3	0.39	3.9	0.76	2.1	0.23	25.2	4.50	7.9	1.64	17.3	2.99	8
CULTCH	12	7.4	0.48	4.0	0.45	2.0	0.23	24.4	5.96	7.7	1.75	16.7	4.32	8

Table 26. Results of the net and percent increases per oyster for the six growth variables, including significance levels for the effect of size and density on growth. The *,**,*** indicate a significant linear relation at the .05, .01 and .001 levels respectively.

	NETL			NETW			NETD		
EXP	MEAN	SIZE	DENS	MEAN	SIZE	DENS	MEAN	SIZE	DENS
I	.104	.112	.121	.145	.003	.271	.040	.007	.003
		*	*					*	**
II	.174	.012	.407	.242	.849	.106	.076	.122	.008
		**							**
III	.065	.533	.578	.168	.084	.541	.056	.532	.911
IV	.040	.492	.623	.022	.536	.817	.018	.457	.962

	NETWT			NETWM			NETWS		
EXP	MEAN	SIZE	DENS	MEAN	SIZE	DENS	MEAN	SIZE	DENS
I	1.28	.041	.000	0.48	.070	.005	0.81	.156	.000
			***			***			***
II	1.79	.023	.003	0.65	.007	.001	1.13	.103	.006
		**	**		***	*		*	**
III	1.24	.036	.315	0.21	.450	.032	1.03	.028	.570
		*				*		*	
IV	2.06	.014	.002	0.72	.000	.098	1.35	.259	.000
									***

	PERL			PERW			PERD		
EXP	MEAN	SIZE	DENS	MEAN	SIZE	DENS	MEAN	SIZE	DENS
I	.012	.003	.252	.047	.009	.443	.027	.002	.010
		***						**	**
II	.032	.000	.653	.075	.847	.117	.047	.025	.023
		***						*	**
III	.011	.196	.318	.048	.023	.258	.033	.519	.956
		*							
IV	.007	.597	.564	.006	.545	.766	.012	.436	.972

	PERWT			PERWM			PERWS		
EXP	MEAN	SIZE	DENS	MEAN	SIZE	DENS	MEAN	SIZE	DENS
I	.111	.000	.003	.138	.021	.294	.102	.000	.006
		***	**		**			***	**
II	.135	.000	.083	.154	.008	.117	.126	.000	.140
		***	*		**			***	
III	.081	.003	.277	.044	.249	.103	.099	.003	.606
		*						*	
IV	.125	.005	.002	.139	.674	.720	.120	.005	.000
		***	***					***	***

Table 27. Non-linear least squares fit (LSF), using a grid search method (Bevington,1969), of the productivity, P^B (ug C/ug CHLA/hr), versus light, PAR (ly/min), data for both the 'TANH' and 'SMITH' hyperbolic models. The parameter A(1) corresponds to PMAX and represents the maximum net productivity (R^B was set to zero for the calculations). The subroutine parameters are described at the end of the Table.

I. TANH MODEL

$$P^B = PMAX*TANH(S*PAR/PMAX) - R^B$$

1. P VS I- 14 DEG,(BLOOM),NALPHA=2,N=7,P.NET

```
ALPHA,S =   11.83
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.320 1.030 1.650 2.500 3.220 3.250 3.380
YFIT(I)=    0.506 1.182 1.705 2.372 2.932 3.217 3.569
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 3.900  FINAL= 3.986
DELTAA(1) INITIAL= 0.050  FINAL= 0.033
SIGMAA(1)= 1.219
CHISQR=     0.039       AVG Y(I)=    2.193
GAMMA=      0.19661     GAMMAM=      0.08566
```

2. P VS I- 16 DEG,(BLOOM),NALPHA=2,N=7,P.NET

```
ALPHA,S =   21.83
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.200 1.510 2.150 3.960 6.050 5.190 5.830
YFIT(I)=    0.932 2.160 3.083 4.205 5.076 5.487 5.952
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 6.200  FINAL= 6.392
DELTAA(1) INITIAL= 0.050  FINAL= 0.067
SIGMAA(1)= 1.012
CHISQR=     0.588       AVG Y(I)=    3.556
GAMMA=      2.93949     GAMMAM=      0.82670
```

3. P VS I- 18 DEG,(BLOOM),NALPHA=2,N=7,P.NET

```
ALPHA,S =   25.83
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.180 1.730 2.680 4.590 6.850 7.260 7.510
YFIT(I)=    1.104 2.578 3.714 5.156 6.356 6.961 7.700
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 8.500  FINAL= 8.553
DELTAA(1) INITIAL= 0.050  FINAL= 0.017
SIGMAA(1)= 1.200
CHISQR=     0.667       AVG Y(I)=    4.400
GAMMA=      3.33268     GAMMAM=      0.75743
```

```
    4. P VS I- 20 DEG,(BLOOM),NALPHA=2,N=7,E.NET
ALPHA,S =   31.89
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.150 1.340 3.690 6.010 7.350 8.780 8.860
YFIT(I)=    1.362 3.165 4.531 6.217 7.557 8.203 8.952
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 9.200   FINAL= 9.707
DELTAA(1) INITIAL= 0.050   FINAL= 0.167
SIGMAA(1)= 1.071
CHISQR=     1.187       AVG Y(I)=    5.169
GAMMA=      5.93326     GAMMAM=      1.14795

    5. P VS I- 20 DEG,(POST-BLOOM),NALPHA=2,N=7,E.NET
ALPHA,S =   31.17
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.160 2.030 3.230 5.950 6.760 7.090 9.000
YFIT(I)=    1.330 3.074 4.371 5.921 7.096 7.635 8.228
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 8.700   FINAL= 8.753
DELTAA(1) INITIAL= 0.050   FINAL= 0.017
SIGMAA(1)= 0.982
CHISQR=     0.953       AVG Y(I)=    4.889
GAMMA=      4.76638     GAMMAM=      0.97501

    6. P VS I- 18 DEG,(POST-BLOOM),NALPHA=2,N=7,E.NET
ALPHA,S =   24.50
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.130 1.600 2.690 4.610 5.760 6.640 6.840
YFIT(I)=    1.047 2.432 3.482 4.779 5.811 6.310 6.888
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 7.200   FINAL= 7.474
DELTAA(1) INITIAL= 0.050   FINAL= 0.083
SIGMAA(1)= 1.068
CHISQR=     0.460       AVG Y(I)=    4.039
GAMMA=      2.30191     GAMMAM=      0.56998

    7. P VS I- 16 DEG,(POST-BLOOM),NALPHA=2,N=7,E.NET
ALPHA,S =   20.50
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.120 1.350 2.820 3.780 5.020 4.910 6.010
YFIT(I)=    0.876 2.034 2.912 3.994 4.853 5.268 5.747
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 6.200   FINAL= 6.229
DELTAA(1) INITIAL= 0.050   FINAL= 0.017
SIGMAA(1)= 1.080
CHISQR=     0.264       AVG Y(I)=    3.430
GAMMA=      1.31836     GAMMAM=      0.38436
```

II. SMITH MODEL:

P^B = PMAX*S*PAR/(SQRT((PMAX**2)+((S*PAR)**2))) - R^B

```
    1. P VS I- 14 DEG,(BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   11.83
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.320 1.030 1.650 2.500 3.220 3.250 3.380
YFIT(I)=    0.506 1.178 1.695 2.351 2.910 3.207 3.605
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 3.900  FINAL= 4.615
DELTAA(1) INITIAL= 0.050  FINAL= 0.233
SIGMAA(1)= 1.501
CHISQR=     0.046       AVG Y(I)=    2.193
GAMMA=      0.22868     GAMMAM=      0.10429

    2. P VS I- 16 DEG,(BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   21.83
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.200 1.510 2.150 3.960 6.050 5.190 5.830
YFIT(I)=    0.931 2.149 3.053 4.148 5.020 5.458 6.017
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 6.200  FINAL= 7.292
DELTAA(1) INITIAL= 0.050  FINAL= 0.367
SIGMAA(1)= 1.253
CHISQR=     0.592       AVG Y(I)=    3.556
GAMMA=      2.96142     GAMMAM=      0.83286

    3. P VS I- 18 DEG,(BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   25.83
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.180 1.730 2.680 4.590 6.850 7.260 7.510
YFIT(I)=    1.104 2.568 3.688 5.103 6.295 6.923 7.759
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 8.500  FINAL= 9.844
DELTAA(1) INITIAL= 0.050  FINAL= 0.450
SIGMAA(1)= 1.496
CHISQR=     0.664       AVG Y(I)=    4.400
GAMMA=      3.31827     GAMMAM=      0.75415
```

```
    4. P VS I- 20 DEG,(BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   31.89
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.150 1.340 3.690 6.010 7.350 8.780 8.860
YFIT(I)=    1.361 3.150 4.491 6.137 7.472 8.153 9.033
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 9.200  FINAL=11.093
DELTAA(1) INITIAL= 0.050  FINAL= 0.633
SIGMAA(1)= 1.330
CHISQR=     1.167       AVG Y(I)=    5.169
GAMMA=      5.83592     GAMMAM=      1.12912

    5. P VS I- 20 DEG,(POST-BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   31.17
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.160 2.030 3.230 5.950 6.760 7.090 9.000
YFIT(I)=    1.328 3.055 4.321 5.828 7.003 7.583 8.313
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 8.700  FINAL= 9.927
DELTAA(1) INITIAL= 0.050  FINAL= 0.417
SIGMAA(1)= 1.216
CHISQR=     0.879       AVG Y(I)=    4.889
GAMMA=      4.39499     GAMMAM=      0.89903

    6. P VS I- 18 DEG,(POST-BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   24.50
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.130 1.600 2.690 4.610 5.760 6.640 6.840
YFIT(I)=    1.046 2.420 3.452 4.719 5.747 6.273 6.952
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 7.200  FINAL= 8.546
DELTAA(1) INITIAL= 0.050  FINAL= 0.450
SIGMAA(1)= 1.335
CHISQR=     0.450       AVG Y(I)=    4.039
GAMMA=      2.25042     GAMMAM=      0.55723

    7. P VS I- 16 DEG,(POST-BLOOM),NALPHA=2,N=7,P.NET
ALPHA,S =   20.50
X(I)=       0.043 0.103 0.154 0.231 0.317 0.377 0.488
Y(I)=       0.120 1.350 2.820 3.780 5.020 4.910 6.010
YFIT(I)=    0.875 2.024 2.886 3.944 4.801 5.238 5.802
NPTS=     7
NTERMS=   1
MODE=     0
A(1) INITIAL= 6.200  FINAL= 7.123
DELTAA(1) INITIAL= 0.050  FINAL= 0.300
SIGMAA(1)= 1.319
CHISQR=     0.251       AVG Y(I)=    3.430
GAMMA=      1.25428     GAMMAM=      0.36568
```

DESCRIPTION OF PARAMETERS IN THE NON-LINEAR LSF SUBROUTINE

S - Initial slope, ALPHA (Input Parameter)

R^B - Respiration (Input Parameter)

X - Array of data pts. for indep var (PAR)

Y - Array of data pts. for dep var (P^B)

NTERMS - No. of parameters

MODE - Determines method of wgting LSF

A - Array of parameters of be estimated
(A=1; A(1)=PMAX)

DELTAA - Array of increments for parameter(s) A
SIGMAA - Array of St. Dev. for parameter(s) A

YFIT - Array of calculated values of Y

CHISQR - Reduced Chi Square for fit

AVG - Average Y(I) value

GAMMA - Sum of ((YFIT(I)-Y(I))**2)

GAMMAM - GAMMA/AVG

Figure 1. Experimental facilities for Experiment 1

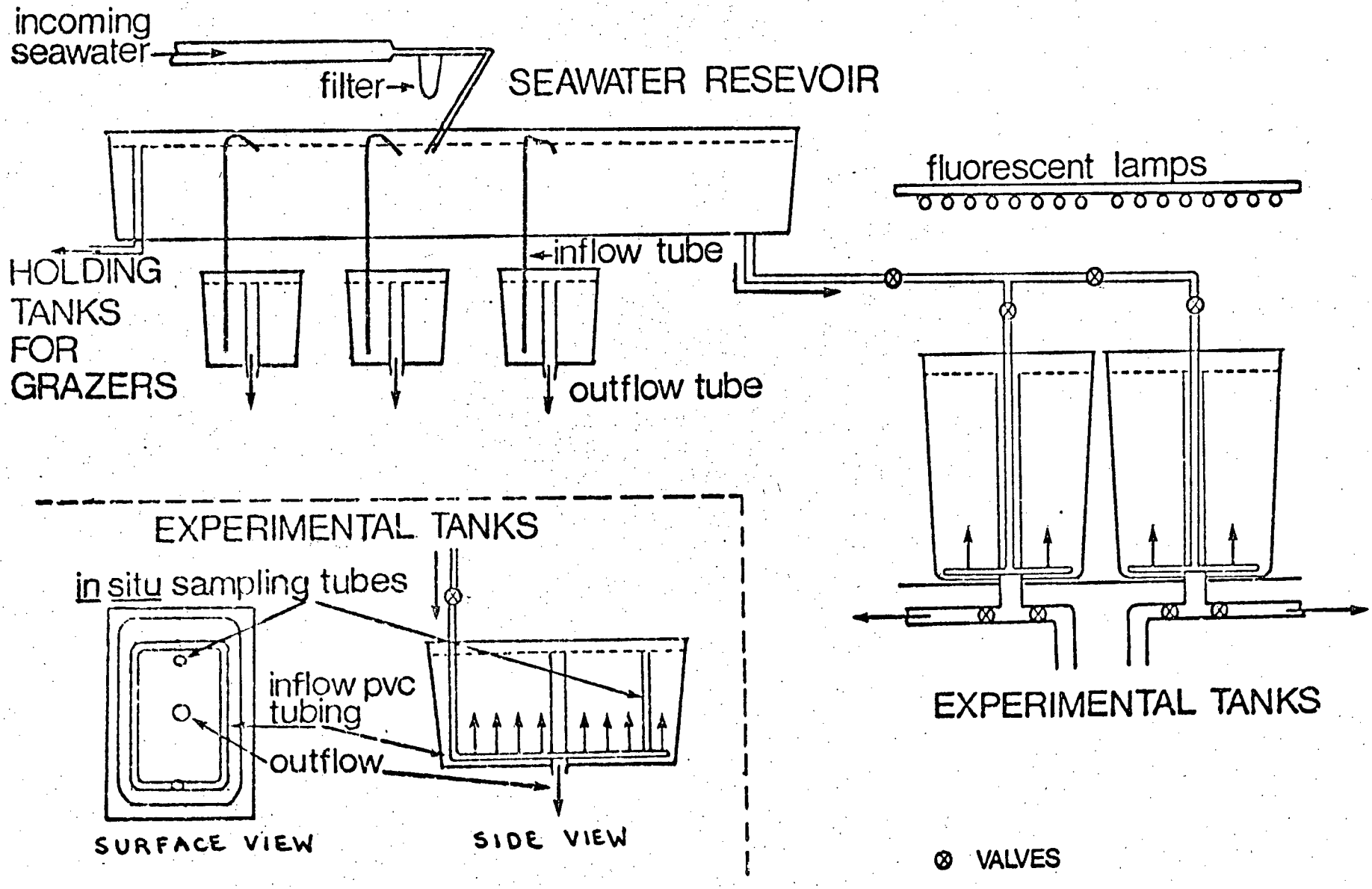


Figure 2. Duplicate tank systems for Experiments 2 and 3

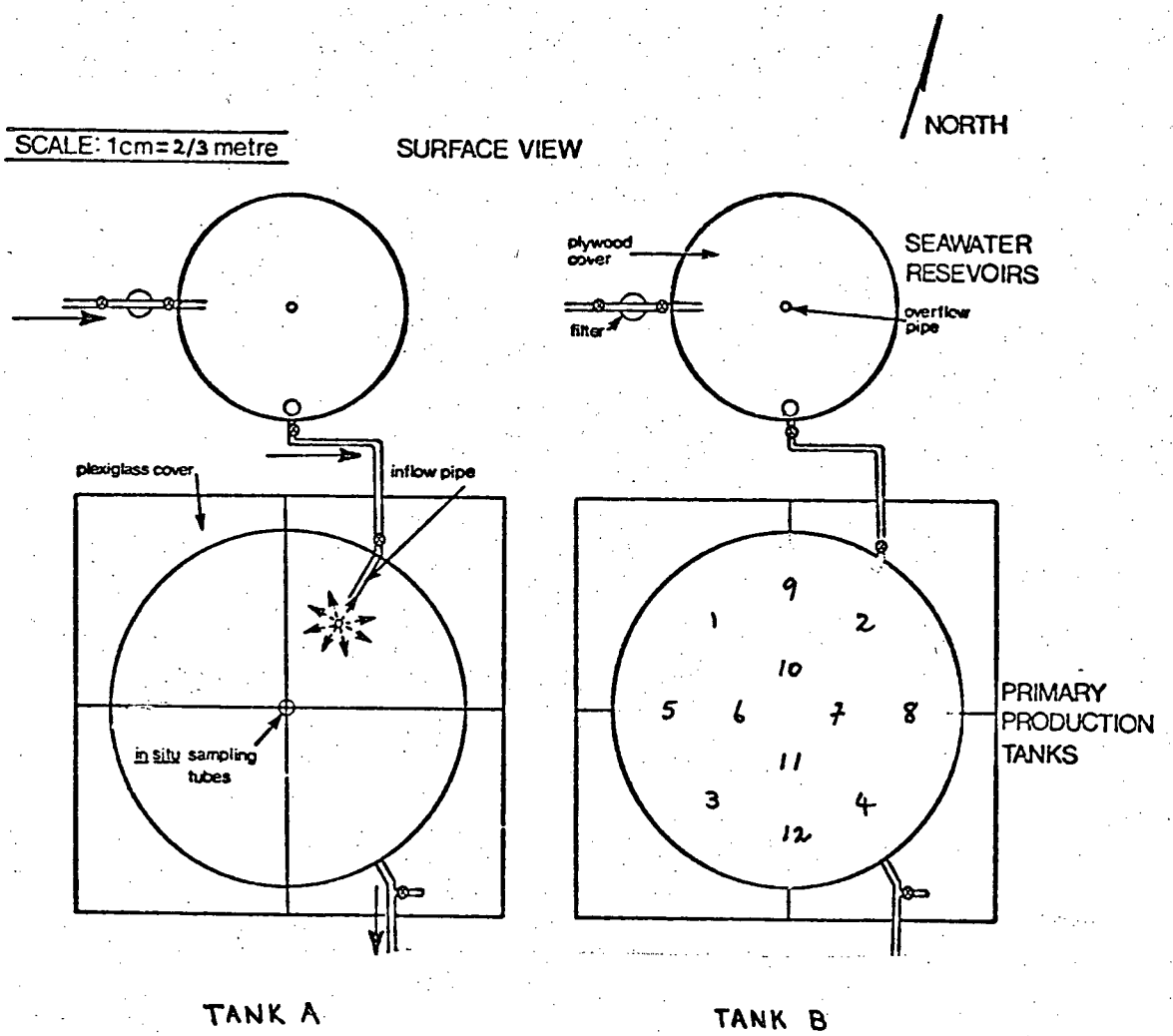


Figure 3. Side view of the experimental facilities for Experiments 2 and 3

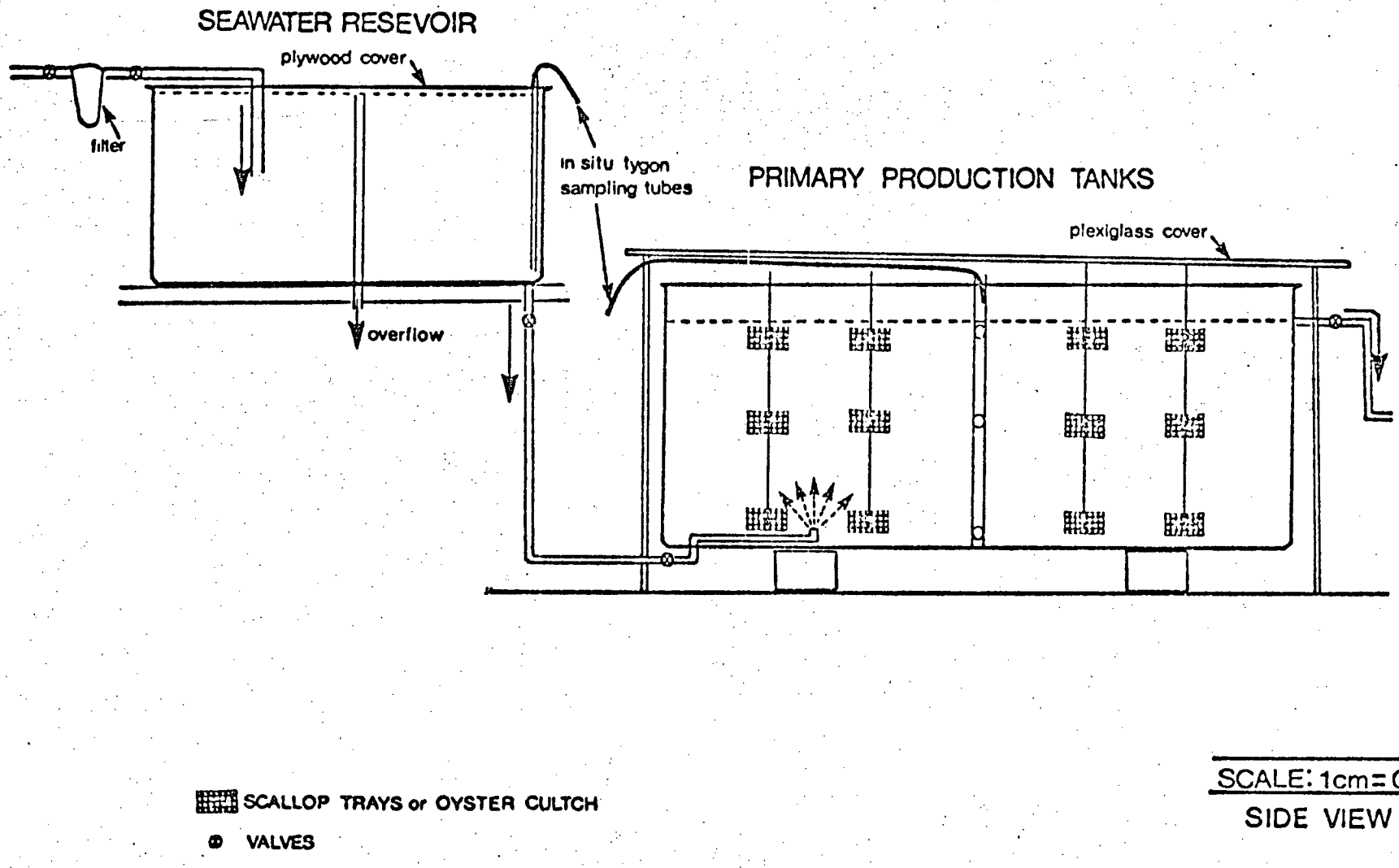
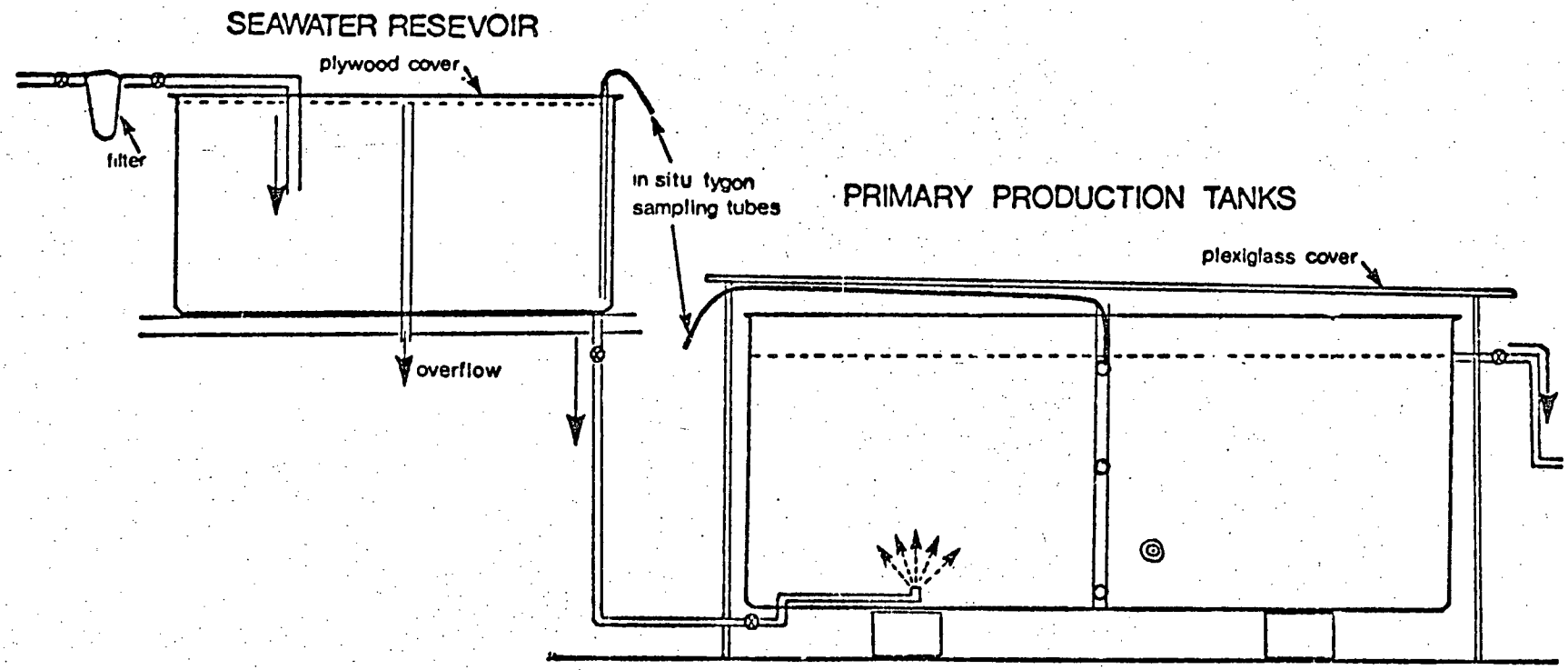


Figure 4. Side view of the experimental facilities for Experiment 4.



SCALE: 1cm = 0.3 metre

SIDE VIEW

VALVES ⊗

PUMP ◎

Figure 5. Two-stage culture systems for Experiment 5

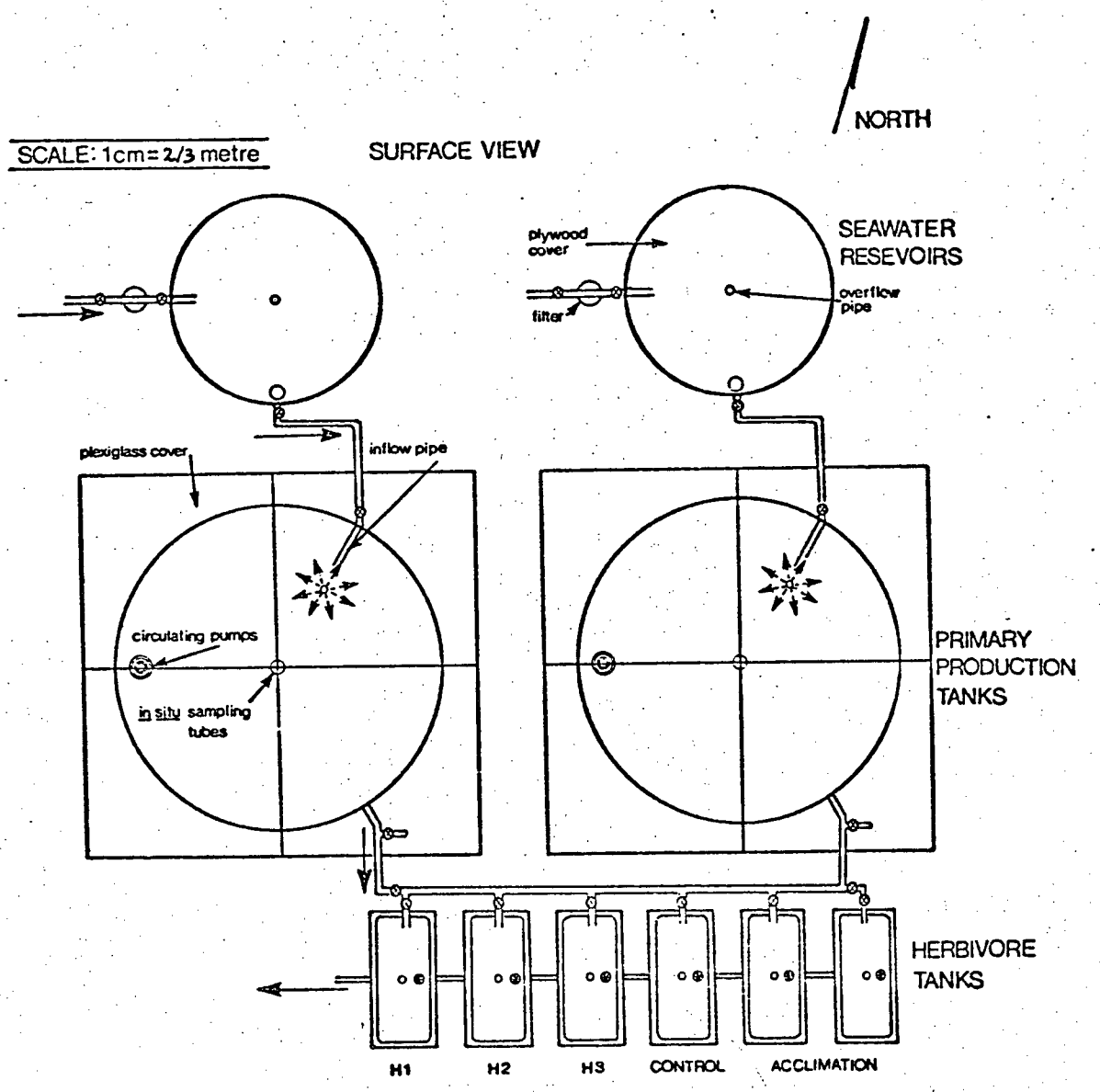


Figure 6. Nitrate concentration during Experiment 1A

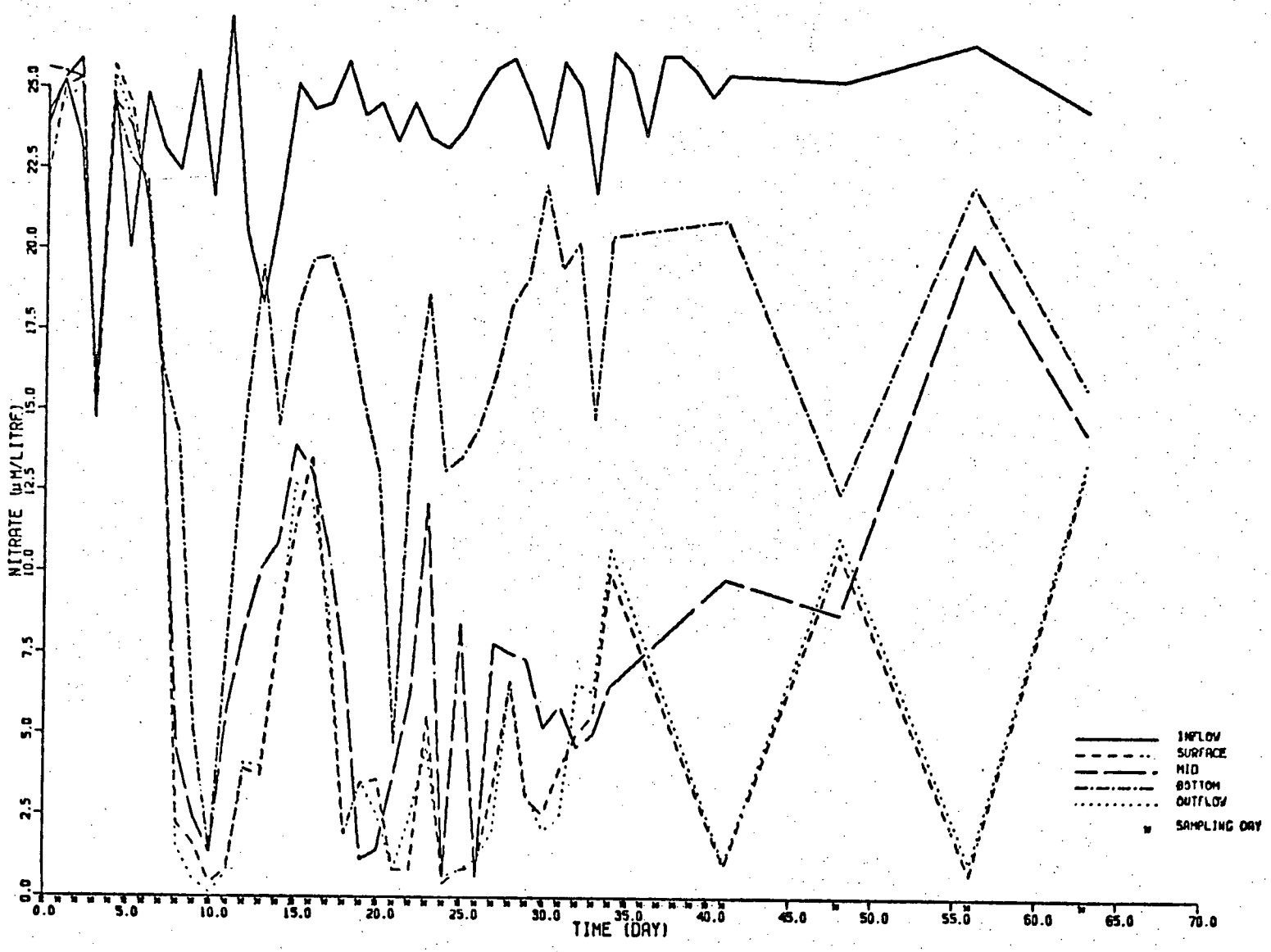


Figure 7. Nitrate concentration during Experiment 1B

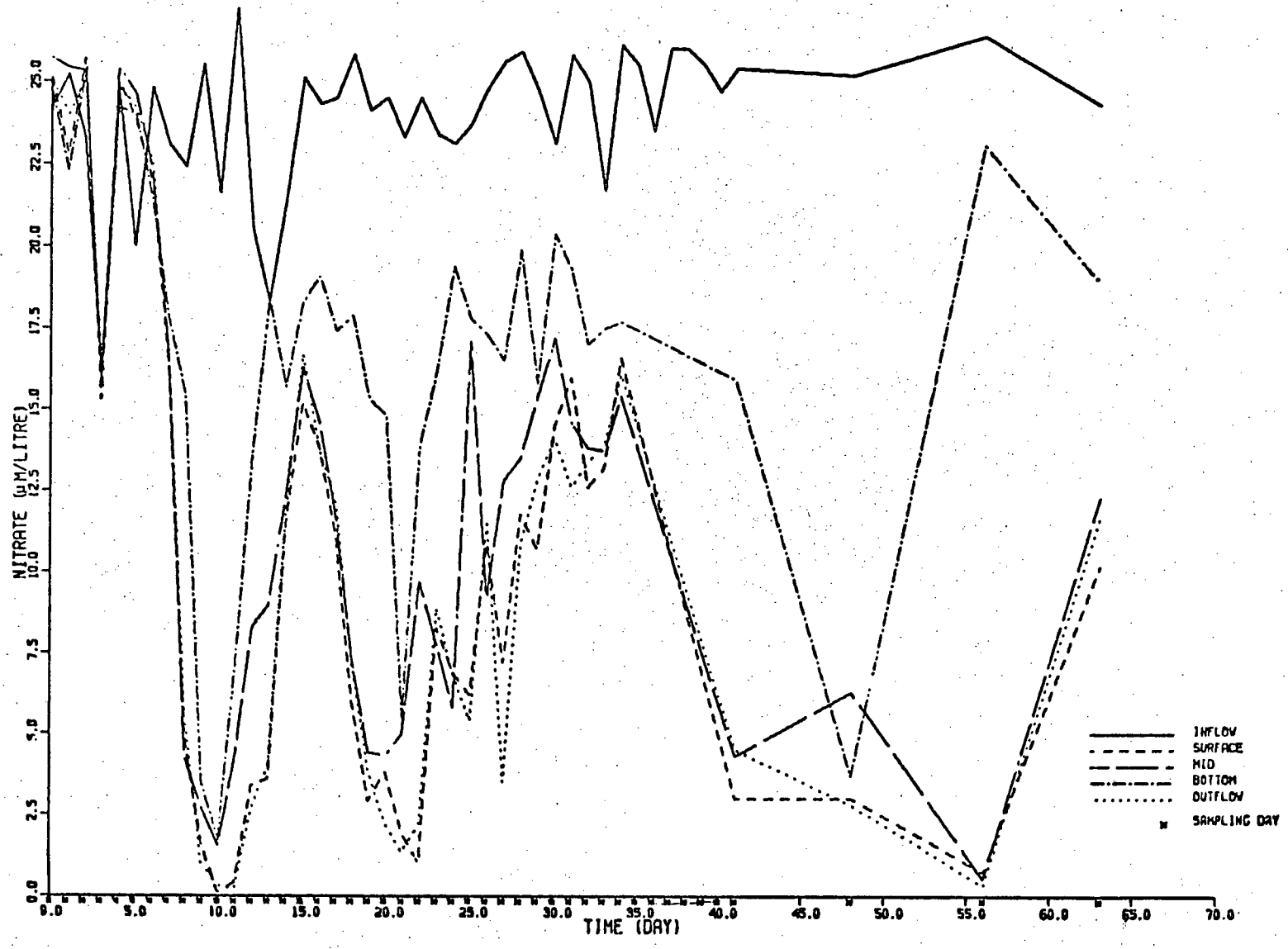


Figure 8. Phytoplankton stock during Experiment 1A

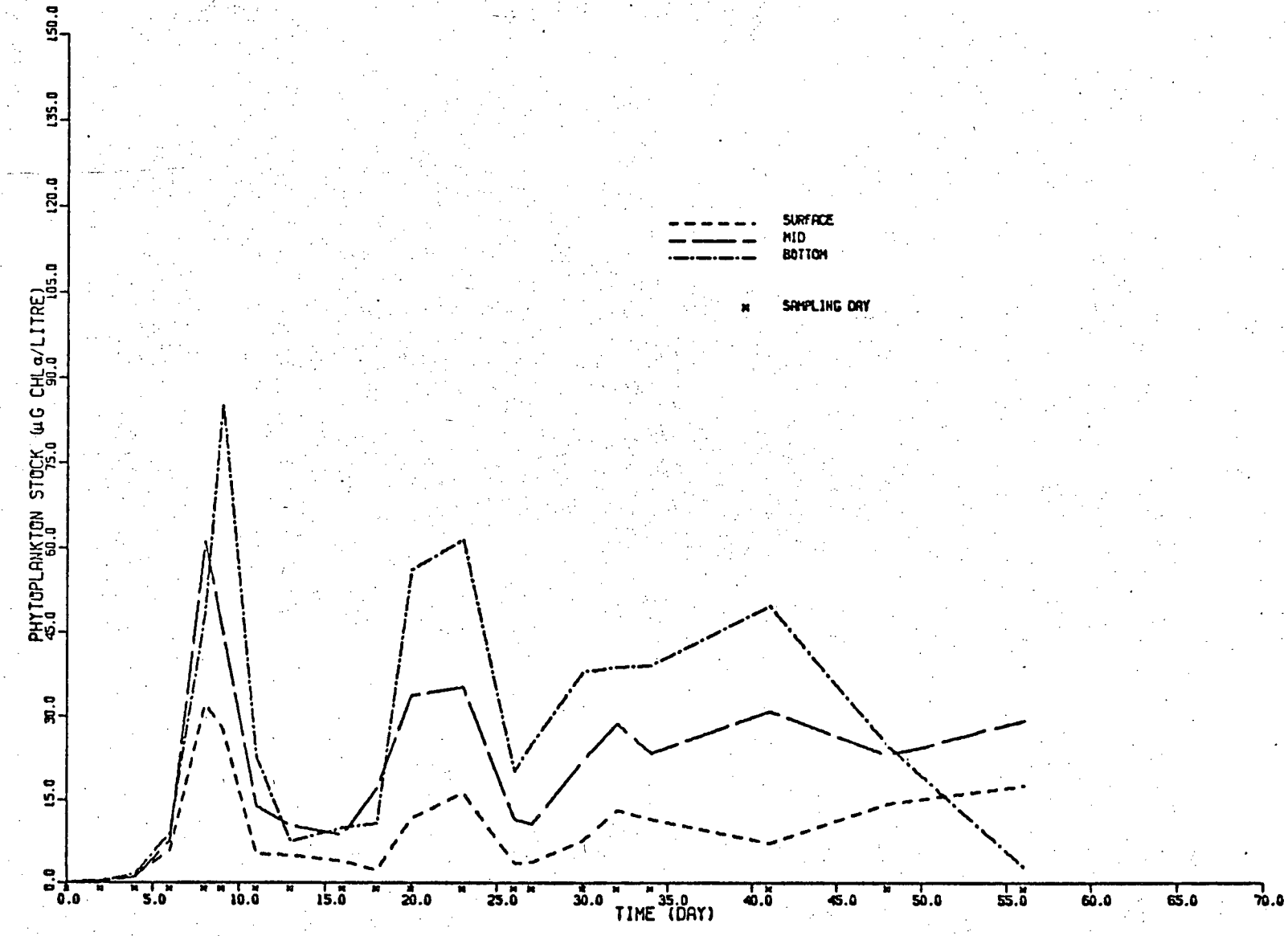


Figure 9. Phytoplankton stock during Experiment 1B

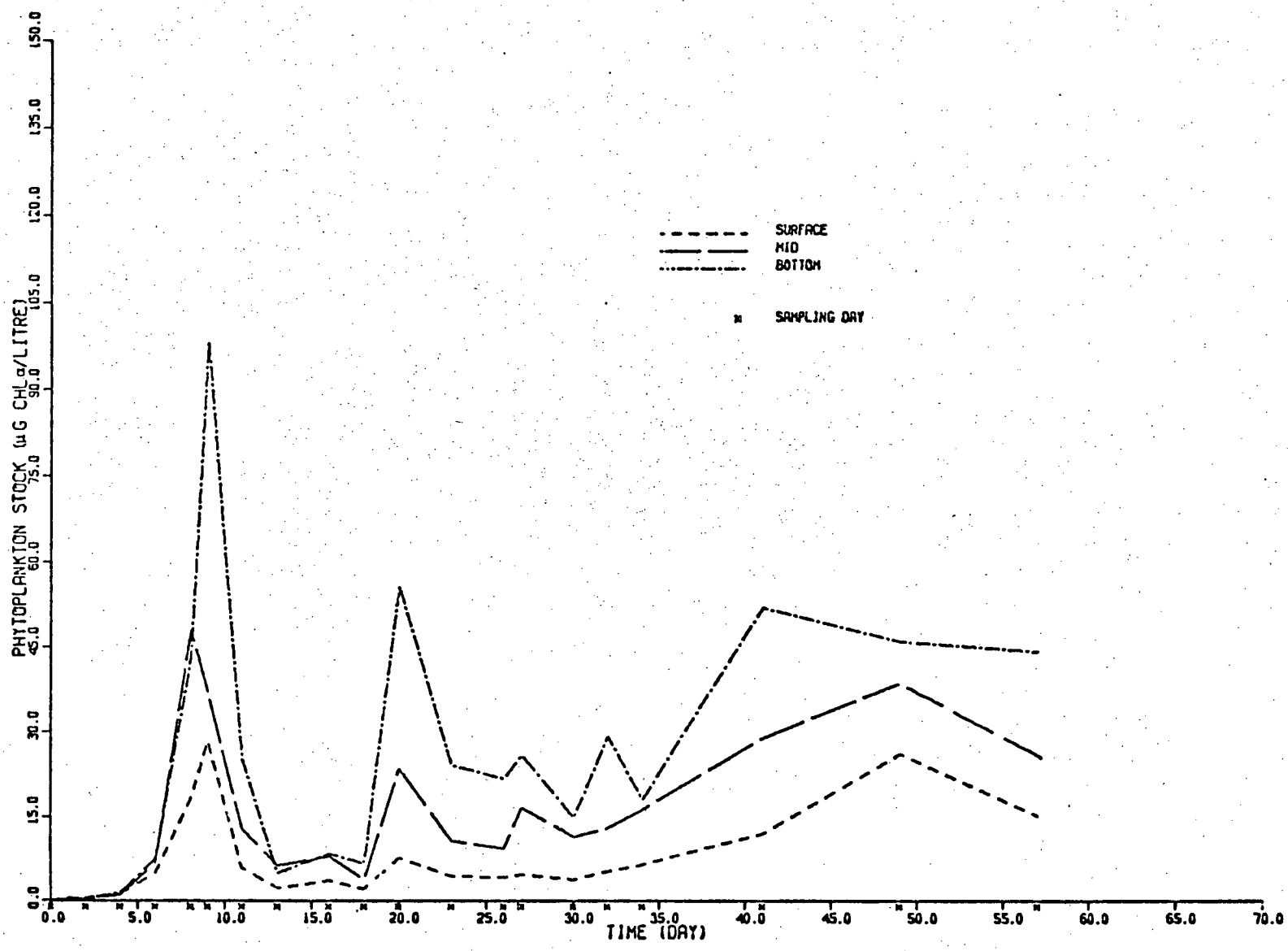


Figure 10. Primary productivity during Experiment 1A

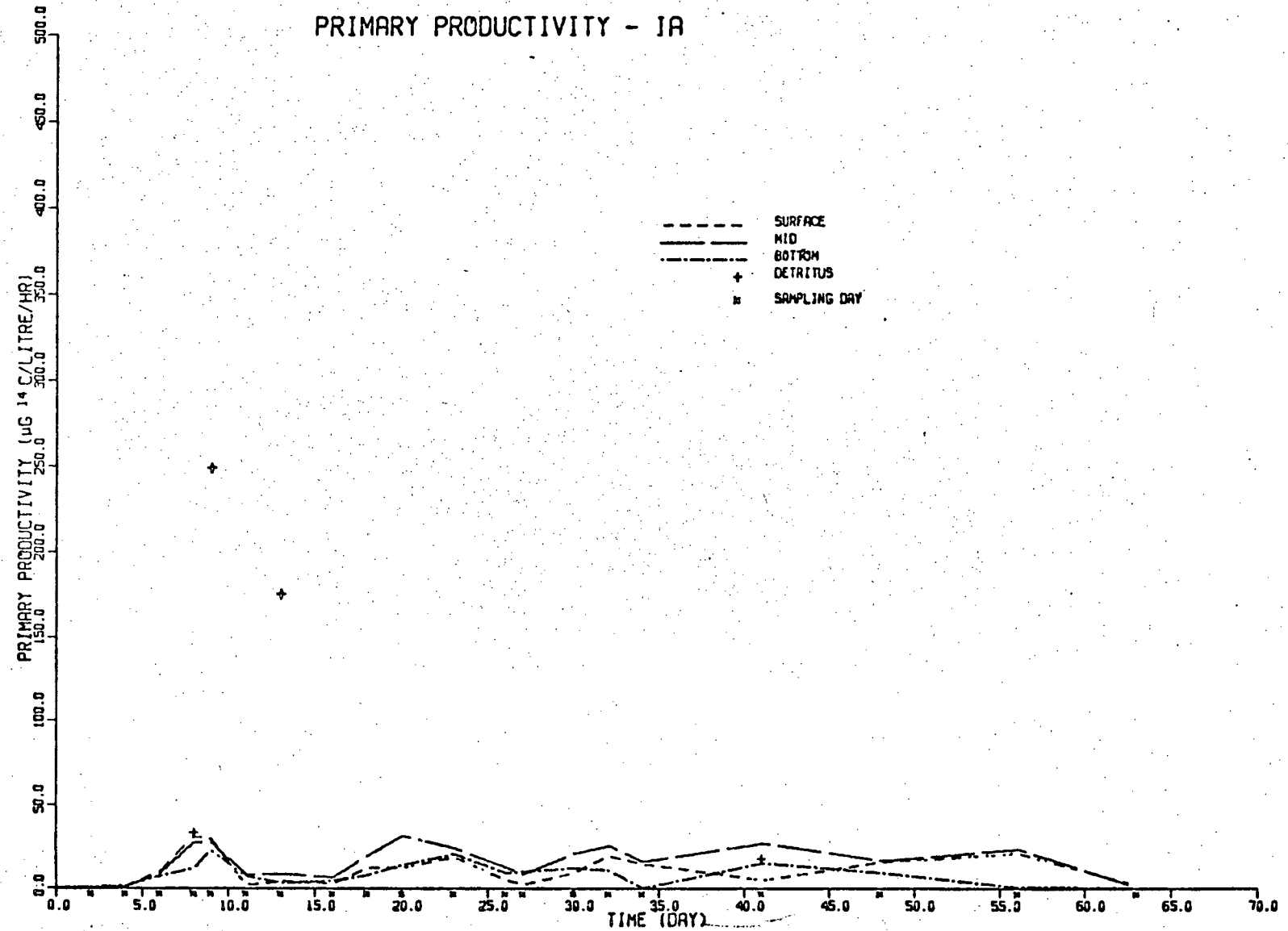


Figure 11. Primary productivity during Experiment 1B

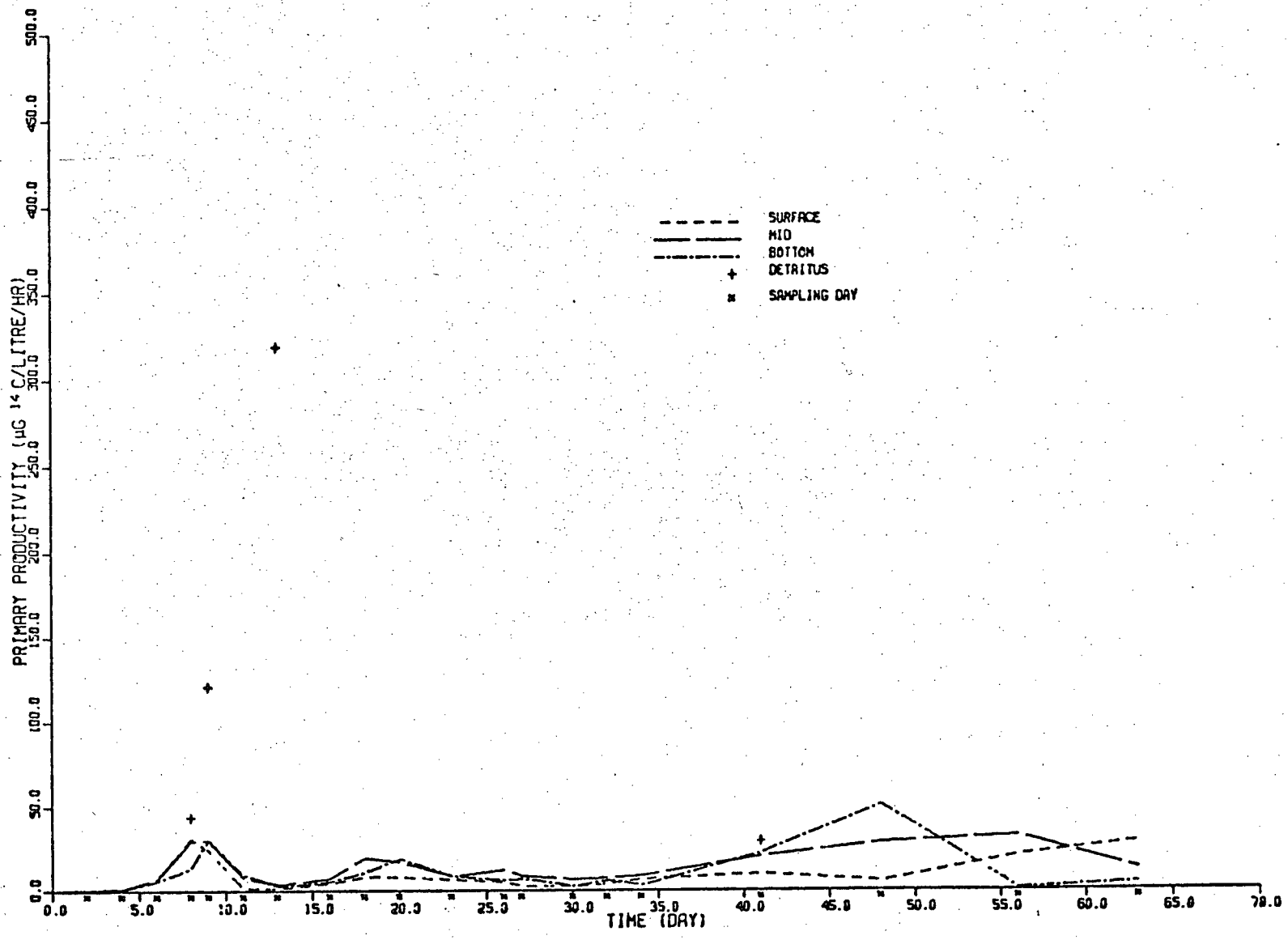


Figure 12. Primary productivity (standardized) during Experiment 1B

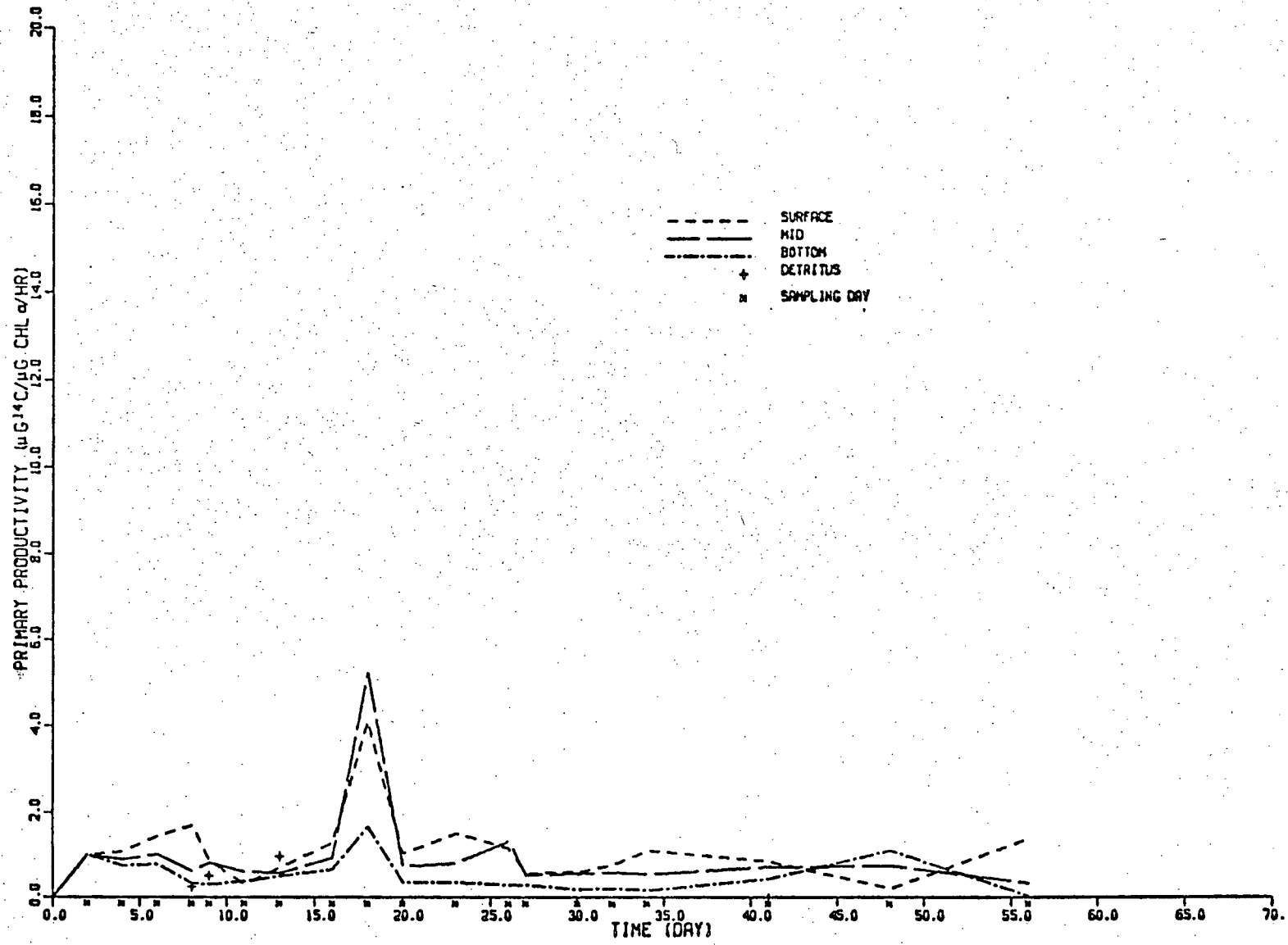


Figure 13. Solar radiation during Experiment 2

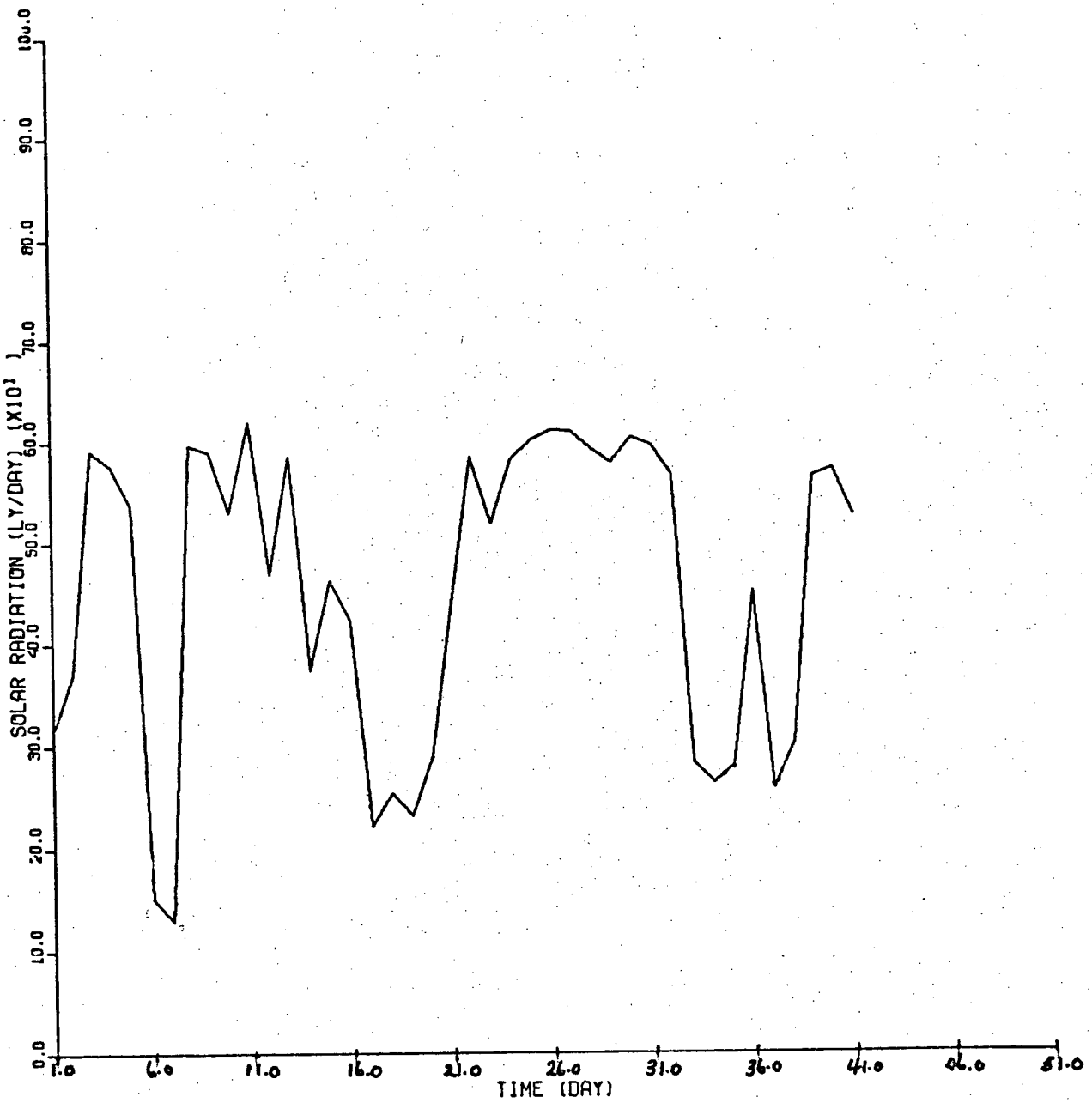


Figure 14. Temperature during Experiment 2A

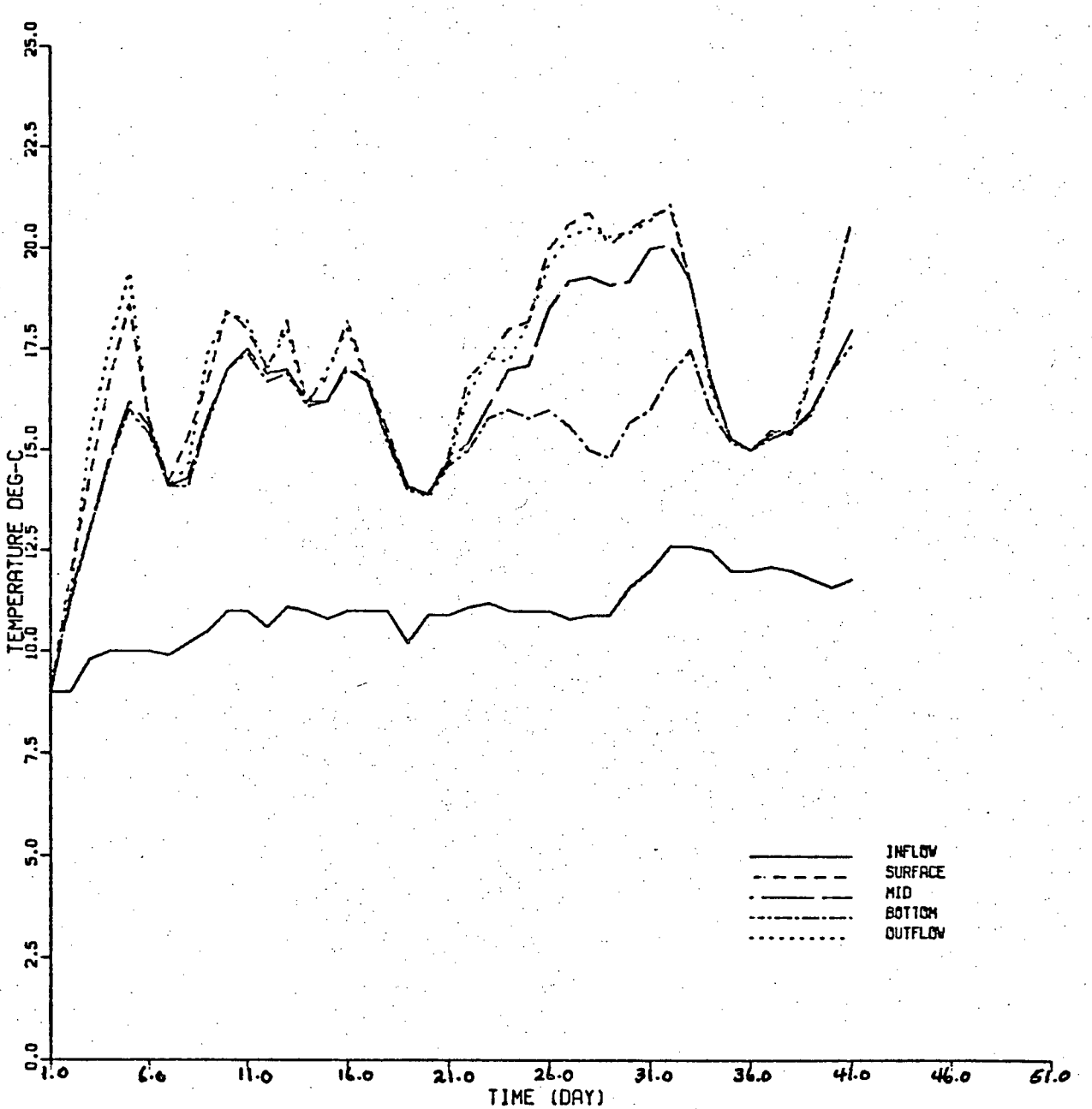


Figure 15. Temperature during Experiment 2B

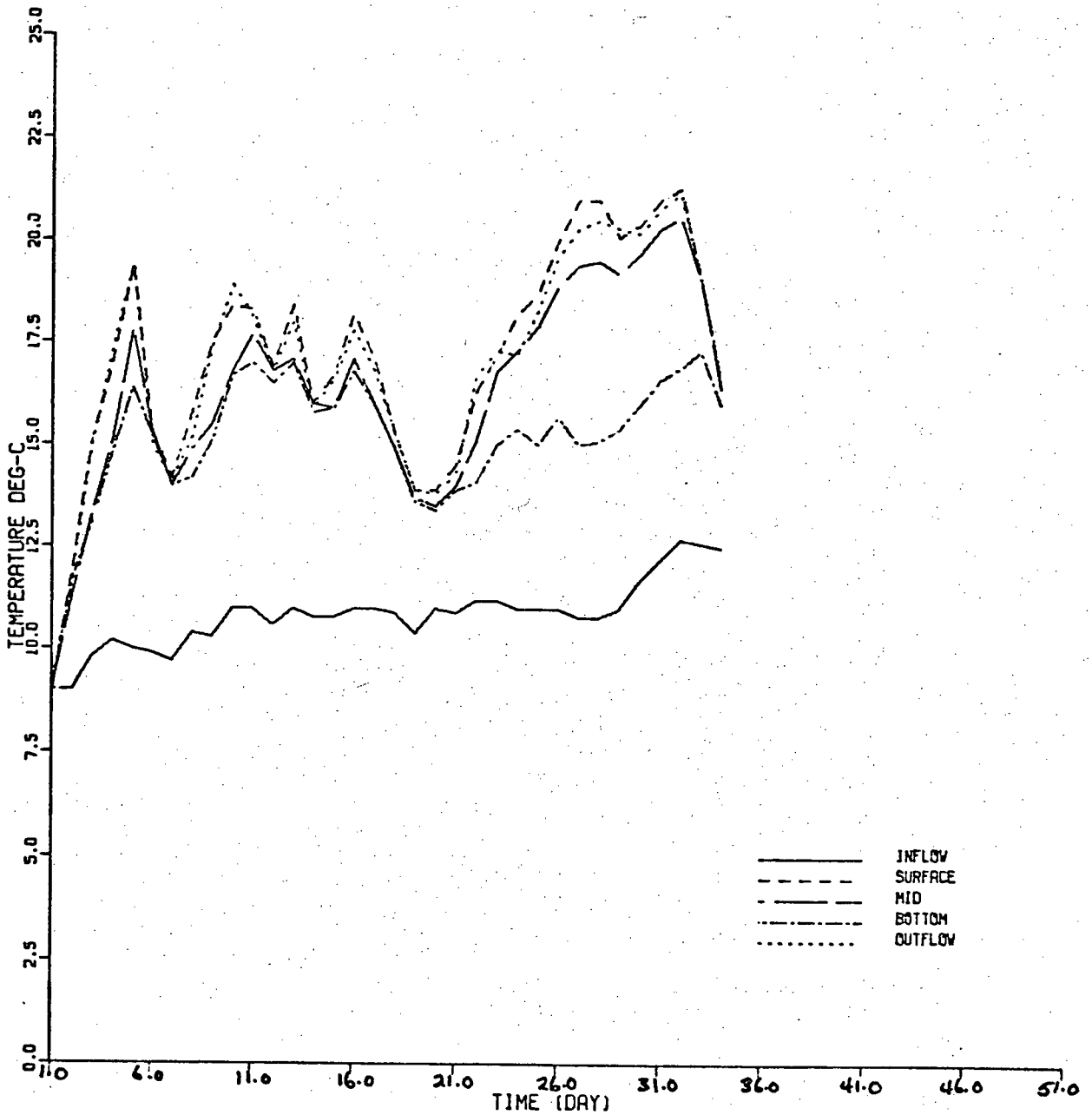


Figure 16. Nitrate concentration during Experiment 2A

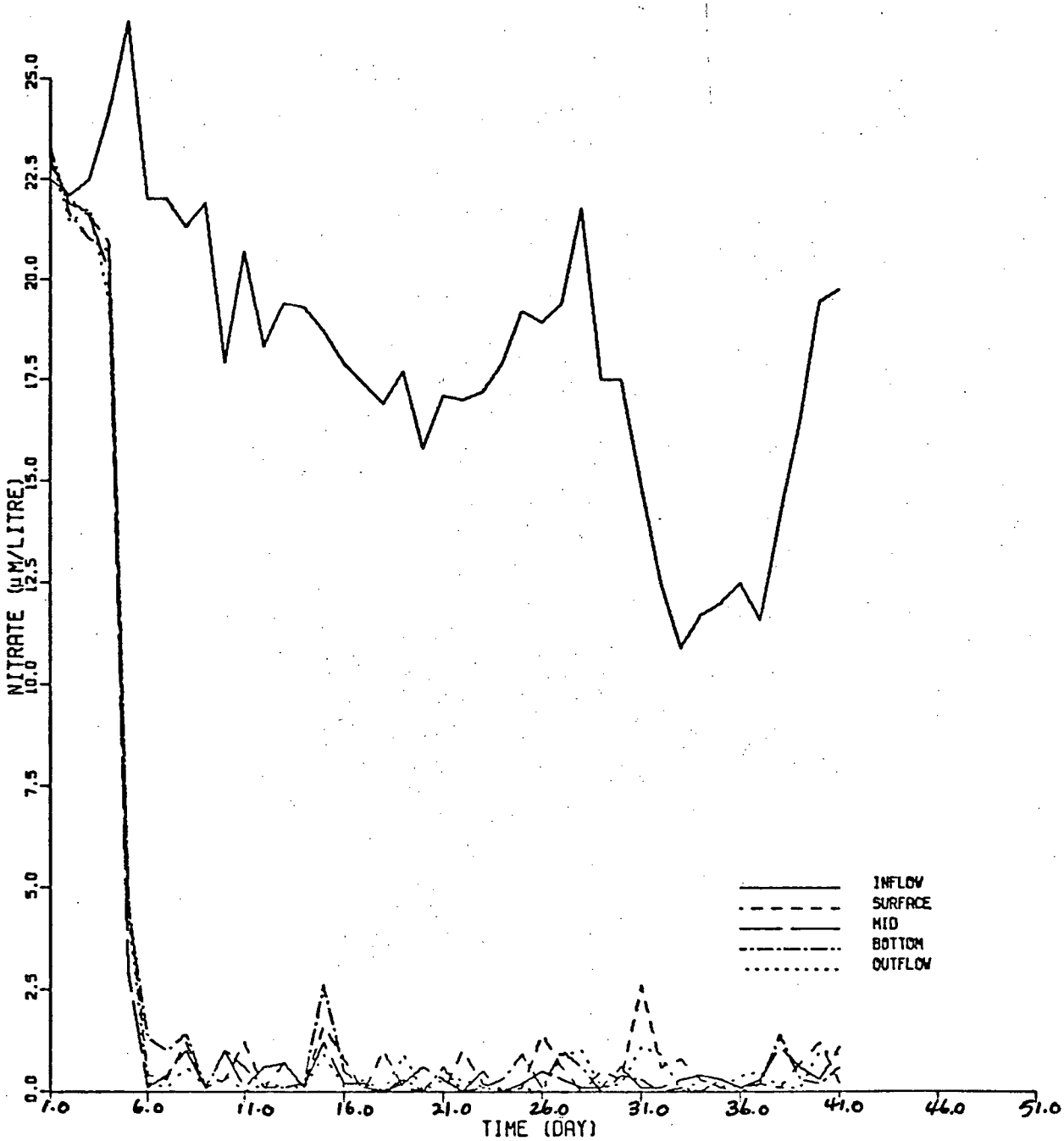


Figure 17. Nitrate concentration during Experiment 2B

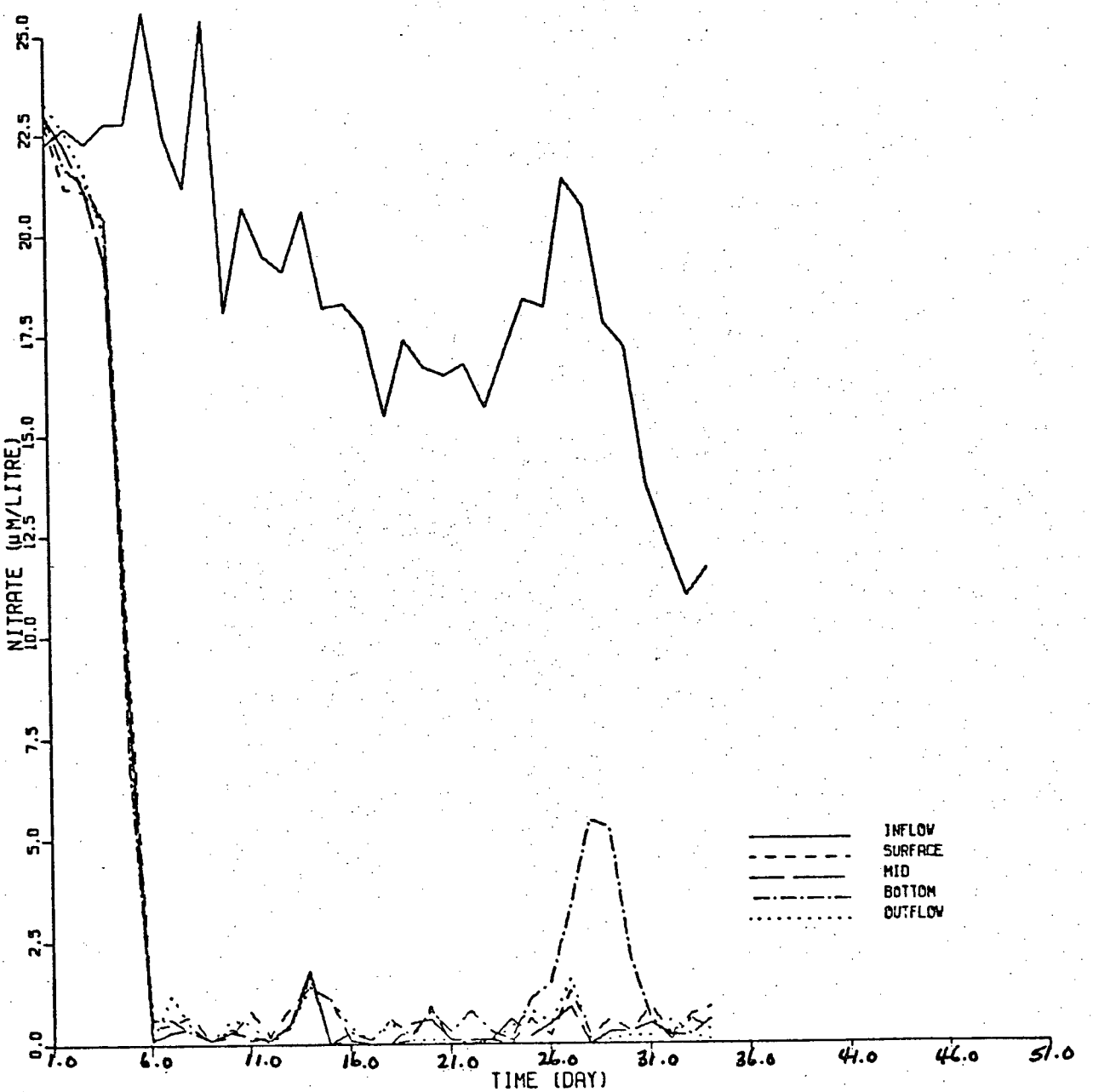


Figure 18. Phytoplankton stock during Experiment 2A

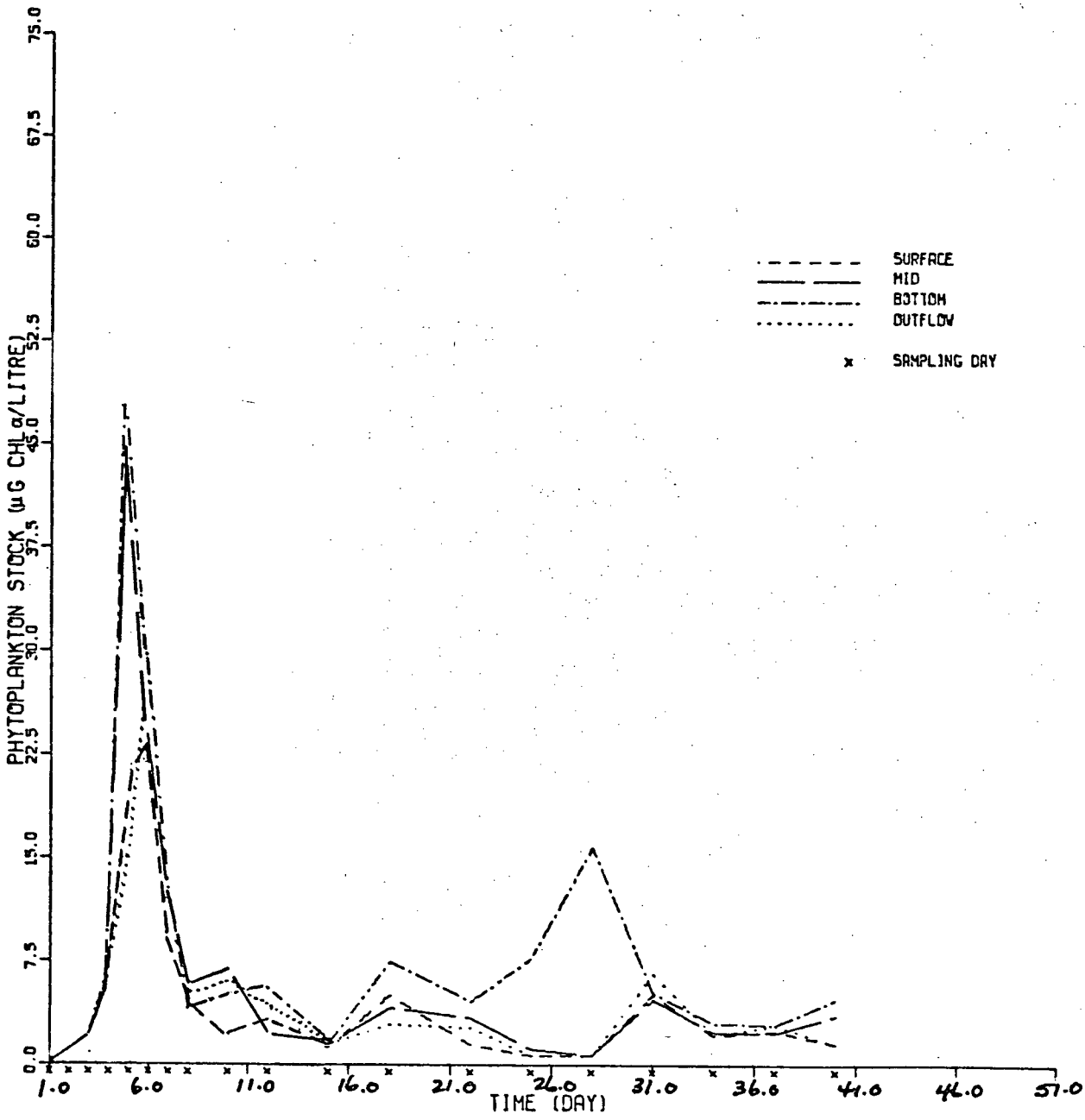


Figure 19. Phytoplankton stock during Experiment 2B

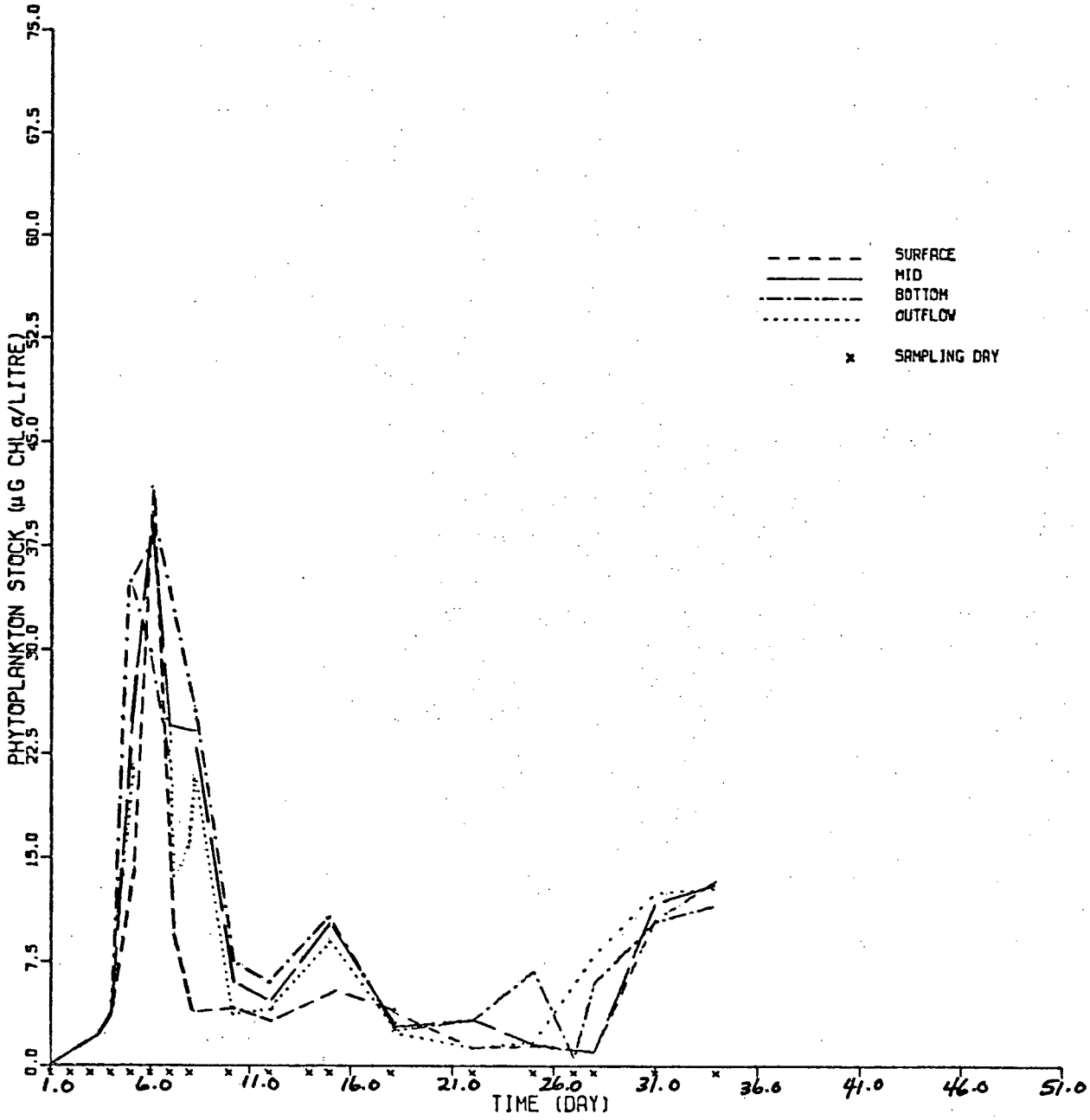


Figure 20. Oxygen concentration during Experiment 2A

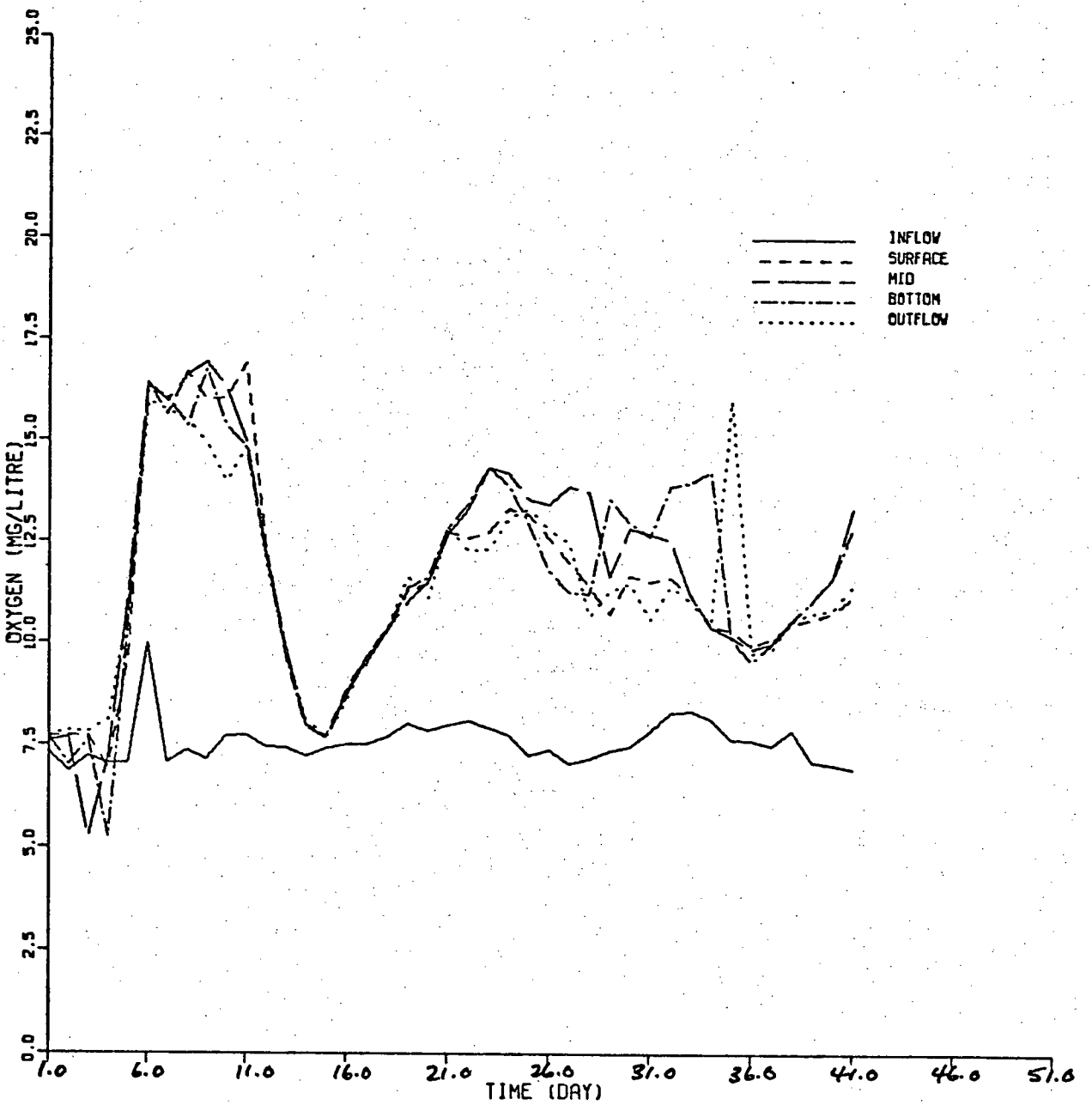


Figure 21. Oxygen concentration during Experiment 2B

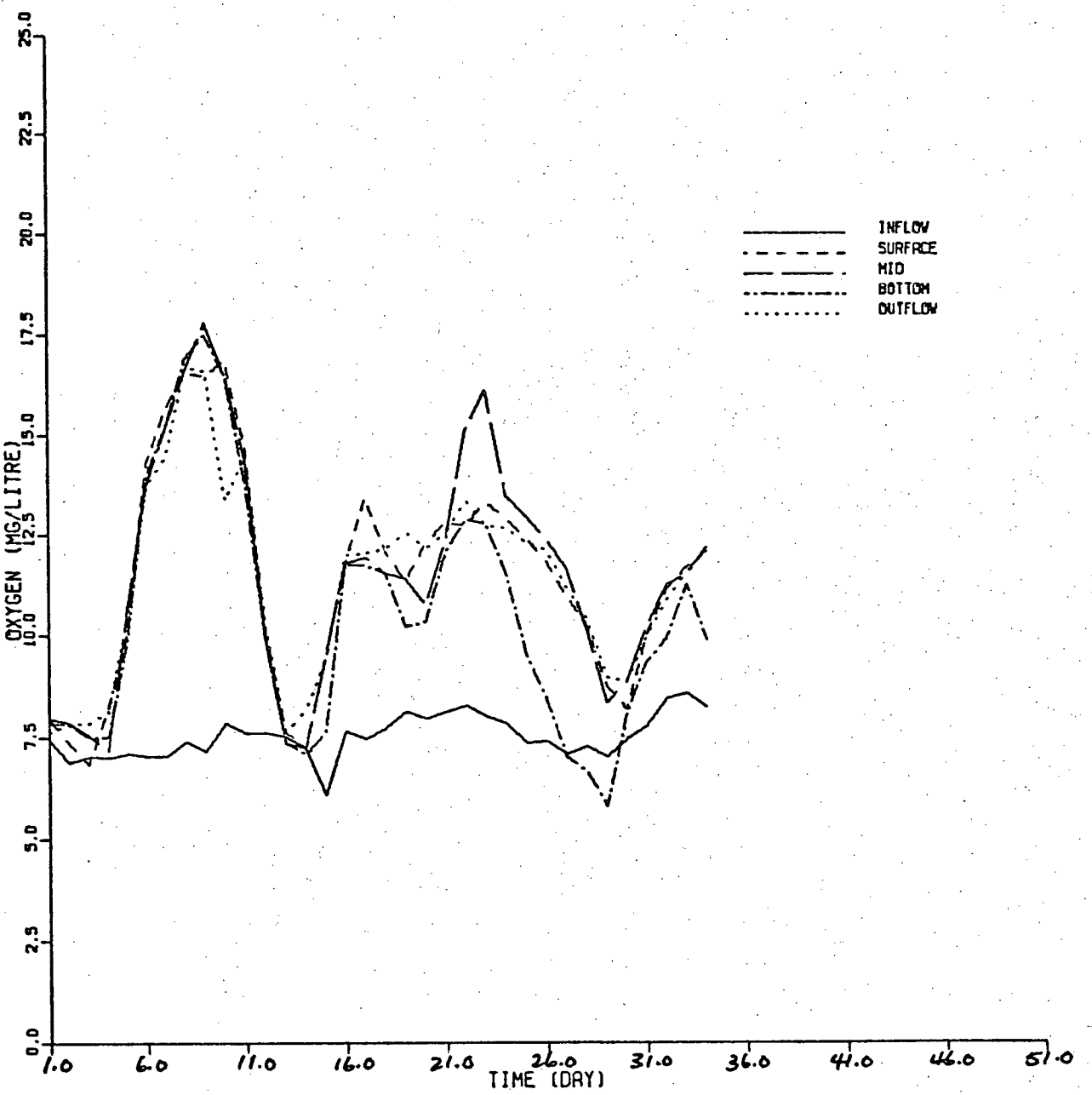


Figure 22. Primary productivity during Experiment 2A

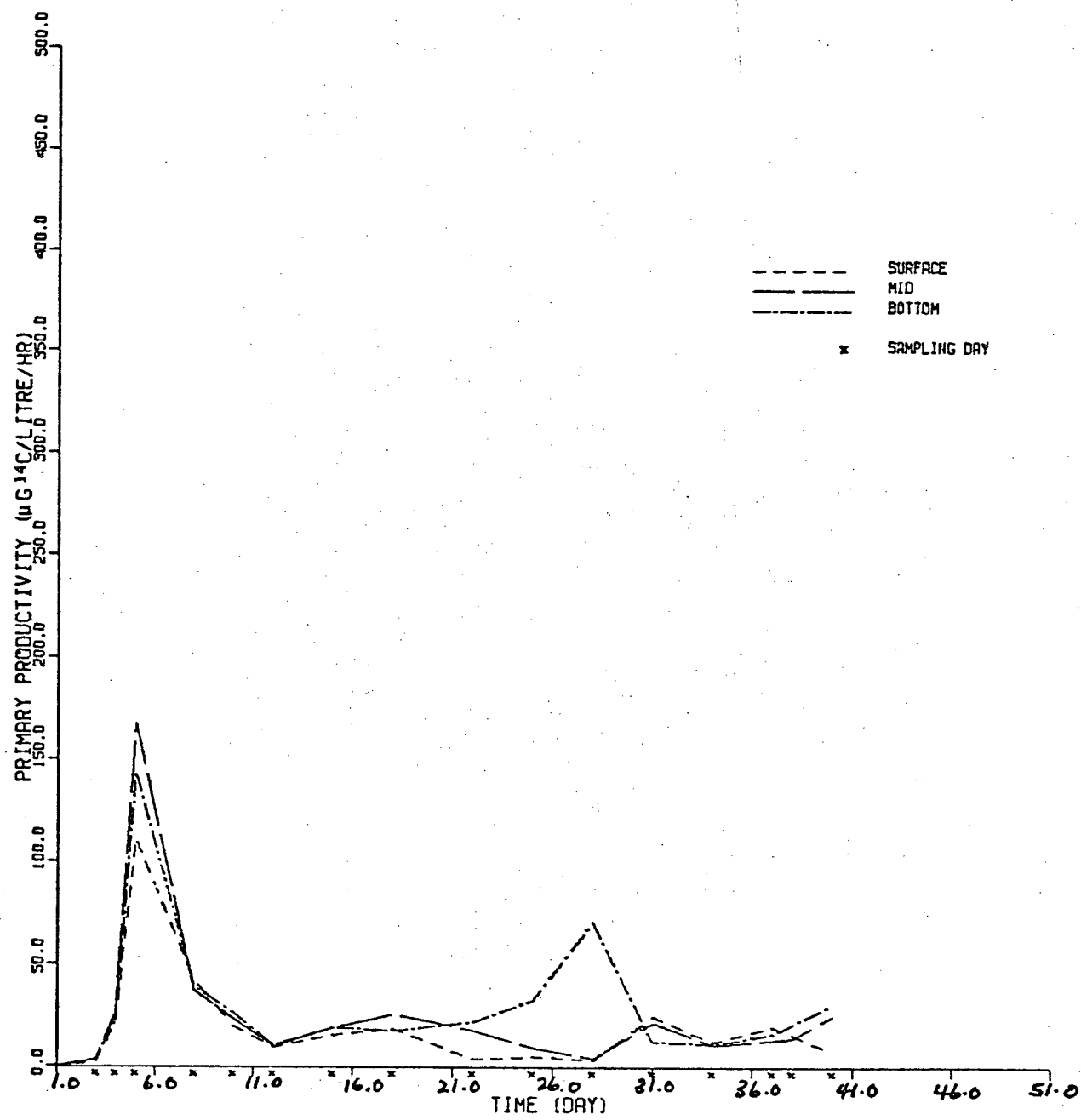


Figure 23. Primary productivity during Experiment 2B

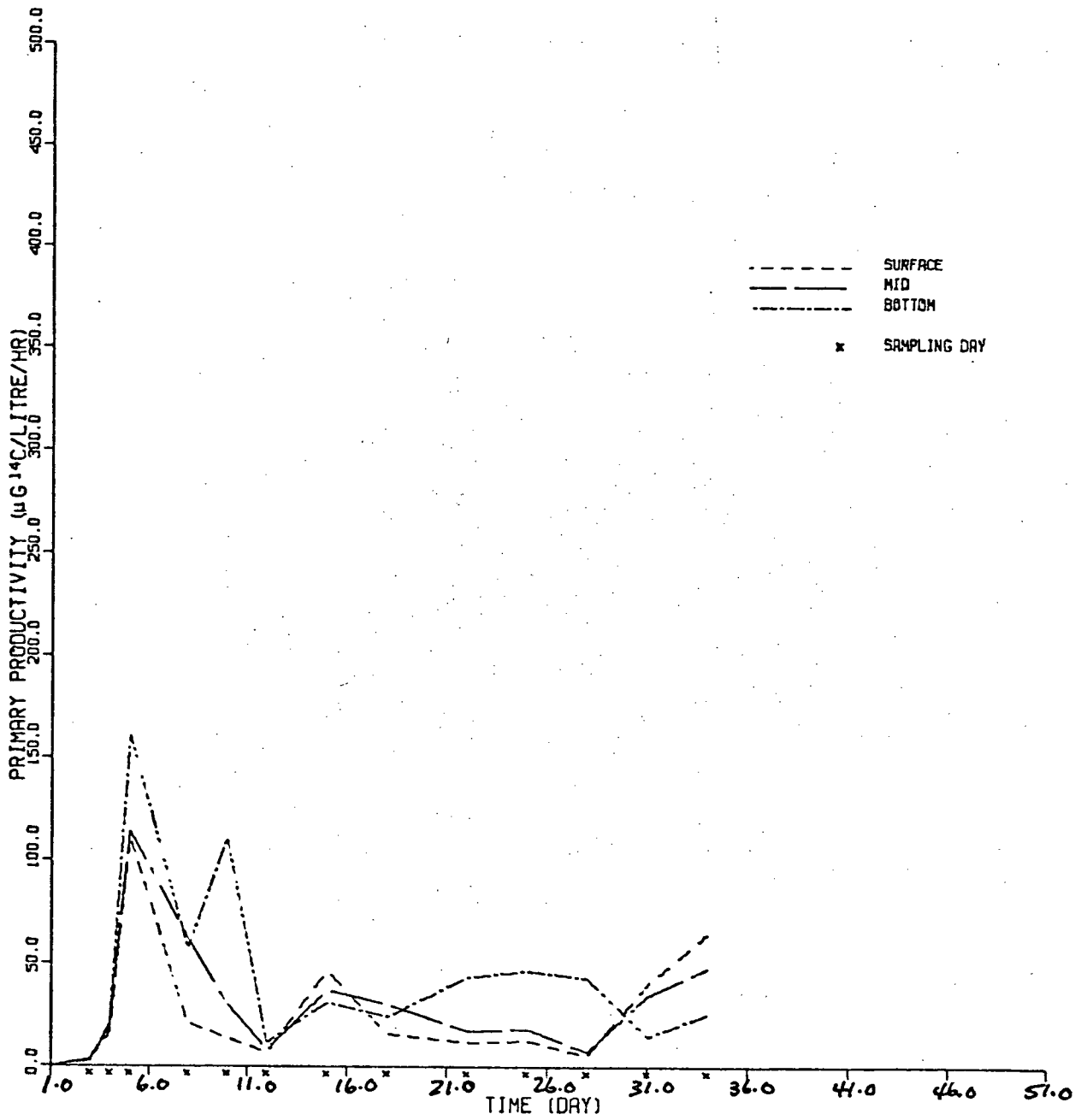


Figure 24. Primary productivity (standardized) during Experiment 2A

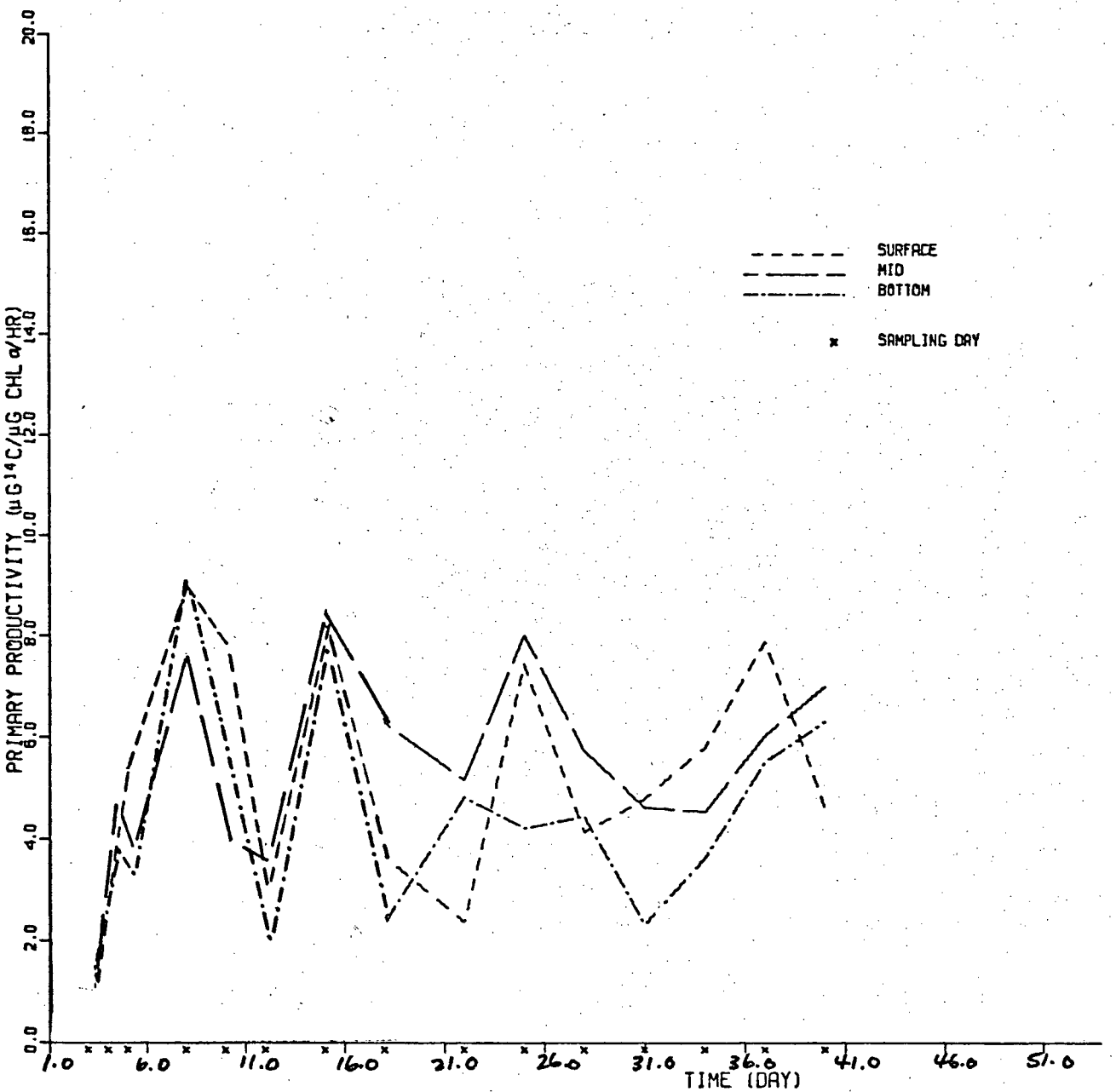


Figure 25. Primary productivity (standardized) during Experiment 2B

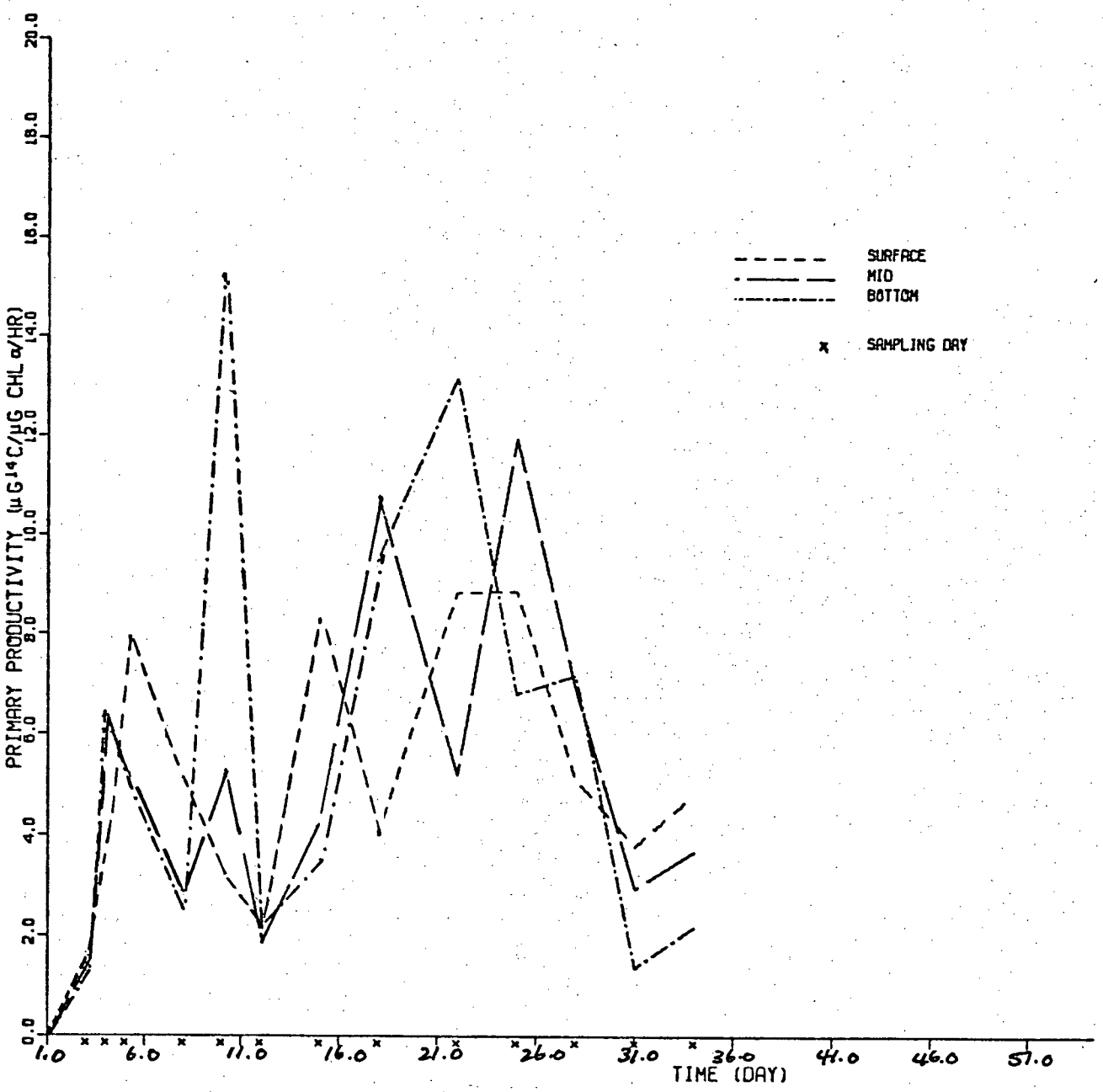


Figure 26. Solar radiation during Experiment 3A

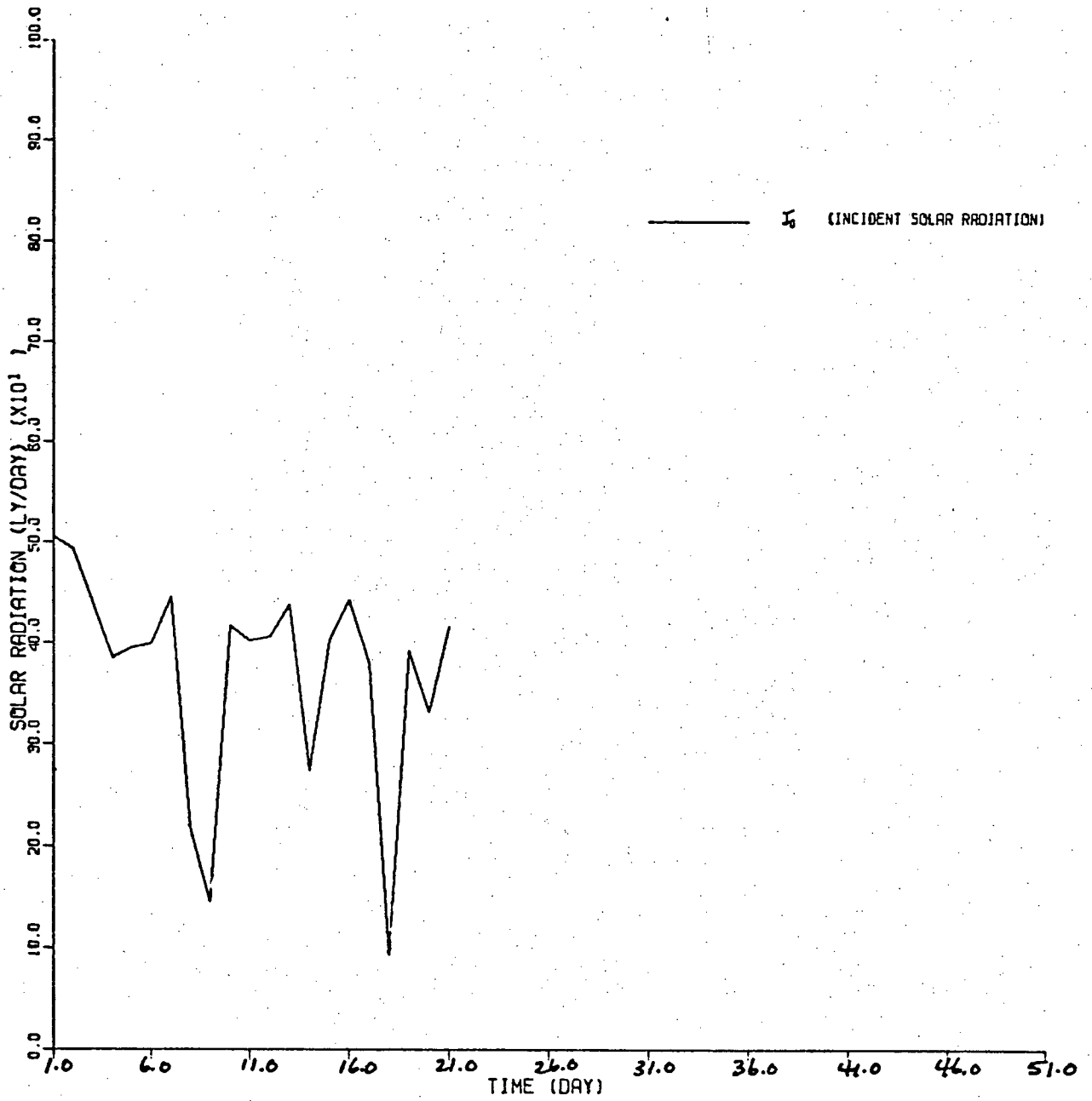


Figure 27. Temperature during Experiment 3A

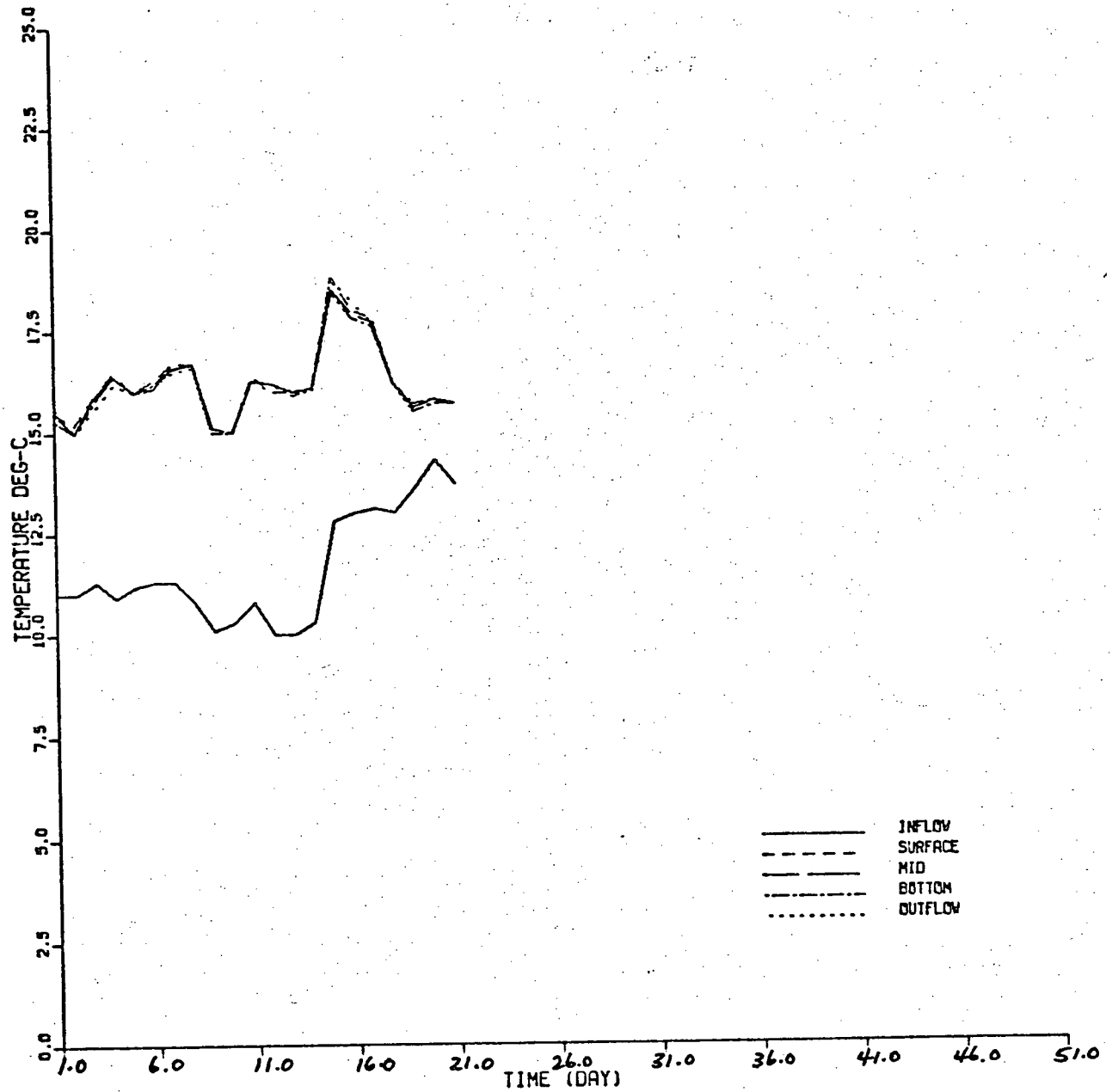


Figure 28. Nitrate concentration during Experiment 3A

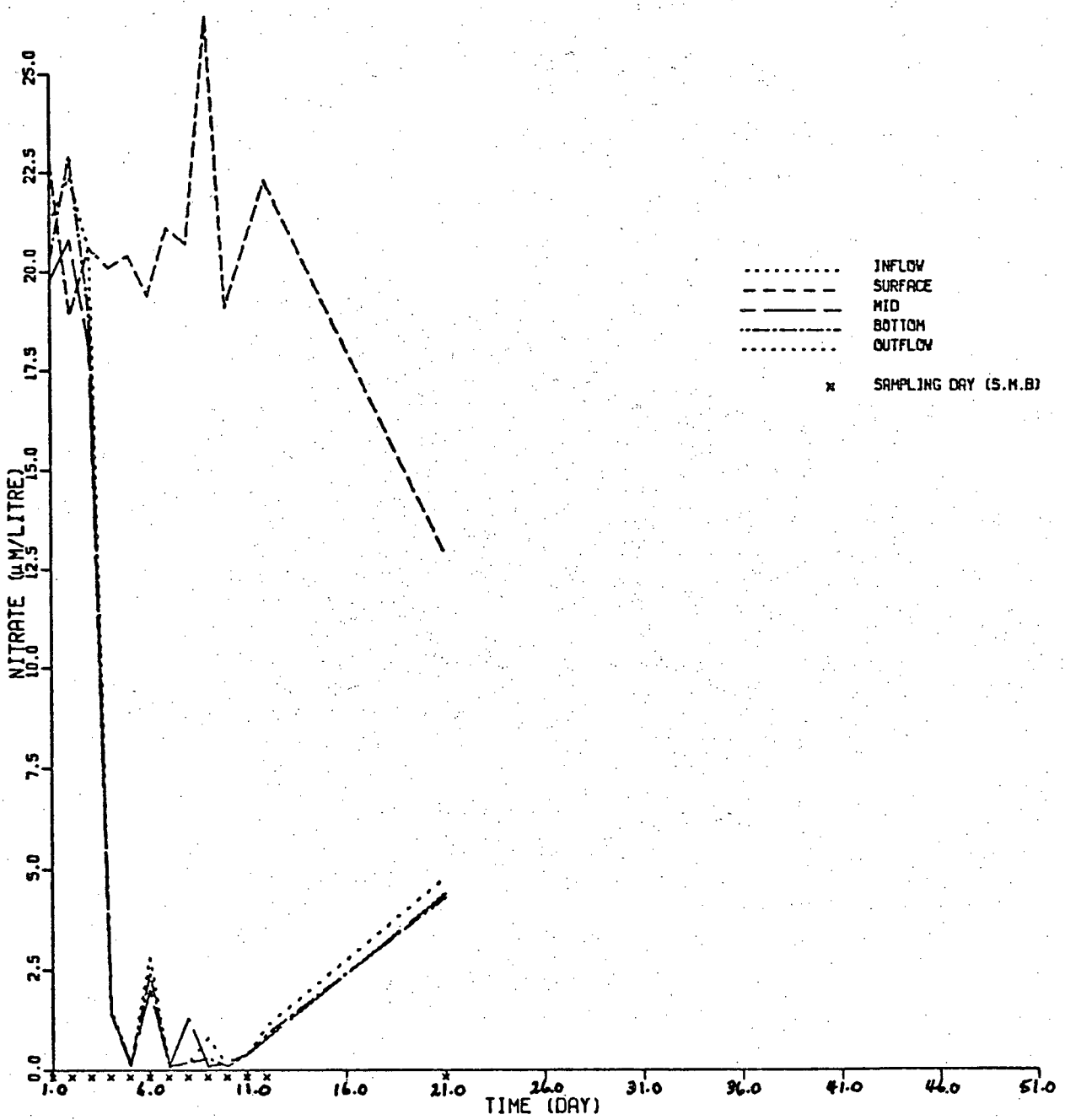


Figure 29. Phytoplankton stock during Experiment 3A

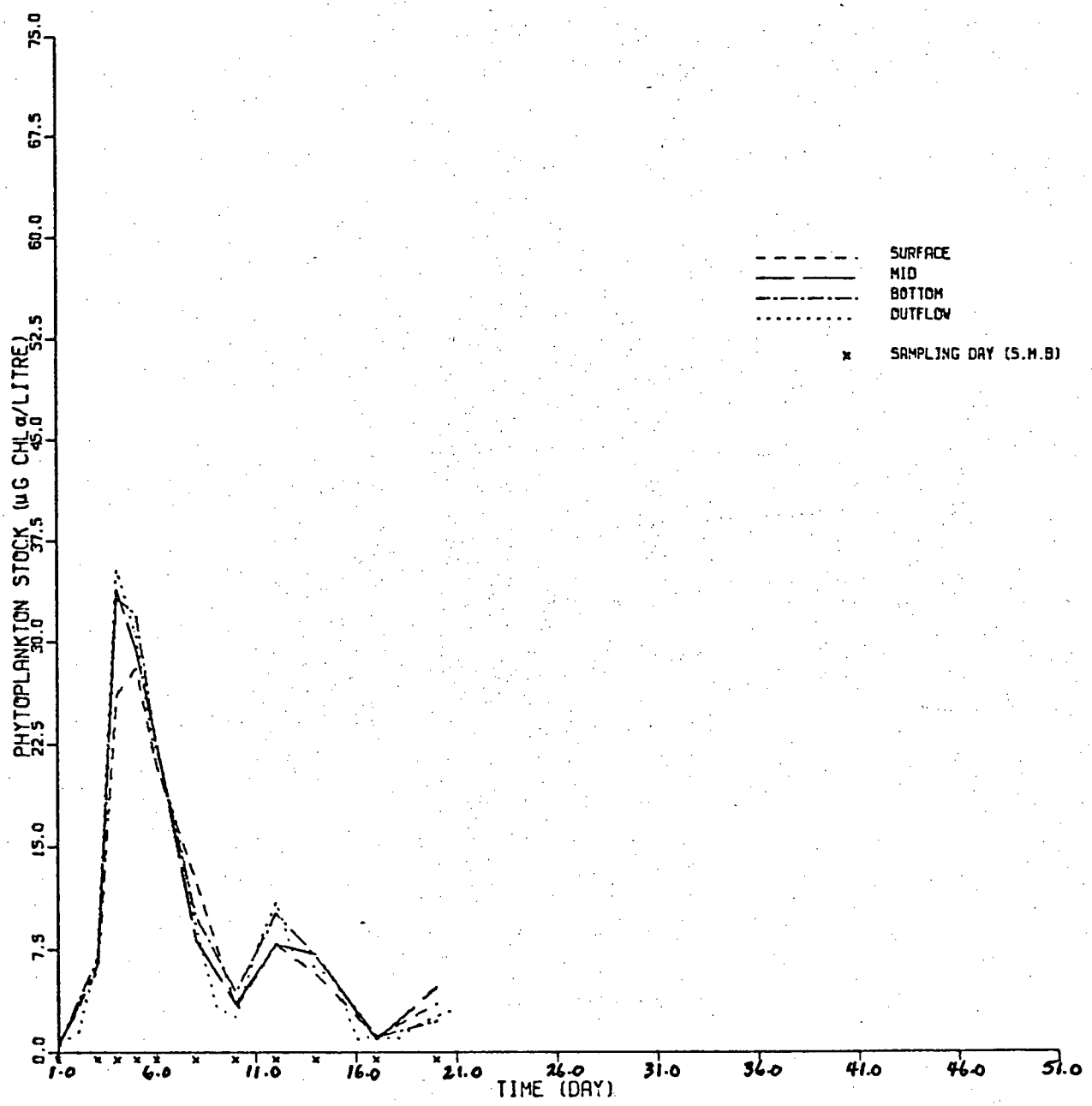


Figure 30. Oxygen concentration during Experiment 3A

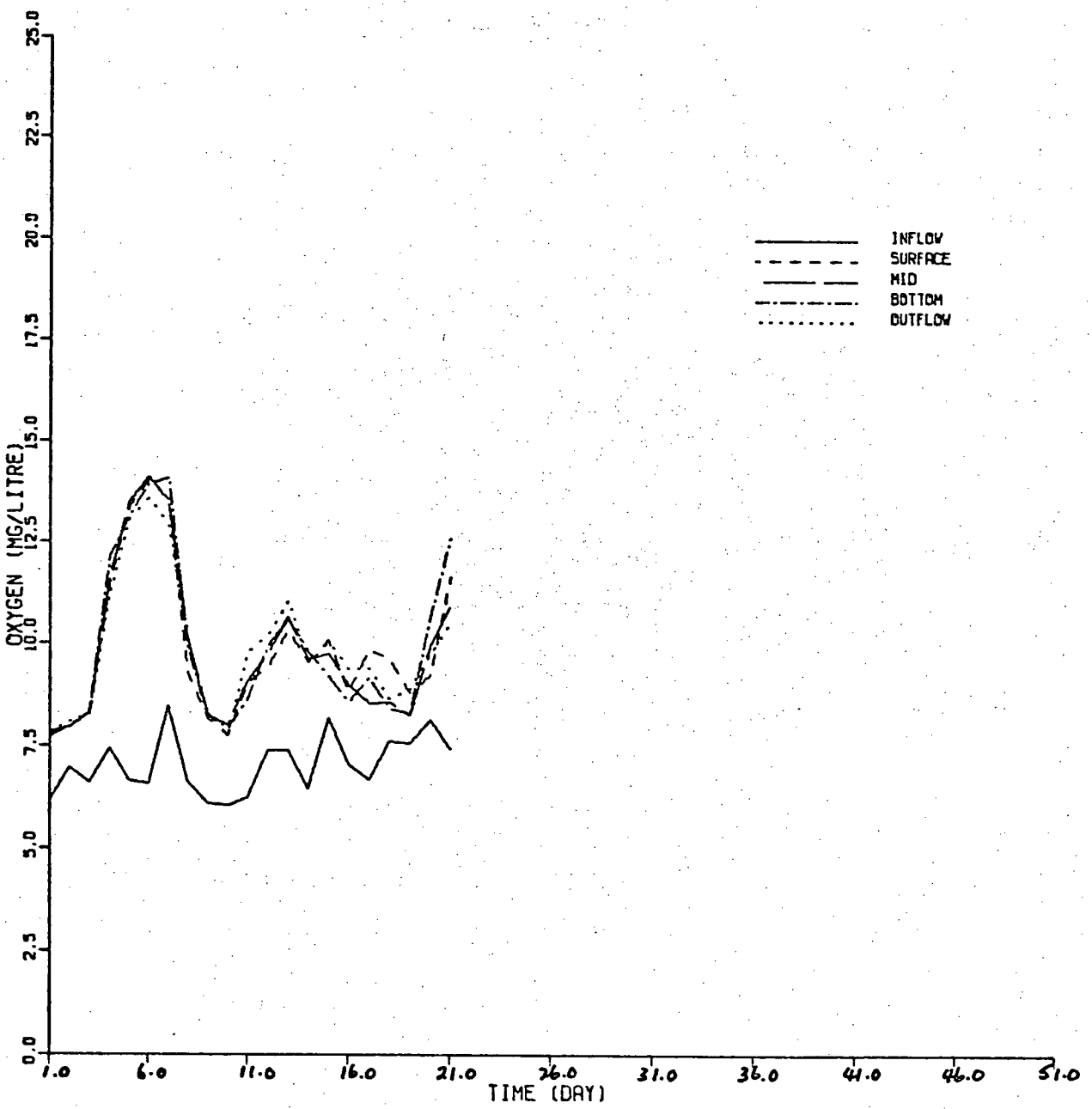


Figure 31. Primary productivity during Experiment 3A

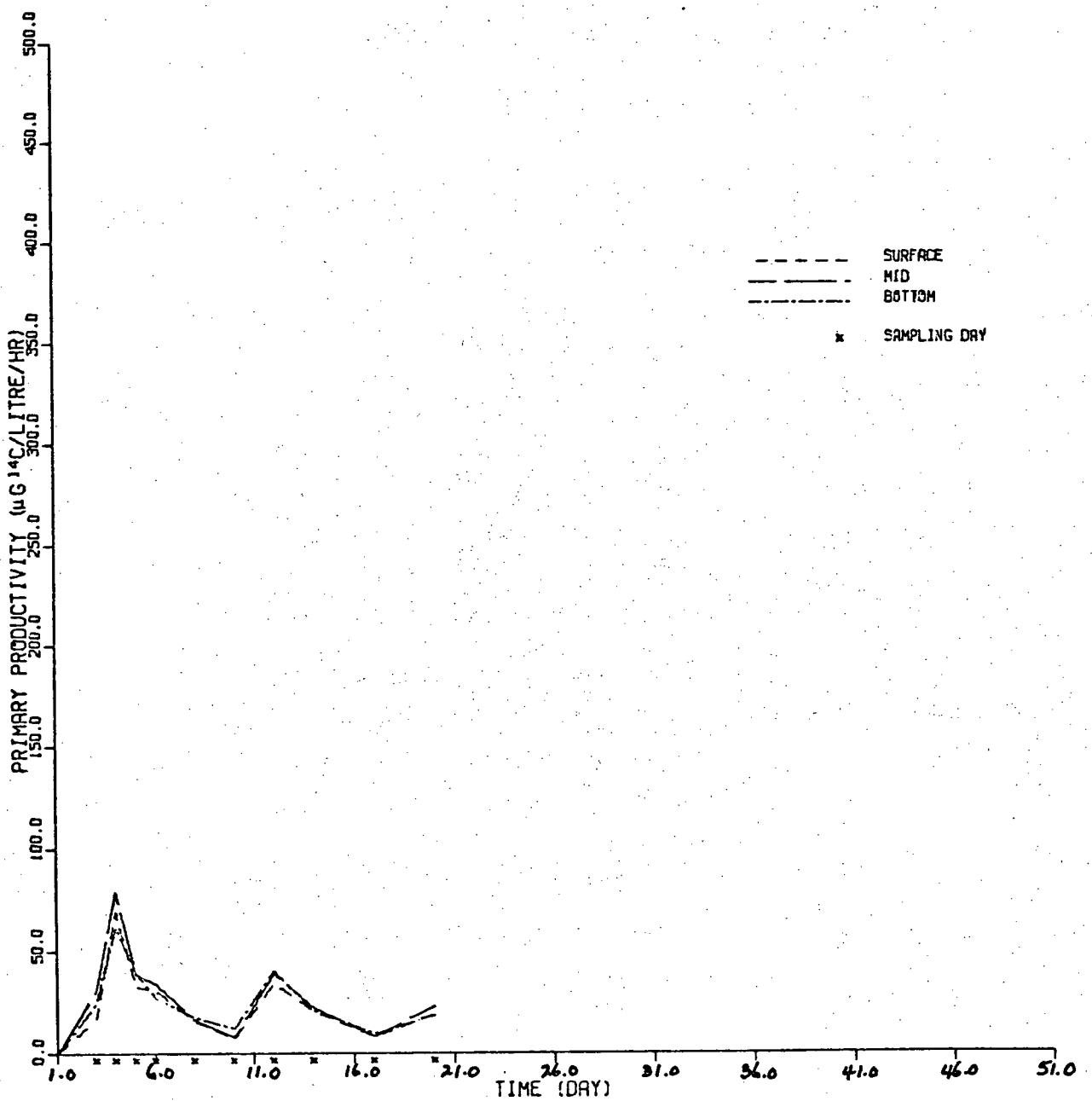


Figure 32. Primary productivity (standardized) during Experiment 3A

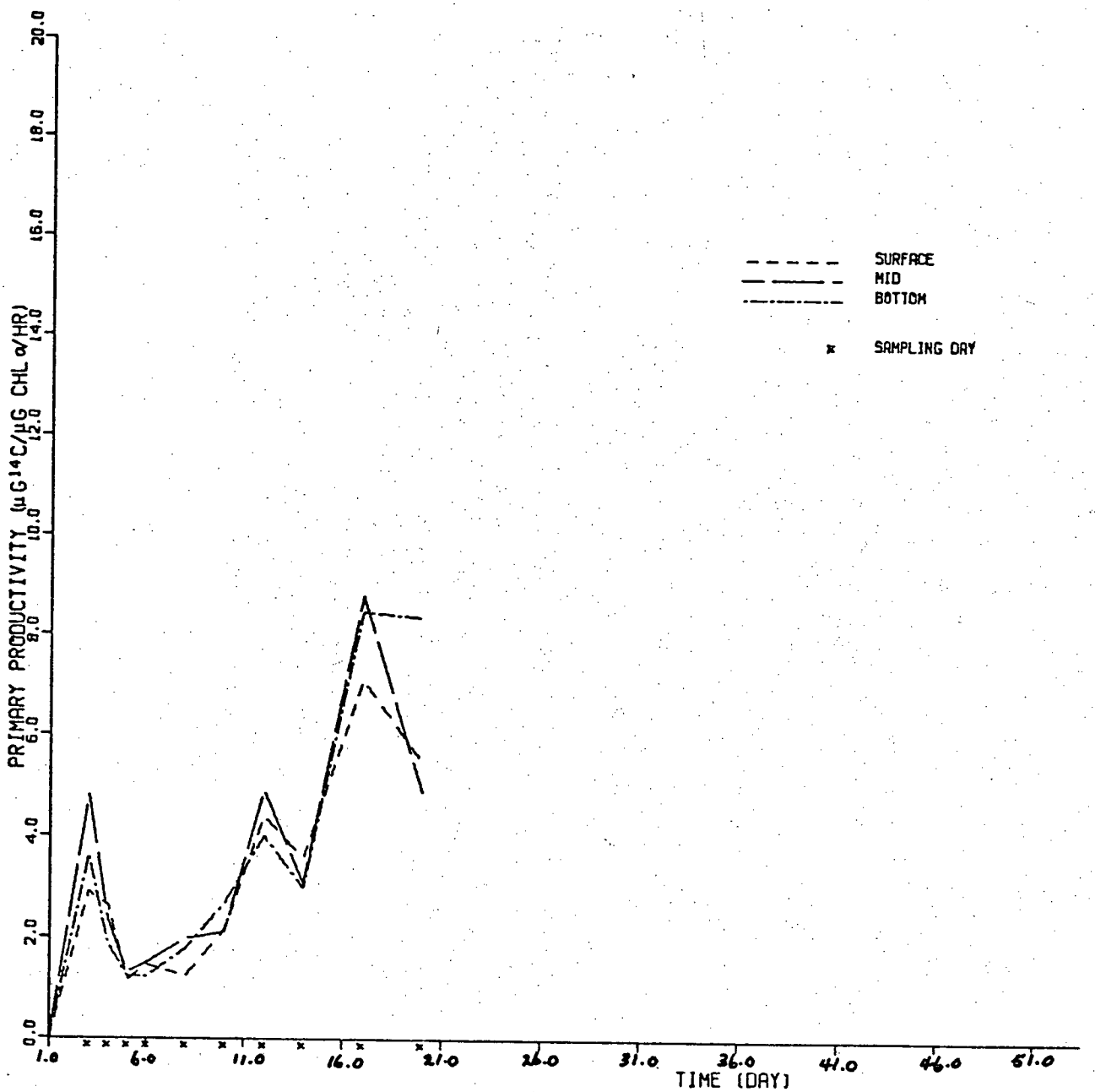


Figure 33. Solar radiation during Experiment 3B

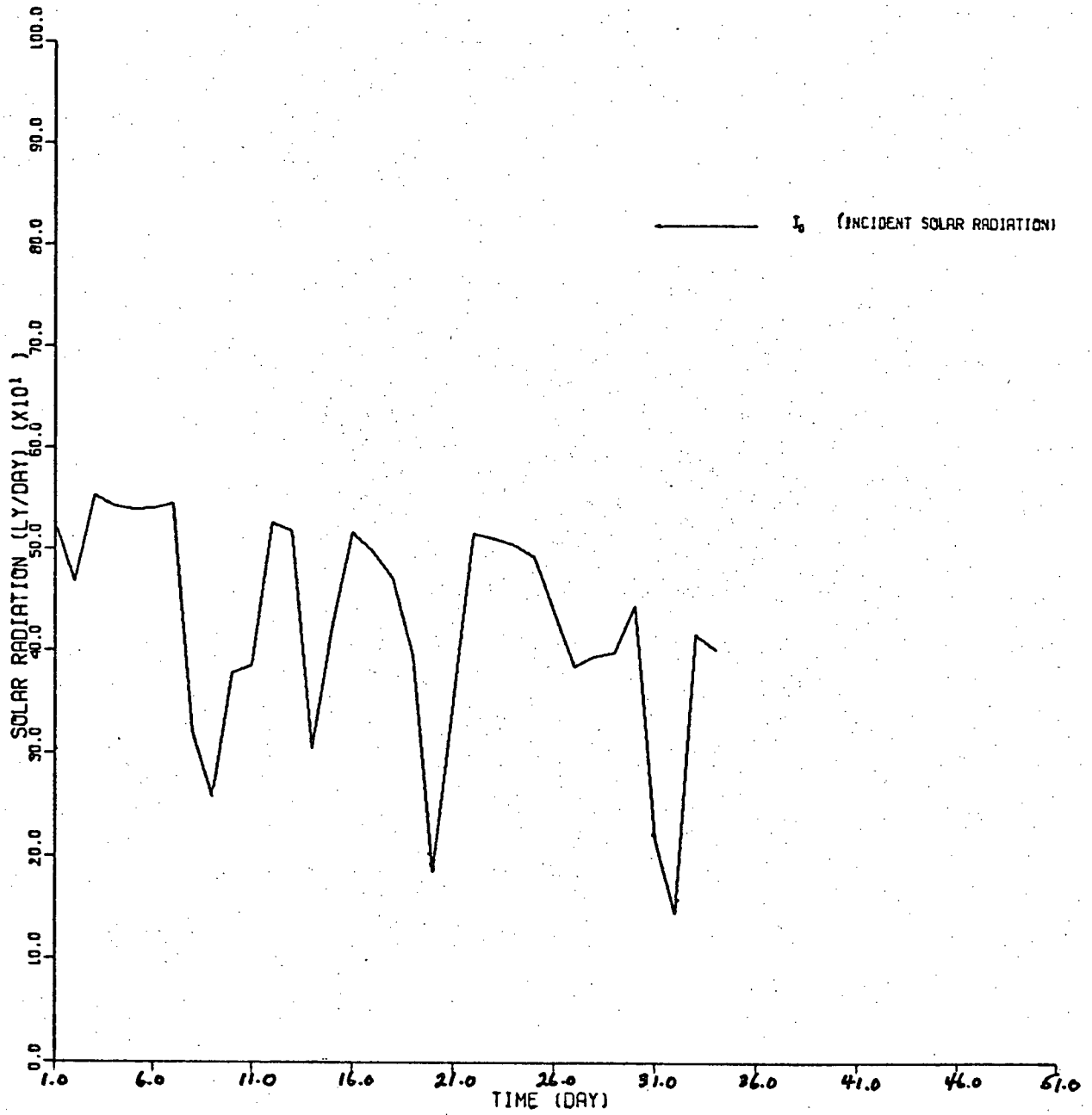


Figure 34. Temperature during Experiment 3B

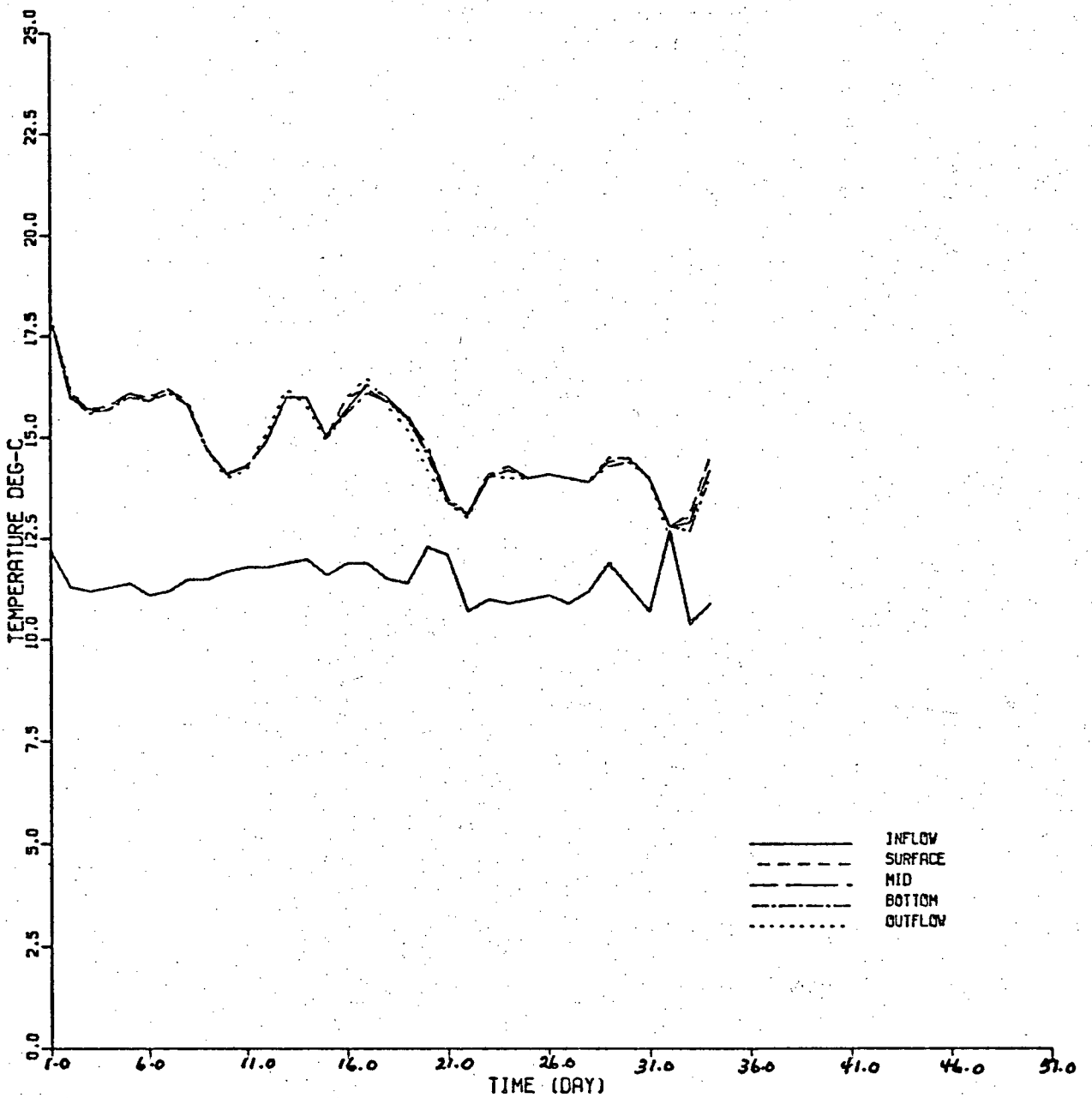


Figure 35. Nitrate concentration during Experiment 3B

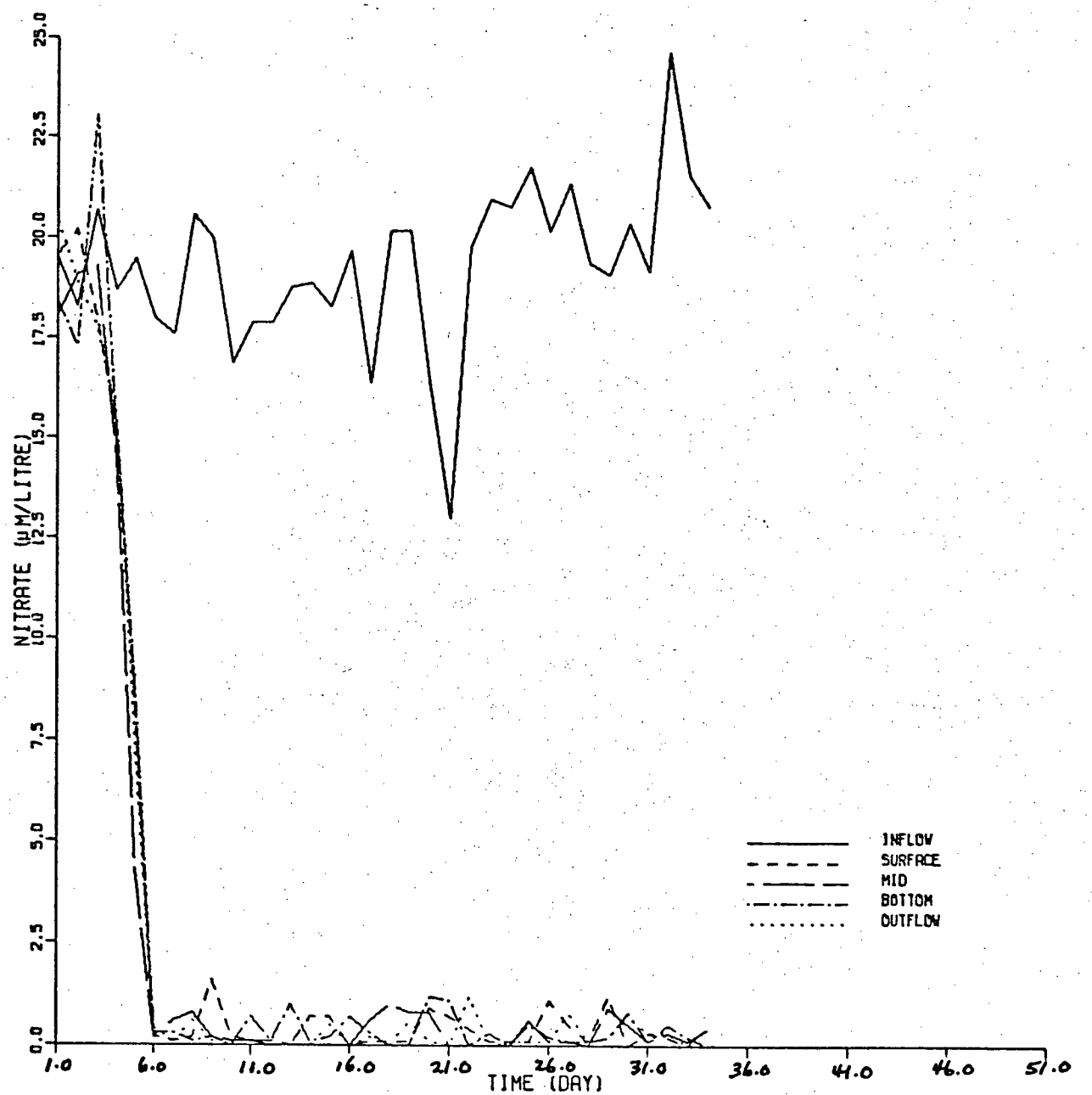


Figure 36. Phytoplankton stock during Experiment 3B

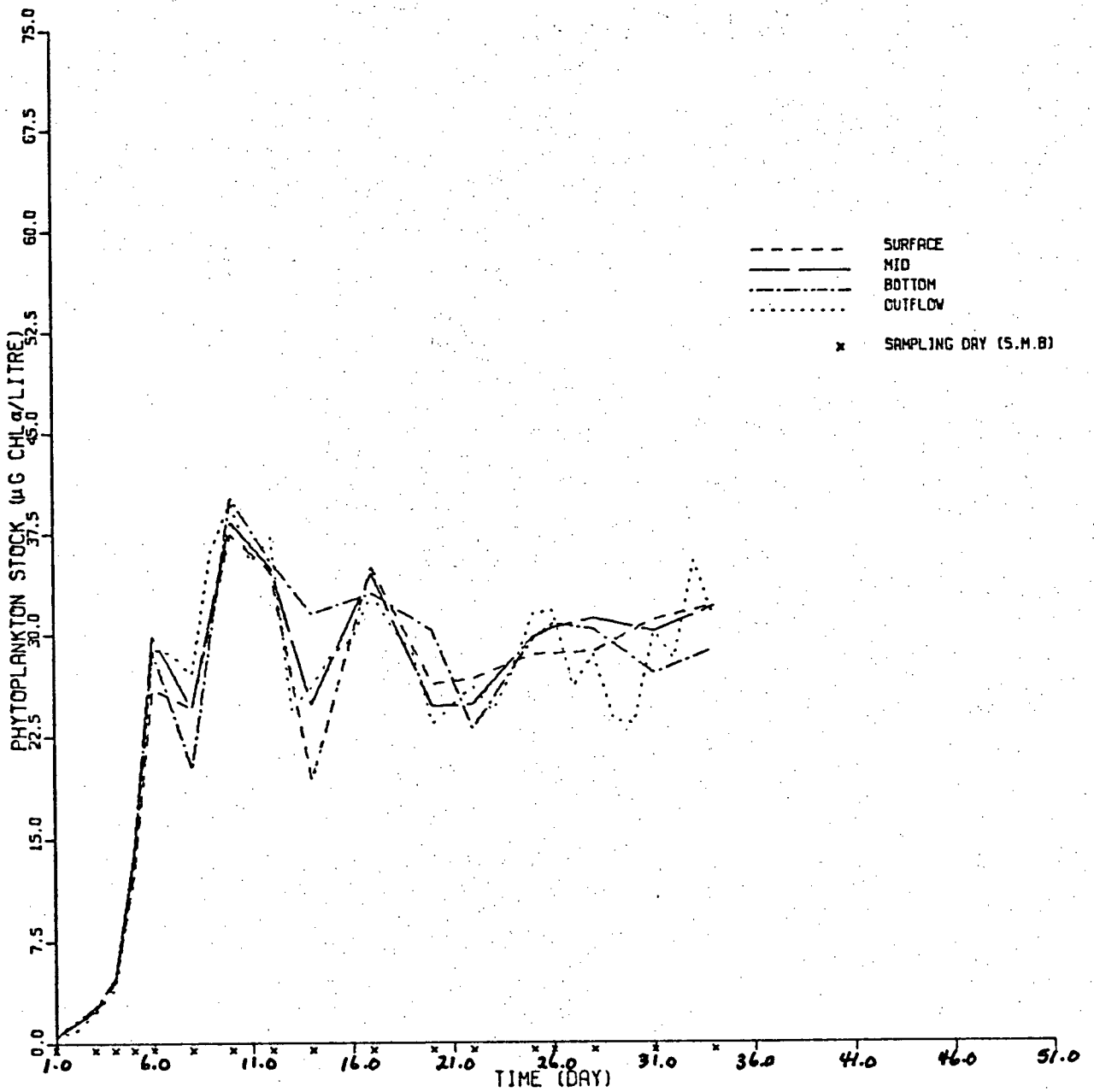


Figure 37. Oxygen concentration during Experiment 3B

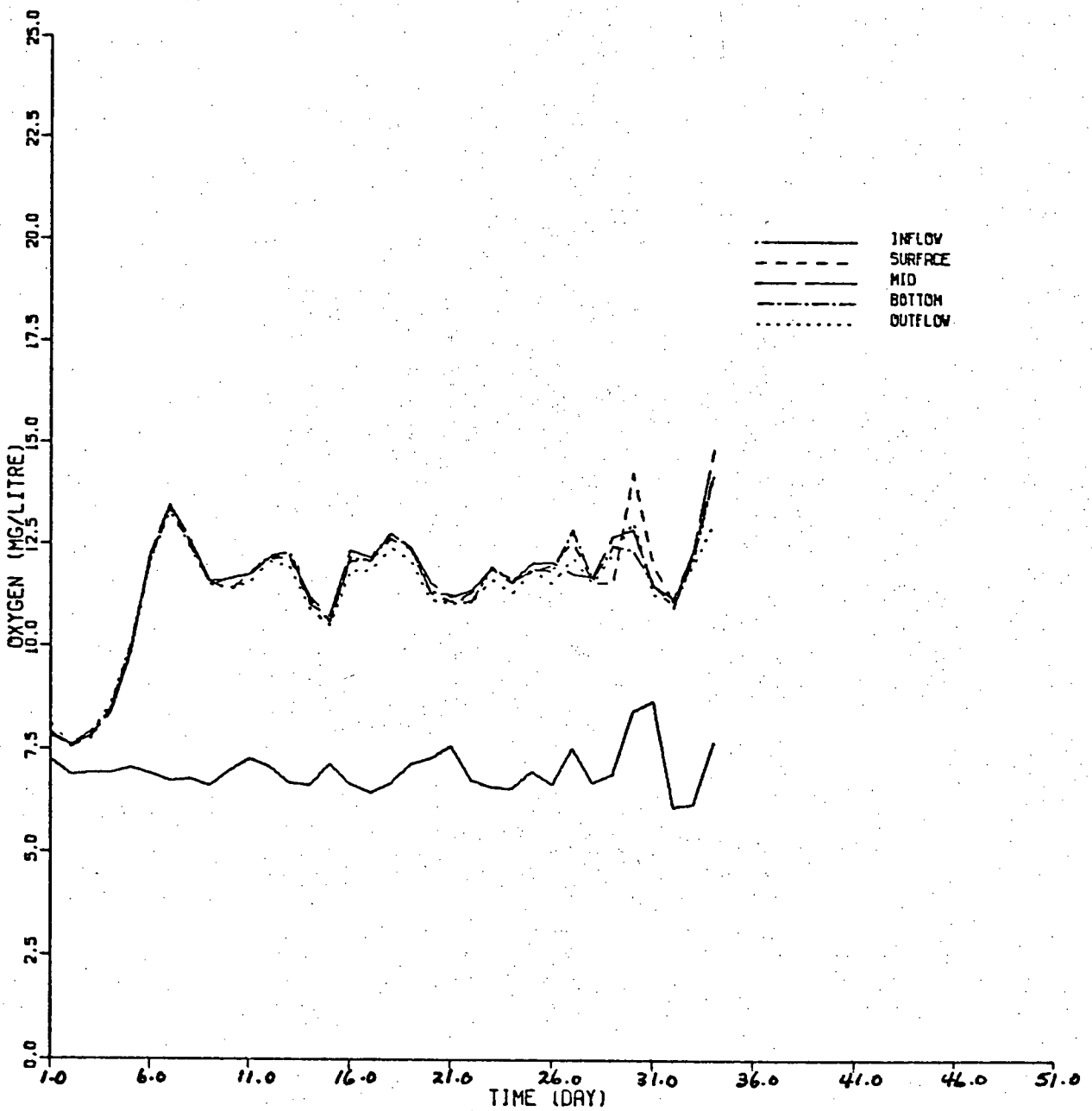


Figure 38. Primary productivity during Experiment 3B

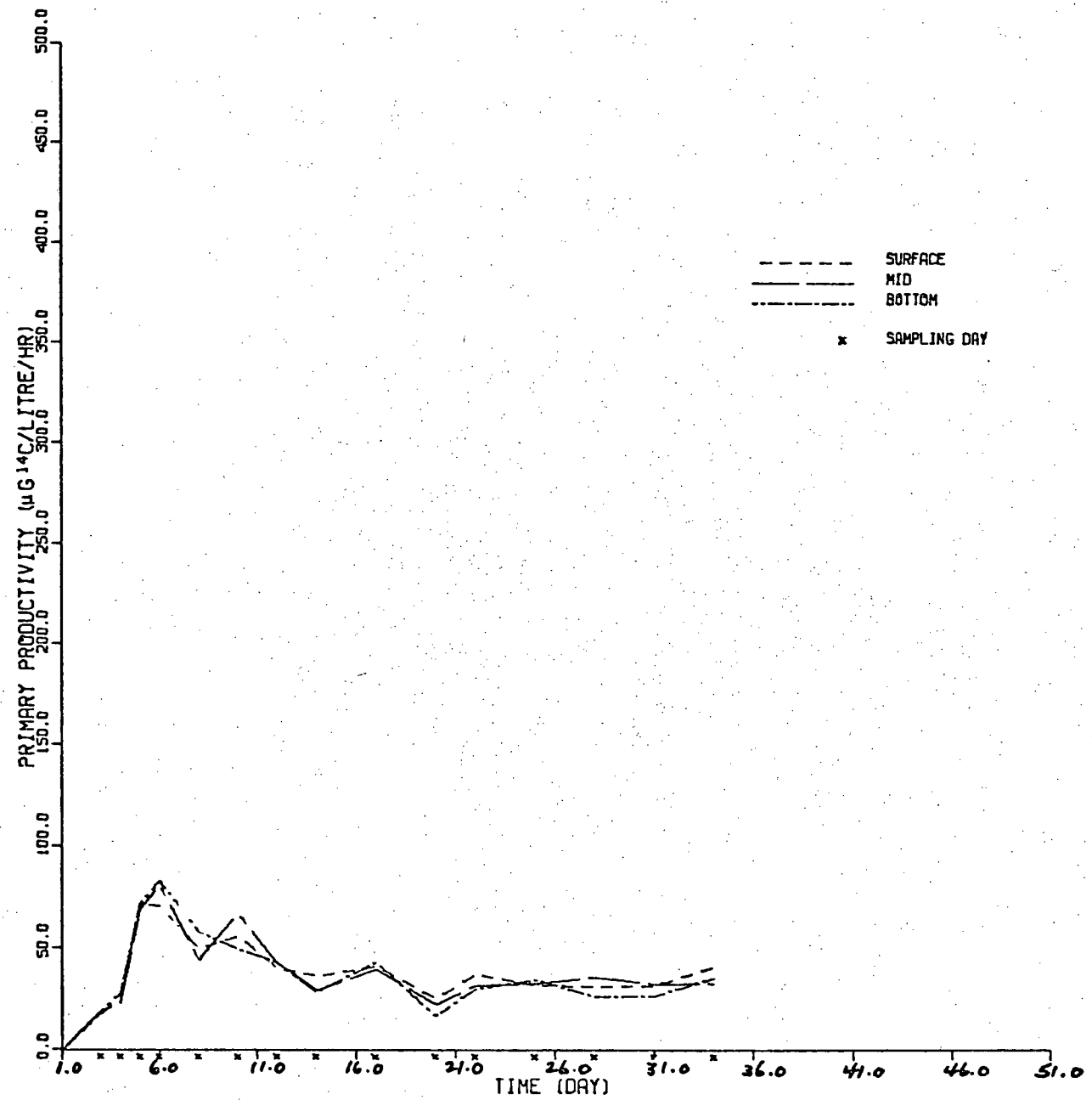


Figure 39. Primary productivity (standardized) during Experiment 3B

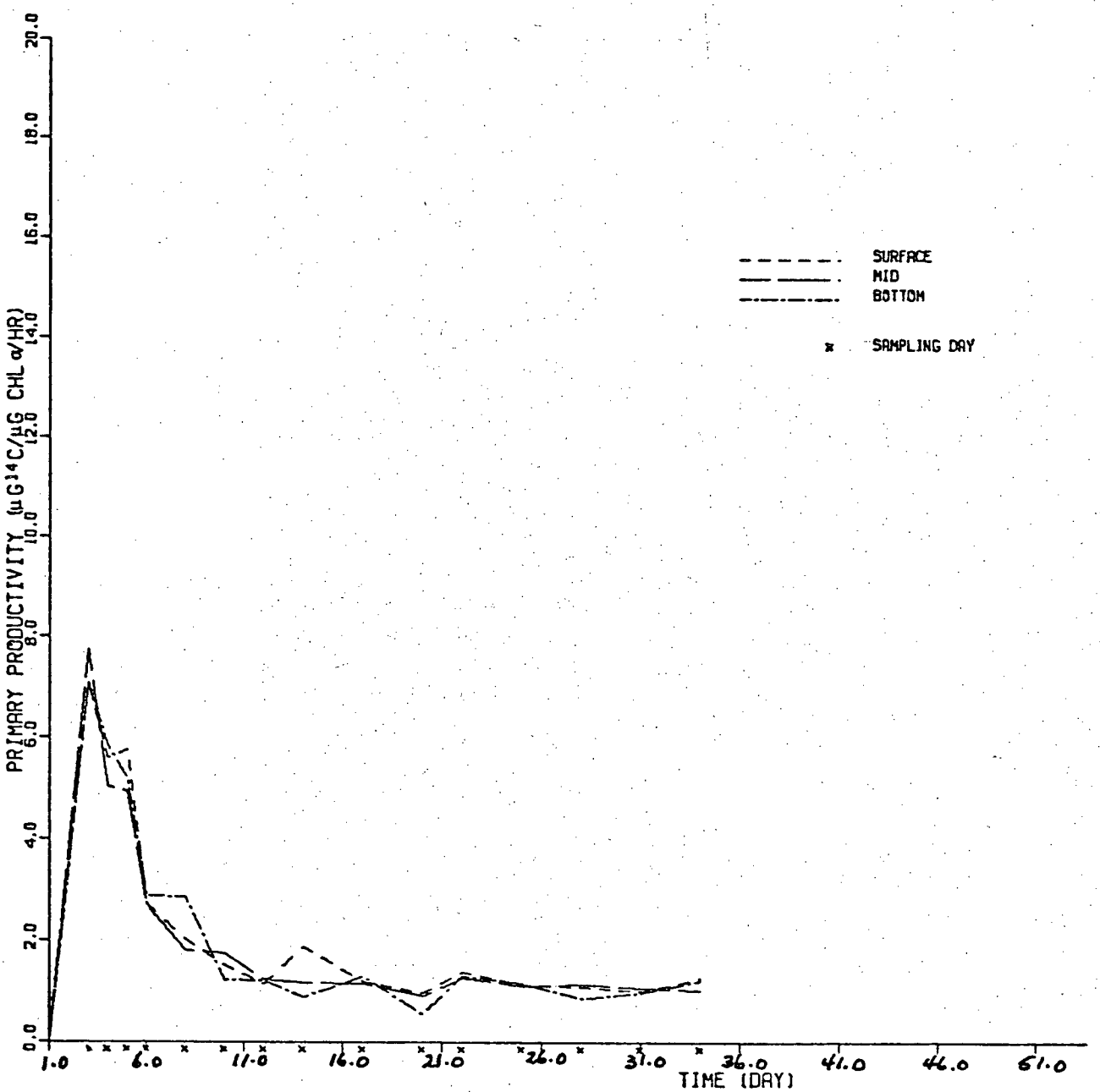


FIGURE 40 FORCING CONDITIONS DURING EXPERIMENT 4

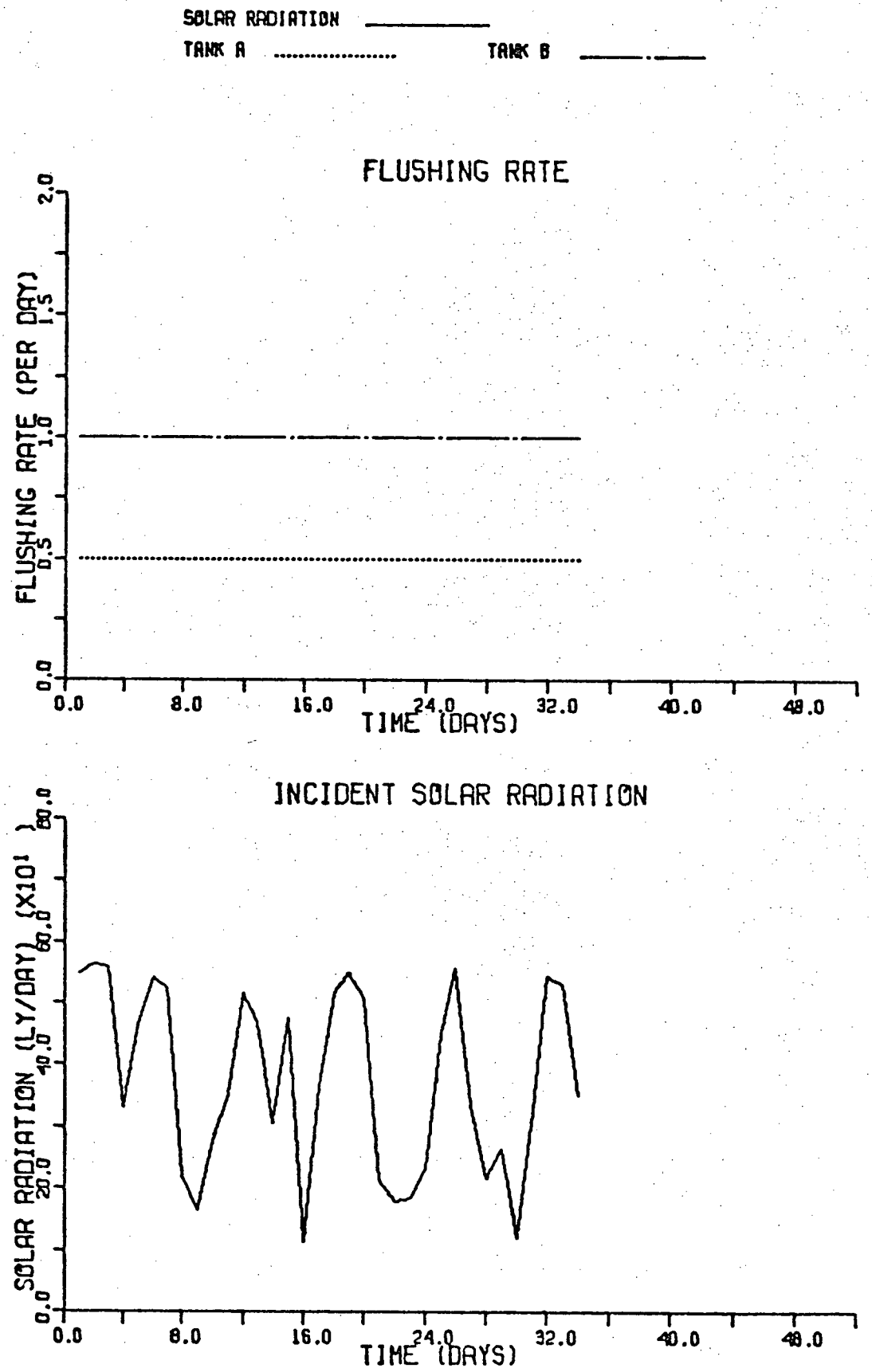


FIGURE 41 TEMPERATURE
DURING EXPERIMENT 4

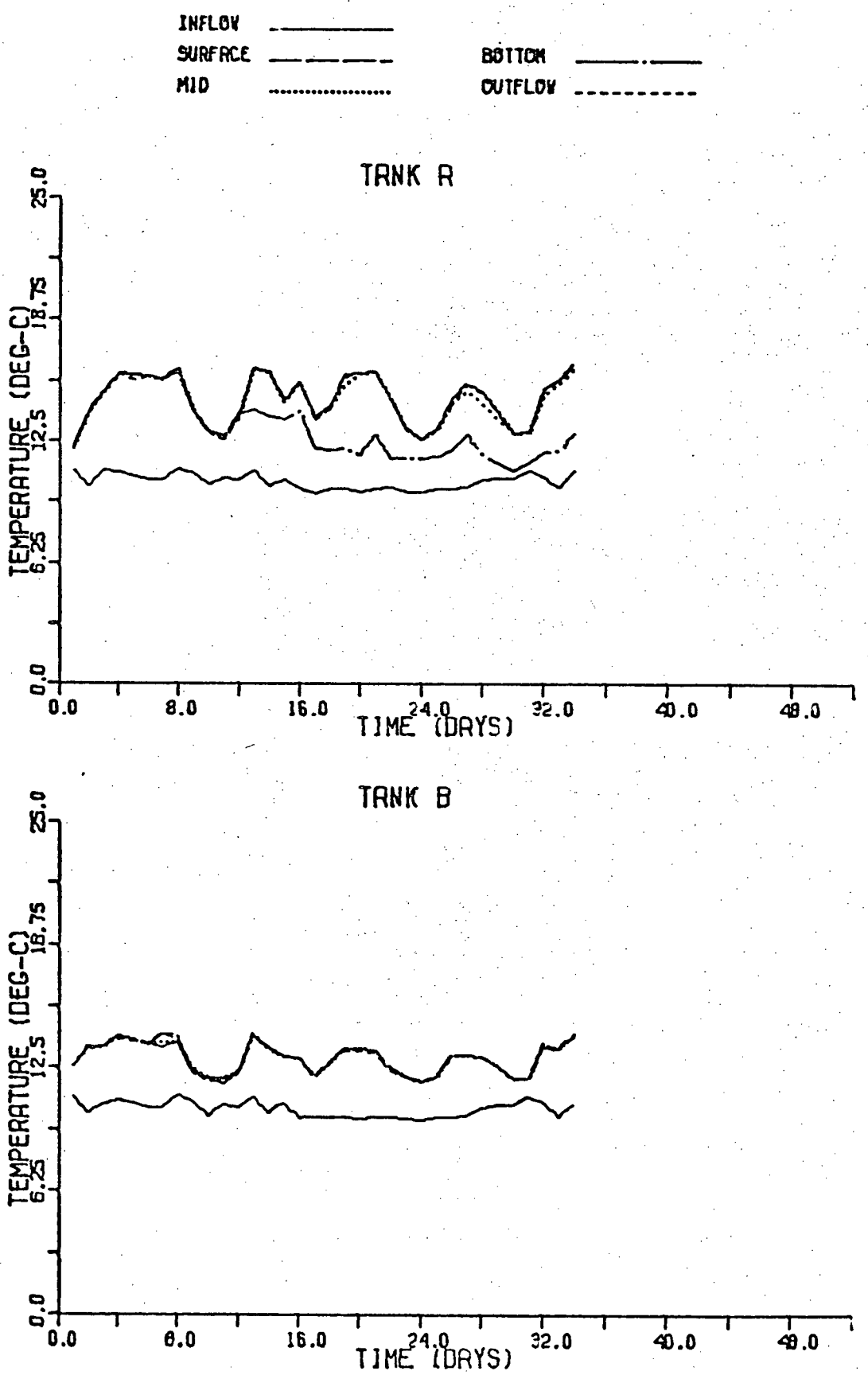


FIGURE 42 NITRATE
DURING EXPERIMENT 4

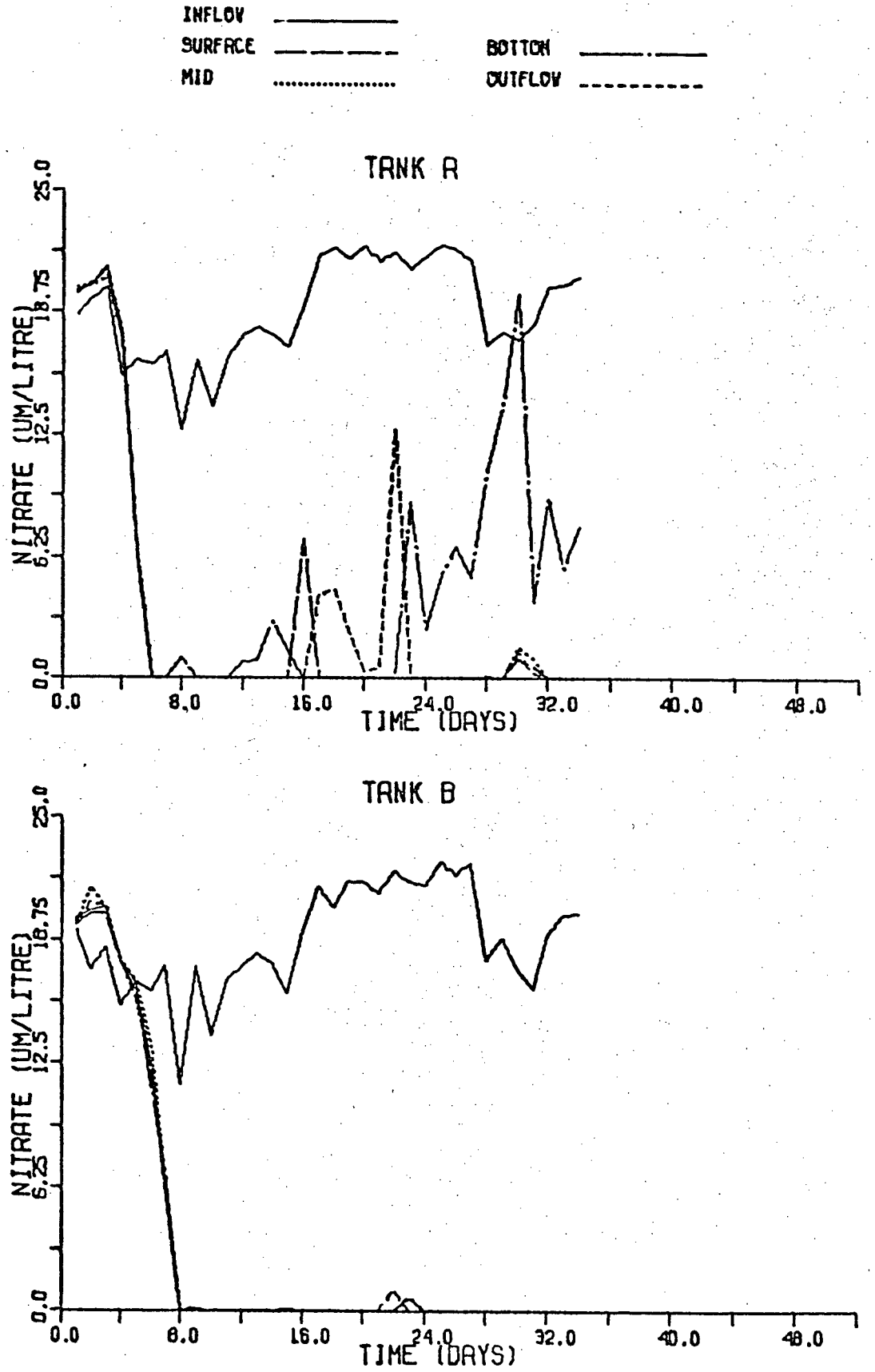


FIGURE 43 PHYTOPLANKTON
DURING EXPERIMENT 4

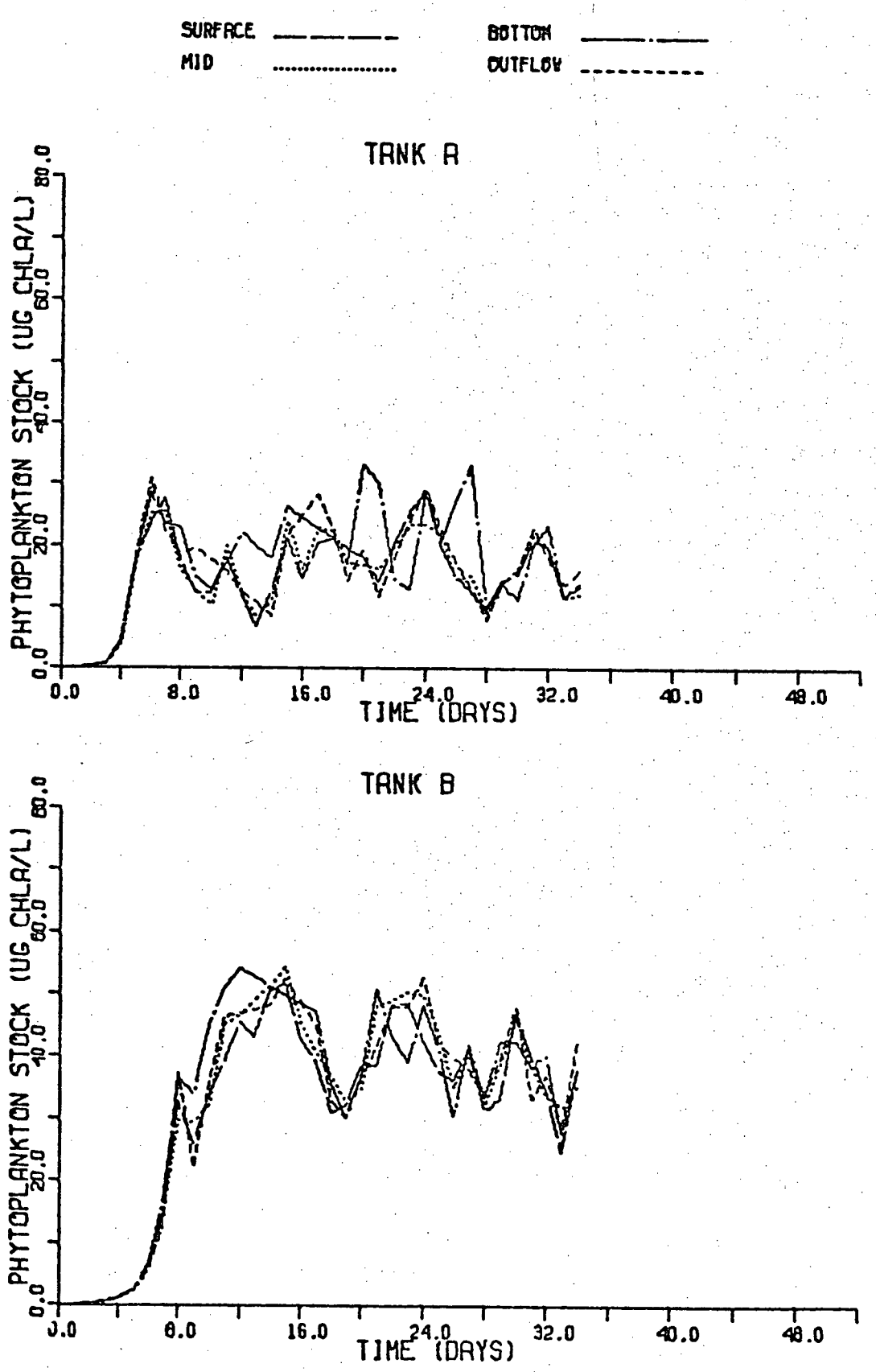


FIGURE 44 CHLB:CHLA RATIO
DURING EXPERIMENT 4

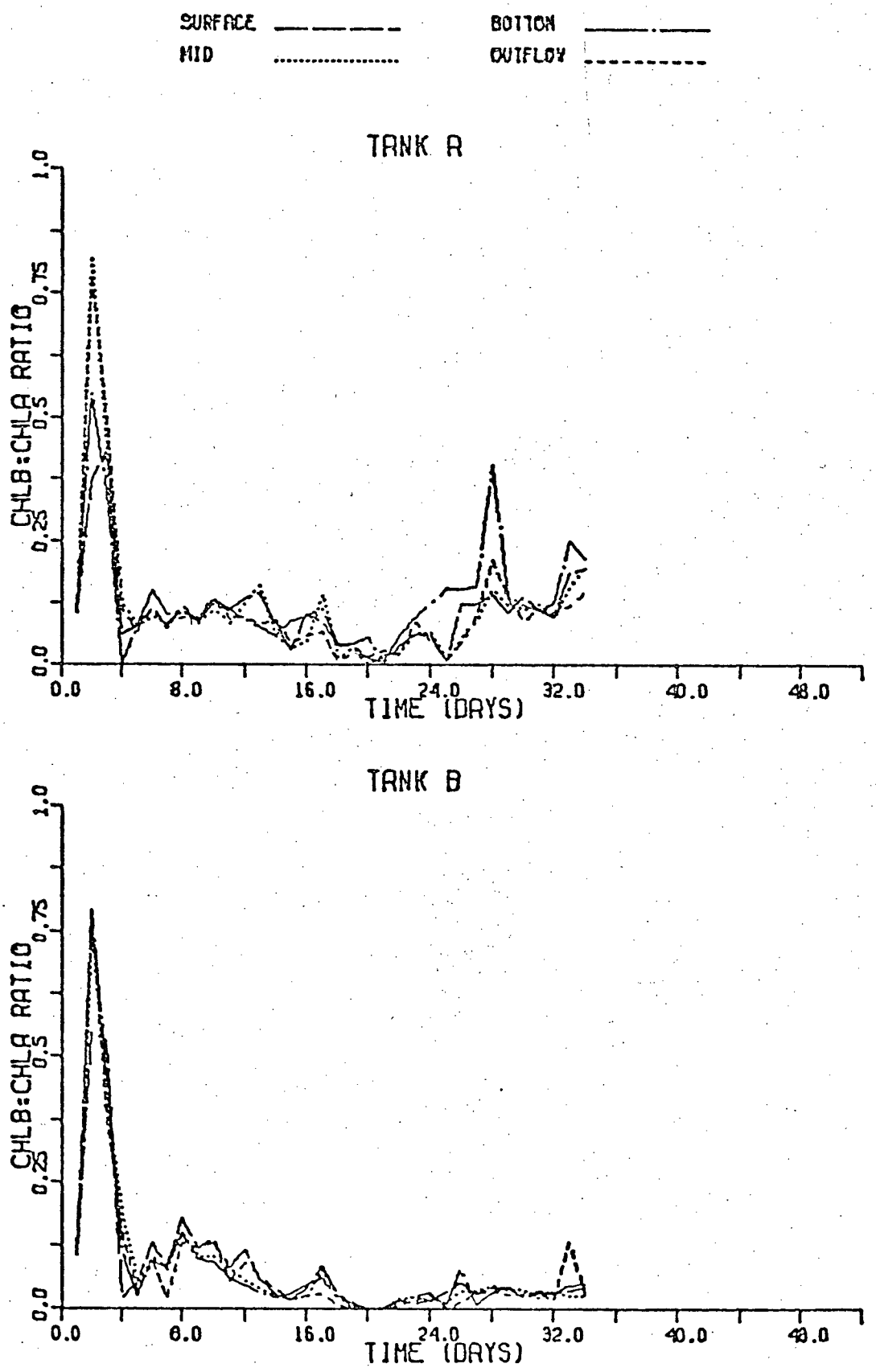


FIGURE 45 CAROTENOID:CHLA
DURING EXPERIMENT 4

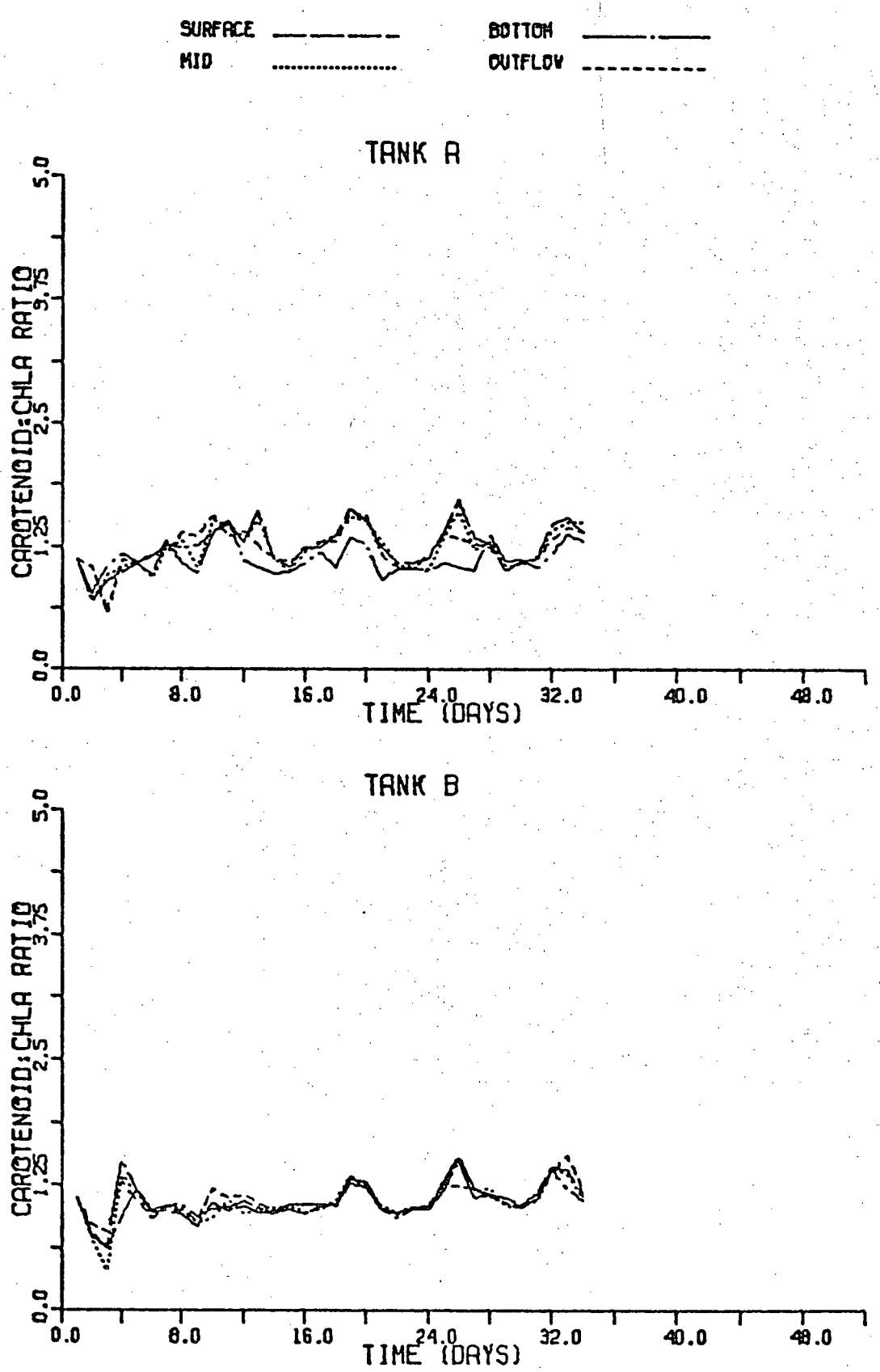


FIGURE 46 OXYGEN
DURING EXPERIMENT 4

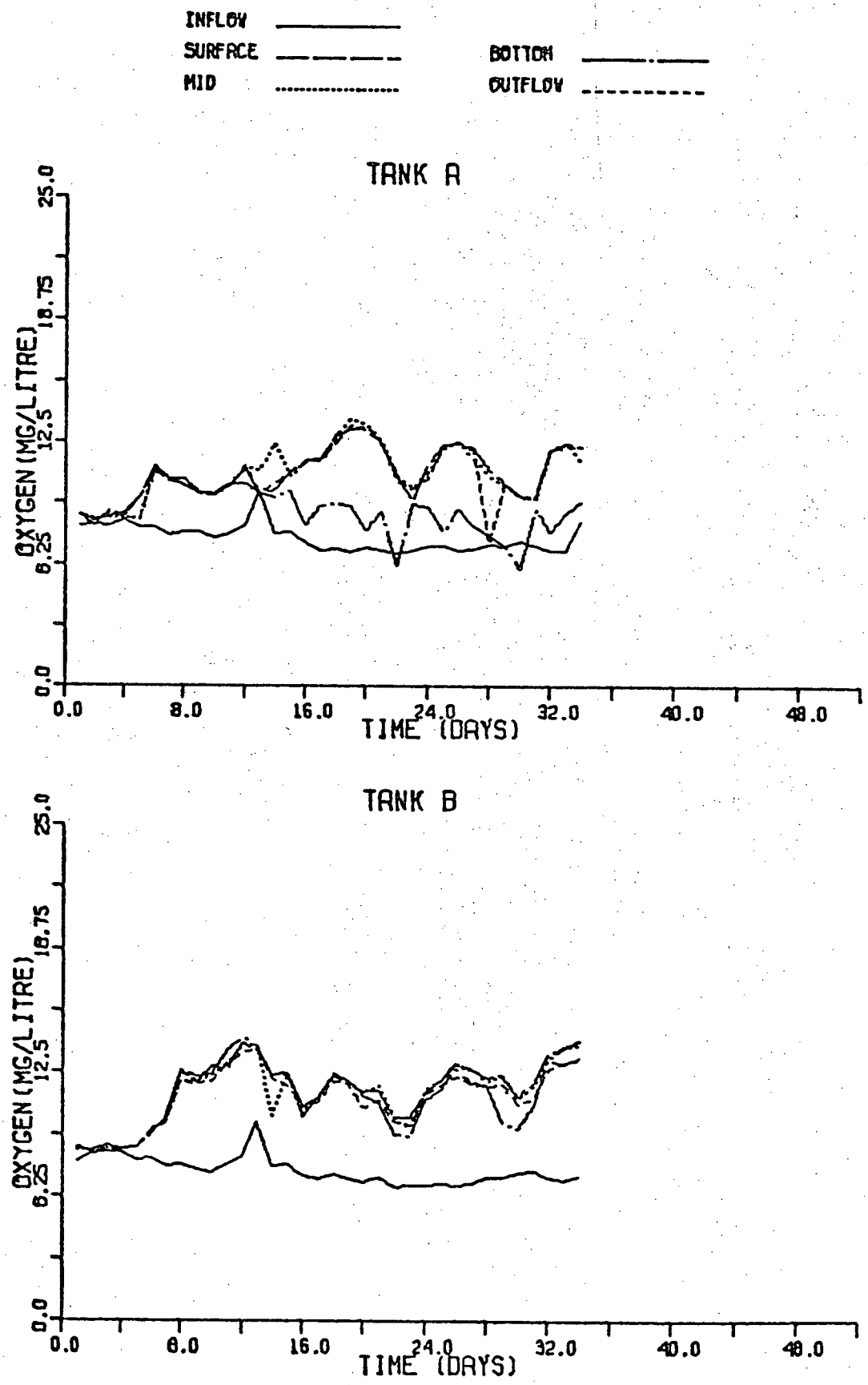


FIGURE 47 GROSS PRIMARY PRODUCTIVITY DURING EXPERIMENT 4

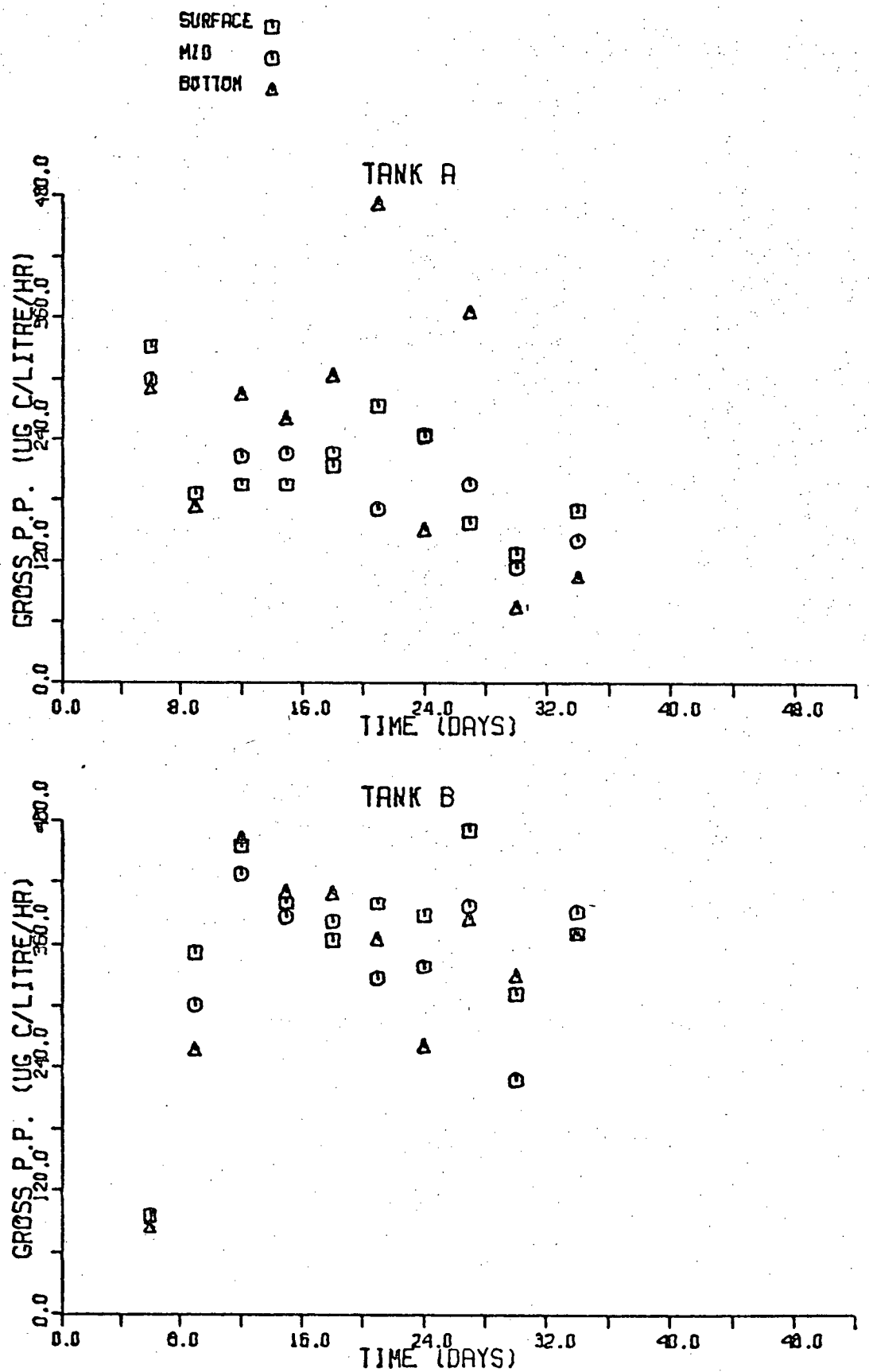


FIGURE 48 RESPIRATION RATE DURING EXPERIMENT 4

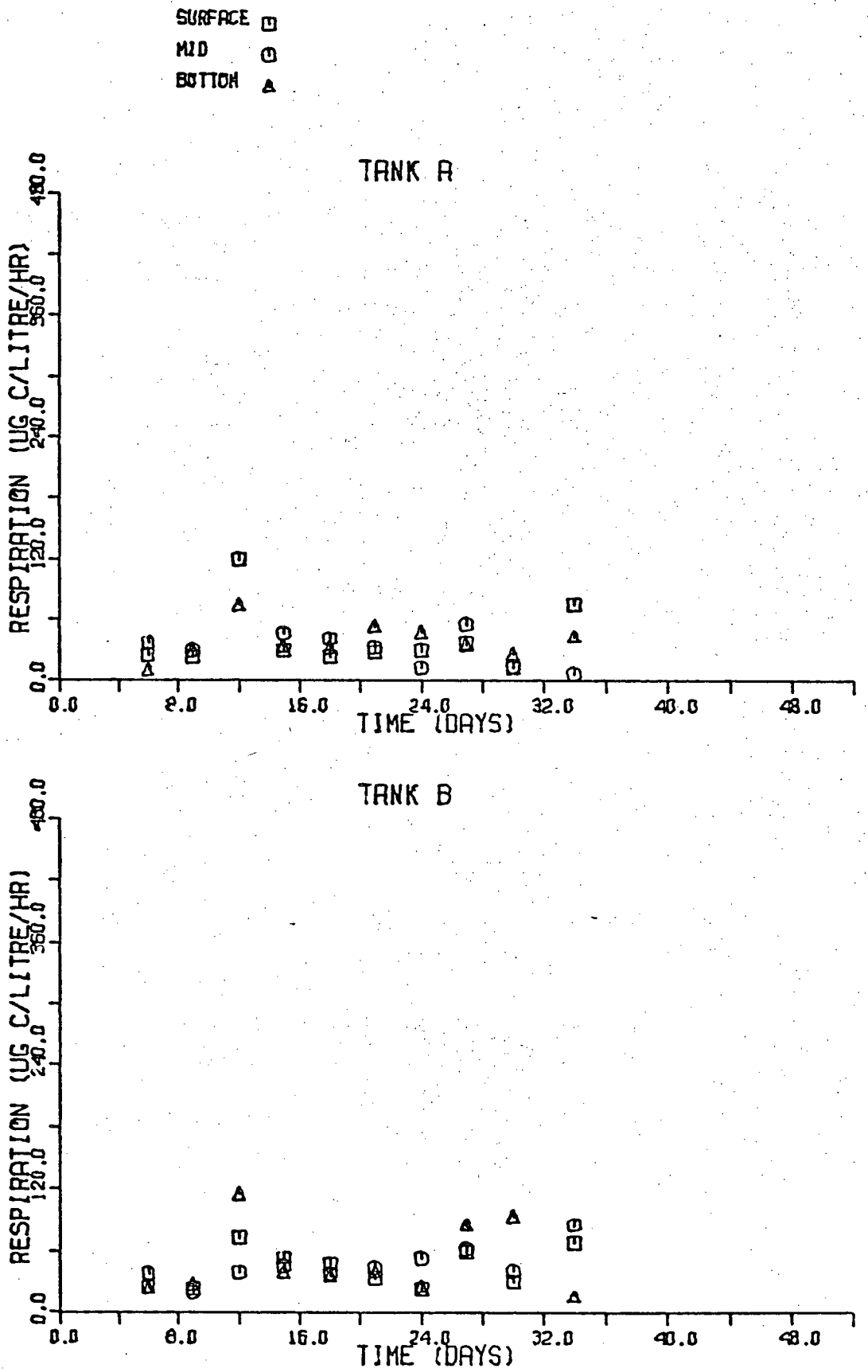


FIGURE 49 NET PRIMARY PRODUCTIVITY DURING EXPERIMENT 4

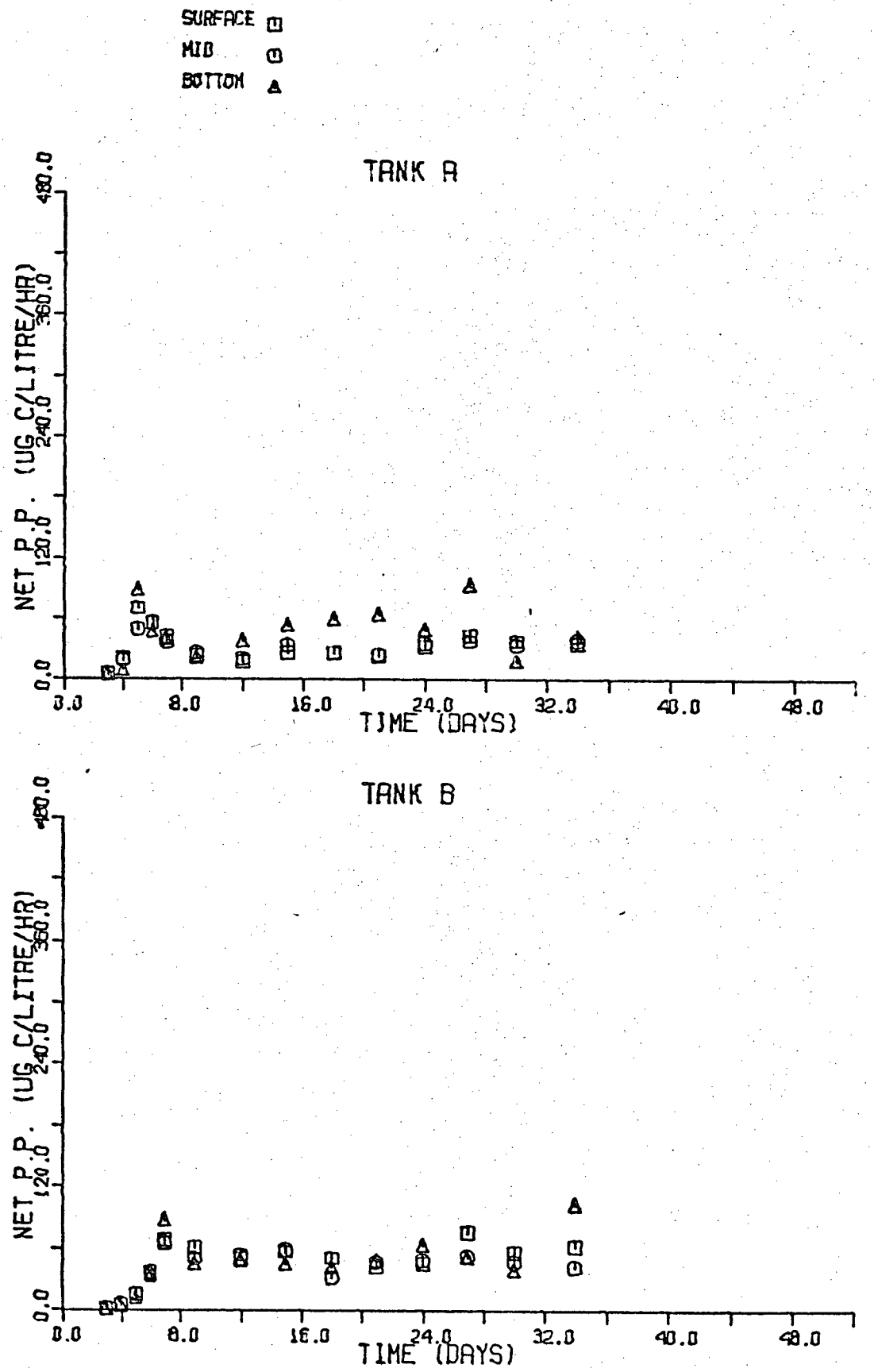


FIGURE 50 NET PRIMARY PRODUCTIVITY (DAILY) DURING EXPERIMENT 4

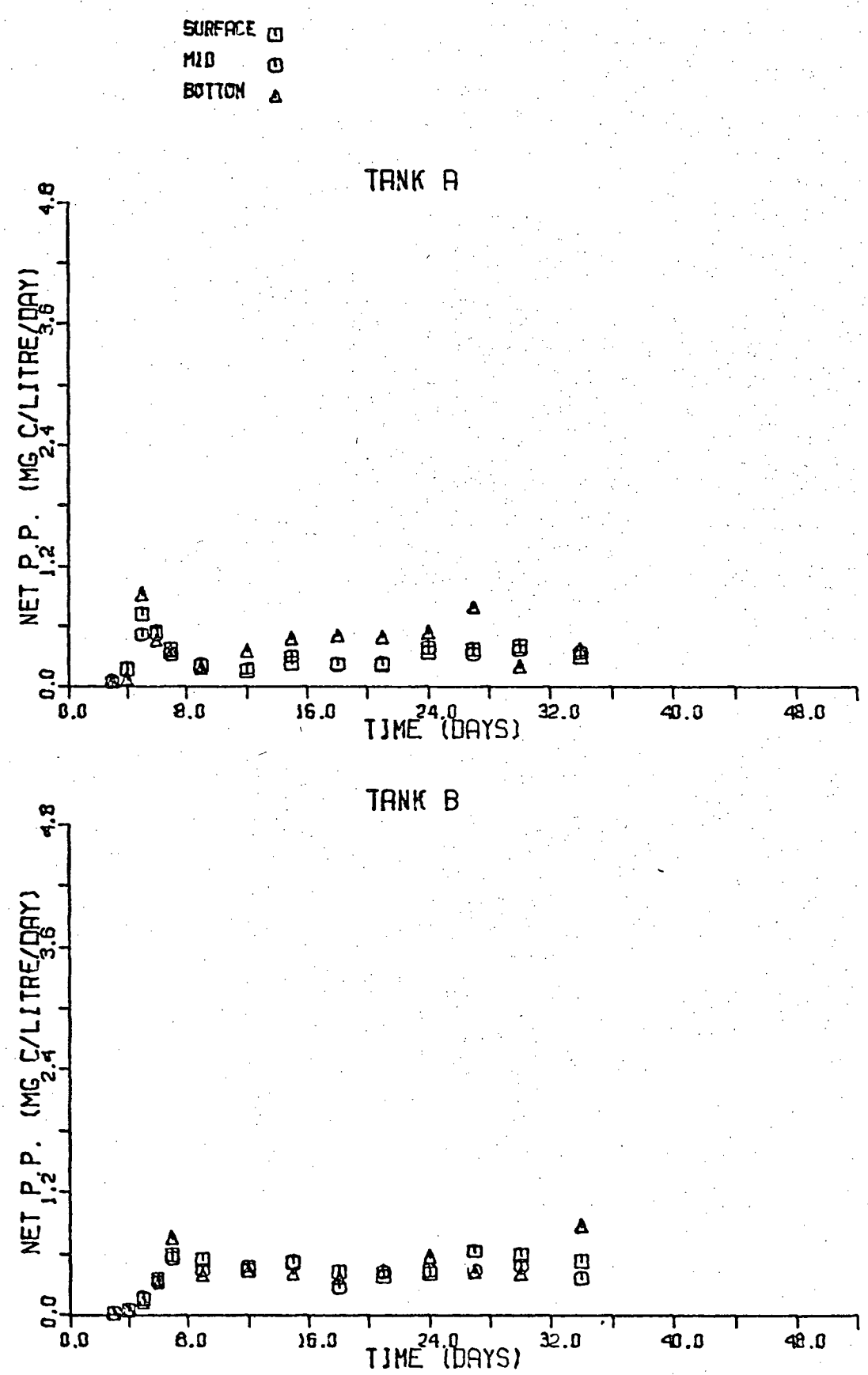


FIGURE 51 GROSS PRIMARY PRODUCTIVITY (DAILY) DURING EXPERIMENT 4

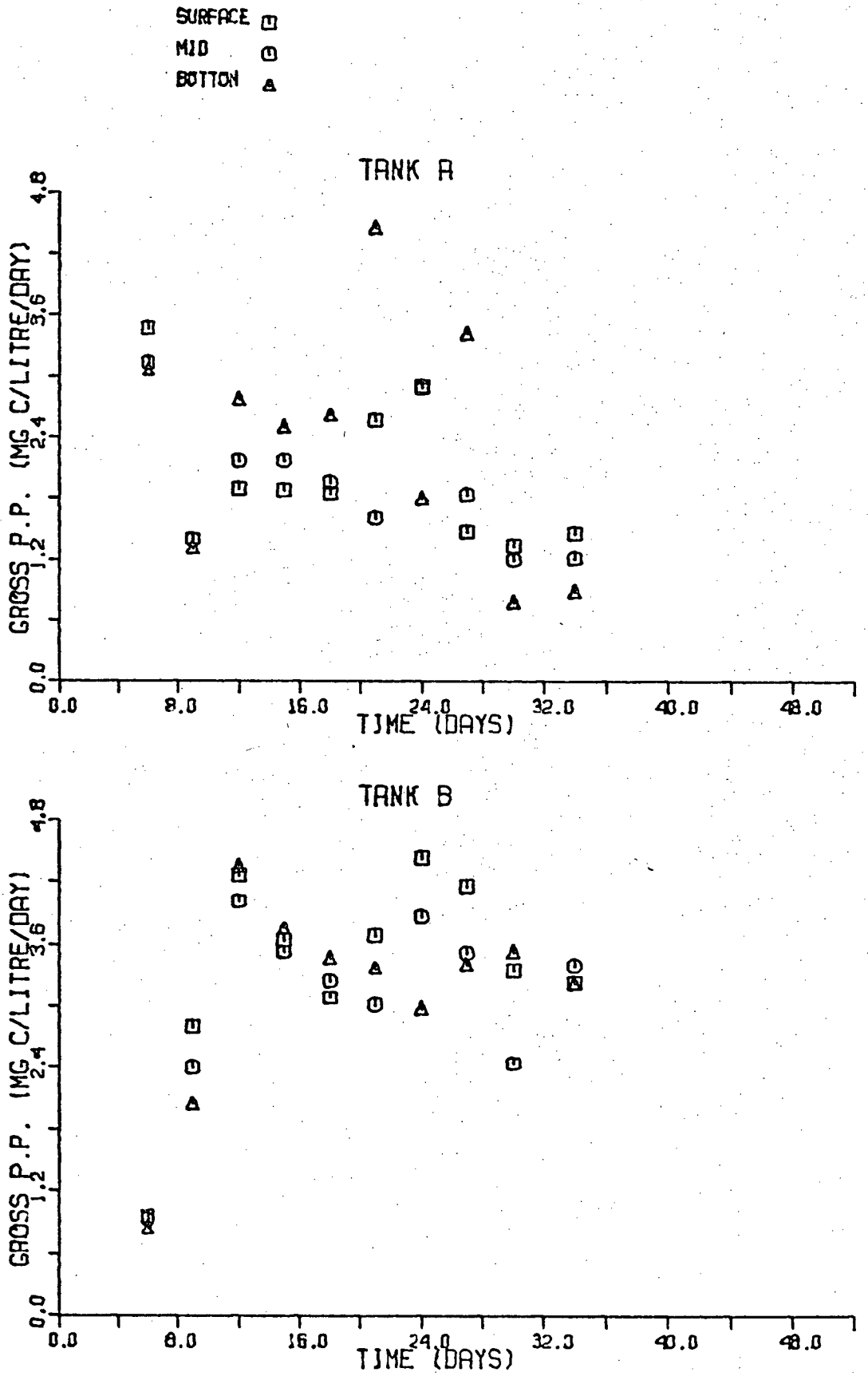


FIGURE 52 GROSS PRIMARY PRODUCTIVITY (STANDARDIZED) DURING EXPERIMENT 4

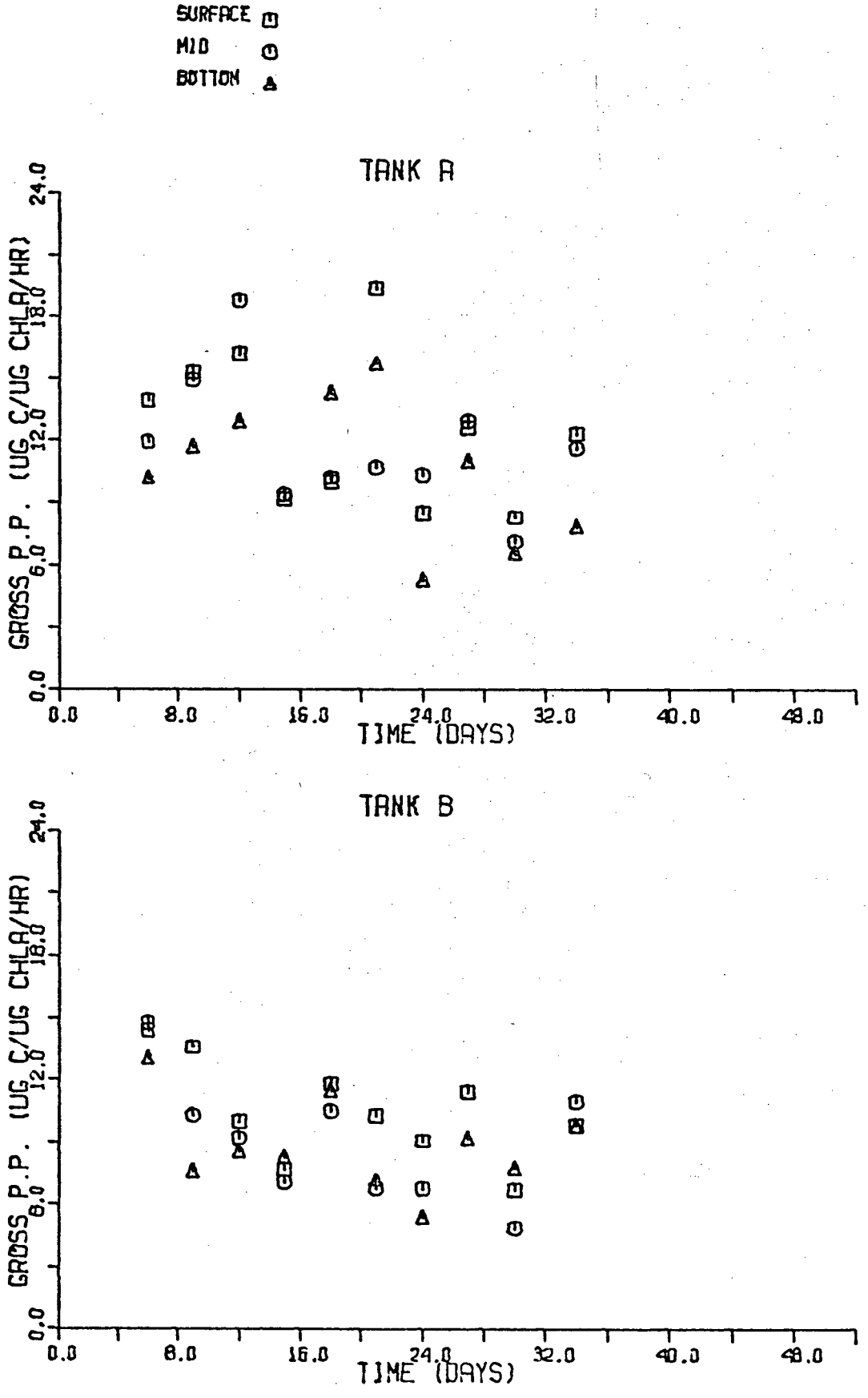


FIGURE 53 NET PRIMARY PRODUCTIVITY (STANDARDIZED) DURING EXPERIMENT 4

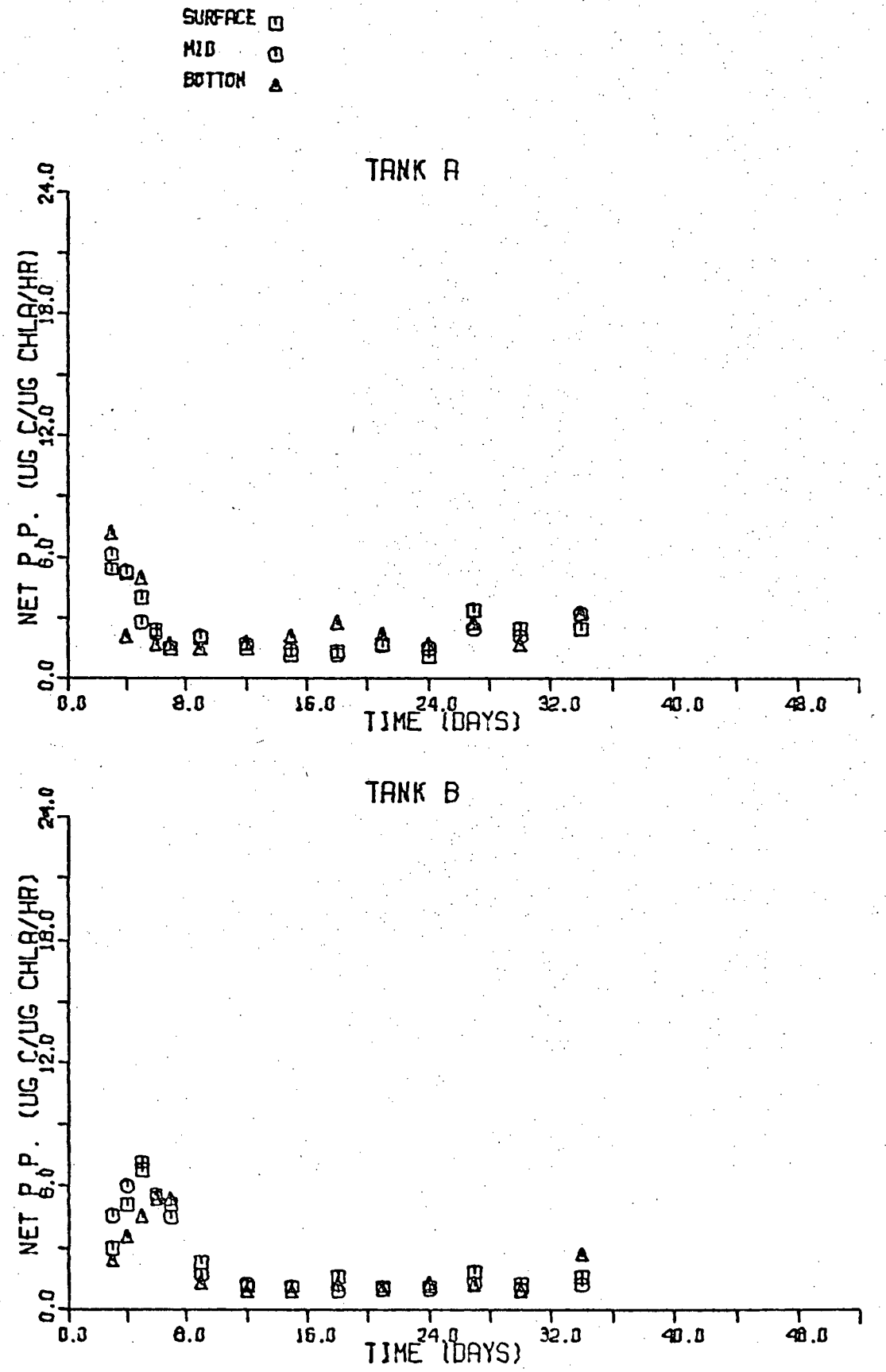


FIGURE 54 RESPIRATION RATE (STANDARDIZED) DURING EXPERIMENT 4

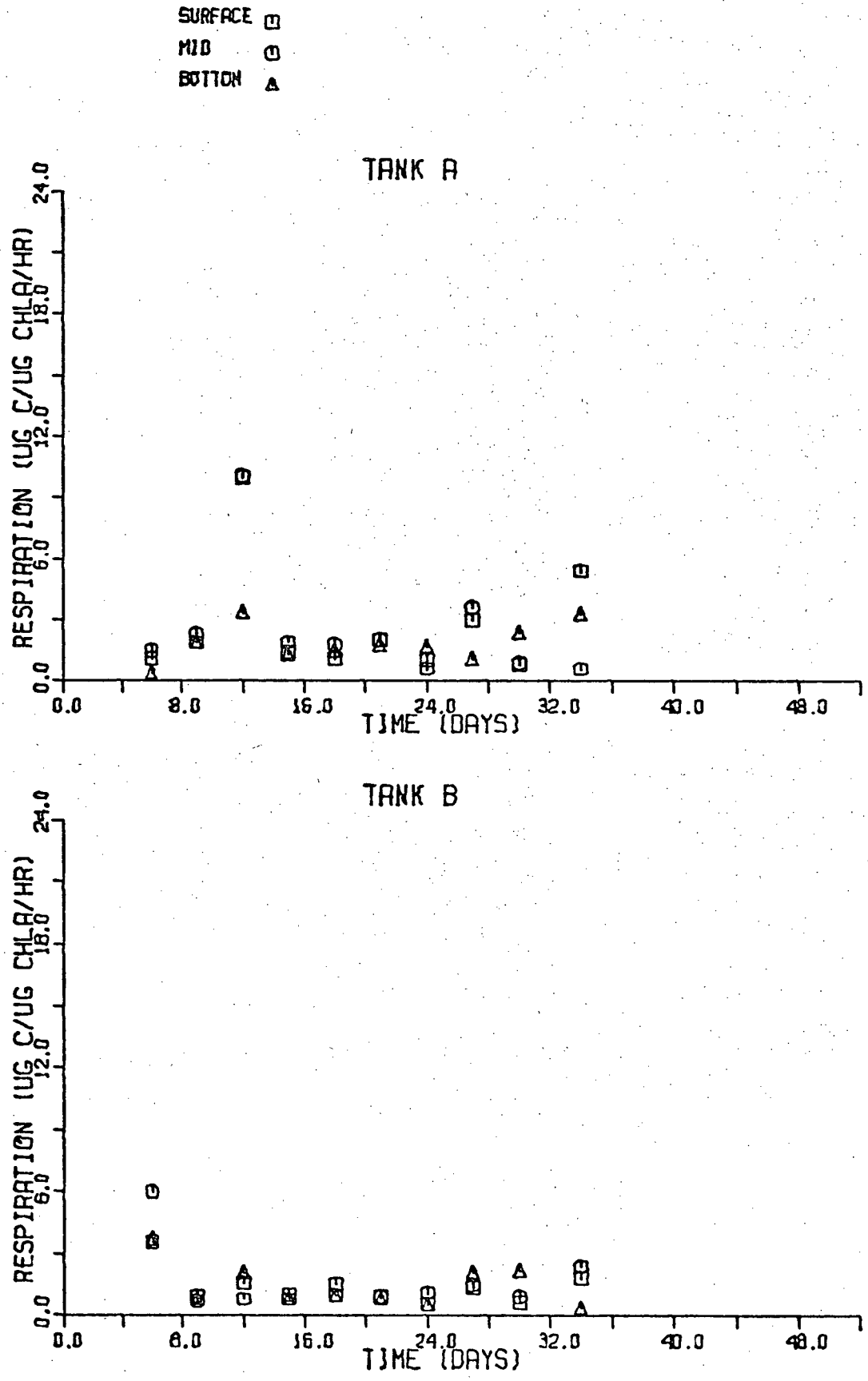


FIGURE 55 ESTIMATES OF ALPHAC
DURING EXPERIMENT 4

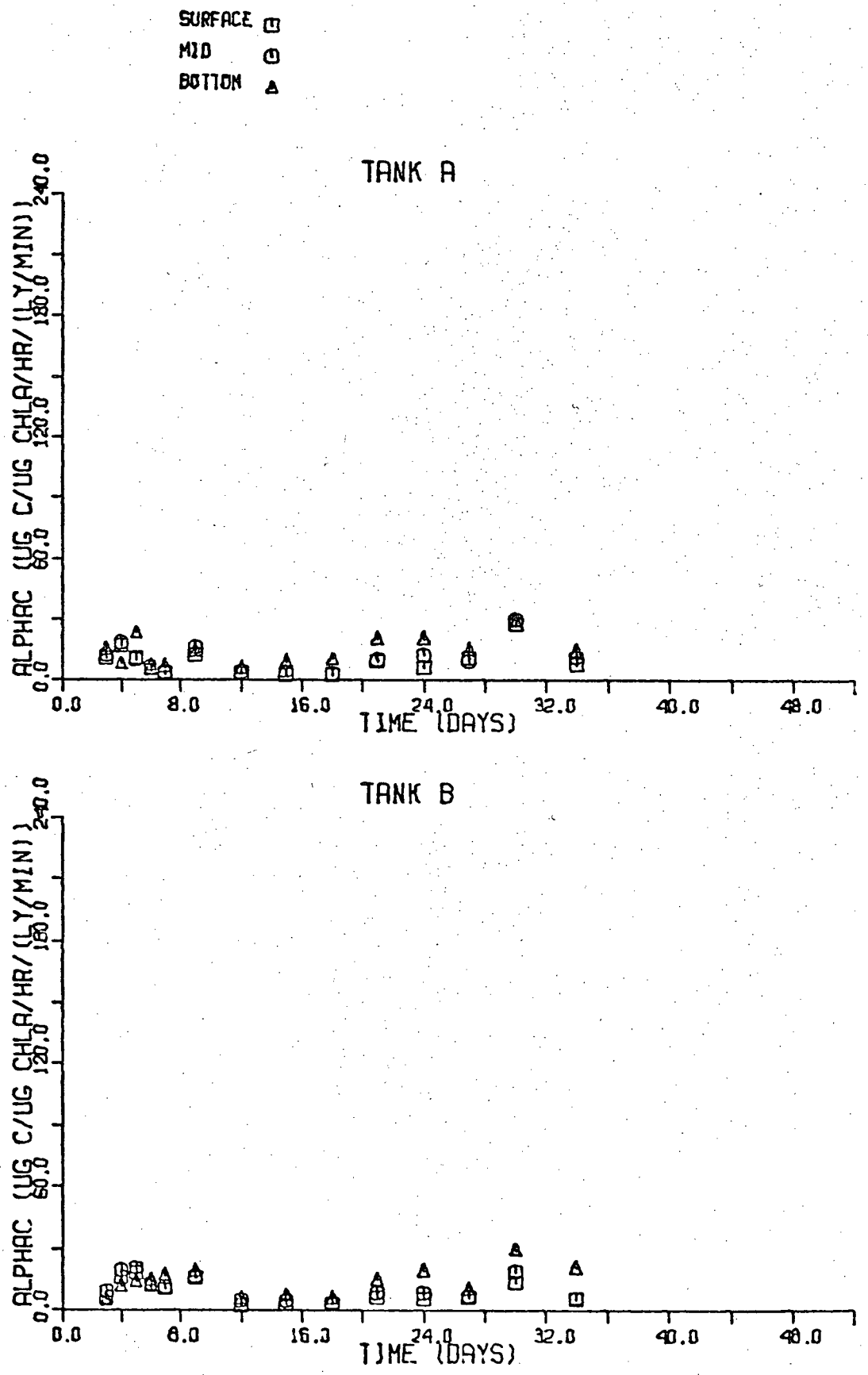


FIGURE 56 ESTIMATES OF ALPHAG DURING EXPERIMENT 4

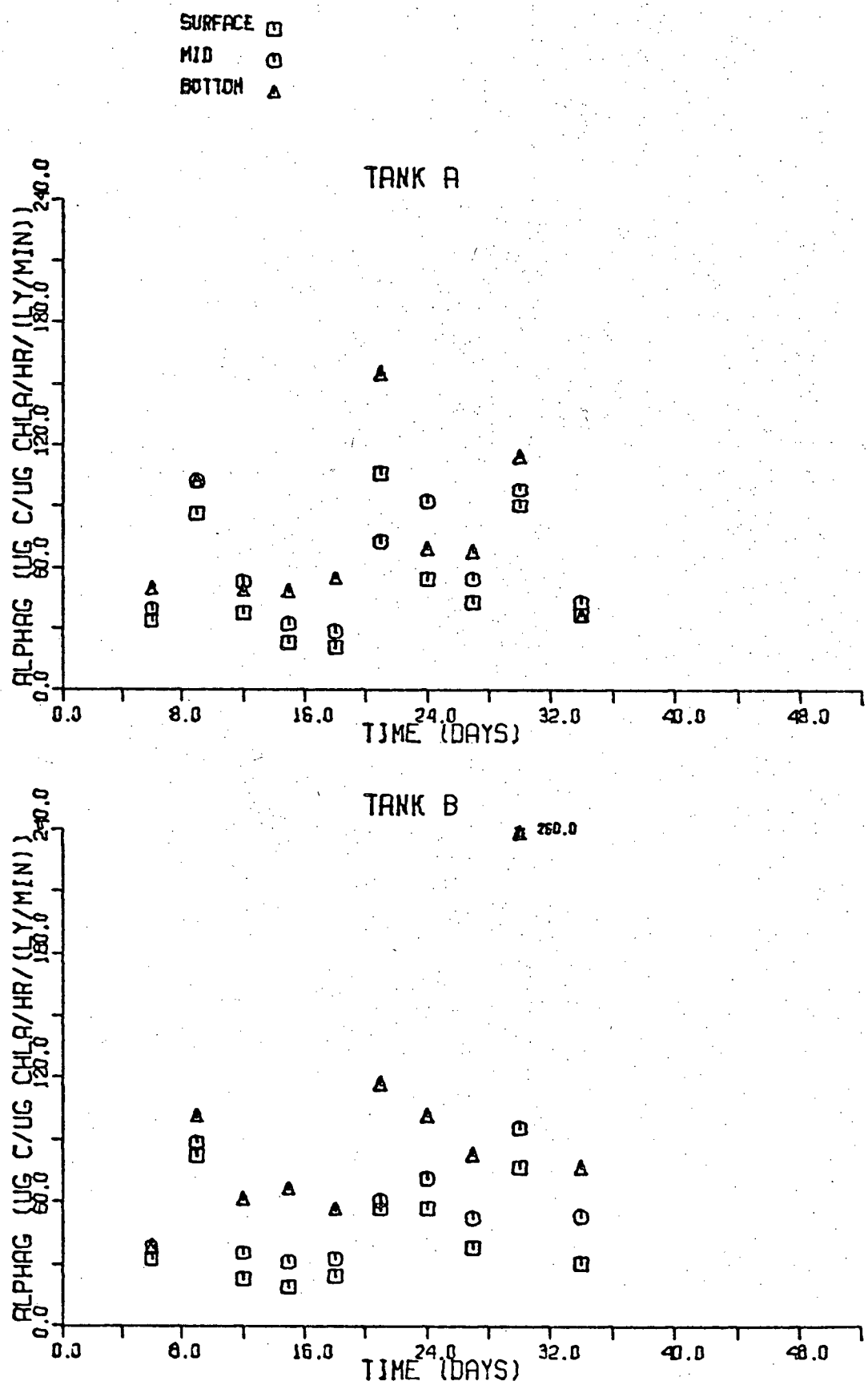


Figure 57. Coulter counts on Day 6 of Experiment 4A

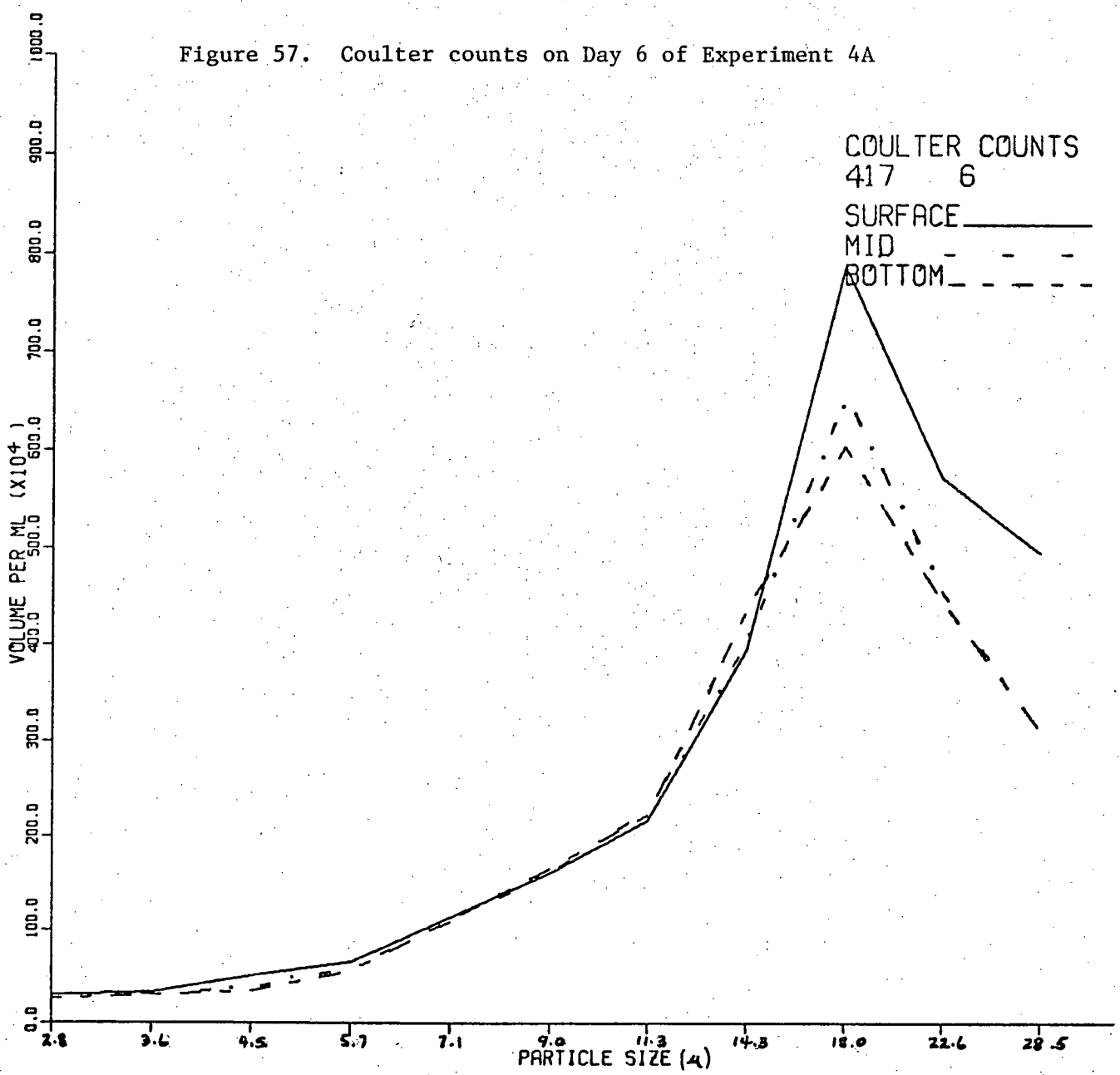


Figure 58. Coulter counts on Day 9 of Experiment 4A

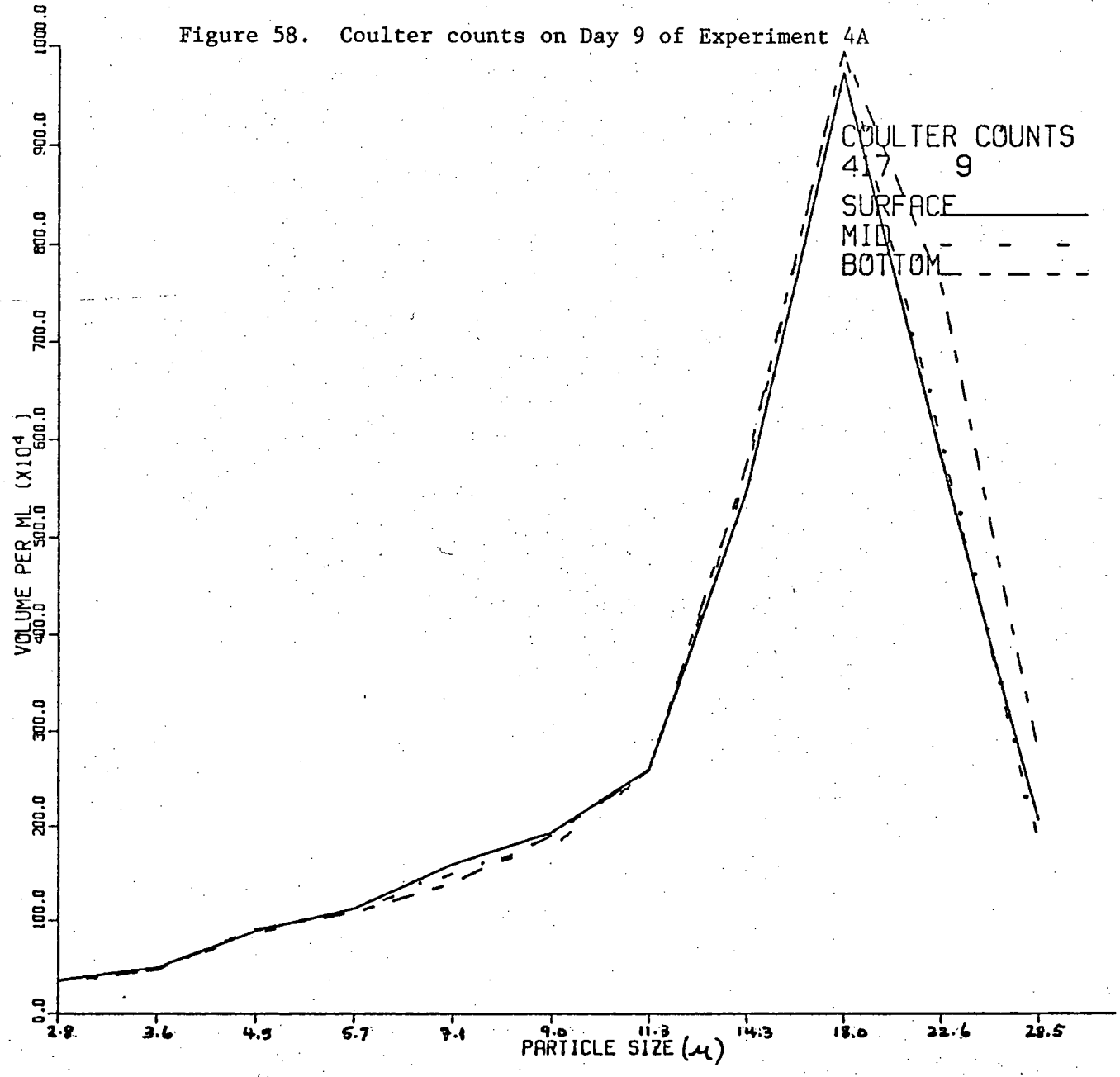


Figure 59. Coulter counts on Day 15 of Experiment 4A

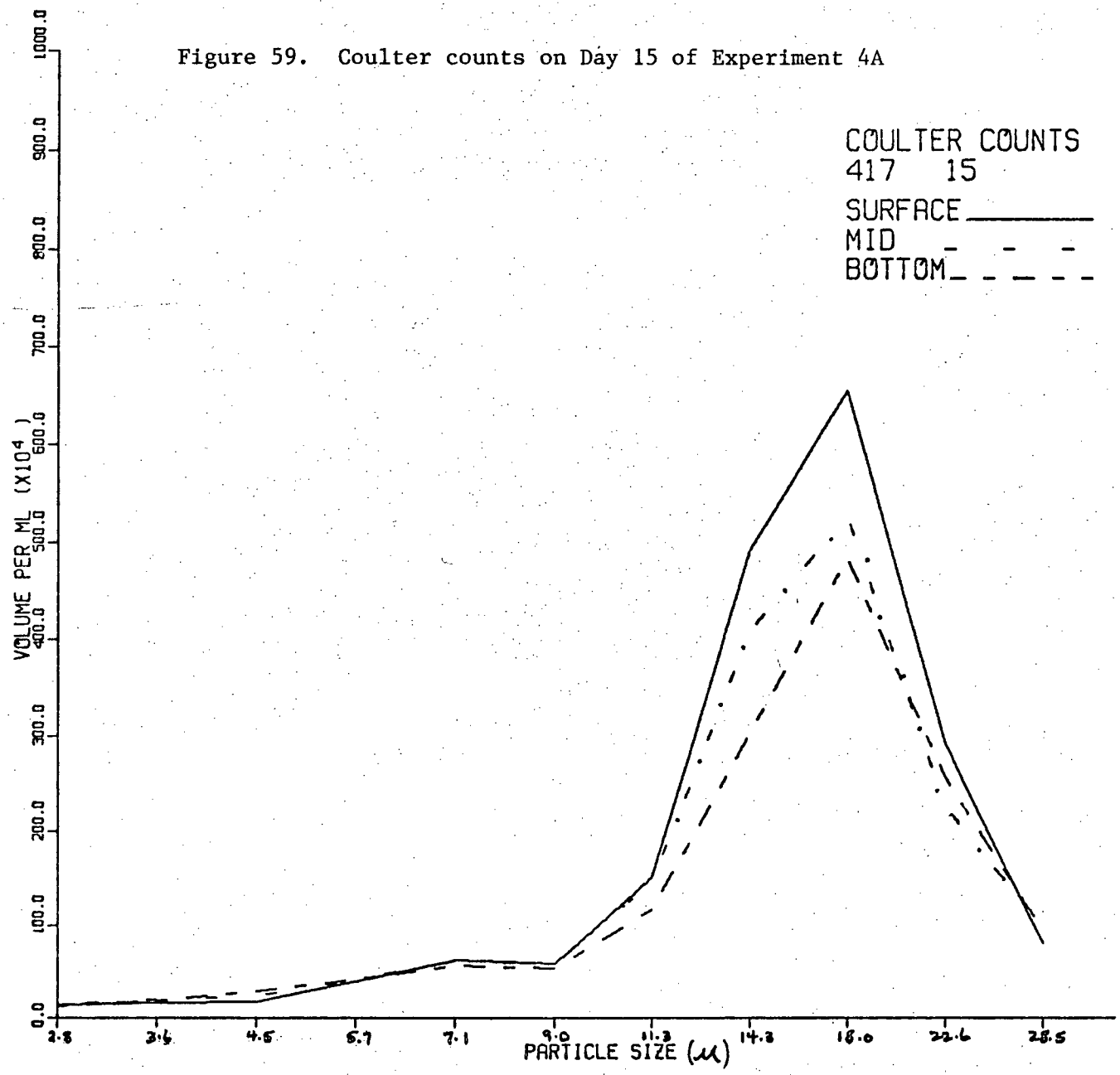


Figure 60. Coulter counts on Day 21 of Experiment 4A

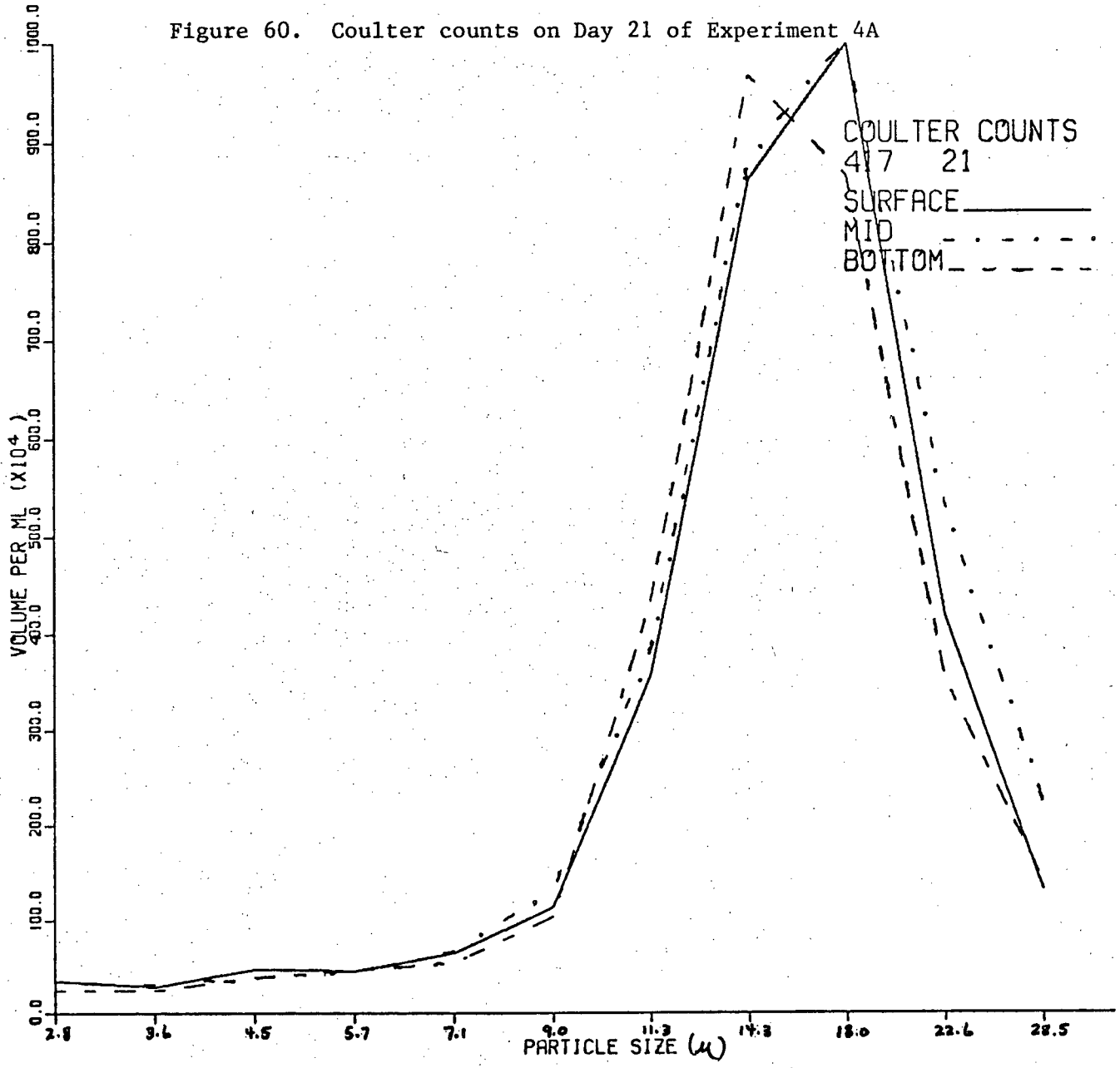


Figure 61. Coulter counts on Day 27 of Experiment 4A

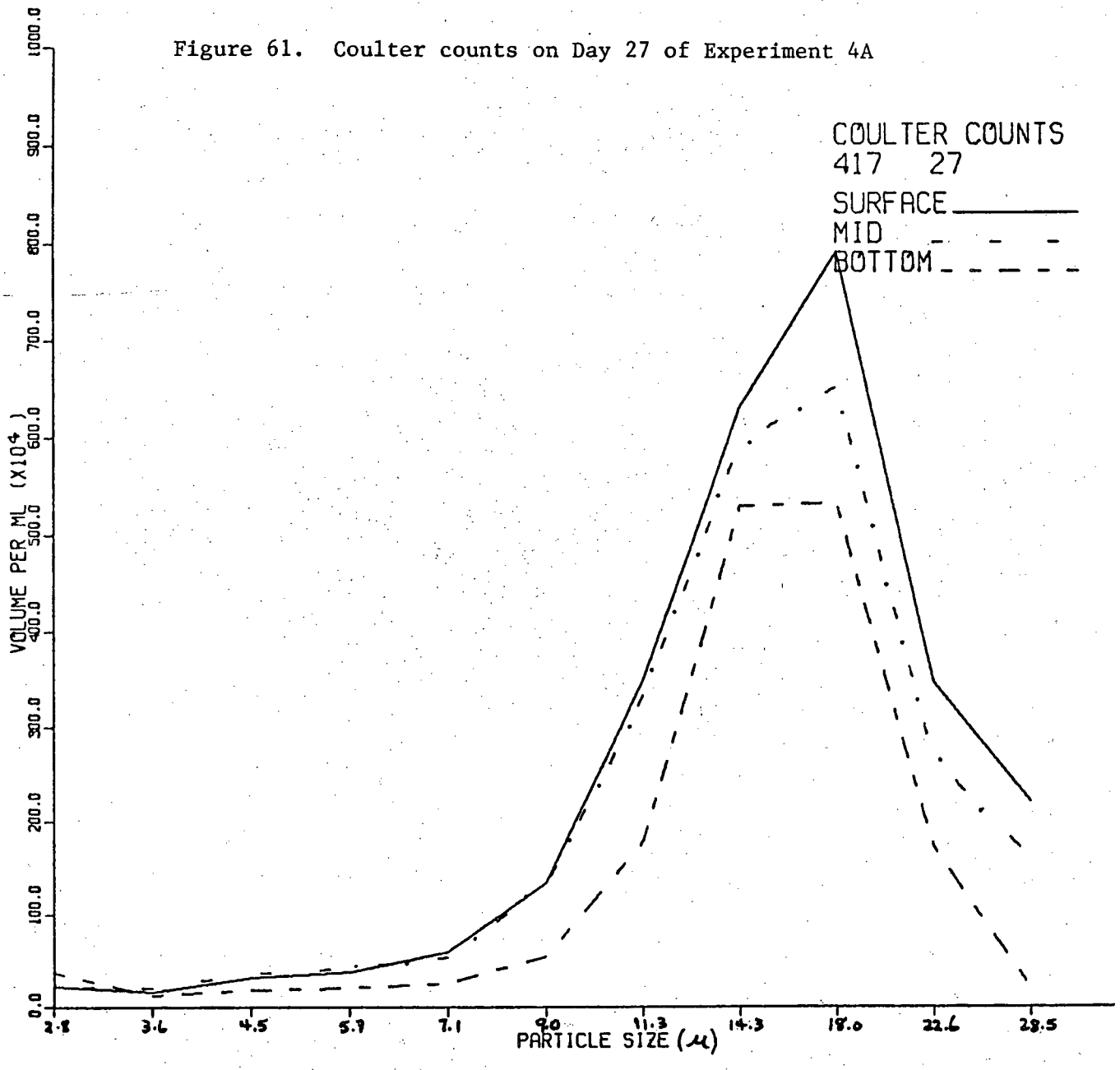


FIGURE 62 FORCING CONDITIONS DURING EXPERIMENT 5

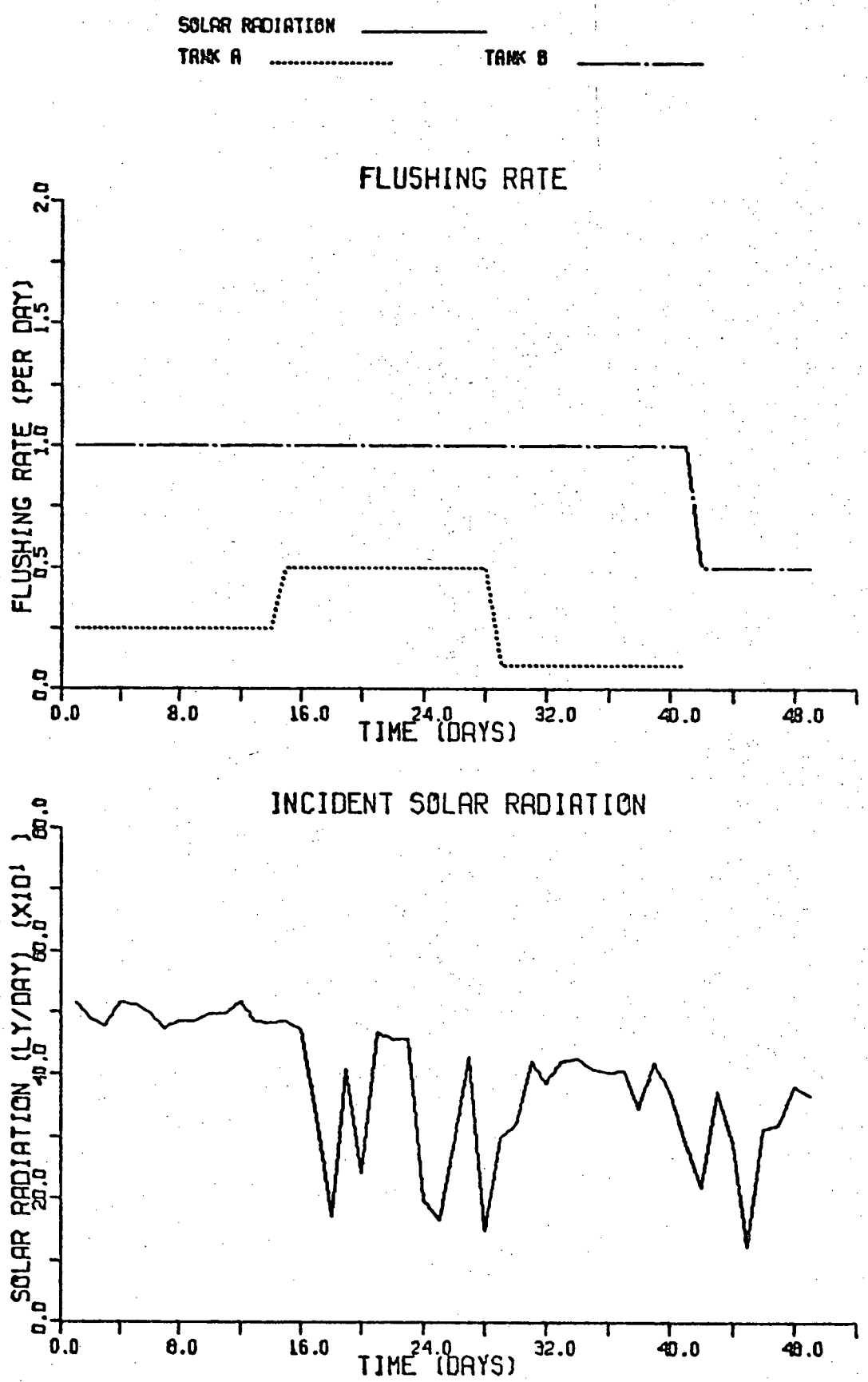


FIGURE 63 TEMPERATURE
DURING EXPERIMENT 5

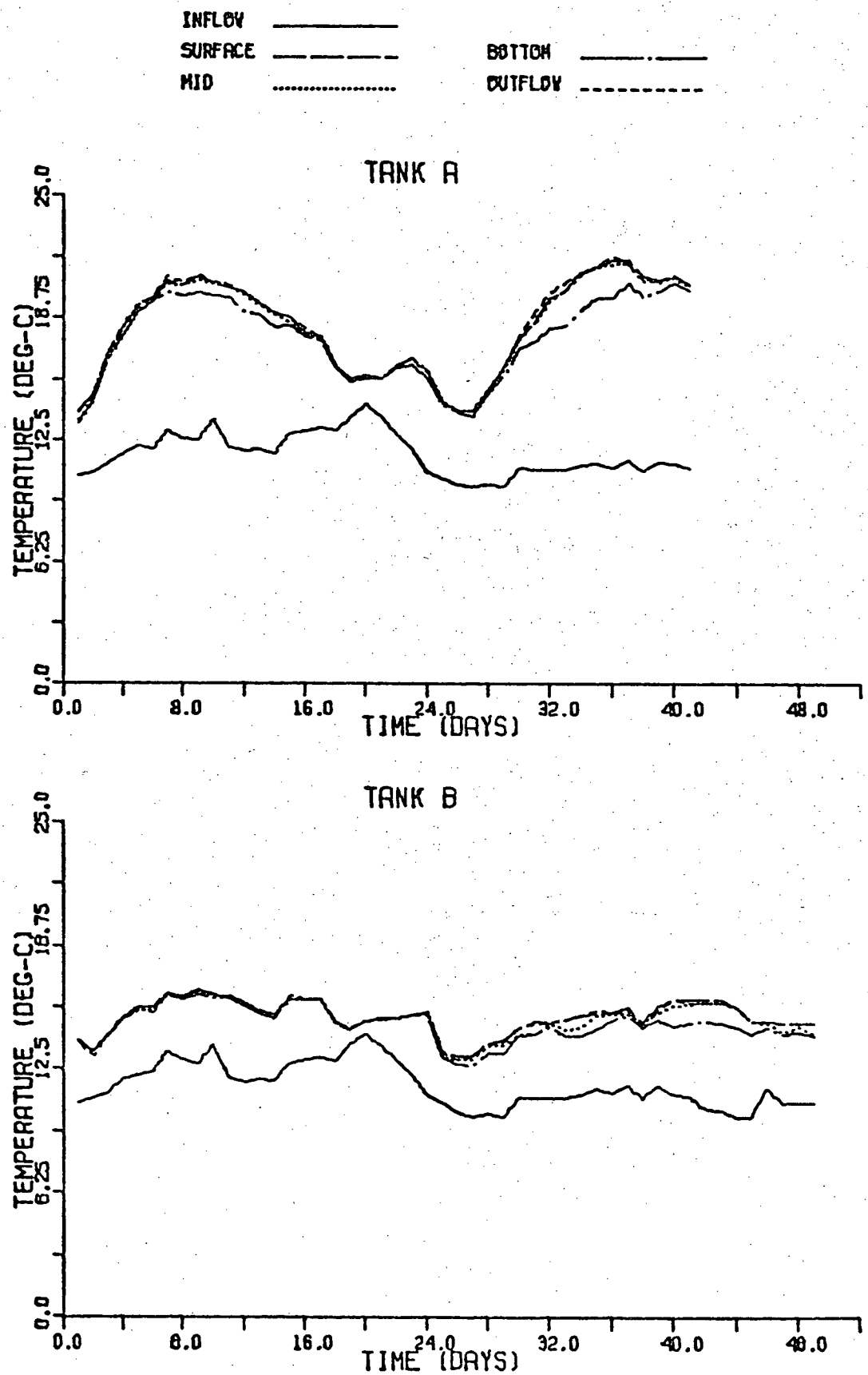


FIGURE 64 NITRATE
DURING EXPERIMENT 5

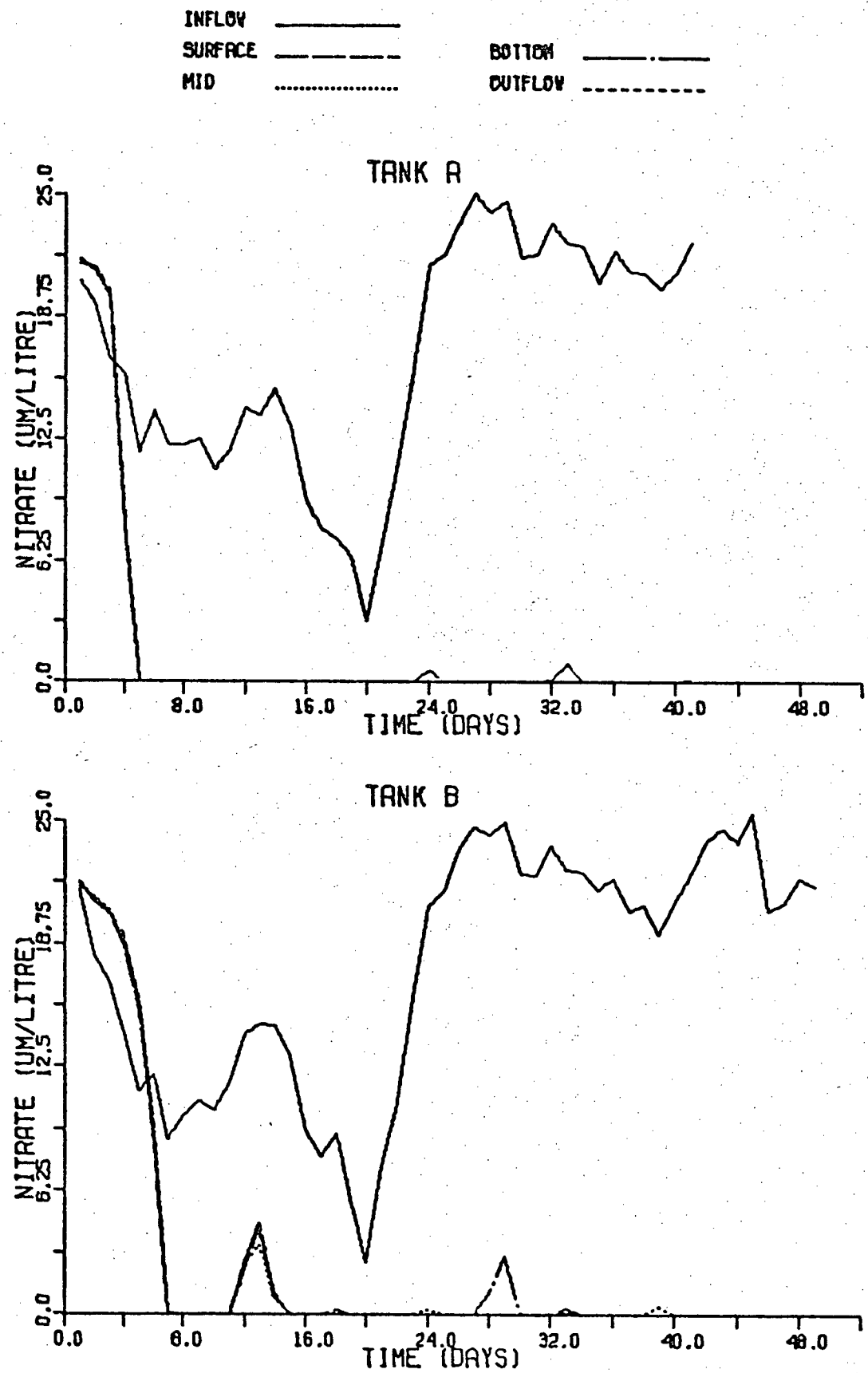


FIGURE 65 PHYTOPLANKTON STOCK DURING EXPERIMENT 5

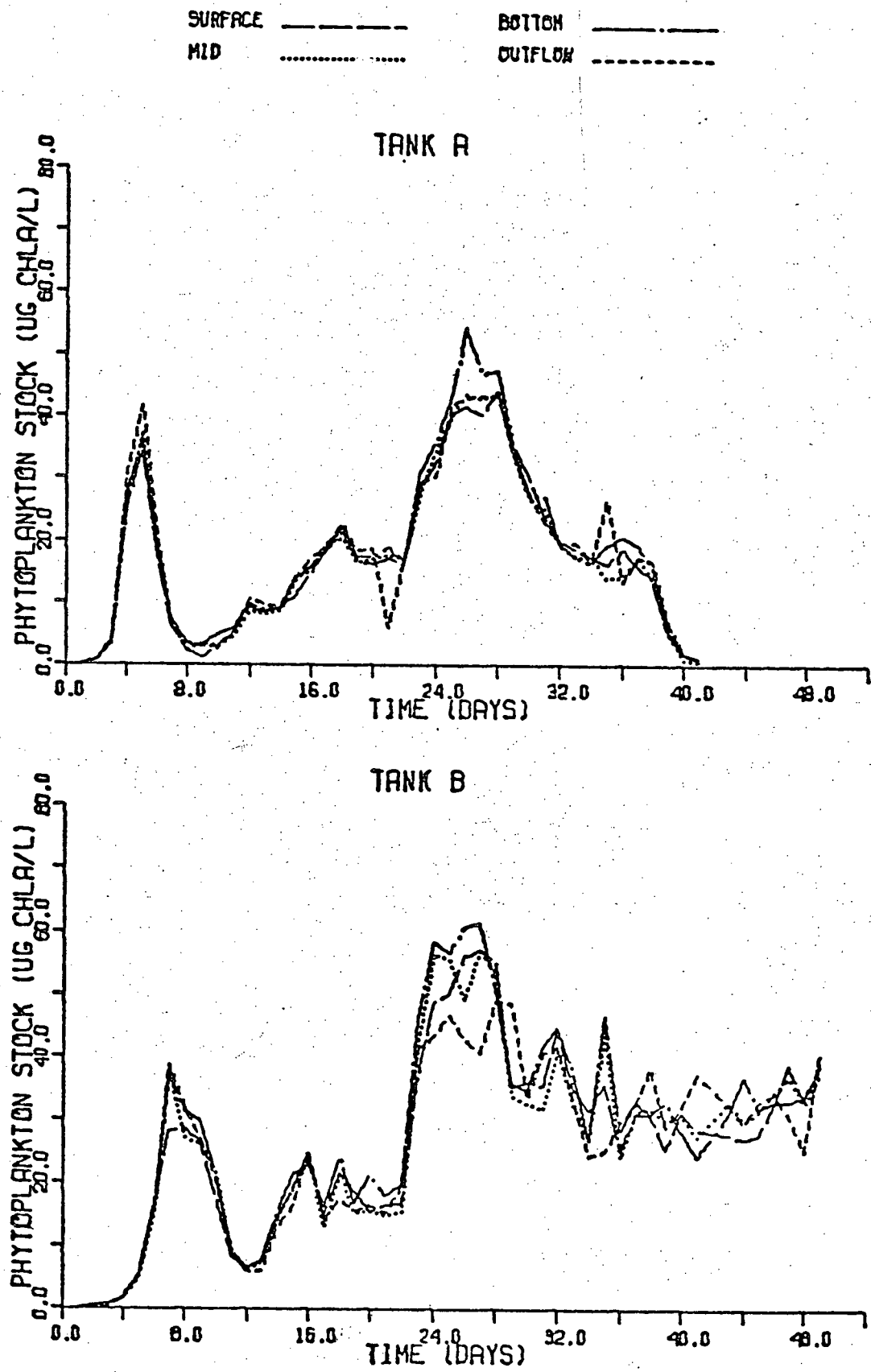


FIGURE 66 CHLB:CHLA RATIO
DURING EXPERIMENT 5

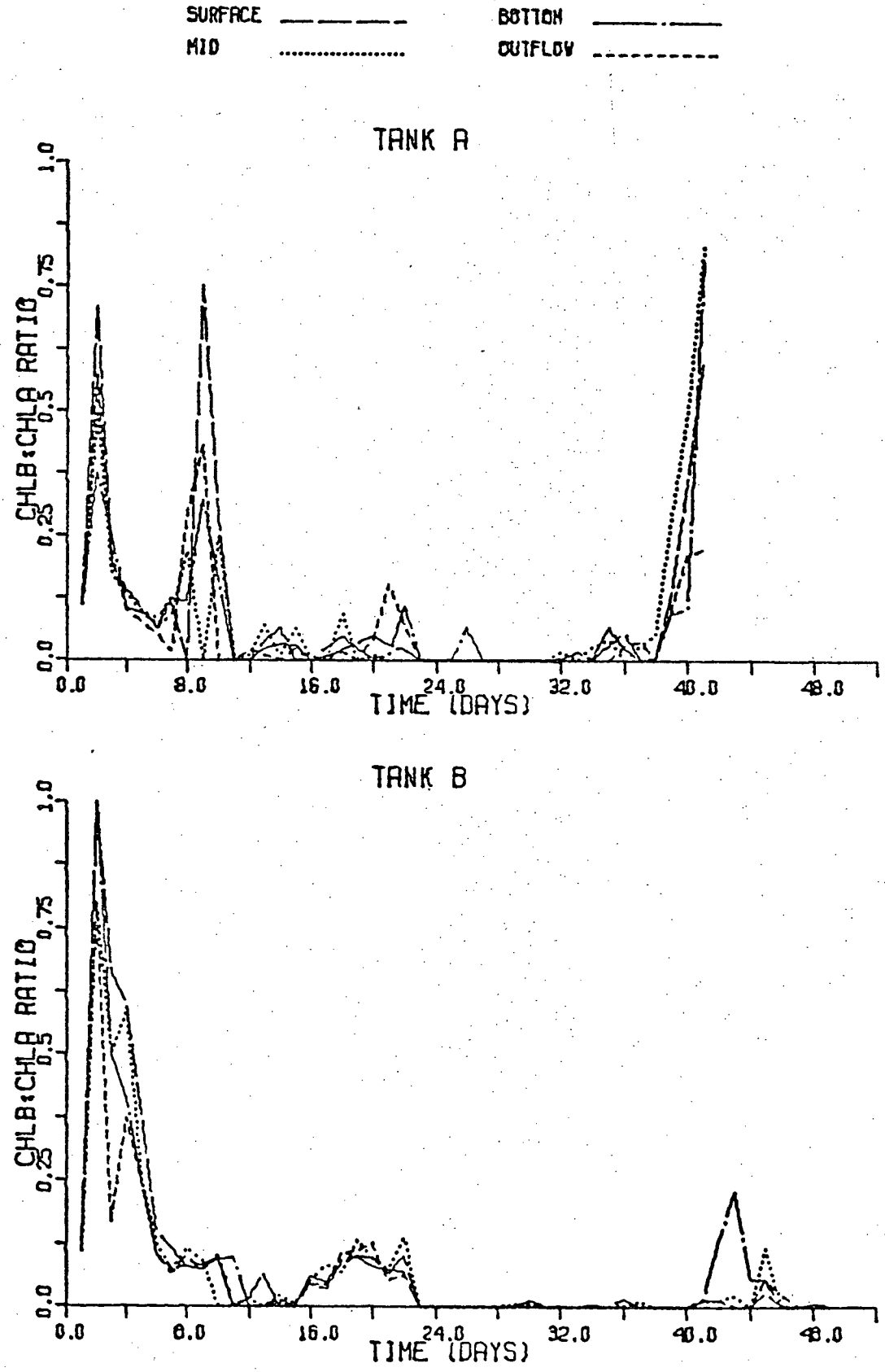


FIGURE 67 CAROTENOID:CHLA RATIO DURING EXPERIMENT 5

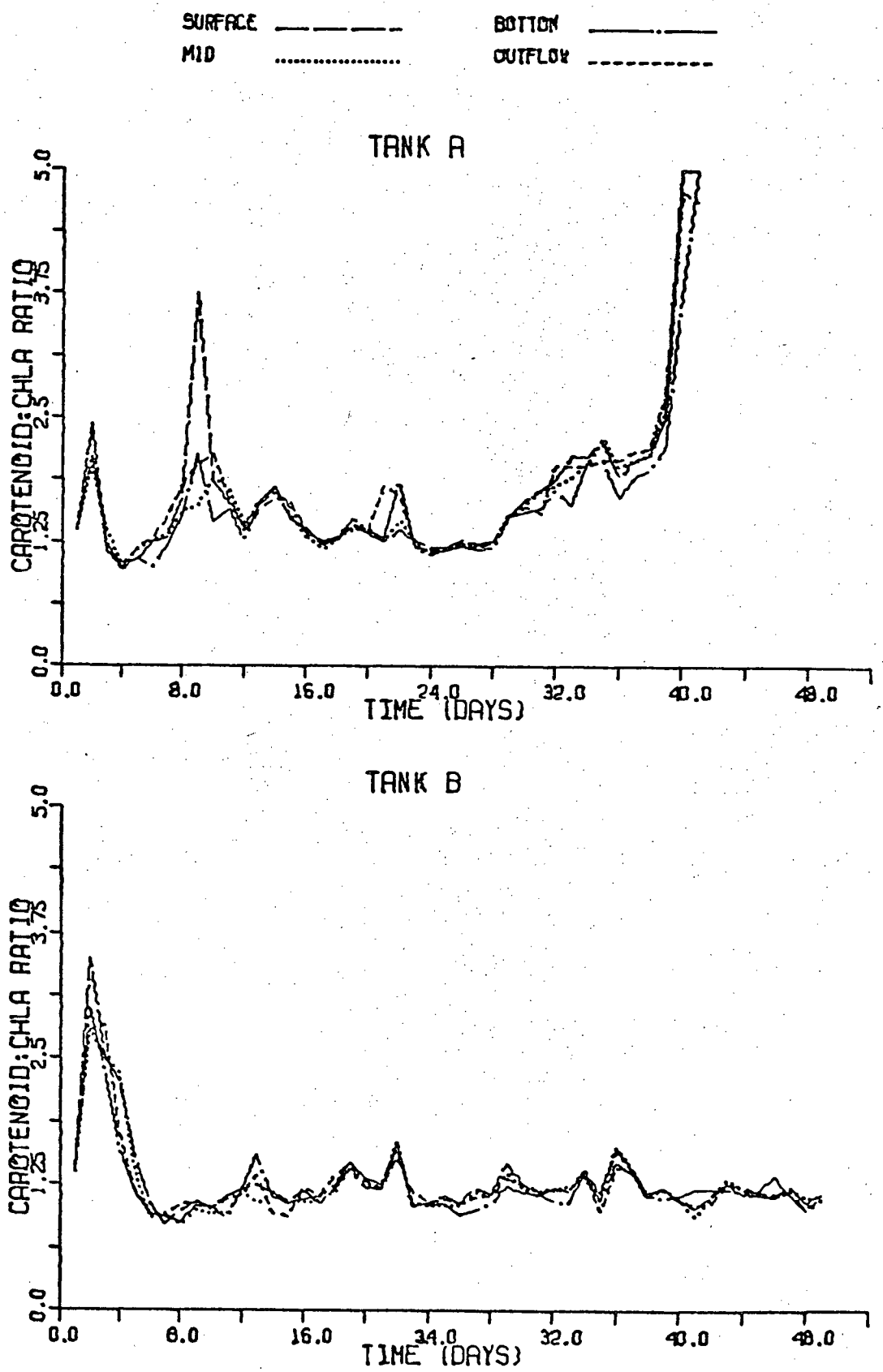


FIGURE 68 OXYGEN
DURING EXPERIMENT 5

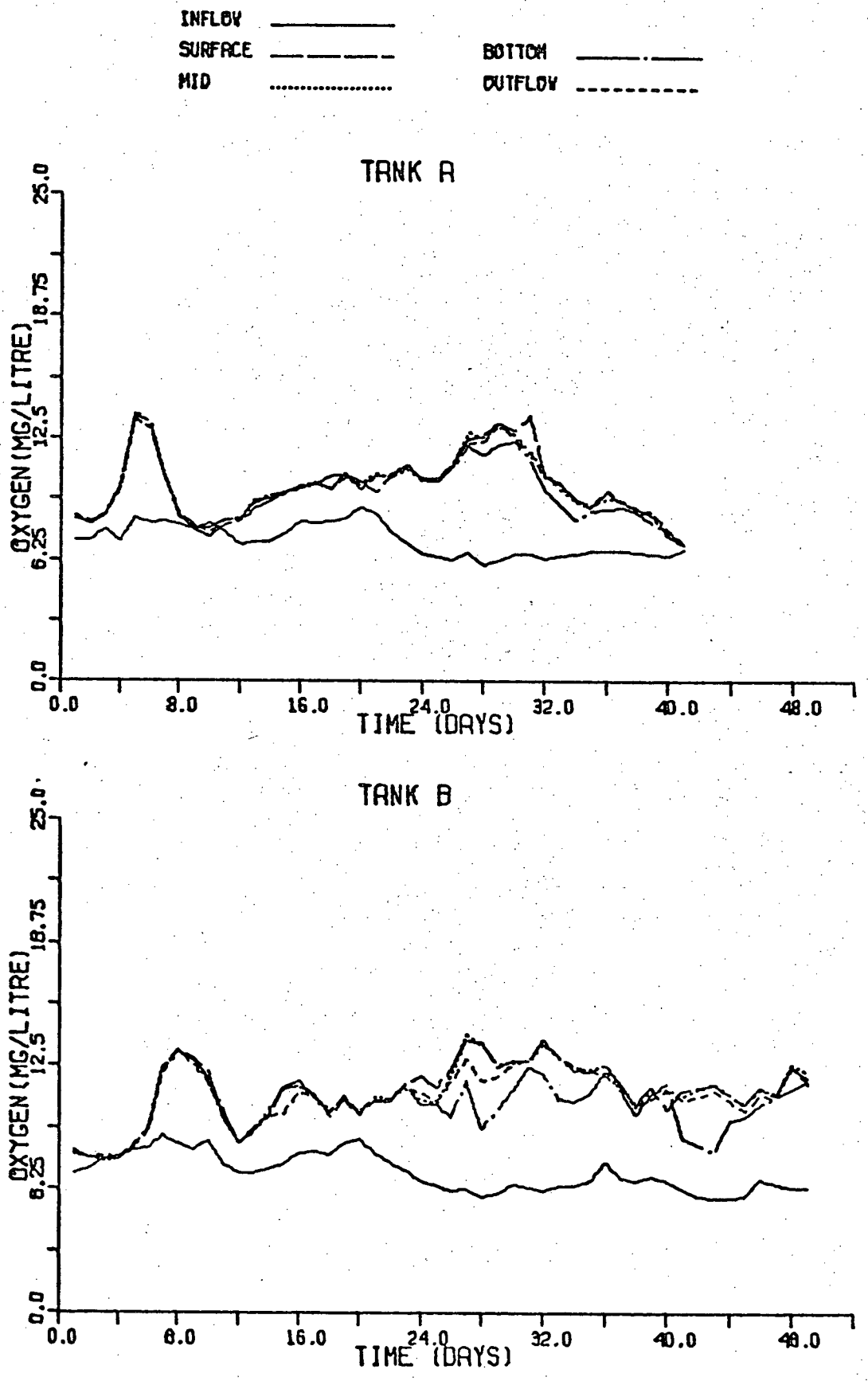


FIGURE 69 GROSS PRIMARY PRODUCTIVITY DURING EXPERIMENT 5

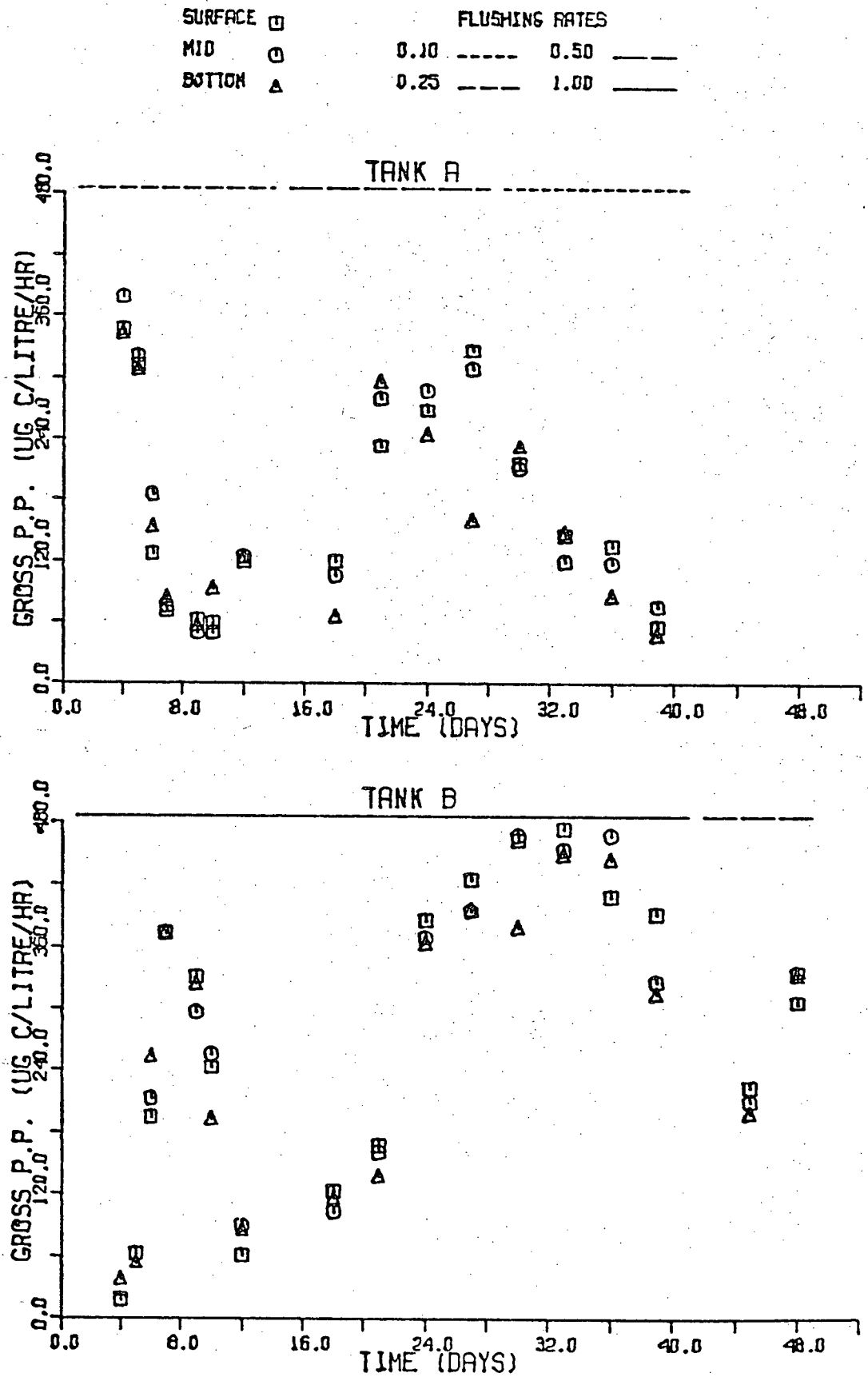


FIGURE 70 GROSS PRIMARY PRODUCTIVITY (DAILY) DURING EXPERIMENT 5

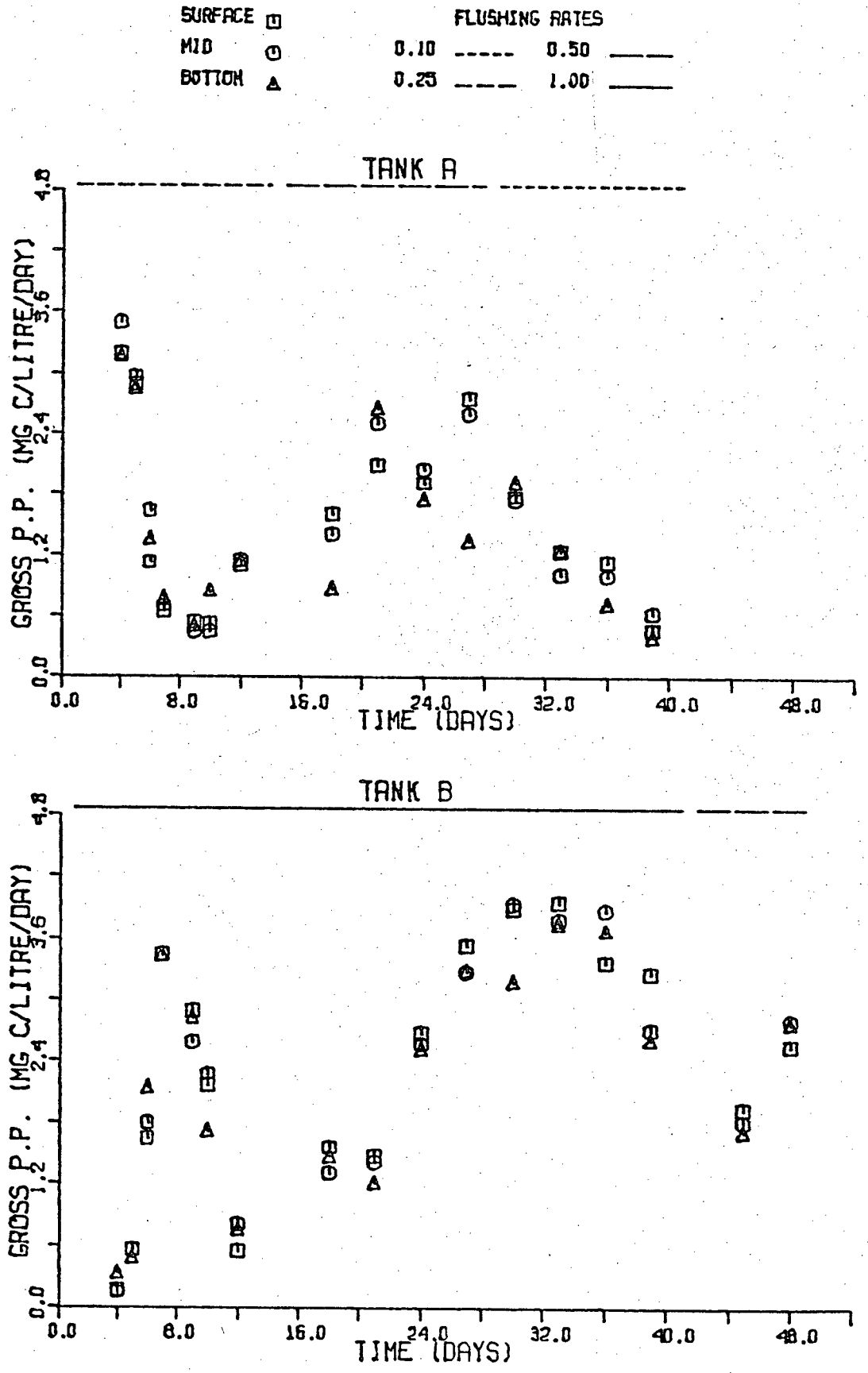
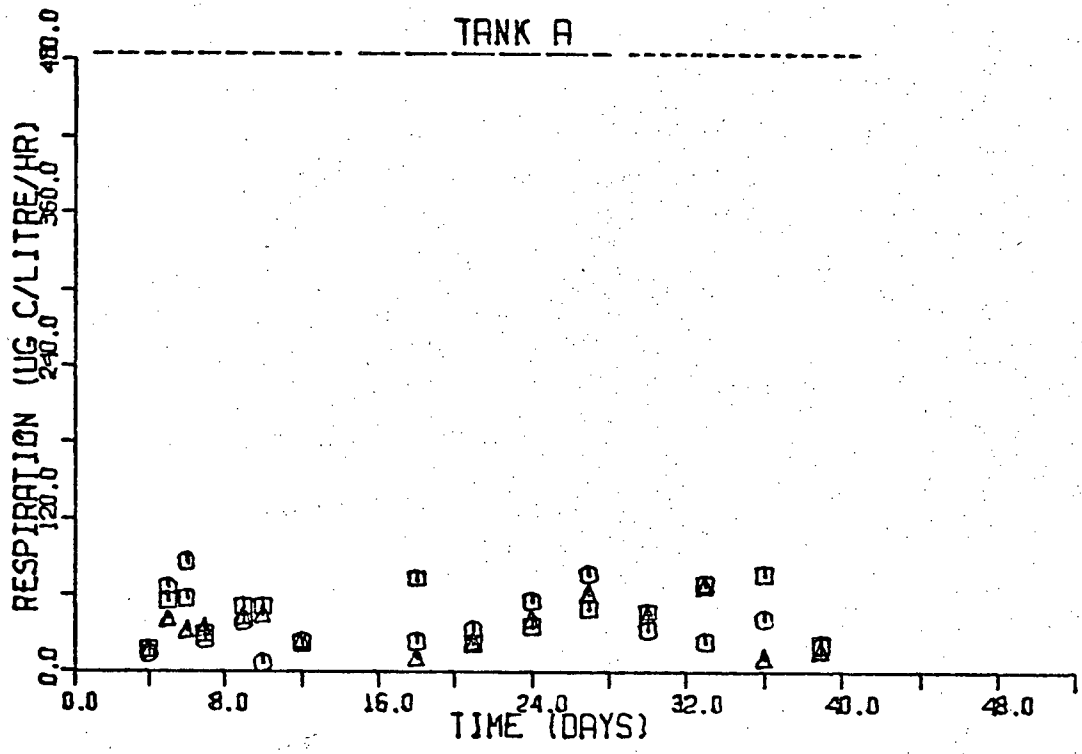


FIGURE 71 RESPIRATION RATE DURING EXPERIMENT 5

SURFACE □
MID ○
BOTTON △

FLUSHING RATES
0.10 ----- 0.50 — —
0.25 — — — 1.00 ———



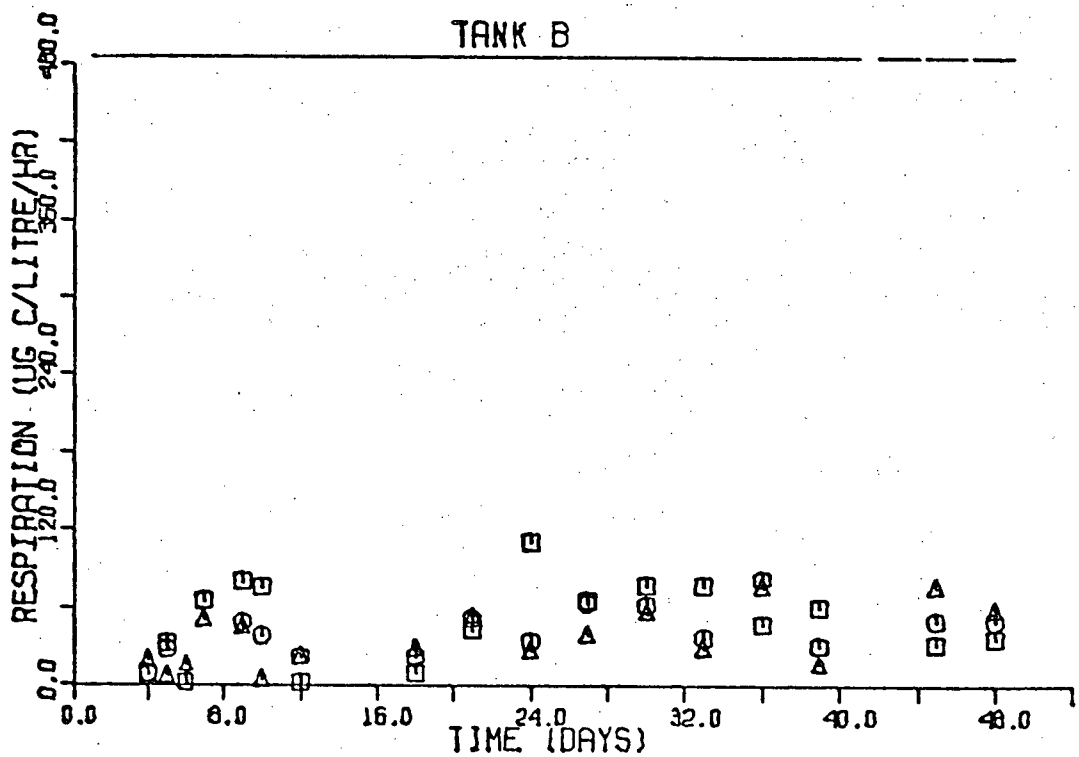


FIGURE 72 NET PRIMARY PRODUCTIVITY DURING EXPERIMENT 5

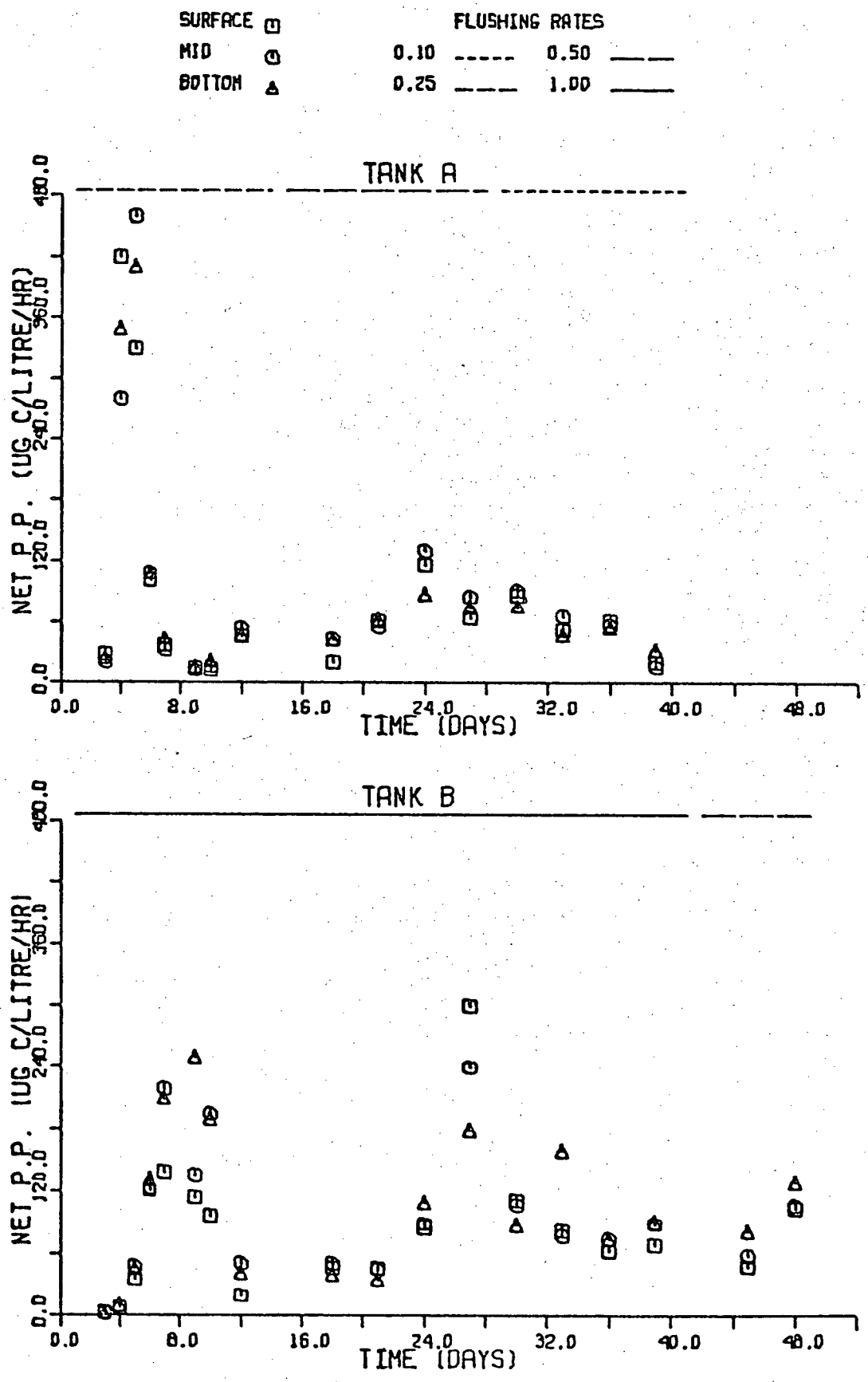


FIGURE 73 NET PRIMARY PRODUCTIVITY (DAILY) DURING EXPERIMENT 5

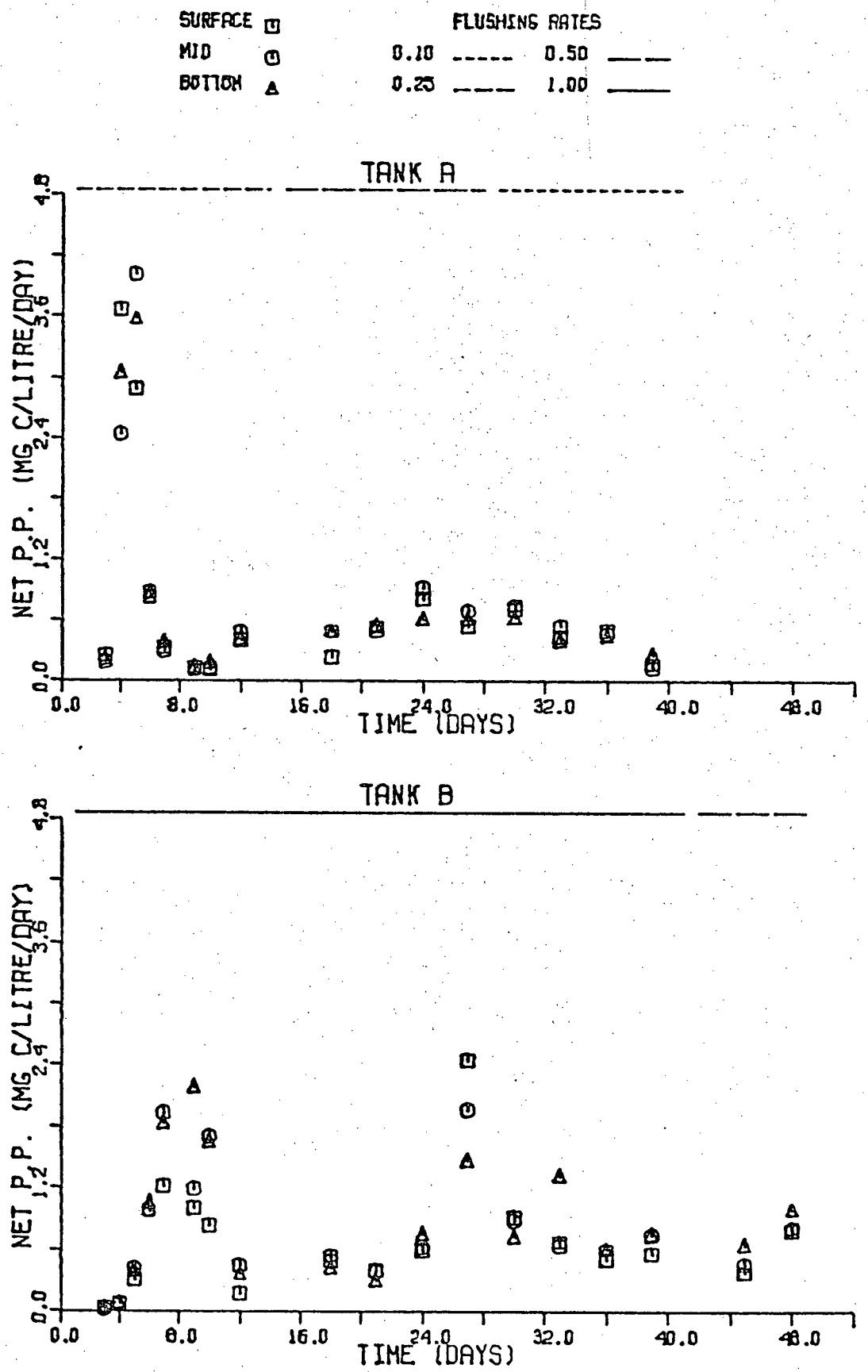


FIGURE 74 GROSS PRIMARY PRODUCTIVITY (STANDARDIZED) DURING EXPERIMENT 5

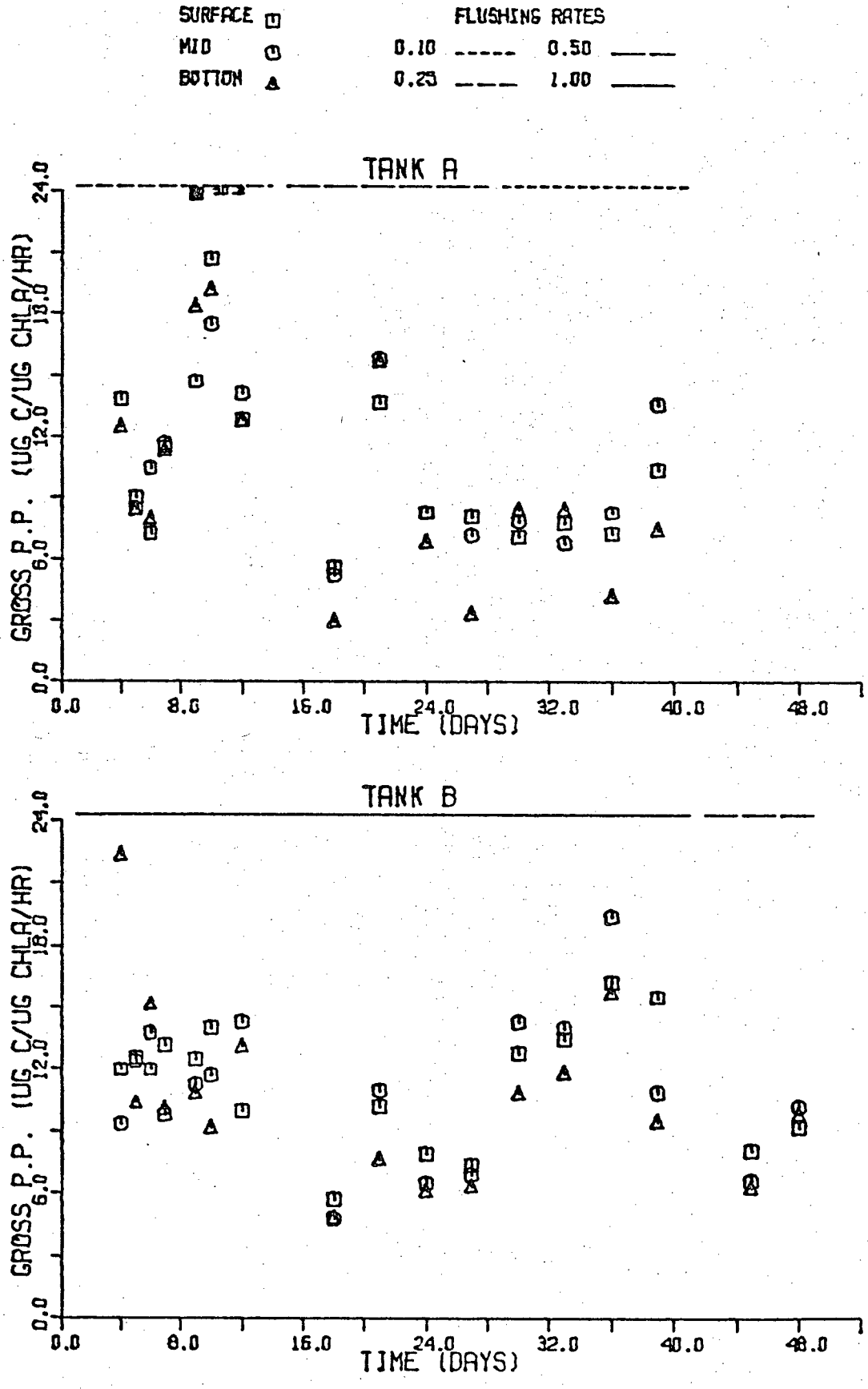


FIGURE 75 RESPIRATION RATE (STANDARDIZED) DURING EXPERIMENT 5

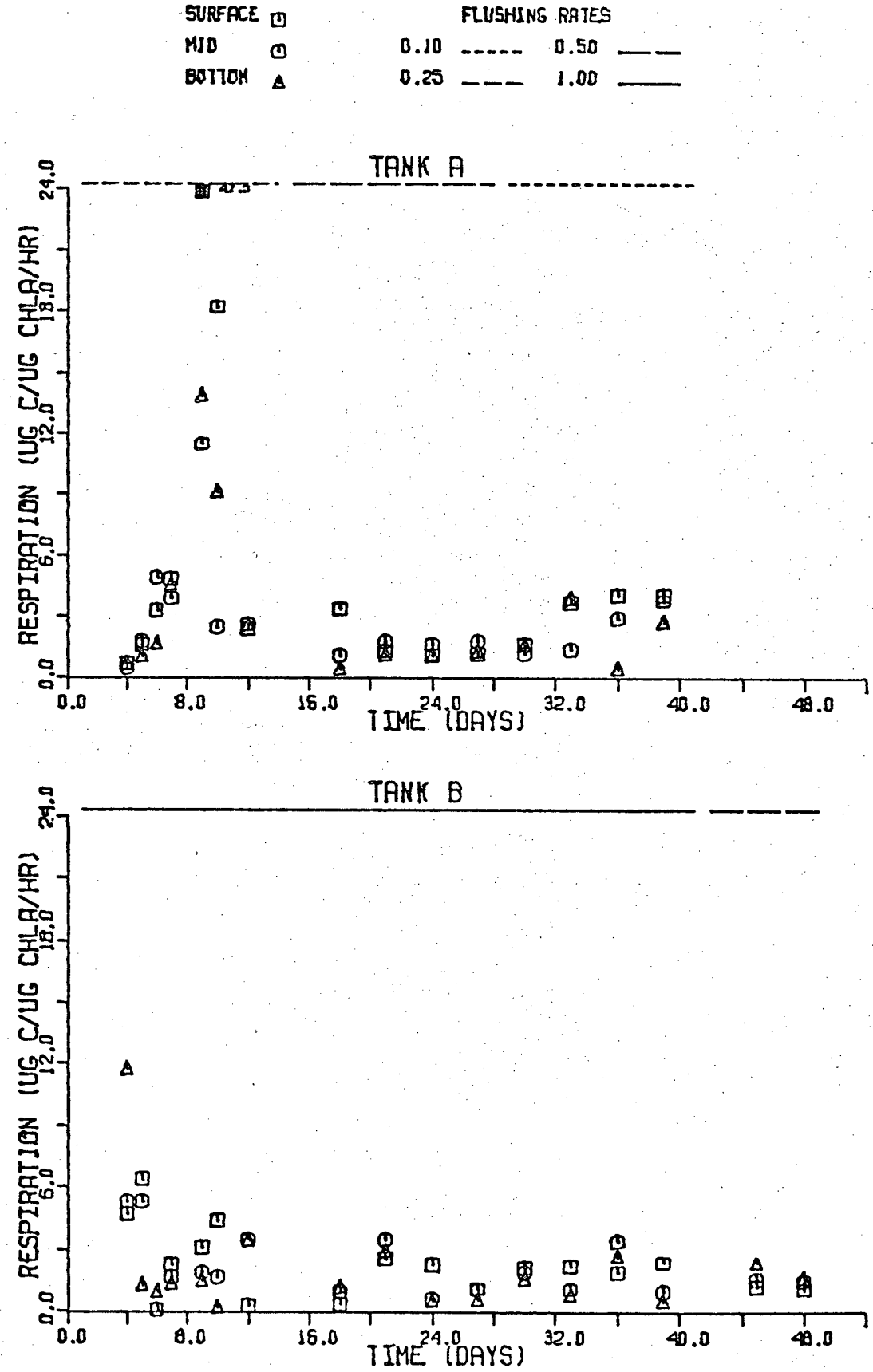


FIGURE 76 NET PRIMARY PRODUCTIVITY (STANDARDIZED) DURING EXPERIMENT 5

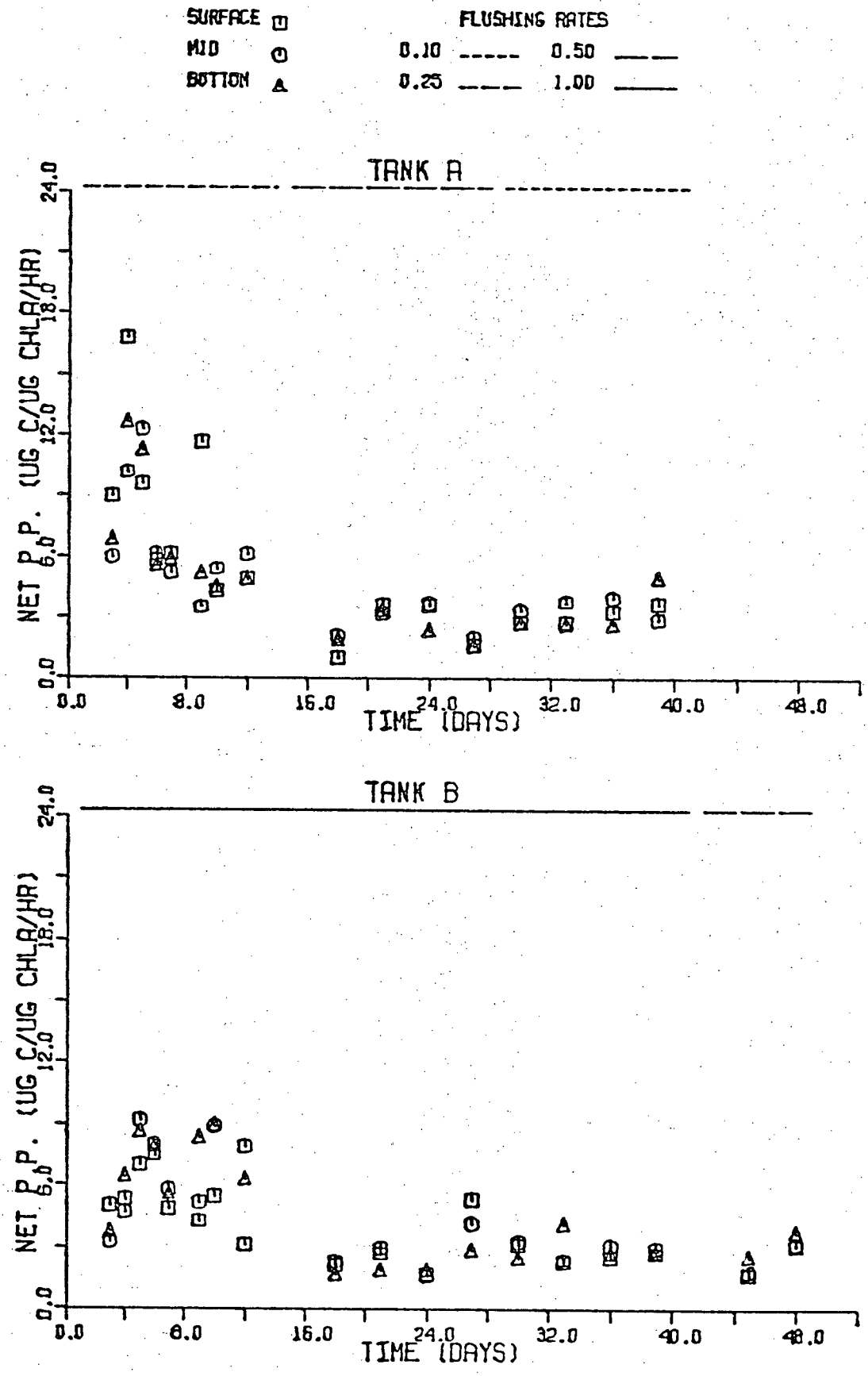


FIGURE 77 ESTIMATES OF ALPHAC DURING EXPERIMENT 5

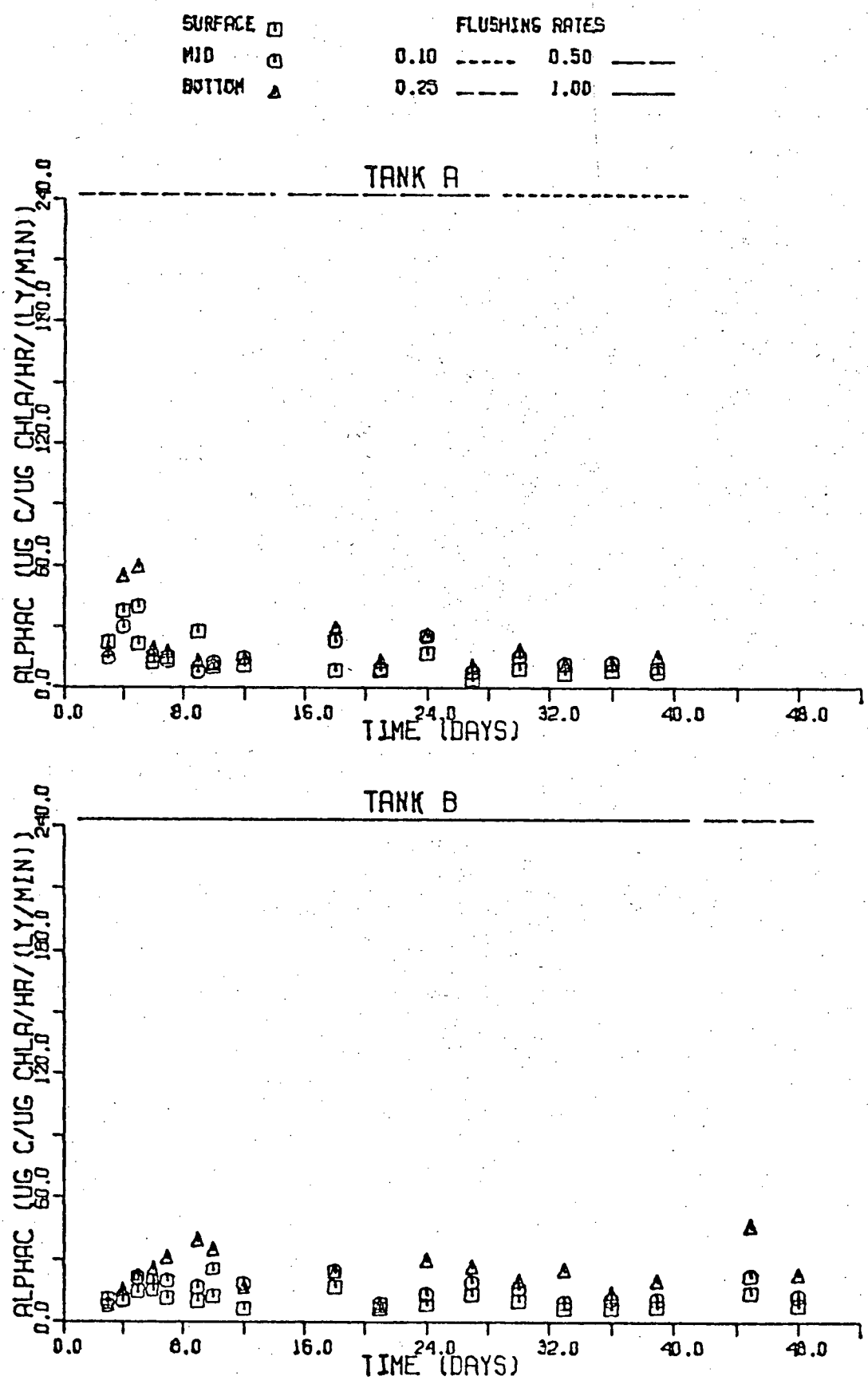


FIGURE 78 ESTIMATES OF ALPHAG DURING EXPERIMENT 5

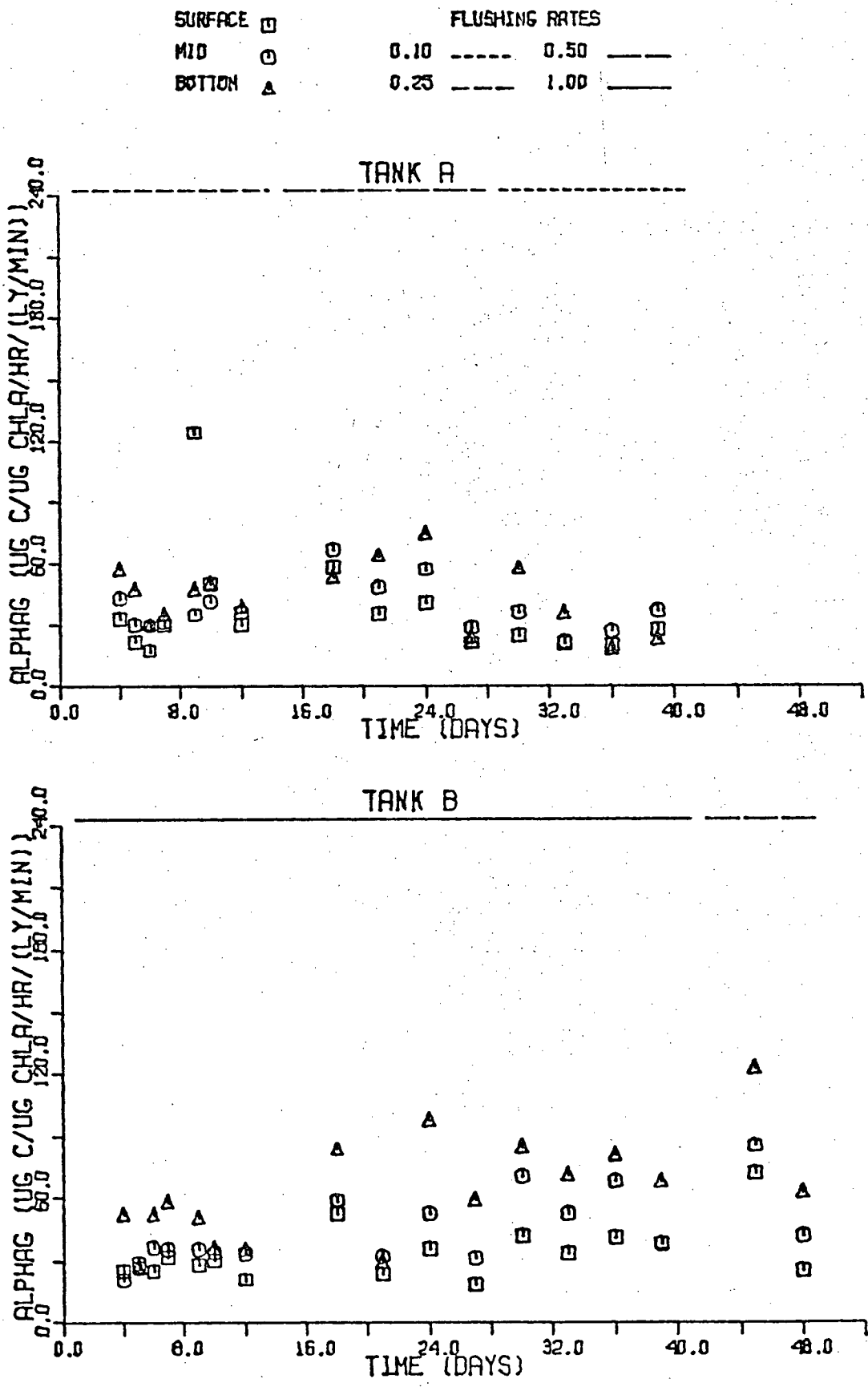


Figure 79. Coulter counts on Day 6 of Experiment 5A

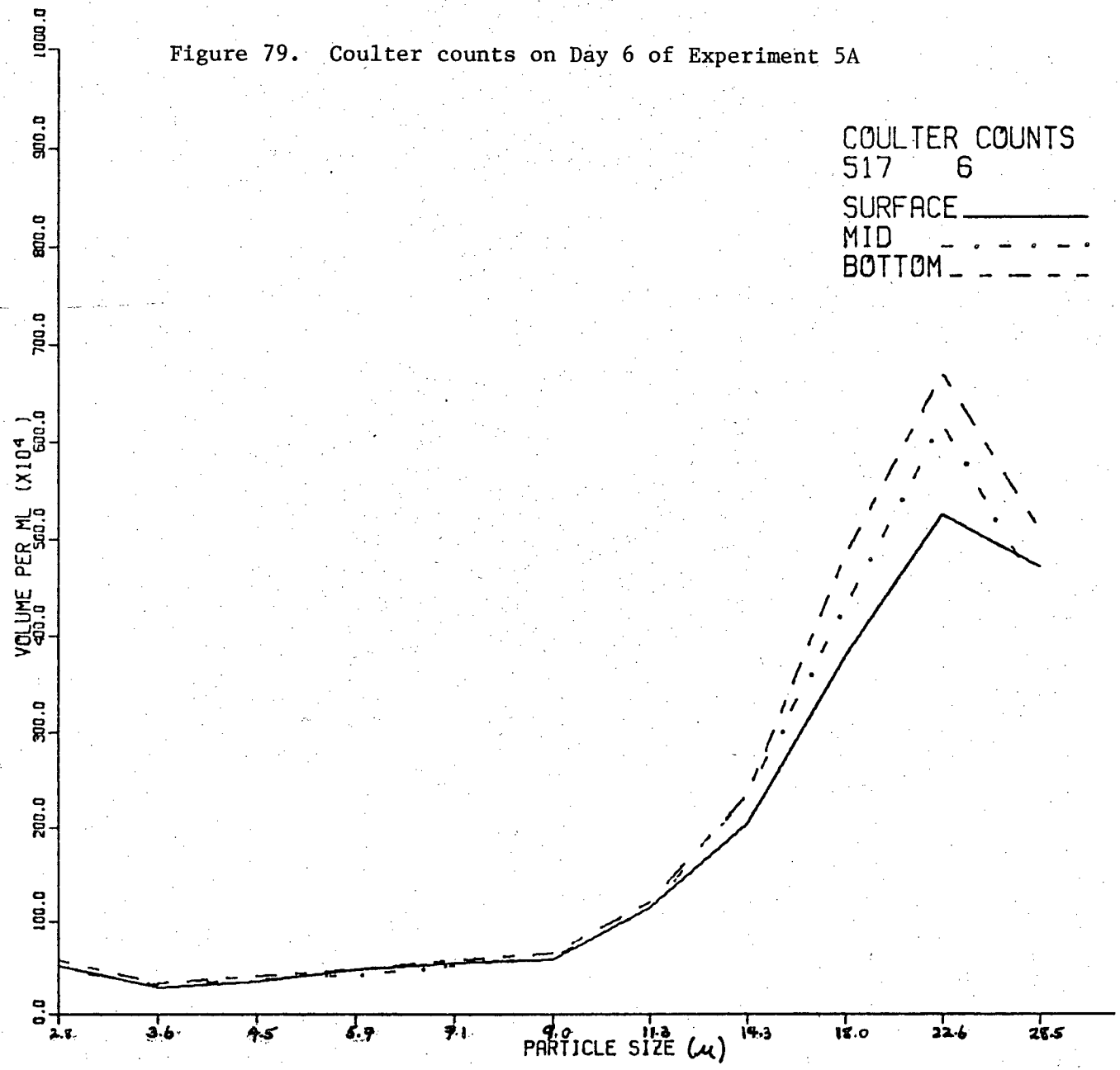


Figure 80. Coulter counts on Day 9 of Experiment 5A

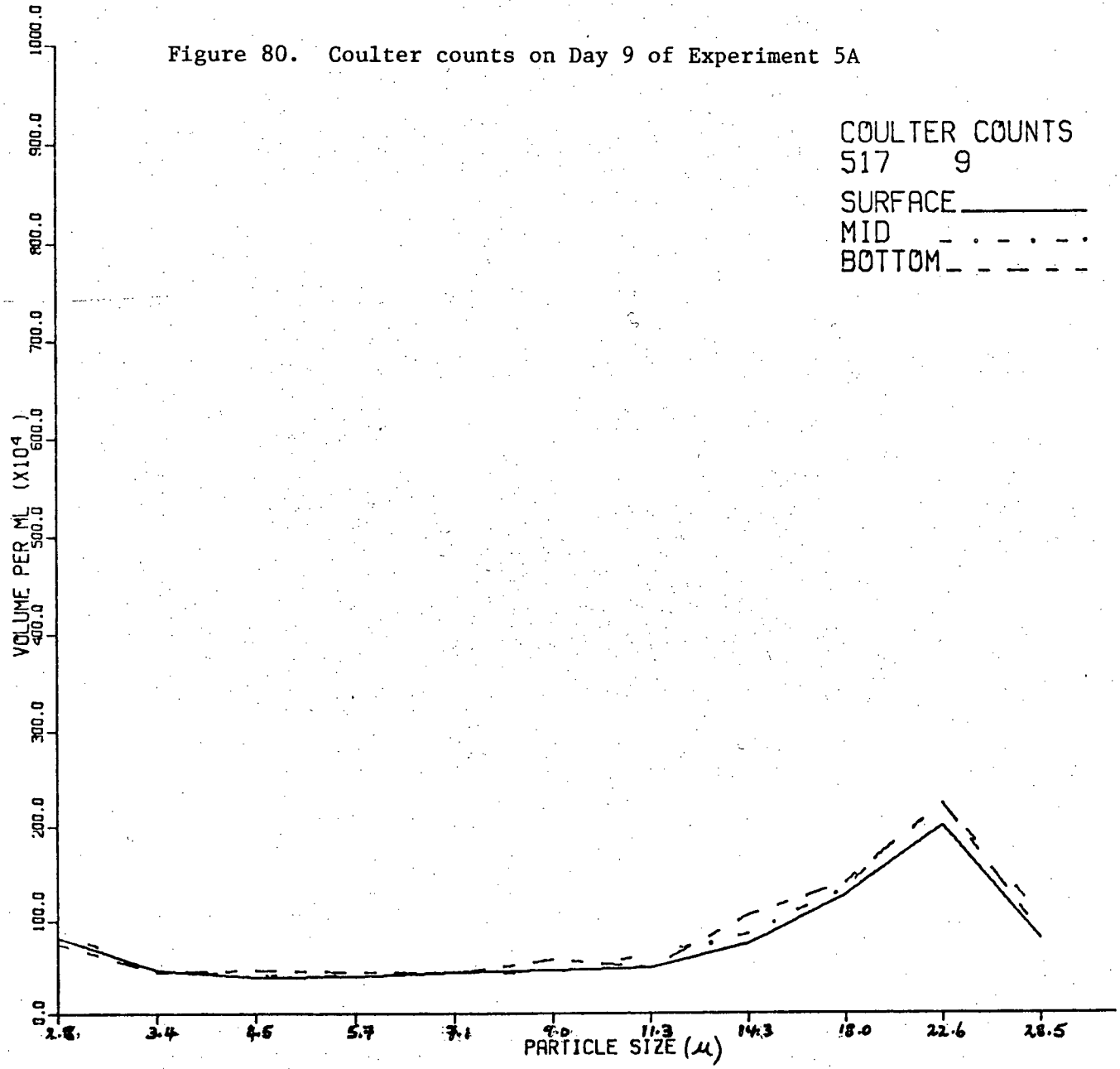


Figure 81. Coulter counts on Day 21 of Experiment 5A

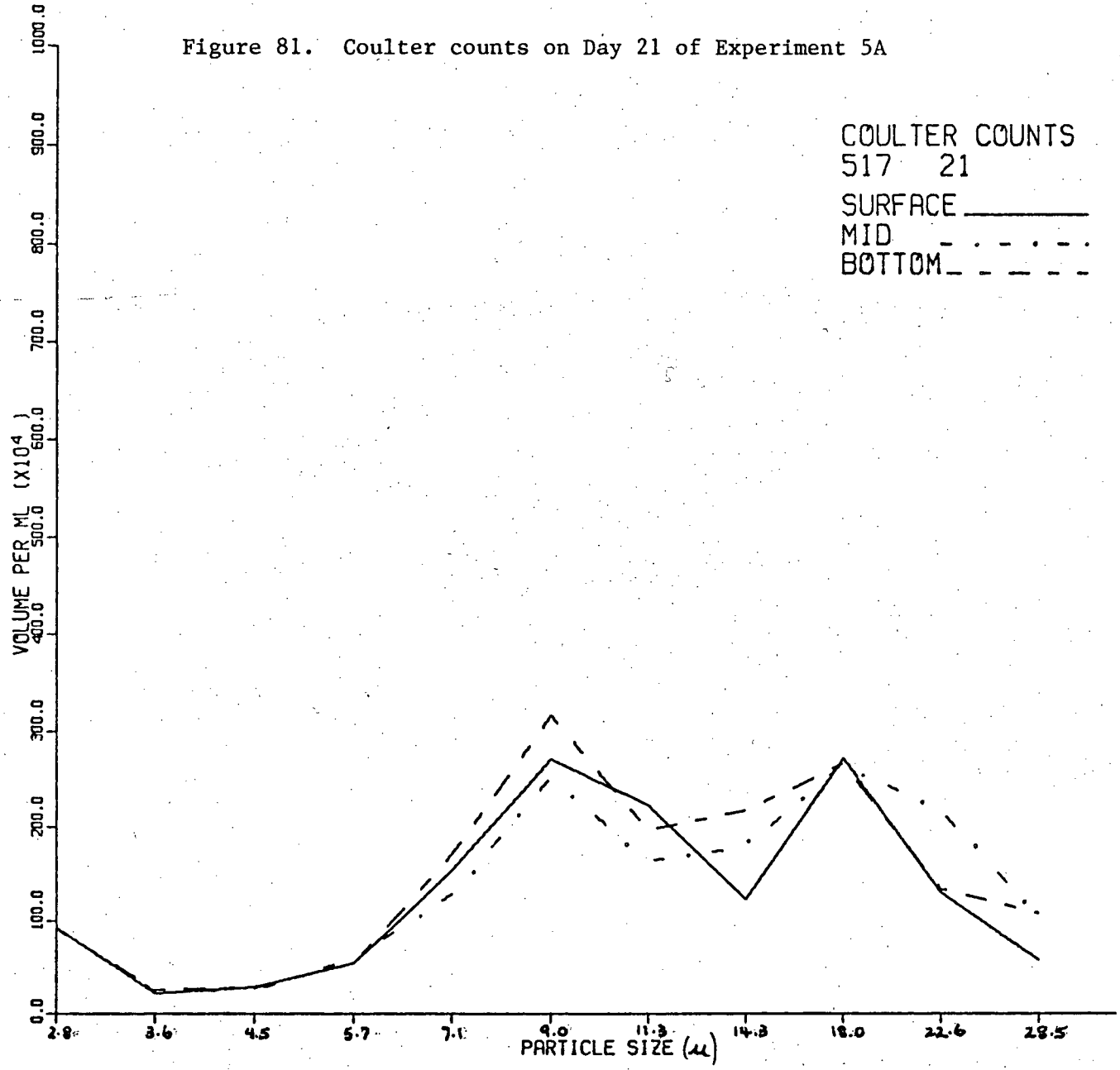


Figure 82. Coulter counts on Day 24 of Experiment 5A

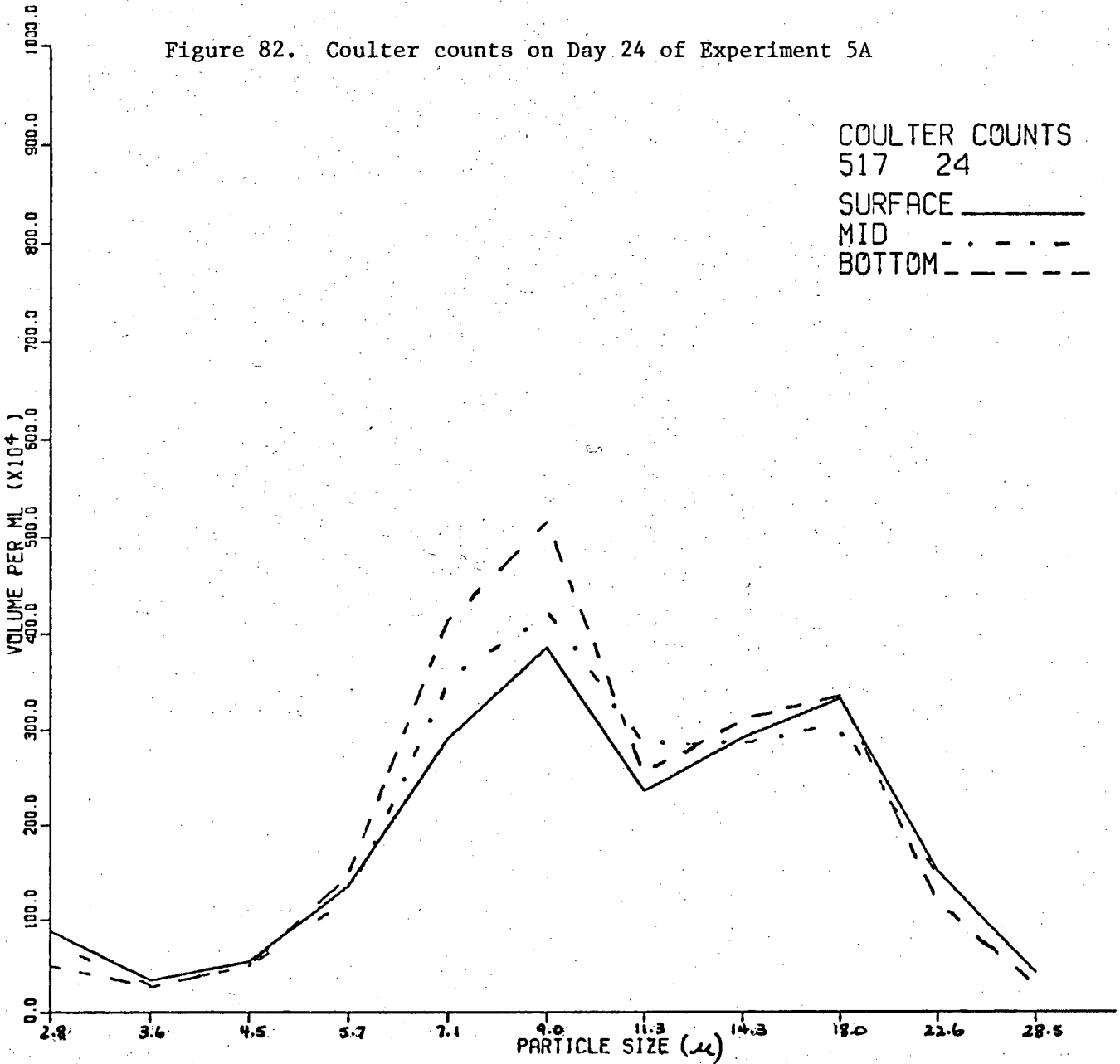


Figure 83. Coulter counts on Day 36 of Experiment 5A

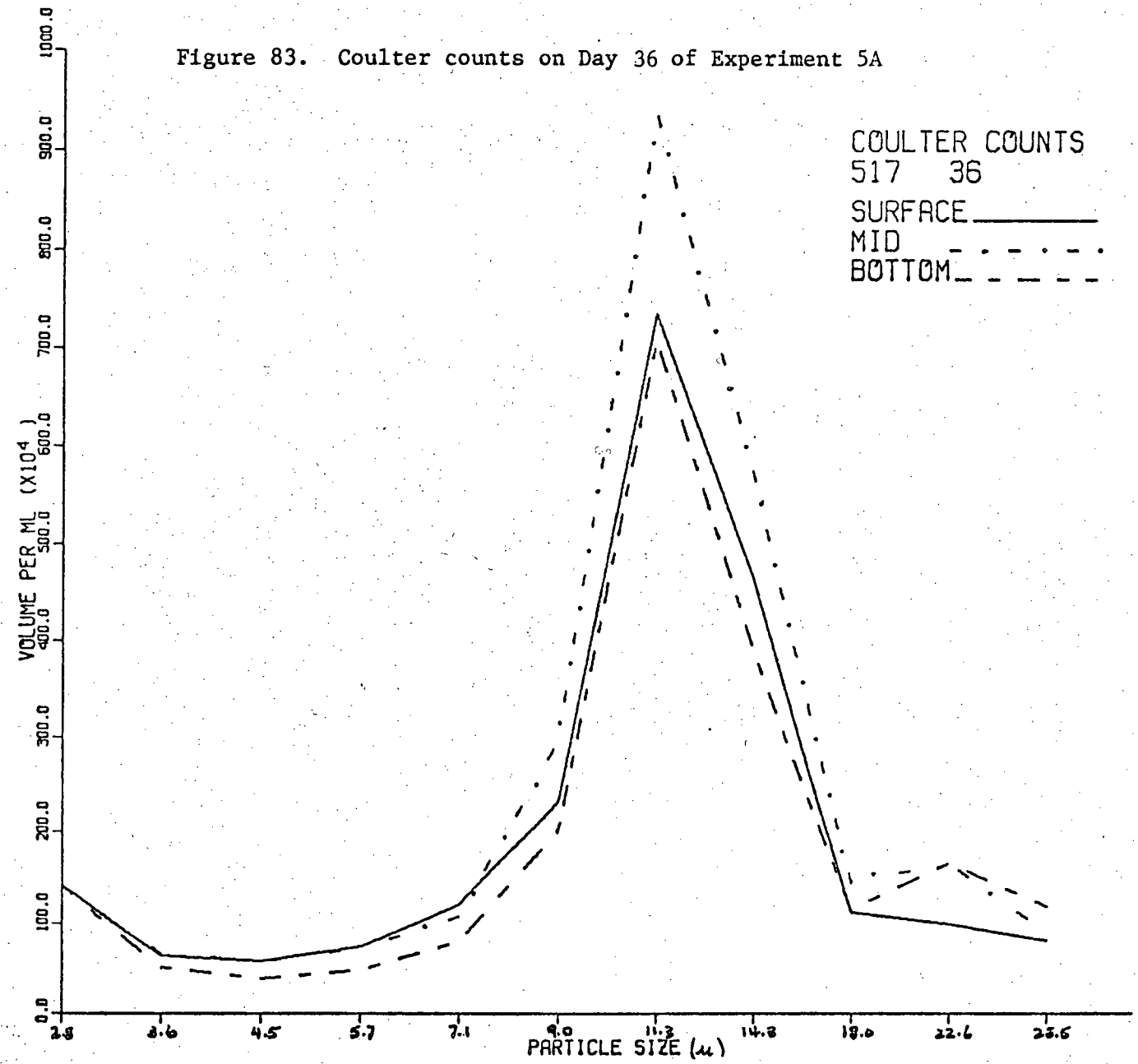


Figure 84. Coulter counts on Day 39 of Experiment 5A

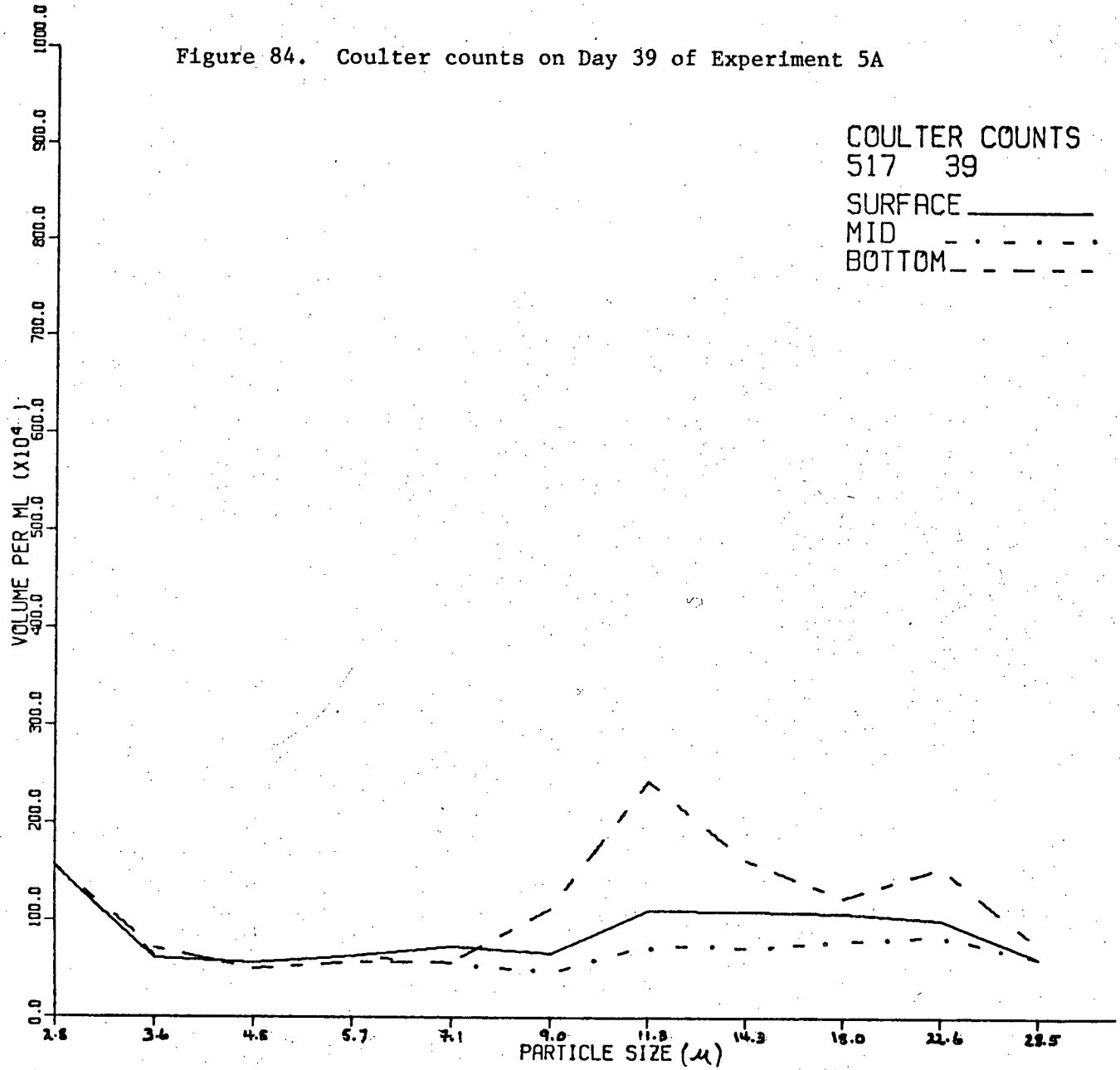


Figure 85. Coulter counts on Day 6 of Experiment 5B

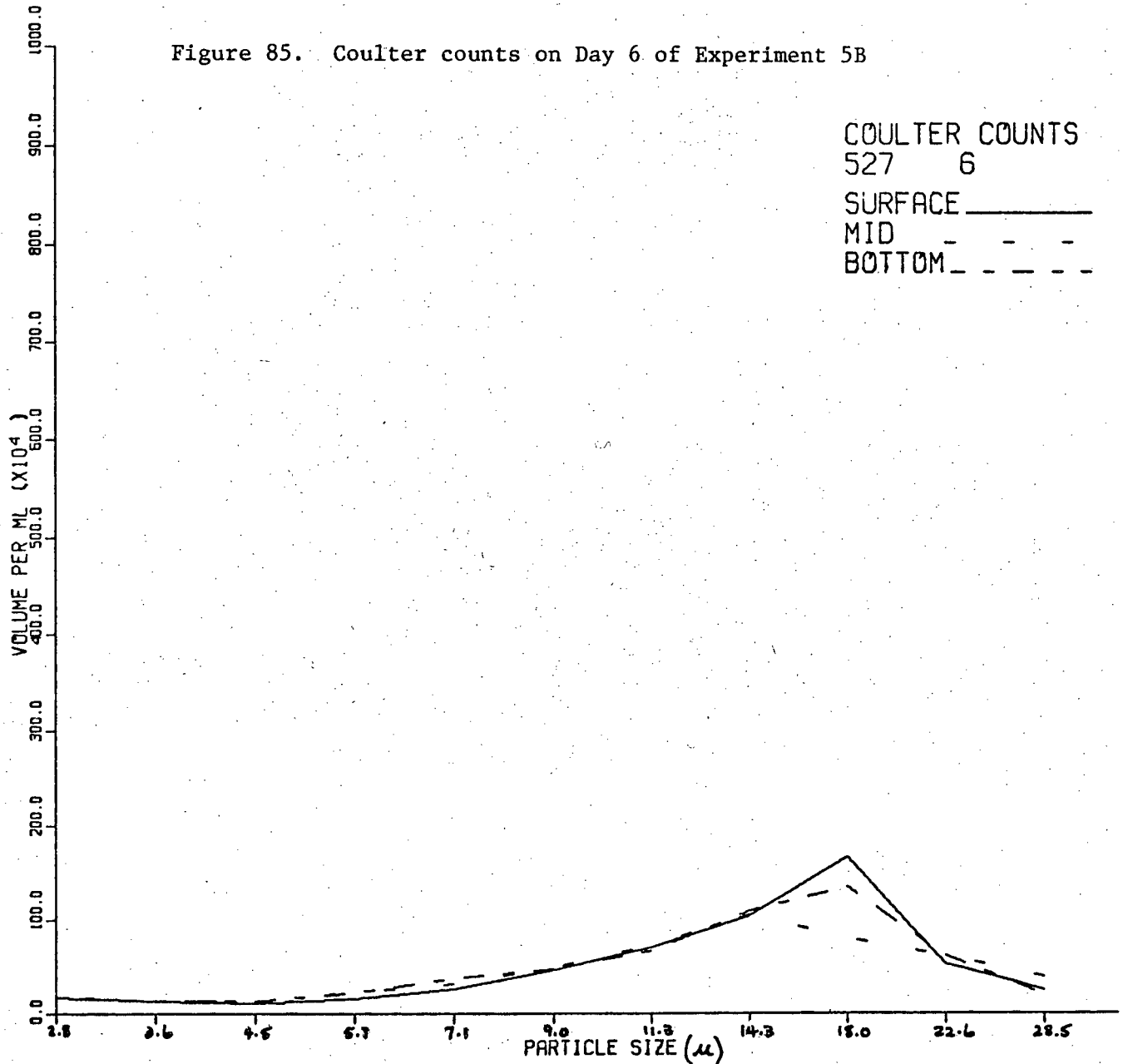


Figure 86. Coulter counts on Day 9 of Experiment 5B

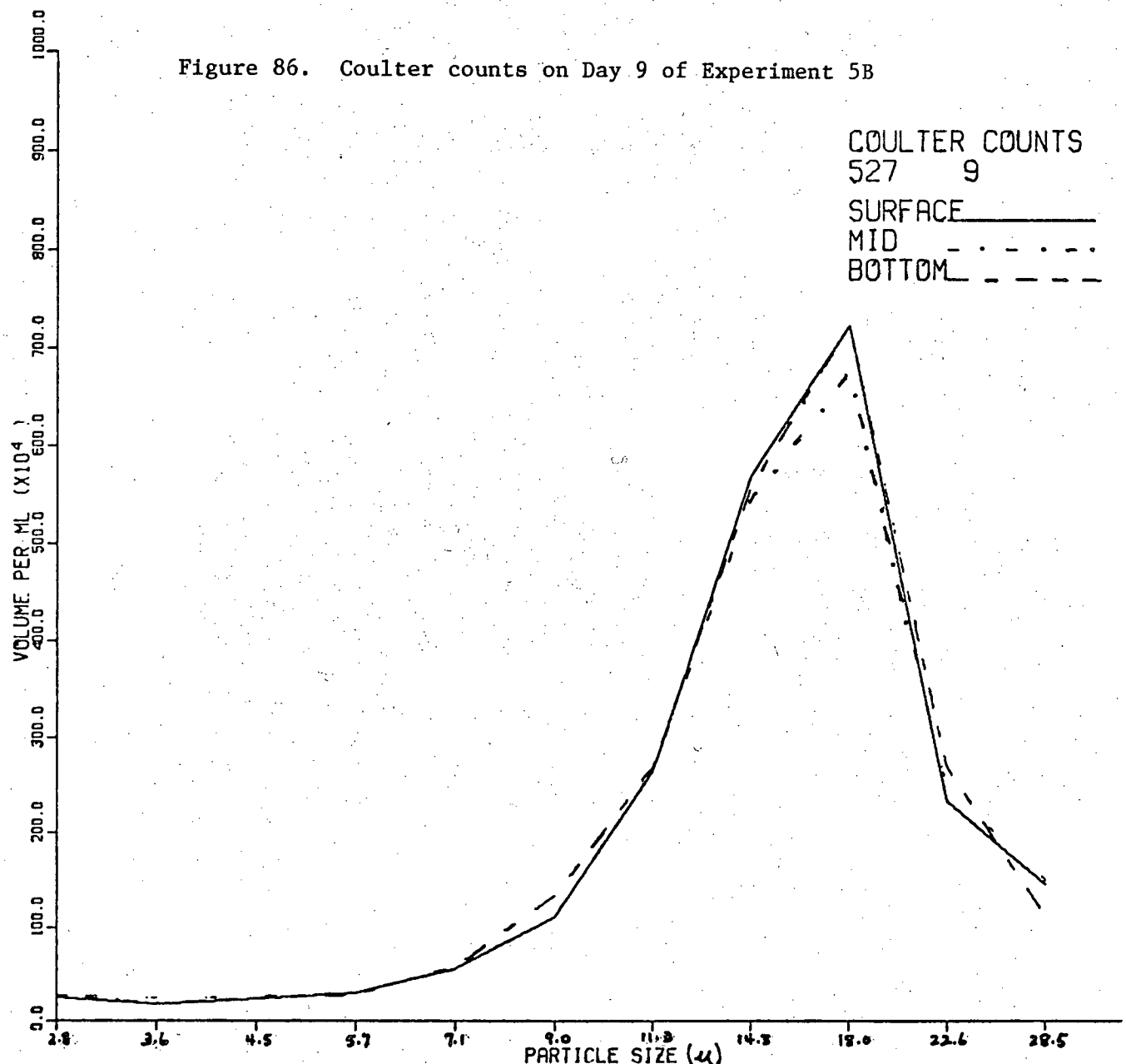


Figure 87. Coulter counts on Day 21 of Experiment 5B

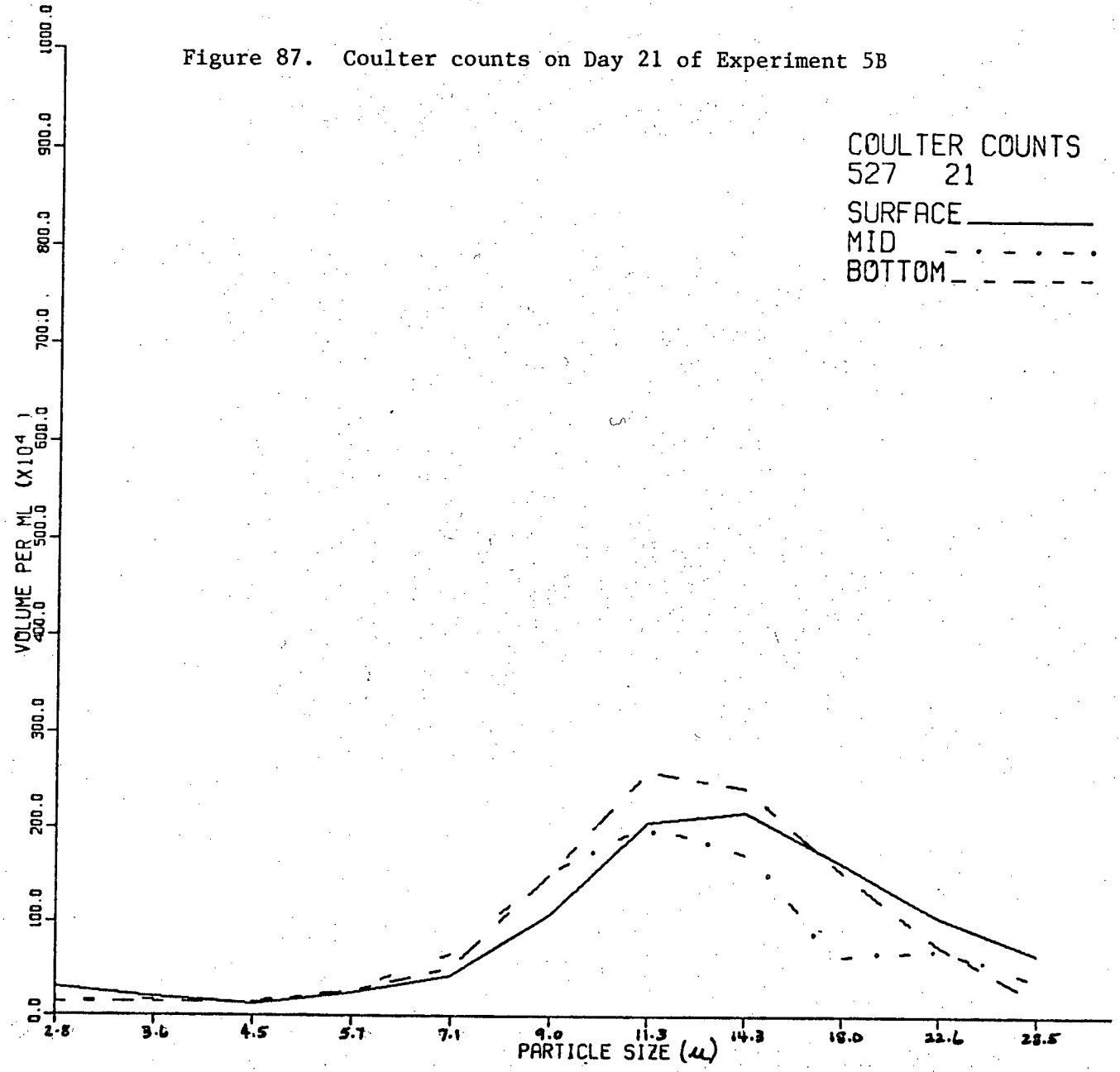


Figure 88. Coulter counts on Day 24 of Experiment 5B

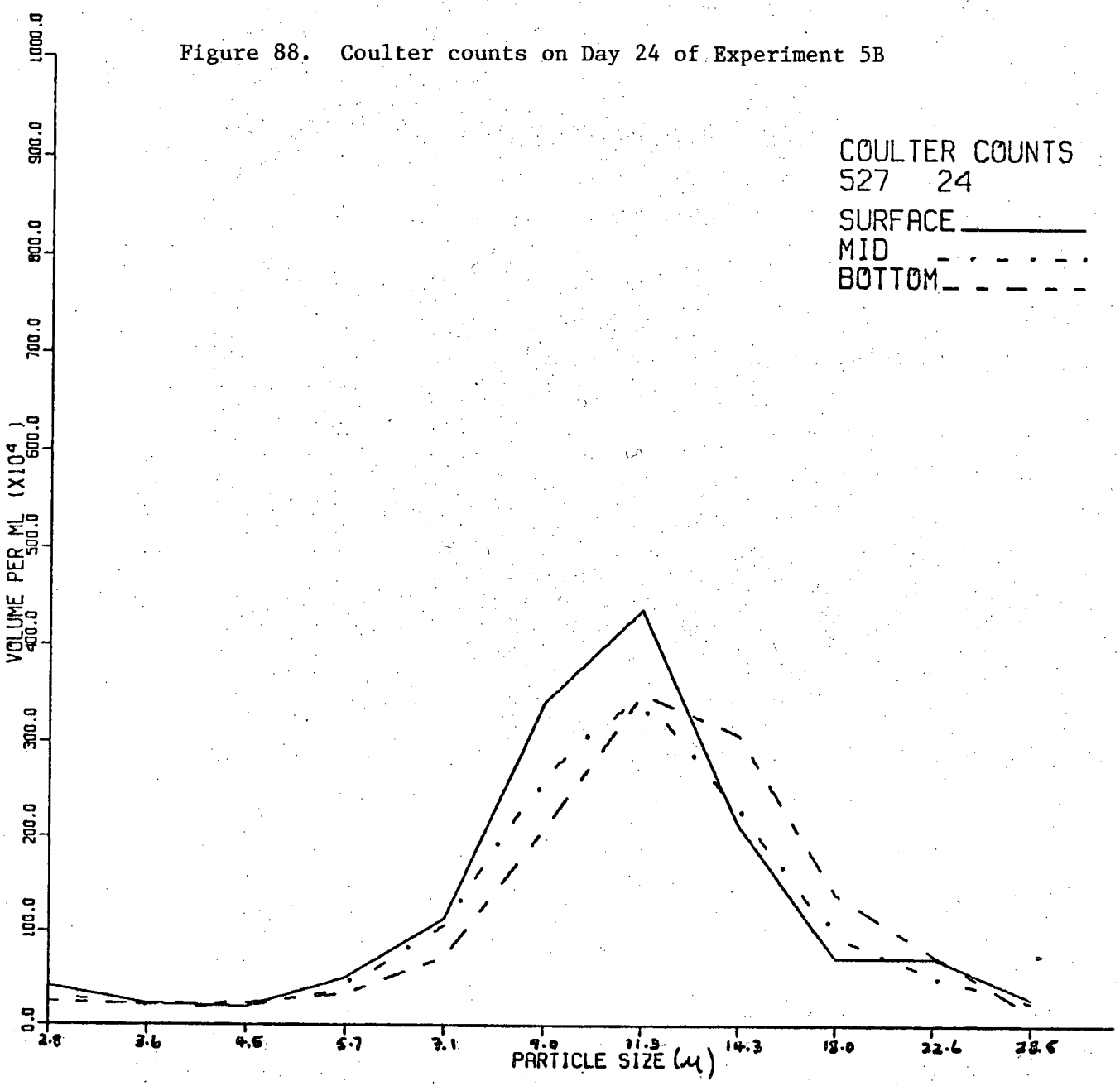


Figure 89. Coulter counts on Day 36 of Experiment 5B

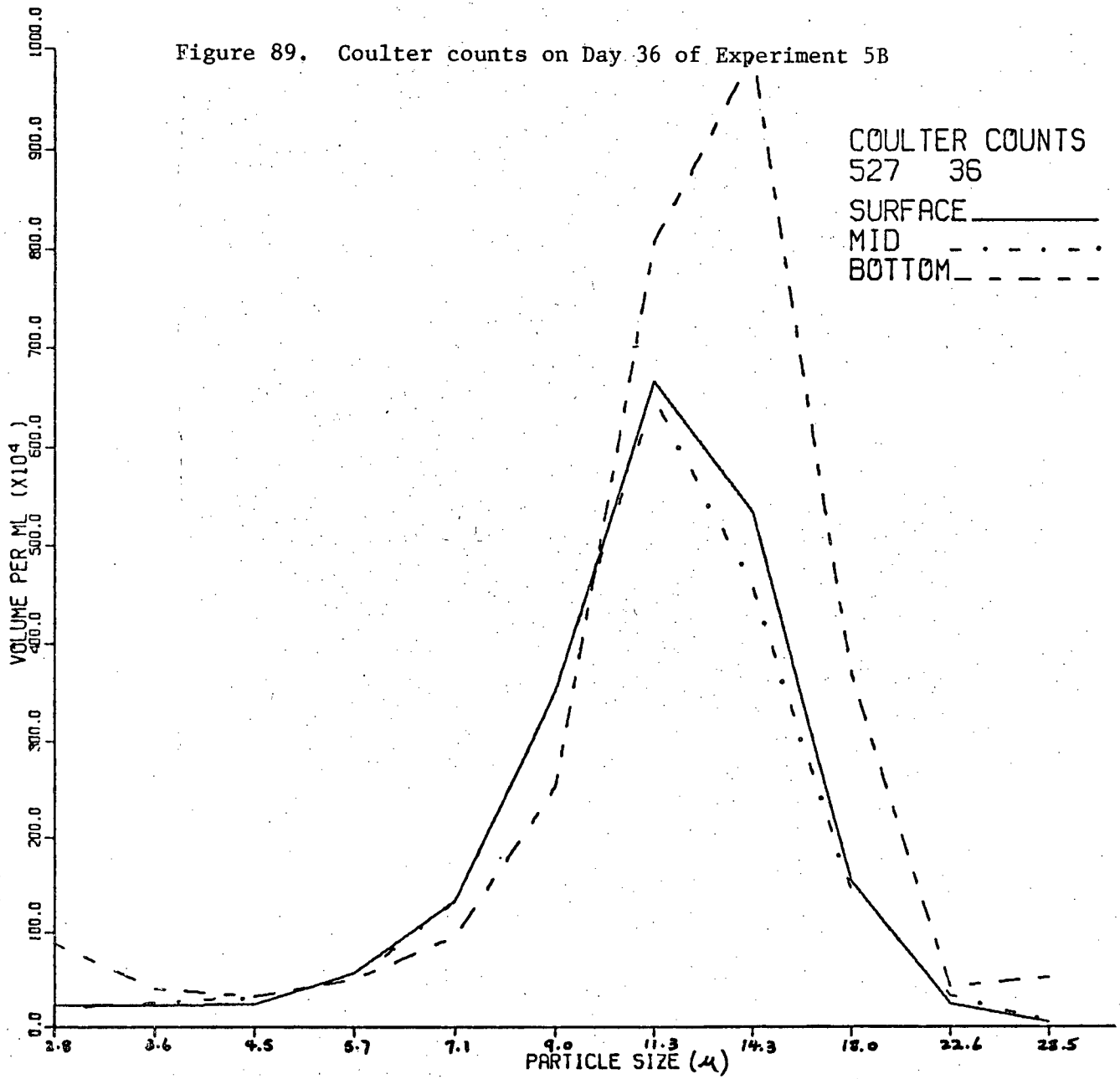


Figure 90. Coulter counts on Day 39 of Experiment 5B

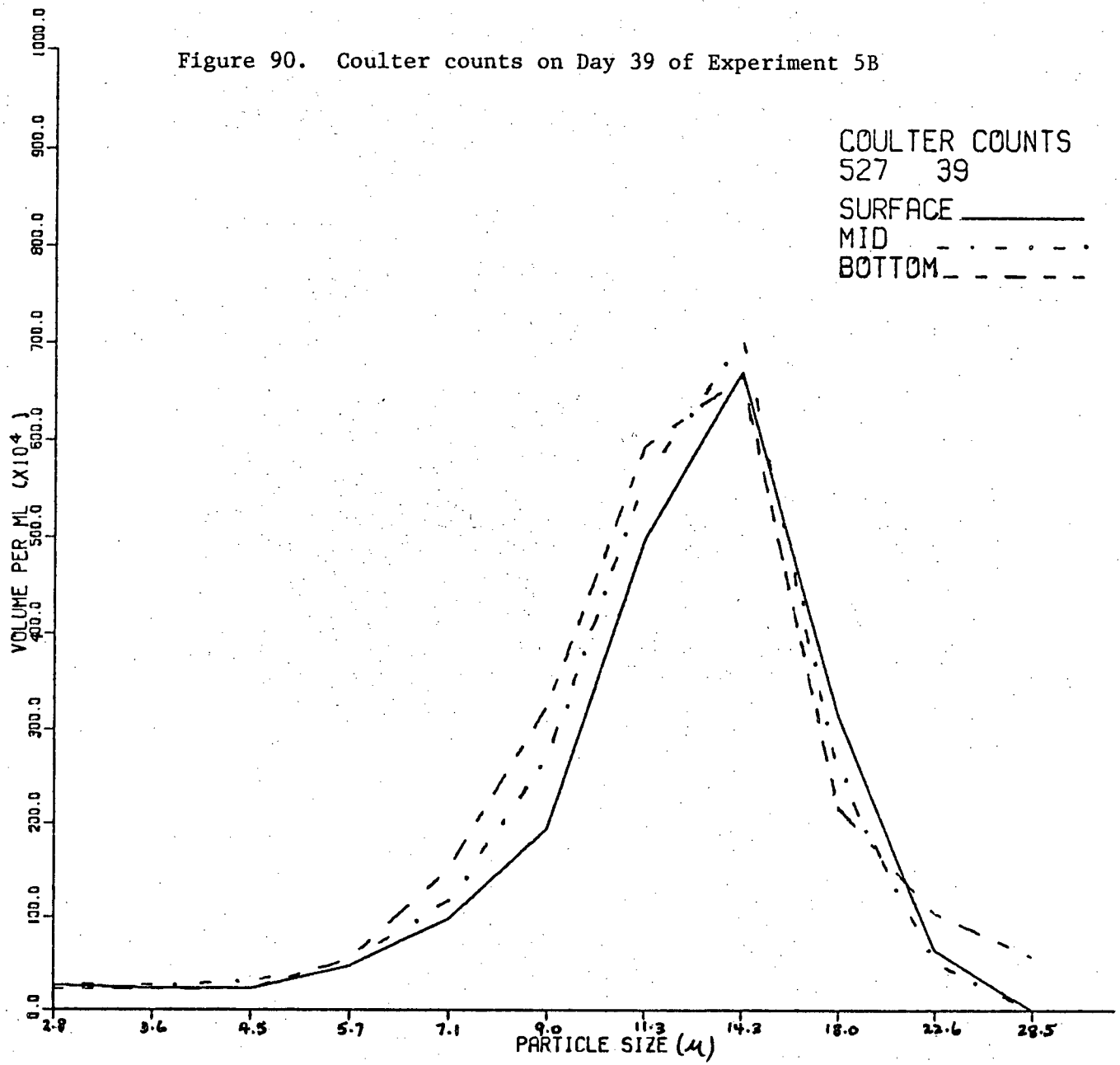


FIGURE 91 TEMPERATURE
IN TWO-STAGE OYSTER CULTURES

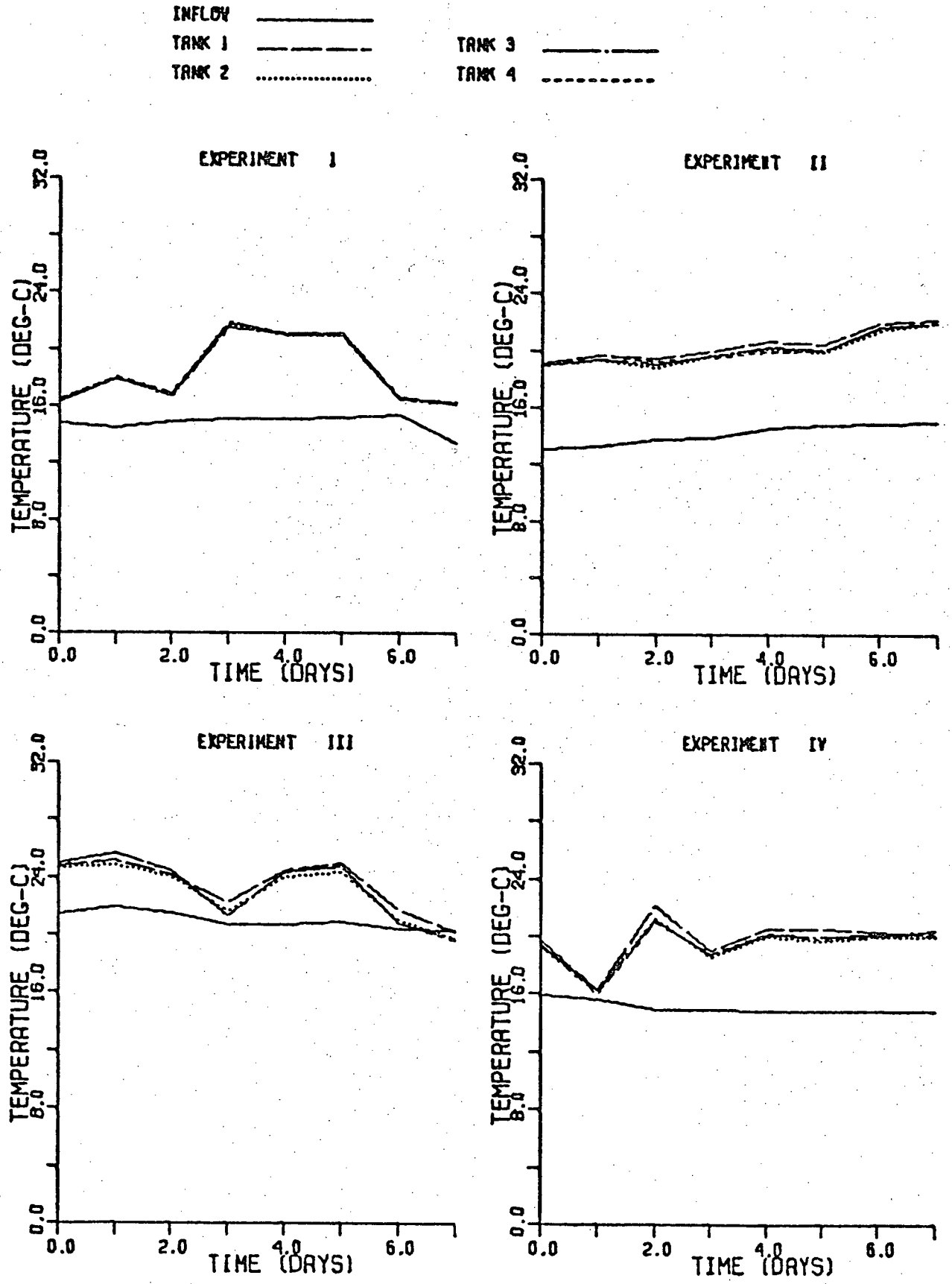


FIGURE 92 CHLOROPHYLL A
IN TWO-STAGE OYSTER CULTURES

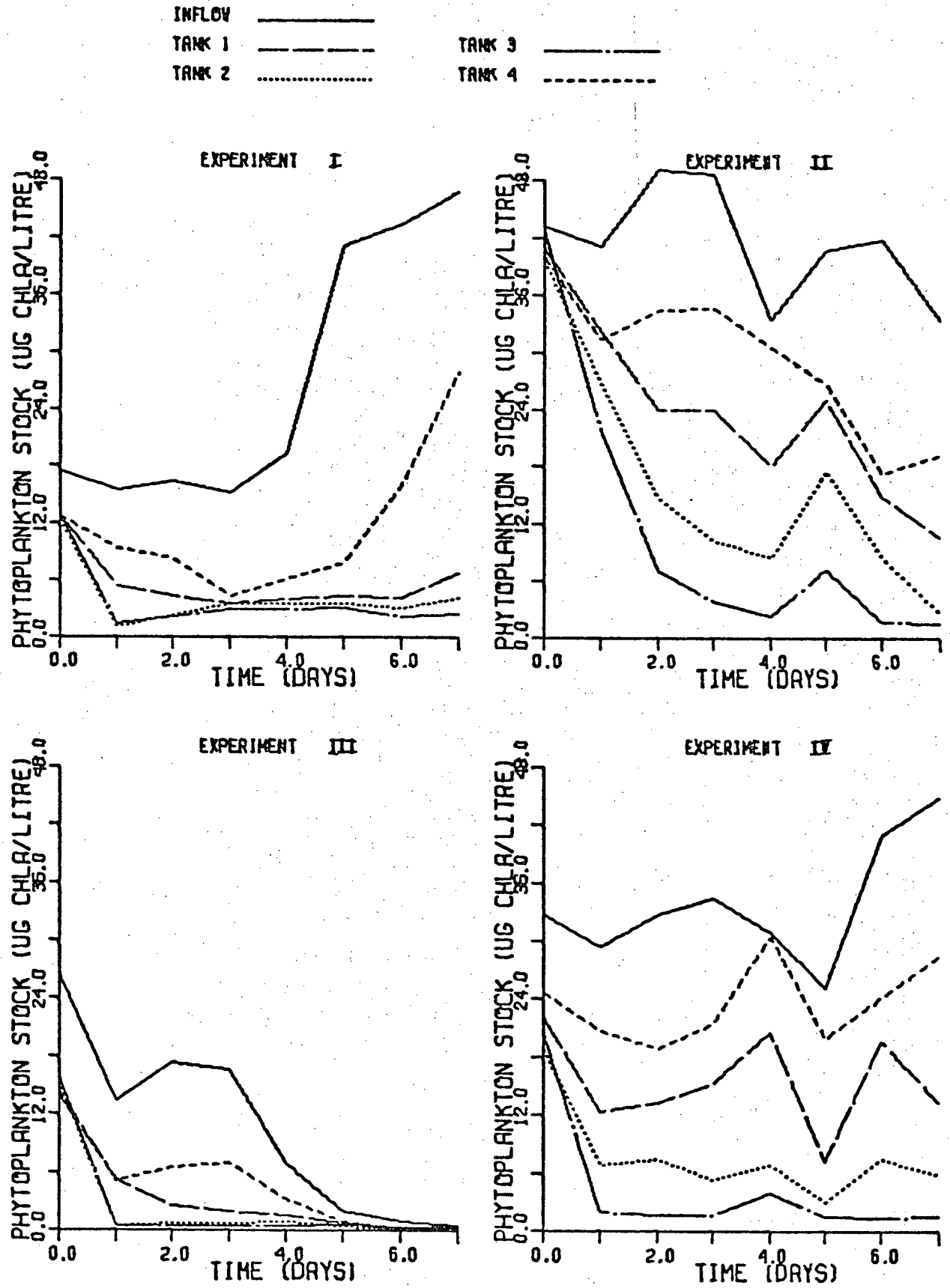


FIGURE 93 OXYGEN LEVELS IN TWO-STAGE OYSTER CULTURES

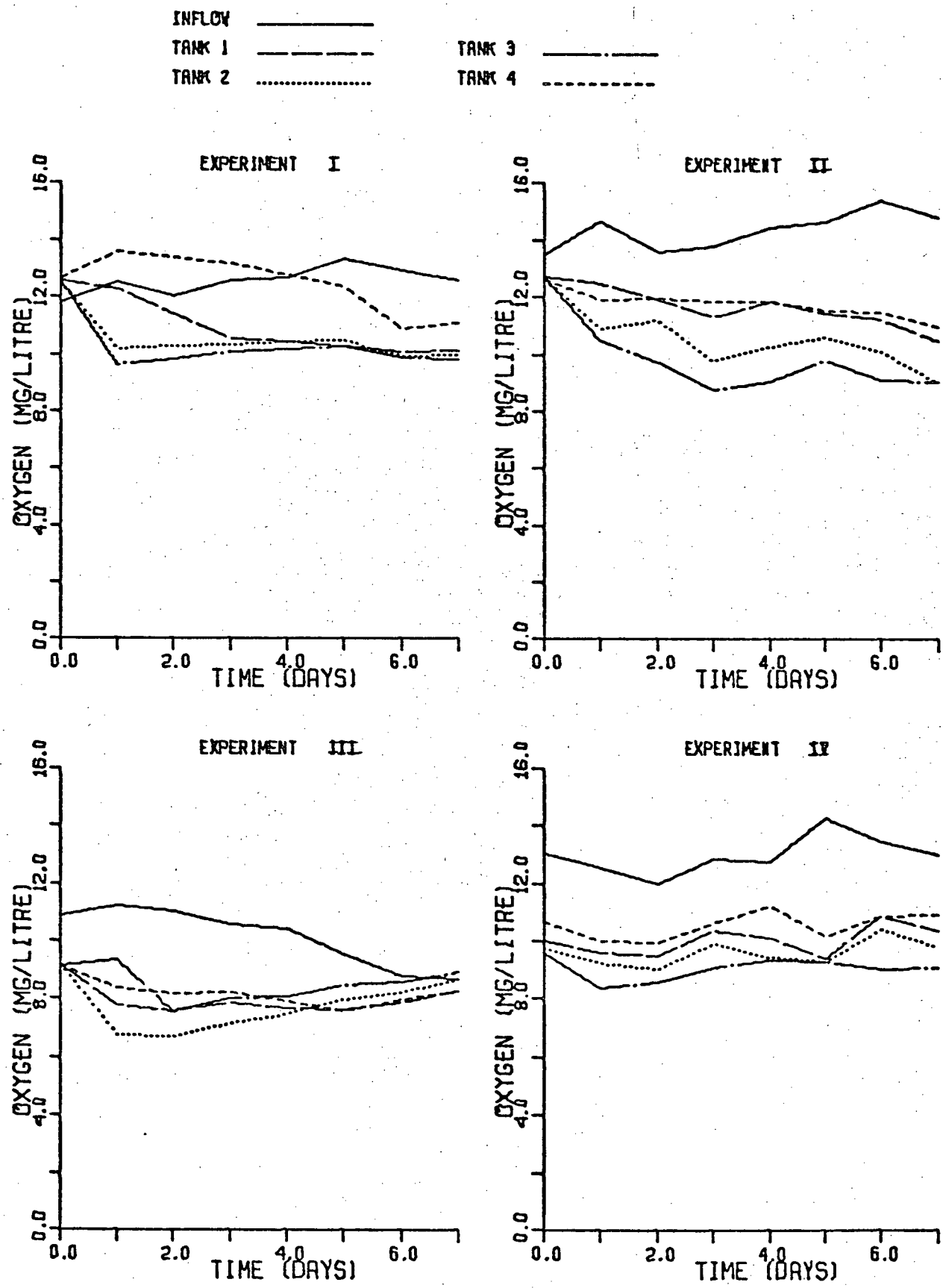


Figure 94. Growth of oysters as a function of DENS in the two-stage culture
(DENS 1 DENS 2 DENS 3)

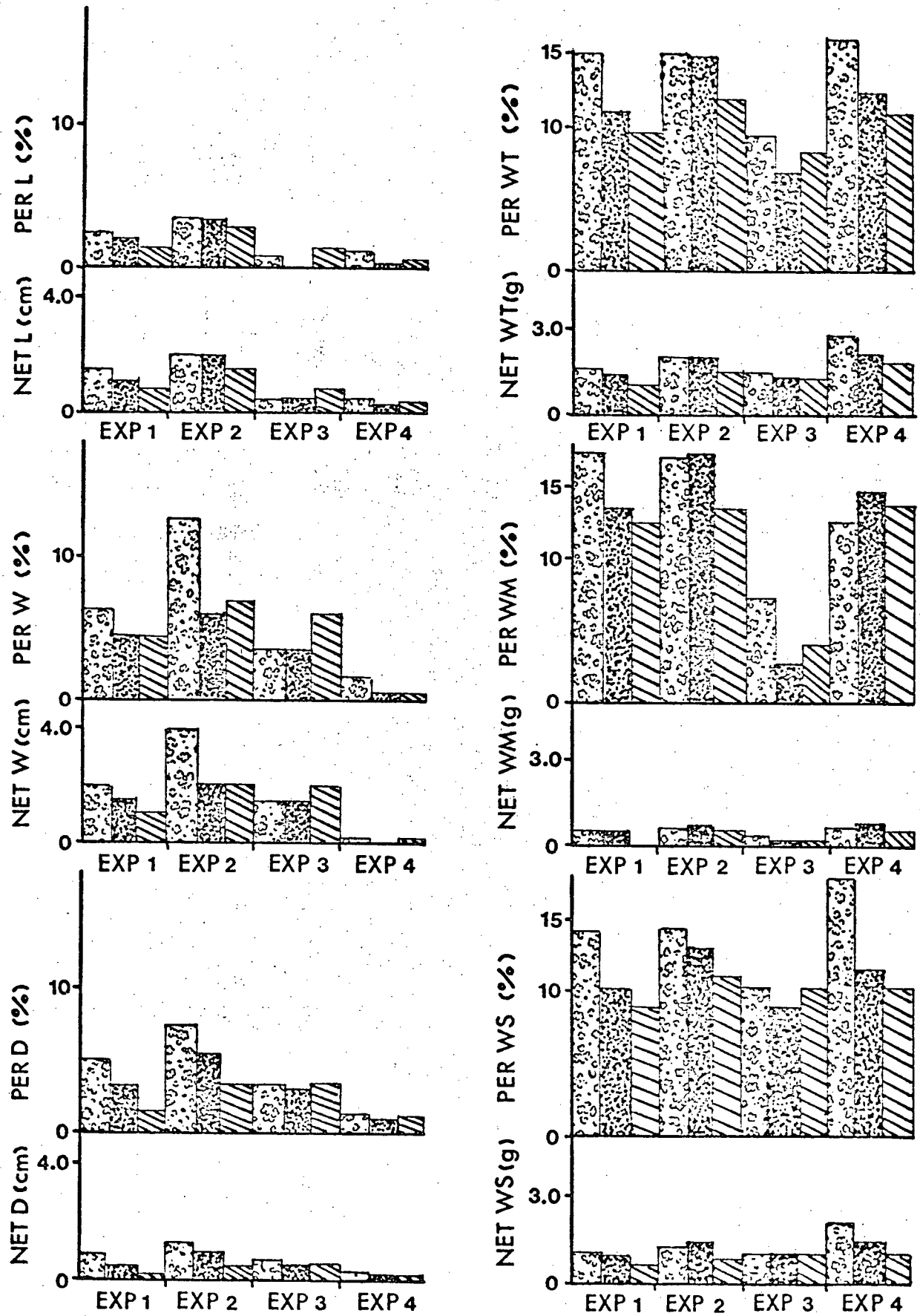


Figure 95. Growth of oysters as a function of SIZE in the two-stage culture
(SIZE 1 SIZE 2 SIZE 3 SIZE 4)

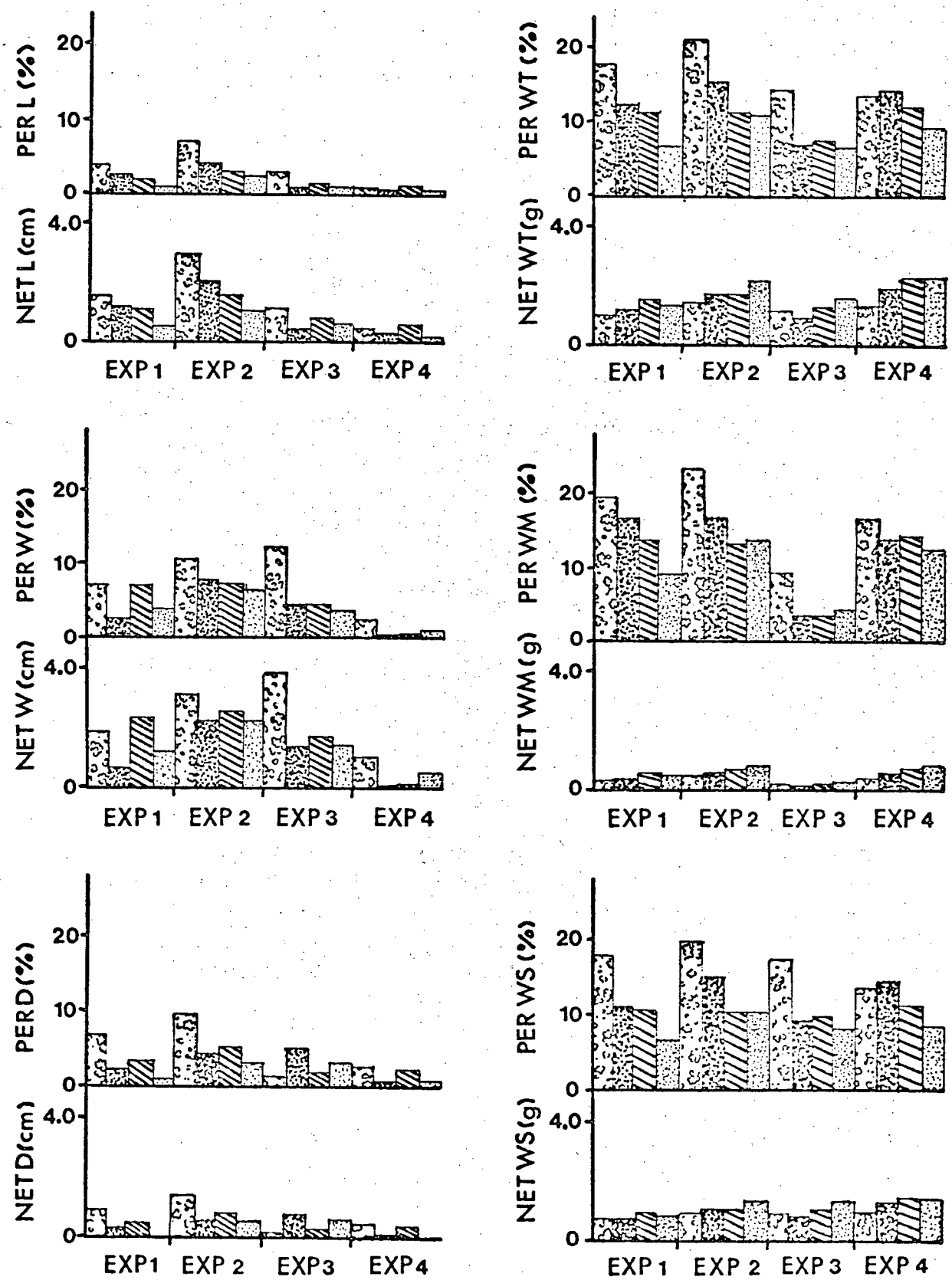


Figure 96. The 'P versus I' curves as a function of temperature and nitrate conditions.

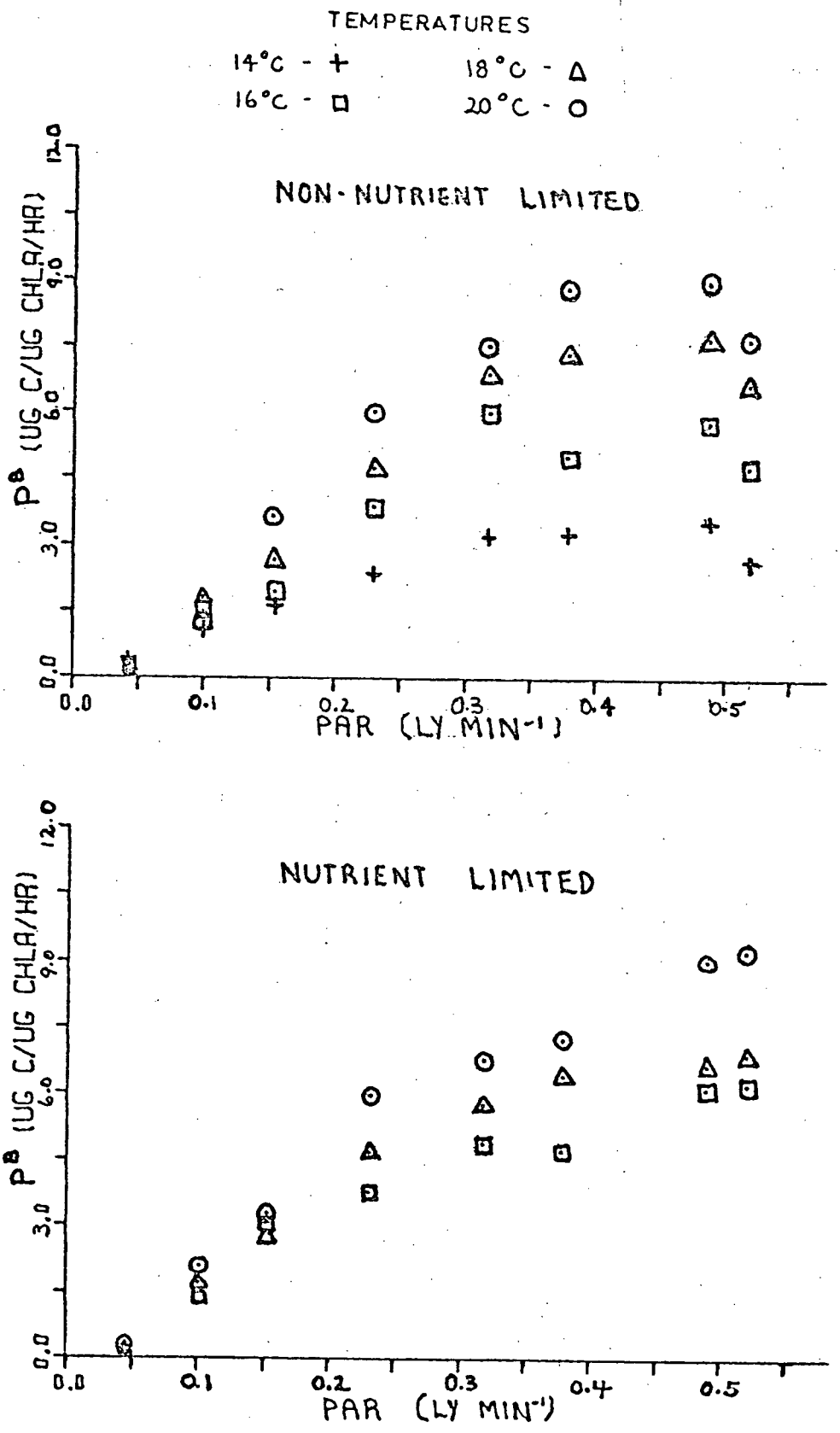


Figure 97. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5B: Run 1

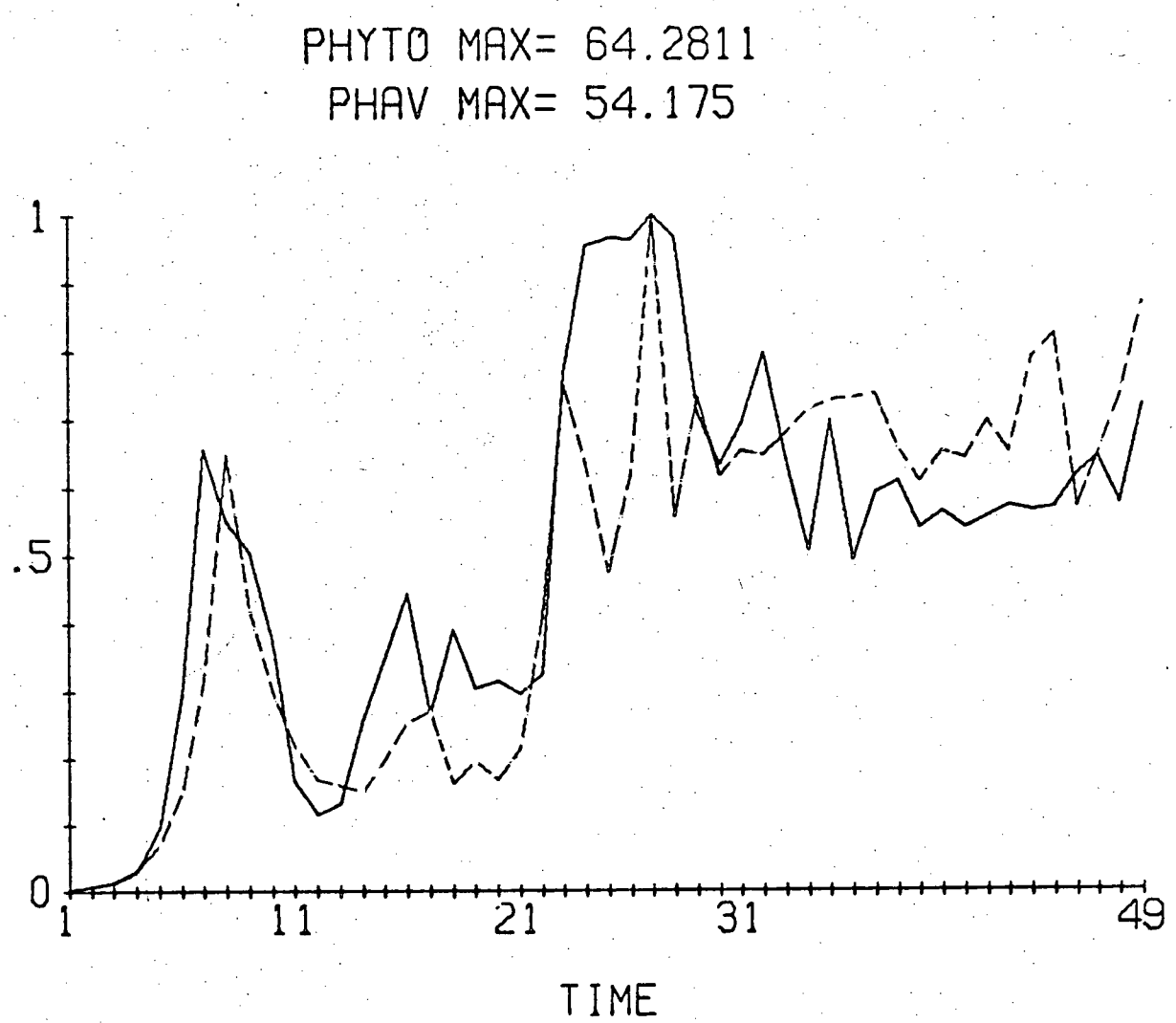


Figure 98. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5B: Run 2

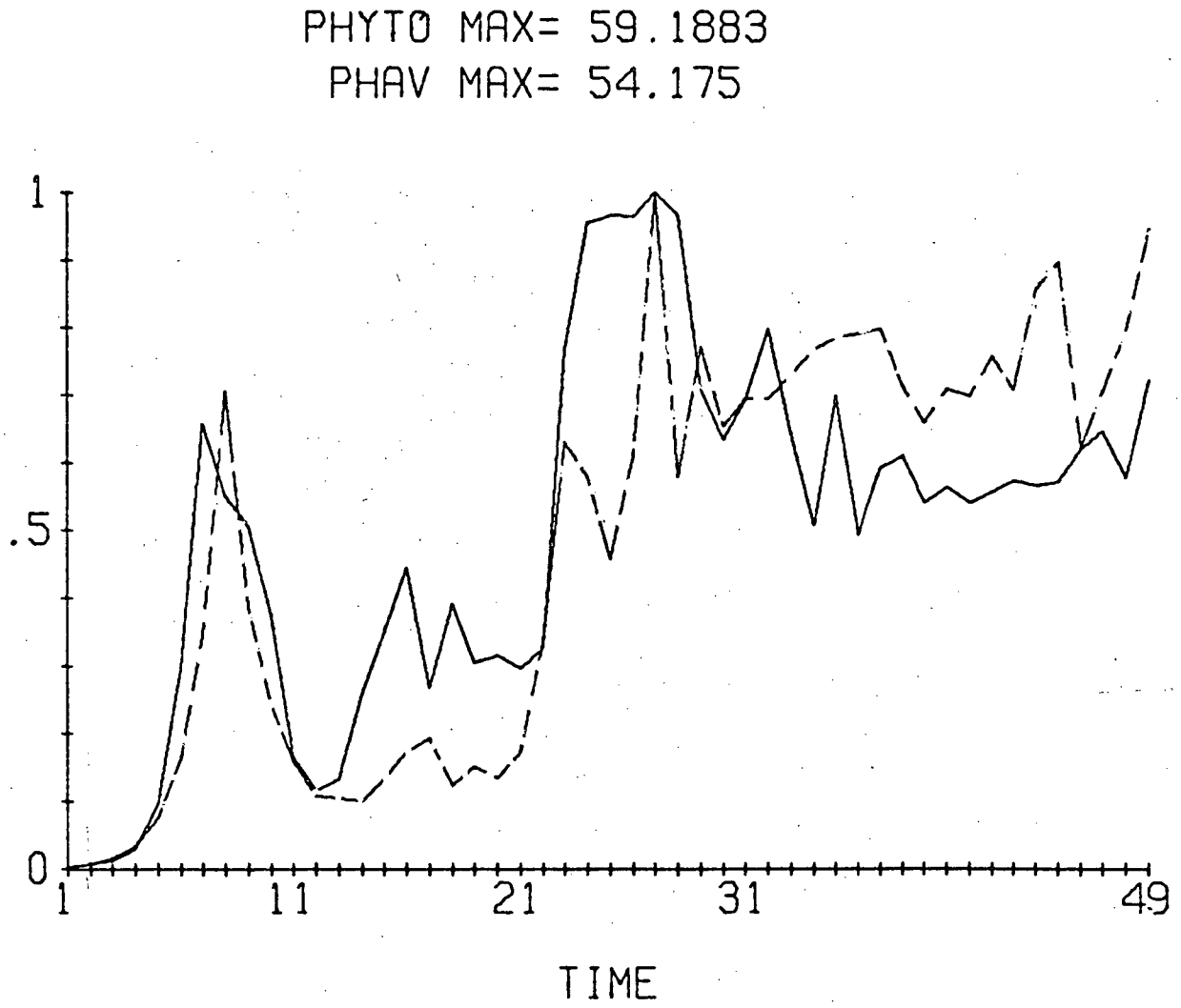


Figure 99. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5B: Run 3

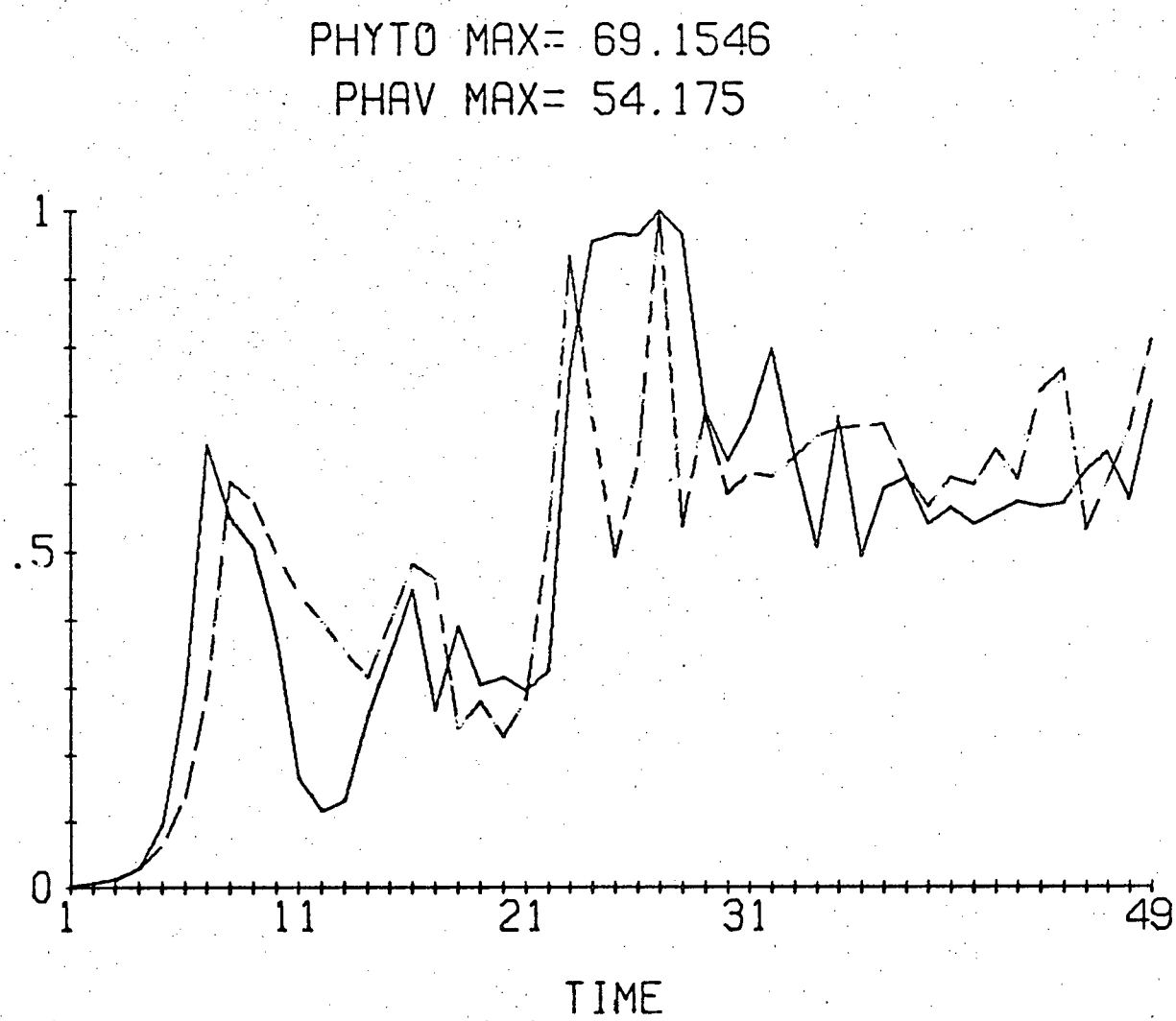


Figure 100. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5B: Run 4

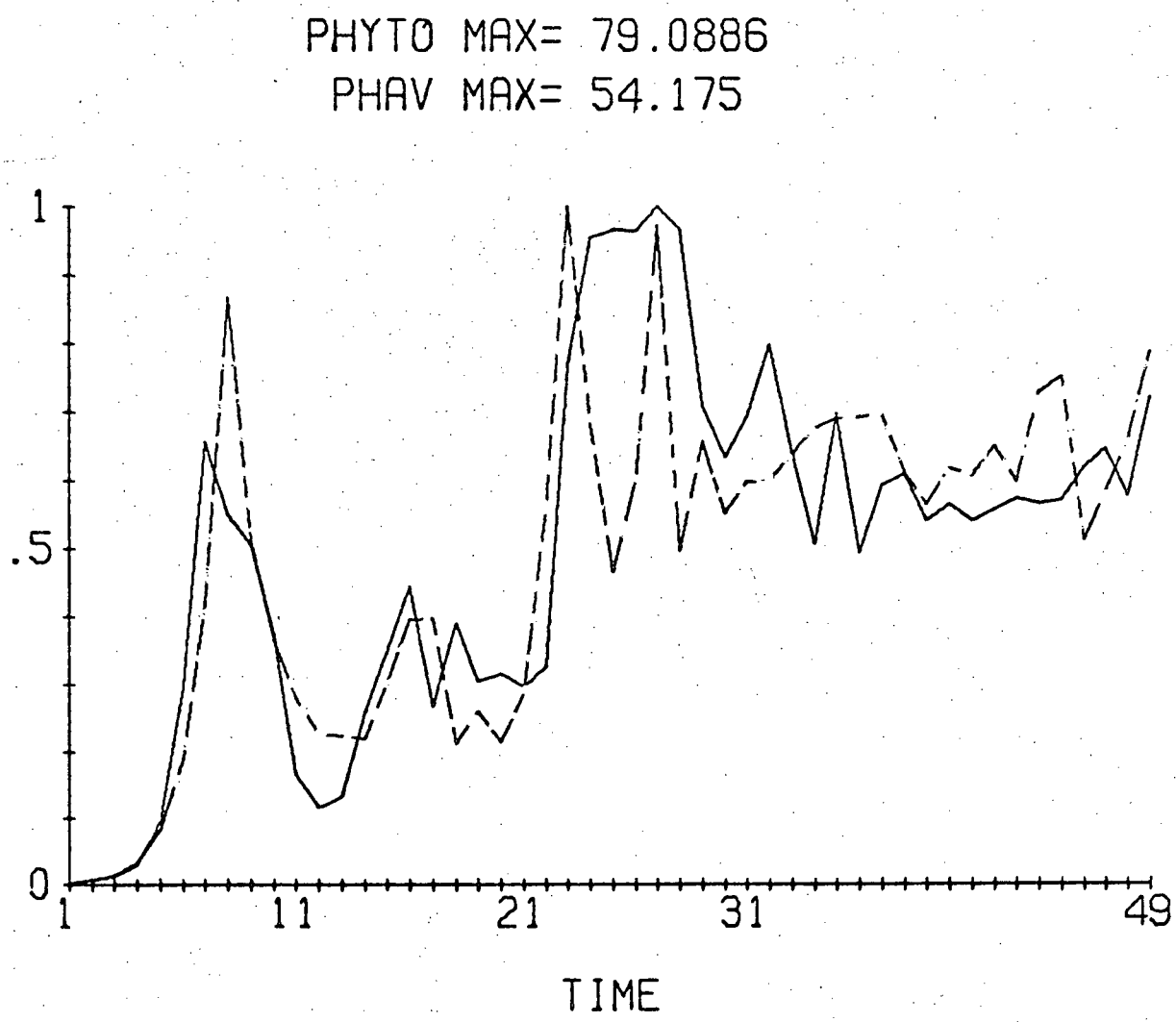


Figure 101. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5A: Run 1

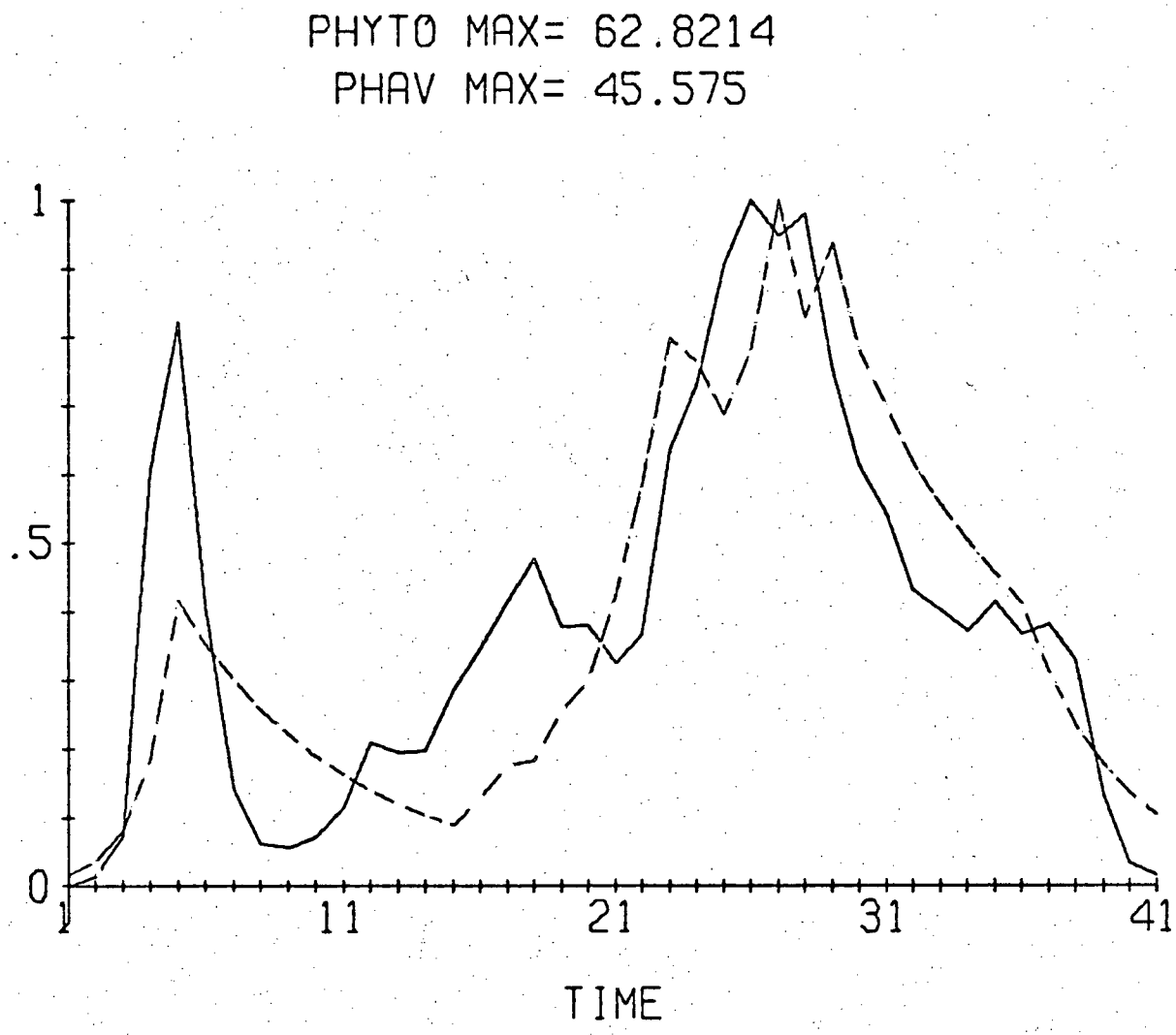


Figure 102. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5A: Run 2

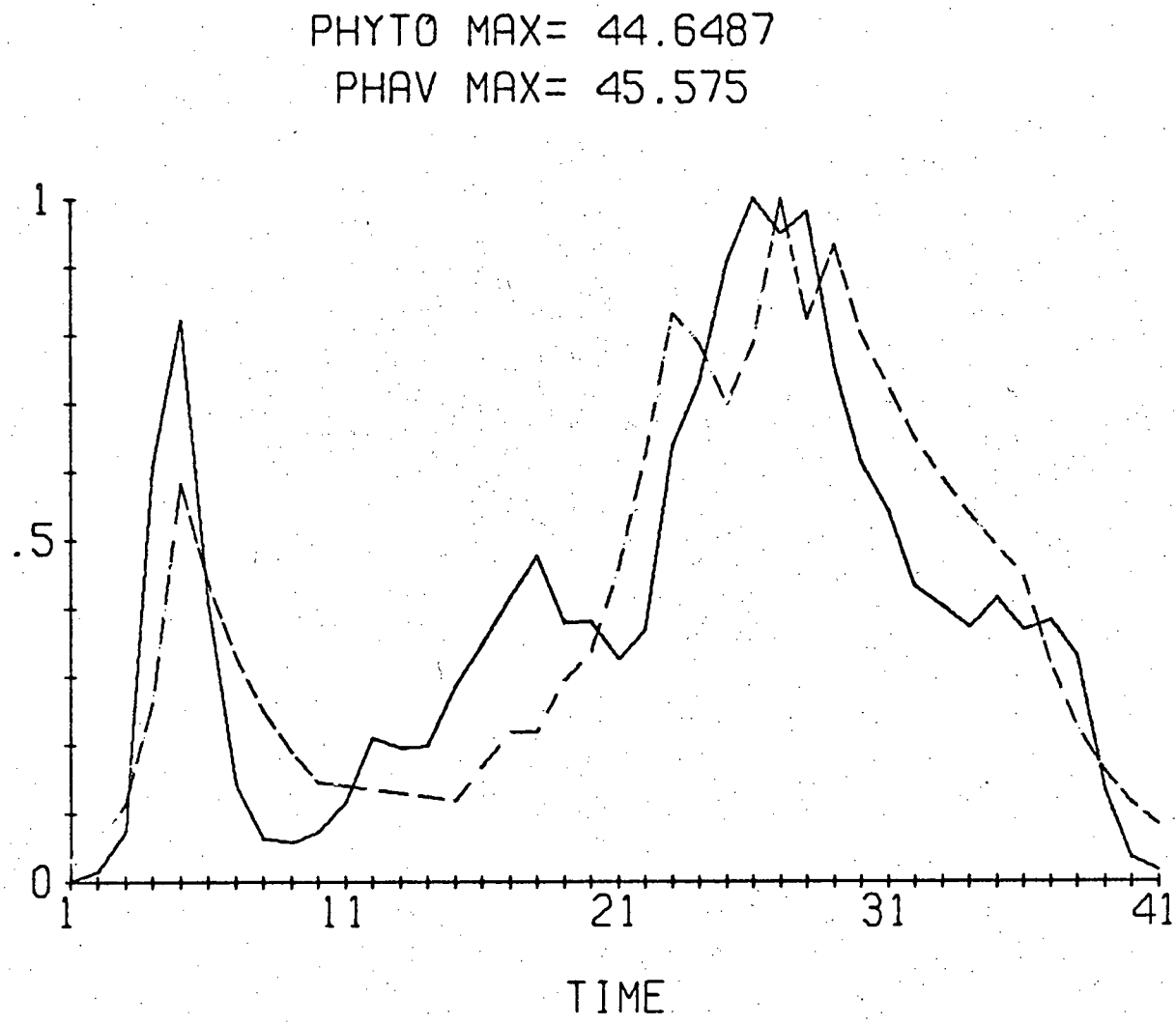


Figure 103. Comparison of the simulated (PHYTO---) versus actual (PHAV) phytoplankton stock during Experiment 5B: Run 1 with a grazing term added on Day 27

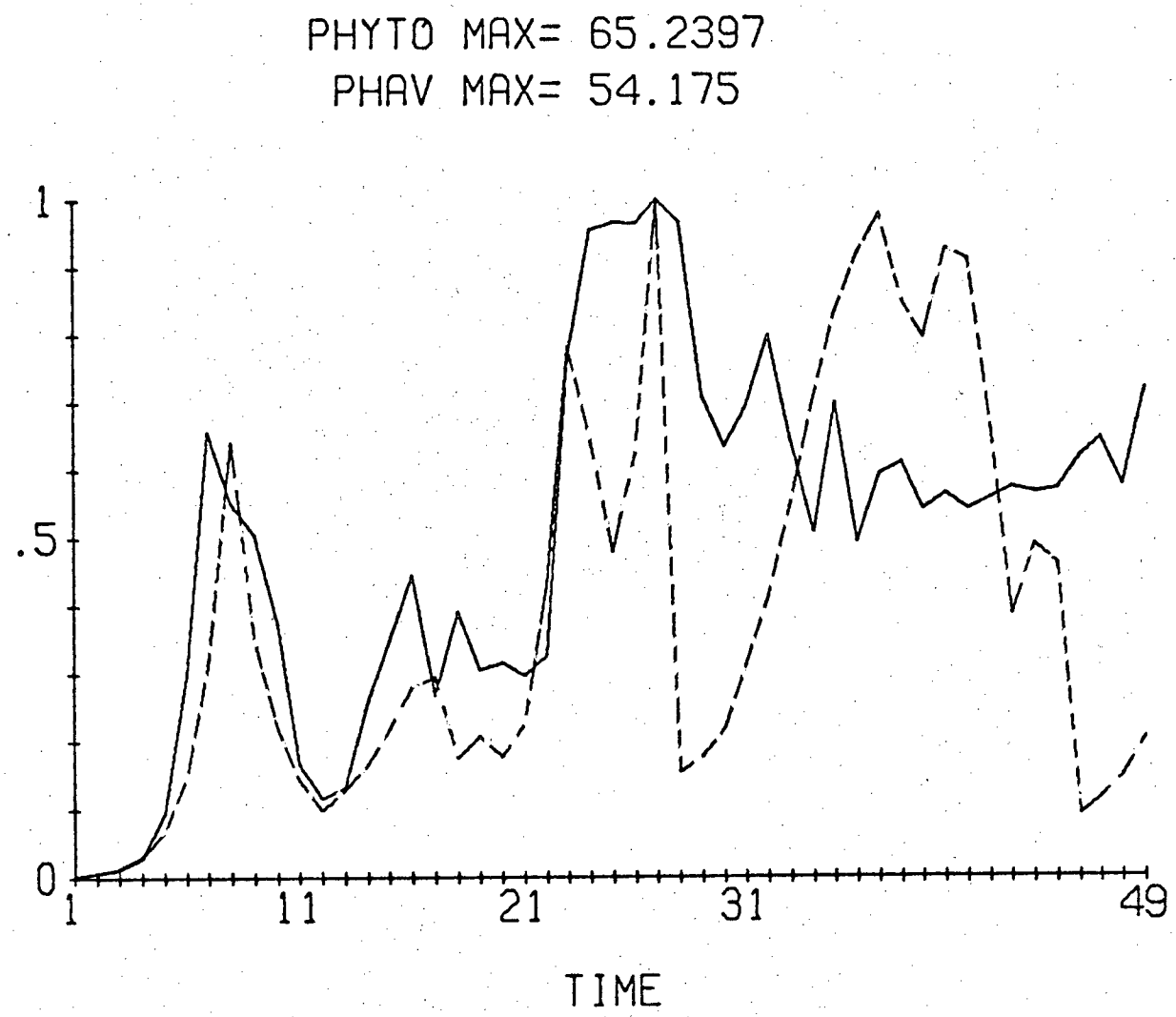


PLATE I

Herbivore tanks in the two-stage culture experiments

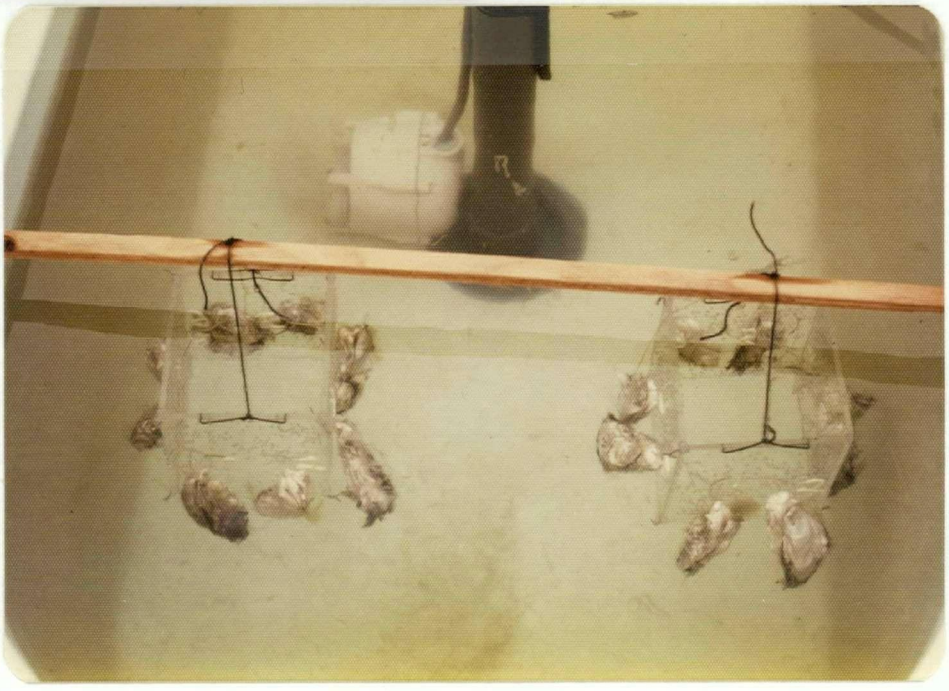


PLATE II

Artificial cultch in the two-stage culture experiments

BIBLIOGRAPHY

Anderson, G.C. and Zeutschel, R.P. 1970. Release of dissolved organic matter by marine phytoplankton in coastal and offshore areas of the N.E. Pacific Ocean. Limnol.Oceanogr. 15:402-407.

Ansell,A.D., Raymont,J.E.G., Lander,K.F., Crowley,E. and Shackley,P. 1963. Studies on the mass culture of Phaeodactylum II.The growth of Phaeodactylum and other species in outdoor tanks. Limnol.Oceanogr. 8:184-206.

Antia,N.J., McAllister,C.D., Parsons,T.R., Stephens,K. and Strickland,J.D.H. 1963. Further measurements of primary production using a large-volume plastic sphere. Limnol.Oceanogr. 8:166-183.

Baab,J.S., Hamm,G.L., Haines,K.C., Chu,A. and Roels,O.A. 1973. Shellfish mariculture in an artificial upwelling system. Nat.Shell.Ass.Proc. 63:63-67.

Bella, D.A. 1970. Simulating the effect of sinking and vertical mixing on algal population dynamics. J.Water Poll.Cont.Fed. 42(5,Part2): R140-R152.

Bevington, P.R. 1969. Data reduction and error analysis for the physical sciences. McGraw-Hill Publishers, N.Y. 336p.

Bierman,V.J.Jr., Verhoff,F.H., Poulson,T.L., and Tenney,M.W. 1974. Multi-nutrient dynamic models of algal growth and species competition in eutrophic lakes. In. Modelling the eutrophication process. Eds. E.J. Middlesbrook, D.H. Falkenburg and T.E. Maloney. Ann Arbour Sc. Publ. Inc., Ann Arbour, Michigan. p. 89-110.

Brown,P.S. and Parsons,T.R. 1972. The effect of simulated upwelling on the maximization of primary productivity and the formation of phytodetritus. Mem. Ist. Ital. Idrobiol. 29 Suppl.:169-183.

Caperon,J. 1967. Population growth in micro-organisms limited by food supply. Ecology 48:715-722.

Caperon,J. and Myer,J. 1972. Nitrogen-limited growth of marine phytoplankton I.Changes in population characteristics with steady-state growth rates. Deep-Sea Res. 19:601-618.

Caperon,J. 1973. A trophic level ecosystem model analysis of the plankton community in a shallow water subtropical estuarine embayment. In. Estuarine Research, V1. Ed. L.E. Cronin. Academic Press, N.Y. p. 691-701.

Cassin,J.M. and McLaughlin,J.J.A. 1971. Phytoplankton cycle of Goose Creek, New York. In. Estuarine Microbial Ecology. Eds. L.H. Stevenson and R.R. Colwell. University of S. Carolina Press. p. 365-386.

Conway,H.L. 1977. Interactions of inorganic nitrogen in the uptake and assimilation by marine phytoplankton. Math.Biosc. 39:222-232.

Conway,H.L., Harrison,P.J., and Davis,C.O. 1977. Marine diatoms grown in chemostats under silicate or ammonium limitation II.Transient response of Skeletonema costatum to a single addition of the limiting nutrient. Math.Biosc. 35:187-199.

Cushing,D.H. 1971. Upwelling and the production of fish. Adv.Mar.Biol. 9:255-334.

Davis,C.O. 1976. Continuous culture of marine diatoms under silicate limitation II.Effect of light intensity on growth and nutrient uptake of Skeletonema costatum. J.Phycol. 12:291-300.

Davis,C.O., Harrison,P.J., and Dugdale,R.C. 1973. Continuous culture of marine diatoms under silicate limitation I.Synchronized life cycles of Skeletonema costatum. J. Phycol. 9:175-180.

Degobbis, D. 1973. On the storage of seawater samples for ammonia determination. Limnol.Oceanogr. 18:146-150.

Dickman,M. 1969. Some effects of lake renewal on phytoplankton productivity and species composition. Limnol.Oceanogr. 14:660-666.

Di Toro, D.M., O.Connor, D.J., and Thomann, R.V. 1975. Phytoplankton-zooplankton-nutrient interaction model for Western Lake Ontario. In. Systems Analysis and Simulation in Ecology, V.3. Ed. B.C. Patten. Academic Press, N.Y. p.423-474.

Dunstan,W.M. and Tenore,K.R. 1972. Intensive outdoor culture of marine phytoplankton enriched with sewage effluent. Aquaculture 1:181-192.

Dunstan,W.M. and Tenore,K.R. 1974. Control of species composition in enriched mass cultures of natural phytoplankton populations. J.Appl.Ecol. 11:529-536.

Epifano,C.E. and Mootz,C.A. 1976. Growth of oysters in a recirculating mariculture system. Nat.Shell.Ass.Proc. 65:32-37.

Eppley,R.W. and Sloan, P.R. 1965. Carbon balance experiments with marine phytoplankton. J.Fish.Res.Bd.Can. 22:1083-1097.

Eppley,R.W. and Dyer,D.L. 1965. Predicting production in light-limited continuous cultures of algae. Arch.Microbiol. 13:833-837.

Eppley,R.W., Rogers,J.N., and McCarthy,J.J. 1971. Light/dark periodicity in nitrogen assimilation of the marine phytoplankters Skeletonema costatum and Coccolithus huxleyi in N-limited chemostat cultures. J.Phycol. 7:150-154.

Goldman,J.C., Ryther,J.H. and Williams,L.D. 1975. Mass production of marine algae in outdoor cultures. Nature 254:594-595.

Grenney, W.J., Bella, D.A. and Curl, H.C.,Jr. 1973a. A theoretical approach to interspecific competition in phytoplankton communities. Amer.Naturalist 107:405-425.

Grenney, W.J., Bella, D.A. and Curl, H.C.,Jr. 1973b. A mathematical model of the nutrient dynamics of phytoplankton in a nitrate limited environment. Biotech.Bioeng. 15:331-358.

Gross,P., Nutman,S.R., Gauld,D.T. and Raymont,J.E.G. 1950. A fish cultivation experiment in an arm of a sea loch. I-V. Proc.Roy.Soc.Edinb.,B, 64:1-135.

Hager, S.W., Atlas, E.L., Gordon, L.I., Mantyla, A.W. and Park,P.K. 1972. A comparison at sea of manual and AutoAnalyzer analysis of phosphate, nitrate and silicate. Limnol.Oceanogr. 17: 931-937.

Harrison,P.J., Conway,H.L. and Dugdale,R.C. 1976. Marine diatoms grown in chemostats under silicate or ammonium limitation I.Cellular chemical composition and steady-state growth kinetics of Skeletonema costatum. Math.Biosc. 15:177-186.

Haynes,R.C. 1973. Some ecological effects of artificial circulation on a smalll eutrophic lake with particular emphasis on phytoplankton. Hydrobiol. 43:463-504.

Imai,T. 1967. Mass production of molluscs by means of rearing larvae in tanks. Venus 25:159-167.

Jassby, A.D. and Platt, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol.Oceanogr. 21:540-547.

Ketchum, B.H., Lillick,L. and Redfield, A.C. 1949. The growth and optimum yields of algae in mass culture. J.Comp.Cell.Physiol. 33:267-279.

Kirby-Smith,W.W. and Barber,R.T. 1974. Suspension feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of bay scallops. Aquaculture 3:135-145.

Kremer,J.N. and Nixon,S.W. 1973. An ecological simulation model of Narraganett Bay - the plankton community. In. Estuarine Research, V1, p.691-701. (ed. Cronin,L.E.). Academic Press, N.Y.

Loosanoff,V.L. and Davis,H.C. 1963. Rearing of bivalve molluscs. Adv.Mar.Biol. 1:1-136.

Lummi Indian Tribal Enterprise. 1970. Lummi Indian progress. L.I.T.E. Report, September, 1970. 4p.

McAllister, C.D., Parsons, T.R., Stephens, K. and Strickland,J.D.H. 1961. Measurements of primary production using a large-volume plastic sphere. Limncl.Oceanogr. 6:237-258.

McAllister, C.D., Shah, N. and Strickland, J.D.H. 1964. Marine phytoplankton photosynthesis as function of light intensity: a comparison of methods. J.Fish.Res.Bd.Can. 21: 159-181.

McAllister, C.D., LeBrasseur, R. and Parsons, T.R. 1972. Stability of enriched aquatic ecosystems. Science 175:562-564.

Maddux, W.S. 1966. A 4π light meter. Limncl.Oceanogr. 11:136-137.

Maddux, W.S. and Jones, R.F. 1964. Some interactions of temperature, light intensity and nutrient concentration during the continuous culture of Nitzschia closterium and Tetraselmis sp. Limnol.Oceanogr. 9:79-86.

Malone,T.C., Garside,C., Haines,K.C. and Roels,O.A. 1975. Nitrate uptake and growth of Chaetoceros sp. in large outdoor continuous culture. Limnol.Oceanogr. 20:9-19.

Odum, E.P. and Schelske, C.L. 1961. Mechanisms for maintaining high productivity in Georgia estuaries. Gulf Carib. Fish. Inst. Proc. 14: 75-80.

Oppenheimer,C.H. 1966. Marine Biology , V.2. A.I.B.S., Washington,D.C. p. 321-335.

Paloheimo, J.E. and Dickie, L.M. 1970. Production and food supply. In. Marine Food Chains. Ed. J.H. Steele. Oliver and Boyd, Edinburgh. p. 499-527.

Parsons,J. 1974. Advantages in tray cultivation of Pacific oysters (Crassostrea gigas) in Strangford Lough, N. Ireland. Aquaculture 3:221-229.

Parsons, T.R. and Takahashi, M. 1973a. Biological oceanographic processes. Pergamon Press, Toronto. 186p.

Parsons,T.R. and Takahashi,M. 1973b. Environmental control of cell size. Limnol.Oceanogr. 18:511-515.

Patten, B.C. and Van Dyne, G.M. 1968. Factorial productivity experiments in a shallow estuary: energetics of individual plankton species. Limnol. Oceanogr. 13:309-314.

Phillips, O.M. 1974. The equilibrium and stability of simple marine biological systems II. Herbivores. Arch. Hydrobiol. 73:310-333.

Pillay, T.V.R., ed. 1970. Coastal aquaculture in the Indo-Pacific region. Fishing News (Books) Ltd., London. 497p.

Platt, T. 1972. Local phytoplankton abundance and turbulence. Deep-Sea Res. 19:183-188.

Platt, T. and Subba Rao, D.V. 1970. Energy flow and species diversity in a marine phytoplankton bloom. Nature 227:1059-1060.

Platt, T. and Jassby, A.D. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. 12:421-430.

Platt, T., Denman, K.R. and Jassby, A.D. 1977. Modelling the productivity of phytoplankton. In. The Sea, V.6. Eds. E.D. Goldberg, I.N. McCave, J.J. O'Brien and J.H. Steele. Interscience Publishers, N.Y. p. 807-856.

Quayle, D.B. 1969. Pacific oyster culture in British Columbia. Bull. Fish. Res. Bd. Can. 169. 192p.

Quayle, D.B. 1971. Pacific oyster raft culture in British Columbia. Bull. Fish. Res. Bd. Can. 178. 34p.

Riley, G.A. 1956. Oceanography of Long Island Sound, 1952-1954. Production and utilization of organic matter. Bull. Bingham Oceanogr. College 15:324-344.

Ross, G.G. 1973. A model for competitive growth of two diatoms. J. Theor. Biol. 42:307-331.

Ryther, J.H. 1969. The potential of the estuary for shellfish production. Nat. Shell. Ass. Proc. 59: 18-22.

Saila, S.B. 1971. Systems analysis applied to some fisheries problems. In. Systems Analysis and Simulation in Ecology, V.2. Ed. B.C. Patten. Academic Press, N.Y. p. 331-372.

Saila, S.B. 1973. Some aspects of fish production and cropping in estuarine systems. In. Estuarine Research, V1. Ed. L.E. Cronin. Academic Press, N.Y. p.691-701.

Sheldon, R.W. and Parsons, T.R. 1967. A practical manual on the use of the Coulter Counter in marine science. Coulter Electronic Sales Co. Canada, Toronto. 66p.

Shiels,W.E. and Hood,D.W. 1970. Artificial upwelling in Alaskan fjord estuaries. Northern Engineer 2:1-5.

Smith, E.L. 1936. Photosynthesis in relation to light and carbon dioxide. Proc.Nat.Acad.Science,Wash. 22:504-511.

Smayda,T.J. 1973. The growth of Skeletonema during a winter-spring bloom in Narragansett Bay, Rhode Island. Norweg.J.Bot. 20:219-247.

Snra,R.F. and Baggaley,A. 1976. Rate of excretion of ammonia by the hard clam, Mercenaria mercenaria and the American oyster, Crassostrea virginica. Math.Biosc. 36:251-256.

Steele,J.H. 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, Mass. 128p.

Steele, J.H. and Menzel, D.W. 1962. Conditions for maximum primary production in the mixed layer. Deep-Sea Res. 9:39-49.

Steele,J.H. and Mullin,M.M. 1977. Zooplankton dynamics. In. The Sea, V.6. Eds. E.D. Goldberg, I.N. McCave, J.J. O'Brien and J.H. Steele. Interscience Publishers, N.Y. p.807-856.

Steeman Nielsen,E. 1962. On the maximum quantity of plankton chlorophyll per surface unit of a lake or the sea. Int.Rev.Ges.Hydrobiol. 47:333-338.

Strickland, J.D.H., Holm-Hansen, O., Eppley, R.W. and Linn, R.J. 1969. The use of a deep tank in plankton ecology I. Studies of the growth and composition of phytoplankton crops at low nutrient levels. Limnol.Oceanogr. 14:23-34.

Strickland, J.D.H. and Parsons, T.R. 1972. A practical handbook of seawater analysis. Bull.Fish.Res.Bd.Can. 167. 311p.

Suckling, P.W. 1974. Radiant exchange above and within a dwarf apple orchard. M.Sc. Thesis, McMaster University. 78p.

Szeicz, G. 1966. Field measurements of energy in the 0.4-0.7 micron range. In. Light As An Ecological Factor. Eds. R. Bainbridge, G.C. Evans and O. Raetham. Blackwell Sc. Publ.,Oxford. p. 41-51.

Takahashi, M. and Parsons, T.R. 1972. Maximization of the standing stock and primary productivity of marine phytoplankton under natural conditions. Ind.J.Mar.Sci. 1:61-62.

Takahashi, M., Fujii, K. and Parsons, T.R. 1973. Simulation study of phytoplankton photosynthesis and growth in the Fraser River estuary. Math.Biosc. 19:102-116.

Takahashi,M., Thomas,W.H., Seibert,D.L.R., Beers,J., Koeller,P. and Parsons,T.R. 1975. The replication of biological events in enclosed water columns. Arch.Hydrobiol. 76:5-23.

Taylor,W.R. 1960. Some results of studies on the uptake of radioactive waste materials by marine and estuarine phytoplankton organisms using continuous culture techniques. Chesapeake Bay Institute, The John Hopkins University, Technical Rpt. 21. 72 p.

Teal, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614-624.

Tenore, K.R., Dunstan, W.M. and Clarner, J.P. 1973. The food chain dynamics of the oyster, clam and mussel in an aquaculture food chain. J.exp.mar.Biol.Ecol. 12:157-165.

Tenore, K.R. and Dunstan, W.M. 1973a. Growth comparisons of oysters, mussels and scallops cultivated on algae grown with artificial medium and treated sewage effluent. Chesapeake Sci. 14:64-66.

Tenore, K.R. and Dunstan, W.M. 1973b. Comparison of rates of feeding and biodeposition of the American oyster, Crassostrea virginica Gmelin, fed different species of phytoplankton. J.exp.mar.Biol.Ecol. 12:19-26.

Tenore,K.R. and Dunstan,W.M. 1973c. Comparison of feeding and biodeposition of three bivalves at different food levels. Math.Biosc. 21:190-195.

Uno,S. 1971. Turbidometric continuous culture of phytoplankton. Construction of the apparatus and experiments on the daily periodicity in photosynthetic activity of Phaeodactylum tricornutum and Skeletonema costatum. Plank. Soc. Jap. Bull. 18:14-27.

Walker, P.N. and Zahradnik, J.W. 1976. Scale-up of food utilization by the American oyster Crassostrea virginica Gmelin. Nat.Shell.Ass.Proc. 65:63-75.

Walne,P.R. 1970. Studies on the food value of nineteen genera of algae to juvenile bivalves of the genera Ostrea, Crassostrea, Mercenaria and Mytilus. Fish. Invest., Ser. 2, 26(5). 62p.

Walne,P.R. 1972. The influence of current speed, body size and water temperature on the filtration rate of five species of bivalves. J.Mar.Biol.Ass.U.K. 52:345-374.

Walsh, J.J. and Dugdale, R.C. 1971. A simulation model of the nitrogen flow in the Peruvian upwelling system. Inv. Pesq. 35:309-330.

Wiegert, R. G., Christian, R. R., Gallagher, J.L., Hall, J.R., Jones, R.D.H. and Wetzel, R.L. 1973. A preliminary ecosystem model of coastal Georgia Spartina marsh. In. Estuarine Research, V1. Ed. L.E. Cronin. Academic Press, N.Y. p.583-601.

Winter,D.F., Banse.K and Anderson,G.C. 1975. The dynamics of phytoplankton blooms in Puget Sound, a fjord in the Northwestern United States. Math.Biosc. 29:139-176.

APPENDIX 1. Description and derivation of the variables and parameters used in this study.

VAR	DESCRIPTION	UNITS	DERIVATION
EXP	EXPERIMENT		
T	TIME	DAY	FIXED SAMPLING T (0830 HR EST)
Z	DEPTH	METRE	FIXED LOCATION
STN	STATION (INFLOW, OUTFLOW, S,M,B DEPTHS)		FIXED AREAL LOC.
SUBSTN	SUBSTATION		MEASURED
V	FLOW RATE	LITRE/DAY	CALCULATED
V	VOLUME	LITRE	v/V
FR	FLUSHING RATE	PER DAY	MEASURED
SINK	SINKING RATE	M/DAY	MEASURED
SB	INCIDENT SOLAR RADIATION	LANGLEY/DAY (LY/DY)	0.50*SB
PAR	PHOTOSYNTHETICALLY AVAILABLE RADIAT'N	LANGLEY/DAY (LY/DY)	MEASURED
PARO	PAR DURING O2 INCUB'N PERIOD	LANGLEY/4 HR (LY/INCUB)	MEASURED
PARC	PAR DURING C14 INCUB'N PERIOD	LANGLEY/4 HR (LY/INCUB)	.04+.0088CHLA+ .054(CHLA**.6667)
EXTK	EXTINCTION COEFF.	PER METRE	PAR*EXP(-EXTK*Z)
PARAV	PAR AT DEPTH	LANGLEY/MIN	(.5*PARO/240.)* EXP(-EXTK*Z)
PARZO	PAR AT DEPTH FOR O2 INCUB'N PERIOD	LANGLEY/MIN (LY/MIN)	(.5*PARC/240.)* EXP(-EXTK*Z)
PARZC	PAR AT DEPTH FOR C14 INCUB'N PERIOD	LANGLEY/MIN (LY/MIN)	MEASURED
SAL	SALINITY	PPT (0/00)	MEASURED
TEMP	TEMPERATURE	DEGREES C. (DEG-C)	MEASURED
TEMPN	NET TEMPERATURE	DEG-C.	TEMP(Z)-TEMP(I)
NO3	[NITRATE]	UM NO3-N/LITRE	MEASURED
NO3N	NET [NITRATE]	UM NO3-N/LITRE	NO3(I)-NO3(Z)
NH3	[AMMONIA]	UM NH3-N/LITRE	MEASURED
UREA	[UREA]	UM UREA-N/LITRE	MEASURED
PO4	[PHOSPHATE]	UM PO4-P/LITRE	MEASURED
SIO3	[SILICATE]	UM SIO3-SI/LITRE	MEASURED
OXY	[OXYGEN]	MG O2/LITRE	MEASURED
OXYN	NET [OXYGEN]	MG O2/LITRE	OXY(I)-OXY(Z)
SAT	OXYGEN SATURATION	PERCENT (%)	OXY/SOLUBILITY
CHLA	[CHLOROPHYLL a]	UG CHLA/LITRE	MEASURED
CHLB	[CHLOROPHYLL b]	UG CHLB/LITRE	MEASURED
CHLC	[CHLOROPHYLL c]	UG CHLC/LITRE	MEASURED
CT	[CAROTENOIDS]	UG CT/LITRE	MEASURED
BA	RATIO CHLB TO CHLA	DIMENSIONLESS	CHLB/CHLA
CA	RATIO CHLC TO CHLA	DIMENSIONLESS	CHLC/CHLA
CTA	RATIO CT TO CHLA	DIMENSIONLESS	CT/CHLA
BC	RATIO CHLB TO CHLC	DIMENSIONLESS	CHLB/CHLC
BCT	RATIO CHLB TO CT	DIMENSIONLESS	CHLB/ CT
CCT	RATIO CHLC TO CT	DIMENSIONLESS	CHLC/ CT
CCHLA	CARBON/CHLA	DIMENSIONLESS	CARBON/CHLA

PGO	GROSS PROD. (O2)	UG C/LITRE/HR	(UG O2/L/HR)/1.2
PNO	NET PROD. (O2)	UG C/LITRE/HR	(PGO)-(RES)
RES	RESPIRATION	UG C/LITRE/HR	(UG O2/L/HR)/1.0
PROD	NET PROD. (C14)	UG C/LITRE/HR	MEASURED(4 HR)
EXC	EXUDATION (C14)	UG C/LITRE/HR	MEASURED(4 HR)
PGOST	PGO(NORMALIZED)	UG C/UG CHLA/HR	PGO/CHLA
PNOST	PNO(NORMALIZED)	UG C/UG CHLA/HR	PNO/CHLA
RESST	RES(NORMALIZED)	UG C/UG CHLA/HR	RES/CHLA
ASS	PROD(NORMALIZED)	UG C/UG CHLA/HR	PROD/CHLA
EXCST	EXC(NORMALIZED)	UG C/UG CHLA/HR	EXC/CHLA
PGODY	DAILY PGO	MG C/LITRE/DY	PGO*(SE/PARC)*4.
PCDY	DAILY PROD	MG C/LITRE/DY	PROD*(SE/PARC)*4.
ALPHAG	P.VS.I INIT.SLOPE	UGC/UGCHLA/HR-LY/M	PGO/CHLA/PARZO
ALPHAC	P.VS.I INIT.SLOPE	UGC/UGCHLA/HR-LY/M	PROD/CHLA/PARZC
APGO	PROD/PGO	DIMENSIONSLESS	PROD/PGO
RPGO	RES/PGO	DIMENSIONSLESS	RES/PGO
EPGO	EXC/PGO	DIMENSIONSLESS	EXC/PGO
ESTPGO	ESTIMATED PGO	DIMENSIONSLESS	APGO+RPGO+EPGO
PMAX	MAX. ASS	UGC/UGCHLA/HR	LSF ESTIMATE
PTMAX	MAX. PMAX	UGC/UGCHLA/HR	LSF ESTIMATE
PHYTO	SIMULATED CHLA	UG CHLA/LITRE	SIMULATION
PHAV	AVERAGE CHLA	UG CHLA/LITRE	MEASURED
P	SIMULATED ASS	UGC/UGCHLA/HR	SIMULATION
GROWR	SIMULATED GROWTH RATE	PER DAY	SIMULATION
GRAZE	SIMULATED RATE OF GRAZING	PER DAY	SIMULATION

APPENDIX 2. Description and derivation of additional variables pertaining to herbivore growth.

VAR	DESCRIPTION	UNITS	DERIVATION
L	LENGTH	CM	MEASURED
W	WIDTH	CM	MEASURED
D	DEPTH	CM	MEASURED
WGTT	TOTAL WEIGHT	GRAMS	MEASURED
WGTM	MEAT WEIGHT	GRAMS	MEASURED
WGTS	SHELL WEIGHT	GRAMS	MEASURED
NETL	NET LENGTH	CM	L(f)-L(i)
NETW	NET WIDTH	CM	W(f)-W(i)
NETD	NET DEPTH	CM	D(f)-D(i)
NETWT	NET TOTAL WEIGHT	GRAMS	WGTT(f)-WGTT(i)
NETWM	NET MEAT WEIGHT	GRAMS	WGTM(f)-WGTM(i)
NETWS	NET SHELL WEIGHT	GRAMS	WGTS(f)-WGTS(i)
PERL	% INCR. LENGTH	%	NETL/L(i)
PERW	% INCR. WIDTH	%	NETW/W(i)
PERD	% INCR. DEPTH	%	NETD/D(i)
PERWT	% INCR. WGTT	%	NETWT/WGTT(i)
PERWM	% INCR. WGTM	%	NETWM/WGTM(i)
PERWS	% INCR. WGTS	%	NETWS/WGTS(i)
GRWM	NETWM/WEEK	G/ZOO/WK	CALCULATED
GRWS	NETWS/WEEK	G/ZOO/WK	CALCULATED
MSRATIO	NETWM:NETWS	DIMENSIONLESS	CALCULATED
NSURV	# SURVIVORS	NUMBER	
SIZE	HERBIVORE SIZE	N/A	Factor with 4 classes (1=smallest;4=largest)
DENS	HERBIVORE DENSITY	N/A	Factor with 3 classes (1=lowest;3=highest)
STKUP	UPTAKE CONC. OF PHYTOPLANKTON	UG CHLA/LITRE	CHLA(I)-CHLA(O)
STKUPR	UPTAKE RATE OF PHYTOPLANKTON	UG CHLA/DAY	STKUP*FR
OXYUP	UPTAKE CONC. OF OXYGEN	MG O2/LITRE	OXY(I)-OXY(O)
OXYUPR	UPTAKE RATE OF OXYGEN	MG O2/LITRE	OXYUP*FR