INVESTIGATIONS ON THE ROLE OF DISSOLVED ORGANIC MATTER IN DETERMINING ECOSYSTEM STRUCTURE AND FUNCTION: THE PLANKTON AND PHOTOHETEROTROPHY

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ABSTRACT

INVESTIGATIONS ON THE ROLE OF DISSOLVED ORGANIC MATTER IN DETERMINING ECOSYSTEM STRUCTURE AND FUNCTION: THE PLANKTON AND PHOTOHETEROTROPHY

By

Kelton R. McKinley

Within the broader context of the cycling of dissolved organic materials, this study examines the occurrence of the phenomenon of photoheterotrophy, the light-mediated assimilation of organic compounds at or near natural substrate concentrations, in the phytoplankton of lake systems.

The pelagic zone of Lawrence Lake, an oligotrophic, dimictic, temperate, hard-water lake in southwestern Michigan, was selected as the study site. Extensive information is already available on Lawrence Lake, the result of intensive study for a number of years. The uptake of an organic compound, glucose, and photolithotrophic carbon fixation were monitored simultaneously. Light and dark bottle uptake of organic and inorganic carbon was measured throughout the annual period during three sampling periods throughout the daylight hours and at three depths within the water column.

The study revealed that light bottle uptake of organic material was significantly greater than dark bottle uptake on the average, 9.2 μgC m^{-3} hr^{-1} vs. 6.3 μgC m^{-3} hr^{-1} (n=252). Annual averages attributable to photoheterotrophic uptake and chemoheterotrophic uptake were 2.6 μgC m^{-3} hr^{-1} and 6.9 μgC m^{-3} hr^{-1} (n=360) respectively. Photoheterotrophic activity represented 67.6% of chemoheterotrophic activity on a comparative, annual basis for the daylight period (n=360).

The patterns of chemoheterotrophic activity and photoheterotrophic activity were significantly related to the variables of months, depths, and time of day. Chemoheterotrophic activity generally increased throughout the daylight period and with depth in the water column, with maximal values generally observed during the sunset-incubation series and the 10-meter series. Generally high and uniform activities with respect to depth were observed during periods of water circulation. Increasing activity at depth during the stratified summer period was also observed. Maximal values of photoheterotrophic activity were observed during spring circulation and during late summer stratification. Activity was generally greater at depth and during morning and midday incubation periods. There was an apparent shift during the daylight period in the area of maximal uptake from 2 and 6 meters in the morning to 6 and 10 meters as the day progressed. Thus it

appears that chemoheterotrophy and photoheterotrophy may be both temporally and spatially separated with respect to activity within the water column on a diurnal as well as seasonal basis.

Heterotrophic uptake was compared to observed photolithotrophic fixation. Comparisons between the two techniques were difficult because of differing levels of precision. However, it is clear that photoheterotrophy may contribute significant additional carbon to photosynthetic organisms under conditions not favorable to inorganic fixation (e.g., at depth and under ice cover). The study revealed that dark bottle chemoheterotrophic estimates may lead to serious underestimates of organic cycling, since significant quantities of organic carbon were assimilated in the light.

Photoheterotrophy represents a key feedback loop at a trophically significant level and may play an important determining role in phytoplankton succession and community structure over time.

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By

Kelton R. McKinley

A DISSERTATION

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DEDICATED to the memory of the late and dear
MARTHA FARRY

Whose woods these are I think I know.
His house is in the village, though;
He will not see me stopping here
To watch his woods fill up with snow.

My little horse must think it queer
To stop without a farmhouse near
Between the woods and frozen lake
The darkest evening of the year.

He gives his harness bells a shake
To ask if there is some mistake.
The only other sound's the sweep
Of easy wind and downy flake.

The woods are lovely, dark, and deep,
But I have promises to keep,
And miles to go before I sleep,
And miles to go before I sleep.

Robert Frost

Don Genaro glanced at me with piercing eyes and then turned his head to look into the distance, towards the south.

"I will never reach Ixtlan," he said.

His voice was firm but soft, almost a murmur.

"Yet in my feelings . . . in my feelings sometimes I think I'm just one step from reaching it. Yet I never will. In my journey I don't even find the familiar landmarks I used to know. Nothing is any longer the same . . . ."

"I left. And the birds stayed, singing."

Carlos Castaneda
Journey to Ixtlan

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I would also like to express my love for my wife, Linda. We have come a very long way together.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

Figure Page

INTRODUCTION

General Introduction and Historical Considerations

Dissolved organic matter (DOM) has received considerable attention in recent years and much effort by many individuals has led to information concerning the sources, cycling, and measurement of DOM in natural waters. However, while we do know a great deal about DOM, we have yet to understand its roles as they relate to the organisms of the freshwater community. There has been much speculation and investigation in an attempt to elucidate these functional roles.

As early as 1885 various workers (Pearcey, 1885) reported mutually antagonistic relationships between various members of freshwater and marine communities. This resulted in a fairly extensive literature concerning the possible role of non-predatory relationships in the sea (e.g., Bigelow, 1931; Russell, 1936; Herdman, 1924, as cited by Lucas, 1947). Johnstone, Scott, and Chadwick (1924) were among the first to suggest that plankton communities somehow influence one another via a large scale group symbiosis, so that the plankton present in one area of the sea must depend, in part, on the type of plankton

which preceded it in time. As noted by Lucas (1947), their suggestions seemed to be the direct result of earlier statements by Brandt (1898) and Nathansohn (1909).

In 1931, Akehurst proposed his famous scheme of "starch and oil" groups in the phytoplankton, which is now only of historical interest. Working out an elaborate and detailed theory of the seasonal succession of algal types, he proposed that the phytoplankton comprised two distinct groups, which he distinguished on the basis of metabolic storage products (i.e., starch and oil). He further proposed that each population produced a toxin inhibitory to its own members, but at the same time stimulatory to members of the other metabolic group. Contemporaries of Akehurst began emphasizing the importance of non-predatory interactions on both an ecological and an evolutionary scale.

Hardy (1935) proposed his well known and often discussed theory of "animal exclusion." Allee (1931, 1934), in a view which included both community and evolutionary considerations, discussed the problems of mass physiology wherein the influence of aquatic organisms in conditioning the medium surrounding them by the addition of secretions and excretions also influenced the actual association of organisms. In this scheme "animal exclusion" appeared to be but an instance of a much more general class of non-predatory relationships dependent upon and related to the

production and subsequent accumulation of external organic substances (Lucas, 1947).

Perhaps the most vociferous proponent for non-predatory interactions was C. E. Lucas, who examined the phenomena of the influence of organism upon organism through the release of extracellular materials in a series of extensive reviews and provocative papers (1936, 1938, 1944, 1947, 1949, 1955, 1961). He coined the term "ectocrine substances," based in part upon the considerations of Huxley (1935) and as a direct analogy to the endocrine system and hormones, for that group of substances mediating ecological relationships by non-predatory means (Lucas, 1947). His examples of relationships mediated by "ectocrine substances" were drawn from almost all areas of science ranging from the close association of many insects and plants and the proposed role of nectar and scent, to animal phermones, and to the simple observation that oxygen was at one time merely a metabolic by-product on which a large number of important interactions are now based.

Lucas accurately observed that while an important part of the study of antibiotics and microbiology is specifically concerned with extracellular products and the interaction of organisms via those extracellular products, little attention is paid to the occurrence of those interactions in nature. As McIlwain (1944) and Waksman (1945) pointed out, microorganisms are in particularly intimate

contact during their growth in common media and are found to exhibit mutual interactions to a high degree, both in the sense of symbiosis and antibiosis. There is no reason to suspect that this is not the case in nature. To the contrary, this is probably good evidence to support the claim that such interactions play an important role in the environment (Pan and Umbreit, 1972).

Since that time a number of excellent, extensive reviews concerning the nature of dissolved organic matter and the roles which extracellular products are believed to play have been published (Fogg, 1962, 1966, 1971; Hellebust, 1974; Provasoli, 1958, 1963; Saunders, 1957). No attempt will be made to review this literature concerning DOM and extracellular products. However, since some treatment of the subject is in order, only that material of particular significance, or of more recent publication will be discussed.

Dissolved Organic Matter - Distribution and Sources

Some of the first attempts at the quantification of dissolved organic matter in lakes were performed by Birge and Juday (1926) during their survey of Wisconsin lakes, 1911 to 1917. They found that the concentration of dissolved organic carbon (DOC) in 13 Wisconsin lakes ranged from 4.00 to 13.22 mg DOC l^{-1} with a mean value of 6.23 mg DOC l^{-1} (n=28). In their work on two Wisconsin

rivers the range was from 9.58 to 15.23 mg DOC l^{-1}. The average concentration in seawater is approximately 2 mg DOC l^{-1} with a maximum of 20 mg l^{-1} (Provasoli, 1963).

There are many sources of DOM (Saunders, 1957; see also the review by Hellebust, 1974), but in the oceans the major source is undoubtedly due to the secretions or lysis of the plankton, particularly the phytoplankton (Provasoli, 1963). This is probably not true of most bodies of freshwater, however.

Thomas (1971) found the release of DOM by phytoplankton to range from 0.11 mg C m^{-3} hr^{-1} in the Continental Shelf waters to 1-2 mg C m^{-3} hr^{-1} in the estuarine waters. There was a general seaward trend of decreasing productivity and the quantity of DOM released, but an increasing percentage release of fixed carbon as DOM in a seaward progression. Values for percentages of photoassimilated carbon released as DOM ranged from < 7% in estuarine waters and < 11.6% in Continental Shelf waters to < 44% in the western-most Sargasso Sea. Extracellular release of dissolved organic materials approximated 1-20% of the total carbon fixed in the tropical coastal waters off India (Samuel, Shah, and Fogg, 1971).

In general the quantity of excreted organic matter seems to be proportional to photosynthetic carbon fixation over a wide range, increasing markedly under conditions of light inhibition, low light, or near the end of a bloom

condition (Fogg, Nalewajko, and Watt, 1965; Hellebust, 1965; Ignatiades and Fogg, 1973).

In the near shore and estuarine areas a significant contribution to the DOM pool may be made by the macrophytic vegetation. Sieburth (1969; Sieburth and Jensen, 1968) demonstrated a release of carbon in organic form from 4.4 mg C $100g^{-1}$ hr^{-1} for Chondrus to 54.2 mg C $100g^{-1}$ hr^{-1} for fruiting Ascophyllum. A carbon balance for Fucus during spring conditions indicates that approximately 30% of the total carbon, or 40% of the net carbon fixed daily is exuded by the plant. Fucus beds, which can exceed a density of 1000g C m^{-2} and fix approximately 16.5g C m^{-2} day^{-1}, are capable of the release of extracellular organic material equivalent to 5-7g C m^{-2} day^{-1}. Khailov and Burlakova (1969) in their study of DOM release from 18 species of macrophytes from the Barents Sea and Black Sea regions found similar rates of release. In the Barents Sea macrophytes release rates for different species ranged from 0.9 to 2.9 mg organic matter per gram dry weight of plant per hour (mg g^{-1} hr^{-1}) in March to 1.7 to 9.8 mg g^{-1} hr^{-1} in June. The release rates for the species of the Black Sea area ranged from 0.5 to 1.6 mg g^{-1} hr^{-1} in slowly growing plants to 1.25 to 6.1 mg g^{-1} hr^{-1} in fast growing plants. They calculated the quantity of total DOM released on a yearly basis as a percentage of gross production to be 39% for brown algae, 38% for red

algae, and 23% for green algae. With these estimates and the consideration that approximately 30% of gross production may be released as DOM through decomposition, the remainder being consumed by herbivores, they further estimated that as much as 70% of gross production may be released as DOM.

The picture in freshwater is complex, but it has been studied in some detail. In Lawrence Lake, a small hard-water lake in southwestern Michigan, the concentration of the DOM pool varies from 1.5 to 9.6 mg C l^{-1} on a yearly basis with a mean of 5.6 mg C l^{-1} for all depths and sampling periods (Wetzel, et al., 1972). A maximum quantity of DOC generally occurs in September and October prior to overturn.

The in situ measurement of the secretion of dissolved organic compounds by phytoplankton has been followed for nearly five years (Miller, 1972; Wetzel, unpublished). The rates of algal release of extracellular products during photosynthesis in Lawrence Lake ranged from 0.0 to 22.5 mg C m^{-2} day^{-1} with a mean of 7.3 mg C m^{-2} day^{-1}. The maximum observed rates never exceeded 3.8 mg C m^{-2} day^{-1} in the epilimnion. The annual mean percentage secretion of phytoplanktonic primary production was 5.7%. A higher percentage of secretion occurred at lower depths. Expressed as the mean percentage secretion of all dates and samples, 23.5% of the phytoplanktonic particulate production was

secreted, an annual average determination which includes all depths.

The release of dissolved organic matter by submersed macrophytes has been studied extensively in axenic cultures (Wetzel, 1969a, 1969b; Allen, 1971b; Wetzel and Manny, 1972b; Hough and Wetzel, 1972, 1975). The rates of secretion of DOC by both submersed and floating-leaf macrophytes varied from 0.05 to over 100% of photosynthetically fixed carbon. The rate of release was dependent upon a number of environmental variables including light and ionic composition of the medium (Hough and Wetzel, 1972; Wetzel, 1969a, 1969b). In situ analysis of secretion rates by Najas flexilis in Lawrence Lake ranged from 1-3% of photosynthetically fixed carbon during the day-light period (Miller, 1972). Nearly a two-fold (2X) increase in percentage of secretion rates was found in the dark (Hough and Wetzel, 1972).

A significant portion of the DOC entering Lawrence Lake is allochthonous, approximately 20.95g C m^{-2} $year^{-1}$ (Wetzel, et al., 1972). However, these materials, largely terrestrial, humic compounds, are highly refractory biologically and as such not subject to rapid bacterial degradation (see also Wetzel and Manny, 1972a, 1972b; Wetzel and Otsuki, 1973).

These studies coupled with work on the decomposition rates of DOM in both marine and freshwaters

(Wetzel and Manny, 1972a; Ogura, 1972) and on the anaerobic and aerobic decomposition of algal cells (Otsuki and Hanya, 1972a, 1972b) have resulted in a fairly complete knowledge of the material transport of DOC (see especially Wetzel, et al., 1972, for freshwaters).

Dissolved Organic Matter - Nature and Action

Knowledge of the nature of the DOM and its mode of action is more limited. The qualitative composition of the DOM varies considerably in both time and space. Some attempts have been made to clarify that composition and an extensive literature has developed. Much of the work has been done with isolates of extracellular products from various algal cultures (e.g., Berland, et al., 1972; Myklestad and Haug, 1972; Hellebust, 1965; Otsuki and Hanya, 1972a, 1972b; Nalewajko and Lean, 1972; Kroes, 1971, 1972; Fogg and Watt, 1965; Sieburth, 1969; Sieburth and Jensen, 1968, 1969). Work has also been done in both salt and freshwaters (e.g., Birge and Juday, 1926; Carlucci and Bowes, 1972; Clark, Jackson and North, 1972; Ohwada and Taga, 1972). The composition of DOM has been approached by a number of different means, including examination and classification by various extractive chemical techniques (e.g., ether extract, chloroform soluble, steam volatile, yellow water soluble pigments), or by functional group (e.g., amino acids, peptides, proteins, carbohydrates,

lipids, fatty acids, organic acids, aldehydes, ketones). Some isolation and characterization of specific compounds have been performed (e.g., glycolate, mannitol, glycerol, proline, a number of vitamins, enzymes, some sexual substances, and hormones). Often, particularly with vitamins, the concentrations of specific compounds were followed through time using bioassay techniques. The most comprehensive, but dated, review of this entire subject was written by Vallentyne (1957) (see also Provasoli, 1963). Hellebust (1974) has written the most recent review of extracellular products.

The functions which DOM is believed to perform in nature were summarized by Saunders (1957) under the following four topics: (1) as an energy source, or providing essential, basic elements for the synthesis of cellular materials; (2) as accessory growth factors either essential to the growth of the organism, or stimulatory to the growth of the organism; included here could also be the various enzymes and sexual substances which, while often not directly linked with the growth of the organism, may be indirectly linked to that process and the propagation of the species; (3) as a toxic substance, including both auto- and heteroantibiosis; and (4) as an organic complex with various trace elements, chelation, which may produce either a beneficial or a detrimental effect depending upon the element and the nature of the chelatory binding. Much

evidence for the above processes is offered both in Saunder's review (1957) and in the other general reviews mentioned earlier. More recent work has generally tended to support these proposed roles, for example: chelation (Kroes, 1972; Moebus, 1972; Wetzel, 1965, 1971); accessory growth factors (Provasoli, 1969; Carlucci and Bowes, 1970); and antibiosis (Moebus, 1972; Berland, et al., 1972; Fitzgerald, 1969; Kroes, 1972).

An apparent contradiction is evident in studies concerning organic materials as an energy source. Much of the work in all categories has been carried out in pure or axenic cultures with artificially high concentrations of organic substrates, concentrations which would virtually never be encountered in the environment. This has been particularly true concerning organic materials as energy sources. Therefore, while a number of species were shown in culture to be capable of either heterotrophic growth, or the utilization of organic substrates, it appeared that this potential could not be realized in nature. In a series of experiments, primarily the work of Wright and Hobbie (1965; Hobbie and Wright, 1965a, 1965b; Hobbie, 1969; Allen, 1969a, 1971b; Wetzel, 1967, 1968; Parsons and Strickland, 1962), it was demonstrated that the kinetics of uptake for planktonic algal species followed zero order principles (diffusion kinetics), while bacteria were able to actively transport organic materials across membranes

(first order kinetics) and simply out-compete the algae at natural substrate concentrations. It was further demonstrated (e.g., with the marine pennate diatom Cocconeis diminuta; Cooksey, 1972) that the uptake of organic substrates by algae was not energy dependent (i.e., again diffusion mechanisms were shown to be operative). This was particularly true for the green algae on which many of the studies were performed (N. B. Wright and Hobbie's classic work (1966) is based on work with a single species of Chlamydomonas sp.). However, it should be noted that the green algae are especially suited for culture work because of the relative ease of their propagation on defined, synthetic media. Those species which require more complex or exotic media (e.g., soil extracts, and other less clearly defined mixtures) simply cannot be as easily maintained. Many species, particularly in the Chrysophyta, Cyanophyta and Pyrrhophyta, cannot be isolated and maintained at all with the methods presently employed. Within this context it is important to note the heterotrophic utilization of organic compounds by cryptomonad species demonstrated by Wright in 1964.

Work notably by Allen (1971a) and Saunders (1972), has indicated that the uptake or organic substrates by various algal species is possible at near natural substrate concentration levels (see also Bennett and Hobbie, 1972). Allen's (1971a) work (with some substantiation in a similar

approach by Remsen, Carpenter, and Schroeder, 1972; and more recently P. A. Wheeler, University of California, Irvine, personal communication) consisted of a size fractionation of a plankton sample after exposure to ^{14}C-organic compounds by filtration through a series of nine membrane filters ranging in porosity from 14.0 μm to 0.22 μm. The reduction in the maximum velocity of active transport following the size fractionation demonstrated that organisms between 3 μm and 8 μm were responsible for the majority of the active uptake of glucose and acetate and that organisms of less than 1.2 μm (i.e., bacterial size-categories) were responsible for only a minor portion of the substrate uptake. An examination of the control sample revealed that the algal organisms were predominately micro-flagellates in the size range of 4 μm to 8 μm. Few bacteria were observed. Those algae which were apparently responsible for the active substrate uptake are those organisms which are often overlooked (see for example Horner and Alexander, 1972) and are generally not, or not easily, maintained in culture collections. While there is some confounding associated with Allen's technique (e.g., particles in the 3 μm to 8 μm range to which bacteria would be expected to be attached) some limited autoradiography by Allen supports his conclusions.[1]

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[1]It should be pointed out that these statements concerning the importance of dissolved organic materials do not supplant the work concerning physical and abiotic

Within this broad context the particular subject to be addressed in this work will be the utilization of organic materials as energy sources. In later works, aspects of stimulation-inhibition interactions and a theoretical overview will be addressed (McKinley, in prep.; McKinley and Wetzel, in prep.).

The interesting and provocative papers by Ingram et al. (1973a, 1973b) suggested that the key to understanding the importance of algal heterotrophy might lie in the interplay concerning the presence or absence of light.

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chemical factors and the productivity of the phytoplankton. Much informative work has been done in the past and is currently being performed (e.g., see Moss, 1972 and also the work on the importance of pH by Kroes (1971, 1972) and O'Brien and deNoyelles (1972), but see also the discussion by Proctor (1957)). However, after reviewing the subject Hutchinson (1967) concluded that, while there was good correlative evidence between the physical and abiotic chemical factors and the phytoplankton, those factors alone could not account for the observed algal associations, productivity, and variations through time. In order to more fully understand the total picture of algal associations and productivity, the abiotic material must be coupled with the elucidation of the role of dissolved organic substances. A major contributing factor to the paucity of insight into the functional interactions of DOM has been the failure both in the past and currently (e.g., see the discussion by Kroes, 1972) to recognize that the interactions mediated via DOM are generally likely to be subtle. The ecological impact of red tide for example, is rather spectacular, but very rare. However, examination of competition equations (see Hutchinson's discussion, 1967) reveals that for organisms with as short a generation time as the plankton, subtle differences, of which these organic substances are certainly capable, can make substantial differences in competitive interactions and consequently in community structure in relatively few generations. This may seem obvious, but the technology and the techniques of the necessary sensitivity to detect those differences in nature and on a species-specific basis, as these interactions are likely to be (Lucas, 1947; Pan and Umbreit, 1972), have been lacking (Wetzel and Allen, 1972).

Indeed, by examining a number of papers already cited it appeared that often the difference between those observing heterotrophy, or not observing heterotrophy, revolved around whether or not the tests were conducted in the light, or in the dark.

The light mediated uptake or organic compounds at, or near natural substrate concentrations by photosynthetic organisms has been termed photoheterotrophy. Although this subject has received considerable work and a significant resultant literature has accumulated over the years, little work has been done concerning its potential ecological role.

Photoheterotrophy

In 1928 Bristol Roach noted that a strain of soil alga, Scenedesmus costulatus, was able to accumulate cell carbon at low light intensities by a combination of photolithotrophic and photoheterotrophic pathways. Since that time much discussion and experimentation has occurred concerning algal heterotrophy. Several recent and excellent reviews are now available on this topic (notably Droop, 1974; Neilson and Lewin, 1974; and earlier, Danforth, 1962).

It has generally been conceded that true chemoheterotrophic utilization (i.e., utilization in the dark) of organic compounds is in large part dominated by bacterial forms. This is particularly true, because of the

relatively rare occurrence of chemoheterotrophic algal forms, the often artificially high concentrations of organics necessary for sustained dark growth, and since the appearance of the papers by Wright and Hobbie (1965, 1966) and Hobbie and Wright (1965a, 1965b; see also Sloan and Strickland, 1966; Munro and Brock, 1968); the concepts having gained nearly universal acceptance.

However, while it is now clear that chemoheterotrophy probably represents a bacterial specilization, it is not clear that algal heterotrophy per se must be completely ruled out. Although little direct work has been done concerning the photoheterotrophic assimilation of organics since Bristol Roach's work with Scenedesmus, it is now apparent that a number of algae are capable of utilizing organic compounds at, or near, natural substrate concentrations in the light.

A number of algal types from a variety of different taxa have shown this ability (see Droop, 1974). A brief examination of the pertinent ecological literature also reveals that those persons observing "algal uptake" of organic compounds at natural substrate concentrations have generally run their experiments in the light (e.g., see Ingram et al., 1973a, 1973b; Pintner and Provasoli, 1968; Sheath and Hellebust, 1974; Lylis and Trainor, 1973; Bunt, 1969; Eppley and MaciasR, 1963).

While evidence for photoheterotrophy has accumulated, little has been done with this information and photoassimilation has generally only been viewed in terms of a laboratory phenomenon. A brief review of what is known of the process is instructive. It should be pointed out that portions of this discussion are in large part based upon more extensively studied pathways in bacteria and higher plants. However, as Neilson and Lewin (1974) point out in their more extensive review, algal biochemical pathways have generally not been shown to be truly unique and in general follow closely those of higher plants and other organisms.

A contrast may be made between those organisms which are capable of growth at the expense of organic compounds in the dark (i.e., chemoheterotrophs) and those organisms which are able to grow by utilizing organic compounds in the light (i.e., photoheterotrophs). There is not necessarily a good correlation between the two processes (Stanier, 1973). The majority of photosynthetic organisms capable of organic utilization must be considered to be facultative chemoheterotrophs, or facultative photoheterotrophs, since CO_2 generally remains the predominant source of cellular carbon.

Chemoheterotrophic and photoheterotrophic assimilation and metabolism of organic compounds may be discussed in terms of the utilization of three compounds and their

respective families of related compounds: (1) glucose, (2) acetate, and (3) glycolate. These substances probably represent major, lower molecular weight compounds available within the environment. Little work has been completed on other compounds.

Glucose is the best understood of these compounds. Only two pathways for the dissimilation of glucose appear to be operational in algae: (1) the Embden-Meyerhof-Parnas (EMP) pathway and the pentose-phosphate pathway (Neilson and Lewin, 1974). Under aerobic conditions the pyruvate generated by the EMP pathway enters the tricarboxylic acid (TCA) cycle where it is oxidized to carbon dioxide. The second pathway, and for blue-green algae the major pathway, for glucose utilization is the pentose-phosphate pathway. Here the initial product is glucose-6-phosphate which is dehydrogenated and oxidatively decarboxylated to carbon dioxide and ribose phosphate. Under aerobic conditions ribose phosphate may be further oxidized to CO_2.

The regulation of glucose metabolism and photoassimilation is not well understood in algae. It has been most extensively studied with blue-green algae. Pelroy *et al.* (1972) and others (see also Pearce and Carr, 1969) have shown that the synthesis of glucose-6-phosphate dehydrogenase was specifically inhibited by ribulose-1,5-diphosphate generated during carbon fixation in the light

via the Benson-Calvin cycle, thus suppressing the pentose-phosphate pathway. Under these conditions exogenous glucose is then assimilated almost entirely as polysaccharide (Neilson and Lewin, 1974). This suppression is reversed by the inhibition of photosystem II through use of DCMU (Stanier, 1973).

Pelroy et al. (1972) suggest that some type of constituitive permease which mediates glucose uptake by Aphanocapsa would account for the relatively high substrate affinities observed. Ohki and Katoh (1975) have some evidence for the operation of a sodium pump in the transport of glucose by having observed accelerated organotrophic growth upon the addition of sodium chloride. Thus chemoheterotrophic utilization in the dark is dependent upon the ATP generated through the pentose-phosphate pathway. However, where cyclic photophosphorylation is operational, adequate ATP may be generated for glucose transport. (See also Neilson and Lewin, 1974 and Tanner, Grünes, and Kandler, 1970, for a discussion of transport of hexose in green algae).

A coupling with light, and of particular interest concerning the distribution of light availability at depth within lakes, is also shown by a shift in the absorption peaks of pigments. The absorption spectra of organotrophically cultured cells of Anabaena variabilis show a marked reduction in the red range 600-700 nm, but little

reduction in the blue range 400-500 nm (Ohki and Katoh, 1975). Greatest overall relative changes in pigment absorption were also noted when cultures of organotrophically grown Chlorella vulgaris were illuminated with monochromatic light at a wavelength of 450 nm (Karlander and Krauss, 1966).

The effect of light was additionally revealed by Ohki and Katoh (1975), who observed increasing growth rates for both lithotrophically and organotrophically grown cells with increasing light intensity to a maximum of 15 hours per doubling. The maximum values were attained at 2.2 mw cm^{-2} for organotrophic growth and at the higher intensity of 3.5 mw cm^{-2} for lithotrophic growth. Additionally they observed low, but significant rates of organotrophic growth under conditions of light limitation where no discernible lithotrophic growth could be observed.

Much work has been completed with acetate, also. Acetate is generally oxidized through intermediates of the TCA cycle. In order to provide carbon skeletons for biosynthesis, acetate must be cycled through the glyoxylate pathway. In Chlamydobotrys and Chlamydomonas cells are apparently dependent upon photosystem II for reducing power under anaerobic conditions. Droop (1974) interprets this to indicate an O_2 dependence for the re-oxidation of $NADH_2$ irrespective of the source of ATP generation (i.e., either through metabolic pathways or from cyclic

photophosphorylation). He further points out the close association between oxidative and photosynthetic assimilation of acetate by noting that photoassimilation is associated with high activity of the glyoxylate cycle and that a reduction in the enzyme activity of the carbon reduction cycle has been observed during the photoheterotrophic growth of several species. However, the photoheterotrophic uptake of acetate by Chlorella pyrenoidosa, Euglena gracilis, and Anacystis nidulans is apparently different in that they are dependent upon non-cyclic photophosphorylation.

In Chlamydobotrys stellata and Chlamydomonas mundana, species which apparently photoassimilate acetate directly utilizing energy derived from cyclic photophosphorylation, Wiessner (1969) has shown a shift in photosynthetic pigment spectra during photoheterotrophic growth. This shift is related to an increase in the chlorophyll proteins associated with photosystem I with a maxima near 695 nm and an apparent decrease in the 655 to 675 nm range associated with photosystem II. (See the discussion on the composition of the two pigment systems by Govindjee and Braun, 1974.)

Glycolate, while not generally a normal product of photosynthesis, may be formed in abundance under conditions unfavorable for inorganic carbon fixation and favorable for photorespiration (i.e., low CO_2, high O_2, and light).

Under these conditions glycolate may represent the major excretory product (Tolbert, 1974). Because of this fact, glycolate has received considerable attention. Glycolate has not been shown to support heterotrophic (i.e., dark) growth of any alga (Neilson and Lewin, 1974). It has been shown to be utilized by a number of species in the light (K. G. Sellner, Dalhousie University, Halifax, personal communication, Thalassiosira; see also Palmer and Star, 1971, Pandorina; Miller, Chang, and Colman, 1971, and Lex, Silvester, and Stewart, 1972, blue-green algae; Nalewajko, Chowdhuri, and Fogg, 1963, Chlorella; and others). Glycolate is metabolized first by an oxidation to glyoxylate and then in blue-green algae to malate and for several types of green algae to glycine, serine, hydroxypyruvate and glycerate (Neilson and Lewin, 1974).

Thus in summary, what is implicated is a system of active transport for glucose involving light generated ATP and cyclic photophosphorylation. The metabolism of glucose, but not necessarily the uptake, may be regulated by the products of photosystem II and the Calvin cycle. The system apparently operates at light intensities below that for inorganic carbon fixation and may involve pigments in the blue range, a range of wavelengths which most often dominates at depth within aquatic systems. Other compounds which may also fit this general pattern would

include fructose, galactose and a few dissacharides (Ohki and Katoh, 1975; Stanier, 1973).

The metabolism and transport of acetate and glycolate are less well understood. Certain species of algae, which may utilize acetate directly, follow a pattern similar to that given above. Shifts in pigment maxima are observed and energy derived from cyclic photophosphorylation is used in conjunction with photoassimilation. Other species, some converting acetate to carbon dioxide before utilization, follow different patterns.

PURPOSE OF THE INVESTIGATION

Given this brief background concerning the phenomenon of photoheterotrophy, it is necessary that that phenomenon be placed within some frame of reference with regard to the cycling of carbon and the dynamics of lake systems. An attempt was made in this study to examine whether, or not photoheterotrophic utilization of organic compounds could represent a significant pathway in the cycling of carbon and second whether it has any potential for further study in the elucidation of the spatial and temporal patterns of plankton within lake systems. With this objective in mind, the conditions of incubation, the area selected for study and the methods employed were all dictated by the attempt to achieve sensitive, short term measures with as little change as possible from natural systems. Until the importance of photoheterotrophy was demonstrated within an ecological context, work on the elucidation of its role in species specific responses, or maximum potentials through use of metabolic inhibitors could not be justified.

A number of those species previously discussed as having demonstrated the greatest potential for

photoheterotrophic utilization are those species generally associated with a substrate; either soil algae, epiphytic algae on macrophytes, or algae in association with the benthic sediments or other areas where one might expect to find naturally higher concentrations of organic compounds. One would probably expect that the greatest contribution to algal organic carbon metabolism within natural systems will always be predominately associated with those areas. However, the strongest test case would be made by measuring the response of phytoplanktonic species, those not in association with substrates or organic concentration gradients. Certainly an important case may be made for photoheterotrophic cycling of materials in general, if it is shown to be significant where one would least expect it to contribute strongly.

The site selected was therefore based upon ease of experimental manipulation and sampling, since the general mechanisms for photoheterotrophic utilization as proposed to date are basic cellular constituent pathways and probably do not represent any specialization, or radical departure from normal cellular metabolism.

SITE FOR THE STUDY

Lawrence Lake, a small hardwater lake in southwestern Michigan (85° 21' W, 42° 27' N), was selected for the study site. Lawrence Lake has been described in some detail elsewhere (Wetzel et al., 1972; Rich, 1970; Allen, 1969b).

All samples for this study and for concurrent studies to be referred to throughout this work were taken at the central depression (designated A in the accompanying morphometric map, Figure 1). The total surface area is 5.0 hectares; the maximum depth is 12.6 meters with a mean depth of 5.9 meters.

The lake represents a typical temperate, dimictic lake. It experiences periods of temporary meromixis about every fourth year. The lake is strongly stratified throughout the summer period (Figure 2) with maximum temperatures in 1974 of 25°C and minimum temperatures under ice of < 1°C. Complete mixing occurred in 1974 following ice loss in March and continued until stratification began during April. Maximum thermal gradients were achieved during the period July-August at a depth interval between 4 and 8 meters. Disruption of stratification began in September

Figure 1.--Morphometric map of Lawrence Lake, Barry County, Michigan. Contour lines in one meter intervals. Central sampling station indicated at point A.

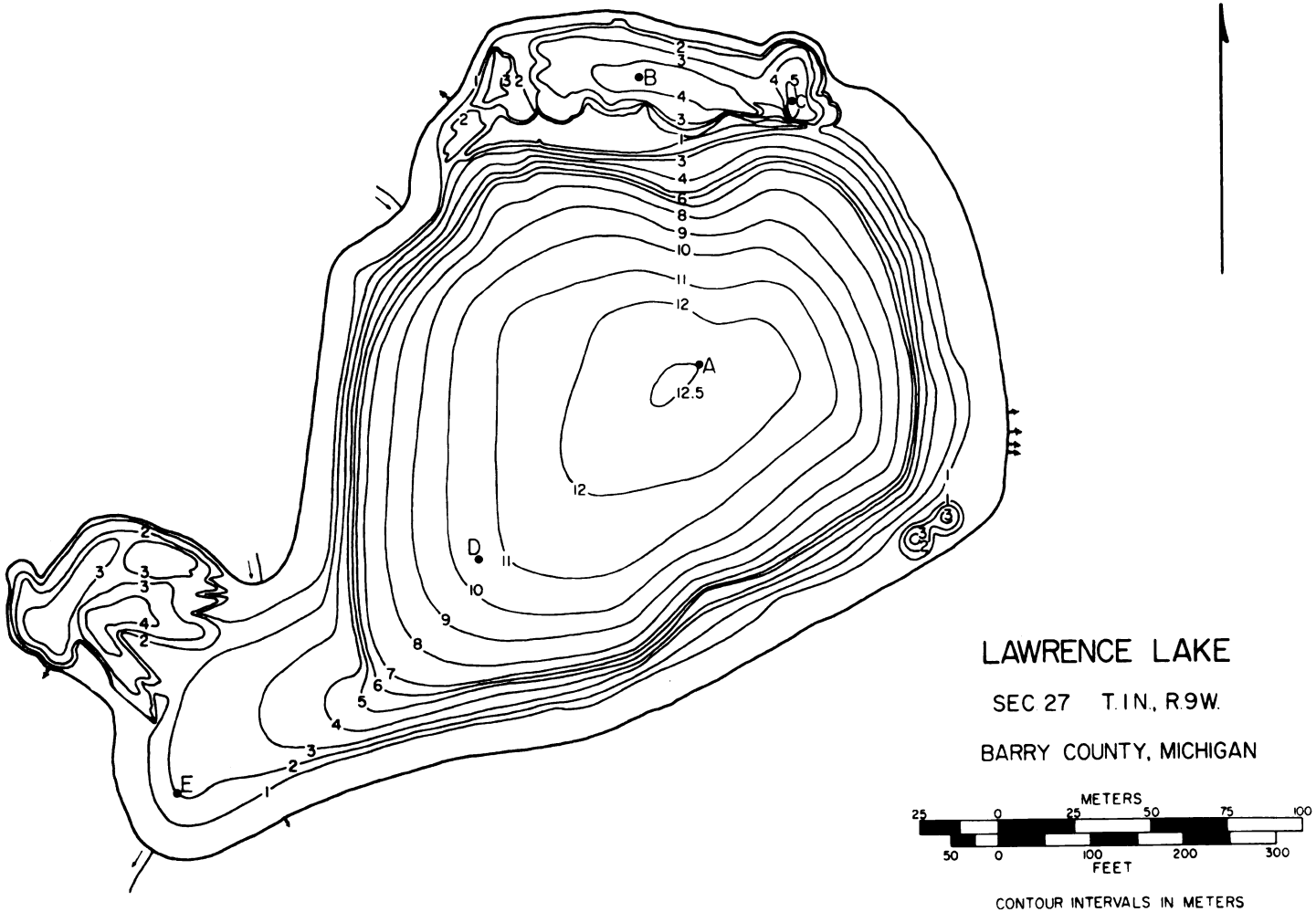
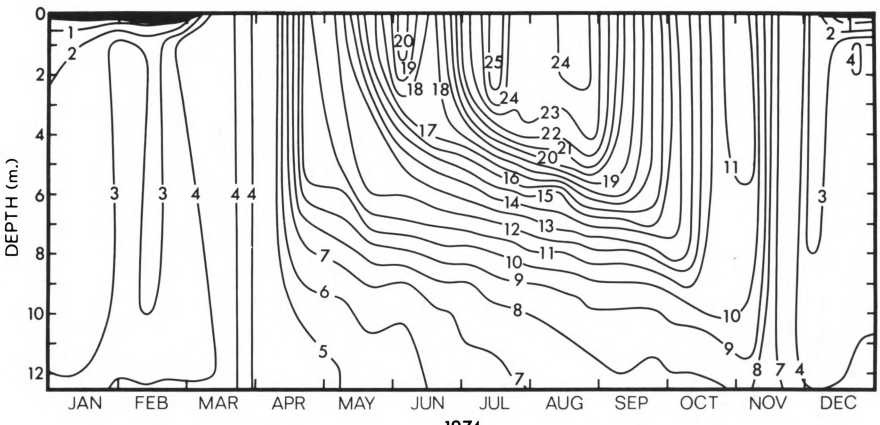

B.M.
281.6m
N
A
B
C
D
E
12.5
LAWRENCE LAKE
SEC 27 T.1N., R.9W.
BARRY COUNTY, MICHIGAN
METERS
25 0 25 50 75 100
50 0 100 200 300
FEET
CONTOUR INTERVALS IN METERS

Figure 2.--Isopleths of temperature distribution (°C) in Lawrence Lake, 1974.


DEPTH (m.)
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AUG
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OCT
NOV
DEC
1974

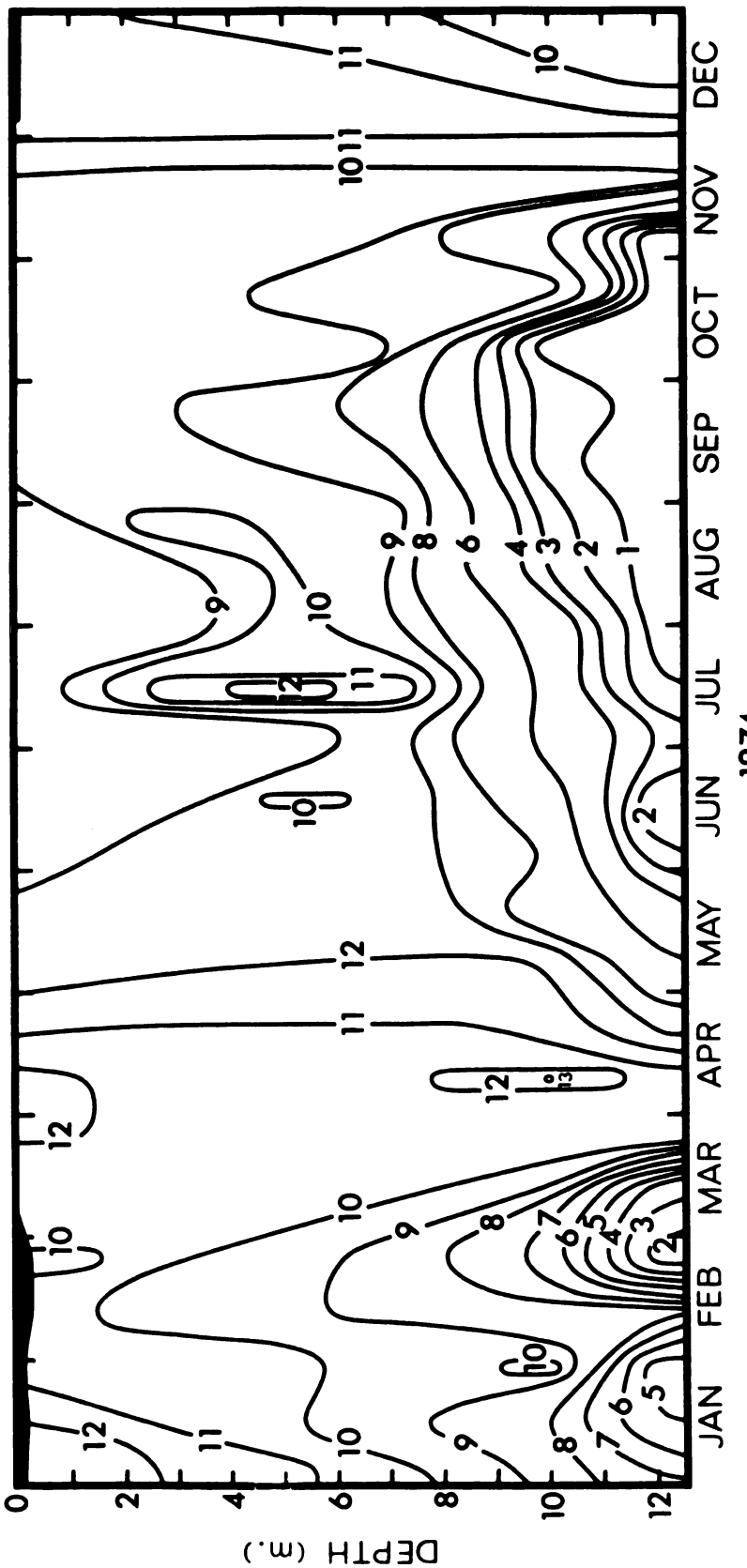
with surface water cooling and an increase in depth of mixing. Autumnal turnover began in November and continued until ice cover was established in December.

The oxygen profile (Figure 3) is typical for a lake of moderate to low productivity with maxima under ice and at all depths during spring mixing and a metalimnetic summer maximum in July associated with high values of photosynthetic production. The range of O_2 concentration was from > 13 mg l^{-1} to < 1 mg l^{-1}. The lake, while experiencing reduced oxygan levels at depth during summer stratification did not become axoxic during 1974, although the relatively small volume of water below the 12 meter interval has occasionally had no detectable oxygen during late summer stratification in other years.

The pH and alkalinity are typical of hardwater lakes in the region. Because of the buffering capacity of the bicarbonate system little change in pH is observed over the annual period (i.e., a range of 8.0 to 8.2 for the epi- and metalimnetic waters). Only at depth just above the sediments and near the end of summer stratification do values approach a pH of < 7.6.

Alkalinity values ranged generally from 4.2 to 4.4 meq l^{-1} for the epilimnion and metalimnion during the ice free period. Values increased with depth under the ice (i.e., to 4.8 meq l^{-1}) and during the summer stratification period, approaching 5.0 meq l^{-1} in late summer.

Figure 3.--Isopleths of oxygen concentrations (mg l^{-1}) in Lawrence Lake, 1974.


DEPTH (m.)
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MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
1974

The typical late summer phenomenon of epilimnetic decalcification was observed in 1974, with a concomitant increase at depth (i.e., a minimum epilimnetic value of < 4.0 meq l^{-1}, see the discussion by White and Wetzel, 1975). A low value of 3.6 meq l^{-1} during winter directly under the ice was probably associated with ground water intrusion during a period of melting.

SAMPLING DESIGN

The design selected for the study was a three-way factorial split plot design of the following model:

$$Y = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + E_{(ijk)l} + \delta_m + \alpha\delta_{im} + \beta\delta_{jm} + \gamma\delta_{km} + \alpha\beta\delta_{ijm} + \alpha\gamma\delta_{ikm} + \beta\gamma\delta_{jkm} + \alpha\beta\gamma\delta_{ijkm} + R_{(ijk)lm} + U_{(ijklm)n}$$

where:

$i = 1 \ldots a = 7$

$j = 1 \ldots b = 3$

$k = 1 \ldots c = 3$

$l = 1 \ldots s = 4$

$m = 1 \ldots d = 2$

$n = 504$

All factors were fixed with the exception of replicate sampling, which was considered to be random.

Monthly samples were taken at fixed intervals at sampling site A throughout 1974. Within the constraints of sampling and the design seven months were utilized for the statistical analysis. Three additional months, differing slightly in sampling procedure, are included in

annual estimates. No attempt was made to select either cloudy or cloudless days.

For each month three incubations were completed during the daylight hours. These fixed sampling periods of approximately equal duration consisted of incubations which were begun at sunrise (SR), incubations which ended at sunset (SS), and midday incubations (MD), the midpoint of which was temporally at the midpoint of the daylight hours between sunrise and sunset.

For each month and sampling period, three fixed depths within the water column were selected: 2, 6, and 10 meters respectively.

For each month, sampling period and depth, four separate Van Dorn samples were taken. The contents were mixed and paired light and dark bottles filled simultaneously by alternating between the two bottles during filling. Separate Van Dorn samples were taken in order to better represent the sampling heterogeneity at a single point in space within the water column. In previous experiments it was shown statistically that replicate samples from a single mixed Van Dorn were not significantly different (McKinley, unpublished).

The design permits not only an assessment of main effects (i.e., Month, Time of Day, Depth, and Light/Dark Treatment), but also of any interaction terms resulting in non-parallel responses across these effects. (See the discussion in the section on Statistical Analysis.)

METHODS

The treatment consisted of a simple light/dark contrast, as in ^{14}C-inorganic photosynthesis estimates, here with the addition of tracer quantities of a radioactive organic compound. This method was selected in preference to the use of metabolic inhibitors, because of a desire to maintain the populations in as natural a state as possible during the treatment period. Inhibitors of photosystem II would certainly force potential photoheterotrophic organisms to utilize organic carbon. However, the contribution that photoassimilated organic carbon might make toward the total cycling of carbon in lake systems would be difficult to assess, since it is undoubtedly the interplay between available light and inorganic carbon sources which determine any role photoheterotrophy might play.

It was with this consideration in mind that a tritiated organic compound was selected in preference to ^{14}C-organic compounds despite the greater difficulties in handling and counting. First to assure that the increase in light bottles over that in dark bottles is indeed due to organic fixation, one must minimize any potential

re-fixation by the algae of inorganic by-products of chemoheterotrophic utilization in the light. Since the utilization of the organic material added was acceptably low (i.e., in one case 8% of the glucose added, and in general less than 2% of the 4-5 μg glucose l^{-1} added), even if 100% of the material utilized was metabolized and released as $^{14}CO_2$, one would probably not expect great amounts of activity to be observed due to refixation. Nevertheless it was felt that a more reasonable course would be to utilize ^{3}H-glucose rather than ^{14}C-glucose; the resultant $^{3}H_2O$ would thus be diluted by 10^6 rather than 10^2 as with CO_2.

An additional factor considered was the desire to assess the importance of photoheterotrophy to algal nutrition as well as overall lake metabolism. Therefore, if ^{3}H-organic compounds were utilized for studying chemoheterotrophic and photoheterotrophic responses, ^{14}C-bicarbonate could be utilized simultaneously to measure inorganic photosynthesis. This was accomplished following standard in situ light bottle/dark bottle techniques (see Strickland and Parsons, 1972).

Glucose was selected from a variety of compounds that could have been used, for a number of practical considerations. First, as discussed previously, there is a relatively small family of compounds which have been shown to be utilized photoheterotrophically and glucose is one

compound that has been fairly well studied. Second, much work has been completed using glucose and its utilization by both photoheterotrophic and chemoheterotrophic organisms is well established. One other compound which was considered was glycolate.

Glycolate has often been considered to be the major excretory product of the phytoplankton. However, it is no longer clear that this is universally the case (Tolbert, 1974). There are certainly wide variations concerning quantities released both in space and time and from species to species (see the discussion by Hellebust, 1974). It is important to note that earlier estimates of excreted glycolate by the Calkins colorimetric test with acidified 2,7-dihydroxynapthalene may have often given overestimates, since the color reaction is not specific and aldehydes, organic materials oxidizable to aldehydes and, of most interest, nitrate interfere with the assay (Tolbert, 1974).

It is also important to note the discussion of light quality versus glycolate excretion by Ignatiades and Fogg (1973). The quality of light used in the majority of the work with cultures does not closely resemble the quality of light available at depth in aquatic and marine systems. Studies with Chlorella have shown higher uptake of aspartic acid when cultures were supplemented with blue light. On the other hand, glycolate excretion is apparently enhanced by red and white light, while no detectable amounts of

glycolate were observed under illumination by blue light (Becker, Döhler, and Egle, 1968). (See also the review by Voskresenskaya (1972) on the effects of blue light on carbon metabolism.) However, glycolate remains an important excretory product, especially under conditions favorable for high rates of photorespiration (i.e., high concentration of O_2, low concentration of CO_2, and high pH (Tolbert, 1974)).

Of critical importance to this experiment was the assessment of photoheterotrophic utilization in relation to chemoheterotrophy. In addition to some problems concerning the physical handling of glycolate, there is some confusion concerning its utilization by bacteria. R. T. Wright (Gordon College, Massachusetts, personal communication) has shown high respiration values by bacteria incubated with glycolate, but virtually no growth, or cellular accumulation of radioactive label. He hypothesizes that glycolate may represent an energy source rather than a carbon source, and/or a co-factor in the metabolism of other organic carbon skeletons. By adding up to 300 mg l^{-1} glucose he was able to show an increase in growth in the presence of glycolate. Until the role of glycolate metabolism in bacterial chemoheterotrophy is better understood, its utilization in the assessment of photoheterotrophic utilization versus chemoheterotrophic utilization must be held in question for mixed populations.

D-Glucose-2-^{3}H (specific activity, 500mCi $mmol^{-1}$) was selected for use because of the relatively stable metabolic carbon site for ^{3}H attachment. The quantity of glucose added for these studies was 4-5 µg glucose $liter^{-1}$. This concentration of glucose was achieved by dilution of the radioactive substrate without the addition of any non-radioactive carrier. The quantity of material was sufficient and not depleted significantly during the short incubation intervals, 2.4 to 3.4 hours. The quantity utilized is also well below those levels normally observed for diffusion mechanisms and is within the range of concentrations reported for naturally occurring glucose (i.e., from undetectable levels to nearly 200 µg glucose $liter^{-1}$ in sea water (Vaccaro et al., 1968; Hicks and Carey, 1968)).

The utilization of an organic compound to measure the "heterotrophic potential" of planktonic populations, in much the same manner that tracer quantities of ^{14}C-bicarbonate are used to estimate photosynthetic activity, is not a new idea. Parsons and Strickland (1962) proposed its use and discussed the accompanying problems. It has since been used in that way by Paerl and Goldman (1972) and McKinley (1971, unpublished manuscript).

One milliliter of ^{14}C-bicarbonate (@ 4.6 or 5.1 µCi ml^{-1}) was added simultaneous to the addition of one milliliter of ^{3}H-glucose solution to each light/dark pair of bottles (125 ml Pyrex glass-stoppered bottles).

Procedures for isotope utilization followed closely that of Strickland and Parsons (1972). In situ incubations were generally less than 3.4 hours for organic uptake and 3.5 hours for inorganic fixation.

Three-hour incubations preclude any conclusions concerning maximal instantaneous rates of fixation, since measures are averaged over a relatively long period of time. Therefore, as will be seen later, while the maximum instantaneous rates of inorganic carbon fixation would be expected prior to the midday maximum and the concomitant maximum of solar irradiance, the highest average sustained rates of fixation were found during the midday incubation periods.

Samples were returned to the laboratory and 50 ml aliquants from each bottle were filtered through 0.22 μm Millipore filters (< 1/2 atm pressure). Filters were stored under dessication, until acid fumed to remove any residual $Ca^{14}CO_3$ which may have precipitated during the incubation period. Filters were then combusted in an oxygen atmosphere in a Packard Tri-Carb Oxidizer (Model 305).[2] The combustion materials were thus isotopically

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[2]Blanks were burned between each sample to reduce the possibility of cross contamination. "Carry-over" and "memory" on the collecting columns were carefully monitored for each oxidation series.

separated and collected as $^{3}H_2O$ and $^{14}CO_2$ in scintillation vials.[3]

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[3]Scintillation cocktails:

a) ^{3}H-cocktail
   10 ml Insta-gel (Packard Instrument Co.)

b) ^{14}C-cocktail
   3 ml Monoethanolamine (CO_2 trap)
   9 ml Absolute Methanol (Solvent)
   7 ml Scintillator consisting of
      15 g PPO
      1 g bis-MSB
      Scintillation grade Toluene to
         make 1 liter.

ASSUMPTIONS, CALCULATIONS, AND STATISTICAL ANALYSIS

The following assumptions were made in calculating the activity represented by the observed uptake of ^{3}H-glucose:

(1) That the isotopic discrimination effect for ^{3}H-glucose is 1.00. One can calculate on a random probability and weight basis that the discrimination against $^{14}CO_2$ should be 1.045. Empirical observation has given support to the figure 1.06 which has received general acceptance. $^{3}H_2O$ on the other hand because of a proportionally smaller weight for the water molecule would be expected to have an associated factor of 1.11 or 1.10. For ^{3}H-glucose, because of its relatively greater weight, one could calculate a figure of 1.01 (i.e., 182 g $mole^{-1}$/180 g $mole^{-1}$). Since this factor is generally unknown and close to 1.0 it was felt that 1.00 would give the least biased minimum estimate for glucose uptake.

(2) Since the natural glucose concentration at the time of incubation was not determined it was assumed that the minimum conservative estimate would be represented by the following:

$$\frac{^{3}\text{H-glucose added}}{^{3}\text{H-glucose measured}} = \frac{\text{H-glucose available}}{\text{H-glucose utilized}}$$

The result of this assumption is two-fold. First the amount of organic uptake calculated by this method represents a minimum figure. Any naturally occurring glucose concurrent to observed utilization rates would be in addition to that injected. Therefore the glucose available would have been increased and the radioactive pool diluted proportionately. In other words if there were 10 μg glucose liter^{-1} available naturally, the addition of 5 μg glucose liter^{-1} would raise the total figure to 15 μg and the estimate of the quantity utilized should have been increased by 3X.

As the natural concentration approaches zero the proportional comparison between observed and projected approaches 1.00. Should values of naturally occurring glucose, or total similar competing organic compounds, approach 50 or 100 μg liter^{-1}, the appropriate factors become 11X and 21X respectively, assuming these concentrations are below saturation levels for uptake kinetics. Thus for values within the expected range of 10 to 20 μg glucose liter^{-1} the estimates must be considered to be very conservative minimal estimates.

The second result of this assumption is that the amount added is independent of concentration except on a

random strike probability basis. This will be true only within the additional constraints of the physiological tolerance limits for the organisms, that no substrate limitation occurs, and that the concentrations are within the expected range for the environment. The figure of concern for additions of the same relative magnitude then equals the specific activity of the material utilized (e.g., in this case SA = 1 mmol/500 mCi).

Organic Uptake

The calculation for converting the raw counts per minute (CPM) from the ^{3}H-glucose uptake series was as follows:

$$\mu gC\ m^{-3}\ hr^{-1} = (CPM*CON1*CON2*CON3*CON4*CON5*SA*TOPEF)/((A*ESR)+B)*BF*SS*TIME(J)*RE(K)*DF(K)$$

where:

CPM = raw counts per minute

A = the slope for the calculated quench correction curve

B = the intercept for the quench curve

ESR = the External Standard Ratio (quench)

BF = the bottle factor (corrects all bottles to 125 ml)

SS = sample size (50 ml)

TIME(J) = the incubation time in hours

RE(K) = the recovery efficiency for known standards with the oxidizer instrumentation

DF(K) = the isotopic decay factor for ^{3}H

TOPEF = the isotopic discrimination effect (assumed to be 1.00)

CON1 = 1.0 (weighting function, not needed here)

$$CON2 = \frac{1000ml}{1} \times \frac{1000\ l}{m^3} = 10^6$$

$$CON3 = 1\mu Ci/(2.22 \times 10^6\ dpm)$$

SA = the specific activity (1μmol/500μCi)

$$CON4 = \frac{6\mu mol\ C}{\mu mol\ ^{3}H\text{-glucose}} \times \frac{12.001\mu g\ C}{\mu mol\ C} \times \frac{mg\ C}{1000\ \mu g\ C}$$

CON5 = 1000 μg C/mg C

This basic calculation was performed for every sample and the results from paired light bottles and dark bottles were used for further statistical analysis and estimation. Samples within the design for statistical analysis numbered 504; total n equaled 720.

Photoheterotrophic Uptake

Photoheterotrophic uptake was estimated as the difference between light and dark bottle pairs. In order to arrive at the estimate it is necessary to assume the following:[4]

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[4]This is much the same assumption used to estimate photolithotrophic uptake of CO_2 (i.e., photosynthesis); calculated as the difference between photolithotrophic uptake less chemolithotrophic uptake.

Light bottle uptake = Photoheterotrophic uptake + Chemoheterotrophic uptake + Background

Dark bottle uptake = Chemoheterotrophic uptake + Background

Therefore light bottle less dark bottle yields an estimate of the proportion of the total heterotrophic uptake observed due to photoheterotrophic uptake (i.e., "PHOTO" in Appendices A and B).

Chemoheterotrophic Uptake

Chemoheterotrophic (i.e., "BACTERIAL") uptake was estimated by the following:

$$\mu gC\ m^{-3}\ hr^{-1} = \left[\frac{CPM_{dark}}{(A*ESR) + B} - BKG(K)\right] *(CON1*CON2*CON3*CON4*CON5*SA*TOPEF)/BF*SS*TIME(J)*RE(K)$$

where:

BKG(K) = background calculated for each oxidation series

This calculation overestimates the contribution to total heterotrophic fixation by chemoheterotrophic organisms, since the background used for the calculation represents machine background (i.e., background associated with the oxidizer and scintillation counter). A proper control would have consisted of a sample "killed" at the time of

injection of the organic compound to account for any absorption and adsorption in the sample.

With this in mind, any comparisons between chemoheterotrophic uptake and photoheterotrophic uptake must be considered minimal estimates of photoheterotrophic potential. Any increase above this machine background would lower chemoheterotrophic estimates and proportionally increase the proportion due to photoassimilation in any comparison of the two.

Percent Comparison

The percent contribution of photoheterotrophic utilization with respect to chemoheterotrophic uptake was calculated as:

PCTBC = (Photoheterotrophic uptake/
Chemoheterotrophic uptake)*100.0

Mean Values and Annual Means

Mean values for all estimates were calculated from the four paired samples for each time, depth, and month (see Appendix A). Standard deviation and standard error were calculated to aid in graphing.

Annual means were calculated from all sample estimates (n=360) for photoheterotrophic uptake, chemoheterotrophic uptake, and percent bacterial uptake (i.e., (Photo/Chemo)*100.0). Standard deviation, standard error, coefficient of variation (CV), and 99% confidence intervals

about the mean were also calculated. An arcsine transformation was used for the percentile data, since the range of observed values was greater than the interval from 30 to 70%.

Inorganic Fixation

Calculations for inorganic carbon fixation followed a similar pattern:

$$mgC\ m^{-3}\ hr^{-1} = CPM*CON2*CON3*ALK(JJJ)*PHFTR(JJJ)*$$
$$CON1*CON5*TOPEF/RE(K)*((A*ESR)+B)*$$
$$BF*SS*AA*TIME(J)$$

where:

TOPEF = the isotopic discrimination effect (1.06)

CON1 = dilution factor for alkalinity determination (20.0)

CON2 = ml per bottle (125.0)

AA = the activity per ml added in μCi

ALK(JJJ) = the alkalinity determination per depth and month (ml 0.02N H_2SO_4 from titrations)

PHFTR(JJJ) = the pH factor for each depth and month[5]

Other factors remain the same as previously given.

Photosynthetic (photolithotrophic) fixation was estimated as the difference between light bottles and dark

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[5]See the table of values by Bachmann in Saunders, Trama, and Bachmann (1962).

bottles. Chemolithotrophic production (dark bottle less background) was not calculated.

Mean values for each of the differences of the four pairs were calculated along with standard deviation and standard error. These values were tabulated along with estimates of photoheterotrophic and chemoheterotrophic production from the same sample for comparison purposes (see Appendix B). Percent comparisons for mean values of photolithotrophic, photoheterotrophic, and chemoheterotrophic production were also calculated. The preceding calculations were carried out on a Hewlett-Packard HP 2100A computer. The statistical analysis was accomplished through cooperation with the Application Programming section of the Michigan State University Computer Laboratory. A Control Data Computer System CDC 6500 was used for the analysis.

RESULTS AND DISCUSSION

Heterotrophic Activity

An examination of the analysis of variance table for the heterotrophic uptake of ^{3}H-glucose reveals a number of significant effects (Table 1). Most notable of the main effects is the "Bottle" effect, for which the treatment contrast light versus dark is highly significant. The exact probability that the difference observed is due to random chance alone is <0.0005. Thus there is very strong evidence of a difference between light and dark bottles. It is also clear that light activity is greater on the average than dark (i.e., 9.2 $\mu gC\ m^{-3}\ hr^{-1}$ vs. 6.3 $\mu gC\ m^{-3}\ hr^{-1}$).

The treatment main effects consisted of Months (J,J,A, etc.), Time of Day (SR, MD, SS), Depth (2, 6, 10 m.), and Bottles (Light, Dark). Other than the main effect "Bottles," which represents a clear, controlled treatment, the other main effects represent fixed treatments which are confounded by a number of environmental changes. In order to correctly interpret the resulting differences it is necessary to remember the numbers and types of changes these treatments may represent. For example, changes observed over months may be due to species population changes,

Table 1.--Analysis of Variance table for photoheterotrophic uptake of glucose. Three-way factorial split plot design. Significance levels are indicated by asterisks: (***) significant at the 0.1% level, or better; (**) significant at the 1% level; (*) significant at the 5% level; (n.s.) not significant at the 5% level, or better.

Analysis of Variance Table

Source of Variance	Sum of Squares	Degrees of Freedom	Mean Square	F Statistic
Month	2076.22	6	346.04	51.97***
Time	739.83	2	369.91	55.56***
Depth	639.90	2	319.95	48.06***
Month x Time	334.07	12	27.84	4.18***
Month x Depth	938.58	12	81.96	12.31***
Time x Depth	131.46	4	32.87	4.94***
Month x Time x Depth	144.78	24	6.03	0.91^{ns}
Error A	1258.35	189	6.66	
Bottle	1075.04	1	1075.04	197.88***
Month x Bottle	237.53	6	39.59	7.29***
Time x Bottle	175.02	2	87.51	16.11***
Depth x Bottle	48.31	2	24.15	4.45**
Month x Time x Bottle	121.86	12	10.16	1.87*
Month x Depth x Bottle	160.32	12	13.36	2.46**
Time x Depth x Bottle	43.78	4	10.94	2.01^{ns}
Month x Time x Depth x Bottle	78.00	24	3.25	0.60^{ns}
Residual Error	1026.79	189	5.43	
Total	9274.86	503		

temperature changes, or organic loading and increasing concentrations of organic materials (N.B. this would be especially true in late summer at depth). Changes of activity throughout the daylight period could be due to changes in light intensity and quality, or a periodism within the organisms themselves due to end product inhibition, or other biochemical feedback systems. Differences over depth at nearly any time of the year could be related to a number of these parameters (e.g., light intensity and quality, temperature differences, population differences among the water strata, and organic loading). Realistically, all of these factors probably interact in such a way as to yield the changes observed.

Since a number of three-way interactions are significant, or very nearly significant,[6] it is necessary that these interactions be examined carefully in order to correctly interpret the differences observed. Understanding main effects alone is not sufficient for a proper interpretation of differences observed. Careful selection of different comparisons may give insight in selecting those parameters most likely to be responsible for the changes observed (e.g., we may contrast differences with depth at turnover with those during a stratified period to

---

[6]

Source of Variance	Probability of F Statistic
Month x Time x Bottle	0.04
Month x Depth x Bottle	0.005
Time x Depth x Bottle	0.09

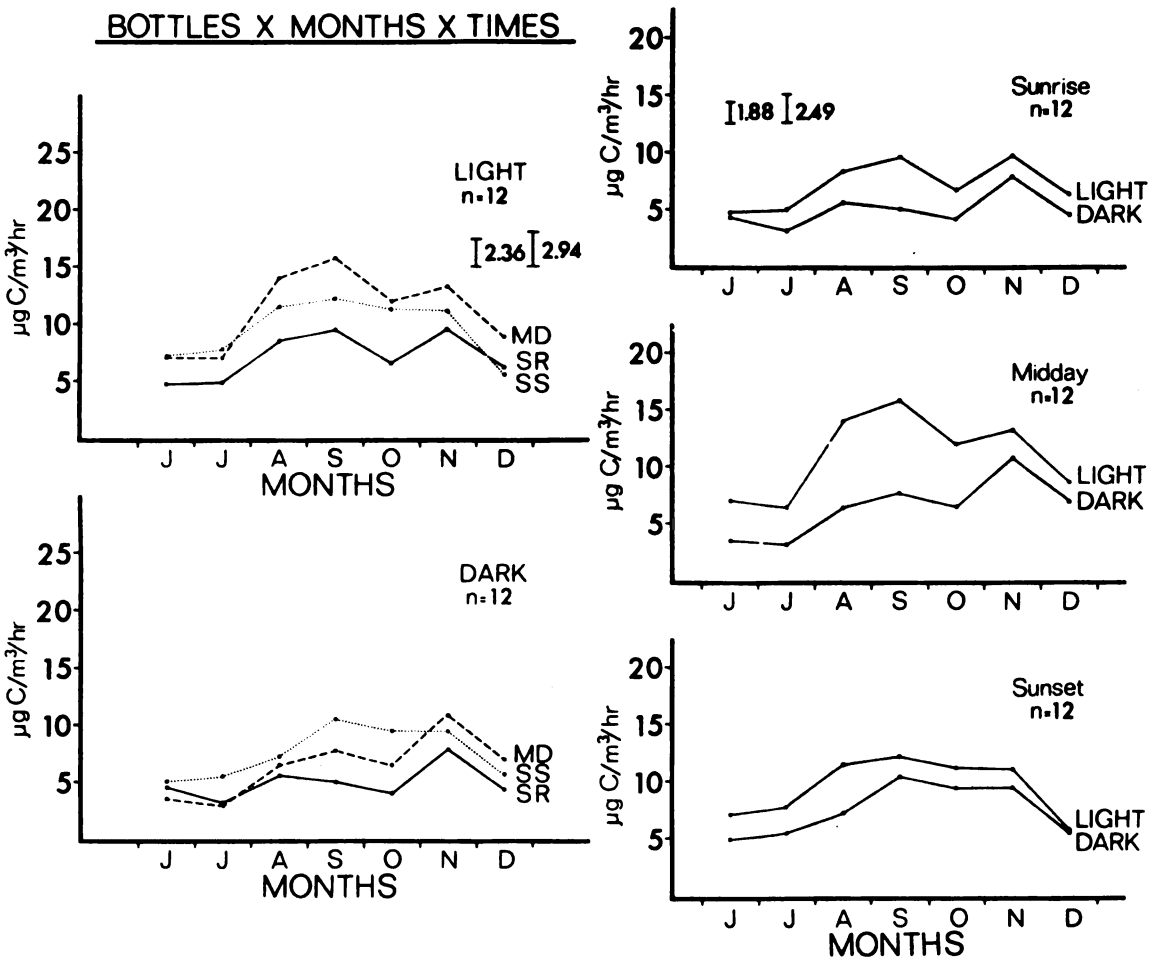
approximate a comparison of light and populations versus temperatures).

Bottles x Months x Times

Figure 4 represents the pattern of uptake observed in light and dark bottles over months and at times of day. Each point is the mean of 12 samples (i.e., replicates summed across depths). The relationship between light and dark uptake is presented in two ways to more clearly demonstrate the patterns observed. On each series of graphs, and those that follow, two distances are denoted by vertical bars (here 2.36 and 2.94, and 1.82 and 2.49). These distances represent the value calculated by the Sheffé S Method for a posteriori comparisons of means (here any two points) (Kirk, 1968). The larger of the two (e.g., 2.94 vs. 2.36) represents the minimum distance two points would be separated to be considered different at the 1% level. In other words, if the distance between two points of interest is greater than this value, they may be considered to be significant at the 1% level. The smaller of the values (here 2.36) represents the distance for the assignment of significance at the 5% level.

While the Sheffé test is useful as a means of selecting those points of interest for comparison, as with all a posteriori tests multiple use at a low significance level will lead to some Type I errors, the rejection of a true null hypothesis. Thus if we are testing whether or not

Figure 4.--Three-way interaction plots (BOTTLES X MONTHS X TIMES). Graphs represent Light and Dark responses in $\mu gC\ m^{-3}\ hr^{-1}$ for all incubation periods across months as SR, sunrise (——); MD, midday (----); and SS, sunset (····). Contrasts between Dark and Light bottles for each incubation period are also given. Sheffé S values for each series of graphs are indicated by vertical bars. The greater of the two, the difference for significance at the 1% level; the lesser, at the 5% level. Each point represents a mean of 12 samples.


BOTTLES X MONTHS X TIMES
LIGHT
n=12
2.36
2.94
MD
SR
SS
DARK
n=12
MD
SS
SR
µg C/m³/hr
J J A S O N D
MONTHS
Sunrise
n=12
1.88
2.49
Midday
n=12
Sunset
n=12
LIGHT
DARK

two population means are the same, we reject the null hypothesis if the distance is greater than the Sheffé S value. If the value at the 5% level is applied numerous times to the same data set we would expect to reject a null hypothesis (i.e., declare the means to be different) which should have been accepted (i.e., the means are not different) one time in twenty on the average. Care must be exercised in this respect.

By comparing dark bottles across all months some general observations may be made. The sunrise (SR) incubation represented the lowest activity across all months. The only exceptions to this statement are observed where mean values were not significantly different. Midday (MD) incubations usually yielded increased activity over that observed at sunrise and intermediate to that of sunset (SS). Late afternoon, pre-sunset (SS), incubations generally resulted in the greatest chemoheterotrophic activity throughout the daylight period. This finding agrees well with the diurnal "bacterial" activities observed by Saunders (see the discussion in Saunders, 1969). An exception to this rule was observed in the November and December incubations, where sunset values represent an intermediate range between midday values and sunrise values (midday and sunrise being significantly different, with midday representing the higher value, but with the sunset value not significantly different from either). In general across all months and times there was a pattern of increasing activity until

turnover and ice cover in December. This is also in agreement with the patterns of chemoheterotrophic activity observed over an annual period by Hobbie (1969).

Light bottle activity (i.e., chemoheterotrophic dark bottle activity plus photoheterotrophic activity) showed a different pattern. Here the greatest total activity was represented by the midday values across nearly all months, followed by sunset and then sunrise values. In general the greatest total activity across all months and times occurred during the late summer period from July to November.

By examining the plots contrasting light and dark incubations at each time and across all months, the relative magnitude of chemoheterotrophic activity can be compared to total activity and to photoheterotrophic activity, the distance between the two lines. The greatest difference between light and dark activity occurred during the midday incubation period. The maximum for the months within the design occurred during the months August, September, and October as previously discussed.

In general the difference between light and dark bottles was greater throughout the year for sunrise incubations than for sunset incubations. The most marked decrease in photoheterotrophic activity occurred during the sunset incubation under ice.

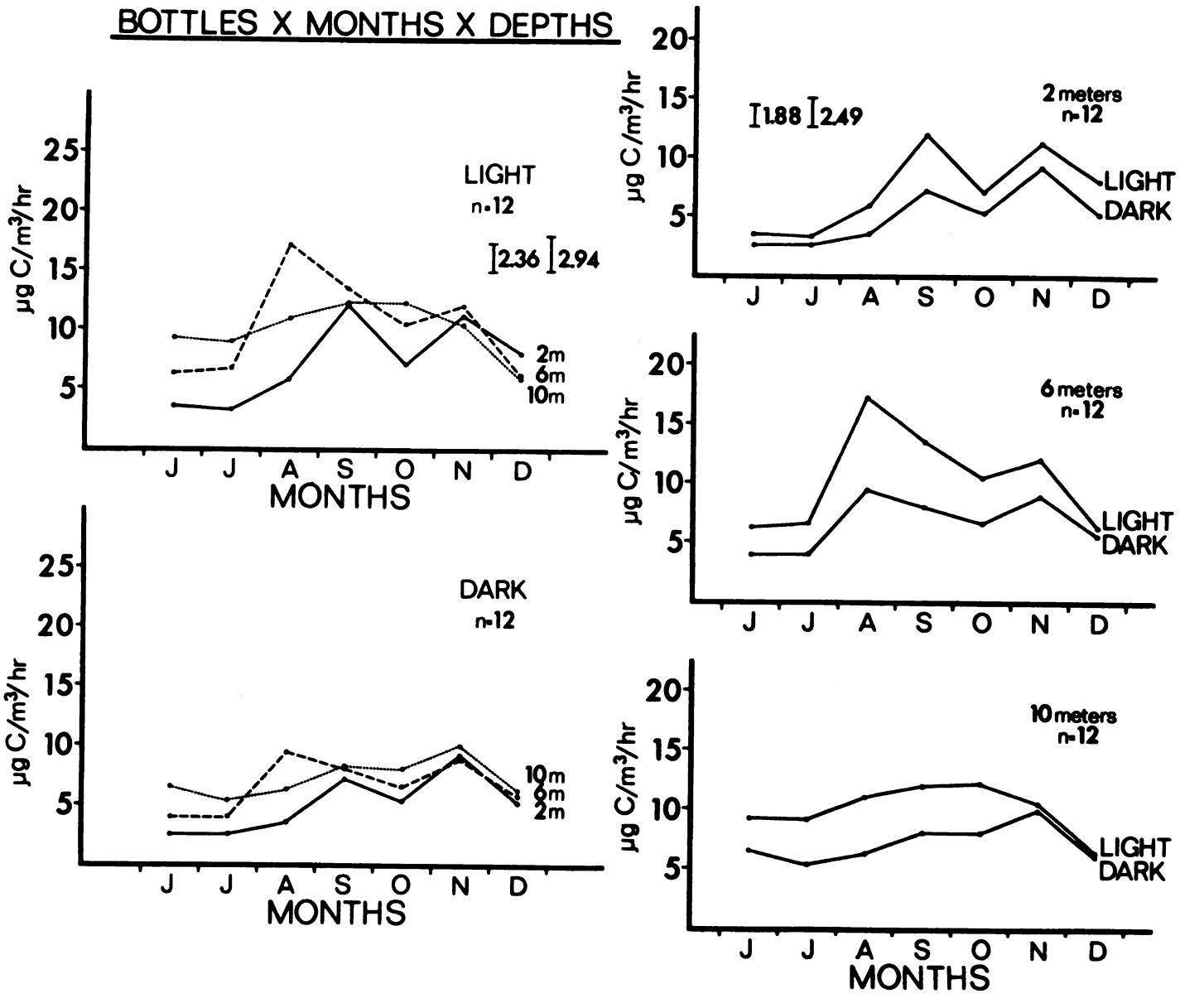
Bottles x Months x Depths

Figure 5 depicts the three-way interaction for BOTTLE X MONTHS X DEPTHS (n=12). Dark bottle activity across all months and depths again showed the general increase up to the time of autumnal circulation and then an apparent decrease under ice.

Activity generally increased with depth across all months. An exception is the elevated 6 meter value during August, which corresponded to peak values for both total and photoheterotrophic activity.

The power of the a posteriori test in examining differences is demonstrated here very well. During June, early in the stratified period, values at 2 meters and 6 meters were not statistically different in activity, but both were different from that of 10 meters. As stratification progressed 6 meters values were not statistically different from those either at 2 or 10 meters, but values for 2 and 10 meters were different. By August with summer stratification fully established the 2, 6, and 10 meters samples represented different strata of water with statistically different uptake rates. During September the peak uptake values at 6 meters decreased with concomitant increasing activity at 2 and 10 meters. During October, uptake rates for the 2 and 10 meter strata were again statistically different, but values at 6 meters were not different from those of either 2, or 10 meters depths. During turnover and under ice with isothermal conditions,

Figure 5.--Three-way interaction plots (BOTTLES X MONTHS X DEPTHS). Graphs represent Light and Dark responses in μgC m^{-3} hr^{-1} for all depths across months, as 2 meters (———), 6 meters (----), and 10 meters (····). Contrasts between Dark and Light bottles for each depth interval are also given. Sheffé S values are indicated by vertical bars. Each point represents a mean of 12 samples.


BOTTLES X MONTHS X DEPTHS
LIGHT
n=12
I2.36 I2.94
2m
6m
10m
DARK
n=12
10m
6m
2m
µg C/m³/hr
MONTHS
J J A S O N D
2 meters
n=12
I1.88 I2.49
6 meters
n=12
10 meters
n=12
LIGHT
DARK

no differences in uptake was observed among depths. This pattern of increasing activity with depth and as the season progressed until uniform activity was achieved at turnover was expected and fits classical patterns of activity.

Total activity (i.e., light bottle activity) is much more difficult to interpret. During June and July activities at all depths are different with greater activity associated with increasing depth. In August the metalimnetic peak of activity was observed, followed by a marked increase in activity at 2 meters and a decrease in activity at 6 meters in September. Total activity then decreased toward turnover. During turnover fairly uniform values were observed, as were values under ice.

It is important that these patterns be contrasted with those patterns of light and dark uptake at the three depths. The general pattern of increased uptake with depth is obvious. Superimposed on the general increase in chemoheterotrophic activity was an increasing difference between light and dark bottles, here considered to correspond to photoheterotrophy. The greatest observed differences occurred at 6 meters during August and September and during other periods at either 6, or 10 meters.

While both total activity and dark bottle activity considered independently are not statistically different with respect to depth at turnover, it is clear that photoheterotrophy (i.e., the difference between the two values at any one depth interval) was markedly different and that

the pattern during the ice free and stratified periods were also quite different. During November with uniform mixing, and probably also populations and organic materials as well, a maximum was observed at mid-depth with a dramatic decrease at 10 meters. Under ice in December the pattern of increasing activity with depth was reversed and highest activity observed near the surface under the ice. This observation suggests that photoheterotrophy is important at decreased light intensities, as would be represented at depth during the ice free period and near the surface under ice cover.

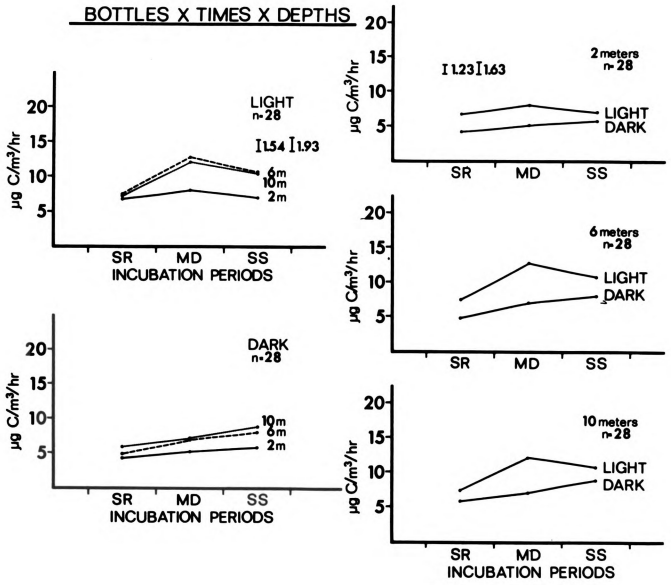
Bottles x Times x Depths

Figure 6 depicts the three-way interaction BOTTLES X TIMES X DEPTHS (n=28). As discussed previously, this interaction was not found to be significant at the 5% level, but was sufficiently close to being significant to warrant its examination for confirming trends. Dark bottle activity was clearly demonstrated as increasing throughout the day-light periods, more so at 6 and 10 meters averaged across all months than at 2 meters.

Light activity was generally greater at midday or sunset. Values at 6 and 10 meters were generally not very different from one another, but both were significantly different from the activity observed at 2 meters during midday and sunset incubation periods.

The contrast between light and dark bottles for the three depths is more instructive. On the average

Figure 6.--Three-way interaction plots (BOTTLES X TIMES X DEPTHS). Graphs represent Light and Dark responses in μgC m^{-3} hr^{-1} for all depths across incubation periods, as 2 meters (——), 6 meters (----), and 10 meters (····). Contrasts between Dark and Light bottles for each depth interval are also given. Sheffé S values are indicated by vertical bars. Each point represents a mean of 28 samples.


BOTTLES X TIMES X DEPTHS
LIGHT
n=28
I 1.54 I 1.93
6m
10m
2m
µg C/m³/hr
SR
MD
SS
INCUBATION PERIODS
DARK
n=28
10m
6m
2m
I 1.23 I 1.63
2 meters
n=28
LIGHT
DARK
6 meters
n=28
10 meters
n=28

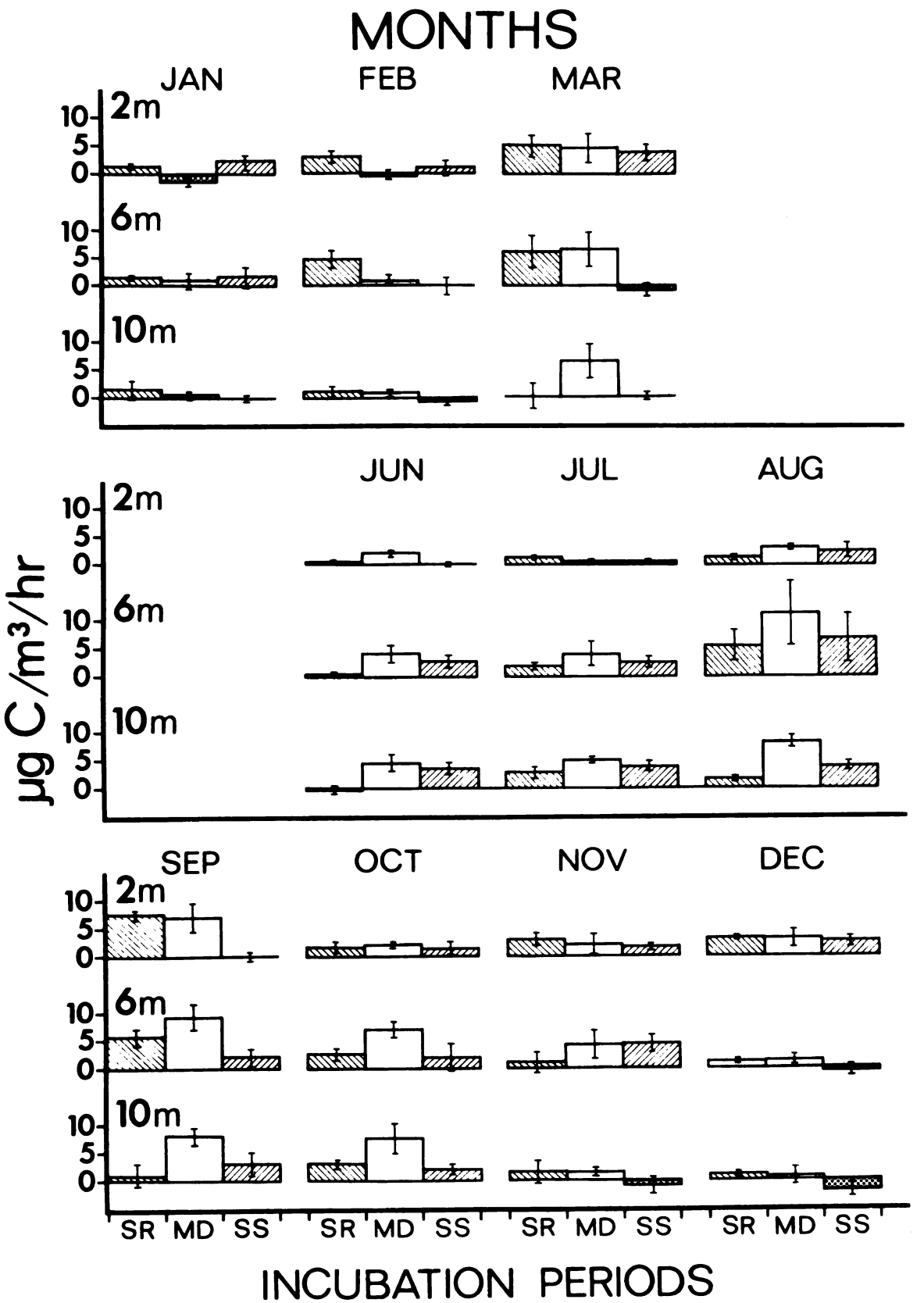
photoheterotrophic activity was greater during sunrise incubations than for sunset incubations with greater activity at 2 and 6 meters in the morning, but with a shift to 6 and 10 meters as the day progresses. The greatest photoheterotrophic activity across all depths was found at 6 meters. A contrast among sunset incubations maintained the highest value at 6 meters, but there was an indication of a shift toward greater activity at 10 meters rather than 2 meters. This pattern of increasing activity from morning to midday and a shifting of depth from morning to sunset implies some type of minimum/maximum threshold for light, coupled with periodism in photoheterotrophic activity, or substrate availability.

With these seasonal, daily, and depth patterns in mind, the pattern of calculated estimates for photoheterotrophic and chemoheterotrophic activity over the annual period can be examined.

Photoheterotrophy and Chemoheterotrophy

The pattern of photoheterotrophic activity observed during 1974 is given in Figure 7. Each bar graph represents the mean of four replicate samples. Individual measures were highly variable and ranged from 0 to 27 $\mu g\ C\ m^{-3}\ hr^{-1}$. An annual mean calculated from all samples (n=360) yielded a value of 2.6 $\mu g\ C\ m^{-3}\ hr^{-1}$. Of particular interest are two periods of fairly high activity, the first of which corresponded to spring turnover (i.e., March) just after

Figure 7.--Estimated values for photoheterotrophic uptake of glucose during 1974 as $\mu gC\ m^{-3}\ hr^{-1}$. Histograms represent the means of four replicate samples. Uptake values for each depth interval (2, 6, 10 meters) and each incubation period (SR, MD, SS) are indicated for each month. Bars denote plus or minus standard error ($\pm$SE) about the mean. Negative mean values are indicated by stippling.


MONTHS
JAN
FEB
MAR
JUN
JUL
AUG
SEP
OCT
NOV
DEC
2m
6m
10m
10
5
0
µg C/m³/hr
SR MD SS
INCUBATION PERIODS

ice loss. The water column was a uniform 4.3°C at this time, generally a period of dominance by diatom species within the lake. The metalimnetic maximum in August and the maxima in September generally corresponded to a period of metalimnetic dominance by non-heterocystous blue-green algae (usually a Chroococcus - Gomphosphaeria - Aphanocapsa association). These periods also corresponded to periods of maximal photosynthetic production for this system.

The estimated chemoheterotrophic activity over the annual period (Figure 8) is also expressed as values where each bar graph represents the mean of four replicate samples. Here the individual measures were less variable than estimates of photoheterotrphic activity and ranged from 1 to 18 μg C m^{-3} hr^{-1}. An annual mean calculated from all samples (n=360) was 6.9 μg C m^{-3} hr^{-1}. One pattern immediately apparent from this graph is the fairly high, uniform rates of uptake throughout the entire year. Values under ice and at 2 to 4°C temperatures were not very much different from maximal values. The greatest activity occurred during periods of circulation in spring and autumn. Early to midsummer values were lowest and activity increased, particularly at depth, as summer progressed. The activities in March, August, and September corresponded to periods of peak photosynthetic activity.

Figure 9 depicts the mean percent comparison of photoheterotrophic activity to chemoheterotrophic estimates. Individual measures were highly variable with a range from

Figure 8.--Estimated values for chemoheterotrophic uptake of glucose during 1974 as $\mu gC\ m^{-3}\ hr^{-1}$. Histograms represent the means of four replicate samples. Uptake values for each depth interval (2, 6, 10 meters) and each incubation period (SR, MD, SS) are indicated for each month. Bars denote plus or minus standard error ($\pm$SE) about the mean.

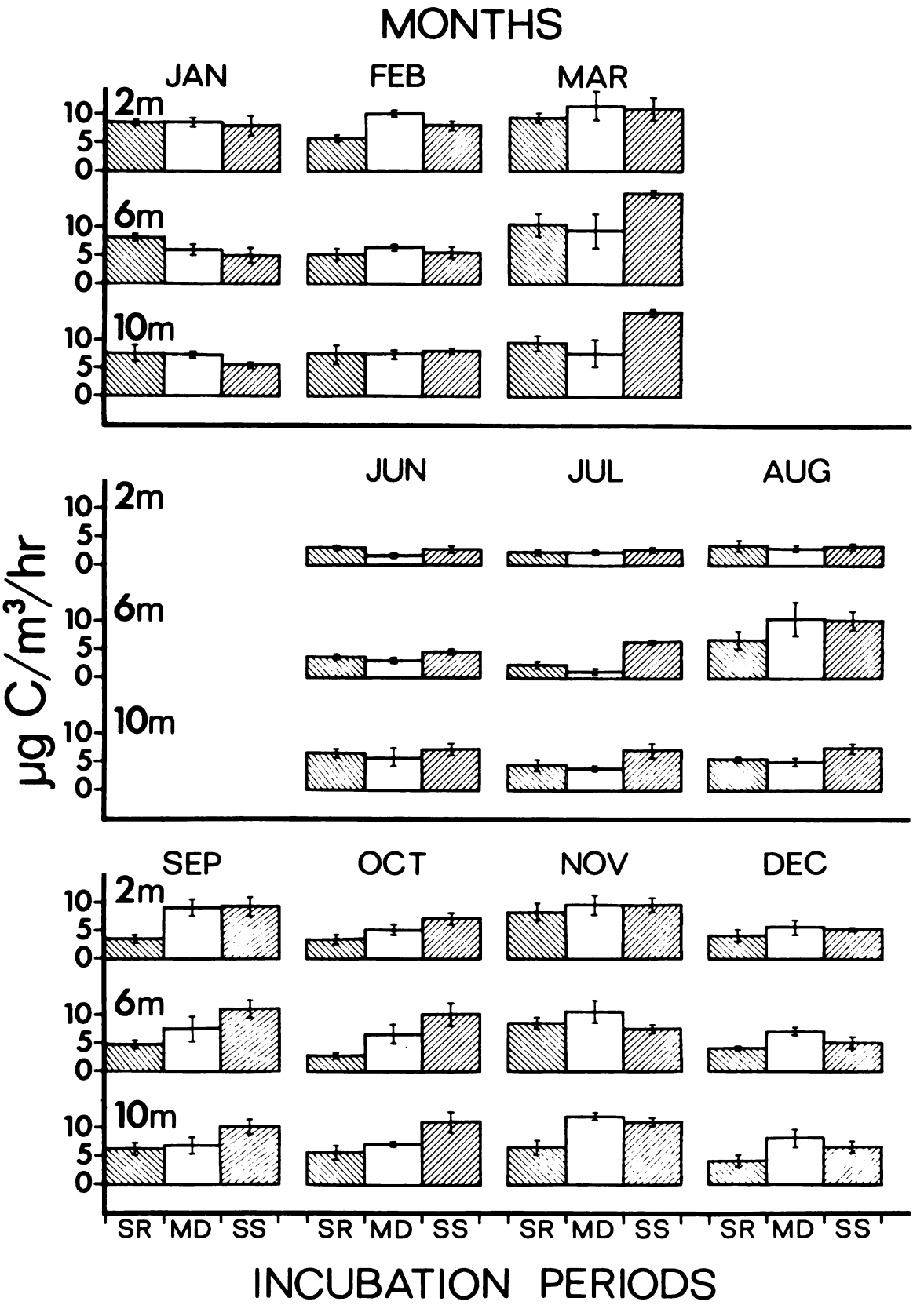
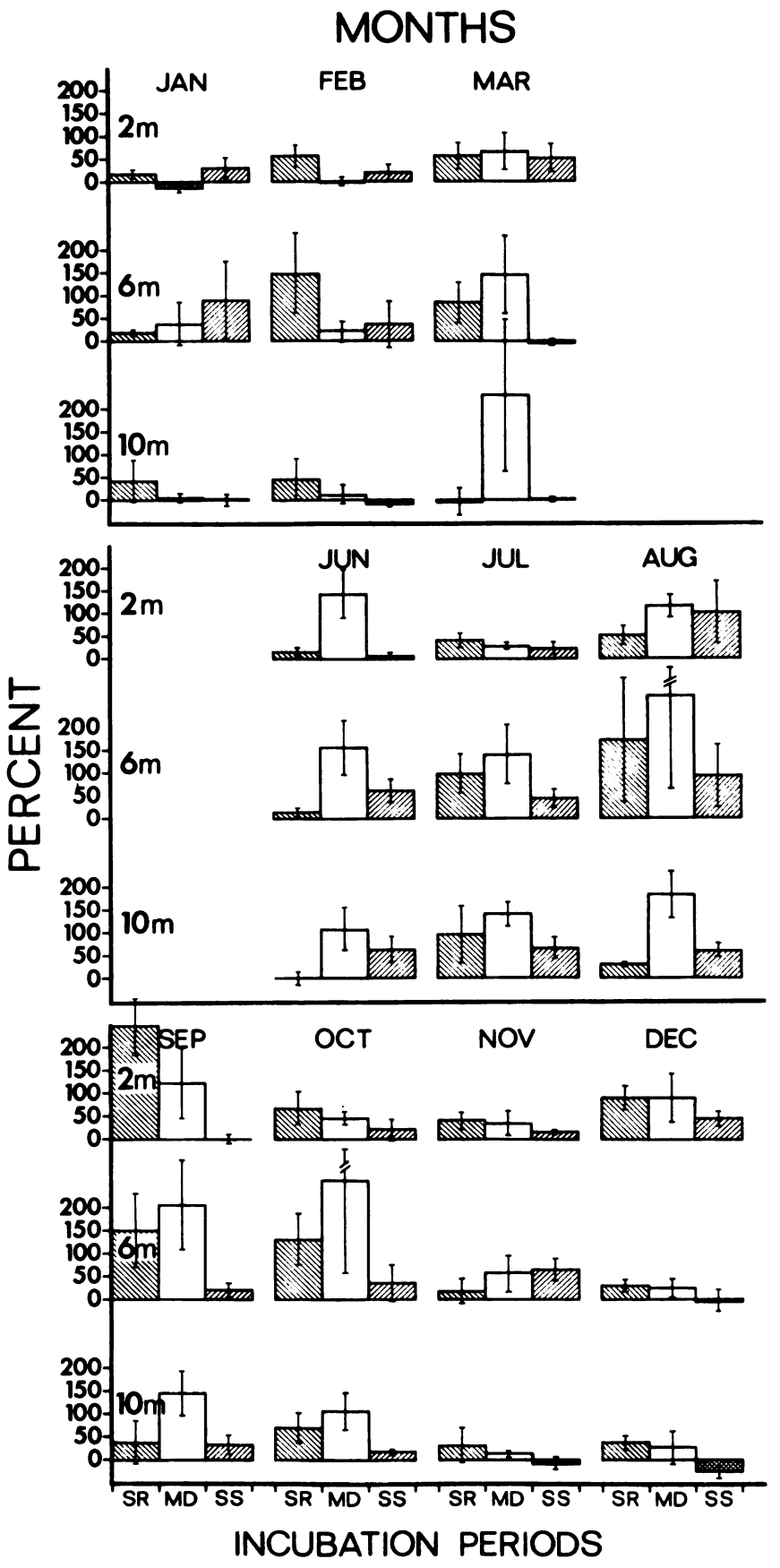

MONTHS
JAN
FEB
MAR
JUN
JUL
AUG
SEP
OCT
NOV
DEC
2m
6m
10m
10
5
0
µg C/m³/hr
SR MD SS
INCUBATION PERIODS

Figure 9.--Percent comparisons between photoheterotrophic and chemoheterotrophic uptake values during 1974. Histograms represent the means of four replicate samples. Percent comparisons at each depth interval (2, 6, 10 meters) and each incubation period (SR, MD, SS) are indicated for each month. Bars denote plus or minus standard error (±SE) about the mean. Negative mean values are indicated by stippling.


MONTHS
JAN
FEB
MAR
JUN
JUL
AUG
SEP
OCT
NOV
DEC
2m
6m
10m
PERCENT
200
150
100
50
0
SR
MD
SS
INCUBATION PERIODS

0 to greater than 870% of chemoheterotrophic activity. The annual average over all samples was 67.6% of chemoheterotrophic activity.

The pattern observed differs little from that already discussed. Maximal values were generally achieved where peak photoheterotrophic activity was found (March and late summer). Exceptions to this occur at all depths in June and at depth during July, both periods of low chemoheterotrophic activity, and at mid-depths during February and October.

It is clear from the annual mean comparisons (Figure 10) and the preceding discussion that photoheterotrophic utilization not only accounts for significant cycling of specific carbon compounds at certain times of the year, but is in general substantial over the entire annual period during the daylight hours.

Photosynthesis

The analysis of variance for the photosynthesis data (Table 2) was highly significant and interactive. Since the four-way interaction (i.e., Month x Time x Depth x Bottle) was significant and one must take all of these factors into consideration for interpretation, a convenient way of viewing the data is in the histogram format used for the photoheterotrophy and chemoheterotrophy estimates (Figure 11). It is evident that these data were much less variable than either of the two heterotrophic measures. Mean values ranged from 0 to 9.1 mgC m^{-3} hr^{-1}. The

Figure 10.--Annual mean values for chemoheterotrophic uptake, photoheterotrophic uptake, and percent comparison values ((Photo/Chemo) *100.0). Heterotrophic uptake as $\mu gC\ m^{-3}\ hr^{-1}$. Error bars give 99% confidence limits about the mean (n=360).

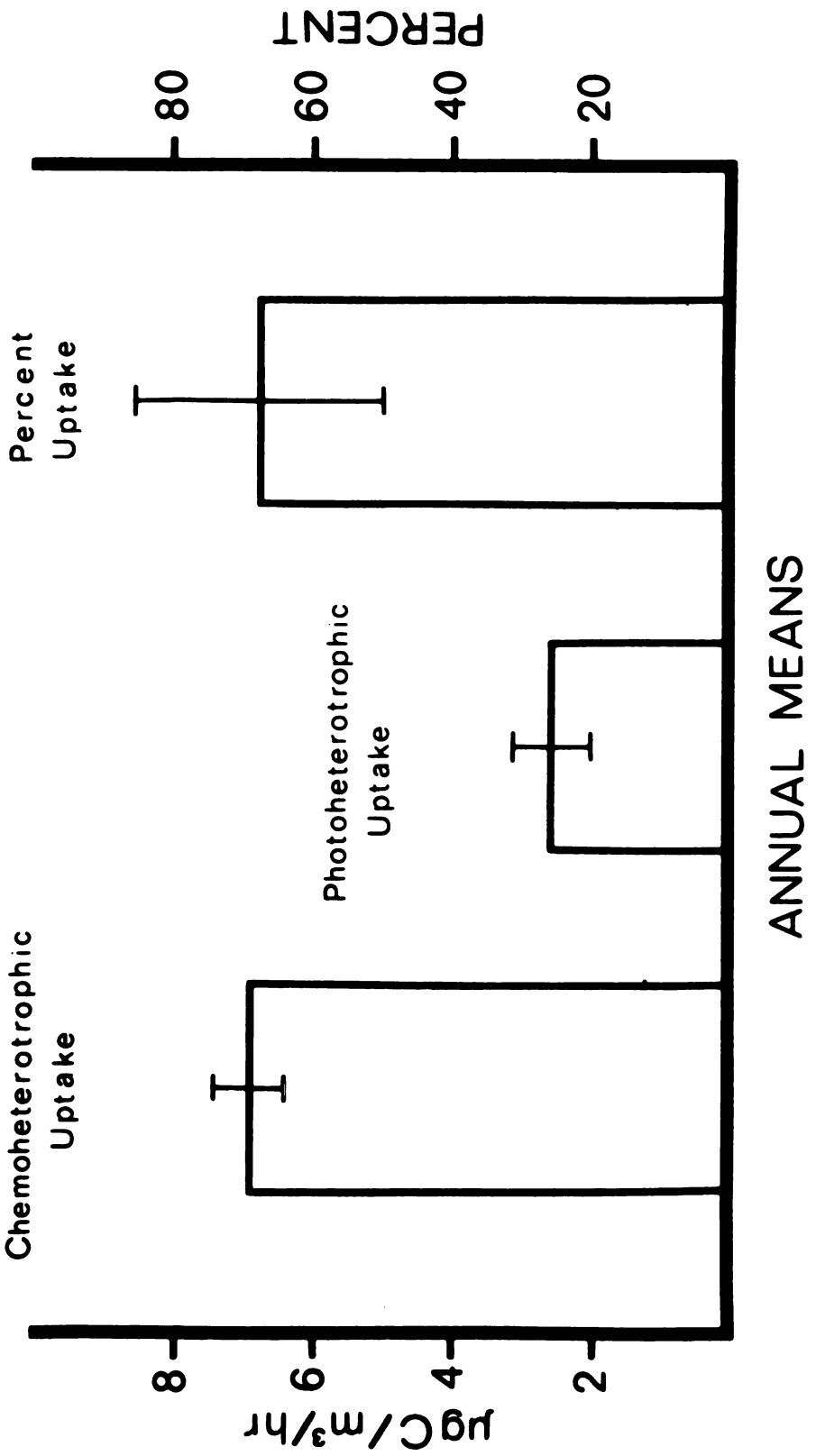
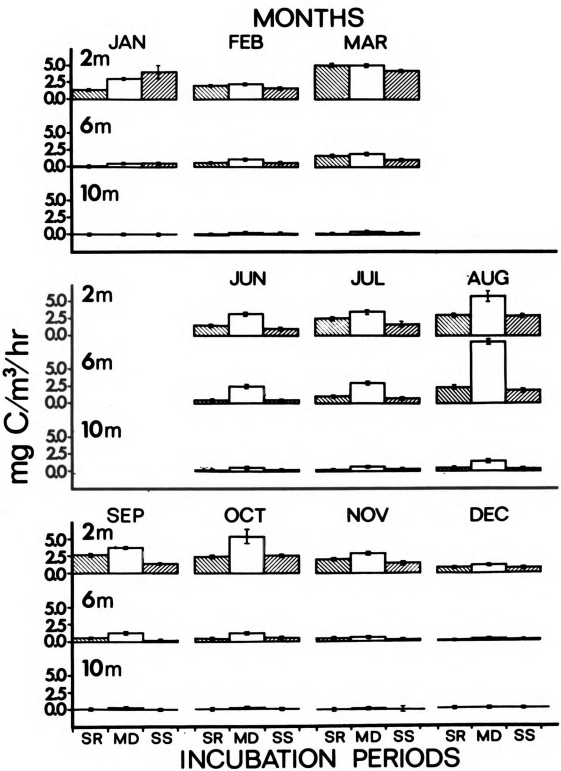

PERCENT
80
60
40
20
Percent Uptake
Photoheterotrophic Uptake
Chemoheterotrophic Uptake
ANNUAL MEANS
8
6
4
2
µgC/m³/hr

Table 2.--Analysis of Variance table for inorganic carbon fixation estimated by the ^{14}C-method. Three-way factorial split plot design. Significance levels are indicated by asterisks: (***) significant at the 0.1% level, or better.

Analysis of Variance Table

Source of Variance	Sum of Squares	Degrees of Freedom	Mean Square	F Statistic
Month	80.31	6	13.38	156.41***
Time	51.74	2	25.87	302.27***
Depth	106.78	2	53.39	623.86***
Month x Time	34.65	12	2.89	33.74***
Month x Depth	43.41	12	3.62	42.27***
Time x Depth	17.39	4	4.35	50.80***
Month x Time x Depth	21.34	24	0.89	10.39***
Error A	16.17	189	0.086	
Bottle	225.49	1	225.49	2457.67***
Month x Bottle	74.13	6	12.35	134.66***
Time x Bottle	53.42	2	26.71	291.09***
Depth x Bottle	107.83	2	53.92	587.64***
Month x Time x Bottle	30.24	12	2.52	27.47***
Month x Depth x Bottle	39.24	12	3.27	35.64***
Time x Depth x Bottle	15.36	4	3.84	41.84***
Month x Time x Depth x Bottle	22.39	24	0.93	10.17***
Residual Error	17.34	189	0.092	
Total	957.23	503		

Figure 11.--Estimated values for inorganic carbon fixation during 1974 as mgC m^{-3} hr^{-1}. Histograms represent the means of four replicate samples. Uptake values for each depth interval (2, 6, 10 meters) and each incubation period (SR, MD, SS) are indicated. Bars denote plus or minus standard errors ($\pm$SE) about the mean.


MONTHS
JAN
FEB
MAR
JUN
JUL
AUG
SEP
OCT
NOV
DEC
2m
6m
10m
5.0
2.5
0.0
mg C/m³/hr
SR MD SS
INCUBATION PERIODS

metalimnetic peak in activity during August was again seen. High epilimnetic values were also found during March and October and under ice in January. Generally the contributions to overall fixation were dominated by epilimnetic values; an exception during the metalimnetic peak in August has been noted. The contribution by 10 meter populations was usually minimal, particularly so under ice cover. As have been reported by others on a number of occasions, greatest activity was generally associated with morning and midday incubation periods.

A comparison was made between those values obtained for chemoheterotrophic uptake, photoheterotrophic uptake, and photosynthesis. On an individual basis the numbers were highly variable ranging from zero (and slightly negative values) to greater than 250% for photoheterotrophic uptake (photoheterotrophic uptake/photosynthesis) and greater than 1000% for chemoheterotrophic uptake (chemoheterotrophic uptake/photosynthesis). Because the values were so variable and, since the precision associated with each of the measures is quite different, these comparisons may be useful in only a very general way.

According to Strickland and Parsons (1972) the precision associated with the radioactive carbon method at the 1.5 mg C m^{-3} hr^{-1} level is approximated by $0.15/n^{0.5}$ mg C m^{-3} hr^{-1} for a 7-hour incubation and 5 μCi of activity added, where n is equal to the number of determinations. For this work n equals 4, therefore the correct value should

lie within the range $\pm$ 0.15/(4)$^{0.5}$, or $\pm$ 75 µg C m^{-3} hr^{-1}. This agrees well with the estimates in this study.

With mean values for photoheterotrophic uptake and chemoheterotrophic uptake of 2.6 and 6.9 µg C m^{-3} hr^{-1} respectively, the only times where one would expect to quantify significant contributions to the carbon pool would be those times where photosynthetic values were near, or below the sensitivity of the ^{14}C-method. This is not to say that these values do not contribute significantly to total carbon metabolism and fixation.

Additionally, while it is instructive and useful to compare the two types of heterotrophic uptake for a single substrate, the natural concentration of which is unknown, comparisons between organic and inorganic carbon pools are more difficult and prone to err. Any percentage must be considered minimal for both photo- and chemoheterotrophic contributions, since (1) the natural, organic substrate concentration and thus the dilution is unknown, and (2) the pool of competing, or readily utilizable compounds which also would increase estimates of total heterotrophy are equally unknown.

These precautions in mind concerning minimal values, the following generalizations were made. The percent contribution of photoheterotrophy to overall carbon fixation in epilimnetic waters is probably always minimal. This is generally true for metalimnetic waters as well, but values greater than 1% are encountered during early morning

incubations and during conditions of low light (e.g., ice cover, cloudy conditions, etc.). In general, based on mean values (n=4), the greatest photoheterotrophic contribution to toal fixation occurs at depth, 10 meters, and during the sunrise incubation period. The midday values at depth contributed greater absolute amounts, but proportionally lesser amounts as compared to photolithotrophic fixation. Sunset values were intermediate to these. The highest values occurred under ice during January and December (i.e., >8%). Higher values were also encountered during late summer.

Bacterial values, chemoheterotrophic uptake, followed a similar pattern. Highest relative values were observed under ice, 20-50%. These values may be an artifact of the method, however, since the mean value for photolithotrophic fixation is less than 75 μg C m^{-3} hr^{-1} in both cases.

At depth heterotrophic activity probably ranges from 0 to 10% of photosynthetically fixed carbon, as minimally estimated here, with photoheterotrophic activity generally 2-5% based on means and chemoheterotrophy <10%.

PERSPECTIVES AND INTEGRATION

Additional work is unquestionably needed. However, this study has clearly demonstrated the direction that work should take and has given considerable insight into the workings of an important feedback pathway in the regulation and cycling of organic carbon in lake systems between the phytoplankton and the dissolved organic carbon pool.

Regardless of the agent of uptake, it has been demonstrated that measures of heterotrophic potential in aquatic systems may lead to serious underestimates depending upon whether, or not these incubations are carried out in the light, or in the dark. Within the constraints of the statistical design (n=252) light bottle uptake averaged 9.2 $\mu g\ C\ m^{-3}\ hr^{-1}$, while dark bottle uptake averaged 6.3 $\mu g\ C\ m^{-3}\ hr^{-1}$; light bottle, or total, represented 146% of dark bottle estimates. Averaged across the annual period, the combined estimate for photoheterotrophic uptake plus chemoheterotrophic uptake yielded a similar figure, 138%, as an estimate of total heterotrophic fixation versus chemoheterotrophic potential.

While these values themselves point out the importance of consideration of this heterotrophic pathway, it must be recalled, that depending upon time of day, depth, and month this error may be many times greater. Thus until better information becomes available we must consider this to be a major pathway in the cycling of certain specific organic compounds within lake systems.

Within the overall scheme of cycling of materials in lake systems it is unimportant whether, or not the agent involved belongs to algal groups within the plankton, or to the bacteria. Stanier (1973) points out that the dominant nutritional mode among non-sulfur purple bacteria is photoheterotrophic uptake of organic materials. However, the wealth of evidence concerning algal uptake already discussed, coupled with limited microautoradiographic studies with ^{14}C-glucose in association with this investigation, point to algal species as being those organisms primarily responsible for the observed, sustained annual uptake.

More important than the annual uptake values and the implications for organic cycling based upon a single organic compound during the daylight period is the importance of this link in the cycling of materials at a significant point in the trophic scheme of organization. Since Lindeman's (1942) provocative paper, ecologists have attempted to place in proper perspective those pathways responsible for the major flux rates in ecological systems. This work in large part has now been accomplished and it is

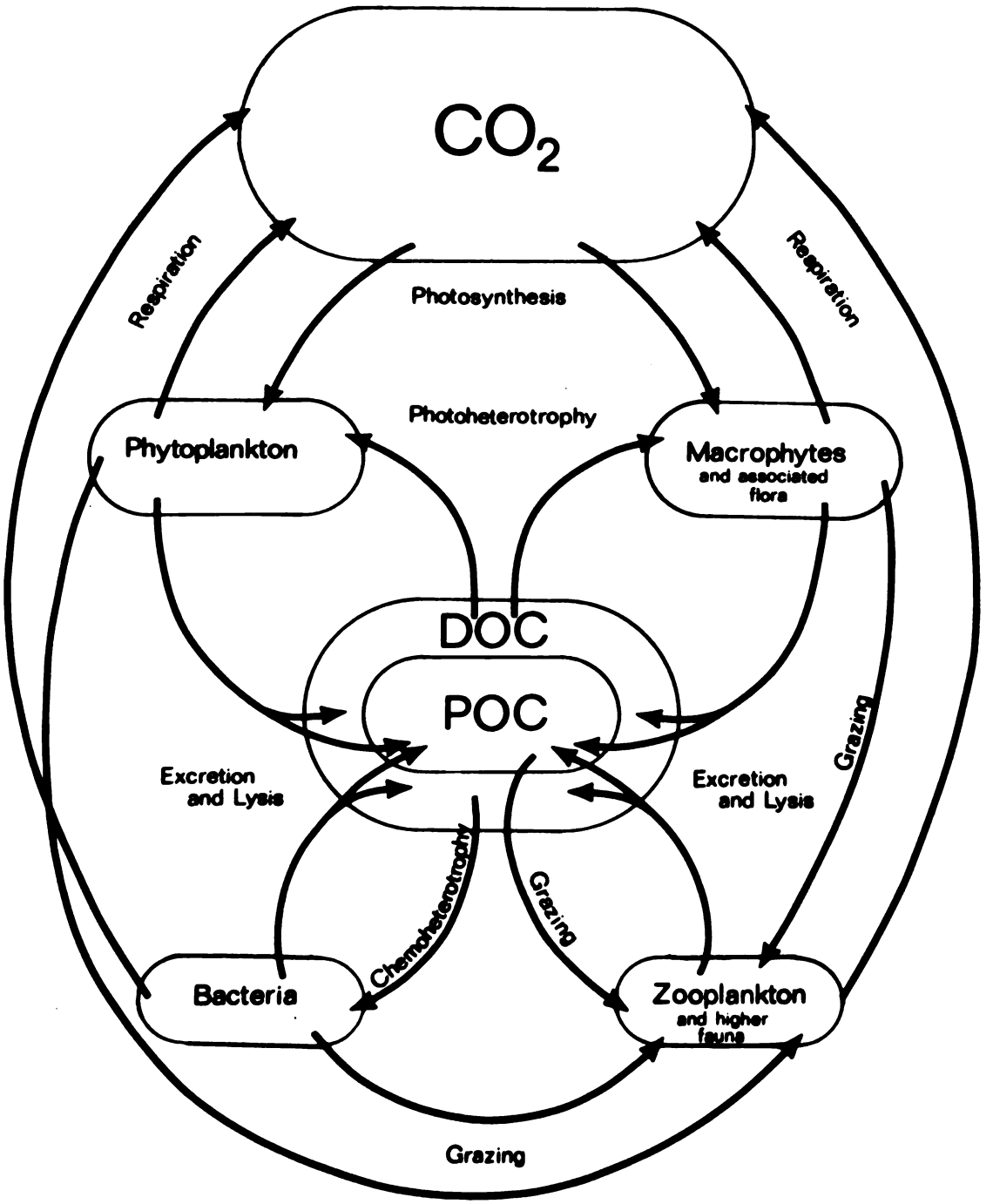
clear that organic carbon (i.e., detritus) plays a central role in the structuring and the functioning of a majority of systems studied in some detail (see the discussion by Wetzel et al., 1972; Saunders, 1969; Jordan and Likens, 1975; and Hobbie et al., 1972).

It is equally clear that we are generally lacking in any understanding of how and why those rates function as they are observed. Key to this understanding is the elucidation of a number of feedback loops within that system. Within this framework those organisms, which influence the pool of dissolved organic carbon and are themselves in some manner directly affected by the composition of that pool, are extremely important insofar as their position within the ecosystem and their influence upon system structure. Those organisms, which occupy these important seats within the system, are without doubt those organisms wherein a majority of carbon cycling occurs and are confined to the lower trophic levels. Figure 12 depicts such an idealized trophic relationship.

Photoheterotrophy thus represents not only an important pathway in the cycling of organic materials, but meets the criterion listed above concerning those loops by which the biogenic drivers in the system may also be regulated.

Chemoheterotrophic assimilation certainly operates as the major mechanism of organic utilization, when one considers the non-daylight hours where photoheterotrophy is

Figure 12.--Idealized trophic scheme emphasizing the cycling of organic carbon. Dissolved organic carbon (DOC), dead particulate organic carbon (POC). Major pathways indicated by arrows.


CO_2
Respiration
Photosynthesis
Respiration
Photoheterotrophy
Phytoplankton
Macrophytes
and associated
flora
DOC
POC
Excretion
and Lysis
Excretion
and Lysis
Grazing
Chemoheterotrophy
Grazing
Bacteria
Zooplankton
and higher
fauna
Grazing

inoperative, and the fact that a much greater variety of organic compounds are probably readily utilizable by chemoheterotrophic pathways. However, the really important questions concerning photoheterotrophic growth have yet to be addressed. If algal species are indeed involved, as the evidence indicates they are, which species possess the ability to photoassimilate organic materials? All species are certainly not equally capable of organic uptake. If the observed uptake is not to be considered a generalized constitutive phenomenon, then it becomes important to ask which species are responsible for the majority of the uptake observed at various times throughout the year. How the structure of the phytoplankton community is influenced over time by the ability of certain organisms to utilize organic substrates is also an important question. Are those species which supplement carbon uptake able to replace other species over time because of this advantage; how then do photoheterotrophic capabilities influence phytoplanktonic succession rates? Photoheterotrophic uptake of organic compounds may also represent a key to the understanding of the existence of populations at depth and under ice, conditions not favorable in the extreme to photolithotrophic fixation (see the discussion by Rodhe, 1955; Bernard, 1963).

Of much interest would be work coupling the release of extracellular products, either during the course of normal cellular metabolism or photorespiratory pathways, to the potential for assimilation. These "wasteful" processes

may not be nearly so costly metabolically, if a measurable proportion of "lost" organic compounds could be successfully recovered at a time when photosynthetic fixation of inorganic carbon is no longer optimal. Photoheterotrophy may represent a partial explanation for the apparent lack of selection for a more complete retention of photosynthetic by-products. Of particular importance on an evolutionary scale would be the species relationships between those capable of photoassimilation and those responsible for the majority of extracellular products found in aquatic systems (whether, or not these processes are concurrent within the same species).

Patterns of excreted organic matter by the plankton with relation to photoassimilation would be instructive. Of importance would be the quantification and qualification of the compounds in the organic carbon pool. A clearer idea of the competing, diluting pool would be gained for a more complete comparative assessment of heterotrophic processes.

Lastly, an important point discussed early in this work concerns the relative importance of photoheterotrophy in the pelagial zone versus its importance in the littoral zone. Certainly strong evidence has been presented for the photoheterotrophic pathway in lake systems. However, as discussed earlier those species most often reported to possess photoheterotrophic potentials were those associated with natural zones of concentrations of organic materials.

Certainly epiphytic algae and those species associated with sediments would be expected to benefit measurably should photoheterotrophic ability be possessed by many members of those associations. Therefore it is probably within the littoral zone and not the pelagial zone where one would find the greatest quantitative contributions to algal nutrition.

Unquestionably the biochemical and physiological mechanisms of organisms at lower trophic levels are intimately tied to the structure of ecosystems. How organic and inorganic carbon pools, photoheterotrophic, photolithotrophic, and photorespiratory pathways, and organic and inorganic nitrogen pools collectively interact to influence metabolism on a diurnal basis and species composition on an annual basis is yet to be addressed. Certainly this interplay will prove to be important. Its elucidation will depend upon insight into questions of broad ecological importance.

SUMMARY

Ample evidence has been presented in this study concerning the importance in nature of the phenomenon of photoheterotrophy. As compared with chemoheterotrophic activity for glucose during the daylight period, photoheterotrophic activity equaled 67.6% on a comparative basis in a hard-water lake in southwestern Michigan. Consequently, studies of heterotrophic uptake utilizing dark techniques may seriously underestimate total activity.

The pattern of photoheterotrophic activity as compared to chemoheterotrophic activity demonstrated that the two heterotrophic processes are separated in space and time on a daily as well as a seasonal basis. Photoheterotrophic activity generally was skewed toward the morning and midday, with predominating activity shifting to increasing depths in the water column as the day progressed. Maximal values were observed during the spring and late summer. Chemoheterotrophic activity generally increased throughout the daylight period and with depth within the water column. During isothermal lake conditions uniform chemoheterotrophic activity with respect to depth was observed.

Heterotrophic fixation as compared to photolithotrophic carbon fixation indicates that photoheterotrophy may contribute significant amounts of carbon to photosynthetic organisms under conditions not favorable to inorganic carbon fixation (e.g., the low irradiance at depth and under ice cover).

The importance of photoheterotrophy in phytoplanktonic species succession, the potential importance in the littoral zone both epiphytically and in association with the sediments, and to the overall cycling of organic carbon and the structure observed in lake systems is discussed.

APPENDICES

APPENDIX A

ORGANIC CARBON UPTAKE VALUES

APPENDIX A

ORGANIC CARBON UPTAKE VALUES

Appendix A is a tabular presentation of calculated values ($\mu gC\ m^{-3}\ hr^{-1}$) for organic carbon uptake in Lawrence Lake during 1974. The data are arranged as four light bottle/dark bottle pairs for each Time, Depth, and Month of sampling. The difference between light and dark estimates (Photoheterotrophy) is found in column "PHOTO UPTAKE." Chemoheterotrophic uptake is presented in column "BACTERIAL UPTAKE." Photoheterotrophic estimates divided by chemoheterotrophic values and multiplied by 100 are placed in column "PERCENT OF BACTERIAL UPTAKE." Means, standard deviations, and standard errors are indicated.

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	10.0349	6.9755	3.0593	6.9055	44.3030
	9.6519	8.8722	.7797	8.8022	8.8583
	9.3663	9.0407	.3255	8.9695	3.6293
	10.8794	9.6633	1.2161	9.5924	12.6780
			X= 1.345	X= 8.567	X= 17.367
			SD= 1.199	SD= 1.159	SD= 18.336
			SE= .600	SE= .579	SE= 9.168
6M					
	9.5076	8.5668	.9409	8.4959	11.0744
	10.5689	9.9207	.6482	9.8484	6.5819
	9.7317	8.0429	1.6888	7.9717	21.1851
	8.9933	6.5803	2.4130	6.5069	37.0839
			X= 1.423	X= 8.206	X= 18.981
			SD= .792	SD= 1.381	SD= 13.526
			SE= .396	SE= .691	SE= 6.763
10M					
	9.1497	9.3286	-.1789	9.2580	-1.9319
	9.3081	3.4060	5.9021	3.3363	176.9055
	8.5683	9.7818	-1.2135	9.7089	-12.4989
	9.6183	8.5130	1.1053	8.4418	13.0931
			X= 1.404	X= 7.686	X= 43.892
			SD= 3.145	SD= 2.947	SD= 89.295
			SE= 1.573	SE= 1.474	SE= 44.648

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	5.2864	7.8607	-2.5743	7.7937	-33.0299
	6.9506	7.1561	-.2054	7.0883	-2.8983
	8.9705	9.0589	-.0884	8.9893	-.9831
	7.6707	10.5799	-2.9092	10.5130	-27.6726
			X= -1.444	X= 8.596	X= -16.146
			SD= 1.505	SD= 1.500	SD= 16.566
			SE= .753	SE= .750	SE= 8.283
6M					
	8.0616	2.9450	5.1166	2.8792	177.7089
	6.5087	6.8954	-.3867	6.8288	-5.6633
	6.8208	7.7764	-.9556	7.7081	-12.3973
	6.4033	6.8336	-.4303	6.7652	-6.3611
			X= .836	X= 6.045	X= 38.322
			SD= 2.865	SD= 2.154	SD= 92.974
			SE= 1.433	SE= 1.077	SE= 46.487
10M					
	8.9430	6.7789	2.1641	6.7094	32.2541
	6.7433	7.1749	-.4316	7.1059	-6.0733
	7.2250	7.8690	-.6439	7.7989	-8.2567
	7.9822	7.4658	.5165	7.3994	6.9800
			X= .401	X= 7.253	X= 6.226
			SD= 1.279	SD= .461	SD= 18.610
			SE= .639	SE= .230	SE= 9.305

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	.0840	.0511	.0328	-.0207	-158.4746
	6.8413	7.4142	-.5728	7.3423	-7.8016
	14.7305	11.7267	3.0039	11.6536	25.7763
	8.9385	5.2860	3.6525	5.2132	70.0631
			X= 1.529	X= 6.047	X= -17.609
			SD= 2.109	SD= 4.852	SD= 99.177
			SE= 1.054	SE= 2.426	SE= 49.588
6M					
	5.8753	4.2395	1.6359	4.1667	39.2608
	6.6084	6.9454	-.3370	6.8712	-4.9047
	6.2102	7.4944	-1.2842	7.4214	-17.3037
	7.9213	1.8410	6.0803	1.7657	344.3542
			X= 1.524	X= 5.056	X= 90.352
			SD= 3.272	SD= 2.614	SD= 171.066
			SE= 1.636	SE= 1.307	SE= 85.533
10M					
	4.7700	5.8053	-1.0352	5.7328	-18.0581
	5.5006	4.4740	1.0266	4.4024	23.3194
	5.4812	6.8937	-1.4125	6.8189	-20.7142
	5.7936	4.7388	1.0548	4.6658	22.6074
			X= -.092	X= 5.405	X= 1.789
			SD= 1.317	SD= 1.104	SD= 24.476
			SE= .658	SE= .552	SE= 12.238

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	11.0309	5.0346	5.9963	4.9577	120.9485
	9.0463	5.5589	3.4875	5.4820	63.6163
	10.0469	7.9505	2.0964	7.8725	26.6295
	5.5795	5.0067	.5728	4.9289	11.6215
			X= 3.038	X= 5.810	X= 55.704
			SD= 2.303	SD= 1.398	SD= 48.676
			SE= 1.152	SE= .699	SE= 24.338
6M					
	10.3282	6.1049	4.2233	6.0271	70.0720
	8.2881	7.1800	1.1081	7.1007	15.6054
	12.5267	6.3721	6.1546	6.2941	97.7838
	10.0079	2.0299	7.9780	1.9494	409.2487
			X= 4.866	X= 5.343	X= 148.177
			SD= 2.937	SD= 2.308	SD= 177.364
			SE= 1.469	SE= 1.154	SE= 88.682
10M					
	8.8294	9.0172	-.1878	8.9397	-2.1003
	6.8298	2.4614	4.3685	2.3848	183.1780
	9.2412	10.3441	-1.1029	10.2642	-10.7454
	9.7458	8.9191	.8267	8.8410	9.3508
			X= .976	X= 7.607	X= 44.921
			SD= 2.395	SD= 3.542	SD= 92.538
			SE= 1.197	SE= 1.771	SE= 46.269

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	10.8919	9.2005	1.6914	9.1324	18.5213
	10.1908	9.9036	.2872	9.8347	2.9203
	10.1066	11.0519	-.9452	10.9811	-8.6079
	9.1302	11.0204	-1.8902	10.9523	-17.2584
			X= -.214	X= 10.225	X= -1.106
			SD= 1.552	SD= .903	SD= 15.477
			SE= .776	SE= .452	SE= 7.739
6M					
	6.5460	6.6861	-.1401	6.6191	-2.1168
	9.3043	5.0662	4.2381	4.9984	84.7898
	6.6309	6.9959	-.3649	6.9175	-5.2755
	7.7877	7.4695	.3182	7.3909	4.3052
			X= 1.013	X= 6.481	X= 20.426
			SD= 2.169	SD= 1.039	SD= 43.094
			SE= 1.084	SE= .519	SE= 21.547
10M					
	10.4016	7.6944	2.7072	7.6145	35.5528
	8.1494	8.8226	-.6732	8.7433	-7.7000
	5.7602	8.0634	-2.3031	7.9829	-28.8507
	8.3764	5.4123	2.9641	5.3361	55.5488
			X= .674	X= 7.419	X= 13.638
			SD= 2.586	SD= 1.466	SD= 38.719
			SE= 1.293	SE= .733	SE= 19.359

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	10.8196	9.4144	1.4052	9.3283	15.0634
	6.6866	9.4424	-2.7559	9.3563	-29.4546
	8.2100	5.9996	2.2104	5.9121	37.3878
	11.0376	7.5626	3.4749	7.4754	46.4848
			X= 1.084	X= 8.018	X= 17.370
			SD= 2.698	SD= 1.657	SD= 33.893
			SE= 1.349	SE= .829	SE= 16.947
6M					
	3.5637	7.5600	-3.9963	7.4728	-53.4780
	6.3970	6.6464	-.2494	6.5575	-3.8034
	6.9152	5.6718	1.2433	5.5843	22.2649
	5.9739	2.1745	3.7994	2.0842	182.2936
			X= .199	X= 5.425	X= 36.819
			SD= 3.259	SD= 2.357	SD= 101.945
			SE= 1.629	SE= 1.178	SE= 50.973
10M					
	6.7038	9.0264	-2.3225	8.9395	-25.9806
	8.3655	9.0070	-.6414	8.9212	-7.1901
	7.1906	7.6199	-.4294	7.5303	-5.7019
	7.9399	7.4134	.5265	7.3259	7.1867
			X= -.717	X= 8.179	X= -7.921
			SD= 1.185	SD= .871	SD= 13.661
			SE= .592	SE= .436	SE= 6.830

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	16.7337	7.3334	9.4003	7.2458	129.7346
	8.3730	8.8618	-.4888	8.7742	-5.5707
	14.2567	10.9401	3.3165	10.8512	30.5639
	18.1880	10.9754	7.2126	10.8868	66.2509
			X= 4.860	X= 9.439	X= 55.245
			SD= 4.364	SD= 1.765	SD= 57.670
			SE= 2.182	SE= .882	SE= 28.835
6M					
	18.2776	6.1970	12.0806	6.1084	197.7707
	14.2285	15.6117	-1.3833	15.5213	-8.9120
	17.7323	12.8098	4.9224	12.7209	38.6958
	15.9194	7.6792	8.2402	7.5874	108.6026
			X= 5.965	X= 10.485	X= 84.039
			SD= 5.706	SD= 4.394	SD= 89.878
			SE= 2.853	SE= 2.197	SE= 44.939
10M					
	11.1322	12.6158	-1.4836	12.5276	-11.8427
	15.9477	9.4465	6.5013	9.3592	69.4637
	!.6486	6.1709	-4.5223	6.0799	-74.3825
	10.6560	10.3380	.3179	10.2491	3.1019
			X= .203	X= 9.554	X= -3.415
			SD= 4.650	SD= 2.673	SD= 59.051
			SE= 2.325	SE= 1.336	SE= 29.526

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	15.9508	7.8863	8.0644	7.8025	103.3576
	16.7433	6.5794	10.1639	6.4944	156.5014
	16.0158	16.1195	-.1037	16.0323	-.6469
	15.4211	15.3148	.1063	15.2309	.6976
			X= 4.558	X= 11.390	X= 64.977
			SD= 5.331	SD= 4.938	SD= 78.077
			SE= 2.666	SE= 2.469	SE= 39.039
6M					
	16.5306	5.5232	11.0073	5.4407	202.3157
	17.4122	14.7235	2.6886	14.6400	18.3649
	16.3830	3.6241	12.7639	3.5295	361.6304
	13.8976	14.3032	-.4056	14.2083	-2.8547
			X= 6.514	X= 9.455	X= 144.864
			SD= 6.371	SD= 5.794	SD= 171.378
			SE= 3.185	SE= 2.897	SE= 85.689
10M					
	12.1873	13.3224	-1.1351	13.2260	-8.5824
	15.1534	5.7930	9.3604	5.6973	164.2956
	14.7523	1.8889	12.8634	1.7918	717.9207
	15.6296	10.5009	5.1287	10.4089	49.2721
			X= 6.554	X= 7.781	X= 230.727
			SD= 6.023	SD= 5.059	SD= 332.649
			SE= 3.012	SE= 2.529	SE= 166.324

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	15.5568	14.3263	1.2305	14.2160	8.6558
	16.3601	14.9835	1.3765	14.8733	9.2551
	13.5578	5.8275	7.7303	5.7155	135.2506
	15.1902	10.1868	5.0034	10.0752	49.6610
			X= 3.835	X= 11.220	X= 50.706
			SD= 3.129	SD= 4.240	SD= 59.541
			SE= 1.564	SE= 2.120	SE= 29.770
6M					
	16.3143	15.1222	1.1921	15.0106	7.9417
	16.8144	16.7022	.1122	16.5883	.6763
	14.5457	15.3422	-.7965	15.2301	-5.2297
	14.6169	18.0758	-3.4589	17.9603	-19.2587
			X= -.738	X= 16.197	X= -3.968
			SD= 1.988	SD= 1.367	SD= 11.530
			SE= .994	SE= .683	SE= 5.765
10M					
	16.0741	16.7316	-.6575	16.6205	-3.9558
	14.7417	13.6894	1.0523	13.5796	7.7491
	14.7401	15.3335	-.5934	15.2188	-3.8988
	15.9934	14.8800	1.1134	14.7679	7.5395
			X= .229	X= 15.047	X= 1.858
			SD= .987	SD= 1.257	SD= 6.681
			SE= .493	SE= .628	SE= 3.341

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	3.3935	3.0375	.3560	2.9532	12.0556
	4.3227	3.0992	1.2235	3.0109	40.6358
	3.1934	2.8227	.3708	2.7383	13.5395
	3.7245	3.7251	-.0007	3.6381	-.0189
			X= .487	X= 3.085	X= 16.553
			SD= .520	SD= .387	SD= 17.165
			SE= .260	SE= .193	SE= 8.583
6M					
	3.1828	2.6057	.5772	2.5180	22.9210
	3.6154	3.9733	-.3579	3.8910	-9.1982
	5.2585	5.0116	.2469	4.9293	5.0089
	5.0277	3.7435	1.2843	3.6584	35.1044
			X= .438	X= 3.749	X= 13.459
			SD= .684	SD= .989	SD= 19.518
			SE= .342	SE= .495	SE= 9.759
10M					
	5.9908	4.4166	1.5742	4.3322	36.3378
	6.4762	6.6403	-.1641	6.5540	-2.5036
	6.4673	7.2005	-.7331	7.1161	-10.3024
	6.3595	8.2856	-1.9261	8.1973	-23.4972
			X= -.312	X= 6.550	X= .009
			SD= 1.456	SD= 1.628	SD= 25.723
			SE= .728	SE= .814	SE= 12.861

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	2.8041	2.0950	.7091	2.0107	35.2676
	3.4365	1.6541	1.7824	1.5709	113.4608
	4.0322	1.7473	2.2849	1.6668	137.0871
	4.8481	1.3127	3.5354	1.2315	287.0908
			X= 2.078	X= 1.620	X= 143.227
			SD= 1.173	SD= .321	SD= 105.318
			SE= .587	SE= .160	SE= 52.659
6M					
	3.6680	4.0648	-.3968	3.9836	-9.9611
	7.5997	2.2881	5.3115	2.2069	240.6783
	7.3802	3.0345	4.3457	2.9539	147.1166
	9.9839	2.9232	7.0607	2.8451	248.1712
			X= 4.080	X= 2.997	X= 156.501
			SD= 3.189	SD= .735	SD= 120.121
			SE= 1.595	SE= .368	SE= 60.060
10M					
	10.1836	3.5488	6.6348	3.4701	191.1968
	11.8002	10.5390	1.2612	10.4603	12.0570
	7.0725	5.2703	1.8022	5.1872	34.7425
	12.5369	4.3506	8.1863	4.2700	191.7148
			X= 4.471	X= 5.847	X= 107.428
			SD= 3.460	SD= 3.155	SD= 97.468
			SE= 1.730	SE= 1.577	SE= 48.734

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	2.4454	2.1252	.3202	2.0394	15.7029
	2.7286	2.4351	.2935	2.3453	12.5124
	3.5775	3.3283	.2492	3.2425	7.6861
	3.2530	3.5261	-.2731	3.4376	-7.9457
			X= .147	X= 2.766	X= 6.989
			SD= .282	SD= .679	SD= 10.488
			SE= .141	SE= .339	SE= 5.244
6M					
	6.1886	4.1880	2.0006	4.0989	48.8076
	6.1931	4.5281	1.6649	4.4444	37.4619
	7.0554	5.9132	1.1421	5.8340	19.5772
	9.9884	4.2449	5.7434	4.1631	137.9589
			X= 2.638	X= 4.635	X= 60.951
			SD= 2.100	SD= .813	SD= 52.730
			SE= 1.050	SE= .407	SE= 26.365
10M					
	9.1632	8.3828	.7804	8.3017	9.4007
	10.1304	4.2124	5.9180	4.1294	143.3144
	11.6107	7.8591	3.7516	7.7779	48.2343
	12.9787	8.7269	4.2518	8.6419	49.2000
			X= 3.675	X= 7.213	X= 62.537
			SD= 2.141	SD= 2.086	SD= 56.953
			SE= 1.070	SE= 1.043	SE= 28.476

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	2.9225	1.7302	1.1923	1.6025	74.4017
	3.0564	1.9432	1.1132	1.8095	61.5198
	3.5253	2.9596	.5657	2.8319	19.9777
	2.9461	2.8599	.0862	2.7282	3.1594
			X= .739	X= 2.243	X= 39.765
			SD= .517	SD= .627	SD= 33.687
			SE= .258	SE= .314	SE= 16.844
6M					
	3.5586	2.8449	.7137	2.7122	26.3150
	4.0114	3.0485	.9630	2.9238	32.9352
	5.5534	1.9818	3.5716	1.8571	192.3246
	3.6323	1.5644	2.0678	1.4357	144.0300
			X= 1.829	X= 2.232	X= 98.901
			SD= 1.302	SD= .703	SD= 82.431
			SE= .651	SE= .352	SE= 41.216
10M					
	5.0726	4.4288	.6437	4.3011	14.9669
	7.3807	2.0393	5.3414	1.9087	279.8475
	9.0408	6.0097	3.0311	5.8820	51.5317
	7.9991	6.1990	1.8002	6.0653	29.6797
			X= 2.704	X= 4.539	X= 94.006
			SD= 2.010	SD= 1.924	SD= 124.801
			SE= 1.005	SE= .962	SE= 62.401

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	2.9082	2.0774	.8307	1.9451	42.7090
	2.5805	2.2670	.3135	2.1366	14.6716
	3.7259	2.7368	.9892	2.6104	37.8942
	3.4179	2.9983	.4196	2.8708	14.6167
			X= .638	X= 2.391	X= 27.473
			SD= .323	SD= .425	SD= 14.943
			SE= .162	SE= .213	SE= 7.472
6M					
	4.1144	2.0748	2.0396	1.9473	104.7395
	4.7136	4.3356	.3780	4.2082	8.9834
	14.6075	3.5809	11.0266	3.4679	317.9626
	4.5318	2.0555	2.4763	1.9461	127.2432
			X= 3.980	X= 2.892	X= 139.732
			SD= 4.784	SD= 1.133	SD= 129.411
			SE= 2.392	SE= .567	SE= 64.706
10M					
	9.6533	3.3193	6.3340	3.2090	197.3799
	9.2748	3.4925	5.7823	3.3804	171.0555
	8.4478	4.5829	3.8650	4.4663	86.5360
	8.7641	4.4083	4.3558	4.2953	101.4082
			X= 5.084	X= 3.838	X= 139.095
			SD= 1.164	SD= .635	SD= 53.545
			SE= .582	SE= .317	SE= 26.773

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	3.1714	3.1234	.0480	3.0096	1.5946
	3.4709	2.0805	1.3904	1.9614	70.8885
	3.9271	3.3421	.5849	3.2284	18.1176
	3.0105	3.0271	-.0166	2.9098	-.5707
			X= .502	X= 2.777	X= 22.508
			SD= .651	SD= .560	SD= 33.316
			SE= .325	SE= .280	SE= 16.658
6M					
	6.4894	6.7003	-.2109	6.5821	-3.2048
	9.9900	5.9712	4.0189	5.8601	68.5797
	10.8115	6.0419	4.7696	5.9308	80.4204
	8.6266	7.1182	1.5084	7.0035	21.5375
			X= 2.521	X= 6.344	X= 41.833
			SD= 2.294	SD= .547	SD= 39.348
			SE= 1.147	SE= .273	SE= 19.674
10M					
	12.5696	10.6419	1.9277	10.5281	18.3099
	1'.6272	5.4329	6.1942	5.3166	116.5079
	10.0891	7.5232	2.5659	7.4095	34.6301
	9.7719	5.0547	4.7172	4.9356	95.5761
			X= 3.851	X= 7.047	X= 66.256
			SD= 1.966	SD= 2.563	SD= 47.201
			SE= .983	SE= 1.281	SE= 23.601

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	2.9460	1.5562	1.3898	1.3244	104.9375
	5.5668	3.5823	1.9845	3.3396	59.4218
	5.1289	3.7921	1.3367	3.5603	37.5454
	6.6772	6.2495	.4277	6.0104	7.1161
			X= 1.285	X= 3.559	X= 52.255
			SD= .642	SD= 1.919	SD= 41.153
			SE= .321	SE= .960	SE= 20.576
6M					
	9.0297	7.1719	1.8578	6.9310	26.8041
	11.2218	9.4858	1.7361	9.2595	18.7491
	15.5224	2.4841	13.0383	2.2578	577.4901
	14.1757	8.8352	5.3405	8.6015	62.0881
			X= 5.493	X= 6.762	X= 171.283
			SD= 5.300	SD= 3.159	SD= 271.458
			SE= 2.650	SE= 1.580	SE= 135.729
10M					
	6.4544	5.2278	1.2265	4.9960	24.5500
	8.1234	5.7186	2.4049	5.4815	43.8727
	6.6377	5.6750	.9626	5.4432	17.6849
	9.1512	6.9492	2.2019	6.7066	32.8324
			X= 1.699	X= 5.657	X= 29.735
			SD= .711	SD= .734	SD= 11.278
			SE= .356	SE= .367	SE= 5.639

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	3.8331	2.1294	1.7036	1.8818	90.5331
	6.7902	2.5443	4.2459	2.3003	184.5787
	6.4579	3.1315	3.3264	2.8949	114.9060
	8.3633	4.9243	3.4390	4.6858	73.3924
			X= 3.179	X= 2.941	X= 115.853
			SD= 1.065	SD= 1.235	SD= 48.881
			SE= .533	SE= .618	SE= 24.441
6M					
	17.0312	17.2101	-.1789	16.9754	-1.0540
	18.9237	14.0795	4.8442	13.8410	34.9991
	29.8833	3.1827	26.7006	3.0563	873.6212
	21.9915	8.3437	13.6478	8.2213	166.0065
			X= 11.253	X= 10.523	X= 268.393
			SD= 11.777	SD= 6.156	SD= 409.820
			SE= 5.889	SE= 3.078	SE= 204.910
10M					
	13.0679	6.7357	6.3323	6.6123	95.7656
	12.4562	4.8480	7.6082	4.7227	161.0981
	13.8195	5.7564	8.0631	5.6260	143.3192
	15.1313	3.6145	11.5168	3.4881	330.1743
			X= 8.380	X= 5.112	X= 182.589
			SD= 2.216	SD= 1.330	SD= 102.182
			SE= 1.108	SE= .665	SE= 51.091

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	3.6244	3.0044	.6200	2.8784	21.5403
	5.6810	4.2914	1.3896	4.1595	33.4071
	8.3314	2.1465	6.1849	2.0205	306.1033
	6.5180	4.6361	1.8819	4.5061	41.7629
			X= 2.519	X= 3.391	X= 100.703
			SD= 2.498	SD= 1.151	SD= 137.184
			SE= 1.249	SE= .576	SE= 68.592
6M					
	13.3600	14.2318	-.8718	14.1009	-6.1826
	23.4511	6.1821	17.2690	6.0592	285.0067
	22.3565	12.0607	10.2958	11.9378	86.2452
	9.7444	9.5006	.2438	9.3736	2.6097
			X= 6.734	X= 10.368	X= 91.918
			SD= 8.634	SD= 3.462	SD= 135.298
			SE= 4.317	SE= 1.731	SE= 67.649
10M					
	10.9128	5.7705	5.1423	5.6446	91.1018
	11.2131	8.4737	2.7394	8.3448	32.8280
	12.4730	6.9934	5.4796	6.8674	79.7917
	12.1835	9.4193	2.7642	9.2875	29.7627
			X= 4.031	X= 7.536	X= 58.371
			SD= 1.484	SD= 1.607	SD= 31.628
			SE= .742	SE= .803	SE= 15.814

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	8.9016	3.5389	5.3627	3.4039	157.5470
	9.9356	2.4055	7.5301	2.2642	332.5656
	12.2908	2.6778	9.6129	2.5428	378.0385
	13.4459	6.1646	7.2813	6.0253	120.8447
			X= 7.447	X= 3.559	X= 247.249
			SD= 1.739	SD= 1.714	SD= 127.029
			SE= .869	SE= .857	SE= 63.515
6M					
	9.2462	6.0310	3.2152	5.8907	54.5806
	8.1621	5.1946	2.9675	5.0628	58.6149
	12.4146	2.6236	9.7910	2.4918	392.9249
	11.5361	5.9332	5.6029	5.7971	96.6495
			X= 5.394	X= 4.811	X= 150.693
			SD= 3.163	SD= 1.590	SD= 162.597
			SE= 1.581	SE= .795	SE= 81.298
10M					
	3.5312	6.6798	-3.1485	6.5448	-48.1078
	10.0147	5.9670	4.0477	5.8289	69.4423
	9.1200	3.7061	5.4139	3.5711	151.6039
	7.1425	9.4435	-2.3009	9.3022	-24.7355
			X= 1.003	X= 6.312	X= 37.051
			SD= 4.354	SD= 2.362	SD= 91.726
			SE= 2.177	SE= 1.181	SE= 45.863

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	10.7450	8.2753	2.4698	8.1481	30.3109
	14.6769	10.9042	3.7726	10.7789	35.0000
	18.9686	4.2731	14.6955	4.1516	353.9680
	16.7922	9.9208	6.8714	9.7983	70.1289
			X= 6.952	X= 8.219	X= 122.352
			SD= 5.482	SD= 2.921	SD= 155.430
			SE= 2.741	SE= 1.460	SE= 77.715
6M					
	13.2648	9.1397	4.1251	9.0192	45.7367
	13.9247	2.5775	11.3472	2.4550	462.2023
	20.3663	5.8517	14.5146	5.6134	258.5715
	19.8709	12.9642	6.9067	12.7334	54.2408
			X= 9.223	X= 7.455	X= 205.188
			SD= 4.614	SD= 4.423	SD= 197.582
			SE= 2.307	SE= 2.212	SE= 98.791
10M					
	16.0232	5.0524	10.9708	4.8198	227.6191
	13.6930	9.6299	4.0630	9.3935	43.2534
	13.8904	4.4648	9.4257	4.2190	223.4105
	17.0027	9.2637	7.7390	9.0254	85.7472
			X= 8.050	X= 6.864	X= 145.008
			SD= 2.967	SD= 2.723	SD= 94.582
			SE= 1.484	SE= 1.362	SE= 47.291

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	5.7671	6.3362	-.5691	6.0934	-9.3400
	6.5092	8.2839	-1.7747	8.0297	-22.1018
	10.6586	8.8176	1.8411	8.5748	21.4709
	15.8032	14.7189	1.0843	14.4685	7.4943
			X= .145	X= 9.292	X= -.619
			SD= 1.628	SD= 3.612	SD= 19.073
			SE= .814	SE= 1.806	SE= 9.537
6M					
	9.1338	7.9950	1.1388	7.7427	14.7075
	12.0661	13.9605	-1.8944	13.7235	-13.8042
	15.4523	9.6426	5.8097	9.4056	61.7679
	16.5949	13.8131	2.7817	13.5684	20.5017
			X= 1.959	X= 11.110	X= 20.793
			SD= 3.216	SD= 3.007	SD= 31.161
			SE= 1.608	SE= 1.503	SE= 15.581
10M					
	10.4136	8.3387	2.0749	8.0959	25.6295
	11.1568	10.9844	.1724	10.7361	1.6057
	17.9279	9.2461	8.6819	9.0033	96.4302
	15.1954	13.8982	1.2972	13.6440	9.5077
			X= 3.057	X= 10.370	X= 33.293
			SD= 3.831	SD= 2.442	SD= 43.262
			SE= 1.915	SE= 1.221	SE= 21.631

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	3.6898	1.8682	1.8216	1.7460	104.3282
	5.3018	5.0241	.2777	4.8962	5.6722
	7.3464	3.0206	4.3258	2.8985	149.2432
	5.3084	4.6870	.6215	4.5610	13.6260
			X= 1.762	X= 3.525	X= 68.217
			SD= 1.833	SD= 1.473	SD= 70.146
			SE= .917	SE= .737	SE= 35.073
6M					
	3.8060	4.5425	-.7365	4.4155	-16.6804
	6.1897	2.3830	3.8067	2.2637	168.1637
	6.0607	2.7037	3.3569	2.5845	129.8886
	6.0422	1.8445	4.1977	1.7213	243.8623
			X= 2.656	X= 2.746	X= 131.309
			SD= 2.288	SD= 1.168	SD= 109.437
			SE= 1.144	SE= .584	SE= 54.719
10M					
	5.9238	4.9964	.9274	4.9190	18.8535
	8.8922	6.0160	2.8762	5.9369	48.4457
	8.0984	3.1067	4.9917	3.0294	164.7755
	12.7655	8.9242	3.8413	8.8432	43.4379
			X= 3.159	X= 5.682	X= 68.878
			SD= 1.721	SD= 2.427	SD= 65.226
			SE= .860	SE= 1.214	SE= 32.613

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	6.2909	3.7618	2.5291	3.6868	68.5981
	7.9556	4.6410	3.3147	4.5670	72.5782
	5.1545	4.2461	.9083	4.1744	21.7596
	9.9067	8.0942	1.8125	8.0220	22.5941
			X= 2.141	X= 5.113	X= 46.383
			SD= 1.026	SD= 1.973	SD= 28.000
			SE= .513	SE= .986	SE= 14.000
6M					
	10.9388	7.0834	3.8555	7.0123	54.9820
	14.7812	8.6345	6.1466	8.5623	71.7874
	13.7693	1.5039	12.2654	1.4322	856.3900
	14.4294	9.5053	4.9241	9.4359	52.1842
			X= 6.798	X= 6.611	X= 258.836
			SD= 3.763	SD= 3.595	SD= 398.463
			SE= 1.882	SE= 1.797	SE= 199.232
10M					
	13.0643	6.8373	6.2270	6.7673	92.0164
	17.3292	8.0407	9.2885	7.9696	116.5492
	7.9631	7.1440	.8191	7.0824	11.5652
	20.7376	6.7937	13.9438	6.7339	207.0681
			X= 7.570	X= 7.138	X= 106.800
			SD= 5.506	SD= .576	SD= 80.492
			SE= 2.753	SE= .288	SE= 40.246

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	4.3549	5.2215	-.8666	5.1576	-16.8028
	9.2747	5.2072	4.0676	5.1403	79.1307
	7.6172	8.3487	-.7315	8.2848	-8.8295
	12.8086	9.8160	2.9925	9.7501	30.6922
			X= 1.365	X= 7.083	X= 21.048
			SD= 2.538	SD= 2.312	SD= 43.939
			SE= 1.269	SE= 1.156	SE= 21.970
6M					
	7.2421	7.0562	.1859	6.9898	2.6597
	12.5989	14.0888	-1.4899	14.0265	-10.6221
	13.5685	13.8435	-.2750	13.7812	-1.9954
	14.8511	5.8466	9.0045	5.7822	155.7293
			X= 1.856	X= 10.145	X= 36.443
			SD= 4.818	SD= 4.369	SD= 79.714
			SE= 2.409	SE= 2.185	SE= 39.857
10M					
	8.8906	7.2725	1.6181	7.2086	22.4465
	10.3352	9.2860	1.0492	9.2206	11.3786
	14.3867	13.4459	.9408	13.3820	7.0302
	19.0970	14.6498	4.4472	14.5829	30.4958
			X= 2.014	X= 11.099	X= 17.838
			SD= 1.649	SD= 3.465	SD= 10.646
			SE= .825	SE= 1.732	SE= 5.323

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	6.8906	5.2331	1.6575	5.1568	32.1412
	12.1306	8.7766	3.3540	8.6967	38.5657
	13.2954	7.0731	6.2223	6.9967	88.9316
	11.9119	12.0863	-.1744	12.0076	-1.4527
			X= 2.765	X= 8.214	X= 39.546
			SD= 2.718	SD= 2.913	SD= 37.308
			SE= 1.359	SE= 1.456	SE= 18.654
6M					
	11.6709	10.0862	1.5847	10.0069	15.8363
	10.7456	5.7235	5.0221	5.6490	88.9019
	11.0226	9.8792	1.1433	9.8047	11.6612
	4.9607	8.9354	-3.9747	8.8584	-44.8693
			X= .944	X= 8.580	X= 17.883
			SD= 3.709	SD= 2.017	SD= 54.847
			SE= 1.855	SE= 1.008	SE= 27.423
10M					
	12.5148	5.4376	7.0772	5.3613	132.0060
	11.9801	8.8613	3.1188	8.7832	35.5086
	3.9692	3.5895	.3796	3.5132	10.8062
	4.5433	8.9332	-4.3899	8.8533	-49.5848
			X= 1.546	X= 6.628	X= 32.184
			SD= 4.819	SD= 2.640	SD= 75.539
			SE= 2.409	SE= 1.320	SE= 37.770

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	9.5051	4.6402	4.8649	4.5614	106.6549
	13.3479	10.1813	3.1666	10.1037	31.3406
	12.9922	10.3472	2.6450	10.2720	25.7501
	10.0118	13.3641	-3.3523	13.2882	-25.2273
			X= 1.831	X= 9.556	X= 34.630
			SD= 3.583	SD= 3.637	SD= 54.345
			SE= 1.792	SE= 1.819	SE= 27.173
6M					
	13.8868	10.7073	3.1796	10.6326	29.9039
	13.8682	15.6213	-1.7531	15.5455	-11.2773
	16.3242	6.1668	10.1574	6.0427	168.0938
	14.5473	10.4247	4.1226	10.3045	40.0076
			X= 3.927	X= 10.631	X= 56.682
			SD= 4.888	SD= 3.886	SD= 77.516
			SE= 2.444	SE= 1.943	SE= 38.758
10M					
	13.3851	10.4557	2.9293	10.3346	28.3450
	13.9695	13.3862	.5833	13.2631	4.3976
	13.7049	11.3349	2.3700	11.2069	21.1476
	12.9305	13.0247	-.0941	12.9006	-.7298
			X= 1.447	X= 11.926	X= 13.290
			SD= 1.434	SD= 1.389	SD= 13.712
			SE= .717	SE= .694	SE= 6.856

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	6.1934	5.7746	.4188	5.6352	7.4055
	11.8289	10.6786	1.1503	10.5536	10.8993
	13.6250	10.5839	3.0411	10.4644	29.0614
	13.4628	11.6826	1.7803	11.5594	15.4013
			X= 1.598	X= 9.558	X= 15.692
			SD= 1.112	SD= 2.649	SD= 9.495
			SE= .556	SE= 1.324	SE= 4.747
6M					
	12.6617	6.7460	5.9157	6.6219	89.3360
	12.8604	6.3568	6.5036	6.2403	104.2196
	12.6852	7.5804	5.1047	7.4638	68.3932
	9.5963	9.8134	-.2172	9.6930	-2.2403
			X= 4.327	X= 7.505	X= 64.927
			SD= 3.083	SD= 1.546	SD= 47.128
			SE= 1.542	SE= .773	SE= 23.564
10M					
	11.2890	11.0272	.2619	10.9077	2.4008
	9.2928	12.5018	-3.2090	12.3796	-25.9214
	11.6992	9.3520	2.3473	9.2325	25.4241
	8.2701	11.9512	-3.6811	11.8262	-31.1268
			X= -1.070	X= 11.087	X= -7.306
			SD= 2.878	SD= 1.377	SD= 26.328
			SE= 1.439	SE= .689	SE= 13.164

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	10.4209	6.6166	3.8042	6.3647	59.7704
	6.6384	2.7900	3.8484	2.5263	152.3307
	5.3408	2.8467	2.4941	2.5948	96.1210
	7.4902	5.2999	2.1903	5.0401	43.4574
		X=	3.084 X=	4.131 X=	87.920
		SD=	.866 SD=	1.893 SD=	48.254
		SE=	.433 SE=	.947 SE=	24.127
6M					
	4.9542	4.8851	.0690	4.6234	1.4933
	5.5619	4.8766	.6853	4.6307	14.7990
	5.6983	3.5777	2.1206	3.3317	63.6478
	6.2683	4.5417	1.7266	4.2877	40.2683
		X=	1.150 X=	4.218 X=	30.052
		SD=	.941 SD=	.612 SD=	27.576
		SE=	.471 SE=	.306 SE=	13.788
10M					
	4.8395	3.1121	1.7274	2.8601	60.3954
	5.3880	3.9139	1.6741	3.6562	45.7876
	5.3816	3.6102	1.7713	3.3583	52.7450
	6.6346	7.2437	-.6092	6.9800	-8.7274
		X=	1.141 X=	4.214 X=	37.550
		SD=	1.167 SD=	1.873 SD=	31.423
		SE=	.584 SE=	.937 SE=	15.712

MIDDAY INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	7.9995	6.6342	1.3652	6.4060	21.3117
	9.6805	3.0569	6.6236	2.8321	233.8763
	8.6726	4.4200	4.2526	4.2020	101.2032
	9.4327	9.2425	.1902	9.0228	2.1075
		X=	3.108 X=	5.616 X=	89.625
		SD=	2.899 SD=	2.707 SD=	105.307
		SE=	1.450 SE=	1.353 SE=	52.653
6M					
	8.6954	6.9153	1.7801	6.6990	26.5731
	8.2226	8.4225	-.1999	8.2027	-2.4374
	9.9738	5.4981	4.4756	5.3963	82.9395
	7.7958	8.4193	-.6236	8.3207	-7.4945
		X=	1.358 X=	7.155 X=	24.895
		SD=	2.327 SD=	1.385 SD=	41.505
		SE=	1.164 SE=	.693 SE=	20.753
10M					
	10.2124	11.3213	-1.1089	11.2218	-9.8814
	10.0325	8.5805	1.4520	8.4794	17.1234
	7.7337	3.4192	4.3145	3.3141	130.1839
	5.7301	7.6958	-1.9657	7.5939	-25.8855
		X=	.673 X=	7.632 X=	27.885
		SD=	2.829 SD=	3.279 SD=	70.471
		SE=	1.414 SE=	1.639 SE=	35.235

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE UGC/M3/HR	DARK BOTTLE UPTAKE UGC/M3/HR	PHOTO UPTAKE UGC/M3/HR	BACTERIAL UPTAKE UGC/M3/HR	PERCENT OF BACTERIAL UPTAKE
2M					
	7.0931	4.8555	2.2376	4.7382	47.2242
	10.0910	5.6238	4.4672	5.5010	81.2063
	7.3769	5.1511	2.2258	5.0338	44.2160
	6.1847	5.6951	.4896	5.5742	8.7827
			X= 2.355 X=	5.212 X=	45.357
			SD= 1.630 SD=	.396 SD=	29.595
			SE= .815 SE=	.198 SE=	14.798
6M					
	3.8603	4.8969	-1.0367	4.7750	-21.7099
	4.5883	8.4269	-3.8386	8.3124	-46.1796
	6.2350	3.9937	2.2413	3.8792	57.7765
	3.4274	3.4553	-.0278	3.3370	-.8343
			X= -.665 X=	5.076 X=	-2.737
			SD= 2.521 SD=	2.238 SD=	44.395
			SE= 1.260 SE=	1.119 SE=	22.197
10M					
	5.0115	5.2705	-.2591	5.1532	-5.0271
	4.0228	6.3478	-2.3250	6.2278	-37.3326
	4.6291	4.8442	-.2151	4.7269	-4.5516
	4.1780	10.0797	-5.9017	9.9569	-59.2723
			X= -2.175 X=	6.516 X=	-26.546
			SD= 2.672 SD=	2.379 SD=	26.672
			SE= 1.336 SE=	1.190 SE=	13.336

APPENDIX B

INORGANIC CARBON UPTAKE VALUES

APPENDIX B

INORGANIC CARBON UPTAKE VALUES

Appendix B is a tabular presentation of calculated values (mgC m^{-3} hr^{-1}) for inorganic carbon uptake in Lawrence Lake during 1974. The data are arranged as four light bottle/dark bottle pairs for each Time, Depth, and Month of sampling. The difference between light and dark estimates (Photolithotrophy) is found in column "C14 UPTAKE." Photoheterotrophic and chemoheterotrophic estimates (µgC m^{-3} hr^{-1}) from the same light bottle/dark bottle pairs are placed in columns "PHOTO UPTAKE" and "BACTERIAL UPTAKE" respectively for comparative purposes. Means, standard deviations, and standard errors are indicated.

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	.2934	.3701	-.0767	3.0593	6.9655
	1.7791	.4454	1.3338	.7797	8.8022
	1.8962	.3241	1.5720	.3255	8.9695
	1.7941	.3417	1.4524	1.2161	9.5924
			X= 1.070	X= 1.345	X= 8.567
			SD= .771	SD= 1.199	SD= 1.159
			SE= .385	SE= .600	SE= .579
6M					
	.4396	.3880	.0516	.9409	8.4959
	.4689	.3987	.0701	.6482	9.8484
	.4800	.3552	.1247	1.6888	7.9717
	.4716	.3814	.0903	2.4130	6.5069
			X= .084	X= 1.423	X= 8.206
			SD= .031	SD= .792	SD= 1.381
			SE= .016	SE= .396	SE= .691
10M					
	.4028	.3916	.0112	-.1789	9.2580
	.4440	.3982	.0458	5.9021	3.3363
	.4170	.4140	.0030	-1.2135	9.7089
	.4464	.4385	.0079	1.1053	8.4418
			X= .017	X= 1.404	X= 7.686
			SD= .020	SD= 3.145	SD= 2.947
			SE= .010	SE= 1.573	SE= 1.474

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.1785	.2858	2.8927	-2.5743	7.7937
	3.3969	.3286	3.0684	-.2054	7.0883
	3.4435	.3356	3.1079	-.0884	8.9893
	.3443	.3379	.0064	-2.9092	10.5130
			X= 2.269	X= -1.444	X= 8.596
			SD= 1.511	SD= 1.505	SD= 1.500
			SE= .756	SE= .753	SE= .750
6M					
	.7024	.3193	.3831	5.1166	2.8792
	.9887	.3382	.6505	-.3867	6.8288
	.7499	.3047	.4451	-.9556	7.7081
	.8355	.3568	.4787	-.4303	6.7652
			X= .489	X= .836	X= 6.045
			SD= .115	SD= 2.865	SD= 2.154
			SE= .057	SE= 1.433	SE= 1.077
10M					
	.4100	.3375	.0725	2.1641	6.7094
	.4043	.4060	-.0017	-.4316	7.1059
	.4173	.3551	.0622	-.6439	7.7989
	.3792	.3844	-.0052	.5165	7.3994
			X= .032	X= .401	X= 7.253
			SD= .041	SD= 1.279	SD= .461
			SE= .021	SE= .639	SE= .230

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	.2751	.2698	.0143	.0328	-.0207
	3.8678	.3507	3.5171	-.5728	7.3423
	6.6937	.4319	6.2618	3.0039	11.6586
	3.8057	.3522	3.4536	3.6525	5.2132
			X= 3.312	X= 1.529	X= 6.047
			SD= 2.559	SD= 2.109	SD= 4.852
			SE= 1.279	SE= 1.054	SE= 2.426
6M					
	.8559	.3199	.5360	1.6359	4.1667
	.9395	.3565	.5829	-.3370	6.8712
	.9196	.3558	.5638	-1.2842	7.4214
	1.0827	.3757	.7070	6.0803	1.7657
			X= .597	X= 1.524	X= 5.056
			SD= .076	SD= 3.272	SD= 2.615
			SE= .038	SE= 1.636	SE= 1.307
10M					
	.4725	.3434	.1291	-1.0352	5.7328
	.4376	.4372	.0004	1.0266	4.4024
	.4941	.3942	.0999	-1.4125	6.8189
	.5023	.4228	.0795	1.0548	4.6658
			X= .077	X= -.092	X= 5.405
			SD= .055	SD= 1.317	SD= 1.104
			SE= .028	SE= .658	SE= .552

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.3730	.4447	1.9283	5.9963	4.9577
	2.2241	.4433	1.7808	3.4875	5.4820
	2.5089	.3951	2.1138	2.0964	7.8725
	2.2220	.4261	1.7959	.5728	4.9289
			X= 1.905	X= 3.038	X= 5.810
			SD= .154	SD= 2.303	SD= 1.398
			SE= .077	SE= 1.152	SE= .699
6M					
	1.0891	.4105	.6786	4.2233	6.0271
	1.1126	.4267	.6860	1.1081	7.1007
	1.1903	.4377	.7525	6.1546	6.2941
	1.0358	.4877	.5481	7.9780	1.9494
			X= .666	X= 4.866	X= 5.343
			SD= .086	SD= 2.937	SD= 2.308
			SE= .043	SE= 1.469	SE= 1.154
10M					
	.5086	.4696	.0390	-.1878	8.9397
	.3237	.4901	-.1665	4.3685	2.3848
	.4946	.4556	.0390	-1.1029	10.2642
	.5646	.5185	.0461	.8267	8.8410
			X= -.011	X= .976	X= 7.607
			SD= .104	SD= 2.395	SD= 3.542
			SE= .052	SE= 1.197	SE= 1.771

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.7109	.5051	2.2057	1.6914	9.1324
	2.5945	.3518	2.2427	.2872	9.8347
	2.6429	.3675	2.2754	-.9452	10.9811
	2.5379	.3816	2.1563	-1.8902	10.9523
			X= 2.220	X= -.214	X= 10.225
			SD= .051	SD= 1.552	SD= .903
			SE= .026	SE= .776	SE= .452
6M					
	1.2213	.3992	.8221	-.1401	6.6191
	1.5862	.4106	1.1756	4.2381	4.9984
	1.4634	.4059	1.0575	-.3649	6.9175
	1.8895	.4388	1.4507	.3182	7.3909
			X= 1.126	X= 1.013	X= 6.481
			SD= .261	SD= 2.169	SD= 1.039
			SE= .131	SE= 1.084	SE= .519
10M					
	.7540	.4579	.2961	2.7072	7.6145
	.6703	.4359	.2344	-.6732	8.7433
	.6351	.4482	.1869	-2.3031	7.9829
	.6876	.4179	.2697	2.9641	5.3361
			X= .247	X= .674	X= 7.419
			SD= .047	SD= 2.586	SD= 1.466
			SE= .024	SE= 1.293	SE= .733

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.0656	.3817	1.6840	1.4052	9.3283
	2.0967	.3883	1.7084	-2.7559	9.3563
	1.8413	.4059	1.4354	2.2104	5.9121
	2.2774	.4221	1.8553	3.4749	7.4754
			X= 1.671	X= 1.084	X= 8.018
			SD= .174	SD= 2.698	SD= 1.657
			SE= .087	SE= 1.349	SE= .829
6M					
	.6105	.4335	.1770	-3.9963	7.4728
	1.1959	.4918	.7041	-.2494	6.5575
	1.2819	.4648	.8178	1.2433	5.5843
	1.0744	.4754	.5990	3.7994	2.0842
			X= .574	X= .199	X= 5.425
			SD= .279	SD= 3.259	SD= 2.357
			SE= .140	SE= 1.629	SE= 1.178
10M					
	.5418	.4334	.1084	-2.3225	8.9395
	.5384	.4889	.0495	-.6414	8.9212
	.5599	.4885	.0714	-.4294	7.5303
	.5751	.4821	.0930	.5265	7.3259
			X= .081	X= -.717	X= 8.179
			SD= .026	SD= 1.185	SD= .871
			SE= .013	SE= .592	SE= .436

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	5.7520	.4448	5.3072	9.4003	7.2458
	5.3855	.4054	4.9801	-.4888	8.7742
	4.9378	.4319	4.5059	3.3165	10.8512
	5.9220	.4313	5.4907	7.2126	10.8868
			X= 5.071	X= 4.860	X= 9.440
			SD= .432	SD= 4.364	SD= 1.765
			SE= .216	SE= 2.182	SE= .882
6M					
	2.3090	.4187	1.8903	12.0806	6.1084
	2.4224	.5269	1.8955	-1.3833	15.5213
	2.0452	.4379	1.6073	4.9224	12.7209
	1.8951	.3945	1.5006	8.2402	7.5874
			X= 1.723	X= 5.965	X= 10.485
			SD= .200	SD= 5.706	SD= 4.394
			SE= .100	SE= 2.858	SE= 2.197
10M					
	.6013	.3928	.2085	-1.4836	12.5276
	.6901	.4656	.2244	6.5013	9.3592
	.3287	.4093	-.0805	-4.5223	6.0799
	.6766	.3998	.2768	.3179	10.2491
			X= .157	X= .203	X= 9.554
			SD= .161	SD= 4.650	SD= 2.673
			SE= .081	SE= 2.325	SE= 1.336

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	5.2753	.3209	4.9544	8.0644	7.8025
	5.3427	.4107	4.9321	10.1639	6.4944
	5.6345	.3690	5.2655	-.1037	16.0323
	5.6422	.3900	5.2522	.1063	15.2309
			X= 5.101	X= 4.556	X= 11.390
			SD= .188	SD= 5.381	SD= 4.938
			SE= .091	SE= 2.666	SE= 2.469
6M					
	2.0609	.3398	1.7210	11.0073	5.4407
	2.2652	.3729	1.8923	2.6886	14.6400
	2.4949	.3721	2.1228	12.7639	3.5295
	2.3054	.3936	1.9118	-.4056	14.2083
			X= 1.912	X= 6.514	X= 9.455
			SD= .165	SD= 6.371	SD= 5.794
			SE= .082	SE= 3.185	SE= 2.897
10M					
	.7482	.4230	.3252	-1.1351	13.2260
	.7553	.3853	.3699	9.3604	5.6973
	.7032	.4139	.2893	12.8634	1.7918
	.7481	.4322	.3160	5.1287	10.4089
			X= .325	X= 6.554	X= 7.781
			SD= .034	SD= 6.023	SD= 5.059
			SE= .017	SE= 3.012	SE= 2.529

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	4.4160	.4300	3.9860	1.2305	14.2160
	4.7429	.4794	4.2635	1.3765	14.8733
	4.4260	.4239	4.0021	7.7303	5.7155
	4.6696	.4438	4.2258	5.0034	10.0752
			X= 4.119	X= 3.835	X= 11.220
			SD= .146	SD= 3.129	SD= 4.240
			SE= .073	SE= 1.564	SE= 2.120
6M					
	1.6453	.4665	1.1789	1.1921	15.0106
	1.3938	.4598	.9340	.1122	16.5883
	1.5982	.4658	1.1324	-.7965	15.2301
	1.4970	.5076	.9894	-3.4589	17.9603
			X= 1.059	X= -.738	X= 16.197
			SD= .116	SD= 1.988	SD= 1.367
			SE= .058	SE= .994	SE= .683
10M					
	.6483	.5155	.1328	-.6575	16.6205
	.7038	.4483	.2555	1.0523	13.5796
	.7833	.5884	.1949	-.5934	15.2188
	.8285	.5782	.2504	1.1134	14.7679
			X= .208	X= .229	X= 15.047
			SD= .057	SD= .987	SD= 1.257
			SE= .029	SE= .493	SE= .628

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.2143	.4703	1.7440	.3560	2.9532
	2.0489	.7444	1.3045	1.2235	3.0109
	2.1912	.4140	1.7772	.3708	2.7383
	2.0204	.7629	1.2575	-.0007	3.6381
			X= 1.521	X= .487	X= 3.085
			SD= .278	SD= .520	SD= .387
			SE= .139	SE= .260	SE= .193
6M					
	.9932	.3892	.6040	.5772	2.5180
	.8358	.5843	.2515	-.3579	3.8910
	1.0173	.3763	.6409	.2469	4.9293
	.8800	.6223	.2577	1.2843	3.6584
			X= .439	X= .438	X= 3.749
			SD= .213	SD= .684	SD= .989
			SE= .106	SE= .342	SE= .495
10M					
	.5629	.3956	.1673	1.5742	4.3322
	.5061	.4728	.0333	-.1641	6.5540
	.7836	.4931	.2905	-.7331	7.1161
	.5061	.8183	-.3121	-1.9261	8.1973
			X= .045	X= -.312	X= 6.550
			SD= .260	SD= 1.456	SD= 1.628
			SE= .130	SE= .728	SE= .814

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.1153	.6954	2.4199	.7091	2.0167
	3.5838	.5487	3.0351	1.7824	1.5709
	4.0537	.4425	3.6112	2.2849	1.6668
	3.9845	.5741	3.4104	3.5354	1.2315
			X= 3.119	X= 2.078	X= 1.620
			SD= .524	SD= 1.173	SD= .321
			SE= .262	SE= .587	SE= .160
6M					
	3.1297	.4400	2.6897	-.3968	3.9836
	2.8168	.6571	2.1597	5.3115	2.2069
	3.2110	.5173	2.6937	4.3457	2.9539
	2.8574	.6983	2.1591	7.0607	2.8451
			X= 2.426	X= 4.080	X= 2.997
			SD= .307	SD= 3.189	SD= .735
			SE= .154	SE= 1.595	SE= .368
10M					
	1.3596	.4109	.9488	6.6348	3.4701
	1.4287	.9390	.4897	1.2612	10.4603
	.8195	.6253	.1942	1.8022	5.1872
	1.3531	.7603	.5929	8.1863	4.2700
			X= .556	X= 4.471	X= 5.847
			SD= .311	SD= 3.460	SD= 3.155
			SE= .156	SE= 1.730	SE= 1.577

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	1.5591	.4992	1.0599	.3202	2.0394
	1.3422	.5179	.8243	.2935	2.3453
	1.4923	.4023	1.0900	.2492	3.2425
	1.7535	.5358	1.2177	-.2731	3.4376
			X= 1.048	X= .147	X= 2.766
			SD= .164	SD= .282	SD= .679
			SE= .082	SE= .141	SE= .339
6M					
	.9791	.6528	.3263	2.0006	4.0989
	.7406	.4597	.2809	1.6649	4.4444
	.7807	.4061	.3746	1.1421	5.8340
	.7678	.4081	.3597	5.7434	4.1631
			X= .335	X= 2.638	X= 4.635
			SD= .042	SD= 2.100	SD= .813
			SE= .021	SE= 1.050	SE= .407
10M					
	.6034	.4156	.1878	.7804	8.3017
	.5203	.4462	.0742	5.9180	4.1294
	.7065	.4880	.2185	3.7516	7.7779
	.5831	.5309	.0522	4.2518	8.6419
			X= .133	X= 3.675	X= 7.213
			SD= .082	SD= 2.141	SD= 2.086
			SE= .041	SE= 1.070	SE= 1.043

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MCC/M3/HR	DARK BOTTLE UPTAKE MCC/M3/HR	C14 UPTAKE MCC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.1235	.6404	2.4831	1.1923	1.6025
	3.5754	1.0301	2.5453	1.1132	1.8095
	3.4432	.9089	2.5343	.5657	2.8319
	2.9165	.9297	1.9868	.0862	2.7282
			X= 2.387	X= .739	X= 2.243
			SD= .268	SD= .517	SD= .627
			SE= .134	SE= .258	SE= .314
6M					
	1.7858	.6981	1.0877	.7137	2.7122
	1.4380	.8742	.5638	.9630	2.9238
	1.9055	.5976	1.3079	3.5716	1.8571
	1.4729	.7111	.7617	2.0678	1.4357
			X= .930	X= 1.829	X= 2.232
			SD= .332	SD= 1.302	SD= .703
			SE= .166	SE= .651	SE= .352
10M					
	1.1471	.6577	.4894	.6437	4.3011
	.8540	1.1352	-.2811	5.3414	1.9087
	1.6757	.7924	.8833	3.0311	5.8820
	1.2422	1.7001	-.4579	1.8002	6.0653
			X= .158	X= 2.704	X= 4.539
			SD= .635	SD= 2.010	SD= 1.924
			SE= .317	SE= 1.005	SE= .962

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MCC/M3/HR	DARK BOTTLE UPTAKE MCC/M3/HR	C14 UPTAKE MCC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.9261	.7692	3.1569	.8307	1.9451
	4.2908	.6783	3.6125	.3135	2.1366
	4.4101	.5373	3.8727	.9892	2.6104
	5.4748	.8096	4.6652	.4196	2.8708
			X= 3.827	X= .638	X= 2.391
			SD= .632	SD= .323	SD= .425
			SE= .316	SE= .162	SE= .213
6M					
	2.9704	.4218	2.5486	2.0396	1.9473
	3.6180	.4409	3.1770	.3780	4.2082
	3.5865	.4212	3.1653	11.0266	3.4679
	3.5017	.4381	3.0636	2.4763	1.9461
			X= 2.989	X= 3.980	X= 2.892
			SD= .298	SD= 4.784	SD= 1.133
			SE= .149	SE= 2.392	SE= .567
10M					
	.9956	.3912	.6043	6.3340	3.2090
	.8724	.3659	.5065	5.7823	3.3804
	1.1994	.3758	.8236	3.8650	4.4663
	.9698	.4107	.5591	4.3558	4.2953
			X= .623	X= 5.084	X= 3.838
			SD= .139	SD= 1.164	SD= .635
			SE= .070	SE= .582	SE= .317

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MCC/M3/HR	DARK BOTTLE UPTAKE MCC/M3/HR	C14 UPTAKE MCC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.6706	.4361	2.2345	.0480	3.0096
	2.1110	1.5606	.5504	1.3904	1.9614
	2.7511	.4417	2.3095	.5849	3.2284
	2.2995	.6032	1.6963	-.0166	2.9098
			X= 1.698	X= .502	X= 2.777
			SD= .812	SD= .651	SD= .560
			SE= .406	SE= .325	SE= .280
6M					
	1.2955	.4786	.8170	-.2109	6.5821
	1.2390	.5324	.7066	4.0189	5.8601
	1.1010	.4055	.6955	4.7696	5.9308
	1.1120	.7350	.3771	1.5084	7.0035
			X= .649	X= 2.522	X= 6.844
			SD= .189	SD= 2.294	SD= .547
			SE= .095	SE= 1.147	SE= .273
10M					
	.7563	.4672	.2890	1.9277	10.5281
	.7121	.5352	.1768	6.1942	5.3166
	.7599	.5201	.2397	2.5659	7.4095
	.6772	.5501	.1272	4.7172	4.9356
			X= .208	X= 3.851	X= 7.047
			SD= .071	SD= 1.966	SD= 2.568
			SE= .035	SE= .983	SE= 1.281

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.6375	.3405	2.2971	1.3898	1.3244
	3.4722	.4123	3.0598	1.9845	3.3396
	3.1127	.3989	2.7138	1.3367	3.5603
	4.1014	.4117	3.6897	.4277	6.0104
		X=	2.940	X= 1.285	X= 3.559
		SD=	.589	SD= .642	SD= 1.919
		SE=	.295	SE= .321	SE= .960
6M					
	2.7991	.4770	2.3221	1.8578	6.9310
	2.5855	.4977	2.0878	1.7361	9.2595
	3.2884	.4887	2.7997	13.0383	2.2578
	2.8332	.5832	2.2500	5.3405	8.6015
		X=	2.365	X= 5.493	X= 6.762
		SD=	.306	SD= 5.300	SD= 3.159
		SE=	.153	SE= 2.650	SE= 1.579
10M					
	.9150	.4752	.4398	1.2265	4.9960
	.8468	.5279	.3189	2.4049	5.4815
	.8784	.5230	.3554	.9626	5.4432
	.9113	.5110	.4003	2.2019	6.7066
		X=	.379	X= 1.699	X= 5.657
		SD=	.053	SD= .711	SD= .734
		SE=	.026	SE= .356	SE= .367

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	4.8302	.4061	4.4241	1.7036	1.8818
	6.7151	.4094	6.3058	4.2459	2.3003
	5.4789	.4457	5.0332	3.8264	2.8949
	8.0051	.4282	7.5769	3.4390	4.6858
		X=	5.835	X= 3.179	X= 2.941
		SD=	1.401	SD= 1.065	SD= 1.235
		SE=	.701	SE= .533	SE= .618
6M					
	10.1668	.6432	9.5235	-.1789	16.9754
	9.0735	.5899	8.4836	4.8442	13.8410
	10.4361	.5610	9.8751	26.7006	3.0563
	9.0137	.6210	8.3927	13.6478	8.2213
		X=	9.069	X= 11.253	X= 10.523
		SD=	.743	SD= 11.777	SD= 6.156
		SE=	.372	SE= 5.889	SE= 3.078
10M					
	2.0976	.4663	1.6313	6.3323	6.6123
	1.6021	.8112	.7909	7.6082	4.7227
	1.9022	.5170	1.3852	8.0631	5.6260
	2.2719	.4948	1.7771	11.5168	3.4881
		X=	1.396	X= 8.380	X= 5.112
		SD=	.435	SD= 2.216	SD= 1.330
		SE=	.217	SE= 1.108	SE= .665

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.9875	.4006	2.5869	.6200	2.8784
	3.0403	.3920	2.6483	1.3896	4.1595
	3.5875	.3639	3.2236	6.1849	2.0205
	3.3998	.4326	2.9672	1.8819	4.5061
		X=	2.856	X= 2.519	X= 3.391
		SD=	.296	SD= 2.498	SD= 1.151
		SE=	.148	SE= 1.249	SE= .576
6M					
	2.6982	.6774	2.0208	-.8718	14.1009
	2.7427	.6474	2.0953	17.2690	6.0592
	2.9151	.6783	2.2368	10.2958	11.9378
	1.7923	.6721	1.1203	.2438	9.3736
		X=	1.868	X= 6.734	X= 10.368
		SD=	.507	SD= 8.634	SD= 3.462
		SE=	.253	SE= 4.317	SE= 1.731
10M					
	.8749	.4919	.3831	5.1423	5.6446
	.8451	.5049	.3402	2.7394	8.3448
	.7830	.4565	.3265	5.4796	6.8674
	.7926	.5164	.2762	2.7642	9.2875
		X=	.331	X= 4.031	X= 7.536
		SD=	.044	SD= 1.484	SD= 1.607
		SE=	.022	SE= .742	SE= .803

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.3922	.5132	2.8789	5.3627	3.4039
	2.8177	.5390	2.2787	7.5301	2.2642
	3.2596	.4933	2.7663	9.6129	2.5428
	3.1423	.4645	2.6778	7.2813	6.0253
		X=	2.650	X= 7.447	X= 3.559
		SD=	.261	SD= 1.739	SD= 1.714
		SE=	.131	SE= .869	SE= .857
6M					
	1.1165	.4874	.6291	3.2152	5.8907
	.9477	.4441	.5037	2.9675	5.0628
	1.1390	.5078	.6312	9.7910	2.4918
	1.0262	.4950	.5312	5.6029	5.7971
		X=	.574	X= 5.394	X= 4.811
		SD=	.066	SD= 3.163	SD= 1.590
		SE=	.033	SE= 1.581	SE= .795
10M					
	.5410	.5829	-.0419	-3.1485	6.5448
	.9216	.6169	.3047	4.0477	5.8289
	.9280	.7808	.1472	5.4139	3.5711
	.9901	.7630	.2272	-2.3009	9.3022
		X=	.159	X= 1.003	X= 6.312
		SD=	.149	SD= 4.354	SD= 2.362
		SE=	.074	SE= 2.177	SE= 1.181

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.7877	.3413	3.4464	2.4698	8.1481
	3.9986	.3611	3.6375	3.7726	10.7789
	4.0868	.3597	3.7271	14.6955	4.1516
	4.4336	.3702	4.0634	6.8714	9.7983
		X=	3.719	X= 6.952	X= 8.219
		SD=	.258	SD= 5.482	SD= 2.921
		SE=	.129	SE= 2.741	SE= 1.460
6M					
	1.7533	.4154	1.3379	4.1251	9.0192
	1.5129	.3517	1.1612	11.3472	2.4550
	1.4447	.3605	1.0842	14.5146	5.6134
	1.7180	.3783	1.3397	6.9067	12.7334
		X=	1.231	X= 9.223	X= 7.455
		SD=	.129	SD= 4.614	SD= 4.423
		SE=	.064	SE= 2.307	SE= 2.212
10M					
	.6946	.3878	.3068	10.9708	4.8198
	.6040	.3859	.2180	4.0630	9.3935
	.6971	.4165	.2806	9.4257	4.2190
	.7788	.4591	.3198	7.7390	9.0254
		X=	.281	X= 8.050	X= 6.864
		SD=	.045	SD= 2.967	SD= 2.723
		SE=	.023	SE= 1.484	SE= 1.362

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	1.8387	.3475	1.4912	-.5691	6.0934
	1.9058	.4796	1.4262	-1.7747	8.0297
	1.6607	.3444	1.3163	1.8411	8.5748
	1.7070	.3825	1.3245	1.0843	14.4685
		X=	1.390	X= .145	X= 9.292
		SD=	.084	SD= 1.628	SD= 3.612
		SE=	.042	SE= .814	SE= 1.806
6M					
	.5695	.3679	.2017	1.1388	7.7427
	.5004	.4078	.0926	-1.8944	13.7235
	.5232	.3807	.1425	5.8097	9.4056
	.5304	.4155	.1149	2.7817	13.5684
		X=	.138	X= 1.959	X= 11.110
		SD=	.047	SD= 3.216	SD= 3.007
		SE=	.024	SE= 1.608	SE= 1.503
10M					
	.4876	.3996	.0880	2.0749	8.0959
	.4722	.4013	.0709	.1724	10.7361
	.5548	.4479	.1069	8.6819	9.0033
	.5083	.4285	.0798	1.2972	13.6440
		X=	.086	X= 3.057	X= 10.370
		SD=	.015	SD= 3.831	SD= 2.442
		SE=	.008	SE= 1.915	SE= 1.221

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.3033	.3207	1.9826	1.8216	1.7460
	2.7160	.3510	2.3650	.2777	4.8962
	2.8646	.3481	2.5165	4.3258	2.8985
	3.1856	.3228	2.8328	.6215	4.5610
		X=	2.424	X= 1.762	X= 3.525
		SD=	.353	SD= 1.833	SD= 1.473
		SE=	.177	SE= .917	SE= .737
6M					
	.7507	.3797	.3710	-.7365	4.4155
	.7547	.3211	.4336	3.8067	2.2637
	.6292	.3503	.2788	3.3569	2.5845
	.6763	.3274	.3488	4.1977	1.7213
		X=	.358	X= 2.656	X= 2.746
		SD=	.064	SD= 2.288	SD= 1.168
		SE=	.032	SE= 1.144	SE= .584
10M					
	.5214	.5233	-.0019	.9274	4.9190
	.5326	.3686	.1640	2.8762	5.9369
	.5754	.5918	-.0164	4.9917	3.0294
	.5940	.4262	.1679	3.8413	8.8432
		X=	.078	X= 3.159	X= 5.682
		SD=	.101	SD= 1.721	SD= 2.427
		SE=	.051	SE= .860	SE= 1.214

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	5.8432	.3227	5.5205	2.5291	3.6868
	6.1290	.3482	5.7809	3.3147	4.5670
	2.7153	.3080	2.4073	.9083	4.1744
	8.0595	.3264	7.7330	1.8125	8.0220
		X=	5.360	X= 2.141	X= 5.118
		SD=	2.202	SD= 1.026	SD= 1.973
		SE=	1.101	SE= .513	SE= .986
6M					
	1.8559	.2830	1.5728	3.8555	7.0123
	1.6887	.3080	1.3806	6.1466	8.5623
	1.6348	.2539	1.3809	12.2654	1.4322
	1.6634	.2961	1.3673	4.9241	9.4359
		X=	1.425	X= 6.798	X= 6.611
		SD=	.098	SD= 3.763	SD= 3.595
		SE=	.049	SE= 1.882	SE= 1.797
10M					
	.6334	.8217	.3116	6.2270	6.7673
	.5506	.2963	.2543	9.2885	7.9696
	.5246	.3534	.1712	.8191	7.0824
	.5867	.3335	.2532	13.9438	6.7339
		X=	.248	X= 7.570	X= 7.138
		SD=	.058	SD= 5.506	SD= .576
		SE=	.029	SE= 2.753	SE= .288

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.8322	.3440	2.4882	-.8666	5.1576
	2.7836	.3983	2.3852	4.0676	5.1408
	3.0043	.3530	2.6513	-.7315	8.2848
	3.2073	.3583	2.8490	2.9925	9.7501
		X=	2.593	X= 1.365	X= 7.088
		SD=	.203	SD= 2.538	SD= 2.312
		SE=	.101	SE= 1.269	SE= 1.156
6M					
	.8506	.3066	.5440	.1859	6.9898
	.8304	.3227	.5077	-1.4899	14.0265
	.7758	.2901	.4857	-.2750	13.7812
	.8538	.3337	.5201	9.0045	5.7822
		X=	.514	X= 1.856	X= 10.145
		SD=	.024	SD= 4.818	SD= 4.369
		SE=	.012	SE= 2.409	SE= 2.185
10M					
	.4246	.3151	.1095	1.6181	7.2086
	.4120	.3150	.0970	1.0492	9.2206
	.4337	.3423	.0913	.9408	13.3820
	.3879	.3288	.0592	4.4472	14.5829
		X=	.089	X= 2.014	X= 11.099
		SD=	.021	SD= 1.649	SD= 3.465
		SE=	.011	SE= .825	SE= 1.732

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.7211	.6159	2.1052	1.6575	5.1568
	2.4872	.5704	1.9168	3.3540	8.6967
	2.6678	.7349	1.9329	6.2223	6.9967
	2.5014	.5818	1.9197	-.1744	12.0076
		X=	1.969	X= 2.765	X= 8.214
		SD=	.091	SD= 2.718	SD= 2.913
		SE=	.046	SE= 1.359	SE= 1.456
6M					
	.9624	.6244	.3380	1.5847	10.0069
	1.1689	.4423	.7266	5.0221	5.6490
	.8508	.5750	.2758	1.1433	9.8047
	.8556	.5238	.3318	-3.9747	8.8584
		X=	.418	X= .944	X= 8.580
		SD=	.208	SD= 3.709	SD= 2.017
		SE=	.104	SE= 1.855	SE= 1.008
10M					
	.4699	.6469	-.1769	7.0772	5.3613
	.6183	.4219	.1964	3.1188	8.7832
	.5956	.7301	-.1345	.3796	3.5132
	.6571	.5809	.0762	-4.3899	8.8533
		X=	-.010	X= 1.546	X= 6.628
		SD=	.176	SD= 4.819	SD= 2.640
		SE=	.088	SE= 2.409	SE= 1.320

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	3.3872	.8430	2.5442	4.8649	4.5614
	3.3849	.6764	2.7086	3.1666	10.1087
	3.8082	.7910	3.0178	2.6450	10.2720
	3.6330	.6706	2.9625	-3.3528	13.2882
		X=	2.808	X= 1.831	X= 9.556
		SD=	.221	SD= 3.583	SD= 3.637
		SE=	.111	SE= 1.792	SE= 1.819
6M					
	1.1424	.7832	.3592	3.1796	10.6326
	1.5347	.6967	.8381	-1.7631	15.5455
	1.3187	.7894	.5294	10.1574	6.0427
	1.1646	.7724	.3922	4.1226	10.3045
		X=	.530	X= 3.927	X= 10.631
		SD=	.218	SD= 4.888	SD= 3.886
		SE=	.109	SE= 2.444	SE= 1.943
10M					
	.6677	.5966	.0712	2.9293	10.3346
	.6449	.5347	.1102	.5833	13.2631
	.6715	.6129	.0586	2.3700	11.2069
	.8202	.5491	.2710	-.0941	12.9006
		X=	.128	X= 1.447	X= 11.926
		SD=	.098	SD= 1.434	SD= 1.389
		SE=	.049	SE= .717	SE= .694

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MGC/M3/HR	DARK BOTTLE UPTAKE MGC/M3/HR	C14 UPTAKE MGC/M3/HR	UGC/M3/HR PHOTO UPTAKE	UGC/M3/HR BACTERIAL UPTAKE
2M					
	2.0065	.4033	1.6032	.4188	5.6552
	1.8466	.5029	1.3437	1.1503	10.5536
	1.6607	.4426	1.2181	3.0411	10.4644
	2.0898	.5549	1.5350	1.7803	11.5594
			X= 1.425	X= 1.598	X= 9.558
			SD= .176	SD= 1.112	SD= 2.649
			SE= .088	SE= .556	SE= 1.324
6M					
	.6665	.3982	.2682	5.9157	6.6219
	.6569	.4271	.2299	6.5036	6.2403
	.6037	.4915	.1122	5.1047	7.4638
	.7551	.5045	.2506	-.2172	9.6930
			X= .215	X= 4.327	X= 7.505
			SD= .070	SD= 3.083	SD= 1.546
			SE= .035	SE= 1.542	SE= .773
10M					
	.4888	.5026	-.0138	.2619	10.9077
	.5884	.5518	.0367	-3.2090	12.3796
	.5599	.6648	-.1049	2.3473	9.2325
	.5631	.5042	.0589	-3.6811	11.8262
			X= -.006	X= -1.070	X= 11.087
			SD= .073	SD= 2.878	SD= 1.377
			SE= .036	SE= 1.439	SE= .689

SUNRISE INCUBATION

	LIGHT BOTTLE UPTAKE MCC/M3/HR	DARK BOTTLE UPTAKE MCC/M3/HR	C14 UPTAKE MCC/M3/HR	UCC/M3/HR PHOTO UPTAKE	UCC/M3/HR BACTERIAL UPTAKE
2M					
	1.2546	.5266	.7280	3.8042	6.3647
	1.3451	.5887	.7564	3.8484	2.5263
	1.4724	.5257	.9467	2.4941	2.5948
	1.1754	.5046	.6708	2.1903	5.0401
		X=	.775	X= 3.084	X= 4.131
		SD=	.120	SD= .866	SD= 1.893
		SE=	.060	SE= .433	SE= .947
6M					
	.5661	.5823	-.0162	.0690	4.6234
	.5986	.4269	.1717	.6853	4.6307
	.5333	.5089	.0243	2.1206	3.3317
	.5564	.5136	.0428	1.7266	4.2877
		X=	.056	X= 1.150	X= 4.218
		SD=	.081	SD= .941	SD= .612
		SE=	.041	SE= .471	SE= .306
10M					
	.4400	.4801	-.0401	1.7274	2.8601
	.5038	.4060	.0977	1.6741	3.6562
	.4270	.4306	-.0036	1.7713	3.3583
	.5001	.5030	-.0029	-.6092	6.9800
		X=	.013	X= 1.141	X= 4.214
		SD=	.059	SD= 1.167	SD= 1.873
		SE=	.030	SE= .584	SE= .937

MIDDAY INCUBATION

	LIGHTBOTTLE UPTAKE MCC/M3/HR	DARK BOTTLE UPTAKE MCC/M3/HR	C14 UPTAKE MCC/M3/HR	UCC/M3/HR PHOTO UPTAKE	UCC/M3/HR BACTERIAL UPTAKE
2M					
	2.2095	.4169	1.7926	1.3652	6.4060
	1.8313	.4251	1.4062	6.6236	2.8321
	1.8407	.4195	1.4212	4.2526	4.2020
	1.5105	.4033	1.1073	.1902	9.0228
		X=	1.432	X= 3.108	X= 5.616
		SD=	.281	SD= 2.899	SD= 2.707
		SE=	.140	SE= 1.450	SE= 1.353
6M					
	.6224	.3919	.2305	1.7801	6.6990
	.5530	.3868	.1662	-.1999	8.2027
	.7136	.4029	.3107	4.4756	5.3963
	.6813	.3915	.2897	-.6236	8.3207
		X=	.249	X= 1.358	X= 7.155
		SD=	.065	SD= 2.327	SD= 1.385
		SE=	.032	SE= 1.164	SE= .693
10M					
	.4033	.3774	.0260	-1.1089	11.2218
	.4004	.4005	-.0001	1.4520	8.4794
	.3923	.3801	.0121	4.3145	3.3141
	.4324	.3799	.0524	-1.9657	7.5939
		X=	.023	X= .673	X= 7.652
		SD=	.023	SD= 2.829	SD= 3.279
		SE=	.011	SE= 1.414	SE= 1.639

SUNSET INCUBATION

	LIGHT BOTTLE UPTAKE MCC/M3/HR	DARK BOTTLE UPTAKE MCC/M3/HR	C14 UPTAKE MCC/M3/HR	UCC/M3/HR PHOTO UPTAKE	UCC/M3/HR BACTERIAL UPTAKE
2M					
	1.2771	.4802	.7969	2.2376	4.7382
	1.1326	.4867	.6459	4.4672	5.5010
	1.1680	.5662	.6018	2.2258	5.0338
	1.1783	.4666	.7117	.4896	5.5742
		X=	.689	X= 2.355	X= 5.212
		SD=	.085	SD= 1.630	SD= .396
		SE=	.042	SE= .815	SE= .198
6M					
	.5267	.4314	.0952	-1.0367	4.7750
	.5332	.3712	.1620	-3.8386	8.3124
	.5503	.4357	.1146	2.2413	3.8792
	.4857	.4190	.0668	-.0278	3.3370
		X=	.110	X= -.665	X= 5.076
		SD=	.040	SD= 2.521	SD= 2.238
		SE=	.020	SE= 1.260	SE= 1.119
10M					
	.4778	.4606	.0172	-.2591	5.1532
	.4808	.4867	-.0059	-2.3250	6.2278
	.5029	.4750	.0280	-.2151	4.7269
	.4300	.4484	-.0184	-5.9017	9.9569
		X=	.005	X= -2.175	X= 6.516
		SD=	.021	SD= 2.672	SD= 2.379
		SE=	.011	SE= 1.336	SE= 1.190

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