Time Series Studies of Phytoplankton Ecology

By

© Dawn Heather Sephton, B. Sc.

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AUTHOR: Dawn Heather Sephton, B.Sc. (Mount Allison University)

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ABSTRACT

Daily measurements were taken during the summer of 1979 in Hamilton Harbour; a eutrophic, physically variable bay situated at the western end of Lake Ontario, to determine the impact of environmental fluctuations on the rates of primary production and growth, species succession and community diversity in the resident phytoplankton community. Nutrient loadings (P, N and C) were high and did not limit algal productivity and growth during the study period. Spatial and temporal heterogeneity was evident in the thermal structure, dissolved oxygen and nutrient distributions. Zm, the mixing depth and N^2, the water column stability were subject to physically induced, short term (<24 h) fluctuations and strong periodic motions in the range of days or weeks. The underwater light field was subject to random, short term oscillations. Zeu and ξPAR were stable over short temporal scales, following fluctuations in algal biomass. The phytoplankton were strongly self-shaded (average $\xi s = 0.0108$ in units m^2 mg chlorophyll a^{-1}) and self-shading increased as Cp; the chlorophyll package size decreased. Fluctuations in Zm were thus, the key environmental factor exerting stress on the phytoplankton, as the algae themselves controlled their own light climate.

Daily variability in the Zeu/Zm ratio, stongly influenced by fluctuations in Zm, and water column stability; N^2 (sec^{-2}) accounted for the low and variable rates of ΣP and max Pv. In situ

Pmax, Pe and Ik values were also low and variable and accounted for the low rates of $\sum P$ and max Pv. The phytoplankton responded to the temporal spectrum of environmental change via a hierarchy of response mechanisms, from physiological regulation to true adaptation. In vivo fluoresecence (IVF, F + DCMU, F ratios and R values) was variable and represented rapid regulation (<24 h) to short term fluctuations in the light field and water column stability. F ratios and R values were low under conditions of water column stability (high N^2 and Zeu/Zm) and high under conditions of vertical mixing (low N^2 and Zeu/Zm). The cellular generation time represented a fundamental period integrating cellular adaptation with environmental change. Pmax varied with depth and time and responded positively to increases in the value of the Zeu/Zm ratio with a 5.0 - 6.0 day lag period. Pe was positively correlated with Pmax, negatively correlated with Ik and high Pe values lagged low Zeu/Zm ratios by 6.0 - 7.0 days. Ik responded to fluctuations in $\sum Io$ over the previous two days and its extreme daily variability obscured its temperature dependence during the study.

The eight dominant algal species responded to water column stability: N^2, with lag periods of one or more generation times (2.0 - 8.0 days). Coelastrum spp., Oocystis borgeii, Scenedesmus sp. and Chlamydomonas sp. responded positively to increasing thermal stability, while Rhodomonas sp, Cryptomonas spp., Stephanodiscus spp. and Cyclotella sp. responded negatively. Species exhibiting the same lag period and the same response in terms of changes in numerical abundance to fluctuations in N^2, avoided competition by utilizing

different scaling strategies. The phytoplankton exploited the nature of environmental fluctuations as a resource permitting the coexistance of species and enhancing community diversity in a physically variable environment.

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ΣP	integral in situ productivity, mg C m^{-2} h^{-1}
max Pv	the maximum volumetric rate of productivity, mg C m^{-3} h^{-1}
Pmax	photosynthetic capacity or assimilation number, mg C mg chlorophyll a^{-1} h^{-1}
Pe	photosynthetic efficiency, mg C mg chlorophyll a^{-1} E^{-1} m^2
E	Einsteins m^{-2} sec^{-1}
Ik	photosynthetic saturation parameter; the light intensity marking the onset of light saturation of photosynthesis, μ E m^{-2} sec^{-1}
Zeu	euphtoic zone depth, m
Zm	mixing zone depth, m
Zeu/Zm	the euphotic zone/mixing zone depth ratio
N^2	water column stability estimate, 10^6 sec^{-2}
PAR	photosynthetically available radiation, 400 - 700 nm
Io	surface (0.1 m) irradiance, μ E m^{-2} sec^{-1}
ξ PAR	vertical extinction coefficient of PAR, ln units m^{-1}
ξ w	vertical extinction coefficient of water, ln units m^{-1}
ξ p	vertical extinction coefficient due to suspended particles, ln units m^{-1}
DOM	dissolved organic matter
ξ DOM	vertical extinction coefficient of DOM, ln units m^{-1}
B, Bmax	chlorophyll a biomass, mg chlorophyll a m^{-3}
ξ min	minimum vertical extinction coefficient of PAR, ln units m^{-1}

P:R	photosynthesis to respiration ratio
Pm	the maximum, light saturated rate of photosynthesis, mg C m^{-3} h^{-1}
Q	proposed electron acceptor of Photosystem II, responsible for fluorescence quenching
DCMU	3-3(3,4-dichlorophenyl)-1,1-dimethyl urea
Σ Io	integral surface irradiance, 1000 - 1400 h EDT, u E m^{-2} sec^{-1}
	average wind speed, m sec^{-1}
TP	total phosphorus, ug l^{-1}
SRP	soluble reactive phosphorus, ug l^{-1}
NO_2-N	nitrite nitrogen, mg l^{-1}
NO_3-N	nitrate nitrogen, mg l^{-1}
NH_4^+	ammonia, mg l^{-1}
Si	soluble silica, mg l^{-1}
ΣCO_2	total carbon (free CO_2 + HCO_3^- + CO_3^{-2}), mg CO_2 l^{-1} concentration
free CO_2	free carbon dioxide , mg CO_2 l^{-1} concentration
HCO_3^{-1}	bicarbonate ion, mg CO_2 l^{-1} concentration
CO_3^{-2}	carbonate ion, mg CO_2 l^{-1} concentration
Tem 1	6 m temperature data, 984 points, 1.0 h intervals
Tem 2	6 m temperature data, 537 points, 0.2 h intervals
Tem 3	6 m temperature data, 219 points, 6.0 h intervals
F	fluorescence ratio; F + DCMU/IVF
R	fluorescence (F + DCMU) and (IVF) per unit chlorophyll a
IVF	in vivo fluorescence
F + DCMU	DCMU induced fluorescence
Δ F	change in the F ratio, maximal to surface depth values

ΣB	integral chlorophyll a biomass in the euphotic zone, mg chlorophyll a m^{-2}
chl a	chlorophyll a
Cp	the chlorophyll a package size, 10^7 cells mg chlorophyll a^{-1}

I. INTRODUCTION

Natural phytoplankton populations exist in intermittantly mixed environments and experience spatial and temporal fluctuations in chemical and physical factors (Harris, 1980a). Primary productivity and ultimately growth and seasonal species succession in natural communities, is controlled by the interaction of nutrient availability and physical factors such as light and temperature, as well as by the endogenous metabolic and physiological properties of the cells (Harris, 1978; Steele, 1962; Talling, 1961). Research in two hypereutrophic lakes: Kinnego Bay (Jones, 1977a,b,c) and Crose Mere (Reynolds, 1976), where nutrients are rarely limiting, indicated that separating the effects of nutrients and physical factors is difficult. Probably, few bodies of water exist where algal growth and productivity is totally independent of nutrient availability (Jones, 1977c). Given continuous and high nutrient loadings to a lake however, the effects of fluctuating light, temperature and mixing processes might be important in determining productivity, growth and succession of the resident phytoplankton community. Such a situation appears to exist in Hamilton Harbour, Lake Ontario, the subject of this study (Harris and Piccinin, 1977,1980; Harris et. al., 1980a,b; Haffner et. al., 1980).

Previous work in Hamilton Harbour indicated that the rates of photosynthesis, integrated over the depth of the euphotic zone where measurable rates of photosynthesis were occurring; ΣP,

were lower than anticipated based on the high and continuous nutrient loadings (Harris et. al., 1980b). The observed algal biomass was lower than expected from the models of Dillon (1974) and Vollenweider (1968). Variability in ΣP was a function of the maximum volumetric rates of photosynthesis (max Pv, mg C $\cdot$ $m^{-3}h^{-1}$) and the photosynthetic capacity of the algae (Pmax, mg C $\cdot$ mg chlorophyll $a^{-1}h^{-1}$) (Harris et. al., 1980b). Pmax was generally low and varied from week to week, as did photosynthetic efficiency (Pe, mg C $\cdot$ mg chlorophyll a^{-1} $E^{-1}m^{2}$). Ik, the saturation parameter of photosynthesis (μE $m^{-2}sec^{-1}$) also varied from week to week and was correlated with the thermal stability in the top five meters of the water column (Harris et. al., 1980b) and the ambient light intensity received over the previous forty-eight hours (Harris, 1978). Changes in Pmax and Pe were associated with changes in the Zeu/Zm (euphotic zone/mixing zone depth) ratio in the previous week, thus linking physiological change in the phytoplankton population with fluctuations in the physical environment (Harris et. al., 1980b). The phytoplankton community in the harbour generally exhibited low values of photosynthetic capacity and reduced growth rates, ensuring that the total algal biomass did not reach predicted levels, based on nutrient loadings (Harris et. al., 1980a,b). Nutrient loadings, however, were never low enough to inhibit algal growth and productivity (Harris, 1976). The physical variability observed in the harbour also resulted in shifts in species composition, largely in response to changes in the value of the Zeu/Zm ratio (Haffner et. al.,1980; Harris and Piccinin, 1980). In Hamilton Harbour then, primary

productivity, growth rates and changes in seasonal species composition appear to be related to fluctuations in a number of physical variables, which are expressed in changes in the Zeu/Zm ratio.

Ecosystems generally respond to random or periodic perturbations by exhibiting temporal and spatial oscillations (Platt and Denman, 1975). In turbulent environments, mixing ensures that temporal and spatial (length) scales of hydrodynamic, chemical and biological change are linked (Boyce, 1974; Ford and Thornton, 1979). Spectral analysis techniques have proven useful in the determination of scales of organization (periodicities) in fluctuating environments, as well as in dealing with the spatial and temporal relationships between physical and biological structure in water bodies (Ford and Thornton, 1979; Platt and Denman, 1975). Spectral analysis has been used to determine the spatial structure of phytoplankton populations (Denman, 1977; Denman and Platt, 1976; Fasham and Pugh, 1976; Platt, 1972, 1978), the temporal structures of environmental parameters such as cycles of temperature (Ford, 1976; Smith and Bella, 1973), horizontal wind flux (Vander Hoven, 1957; Van Meighan, 1973) and the spatial and temporal relationships between phytoplankton populations and their physical environments (Denman, 1976; Denman and Platt, 1974; Estrada and Wagenburg, 1977; Zlobin, 1973 (cited in Platt and Denman, 1975)).

Phytoplankton communities are exposed to many environmental fluctuations with a variety of spatial and temporal scales of variability (Fig. 1) to which they must adaptively respond to survive (reviewed in Harris, 1978). Understanding how environmental

variability affects algal populations requires quantification of these environmental fluctuations in terms of their means, amplitudes, phases, periods and durations (Grenney et. al., 1973; Harris, 1980a), as well as the scale of phytoplankton response to those fluctuations (Allen, 1977). Scale is a form of information flow that compartmentalizes the environmental experience of the cell (Allen, 1977) so that the cell optimizes the quality of its environment. By operating on a particular time scale, algae may exploit a specific niche created by environmental fluctuations and their interaction. By adapting to different time scales algae help compartmentalize the habitat so as to reduce competition (Allen, 1977; Grenney et. al., 1973; Levins, 1979). Thus, different species sense different environmental features so that temporal and spatial fluctuations become a resource to be exploited (Harris, 1980a; Levins, 1979). Slobodkin and Rapoport (1974) suggested that well adapted populations in fluctuating environments responded to environmental changes on many, interlinking levels. Any environmental change causes the algae to respond on the level appropriate to the environmental perturbation (Fig. 1), from individual cellular changes to population and community changes (c.f. Fig. 1 in Slobodkin and Rapoport, 1974).

Keeping in mind then, that algae respond to changes in their environments over various temporal scales, utilizing a hierarchy of response mechanisms, several important parameters and processes will be dealt with in detail. First, temporal and spatial changes in the physical environment will be outlined in terms of mixing processes and variability in light. Second, specific responses to

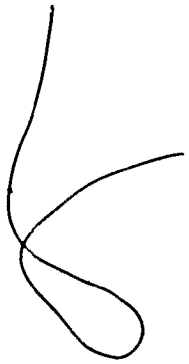
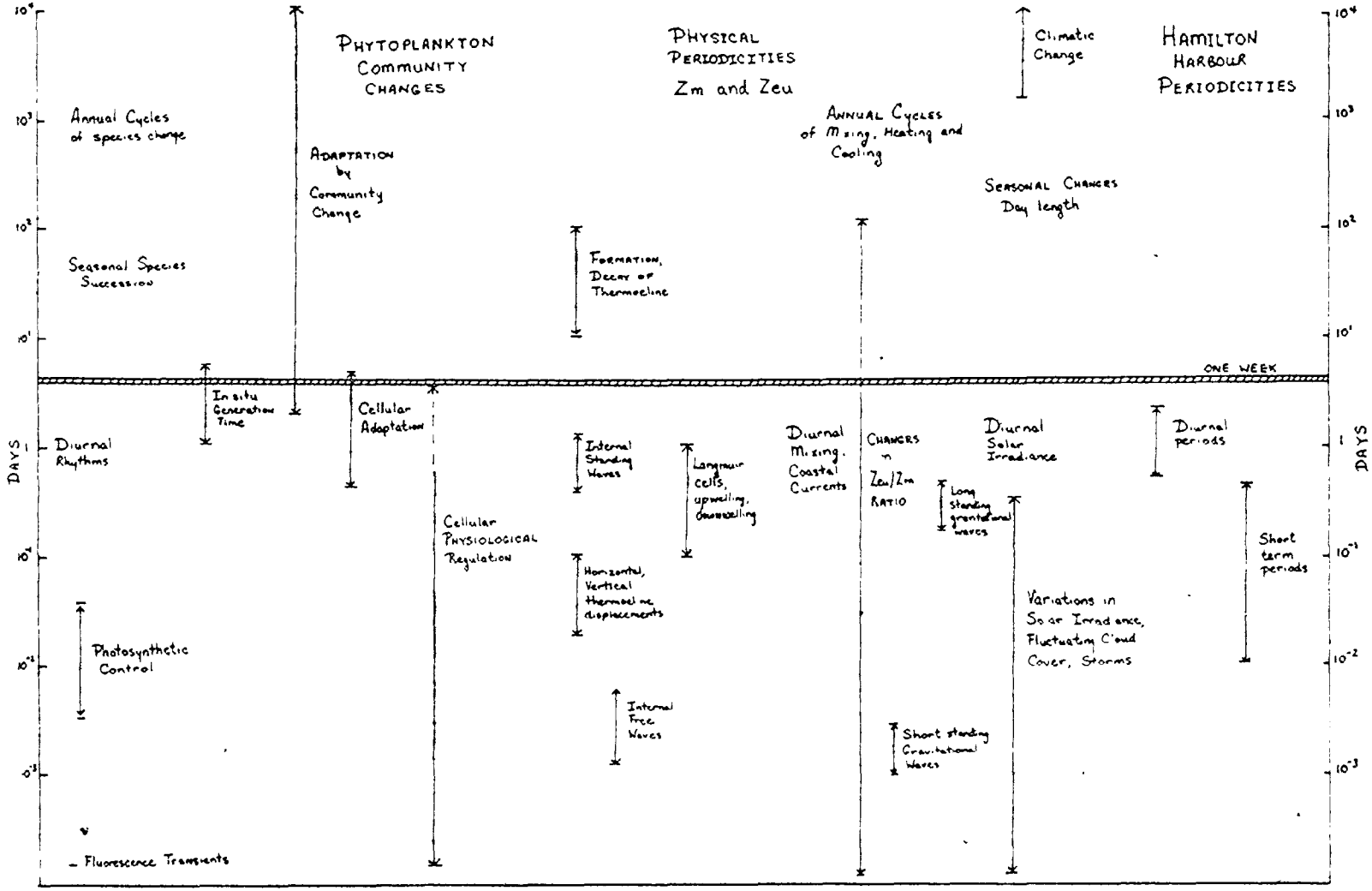


Fig. 1. Temporal scales of variation in the physical environment of large lakes, and the time scales of phytoplankton response. The figure summarizes the temporal scales of phytoplankton response (from Harris et. al., 1980b), the physical periods in mixing (Boyce, 1974), fluctuations in the light climate (Dera and Gordon, 1968; Talling, 1971) and the Hamilton Harbour periods (Palmer and Poulton, 1976). The dashed line represents a weekly sampling interval.


PHYTOPLANKTON COMMUNITY CHANGES
PHYSICAL PERIODICITIES
Zm and Zeu
HAMILTON HARBOUR PERIODICITIES
Climatic Change
Annual Cycles of species change
Adaptation by Community Change
Annual Cycles of Mixing, Heating and Cooling
Seasonal Changes Day length
Seasonal Species Succession
Formation, Decay of Thermocline
ONE WEEK
In situ Generation Time
Cellular Adaptation
Diurnal Rhythms
Internal Standing Waves
Langmuir cells, upwelling, downwelling
Diurnal Mixing, Coastal Currents
Changes in Zeu/Zm Ratio
Diurnal Solar Irradiance
Diurnal periods
Long standing gravitational waves
Short term periods
Cellular Physiological Regulation
Horizontal, Vertical thermocline displacements
Variations in Solar Irradiance, Fluctuating Cloud Cover, Storms
Photosynthetic Control
Internal Free Waves
Short standing Gravitational Waves
Fluorescence Transients
DAYS
DAYS

environmental fluctuations will be discussed in terms of growth and community changes, population changes and pure physiological changes, encompassing the scale of low to high frequency change. Finally, physiological adaptation and community change will be studied in terms of the effects of light and temperature on primary productivity and growth.

Diurnal, seasonal and annual cycles of atmospheric heating and cooling produce corresponding thermal cycles in water bodies (Hutchinson, 1957; Mortimer, 1974). The interaction of opposing physical processes creates spatially and temporally heterogeneous or "patchy" temperature structures. Daily and seasonal patterns of wind flux are the principle source of mechanical energy, generating hydrological turbulence or mechanical mixing along the horizontal and vertical planes. The net flux of heat across the air-water interface, resulting from changes in radiation, heat exchange within the water layers and evaporative cooling processes causes variation in density and buoyancy, thus altering the physical stability in the water column (Ford and Thornton, 1979). The two processes interact both spatially and temporally to produce the broad range of thermal structures and mixing dynamics observed in lakes and oceans. The physical nature of these processes, as well as their spatial and temporal resolution has been extensively documented by several authors (Boyce, 1974; Hutchinson, 1957; Mortimer, 1974; Wetzel, 1975).

Stability in the water column may be expresses in terms of the gradient of density with depth; dp/dz (Mortimer, 1974).

N^2, the numerical estimate of water column stability over a given depth, may be calculated from the square of the Brunt-Väsälä frequency; $N = \sqrt{-\frac{g}{p} \cdot \frac{dp}{dz}}$, where g is the acceleration due to gravity, p, the density of pure water at 4^0C, and dp/dz, the gradient of temperature induced density change over a specified depth interval (Boyce, 1974). The Brunt-Väsälä frequency represents the high frequency limit of all internal waves and may also represent one of the free modes of oscillation of the thermocline in any water body (Boyce, 1974; Mortimer, 1974). High N^2 (sec^{-2}) numbers indicate the presence of thermally induced layering in the epilimnion, which tends to counteract the effects of wind-induced circulation.

Large lakes and closed basins of water act as viscously damped mechanical oscillators (Boyce, 1974). Each basin may be characterized by a spectrum of free modes of surface and internal oscillations, which depend upon its physical dimensions, morphometry and internal density distribution, as well as wind effects (Boyce, 1974; Wetzel, 1975). The full complement of periodic and random oscillatory motions have been reviewed in detail (Boyce, 1974; Hutchinson, 1957; Mortimer, 1974). Several important temporal scales in terms of algal reponse to changes in epilimnial mixing will be discussed at this point (Fig. 1).

Free standing gravitational waves produce small scale, high frequency oscillatory motion, while physically induced, stress type motions produce long scale, low frequency motions. Wind driven surface gravitational waves are relatively short (cm - m), with periods of seconds to minutes. Short, internal freely propagating

waves, caused by internal vertical shifts about the thermocline, have periods of up to 5 minutes. Surface seiche effects produce horizontal and vertical motions with periods of 2 - 10 hours, while internal seiche effects have periods of up to 16 hours. Whole basin horizontal circulations and coastal currents have near circadian periods. Vertical mixing processes such as Langmuir type circulations, upwelling and downwelling currents vary significantly over periods of 1 - 24 hours. In stratified lakes, vertical (frictional shear type) and horizontal (surface wave type) displacements in the thermocline region operate over temporal scales from minutes to hours. The formation and decay of the thermocline itself takes place over longer temporal scales (up to one month) and incorporates changes in wind stress and internal density gradients. Finally, long term climatic changes may induce annual scales of physical mixing and thermal change, which can affect the biology of the system (Cushing and Dickson, 1976). The sum of the observed physical periodicities in the water column at any point in time tend to damp each other temporally, and in turn are damped by previous periods of mixing events (Boyce, 1974; Mortimer, 1974). Complex interaction among the various physical mixing processes occurs over horizontal and vertical spatial scales, further complicated by the broad spectrum of temporal scales involved (Fig. 1). Phytoplankton communities must actively exploit the full spectrum of temporal and spatial fluctuations if they are to survive in a physically variable environment (Harris, 1978).

The light received by an algal cell in the water column

is determined by three principle components; the time course and fluctuations (Dera and Gordon, 1968) of surface irradiance, the penetration of light with depth (Kirk, 1974, 1976, 1977; Talling, 1971) and the proportion of illuminated and dark water in the mixing zone (Sverdrup, 1953; Talling, 1971). The time course of surface irradiance may be described in terms of the fraction of radiation received that is photosynthetically available (P.A.R., 400-700 nm), the duration or daylength and the variable irradiance received during the day (Dera and Gordon, 1968; Hutchinson, 1957; Talling, 1971). About 50 % of the total irradiance received by an algal cell is photosynthetically available (Talling, 1971). Daylength varies seasonally and is longer in the spring and summer when primary production in surface waters is maximal (Hutchinson, 1957) (Fig. 1). The variable irradiance during the day reflects not only diurnal periods in the light field (Fig. 1), but also short term fluctuations in cloud cover. Dera and Gordon (1968) emphasize the effects of high frequency waves, which act like converging lenses, refracting and reflecting light at the surface and thus altering underwater irradiance. The spectral distribution of light and its angular distribution with respect to the water surface are also important in determining surface irradiance (Kirk, 1977).

The lower limit of light penetration in the water column; the euphotic zone depth; Zeu, is defined as the depth at which P.A.R. is reduced to 1 % of its surface value, Io ($\mu E\ m^{-2} sec^{-1}$) (Bindloss, 1976; Ganf, 1974; Talling, 1971). The attenuation or diminution of light with depth is largely caused by scattering and absorption

(Kirk, 1976, 1977). The irradiance, Iz, at depth z (in meters) in the water column is a function of Io and the log e base of the negative extinction coefficient, η, a constant value for specific wavelengths of P.A.R. and ultraviolet light, where: $Iz = Io\ e^{-\eta z}$ and $\ln Iz = \ln Io - \eta z$ (Hutchinson, 1957). The bulk extinction coefficient; εPAR (in units m^{-1}), between 400 and 700 nm, is derived from the absorption of light by the water itself; εw, the absorption of the particles (algae and suspended matter); εp, and the absorption due to dissolved colour, dissolved organic matter (DOM) or Gelbstoff; εDOM (Hutchinson, 1957; Kirk, 1976,1977). In waters highly coloured by DOM, εDOM is the key factor attenuating light (Kirk, 1976, 1977). The average value of εDOM in a body of water may be obtained by plotting εPAR against the chlorophyll a biomass (B, mg chlorophyll a m^{-3}) and extrapolating to zero biomass or by means of a deep tank experiment using a spectroradiometer (Harris, 1980b; Talling, 1960, 1970).

The minimum vertical extinction coefficient of light, εmin, occurs in the 530-575 nm spectral band, which is also the region of minimum absorption by photosynthetic pigments (Talling, 1971). εmin is related to εPAR by an empirical factor; a, where: $\varepsilon PAR = a\,\varepsilon min$. Talling (1971) quotes a general value for a of 1.33, however the estimate varies in different water bodies. εmin is important in the determination of Zeu, where: $Zeu = b/\varepsilon min$, and b = 3.7 (Talling, 1965, 1971; Talling et.al., 1973). Values of b are also variable in different water bodies. εmin is also important in determining εs, the self-shading parameter of the algal population (Harris, 1980b;

Harris et. al., 1980b; Talling, 1970). Self-shading is the degree to which algal cells compete with DOM by capturing light, complete self-shading occurring when all of the light available is absorbed by the algae (Talling, 1960). ξs (ln units mg chlorophyll $a^{-1} m^{-2}$) may be obtained for an algal population by plotting ξ min, corrected for the contribution of DOM at that particular wavelength, against the algal biomass, B (mg chlorophyll a m^{-3}). The ξs value of a population is influenced by the cell size and geometry, the composition and structure of the pigment packages and the number of cells in the population (Harris, 1978; Jewson, 1977; Kirk, 1974, 1975a,b; Lorenzen, 1972). Talling (1960) quotes an average ξs value of 0.020 ln units mg chlorophyll $a^{-1} m^{-2}$, and suggests that due to its magnitude, algae rarely are completely self-shaded. The theoretical maximum biomass of algae in the water column; Bmax (mg chlorophyll a m^{-3}) is equal to $3.7/\xi s$ and allows direct comparison with the actual biomass estimates (Bindloss, 1976; Harris, 1980b; Harris et. al., 1980b; Jewson, 1977; Jones, 1977b). Such comparisons indicate the degree of self-shading in the population, in other words, how the existing population limits its own growth and rates of primary production.

The proportion of illuminated and dark water in which an algal cell is circulated is dependent on the depth of circulation or the mixing depth, Zm of the water column, as well as by the euphotic zone depth (Bindloss, 1976; Harris, 1978; Talling, 1971). Zm is influenced by changes in the thermal structure and wind speed, as well as by fluctuations of solar radiation (Hutchinson, 1957; Mortimer, 1974). Due to rapid fluctuations in wind speed and thermally induced

mixing events (Fig. 1), Zm often fluctuates rapidly and also has larger diurnal and seasonal changes (Mortimer, 1974; Sverdrup, 1953). Summer stratification in lakes is a substantial barrier to increases in Zm (Bella, 1970), while large values of Zm are observed during periods of isothermal mixing (Talling, 1971; Tilzer and Schwartz, 1973). Zeu is influenced by solar irradiance fluctuations (daily and seasonal) and its penetration of the water column (Talling, 1971) (Fig. 1). In eutrophic waters, self-shading by algae is the most frequent cause of reduction of Zeu (Bindloss, 1976; Jewson, 1977). The magnitude of the reduction in Zeu may be species dependent in the case of mono-specific blooms (Berman, 1976; Jewson and Taylor, 1978) and changes in algal biomass are reflected in changing euphotic zone depths (Bindloss, 1976).

The Zeu/Zm ratio incorporates changes in light and the depth of circulation. Zeu does not fluctuate as rapidly as Zm changes (Fig. 1). Thus, the mixing depth determines the time course of circulation through light and dark gradients and the physiological response of the phytoplankton, through changes in the relative rates of photosynthesis and respiration (Harris, 1978; Sverdrup, 1953). Increasing Zm dilutes the algal population over larger volumes of water, increasing respiration losses (Bindloss, 1976; Jewson, 1978; Talling, 1971). Circulating cells are subject to rapid changes in both the proportions of euphotic and sub-euphotic zone water and in underwater light gradients (Jewson and Wood, 1975; Talling, 1971). Gradients in dark respiration occur with depth (Ganf, 1974; Gibson, 1975; Harris et. al., 1980b; Jones, 1977c) and the effect on gross

photosynthesis can be substantial (Jewson and Taylor, 1978). The effects of increasing Zm become important in terms of critical depth (Sverdrup, 1953) or column compensation point (Talling, 1957a, 1965, 1971) models, where an effective depth for photosynthetic activity is defined in terms of the water depth where respiration losses balance gains in gross photosynthesis so that autotrophic growth is prevented.

The P:R ratio of an algal population at any one point in time determines the survival of that population and is a direct consequence of the environment (Harris, 1978; Vollenweider, 1970). The most commonly encountered values of the P:R ratio lie in the range of 10 (Yentsch, 1962) although other researchers quote widely differing values (Humphrey, 1975; Jewson, 1976; Talling, 1957a). Seasonal trends in P:R ratios (Harris, 1973a; Harris and Piccinin, 1977; Jewson, 1976) occur and there is a definite relationship between respiration rates, P:R ratios and the Zeu/Zm ratio (reviewed in Harris, 1978). The observed changes in the P:R ratio with season may be related to the seasonal changes in the Zeu/Zm ratio. Ignoring the seasonal effects, it is probable that the value of the Zeu/Zm ratio may exert a selection pressure on species growing in the mixed layer (Harris, 1978; Harris et. al., 1980b).

In evolutionary and ecological terms, it is reasonable to assume that phytoplankton communities are adapted to or may actually exploit the spectrum of physical periodicities in the mixed layer (Fig. 1) (Harris, 1980a; Harris et. al., 1980b; Haffner et. al., 1980). Both short and long term physical periodicities (seconds-years)

ensure that phytoplankton communities are rarely at equilibrium with the environment because a temporal lag exists between environmental change and the response of the algae at the individual and community levels (Allen, 1977; Allen et. al., 1977; Grenney et. al., 1973; Harris, 1980a). Natural phytoplankton populations are composed of a number of different species with different genotypes (Slobodkin and Rapoport, 1974), with varying sizes, growth and division rates (Banse, 1976; Eppley, 1972; Eppley and Sloan, 1966; Parsons and Takahashi, 1973), which adapt to environmental changes over varying temporal scales linked to their generation times (Harris, 1978,1980a; Marra, 1978). Algae respond to high and low frequency environmental fluctuations over varying temporal scales by utilizing a variety of adaptive strategies (Fig. 1). Each cell responds to the spectrum of environmental change depending on its physiological state (Harris, 1978), its age (Morris and Glover, 1974) and the set of environmental conditions to which it has been exposed (reviewed in Harris, 1978; Harris, 1980a).

Community changes are often correlated with seasonal and annual environmental changes (Jones, 1977a; Pechlaner, 1971; Reynolds, 1976; Round, 1971). Seasonal shifts in species abundance are related primarily to changes in thermal stratification; the reduction in circulation and its influence on average water temperature, underwater light and the reduction of the nutrient rich water where the cells occur (Reynolds, 1976). Under extreme physical change, species which fail to track their environments physiologically may be eliminated from the community (Haffner et. al., 1980; Harris, 1978).

Cellular physiological responses to environmental change such as the alteration of pigment concentrations and enzyme activity are accomplished within the generation time of the algae (Beardall and Morris, 1976; Heron and Mauzerall, 1972). Algal cells may also exercise feedback control and utilize different metabolic pathways in response to environmental stress (Morris et. al., 1974). Harris (1978,1980a) states that the cellular generation time represents a fundamental integration period of algal response to changing environmental conditions. Some species of algae (Cryptomonas spp.) utilize heterotrophic processes of carbon uptake under conditions of increased physical mixing (Haffner et. al., 1980). Buoyancy regulation, prevalent in blue-green algae (Fogg and Walsby, 1971; Lund, 1959; Reynolds, 1975), active vertical migration such as that exhibited by Ceratatium hirundinella (Harris et. al., 1979; Heaney, 1976) and the alteration in life cycle such as flagellation and spore formation in Chlamydomonas spp. (Haffner et. al., 1980) enable algae to occupy niches particularly favorable to them. Structural diversification within a population; alteration of cellular shape and volume, cellular pigments, and chromatophore structures, result in a population of cells in which a few cells are always adapted to current physical conditions (Haffner et. al., 1980).

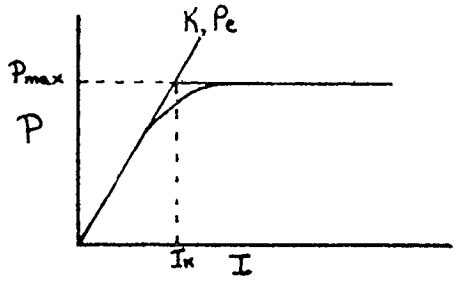
In a highly variable environment, only a fraction of the total species in the community is optimally adapted at any one time (Richerson et. al., 1970; Slobodkin and Rapoport) and those species exhibit maximum growth rates (Richerson et. al., 1970). The growth rate of an algal cell is defined as the rate of increase of cell

substance per unit cell size (Eppley, 1972). Growth rate is species dependent (Eppley and Sloan, 1966; Goldman, 1977a,b) and is subject to environmental factors. Phytoplankton growth is a function of ambient light intensity, temperature and the quality and quantity of nutrients (Goldman et. al., 1979; Reynolds, 1976). Photosynthesis, respiration and growth rates, expressed on a carbon or chlorophyll a basis, increase as cell size decreases (Banse, 1976; Eppley, 1972; Malone, 1971). Cells of varying sizes may exhibit different uptake constants for photosynthesis, light and nutrients, which may alter their growth rates (Parsons and Takahashi, 1973). Cells respond to changes in underwater light by altering growth rates (Hitchcock, 1979) proportional to the intensity and duration of the light period and by varying cellular chlorophyll and pigment contents (Eppley and Sloan, 1966; Goldman, 1977). At high irradiance, the maximum growth rate is dependent on average daytime temperature (Tamiya et. al., 1955). Some marine diatoms exhibit rapid differentiation in division rates following changes in light intensity as temperature increased (Hitchcock, 1979). Eppley (1972) states that temperature sets an upper limit for growth that is seldom realized under natural conditions. Physiological adaptive responses of the cells to fluctuating light and temperature tend to even out environmental fluctuations in such a way that a steady state growth rate is achieved (Harris, 1978).

The generation time of algal cells may represent a fundamental integration period for true cellular adaptation in response to environmental variability (Harris, 1980a). Estimates of generation times or doubling times in the field range in the order of 1 - 7 days

(Eppley, 1972; Goldman, 1977a,b; Goldman and Carpenter, 1974; Haffner et. al., 1980). Cells with different generation times will respond to different features of the temporal spectrum of environmental variability (Harris, 1980a). The link between physiological adaptation and environmental variability is complicated by time lags (Allen, 1977; Allen et. al., 1977) and the fact that different species respond over different temporal scales related to their generation times (Harris, 1980a).

Photosynthesis may be described in terms of a photosynthesis verses light intensity curve (P vs. I) (Fig. 1, Talling, 1957b). P vs. I curves are based upon an empirical mathematical relation first proposed



by Smith (1936): $KI = P(Pm^2 - P^2)^{-\frac{1}{2}}$, where K is a constant representing the initial, light limited linear rate of photosynthesis, P represents the generalized rate of photosynthesis and Pm is the light saturated rate of photosynthesis. Talling (1957a,b) modified Smith's equation to: $KI = p\,(1-p^2)^{-\frac{1}{2}}$, where $p = P/Pm$, and defined a number of photosynthetic parameters from the P vs. I curve. Pm or Pmax, is defined as the maximum, light saturated rate of photosynthesis (mg C incorporated or O_2 evolved per unit volume and time) observed over periods from 0.5 to 4.0 hours (Vollenweider, 1965). Pmax is temperature dependent, increasing with temperature from 5 to 20°C (Talling, 1957a,b) and is probably the effective rate determining step in the photosynthetic

pathway (Heron and Mauzerall, 1972). When Pmax is expressed as a rate of carbon incorporation per unit chlorophyll a, it provides a measure of photosynthetic capacity and has been used as a measure of algal photosynthetic potential (Berman and Eppley, 1974; Jewson, 1976; Jones, 1977b; Platt and Jassby, 1976). Extrapolation from the point of intersection of K and Pmax on the P vs. I curve , gives the value Ik, the light intensity which expresses the onset of light saturation of the photosynthetic apparatus (Talling, 1957a). When K remains constant, Ik shows temperature dependence, since it is defined in terms of Pmax (Jones, 1978; Talling, 1957a). K or Pe, the gradient of the linear, light limited region of the curve is independent of temperature (Jewson, 1976; Talling, 1957a) and is a function of the number of "quantum traps" within the photosynthetic apparatus of the cells, as well as their cross sectional area exposed to incident light, the number of photosynthetic units, the pigment complement of the cells and their total chlorophyll a content (Heron and Mauzerall, 1972). K or Pe is thus a measure of photosynthetic efficiency and is often expressed in terms of photosynthetic capacity and Ik (Heron and Mauzerall, 1972; Talling, 1957a).

Considerable emphasis has been placed on the physiological response and adaptation to low, high and fluctuating irradiance fields by algal cells (Jones, 1978; Jorgensen, 1964, 1968, 1970; Ryther, 1959; Sheridan, 1972a,b; Steemann-Nielsen and Jorgensen, 1962, 1968a,b; Yentsch and Lee, 1966). Phytoplankton cells growing at low light intensities have high pigment concentrations; chlorophyll a and accessory pigments (Heron and Mauzerall, 1972; Jorgensen, 1964), larger and more numerous photosynthetic units (Sheridan, 1972a,b) and

higher Pe values over low light ranges (Harris et. al., 1980b; Ryther and Menzel, 1959). At low light intensities, the photosynthetic rate of low light adapted cells is higher that that exhibited by high light adapted cells (Jones, 1978). Physiological regulation by algal cells in low irradiance results in enhanced abilities to utilize low irradiances and a low light saturation value for photosynthesis (Beardall and Morris, 1976; Heron and Mauzerall, 1972; Yentsch and Lee, 1966). Cells growing in dim light (shade cells) are subject to extensive and rapid photoinhibition; the light saturation of the photosynthetic apparatus followed by photochemical oxidation and the subsequent decline of the rate of photosynthesis with time, when exposed to high light (Ryther and Menzel, 1959), due to their low Ik and Pmax values (Jones, 1978; Talling, 1966; Yentsch and Lee, 1966). Cells grown in high light (sun cells) have lower pigment contents and numbers of photosynthetic units (Heron and Mauzerall, 1972; Sheridan, 1972a,b), lowered photosynthetic efficiencies (Harris et. al., 1980b) and high Pmax and Ik values (Yentsch and Lee, 1966).

True adaptation in terms of alteration of cellular pigment concentrations is accomplished within the generation time of the cell (Harris, 1978, 1980a). Adaptation to a new light intensity by Chlorella spp. occurs in 40-50 hours, the time required for change in chloroplast structure and the formation of new photosynthetic units (Sheridan, 1972a,b; Steemann-Nielsen et. al., 1962). In Hamilton Harbour, cells in the mixed layer respond to ambient light intensities with a 48 hour lag (Harris, 1978). Platt and Jassby (1976) correlated changes in Pe with mean solar radiation over the previous 3 days for

marine algae, while Jones (1978) correlated changes in Ik values in a population of blue-green algae with changes in light intensity over the previous five days. In Hamilton Harbour, Ik varies from week to week, as does Pe (Harris et. al., 1980b).

Physiological regulation of photosynthesis and respiration in response to unfavorable environmental conditions is accomplished over periods considerably shorter than cellular generation times (Fig. 1) (Harris et. al., 1980b). Phytoplankton moving through light gradients in a mixing water column experience rising and falling light and temperature regimes (Harris and Lott, 1973a; Jewson and Wood, 1975), operating over long and short periodicities which depend on wind speed and Zm. Increasing light enhances photosynthesis to the point of light saturation (Harris and Lott, 1973a). Cells moving through light gradients utilize brief periods of surface light exposure optimally and offset to a certain degree, respiration losses incurred during brief periods in dark water (Jewson and Wood, 1975; Marra, 1978). Circulating cells often maintain photosynthetic rates close to Pmax (Jewson and Wood, 1975). In mixing water columns residence times at any given depth are not long enough to produce depth induced light adaptation (Tilzer and Schwartz, 1976) and surface populations may not show photoinhibition (Harris and Piccinin, 1977). Langmuir type circulations are capable of moving cells vertically in the time required to prevent photoinhibition (less than 20 minutes of surface exposure, Harris and Lott, 1973b) which occurs in surface bottles in in situ incubations at surface light intensities above Ik (Harris and Piccinin, 1977).

Photoinhibition is a diurnal phenomenon in thermally stratified waters and is a function of surface irradiance and penetration of P.A.R. (Vollenweider and Nauwerck, 1961).

Ik values may be good indicators of the light adapted conditions of the algal population examined (Jones, 1978; Yentsch and Lee, 1966) and correspond to threshold values for changes in accessory pigment contents as well as for the onset of photoinhibition of in vivo fluorescence (Harris, 1978). Kiefer (1973a,b) noted marked similarities between the photoinhibition of fluorescence and photosynthesis at a constant irradiance (200 $\mu E\ m^{-2}sec^{-1}$). Diurnal changes in the photoinhibition of photosynthesis and in vivo fluorescence reflect each other and the induction process is also similar (Harris and Piccinin, 1977).

In vivo fluorescence may be defined as that portion of quantum energy absorbed by chlorophyll a and accessory pigments that is emitted at 685 nm from Photosystem II of the photosynthetic apparatus. Fluorescence emission occurs rapidly (Fig. 1) at the level of Q, the primary electron acceptor of PS II and in vivo fluorescence emission is quenched once electron transport through Q and on to PS I occurs. Metabolic inhibitors of electron transport at the level of Q, such as 3-3(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU) increase fluorescence emission and consequently inhibit photosynthesis (Samuelsson et. al., 1978). In vivo fluorescence yield or the cellular fluorescence per unit of extractable chlorophyll a in natural populations is extremely variable (Harris, 1978). Changes in the nutrient status of the algal cells,

interspecific differences, chlorophyll concentrations and surface irradiances in excess of 100 $\mu E\ m^{-2}sec^{-1}$ alter in vivo fluorescence yield (Harris, 1980b; Heaney, 1978; Kiefer, 1973a,b; Loftus and Seliger, 1975). At high surface light intensities and in aphotic zones, in vivo fluorescence is inhibited, resulting in depth dependent in vivo fluorescence profiles and diel changes (Harris, 1980b; Kiefer, 1973a,b).

Changes in fluorescence yield induced by light and nutrient stress are important indicators of the physiological state of the phytoplankton (Harris, 1980b; Kiefer, 1973b; Loftus and Seliger, 1975). DCMU induced fluorescence is thought to be directly related to photosynthetic capacity in cultured populations (Samuelsson and Ooquist, 1977; Samuelsson et. al., 1978). Slovacek and Hannon (1977) observed that DCMU induced fluorescence was a constant function of cellular chlorophyll a in pure cultures. These relationships have not, as yet, been observed for field population (Harris, 1980b). Fluorescence yield by natural populations in Hamilton Harbour, shows rapid change and regulation in response to fluctuations in mixing depth, light, the Zeu/Zm ratio and the overall stability of surface waters. No clear relationship was observed between fluorescence properties and photosynthetic capacity, possibly due to the fact that the temporal response scales are different for the two processes (Fig. 1) (Harris, 1980b). At the cellular level, changes in photosynthetic capacity or efficiency may lag behind changes in physical parameters at scales from days to weeks (Harris, 1980b). Changes in in vivo fluorescence however, provide a useful means of

assessing rapid, high frequency regulation and response by algal cells to short term fluctuation in the environment (Harris, 1980b).

The effect of fluctuating temperature on the physiological adaptation of phytoplankton is important in terms of the maximum light-saturated rate of photosynthesis, respiration rates and growth, processes that involve a certain amount of enzymatic regulation (Harris, 1978). Cellular chlorophyll and protein contents increase with growth at low temperatures (Jorgensen, 1968; Morris and Glover, 1974). Low temperature growth may not actually enhance photosynthesis at lower temperatures as much as it reduces photosynthetic activity at higher temperatures (Morris and Glover, 1974). Harris and Piccinin (1977) found that changes in cell size and variation in different species affected the magnitude of the maximum photosynthetic capacity and correspondingly, its relation to temperature. Temperature may set an upper limit for photosynthetic and respiration rates and the values of the photosynthetic capacity, but changes in the environment, species composition and cellular constituents may confound direct correlations with temperature (Eppley, 1972; Harris et al., 1980b; Jones, 1977c).

In summary, the temporal response of algal cells to changing environmental parameters such as light, temperature and mixing depth is important for understanding population growth, photosynthesis and species succession and community diversity. The spectrum of temporal fluctuations in a mixing water column is as diverse as the temporal hierarchy of adaptive responses exhibited by the algal cells living in that particular environment (Fig. 1).

The complete resolution of photosynthesis, productivity and growth in fluctuating environments may only be realized by examination of the temporal patterning of the key factors.

The object of the study in Hamilton Harbour was to examine the effects of environmental variability on changes in the rates of integral photosynthesis and the values of Pmax, Pe and Ik, as well as changes in species succession and community diversity, over the complete temporal spectrum of environmental variability and cellular adaptation and regulation. Hamilton Harbour was suited to these basic aims in two important aspects. First, the Harbour is a eutrophic bay with high and continuous nutrient loadings which do not appear to limit algal growth and productivity (Harris et. al., 1980a). Thus, the effects of physical variability in the absence of nutrient limitation could be assessed. Second, Hamilton Harbour is a physically dynamic body of water both spatially and temporally (Harris et. al., 1980a: Zarull, 1979). Due to its size and basin morphometry, the harbour develops its own high frequency, wind induced motions in the range of 0.1-0.2 hours (Palmer and Poulton, 1976). The harbour is connected to Lake Ontario by a narrow channel and the lake-harbour exchange dominates the physical motions in the harbour (Harris et. al., 1980a;Palmer and Poulton, 1976). The frequent oscillations of the lake are superimposed on the high frequency harbour motions, resulting in an often chaotic mixing regime and thermal structure. Based on the nutrient-biomass equations of Vollenweider (1968) and Dillon (1974), the biomass in Hamilton Harbour is much lower than anticipated

(Harris et. al., 1980a). It was our hypothesis that algal growth and productivity in the harbour was limited by the physical variability of the system.

II. MATERIALS AND METHODS

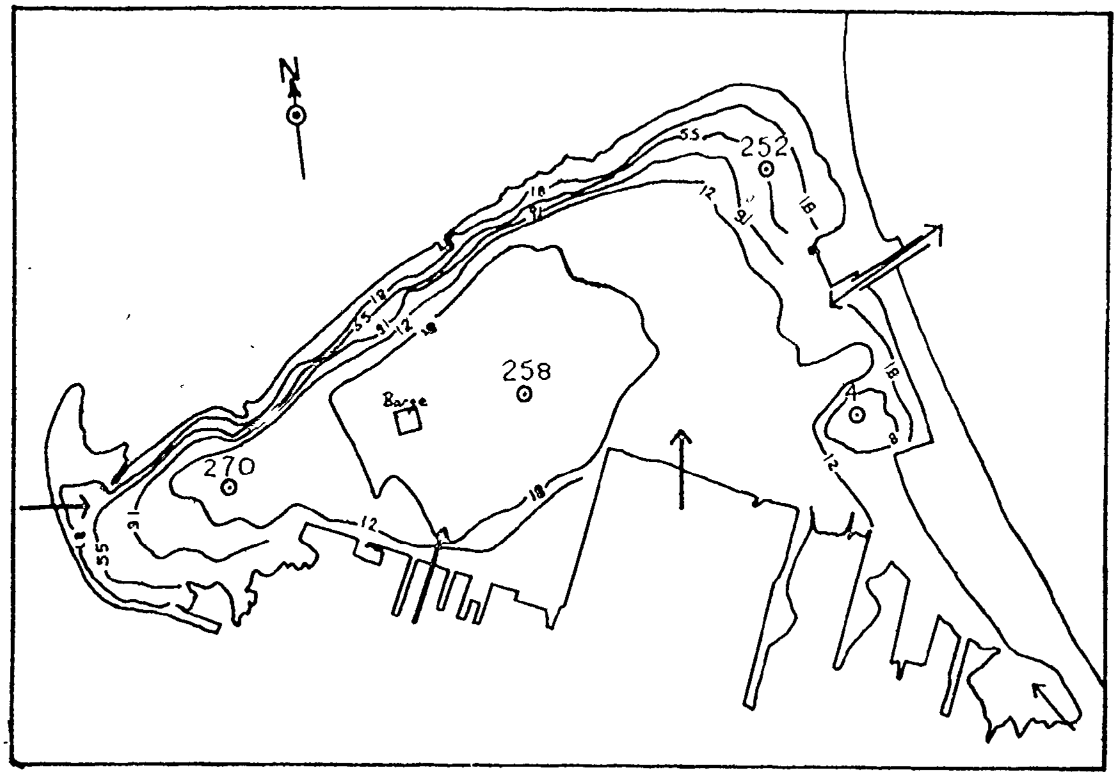
II. 1.0 Description of the Sampling Site

Hamilton Harbour is an enclosed, triangular body of water situated at the western end of Lake Ontario. It has a maximum east-west dimension of 8 kilometers and a maximum north-south dimension of 4 kilometers (Fig. 2). The harbour has a maximum depth of 22 meters ($\bar{x}$ = 13 meters), a surface area of 3.6×10^4 hectares and contains 2.8×10^3 m^3 of water (Harris et. al., 1980a).

The harbour is connected to Lake Ontario by a 732 m long ship canal at its eastern end. The dominant exchange motion in the harbour is the lake-harbour exchange through the ship canal, which modifies the harbour's own internal oscillations and periods by those of Lake Ontario (Harris et. al., 1980a; Palmer and Poulton, 1976). A second narrow channel at the western end of the harbour allows exchange with the Dundas Marsh, a highly eutrophic body of water. The harbour receives loadings from three municipal sewage treatment plants (Dundas, Hamilton and Burlington) as well as from a number of industrial plants on the south shore (Fig. 2).

Hamilton Harbour is a eutrophic, dimictic body of water, with two major periods of overturn (spring and fall), winter ice cover and periods of partial overturn throughout the year. Nutrient loadings are high (P: 10.5 g $m^{-2}y^{-1}$, N: 320 g $m^{-2}y^{-1}$) and continuous. Dissolved oxygen depletion occurs rapidly in the hypolimnion after summer stratification. The harbour is optically

Fig. 2. Hamilton Harbour, Lake Ontario, indicating the basin depth morphometry and the location of the OME sampling stations and the barge. Arrows indicate sources of waste water loadings and the lake-harbour exchange through the ship canal.


N
252
258
Barge
270
4
55
18
12
8

deep, with high background attenuation of light by dissolved organic material or colour (DOM), and the euphotic zone depth ranges from 2 - 4 m (Harris et. al.,1980a).

II. 2.0 Sampling and Measurement Procedures - Physical Measurements

Samples were collected daily from a barge moored in approximately 19 m of water midway between the Ontario Ministry of the Environment (OME, 1974) stations 270 and 258 (Fig. 2). Sampling began on 25 June, 1979 and terminated on 18 August, 1979.

II. 2.1 Temperature and Dissolved Oxygen

Temperature and dissolved oxygen measurements were obtained at 1 m intervals in the water column twice daily (1000 hrs. and 1400 hrs. E.D.T.) using a YSI model 57 dissolved oxygen meter with a Clark type polarographic sensor and built in thermistor.

Continuous temperature measurements were obtained throughout the study at selected depths in the water column to record temperature fluctuations over short time intervals. Eleven YSI series 401 temperature probes were fastened together to form a continuous cable, secured to and suspended through an opening in the barge floor. The probes were suspended at 1 m intervals at depths of 0 through 8 m and at depths of 10 and 12 m. Air temperature was measured using a YSI series 401 probe fastened to the exterior of the barge hut in a shaded corner so that direct solar exposure was avoided. The twelve temperature probes were connected to an 18 channel stepping switch, which selected the electrical signal sequentially from probes at 0 through 12 m, followed by the air

probe and six blank channels. The six blank channels were connected to a variable resistor and were used as a calibration check for the recording system. The complete cycle time of the stepping switch was 230 seconds, so that the signal from each thermistor probe was measured for 13 seconds before the switch stepped to the next probe. The stepping switch was connected to a YSI model 46 Telethermometer and temperature in C° was recorded by a Rikadenki two channel recorder. On August 9 the stepping switch was replaced, due to mechanical failure, by a second switch with a total cycle time of 112 seconds, or 7 seconds for each thermistor probe. The chart speed of the recorder was increased at this point in order to obtain a readable trace.

Zm, the mixing depth, was defined in this study as the depth to the maximum temperature change over a 1 m depth interval and was estimated from the in situ profiles.

N^2 or stability estimates were obtained by determining density differences between surface-(0m) and thermocline region-(6m) temperature profiles. The density values were obtained for specific temperature (θ) using the equation of state for pure water:

$$\rho_{\theta} = \rho_{4^{\circ}C} \times 1 - \left[7.11 \times 10^{-6} (\theta - 4^{\circ}C)^2\right]$$

N^2 estimates, the change in density over the 6 m depth interval were determined using the following equation: $N^2 = \left[\frac{\rho 0m - \rho 6m}{600 cm}\right] \times 10^{-6} \times g$, where $\rho 0m$ and $\rho 6m$ represent the densities of water at 0m and 6m respectively and g is the acceleration due to gravity. N^2 estimates ranged from $10^0 - 10^3 \times 10^{-6}$ sec^{-2}.

II. 2.2 Light

In situ profiles of downwelling irradiance (as $\mu E\ m^{-2} sec^{-1}$ PAR) were obtained prior to and directly after each in situ productivity measurement (1000 and 1400 hrs. EDT) using a Lambda-Licor underwater quantum sensor. The quantum sensor had a flat spectral response from 400 - 700 nm PAR (Biggs et. al., 1971). Measurements were made at 1 m intervals through the euphotic zone, Zeu, defined as the depth in the water column where light intensity is equal to 1% of Io, the surface light intensity (Talling, 1971). Vertical extinction coefficients of PAR were determined from each in situ irradiance profile by least squares linear regression.

The integral downwelling irradiance during the in situ productivity measurement period, $\sum Io$ ($\mu E\ m^{-2} sec^{-1}$) was determined using a Biospherical Instruments QSI-140 Integrating Quantum Scalar irradiance meter. The quantum integrator was suspended in the water column at a depth of 0.5 m, from a float constructed in such a way that the sensor was not shaded. The sensor, a 1.9 cm solid teflon sphere, had a flat spectral response from 400 - 700 nm PAR. Average solar irradiance for the corresponding time period was measured by an Eppley Model 6-90 temperature compensated pyranometer placed on the roof of the barge. The signal was recorded on a Phillips 82-20 chart recorder as 220 $\mu E\ m^{-2} sec^{-1}$ per millivolt.

Spectral irradiance measurements from 400 - 735 nm PAR were determined daily using a Techtum Instruments QSM-2500 Quanta-spectrometer. The quantum sensor of the instrument responded

to discrete wavelengths of light from 400 - 735 nm PAR. The sensor, in its submersible housing, was lowered through the water column so that readings at 4 - 5 discrete 1 m depth intervals could be recorded as continuous plots of irradiance verses wavelength. ε min, the minimum vertical attenuation coefficient of downwelling irradiance, was calculated from 25 nm increments (400-725 nm). During a period of active vertical mixing (June 28 - July 2) when surface waves made field measurements difficult, a 10 l. surface water sample was collected and returned to the laboratory, where ε min was determined by means of a deep tank experiment (Harris, 1978; Harris et. al.,1979; Talling, 1960). Water depth in the tank was 45 cm, the tank diameter was 14 cm and the light source was an overhead fluorescent light bank, whose spectral distribution was a close approximation of the spectral distribution found in the surface waters of the harbour.

II. 2.3 Wind Speed

A record of average wind speed during the in situ productivity measurement period was obtained using a C. F. Casella and Co. Ltd.^{R} Sensitive Anemometer. The anemometer was clamped to a pole, which extended vertically from one corner of the barge roof. Counts per minute were converted to average wind speed in ft sec^{-1} and m sec^{-1} using the conversion graphs provided by the manufacturer.

II. 2.4 Nutrients

Water samples were collected daily at 1100 hrs. EDT from

depths of 0, 1, 2, 4, 6, 12, and 18 m using an opaque, 2 l. Van Dorn water sampler. Aliquots of unfiltered water samples were frozen unpreserved for total phosphate (TP) analysis. Aliquots from the same water samples were filtered through Whatman GF/C filter papers at 12 lbs in^{-2} pressure, preserved with a drop of concentrated HCl and frozen for soluble reactive phosphorus (SRP) and soluble silica (Si) analysis. Filtered aliquots were also preserved with a drop of chloroform and frozen for nitrite nitrogen (NO_2-N), nitrate nitrogen (NO_3-N) and ammonia (NH_4^+) analysis. TP and SRP analyses were performed on the AutoAnalyser II, using the stannous chloride, ammonium molybdate method of Kramer et. al. (1972). Soluble Si was determined on the AAII by the silicon-molybdate-molybdenum blue reaction method (Technicon Corp., 1973). NO_2-N and NO_3-N analyses were performed using the AAII method and a cadmium reduction column (Technicon Corp., 1971a); NO_2-N was determined alone on the AAII after the removal of the reduction column. Ammonia was determined on the AAII using the sodium phenoxide, sodium hypoclorite and potassium tartrate reaction method (Technicon Corp., 1971b).

II. 2.5 pH, Free CO_2 and Total CO_2 Alkalinity

pH measurements were made daily, using a Radiometer Copenhagen pH meter 29, on discrete water samples collected from 1 m depth intervals of 0 - 9 m and at 12 and 18 m. Total CO_2, free CO_2, HCO_3^- and CO_3^{-2} concentrations in the surface water were determined by the Gran titration method of Talling (1973). pH changes were read off a Beckman Model 26 pH meter with expanded scale.

II. 3.0 Biomass Estimation

II. 3.1 Chlorophyll a

Chlorophyll a determinations were made on 2 l. water samples (also used for nutrient analysis) collected from 1 m depth intervals of 0 - 9 m and at 12 and 18 m. An integrated 0 through 8 m samples was collected using an 8 m tube.

A modification of the method of Strickland and Parsons (1968) was employed for chlorophyll analysis. Two hundred to five hundred ml aliquots, depending on biomass, were filtered through Whatman GF/C filter papers at 12 lbs in^{-2} pressure and the filters were frozen. The frozen filters were cut in pieces and ground in a manual tissue grinder in 90% aqueous acetone. The suspension was made up to a volume of 12 ml with 90% acetone and left to extract in the cold and dark for one hour. After centrifugation, the supernatant was decanted into a 10 cm glass cuvette and its optical density was read in a spectrophotometer at 750, 665, 645 and 630 nm. Chlorophyll a was determined using the SCOR/UNESCO equations (Strickland and Parsons, 1968) and the biomass was expressed as mg chlorophyll a m^{-3}.

II. 3.2 Cell Counts

Cell counts were performed on sub-samples from the integrated water sample, collected for chlorophyll a determination, preserved with a few drops of Lugol's iodide. Ten ml of the preserved cell suspension was allowed to settle overnight in a settling chamber (Lund et. al., 1959) and 15 random fields were counted using a Zeiss UPL inverted microscope at a magnification

of 500x with phase contrast. Changes in individual species as cells ml^{-1} were noted on a daily basis.

II. 4.0 In Vivo Fluorescence

Natural phytoplankton populations were collected as previously described and in vivo fluorescence was determined on populations at 1 m depth intervals from 0 through 9 m. Water samples were taken inside the barge hut immediately upon collection, aliquots were placed in 13 x 100 mm cuvettes and then placed in a fluorometer. Fluorescence was measured using a Turner Designs Model 10 Fluorometer with a red sensitive photomultiplier and the combination of filters and lamp previously described by Harris (1980b). The fluorometer was zeroed with distilled water before each in vivo measurement. After the in vivo fluorescence determination, DCMU (3-(3,4-dichlorophenyl)-1,1-dimethyl urea) was added to the water sample to a final concentration of 10^{-5}M and a second fluorescence reading was obtained. Less than one minute elapsed between the in vivo reading and the +DCMU reading.

II. 5.0 Photosynthesis Measurements

Measurements of primary productivity in situ and in an incubator tank were carried out daily by means of the ^{14}C technique (Strickland and Parsons, 1968; Vollenweider, 1974). Soft glass, 125 ml bottles were filled with the appropriate water samples and 100 µl of $H^{14}CO_3^-$ (New England Nuclear, 2 µci ml^{-1} and 50 µg ml^{-1} $NaH^{14}CO_3$) was added to each bottle, the bottle stoppered and incubated for a 3 - 4 h period. Fifty ml aliquots were filtered

from each bottle onto 0.45 μ membrane filters, washed with distilled water (Harris and Piccinin, 1977) and ^{14}C activity was counted by liquid scintillation techniques in Aquafluor (Amersham Corp.) using a Beckman 260 liquid scintillation counter. Dark bottle ^{14}C uptake was subtracted from ^{14}C uptake in the light bottles. Counting efficiencies were determined by external standards and by the channels ratio method. Known ^{14}C-glucose activities were used to construct a quench curve and to check counting efficiencies. All counts were corrected to 100% counting efficiency and converted to values of carbon uptake in mg C m^{-3} h^{-1}.

II. 5.1 In Situ Measurements

Water samples were collected using an opaque, 2 l. Van Dorn bottle from depths of 0, 2, 4 and 7 m. Water collected from 0 m was resuspended in bottles at 0, 0.5, 1.0, and 1.5 m; from 2 m at 2.0, 2.5 and 3.0 m; from 4 m at 4.0 and 5.0 m and from 7 m at 7.0 m. Care was taken not to expose the water samples to surface light intensities during filling. After addition of ^{14}C, the bottles were hung in duplicate pairs on a chain of clear plastic supports at 50 cm intervals from the surface to 3.0 m, and at 4.0, 5.0, and 7.0 m. Dark bottles were suspended at 0.5, 3.0 and 7.0 m. The chain was fastened to a float constructed of two polystyrene cubes joined by a metal bar, tied to the barge in such a way that it was not shaded. In situ incubations were carried out between 1000 and 1400 hrs. EDT.

II. 5.2 Tank Measurements

Productivity measurements were conducted in an incubator tank inside the barge hut in order to determine if the natural algal populations were vertically structured in terms of their photoysnthesis over a series of fixed light intensities. The tank measured 2 ft. wide x 3 ft. high x 4 ft. long and was constructed of opaque, Nalgene plastic (Can Bar Products Ltd., Waterloo, Ontario). A clear plexiglass window measuring 18 in x 18 in was bolted into one end of the tank. An aluminum frame was constructed to hold six, 12 in, diameter wheels fitted with clips to hold productivity bottles, in place on a stainless steel shaft directly in front of the clear window. The shaft and wheels were turned at a constant speed of 70 sec revolution^{-1} by means of a rotisserie motor, connected to a vertical pulley system fastenened to the opposite end of the aluminum frame, away from the clear window. A light bank measuring 2 ft. x 2 ft. was constructed from seven, 24 in. fluorescent tubes and was placed in front of the clear window. The tank was pumped full of surface harbour water using a submersible pump connected to a bulkhead type inflow fitting at the lower corner of the tank. Water circulated through the tank and drained through a second bulkhead fitting, for a replacement time of twenty minutes, maintaining the water temperature in the tank. Irradiance at each of the wheels was similar to the spectral distribution in the harbour, and backscattering off the sides of the tank was estimated at 10 - 15%. Irradiance at each wheel fluctuated slightly, due to changes in the vertical extinction coefficient of the harbour

water, so that it was necessary to adjust the position of the wheels on the shaft to maintain constant irradiances. Wheels 1 (closest to the light bank) through 6 received 238, 133, 84, 42, 21 and 7 $\mu E\ m^{-2}sec^{-1}$ of light respectively. The tank was fitted with a plywood cover to minimize exposure to outside light.

Water was collected from depths of 0, 1, 2 and 4 m at the same time as the in situ productivity water samples were collected, replaced in duplicate bottle pairs, spiked with ^{14}C and clipped on each of the six wheels. Two dark bottles were also incubated in the tank from each of the four depths. The incubation period in the tank corresponded to the in situ incubation period.

II. 5.3 Photosynthetic Parameter Analysis

Several photosynthetic parameters were derived from the in situ and tank estimates of the maximum volumetric rates of photosynthesis; max Pv (mg C $m^{-3}h^{-1}$). In situ integral productivity, ΣP (mg C $m^{-2}h^{-1}$) was obtained by the integration of the volumetric photosynthesis estimates over 0.5 m depth intervals from 0 - 5 m. Carbon uptake in the light ceased to be significant in terms of dark carbon uptake below 5 m in the water column. In situ Pmax, the assimilation number or photosynthetic capacity (mg C mg chl $a^{-1}h^{-1}$) was determined from max Pv and the volumetric chlorophyll a value (mg chl a m^{-3}) from the appropriate depth. In situ Pe, the photosynthetic efficiency (mg C mg chl $a^{-1}E^{-1}h^{-1}$) was determined from Pmax and in situ Ik ($\mu E\ m^{-2}sec^{-1}$) where Ik was defined as the irradiance at which the linear, rising portion of the photosynthesis verses irradiance curve determined for each in situ incubation,

intersects the light saturated rate of photosynthesis, Pm.

Tank Pmax values were determined from max Pv estimates from each population in the tank and the appropriate volumetric chlorophyll a estimate. Analysis of variance (Factorial design, two way classifiaction) was performed on the four depth estimates of Pmax to determine the effect of depth and time on changes in the values of Pmax. Po and Ik were not determined from the tank data, since Pm may not have been achieved on occasion in the tank due to the limiting range of light intensities used.

II. 6.0 Power Spectral and Time Series Analysis

A time series represents a random sequence of data; x, which is a sequential function of time; x(t). A time series may be described fully in terms of its mean value and the variance about the mean and its future behaviour may be predicted in a statisitical sense only (Chatfield, 1975; Jenkins and Watts, 1968; Rayner, 1971). Spectral analysis is the process of calculating and interpreting the variance spectrum from a time series of data to better understand the inherent pattern and the system producing it (Rayner, 1971). Spectral analysis assumes that a time series is statistically a single realization or representative portion of a stochastic process, in simple terms, the complete set of all random variables; x, with time along with their probability density distributions (Box and Jenkins, 1970; Jenkins and Watts, 1968; Platt and Denman, 1975; Rayner, 1971).

Sequenced observations are often related to each other through their variance functions and are said to be autocorrelated

(Chatfield, 1975; Rayner, 1971). The autocorrelation or autocovariance function of a time series is the result of fitting the time series to an exact copy of itself and sliding it backwards and forwards, using a specific number of lags; equally spaced intervals of time or length (Platt and Denman, 1975). The autocovariance function provides information about how adjacent points are correlated and gives a frequency breakdown of the variance (Rayner, 1971). High values of the autocovariance function indicate that the data set tends to repeat itself, when compared over specific temporal or spatial intervals which represent some fraction of the number of lags used in the analysis. The power spectrum of a time series is defined as the Fourier cosine transformation of the autocovariance function (Jenkins and Watts, 1968). Fourier analysis is the process of fitting, by least squares estimation, a Fourier cosine transformation to the autocovariance function and calculating the amplitudes and phase angles of the sine and cosine waves obtained at different frequencies (Box and Jenkins, 1970; Jenkins and Watts, 1968). In other words, the variance function of the original data series is smoothed by least squares regression, into a series of sine and cosine waves. The power spectrum thus gives the variance of the stochastic process as a function of frequency (Platt and Denman, 1975). High power spectral estimates at given frequencies indicate repetitions or periodicities in the data set.

Spectral analysis techniques may be expanded to deal with pairs of time series to determine the relationships between

them (Jenkins and Watts, 1968). The crosscovariance function between two time series is analagous to the autocovariance function from a single time series. A value of the cross covariance function significantly different from zero indicates that at the number of lags specified, the two series are positively or negatively related to each other. The cross spectrum is calculated in the same manner as the power spectrum and gives a frequency or scale breakdown of the regression parameters (covariance and correlation) between the two time series (Rayner, 1971). The coherence spectrum or squared coherency of the cross spectrum describes the degree of correlation between the two series, now transformed into waves, at specific frequencies. If the coherence value is high at a specific frequency, the reciprocal of that frequency represents a significant period at which the time series are strongly correlated. The phase angle of the cross spectra, expressed as fractions of a circle , indicate how far out of phase the two waves are or whether one time series leads or lags the other. The amplitude of the transfer function provides the vertical distance between the waves at a given frequency and allows one to predict statisitically the value of a point on one wave at a specific frequency from the value of a point on the second wave at that frequency (Jenkins and Watts, 1968; Platt and Denman, 1975; Rayner, 1971).

II. 6.1 Autocovariance and Power Spectral Analysis - Physical Parameters

Autocovariance and power spectral analysis (BMD 02T) was performed on three sets of temperature data. The three data sets

incorporated temperature records with fixed, but differing time intervals, all at depths of 0, 6 and 12 m in the water column. Tem 1; represents the data set with 984 records at 1 h constant intervals, Tem 2; the data set with 537 records at 0.20 h constant intervals and Tem 3; the long term data set with 219 records at 6 h time intervals. Fifty lags were fitted over the entire data sets and provided a suitable compromise between the number of degrees of freedom and the corresponding 80% confidence intervals. The number of lags that can be fitted to a data set is determined as N/4, where N is the number of observations or data points, since the smoothing process involved in spectral analysis becomes statisitically invalid when dealing with less than one quarter of the full data set (Platt and Denman, 1975). Using BMD 02T, the degrees of freedom are equal to 2.5N/M, where N is the number of data points and M is the number of lags, and the degrees of freedom allow one to determine the 80% or 95% confidence intervals for the spectral estimates (Jenkins and Watts, 1968). Autocovariance and power spectral analysis was also performed on N^2 numbers, derived from temperature data at 0 and 6 m depths, for the three data sets.

II. 6.2 Cross Spectral Analysis - Physiological verses Physical Parameters

Autocovariance and power spectral analysis were performed on time series data for two photosynthetic parameters; Pmax and Pe. Cross covariance and cross spectral analysis (BMD 02T) was performed on both Pmax and Pe, using the noon Zeu/Zm ratio data series as the second series in the analysis, in an attempt to

compare physiological periodicities with those of the environment. In situ Pmax values, as well as incubator tank estimates were compared to the noon Zeu/Zm ratios on the same day. In situ Pmax was also compared to a day to day change in the Zeu/Zm ratio, as it was thought that the magnitude of the change from one day to the next might be as important in terms of physiological change as the actual value of the ratio alone. Pmax was thus compared to the change in Zeu/Zm from the day before, from two days before and from three days before (Zeu/Zm -1day to Zeu/Zm 0 day, Zeu/Zm -2 days to Zeu/Zm 0 day and Zeu/Zm -3 days to Zeu/Zm 0 day). Pe was compared to another variation of the Zeu/Zm ratio, since preliminary analysis indicated that Pe might not have been responding to changes in Zeu and Zm on the same temporal scale. Pe was compared first to the Zeu/Zm ratio on the same day and then to the Zeu(day 0)/Zm (day-1) ratio and the Zeu (day 0)/Zm (day -2) ratio. Since all previously described analyses involved time series of 55 observations, 12 lags were selected for the analyses.

II. 6.3 Cross Spectral Analysis - Species Numbers and N^2

Autocovariance and power spectral analysis was performed on time series data for the daily cells ml^{-1} counts for the eight dominant species during the study period (Chlamydomonas spagnicola, Coelastrum spp, Oocystis borgeii, Scenedesmus quadricauda, Stephanodiscus spp, Cyclotella spp, Cryptomonas spp and Rhodomonas sp) and the noon N^2 number. Cross covariance and cross spectral analysis (BMD 02T) was performed on each of the species data series and the N^2 number, in order to determine the periodicity of the species response to

a measure of environmental stability and change. A twelve day lag was selected for the analysis.

III. RESULTS

III. 1.0 General Limnology

III. 1.1 Thermal Regime, Wind Speed and Dissolved Oxygen

During the summer of 1979 there was a period of warmth and relative stability in the harbour (early to late July), braketed by periods of cooler, windy conditions. Average daily wind speed was generally high in late June and in August and lower during the month of July (Fig. 1b, Appendix I). Daily mid-morning air temperatures were low in late June (17 - 24 °C), increased through early July to a maximum on July 15 (31.6 °C), remained high until late July and then steadily declined after July 28 (Fig. 1c, Appendix I).

The thermal structure in the harbour showed high spatial and temporal patchiness (Fig. 2, Appendix I). Water temperatures decreased gradually with depth until July 9, when increasing air temperatures and decreasing wind speeds led to surface heating and the onset of thermal stratification in the epilimnion. Thermal stratification persisted through July and was destroyed in August as epilimnial water temperatures and wind speed increased, resulting in partial overturn conditions in mid August (Fig. 3, Appendix I). Zm, the mixing depth, oscillated from 6 - 10 m during periods of active vertical mixing, and from 2 - 6 m during periods of relative stability in the water column (Fig. 1a, Appendix I). The temperature in the region of the thermocline

(5 - 10 m) was highly variable, reflecting short term changes in vertical mixing, as well as internal harbour periodicities and lake oscillation effects. Below the thermocline, temperature was more stable and increased slightly with time. Rising of cooler, bottom water was noted on July 28, possibly due to an incursion of cold Lake Ontario water through the ship canal, and may have contributed to the onset of partial overturn conditions in mid August.

Dissolved oxygen concentrations showed spatial and temporal patchiness and declined with depth (Fig. 3, Appendix I). Due to the high sediment and water column oxygen demands in the harbour (Polak and Haffner, 1978), hypolimnial waters were low in oxygen at the onset of sampling and anoxic conditions were evident near the sediments by July 1, gradually penetrating the region of the thermocline (Fig. 3, Appendix I). Dissolved oxygen concentrations rose significantly in the top three meters of the water column in early July, due to increased algal activity and surface heating. Partial reoxygenation of the hypolimnion occurred early in August, due to the possible incursion of Lake Ontario water in late July, and as surface heating and algal productivity declined, epilimnial oxygen concentrations declined. The effect of these two processes and the increased mixing due to wind activity resulted in a clinograde oxygen profile, similar to that observed at the onset of sampling.

The thermal strucure and dissolved oxygen concentrations evident during the study were comparable to previous observations

in the harbour during the summers of 1975 - 1978 (Harris, 1976; Harris et. al., 1980 a; Piccinin, 1977, 1979). The degree of spatial and temporal patchiness evident in the thermal structure and mixing events in the harbour means that the phytoplankton living in this environment were exposed to many rapid environmental changes.

III. 1.2 Nutrients

Total phosphorus (TP) concentrations in the water column showed spatial and temporal patchiness (Fig. 4, Appendix I). Although slight declines and fluctuations were noted, TP was generally stable with time at all depths. Average surface and epilimnial concentrations ranged from 80 - 130 $\mu g\ l^{-1}$ in June to 30 - 50 $\mu g\ l^{-1}$ in August. Significant rises in the surface TP from day to day were observed, possibly the result of increased external loadings and surface runoff to the harbour following storms. Hypolimnial TP concentrations were stable with time, ranging from 70 - 90 $\mu g\ l^{-1}$ in June and July to 40 - 60 $\mu g\ l^{-1}$ in August. The slight decline was probably due to mixing with the epilimnion or precipitation to the sediments.

Soluble reactive phosphorus (SRP) showed patterns similar to TP concentrations (Fig. 5, Appendix I). Patchiness was observed in the epilimnion in June and early July and in the metalimnion in mid July, when algal biomass was rising and thermal stratification was evident. With the increasing algal biomass from July 7 to its peak on July 24, epilimnial SRP declined,

dropping to mean concentrations of 5 - 20 $\mu g\ l^{-1}$ in mid July to 5 - 10 $\mu g\ l^{-1}$ in August. The decline was also evident in the metalimnion; 15 - 30 $\mu g\ l^{-1}$ in mid July to 5 - 15 $\mu g\ l^{-1}$ in August, and in the hypolimnion; 20 - 30 $\mu g\ l^{-1}$ in mid July to 10 - 20 $\mu g\ l^{-1}$ in August. It appeared that some hypolimnial SRP was mixing into the epilimnion as depletion of SRP was not evident late in July despite high algal activity.

Nitrate (NO_3) was the most abundant nitrogen source in the harbour (1.1 - 2.8 mg l^{-1}) and was generally stable, decreasing only slightly with depth (Fig. 6, Appendix I). Nitrate concentrations decreased with time in the epilimnion due to increased algal utiliziation in July and August and exhibited a metalimnetic maximum in mid July to early August, when algal biomass was high. Nitrate concentrations also decreased with time in the hypolimnion, following a period of anoxia in July, possibly due to denitrification.

Nitrite (NO_2) represented a small portion of the total nitrogen in the harbour (0.35 - 0.50 mg l^{-1}) and decreased with depth (Fig. 7, Appendix I). A clear separation between epilimnial and hypolimnial concentrations was evident during mid July to early August, when oxygen depletion occurred in the hypolimnion and nitrite concentrations were conservative with depth. Nitrite concentrations increased at all depths after August 5, after a period of active vertical mixing and some reoxygenation in the hypolimnion.

Ammonia (NH_4+) concentrations were higher in the epilimnion (1.0 - 2.0 mg l^{-1}) compared to the hypolimnion (0.5 -

1.0 mg l^{-1}) and represented the second major source of inorganic nitrogen (Fig. 8, Appendix I). Ammonia concentrations declined in the epilimnion in mid July and were rapidly depleted by July 21. Ammonia depletion extended to all depths and no ammonia was detected after August 6. Several releases of ammonia from the sediments in July were associated with hypolimnial anoxia.

Total nitrogen concentrations ($NO_3 + NO_2 + NH_4^+$) showed slight fluctuations with depth and time but were generally stable (Fig. 9, Appendix I). Slight declines in total nitrogen occurred with time at all depths. Surface waters showed slightly higher concentrations (1.5 - 4.5 mg l^{-1}) compared with the metalimnion (2.0 - 4.0 mg l^{-1}) and the hypolimnion (1.0 - 3.5 mg l^{-1}).

Soluble reactive silica (Si) concentrations remained stable with time throughout the sampling period and increased slightly with depth (Fig. 10, Appendix I). Si concentrations were lowest in the epilimnion in late June and early July (0.1 - 0.4 mg l^{-1}) due to utilization by centric diatoms. Epilimnial Si concentrations were slightly higher in mid July (0.6 - 0.8 mg l^{-1}) and declined again in August with the appearance of Cyclotella sp. Higher concentrations were noted at all depths between mid July and early August. Hypolimnial concentrations were higher (0.4-1.0 mg l^{-1}) than epilimnial concentrations, the result of either diatoms sinking or of release from the sediments.

It is important to note that the concentrations of the major nutrients essential for algal growth and productivity observed during the study were comparable to previous studies

(Harris, 1976; Harris et. al., 1980a; Piccinin, 1977, 1979) and were not low enough to limit algal growth (Harris, 1976; Harris et. al., 1980a). The spatial and temporal patchiness observed in the patterns of nutrient distribution in the harbour reflected the high frequency periodic and random mixing events to which the phytoplankton were continuously exposed.

III. 1.3 pH, Conductivity and Carbonate Alkalinity

pH decreased with depth, ranging from 7.8 - 8.8 in the epilimnion to 7.2 - 7.6 in the hypolimnion. A gradual increase in epilimnial pH was observed with time, peaking between July 18 and July 24 and again in mid August (Fig. 11, Appendix I). Conductivity ranged from 340 - 540 μmhos, with a mean value of 476.6 ± 46.7. Total CO_2 alkalinity ranged from 57.25 - 101.58 mg l^{-1}, with a mean value of 74.02 ± 7.84. The bicarbonate ion, HCO_3^-, accounted for most of the total CO_2 in the water (55.96 - 98.94 mg l^{-1}, $\bar{x}$ = 71.75 ± 7.66) followed by free CO_2 (0.42 - 5.27 mg l^{-1}, $\bar{x}$ = 1.58 ± 1.53) and carbonate CO_3^{-2} (0.04 - 1.52 mg l^{-1}, $\bar{x}$ = 0.60 ± 0.35) (Appendix II).

No consistant relationship was noted between the daily flucutations in in situ integral productivity, ΣP and changes in total CO_2 and free CO_2 concentrations or rises in surface pH and changes in the bicarbonate ion concentration (Appendix II). The dynamic nature of the physical processes in the harbour again accounted for the patchiness observed in the concentrations of the major carbon species, which did not appear low enough to limit algal growth and productivity.

III. 2.0 The Thermal Structure and its Internal Periodicities

III. 2.1 Thermal Periodicities; 0, 6 and 12 m

Autocovariance and power spectral analysis of three sets of temperature data identified a broad spectrum of high and low frequency motions in the harbour (Table I). Analysis of hourly temperature data (Tem 1) revealed significant periods in the 2 - 17 h range, with highest power spectral estimates at scales of 20 - 200 h. Analysis of 0.20 hourly temperature data (Tem 2) revealed high frequency periods in the 0.36 - 2.50 h range, with highest power spectral estimates at scales of 3 - 18 h. Analysis of 6.00 hourly temperature data (Tem 3) provided the longest temporal resolution in the data set. Significant periods were noted in the 12 - 24 h range and the maximum power spectral estimates occurred in the 30 - 500 h range. Considerable overlapping in the thermal periodicities were evident in the three analyses and these were consistent with depth (Table I).

Examination of the temporal range of high and low frequency motions at the 6 m depth (thermocline region) illustrated several important points. The power spectral estimates derived from the 0.20 hourly temperature data indicated weak, short period motions in the 0.36 - 2.5 h range (Fig. 3). The highest power spectral estimates occurred in the 3 - 8 h range and represented the strongest periodic motions detected. The analysis of hourly temperature data elucidated these periods, but once again, the highest power spectral estimates occurred at shorter frequencies (longer periods) (Fig. 4). Periods in the 0.40 - 5.0 h

Table I. Theoretical and observed hourly periodicities of important physical and chemical properties in Hamilton Harbour, Lake Ontario, June 25 - August 18, 1979.

Rao and Schwab, 1974.	Ship Canal (1) Upper	Ship Canal (1) Lower	Windermere Basin (1)	Tem 1 (2) 0 m	Tem 1 (2) 6 m	Tem 1 (2) 12 m	Tem 2 (2) 0 m	Tem 2 (2) 6 m	Tem 2 (2) 12 m	Tem 3 (2) 0 m	Tem 3 (2) 6 m	Tem 3 (2) 12 m	N^2 (3) 1	N^2 (3) 2	N^2 (3) 3
										500.0	500.0	500.0			
				200.0	200.0	200.0				333.0	333.0	333.0			
										200.0	200.0	200.0			250.0
										166.0					
										125.0					125.0
				100.0	100.0	100.0				100.0	100.0	91.0	100.0		
															76.0
				50.0	50.0	50.0				59.0	59.0	59.0	50.0		56.0
				33.0	33.0	33.0				37.0	36.0	30.0			37.0
				25.0	25.0	25.0				27.0		24.0			26.0
				20.0	20.0	20.0				20.0	21.0	19.0	20.0		23.0
				17.0		17.0	18.0	18.0	18.0	17.9	18.5				18.5
				15.0		15.0					16.7	15.2			15.6
										13.5	14.1	13.2	14.3		14.3
	12.0	12.0		12.5		12.0				12.1	12.7	12.1			12.5
							9.0	9.0	9.0					10.0	
					8.3	7.5							8.0		
5.11	5.0	5.0			6.0		6.0	6.0	6.0					5.0	
				4.3	4.0	3.3	4.5	4.5	4.5				4.0	4.0	
3.11	3.2	3.1			3.0	2.8	3.0	3.0	3.0				2.8	3.3	
2.31	2.3	2.4	2.6		2.3	2.1		2.5	2.5				2.3	2.5	
1.97			2.0	2.0	2.0								2.0	2.0	
1.78	1.7	1.7	1.7												
1.46	1.4	1.4	1.38					1.5						1.54	
	1.25	1.25	1.18				1.20							1.18	
	1.00	1.00	1.08				0.95	1.10	0.90						
	0.86	0.84						0.80	0.80					0.83	
	0.67	0.67					0.75							0.67	
	0.56	0.56					0.60	0.60	0.56					0.54	
	0.45	0.47					0.48		0.44					0.43	
	0.37	0.37					0.40	0.38						0.40	
0.35	0.35	0.35						0.36	0.36						

(1) Data from Palmer and Poulton, 1976, 95% confidence intervals.

(2) Tem 1; hourly temperature data, Tem 2; 0.2 h temperature data, Tem 3; 6.0 h temperature data, 80% confidence intervals.

(3) N^2 stability estimates derived from Tem 1, Tem 2 and Tem 3 respectively, 80% confidence intervals.

Fig. 3. Power spectral estimates of Tem 2; 0.20 hourly, 6m temperature data, plotted on a $\log_{\sigma}$ scale against frequency in cycles h^{-1}, with 80% confidence intervals.

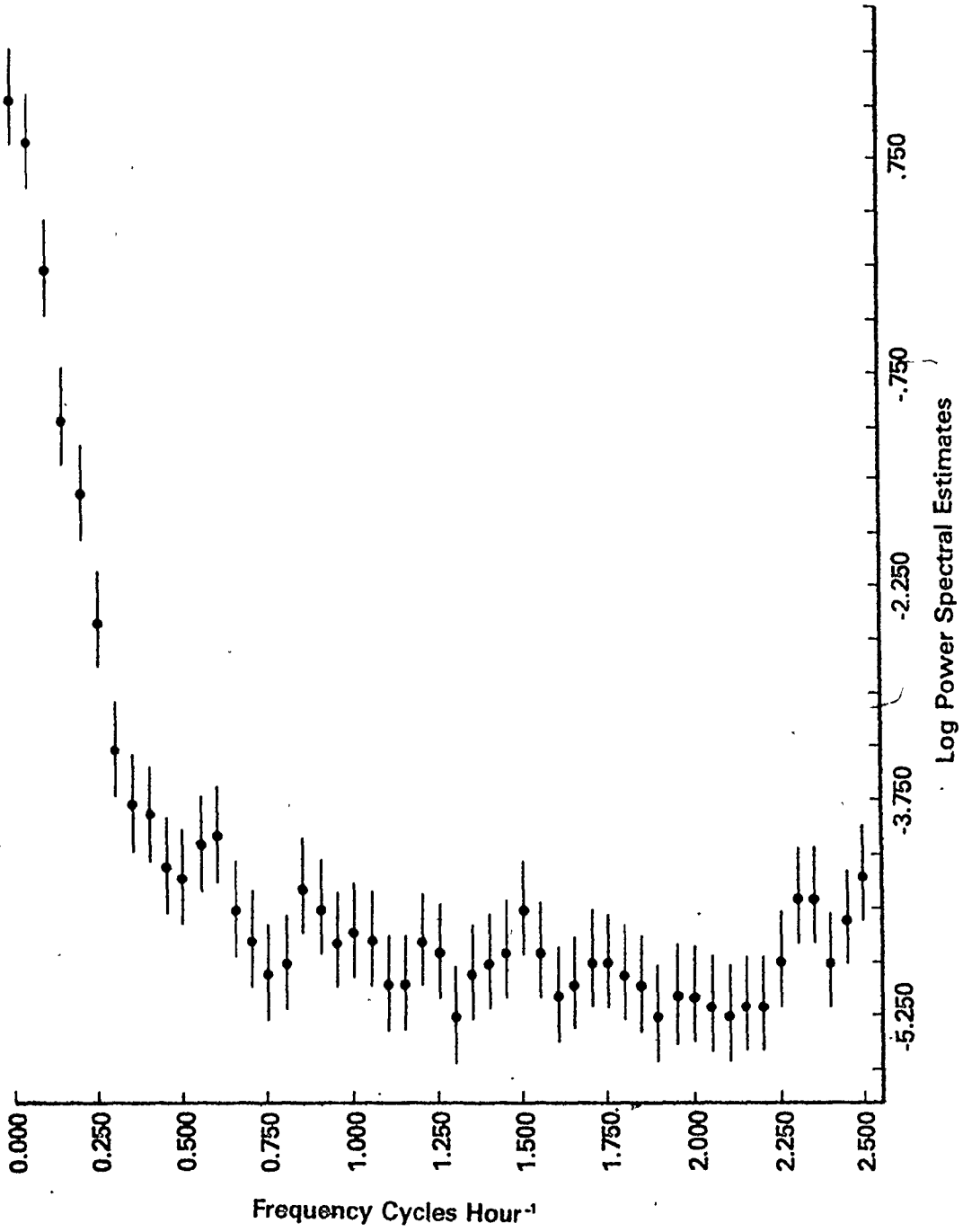
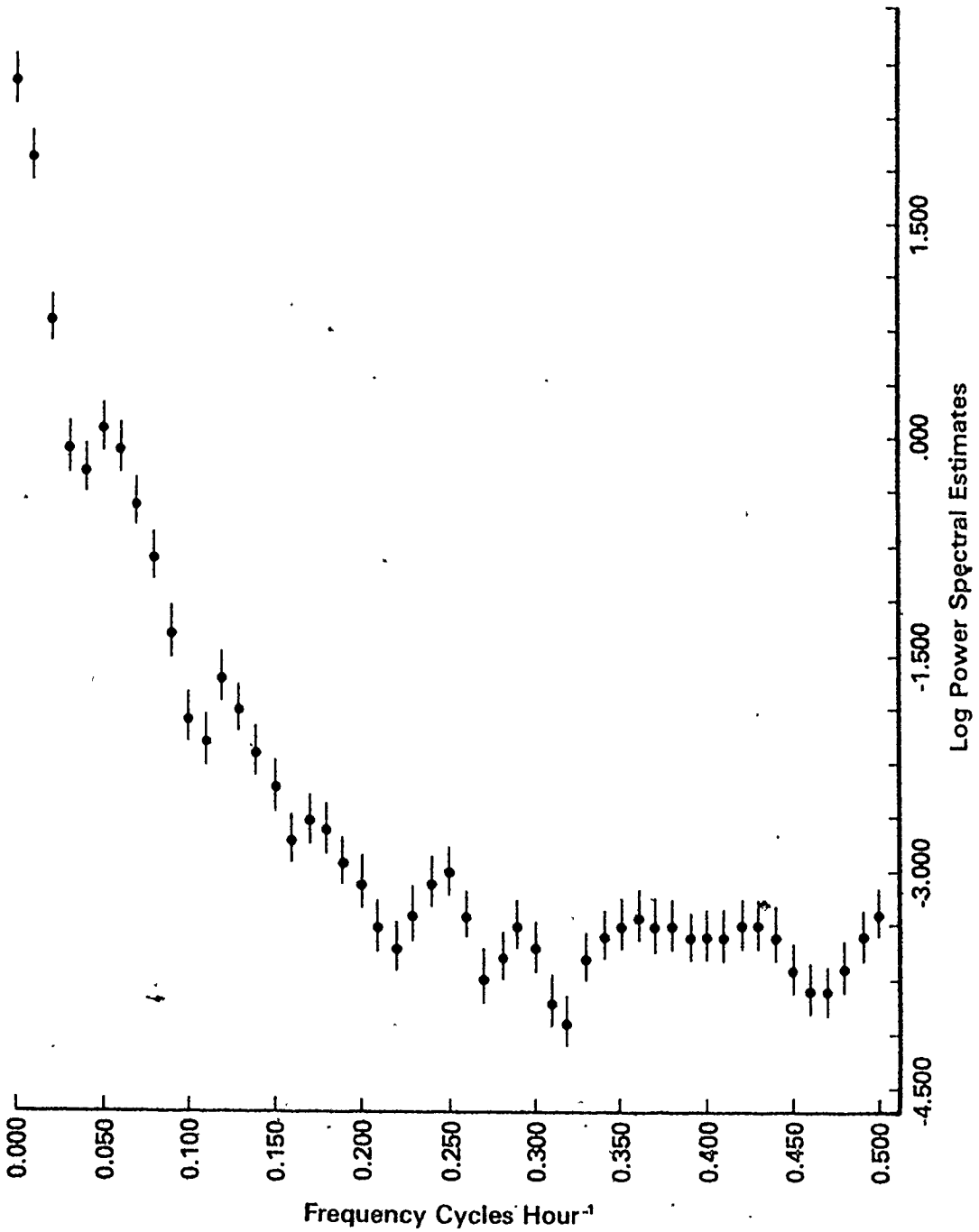

0.000
0.250
0.500
0.750
1.000
1.250
1.500
1.750
2.000
2.250
2.500
Frequency Cycles Hour⁻¹
.750
-.750
-2.250
-3.750
-5.250
Log Power Spectral Estimates

Fig. 4. Power spectral estimates of Tem 1; hourly, 6 m temperature data, plotted on a $\log_e$ scale against frequency in cycles h^{-1}, with 80% confidence intervals.


0.000
0.050
0.100
0.150
0.200
0.250
0.300
0.350
0.400
0.450
0.500
Frequency Cycles Hour⁻¹
1.500
.000
-1.500
-3.000
-4.500
Log Power Spectral Estimates

range were comparable to previous estimates (Palmer and Poulton, 1976) (Table I). The analysis of the 6.00 hourly temperature data elucidated weak periods in the 12 - 24 h range, while the highest power spectral estimates occurred in the 30 - 500 h range (Fig. 5). Thus, the values of the power spectral estimates indicated that the high frequency, short term periodic motions were not as significant as the low frequency, longer period motions evident in the thermal strucutre of the harbour.

III. 2.2 N^2 Stability Numbers

Autocovariance and power spectral analysis of the N^2 stability numbers derived from Tem 1, Tem 2 and Tem 3 revealed periodicities similar to those of the temperature time series (Table I). The highest power spectral estimates occurred at scales in the 3 - 10 h range for the 0.20 hourly data (Fig. 6), in the 8 - 100 h range for the hourly data (Fig. 7) and in the 20 - 500 h range for the 6.00 hourly data (Fig. 8). Weaker periods were noted at 0.40 - 1.54 h (Fig. 6), 2.0 - 8.0 h (Fig. 7) and 12.5 - 23.0 h (Fig. 8) ranges respectively.

The results of the autocovariance and power spectral analyses suggest that although significant, short term periods occurred in the harbour motions, these periods were not as statistically significant or as strong as the longer term periodic motions. The phytoplankton in the harbour thus experienced the full temporal spectrum of periodic motions in the water column, but may have been more strongly influenced by fluctuations in the range of one or more days.

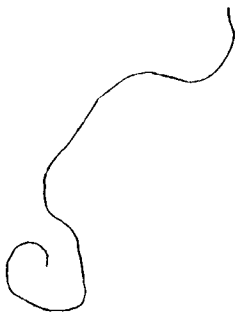


Fig. 5. Power spectral estimates of Tem 3; 6.0 hourly, 6 m temperature data, plotted on a $\log_e$ scale against frequency in cycles h^{-1}, with 80% confidence intervals.

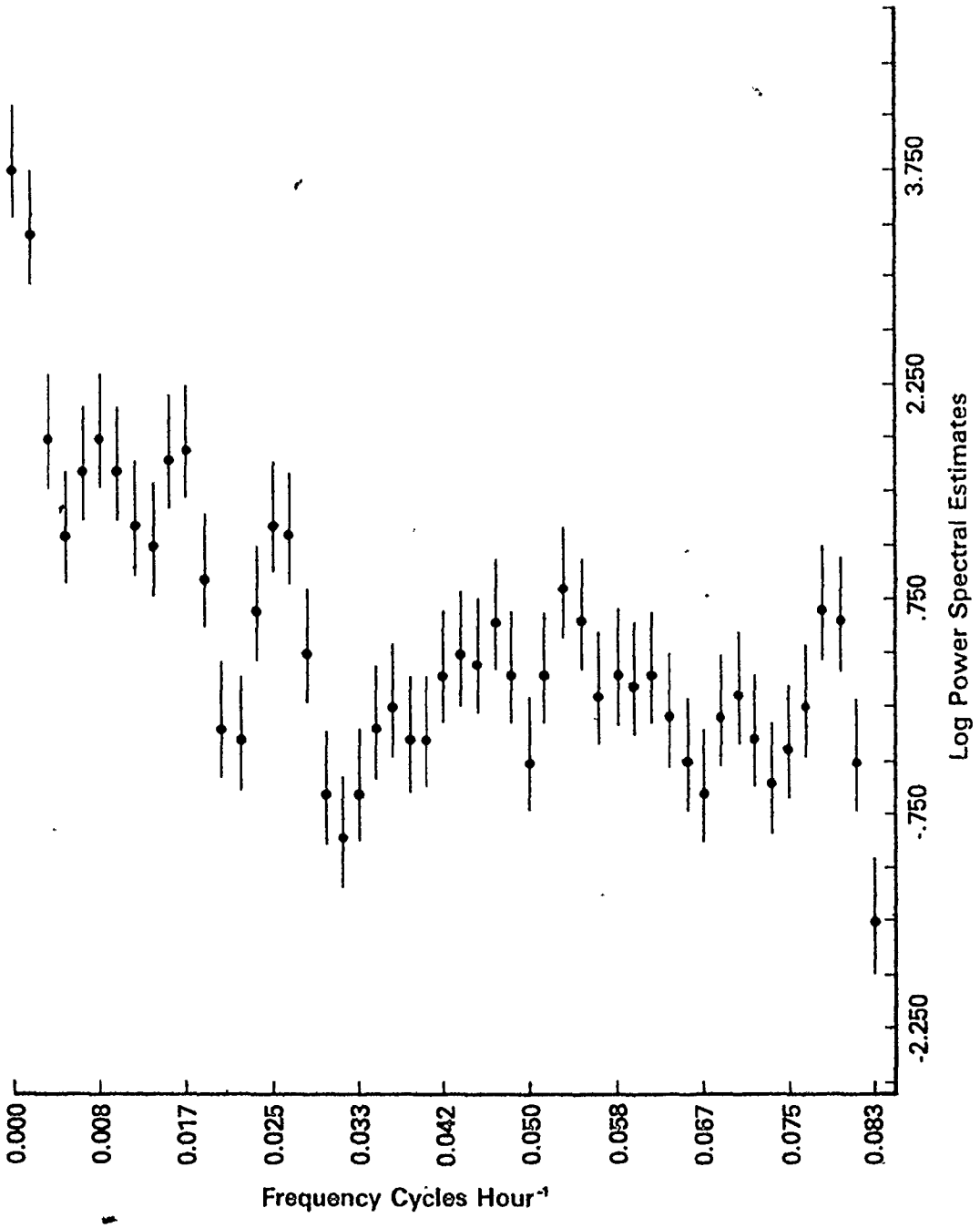

Log Power Spectral Estimates
3.750
2.250
.750
-.750
-2.250
0.000
0.008
0.017
0.025
0.033
0.042
0.050
0.058
0.067
0.075
0.083
Frequency Cycles Hour⁻¹

Fig. 6. Power spectral estimates of N^2 stability numbers derived from 0.20 hourly 0 and 6 m temperature data, plotted on a $\log_e$ scale against frequency in cycles h^{-1}, with 80% confidence intervals.

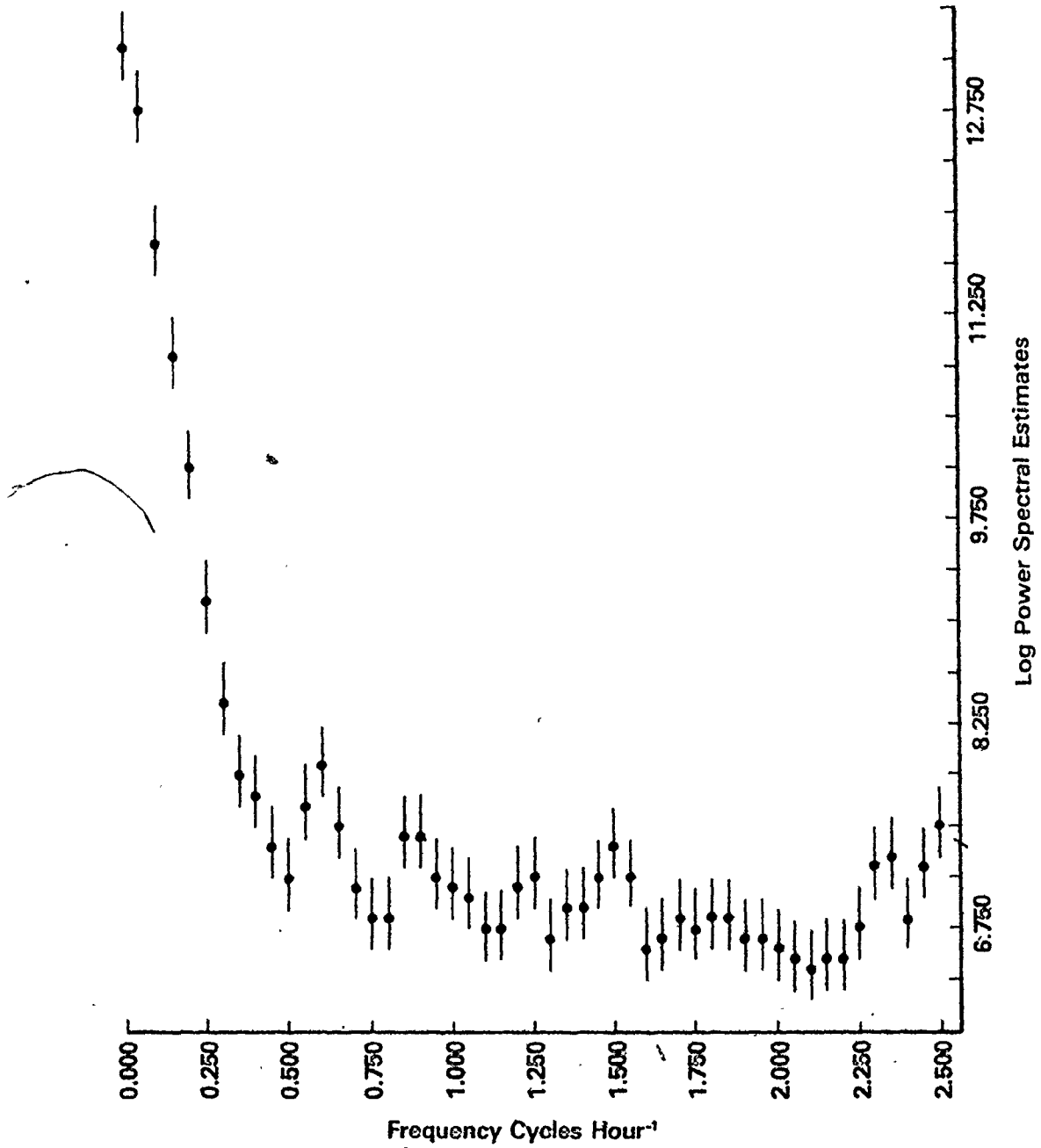

0.000
0.250
0.500
0.750
1.000
1.250
1.500
1.750
2.000
2.250
2.500
Frequency Cycles Hour⁻¹
6.750
8.250
9.750
11.250
12.750
Log Power Spectral Estimates

Fig. 7. Power spectral estimates of N^2 stability numbers derived from hourly 0 and 6 m temperature data, plotted on a $\log_e$ scale against frequency in cycles h^{-1}, with 80% confidence intervals.

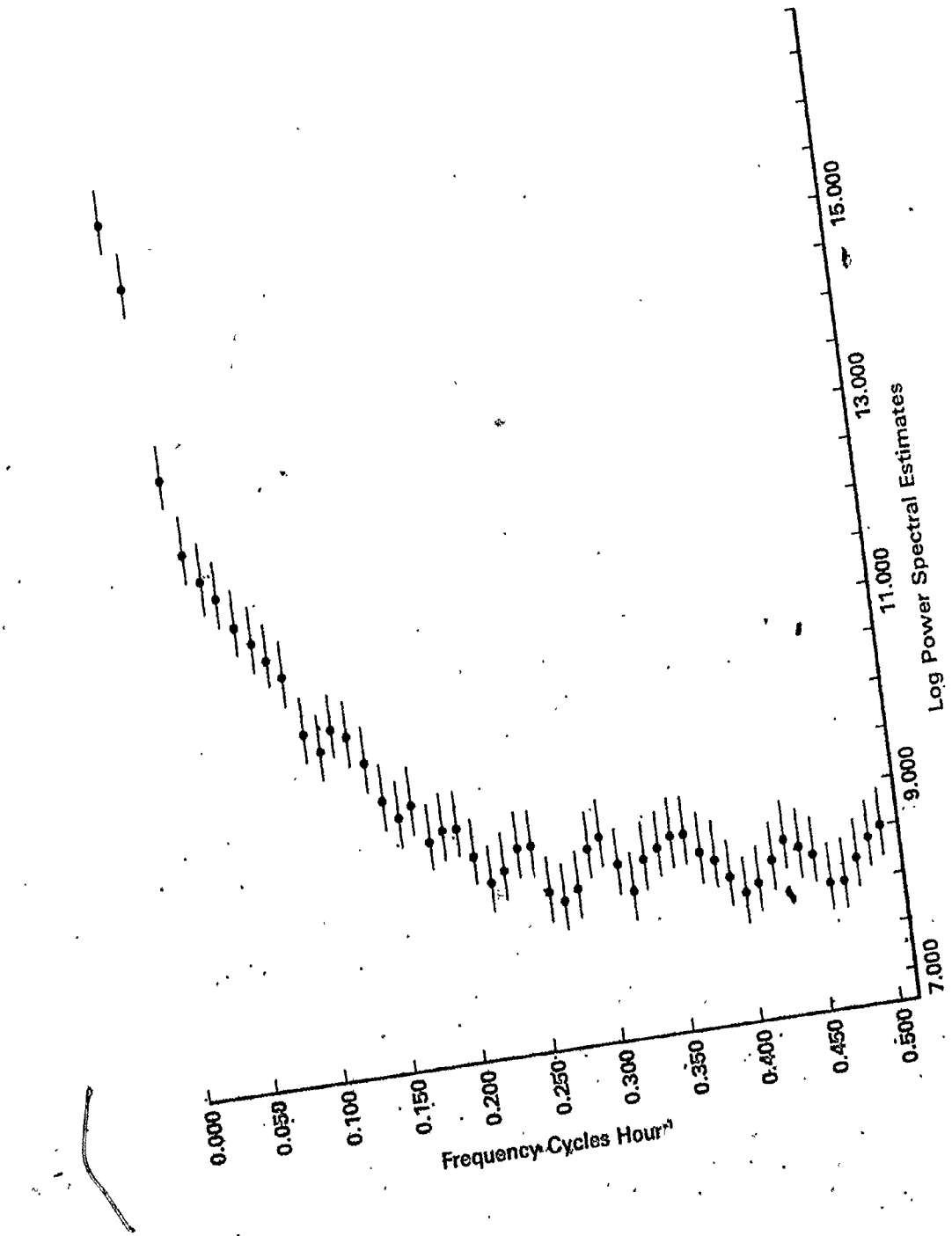
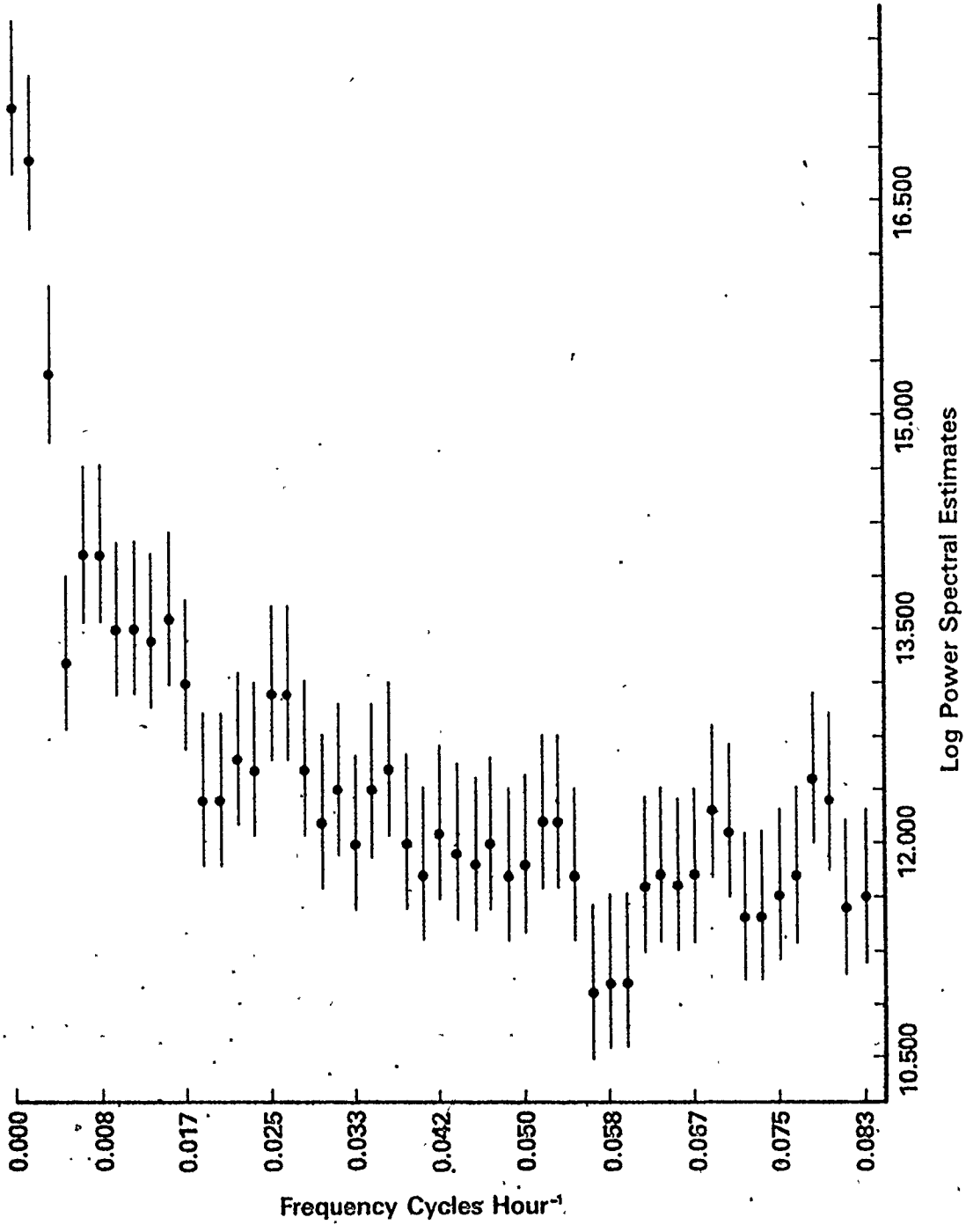

Log Power Spectral Estimates
7.000
9.000
11.000
13.000
15.000
Frequency Cycles Hour⁻¹
0.000
0.050
0.100
0.150
0.200
0.250
0.300
0.350
0.400
0.450
0.500

Fig. 8. Power spectral estimates of N^2 stability numbers derived from 6.0 hourly 0 and 6 m temperature data, plotted on a $\log_e$ scale against frequency in cycles h^{-1}, with 80% confidence intervals.


Log Power Spectral Estimates
10.500
12.000
13.500
15.000
16.500
0.000
0.008
0.017
0.025
0.033
0.042
0.050
0.058
0.067
0.075
0.083
Frequency Cycles Hour⁻¹

III. 3.0 The Light Climate

The daily integrated solar irradiance, ΣIo ($\mu E\ m^{-2}sec^{-1}$, 1000 - 1400 h EDT) was highly variable with time (Fig. 12, Appendix I; Table II). The euphotic zone depth, Zeu, ranged from 1.75 - 5.07 m and decreased through July to a minimum depth late in July, then increased through August (Fig. 12, Appendix I; Table II). The vertical extinction coefficient of PAR, ξPAR (ln units m^{-1}) ranged from 0.94 - 2.63 and increased through July to its maximum value in late July, then declined through August. A significant correlations existed between ξPAR and ξmin, the minimum value of ξPAR in the water column; $\xi PAR = 1.448\,\xi min$ (Fig. 13, Appendix I). Short and long term fluctuations were thus evident in the light climate of the harbour.

The algae in the harbour influenced the amount of solar radiation they received. A significant correlation existed between ξmin and the volumetric algal biomass (mg chlorophyll a m^{-3}), indicating that the algae were self-shaded (Fig. 9). The background extinction coefficient due to non-algal components was high, estimated as 0.797 ln units m^{-1} (Fig. 9). The self-shading parameter of the population, ξ_s (ln units m^2 mg chlorophyll a^{-1}) was 0.0108 , while the daily values (Table II) gave an average value of 0.0368 ± 0.0289, uncorrected for the effect of background extinction of light. Assuming that the integral biomass in the euphotic zone; ΣB (mg chlorophyll a m^{-2}) is equal to $3.7/\xi s$ (Talling, 1971), the maximum biomass in the euphotic zone of Hamilton Harbour during the summer of 1979 was 343 mg chlorophyll a m^{-2}. The actual or observed ξ_s

TABLE II. Daily variation in light climate characteristics; the vertical extinction coefficient of PAR (ℰPAR), the euphotic zone depth (Zeu), the minimum value of the vertical extinction coefficient (ℰmin) and the surface integral light intensity (ΣIo) and the observed and theoretical algal biomass estimates and the self-shading characteristics of the phytoplankton, Hamilton Harbour, June 25 - August 18, 1979.

Date	ℰPAR[1]*		Zeu (m)*		ℰmin[1]	ΣIo[2]	chl a[3]	ℰs obs[4]	ℰs pred[5]	ΣB obs[6]	ΣB pred[6]	Cp[7]
25/06	1.629	1.598	2.82	2.88	0.836	582.8	16.80	0.0498	0.0463	74.30	80.00	19.16
26/06	1.611	1.452	2.85	3.23	0.628	587.7	31.37	0.0200	0.0182	185.00	203.84	15.30
27/06	1.511		2.97		0.921	220.0	23.25	0.0396	0.0371	93.43	99.80	15.91
28/06	1.466	1.451	3.14	3.17	0.629	580.6	19.50	0.0323	0.0292	114.55	126.58	23.72
29/06	1.556	1.490	2.96	3.09	0.638	379.9	33.47	0.0191	0.0173	194.12	213.88	14.70
30/06	1.332	1.392	3.46	3.31	0.848	82.0	27.91	0.0304	0.0283	121.79	130.88	16.31
01/07	1.589	1.824	2.89	2.52	0.579	225.4	28.67	0.0216	0.0194	171.69	191.19	15.28
02/07	1.666	1.639	2.76	2.81	0.928	527.0	30.26	0.0307	0.0287	120.64	128.34	13.82
03/07	1.513	1.556	3.04	2.96	1.112	714.3	26.27	0.0423	0.0401	87.34	92.31	15.83
04/07	1.492	1.386	3.09	3.37	0.700	397.0	21.91	0.0320	0.0293	115.81	126.47	23.98
05/07	1.120	1.397	4.11	3.30	1.148	200.5	34.63	0.0331	0.0314	111.65	117.69	14.95
06/07	1.417	1.689	3.25	2.73	1.303	630.9	43.66	0.0298	0.0235	123.99	129.85	
07/07	1.618	1.518	2.85	3.03	1.140	646.7	24.32	0.0469	0.0445	78.92	83.24	16.28
08/07	1.390	1.716	3.31	2.68	1.167	556.8	31.68	0.0368	0.0350	100.43	105.79	15.65
09/07	1.795	1.728	2.56	2.66	1.356	527.7	39.36	0.0345	0.0329	107.40	112.28	14.57
10/07	1.713	1.957	2.69	2.35	0.752	412.7	47.47	0.0158	0.0146	233.58	253.44	10.68
11/07	1.803	1.890	2.55	2.44	1.465	596.8	42.06	0.0348	0.0334	106.32	110.68	12.93
12/07	1.430	1.715	3.22	2.68	1.478	437.2	42.63	0.0347	0.0333	106.72	111.16	19.18
13/07	1.783	1.919	2.58	2.40	1.188	180.5	30.30	0.0392	0.0373	94.26	99.30	16.85
14/07	1.734	1.626	2.66	2.83	1.442	440.0	78.60	0.0184	0.0176	201.03	210.26	7.34
15/07	1.481	2.135	3.11	2.16	1.810	560.9	28.72	0.0630	0.0610	58.71	60.69	20.87
16/07	2.004	1.891	2.30	2.44	0.931	563.5	39.60	0.0235	0.0220	157.38	168.03	11.77
17/07	1.786	1.757	2.58	2.62	1.664	336.0	44.80	0.0371	0.0358	99.62	103.27	21.56
18/07	1.917	1.841	2.40	2.50	0.680	559.5	46.97	0.0149	0.0132	255.52	279.85	17.25
19/07	2.188	2.140	2.10	2.15	1.892	655.0	52.47	0.0361	0.0349	102.61	105.91	14.60
20/07	2.083	2.076	2.21	2.22	1.734	776.2	22.70	0.0761	0.0735	48.63	50.34	
21/07	2.380	2.637	1.93	1.75	1.938	457.8	26.59	0.0729	0.0710	50.77	52.36	24.07
22/07	2.482	2.634	1.85	1.75	1.629	600.8	44.72	0.0364	0.0351	101.56	105.39	21.43
23/07	2.214	2.090	2.08	2.20	1.612	460.0	69.26	0.0233	0.0224	159.00	165.01	16.56
24/07	2.215	2.205	2.08	2.09	1.812	585.0	50.34	0.0360	0.0348	102.81	106.26	15.80
25/07	1.986	1.865	2.32	2.47	1.650	465.0	35.81	0.0461	0.0444	80.29	83.28	21.18
26/07	2.056	1.959	2.24	2.35	1.522	522.1	39.92	0.0531	0.0374	69.67	98.93	18.72
27/07	1.825	1.770	2.52	3.91	1.431	324.6	44.44	0.0322	0.0309	114.91	119.84	18.98
28/07	2.053	1.787	2.24	2.58	1.376	239.5	30.12	0.0457	0.0437	81.00	84.62	21.99
29/07	1.655	1.565	2.78	2.94	1.599	112.4	27.03	0.0592	0.0570	62.08	64.94	16.29
30/07	1.568	1.449	2.94	3.18	1.210	530.0	26.37	0.0469	0.0436	80.64	84.77	18.66
31/07	1.437	1.377	3.13	3.34	1.330	384.8	27.30	0.0487	0.0466	75.94	79.47	14.50
01/08	1.310	1.336	3.52	3.45	1.028	190.5	23.63	0.0435	0.0410	85.06	90.23	21.61
02/08	1.367	1.265	3.37	3.64	1.036	508.8	33.54	0.0309	0.0291	119.73	127.02	21.18
03/08	1.399	0.941	3.29	4.89	1.103	575.3	16.96	0.0650	0.0616	56.89	60.11	27.49
04/08	1.203	1.046	3.83	4.40	0.972	592.5	27.17	0.0358	0.0336	103.44	109.99	21.65
05/08	0.994	0.909	4.63	5.07	0.945	633.9	19.45	0.0468	0.0455	76.15	81.22	24.38
06/08	1.085	1.195	4.24	3.85	0.661	591.7	19.56	0.0338	0.0308	109.50	120.22	37.26
07/08	1.191	1.055	3.87	4.37	1.255	140.0	18.84	0.0666	0.0635	55.55	58.22	39.28
08/08	1.159	1.036	3.97	4.45	0.724	196.6	33.23	0.0218	0.0200	169.80	184.89	17.59
09/08	0.994	1.102	4.63	4.18	0.699	296.3	26.58	0.0263	0.0241	140.68	153.67	23.11
10/08	1.117	1.018	4.11	4.52	0.757	272.0	35.65	0.0212	0.0196	174.28	188.97	21.17
11/08	1.255	1.210	3.67	3.81	1.155	138.3	31.95	0.0362	0.0343	102.35	107.86	20.85
12/08	1.429	1.209	3.22	3.81	0.757	665.0	51.28	0.0148	0.0136	250.68	271.83	10.75
13/08	1.393	1.327	3.30	3.47	1.263	645.0	52.20	0.0242	0.0231	152.96	160.42	14.81
14/08	1.193	1.159	3.86	3.97	1.109	518.2	42.97	0.0258	0.0244	143.36	151.24	15.67
15/08	1.237	1.188	3.72	3.88	0.909	417.7	34.17	0.0266	0.0249	139.10	148.74	17.76
16/08	1.126	1.096	4.09	4.20	0.905	297.0	27.28	0.0332	0.0310	111.55	119.31	19.12
17/08	1.357	1.031	3.39	4.47	1.174	325.1	29.66	0.0396	0.0376	93.48	98.42	17.84
18/08	1.188	1.371	3.88	3.36	1.092	90.7	30.57	0.0357	0.0338	103.58	109.50	15.24

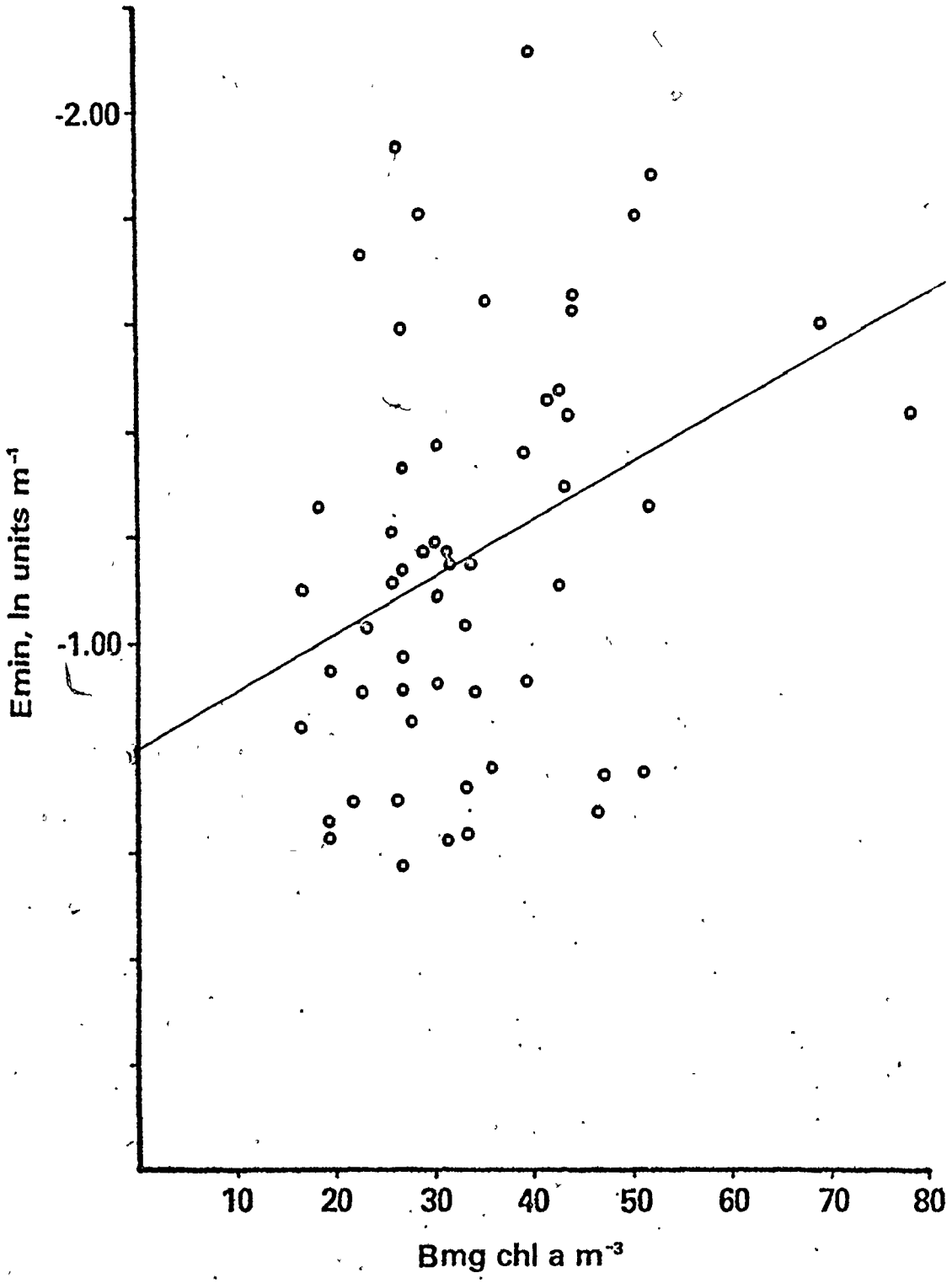
1. Units of ln units m^{-1}.
2. Integral 0.5 m irradiance in $\mu E\ m^{-2} sec^{-1}$, 1000-1400 h EDT.
3. Surface volumetric chlorophyll a value, mg chlorophyll a m^{-3}.
4. The observed or actual self-shading estimate for the algal population; ℰmin/chl a, in units m^2 mg chl a^{-1}.
5. The predicted or theoretical self-shading estimate for the algal populations, derived from the value of ℰmin corrected for the effect of DOM, in units m^2 mg chl a^{-1}.
6. The observed and predicted algal biomass estimates in the euphotic zone, derived from 3.7/ℰs obs and 3.7/ℰs pred respectively, mg chl a m^{-2}.
7. The average chlorophyll a package size, 10^7 cells mg chl a^{-1}.

* ℰPAR and Zeu, morning and afternoon estimates.

Fig. 9. ε_{min}, the minimum value of the extinction coefficient of photosynthetically available radiation, PAR in in units m^{-1} plotted against the algal biomass in mg chlorophyll a m^{-3}.

$\varepsilon_{min} = - 0.0108$ mg chlorophyll a $m^{-3} - 0.0797$

$n = 55$, $r = + 0.341$, $p < 0.01$


-2.00
-1.00
Emin, ln units m-1
10
20
30
40
50
60
70
80
Bmg chl a m-3

and ΣB values were comparable to the predicted or theoretical values of εs and ΣB (Table II). The background extinction coefficient due to DOM at the wavelength appropriate to εmin, was small (0.059 ln units m^{-1} at 575 nm), thus the relative contribution of DOM to the extinction of light was small in comparison to the attenuation due to the algae themselves. A significant, positive correlation existed between εs and the mean chlorophyll package size; Cp (10^7 cells mg chlorophyll a^{-1}) (Fig. 10).

Despite the physical fluctuations in solar irradiance, the algae in the harbour successfully controlled their own light climate. The temporal fluctuations in Zeu and εPAR (Fig. 12, Appendix I) followed changes in volumetric chlorophyll a (Fig. 22, Appendix I) and the numerical abundance of the algae (Fig. 23, Appendix I).

III. 4.0 <u>The Zeu/Zm Ratio</u>

Fluctuations in the Zeu/Zm ratio were caused by changes in the euphotic zone depth, Zeu and in the mixing depth, Zm (Table III). Zeu showed little daily variability and followed a pattern of slow rise and decline corresponding to changes in the algal biomass (Fig. 11b). Zeu declined steadily from June (2.5 - 3.5 m) to its minimum value in late July (1.7 m), rose to its maximum value (5.07 m) in early August, then declined and remained stable near the end of the sampling period. Daily, in situ estimates of Zeu gave a mean $\pm$ 2 SEM value of 3.12 $\pm$ 0.15 m. Zm, on the other hand, was highly variable on a daily basis and often changed significantly from the morning to afternoon in situ estimates

Fig. 10. εs, the self-shading parameter of the algal populations, in ln units m^2 mg chlorophyll a^{-1} plotted against the mean chlorophyll a package size, Cp, 10^7 cells mg chlorophyll a^{-1}.

$\varepsilon s = 0.0012\ Cp + 0.0138$, $n = 53$

$r = + 0.499$, $p < 0.001$

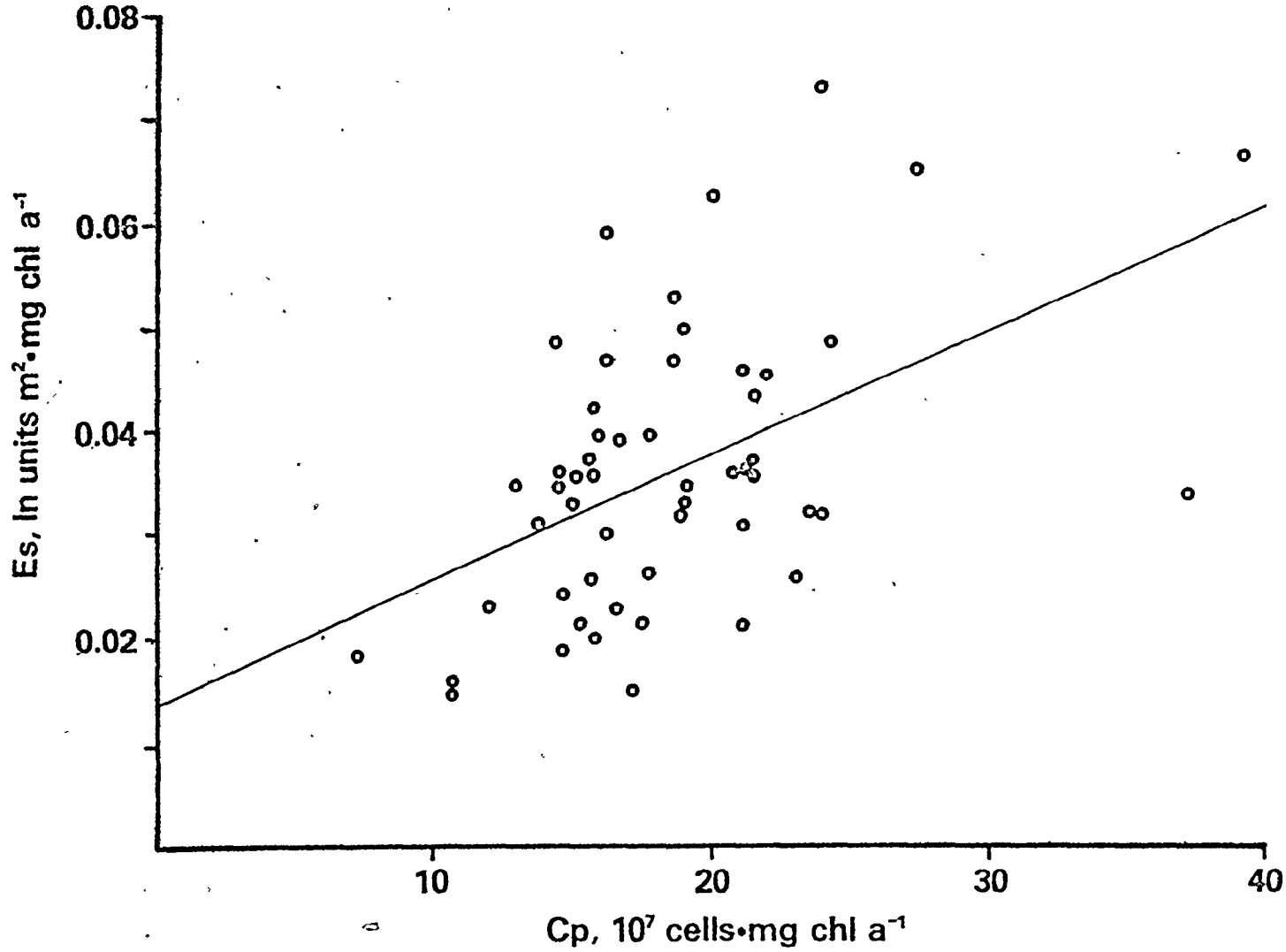

0.08
0.06
0.04
0.02
Es, In units m²•mg chl a⁻¹
10
20
30
40
Cp, 10⁷ cells•mg chl a⁻¹

Table III. Variation in average daily wind speed (μ), mixing depth (Z_m), euphotic zone depth (Z_{eu}), the euphotic zone/mixing zone depth ratio (Z_{eu}/Z_m) and i^2 stability numbers with time in Hamilton Harbour, June 25 - August 18, 1979.

Date	μ (m sec^{-1})	Z_m(m)*		Z_{eu}(m)*		Z_{eu}/Z_m*		N^2(sec^{-2})
25/06	4.95	7	7	2.82	2.88	0.403	0.412	325.30
26/06	3.07	6	7	2.85	3.23	0.475	0.462	393.39
27/06	8.10	7	6	2.97		0.424		419.89
28/06	4.07	7	7	3.14	3.17	0.449	0.453	633.90
29/06	5.42	8	8	2.96	3.09	0.370	0.386	330.15
30/06	6.68	8	8	3.46	3.31	0.433	0.414	33.60
01/07	6.27	5	6	2.89	2.52	0.578	0.420	[illegible]
02/07	6.50	6	5	2.76	2.81	0.460	0.562	825.48
03/07	4.24	5	6	3.04	2.96	0.608	0.493	462.09
04/07	3.94	9	10	3.09	3.37	0.343	0.337	664.94
05/07	6.30	6	5	4.11	3.30	0.685	0.660	415.57
06/07	4.16	5	9	3.25	2.73	0.650	0.303	594.26
07/07	2.59	6	6	2.85	3.03	0.475	0.550	756.66
08/07	1.55	5	6	3.31	2.68	0.662	0.447	1294.66
09/07	6.11	3	4	2.56	2.66	0.853	0.665	1297.33
10/07	6.10	2	3	2.69	2.35	1.345	0.783	1409.98
11/07	3.64	3	3	2.55	2.44	0.850	0.813	1606.09
12/07	2.84	4	3	3.22	2.68	0.805	0.893	2026.79
13/07	4.32	2	3	2.58	2.40	1.290	0.800	2325.09
14/07	2.12	3	3	2.66	2.83	0.887	0.943	2576.65
15/07	4.12	3	3	3.11	2.16	1.037	0.720	2574.21
16/07	4.68	3	3	2.30	2.44	0.767	0.813	2522.59
17/07	5.76	5	6	2.58	2.62	0.516	0.437	582.64
18/07	4.25	5	5	2.40	2.50	0.480	0.500	1654.57
19/07	3.00	5	4	2.10	2.15	0.420	0.538	2063.99
20/07	3.38	6	5	2.21	2.22	0.368	0.444	1724.55
21/07	4.40	5	7	1.93	1.75	0.386	0.253	1439.62
22/07	4.76	5	4	1.85	1.75	0.370	0.438	1509.72
23/07	3.94	4	4	2.08	2.20	0.520	0.550	1300.47
24/07	4.48	4	5	2.03	2.09	0.520	0.418	1714.55
25/07	7.83	7	5	2.32	2.47	0.331	0.494	1057.75
26/07	7.51	5	5	2.24	2.35	0.448	0.470	1372.08
27/07	1.74	6	5	2.52	3.91	0.420	0.782	1185.74
28/07	5.35	5	6	2.24	2.58	0.448	0.430	1533.08
29/07	3.13	6	6	2.78	2.94	0.463	0.490	1080.65
30/07	1.54	5	5	2.94	3.18	0.588	0.636	1640.50
31/07	5.66	3	3	3.13	3.34	1.043	1.113	1785.58
01/08	6.51	5	6	3.52	3.45	0.704	0.575	823.04
02/08	5.70	5	4	3.37	3.64	0.674	0.911	1395.91
03/08	5.91	5	5	3.29	4.89	0.658	0.978	1339.18
04/08	2.49	5	6	3.83	4.40	0.766	0.733	1552.62
05/08	4.85	5	4	4.63	5.07	0.926	1.268	1160.63
06/08	7.44	6	7	4.24	3.85	0.707	0.550	80.44
07/08		5	5	3.87	4.37	0.774	0.874	1149.58
08/08	6.27	6	6	3.97	4.45	0.662	0.742	738.75
09/08	7.20	6	7	4.63	4.18	0.772	0.597	440.81
10/08	9.22	6	4	4.11	4.52	0.685	1.130	1147.02
11/08	5.43	7	8	3.67	3.81	0.524	0.476	145.08
12/08	4.05	7	9	3.22	3.81	0.460	0.423	77.07
13/08	8.16	7	6	3.30	3.47	0.471	0.578	251.45
14/08	9.03	8	5	3.86	3.97	0.483	0.794	476.04
15/08	6.05	10	9	3.72	3.88	0.372	0.431	309.22
16/08	5.37	8	10	4.09	4.20	0.511	0.420	155.19
17/08	5.29	8	8	3.39	4.47	0.424	0.559	287.72
18/08	4.47	9	8	3.88	3.36	0.431	0.420	62.31

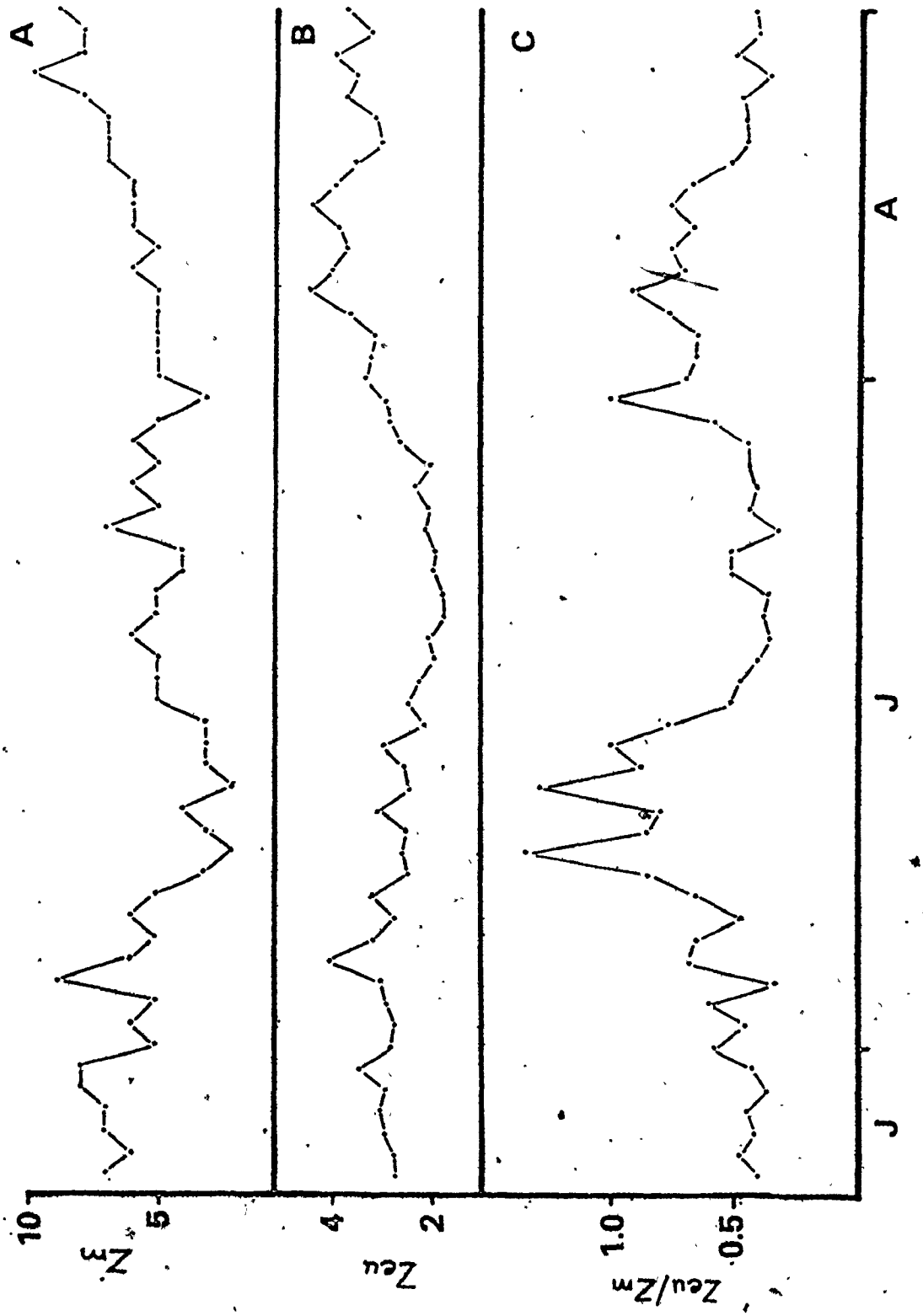
* Morning and afternoon estimates.

Fig. 11. Variation in the morning mixing depth, euphotic zone depth and the Zeu/Zm ratio with time; June 25 - August 18, 1979.

A. Zm, the mixing depth (m)

B. Zeu, the euphotic zone depth (m)

C. Zeu/Zm ratio


A
B
C
10
5
4
2
1.0
0.5
Z_m
Z_{eu}
Z_{eu}/Z_m
J
J
A

(Fig. 11a). Zm ranged from 5 - 10 m during periods of active vertical mixing and from 2 - 6 m during periods of thermal stability and stratification (Table III). Daily in situ estimates of Zm gave a mean ± 2 SEM value of 5.64 ± 0.35 m.

The Zeu/Zm ratio fluctuated daily, ranging from 0.33 - 1.34 and was largely driven by the short term variability in Zm (Fig. 11c). The Zeu/Zm ratio remained low (< 0.5) during June, rose to higher values (0.70 - 1.34) in early July and declined in late July (0.30 - 0.60). A second peak in the Zeu/Zm ratio occurred in early August (0.50 - 1.20) followed by a second decline in mid August (0.30 - 0.50) (Fig. 11c). Since the phytoplankton contributed to the value of Zeu, the variability in Zm was the primary factor determining the response of the algae to variability in the Zeu/Zm ratio.

III. 5.0 In Vivo Fluorescence

The in vivo fluorescence characteristics of the Hamilton Harbour phytoplankton population showed short term variability and regulation in response to high frequency fluctuations in the underwater light fields and the stability of the water column. In vivo fluorescence (IVF) showed no consistent depth pattern and was highly variable from day to day. F + DCMU, the DCMU induced fluorescence values were low in surface and aphotic waters and also varied daily. The F ratio (F + DCMU/IVF) was generally low at the surface and in aphotic waters, but maximal F ratios occurred at the surface on several occasions (Fig. 14, Appendix I). Maximum F ratios usually occurred at or just below the 1% Io light level.

At similar light intensities, the depth effect on F ratios lessened with increasing wind speeds above 5 m sec^{-1} (Fig. 15, Appendix I). F ratios decreased with increasing irradiance in stable water columns and increased under similar irradiance conditions during vertical mixing. A statistically significant relationship was noted between ΔF, the difference between surface and maximal F ratios and wind speed (Fig. 12). With increasing wind speed and active vertical mixing, ΔF decreased as the depth effect on the fluorescence profiles diminished. Vertical mixing in the water column reduced photoinhibition of in vivo fluorescence.

Fluctuations in F ratios and R values; the fluorescence per unit chlorophyll a value, were related to changes in water column stability (Fig. 13). High F ratios were associated with low N^2 values and Zeu/Zm ratios, indicative of mixing conditions, while low F ratios were associated with moderate to high values of N^2 and high Zeu/Zm ratios, representing stable, thermally stratified periods. High R values in June corresponded to low N^2 numbers and Zeu/Zm ratios and R values decreased as N^2 and the Zeu/Zm ratio increased in mid July with the onset of thermal stratification (Fig. 13). Low R values late in the season resulted from a period of stability in early August and changes in the community structure.

The in vivo fluorescence response by Hamilton Harbour algal populations represented the shortest term physiological response to environmental fluctuations in irradiance, mixing depth and water column stability. The algae were capable of rapid regulation of F ratios and R values, which enabled them to cope with short term environmental variability.

Fig. 12. μ, the average daily wind speed in m sec^{-1}, plotted against ΔF, the daily change from the maximum to surface value of the fluorescence ratio.

$$\mu = 5.9678\ e^{-0.4866\,\Delta F}$$

$$n = 47,\ r = +0.291,\ p\ \ 0.05$$

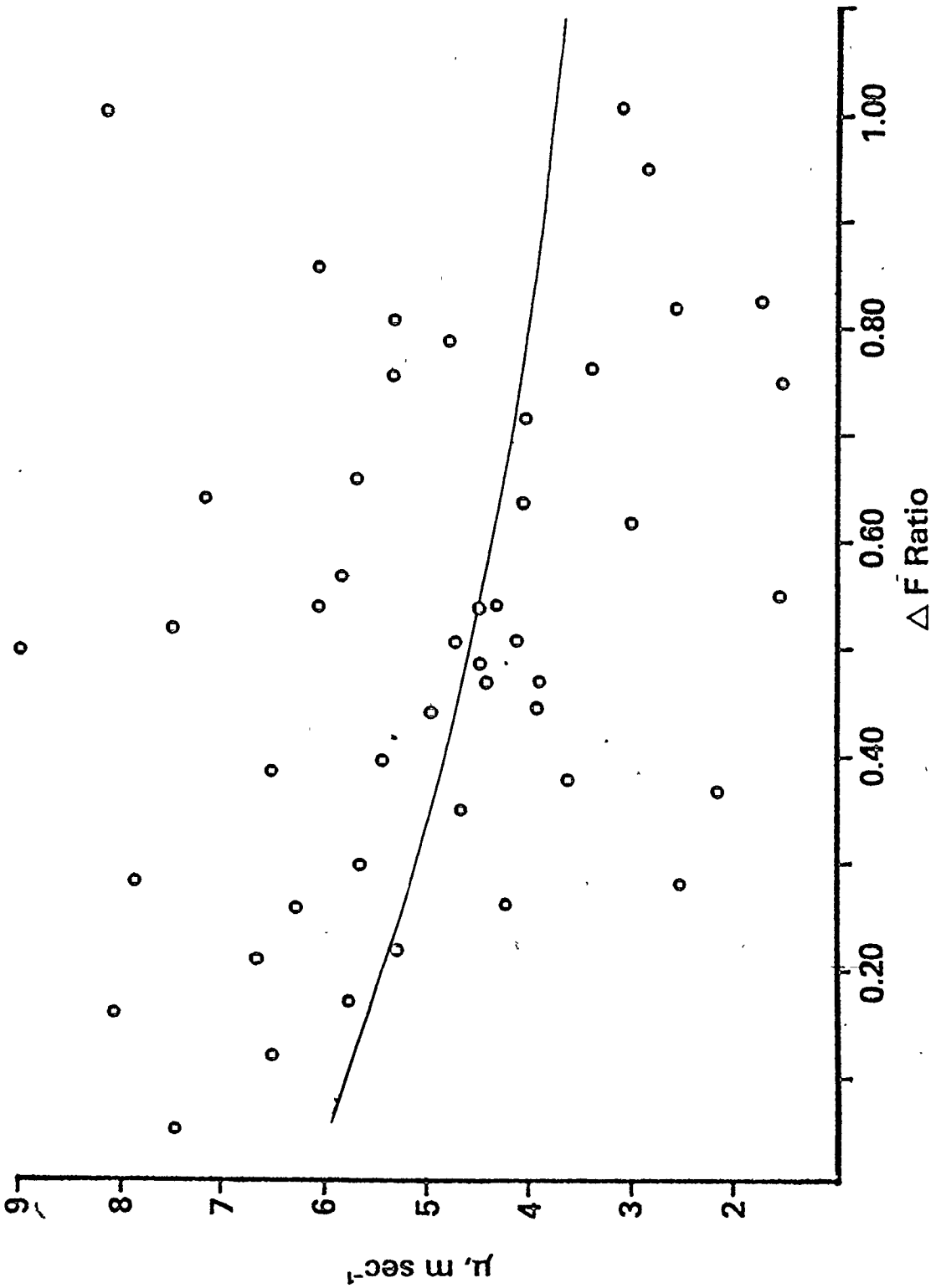

μ, m sec⁻¹
9
8
7
6
5
4
3
2
0.20
0.40
0.60
0.80
1.00
Δ F Ratio

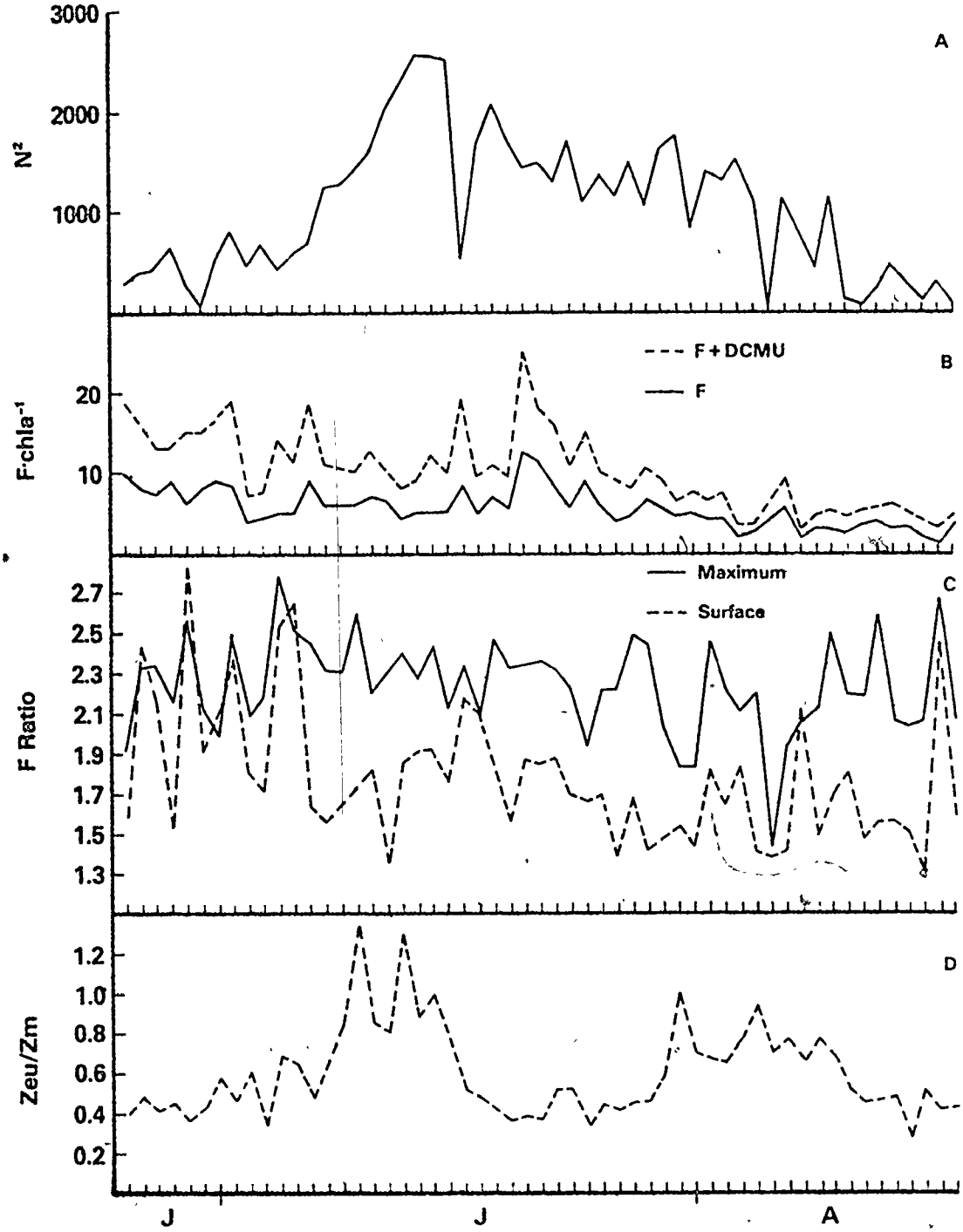
Fig. 13. Variation in the physical environment and fluorescence properties of the Hamilton Harbour phytoplankton population with time; June 25 - August 18, 1979.

A. Noon 0 - 6 m N^2 stability numbers

B. F + DCMU and F ratios per mg chlorophyll a, 1 m

C. Maximal and surface F + DCMU/IVF ratios.

D. Morning Zeu/Zm ratio


3000
2000
1000
N²
A
F+DCMU
F
B
20
10
F·chla⁻¹
Maximum
Surface
C
2.7
2.5
2.3
2.1
1.9
1.7
1.5
1.3
F Ratio
D
1.2
1.0
0.8
0.6
0.4
0.2
Zeu/Zm
J
J
A

III. 6.0 Photosynthetic Measurements and Photosynthetic Parameters

III. 6.1 In Situ Photosynthesis

In situ integral productivity, $\sum P$ (mg C $m^{-2}h^{-1}$) ranged from 23.25 - 232.20 mg C $m^{-2}h^{-1}$ and was highly variable on a daily basis (Fig. 14a; Appendix III). The maximum volumetric rate of photosynthesis, max Pv (mg C $m^{-3}h^{-1}$) ranged from 34.22 - 289.92 mg C $m^{-3}h^{-1}$, was highly variable with time and resembled changes observed in $\sum P$ with time (Appendix III). Max Pv occurred most frequently in the surface bottles and surface photoinhibition was not a predominant phenomenon during the summer of 1979. Extensive day to day variability was also noted in three photosynthetic parameters; Pmax (mg C mg chl $a^{-1}h^{-1}$), the assimilation number or photosynthetic capacity, Pe (mg C mg chl $a^{-1}E^{-1}h^{-1}$) and Ik ($\mu E\ m^{-2}sec^{-1}$)(Fig. 14b,c,d; Appendix III).

Daily variability in photosynthetic parameters was directly linked with environmental variability. Pmax was generally low, ranging from 0.86 - 10.42 mg C mg chl $a^{-1}h^{-1}$ and was positively correlated with the average surface water temperature during the in situ incubation period (Fig. 16, Appendix I). Pmax was positively correlated with Pe (Fig. 17, Appendix I) and with Ik (Pe = 0.0031 Ik + 2.163). High Pmax values corresponded with rising values of Pe and Ik. Pe ranged from 1.13 - 18.69 mg C mg chl $a^{-1}E^{-1}h^{-1}$ and was correlated with Ik (Fig. 18, Appendix I). Ik ranged from 44 - 830 $\mu E\ m^{-2}sec^{-1}$ and its daily variability corresponded to the variability in $\sum Io$ over the previous 2 day period (Fig. 19,

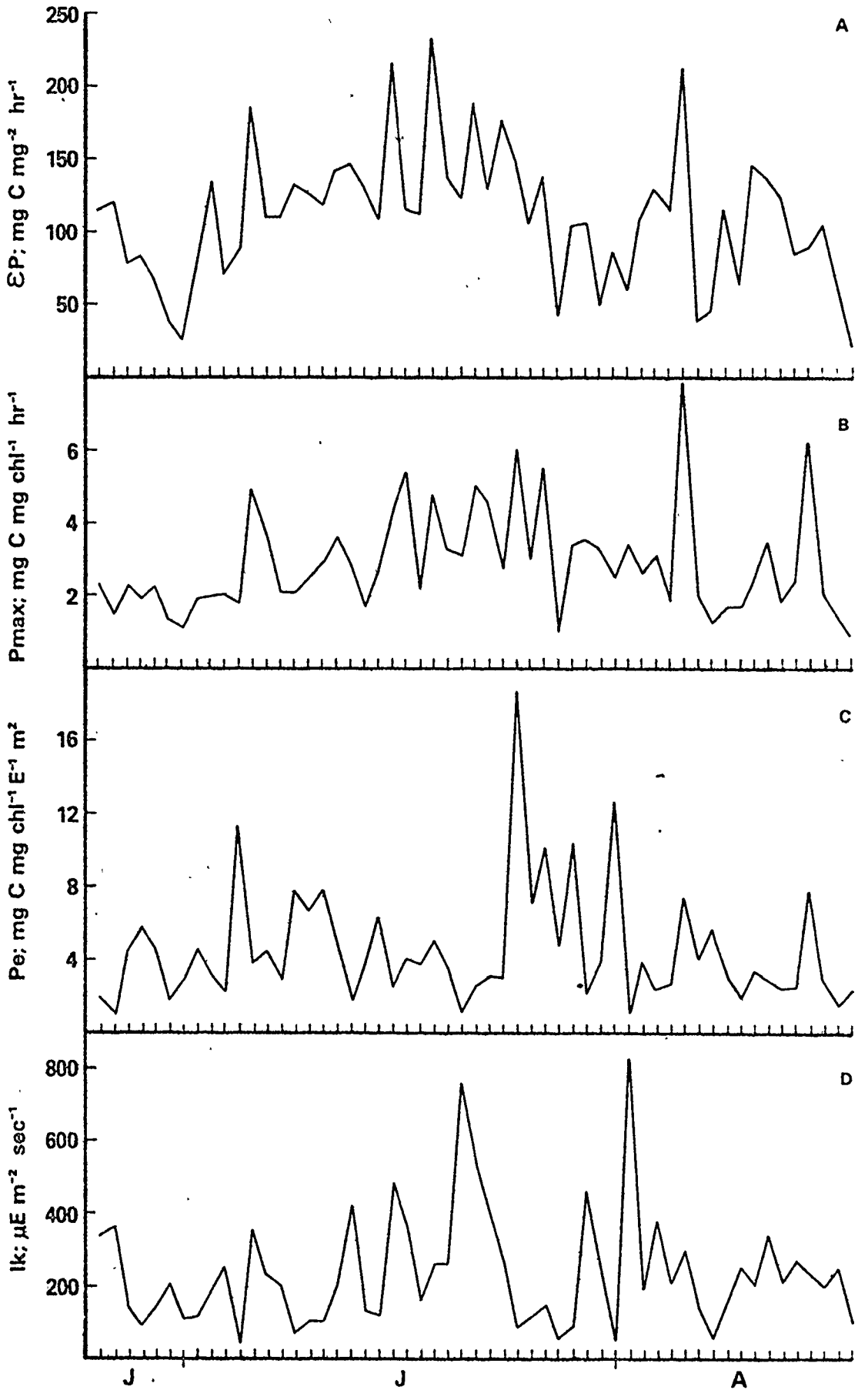
Fig. 14. Variation in the primary productivity and photosynthetic parameters of the Hamilton Harbour phytoplankton population with time; June 25 - August 18, 1979.

A. In situ integral productivity; $\sum P$, mg C $m^{-2}h^{-1}$

B. Photosynthetic capacity; Pmax, mg C mg chl $a^{-1}h^{-1}$

C. Photosynthetic efficiency; Pe, mg C mg chl $a^{-1}E^{-1}m^{2}$

D. Ik, $\mu E\ m^{-2}sec^{-1}$


A
B
C
D
ΣP; mg C mg⁻² hr⁻¹
Pmax; mg C mg chl⁻¹ hr⁻¹
Pe; mg C mg chl⁻¹ E⁻¹ m²
Ik; µE m⁻² sec⁻¹
250
200
150
100
50
6
4
2
16
12
8
4
800
600
400
200
J
J
A

Appendix I). High Ik values corresponded to low Pe values (Fig. 18, Appendix I), indicative of high light adaptation by the algae. Ik and surface water temperature were not significantly correlated, despite the known dependence of Ik on temperature through Pmax (Talling, 1957a,b).

III. 6.2 Tank Photosynthesis

The daily maximum volumetric rates of photosynthesis, max Pv, derived from the four populations in the incubator tank were lower than in situ max Pv rates, due to biomass differences and light limitation in the tank. The highest tank irradiance (235 $\mu E\ m^{-2}sec^{-1}$) was generally lower than the integral average irradiance at the depth of the in situ max Pv estimate and corresponded to in situ irradiance levels at 0.3 - 1.0 m depths. Photoinhibition of photosynthesis was not observed in the tank, due to light limitation and the low incidence of in situ surface photoinhibition during the experimental period.

The daily variation in the Pmax and max Pv rates recorded from the four tank populations resulted from the short term environmental variability. The daily variation ensured that analysis of variance was unsuccessful in determining the presence or absence of depth differentiated algal populations in the water column. The analysis of variance (Factorial design, two way classification) for the Pmax estimates at 0.2, 1.0, 2.0 and 4.0 m (Appendix IV) revealed that the individual effects of depth (A) and day or time (B) were significant over the entire fifty-five day experimental period (Table IV). A significant depth-day

Table IV. Analysis of variance table for the daily estimates of photosynthetic capacity, Pmax (mg C mg chlorophyll $a^{-1}h^{-1}$) exhibited by algal populations sampled from depths of 0.2, 1.0, 2.0 and 4.0 m; Hamilton Harbour, Lake Ontario, June 25 - August 18, 1979.

Source	Sum of Squares	Degrees of freedom	Mean Square	F	P
A(depth)	7.1775	3	2.3925	20.9810	<0.01
B(day)	365.7083	54	6.7724	59.3903	<0.01
AB(interaction)	125.6295	162	0.7755	6.8007	<0.01
Error	25.0869	220	0.1140		
Total	523.6022	439			

interaction was noted but did not lend itself to further analysis, due to the fact that several, inseparable factors (wind speed, water column stability and mixing depth fluctuations) contributed to the variability in the day factor and were in part, responsible for the day-depth interaction. The daily variability in Pmax was much greater than the variability with depth among the four populations. The high frequency vertical mixing processes in the harbour prevented depth stratification of the algal populations, in terms of the cells exhibiting statistically different rates of photosynthesis at the various depths, over extended periods of time.

III. 6.3 Environmental variability; the Zeu/Zm ratio and variability in Photosynthetic Capacity; Pmax.

Cross spectral analysis techniques proved useful in providing insight into the temporal response scales between environmental variability and physiological change in the photosynthetic capacity of the phytoplankton populations. Autocovariance and power spectral analysis performed on the Zeu/Zm time series indicated that the highest variance estimates and the strongest periodicities in the data series occurred at scales of 24 days. No statisitically significant short term periods were evident in the data, indicating that day to day variability in the Zeu/Zm ratio was random (Fig. 11c). Power spectral analysis of the five Pmax time series; Pmax in situ, Pmax at 0.2 m, 1.0 m, 2.0 m and 4.0 m, also showed high variance estimates at frequencies of 0.0833 - 0.0417 cycles day^{-1} and strong 12 - 24 day periods .

Pmax time series also exhibited statistically significant short term periodcities in the 2 - 4 day range, a time scale comparable to the average generation time of 2.50 days observed for algal cells in Hamilton Harbour (Harris, 1980a; Harris et. al., 1980b).

Cross spectral analysis between the Zeu/Zm ratio time series and the five Pmax estimate data series indicated several significant periods over which the value of Pmax lagged the daily values of the Zeu/Zm ratio (Table V). Peak cross-covariance estimates occurred at different number of day lags in the five series, however the highest variance in each case occurred when Pmax lagged the Zeu/Zm ratio by 5 or 6 days. In other words, the daily value of the Zeu/Zm ratio was reflected in the value of Pmax exhibited by the phytoplankton populations 5 or 6 days later (Table V).

High values of the cross-spectral estimate (the variance estimate between two time series at specific, fundamental frequencies of the time series) indicate high variance functions for one or both of the time series examined at the specific frequency examined. A high cross-spectral estimate in combination with a high coherence squared value (correlation coefficient) at a specific frequency, is a good indication of high variance for the two data series and high correlation coefficients between points of both data series at that frequency. The reciprocal value of the specific frequency represents a statistically significant period in the two data series over which one time series lags or leads the other.

Table V. Results of cross-spectral analysis between the daily Zeu/Zm ratio (series 1) and the daily photosynthetic capacity; Pmax (series 2) time series, Hamilton Harbour, Lake Ontario, June 25 - August 18, 1979. The daily Zeu/Zm time series are compared with five Pmax time series; Pmax in situ, and Pmax from populations sampled at depths of 0.2, 1.0, 2.0 and 4.0 m.

Variables	Number of lags (days)[1]	Cross-covariance estimates of series 1 and 2	Period (days)	Cross-spectral estimates of series 1 and 2	Coherence Squared (r^2)
Zeu/Zm vs.	10.00	-0.06577	2.40	-0.04169*	0.4308
Pmax in	9.00	-0.05894	2.67	-0.03402	0.2753
situ	12.00	-0.05588	4.00	-0.03399	0.2220
	5.00	-0.05215	4.81	-0.01812	0.2248
	7.00	-0.05014	6.00	+0.01459	0.2912
Zeu/Zm vs.	10.00	-0.04231	2.67	-0.02793*	0.3358
Pmax 0.2 m	2.00	-0.03215	2.40	-0.01548	0.1995
	12.00	-0.02577	3.00	-0.01240	0.1231
	5.00	-0.02476	6.00	+0.00986	0.3438
	9.00	-0.02171	4.81	-0.00269	0.3637
Zeu/Zm vs.	5.00	-0.05898	∞	-0.04598*	0.0608
Pmax 1.0 m	0.00	-0.03490	4.81	-0.02428	0.3682
	2.00	-0.03374	2.40	-0.02371	0.2811
	10.00	-0.02743	2.67	-0.02184	0.2840
	6.00	-0.02721	6.00	+0.00729	0.1238
Zeu/Zm vs.	6.00	-0.03212	∞	-0.03719*	0.0805
Pmax 2.0 m	3.00	-0.03059	23.81	-0.03258	0.1183
	2.00	-0.02790	12.05	-0.01296	0.1406
	0.00	-0.02346	2.67	-0.00963	0.0624
	1.00	-0.02215	2.00	+0.00177	0.3539
Zeu/Zm vs.	0.00	-0.05052	∞	-0.06249*	0.0807
Pmax 4.0 m	12.00	+0.03672	2.40	-0.03244	0.3067
	1.00	-0.03585	2.67	-0.02208	0.3164
	5.00	-0.03404	2.18	-0.01314	0.2919
	2.00	-0.02576	2.00	+0.00003	0.6865

* Denotes maximum cross-spectral estimates.

1. Number of day lags for the cross-covariance estimates.

2. Period of the cross-spectral estimates.

The highest cross-spectral estimates for the Pmax in situ and Pmax at 0.2 m and the Zeu/Zm ratio data series occurred at periods of 2.40 and 2.67 days respectively, with high correlation coefficients between the series. The coherence squared value between the Zeu/Zm and Pmax at 0.2 m time series was also high with a lag of 4.81 days. The Pmax at 1.0 m, Pmax at 2.0 m and Pmax at 4.0 m time series showed highest cross-spectral estimates with the Zeu/Zm ratio time series at long term periodicities (∞). The coherence squared values were not statisitically significant at these periods, however. High values of both the cross-spectral estimated and the coherence squared were noted at 2.00 - 2.67 day periods for the three analyses. The high coherence squared values combined with high cross-spectral estimates indicated that the daily value of the five Pmax estimates lagged the value of the Zeu/Zm ratio at periods of 2.00 - 2.67, 4.00 - 4.81 and 6.00 days (Table V), representative of one or more generation time periods for the algal cells in the harbour.

The high cross-spectral estimates obtained between the time series representing changes in the Zeu/Zm ratio over one, two and three day periods (Δ Zeu/Zm -1, ΔZeu/Zm -2 and ΔZeu/Zm -3) and the daily in situ Pmax time series indicated that in situ Pmax responded most strongly to changes in the magnitude of the Zeu/Zm ratio (Table VI). The cross covariance estimates showed that in situ Pmax responded negatively to large increases in the Zeu/Zm ratio at scales of 5.0, 4.0 and 3.0 days for ΔZeu/Zm -1, ΔZeu/Zm -2 and ΔZeu/Zm -3, respectively. In situ Pmax

Table VI. Results of cross-spectral analysis between the change in the Zeu/Zm ratio from the daily estimate to one day before; Zeu/Zm -1 , from two days before; Zeu/Zm -2 and from three days before; Zeu/Zm -3 (series 1) and the daily in situ photosynthetic capacity; Pmax (series 2) time series, Hamilton Harbour, Lake Ontario, June 25 - August 18, 1979.

Variables	Number of lags (days)[1]	Cross-covariance estimates of series 1 and 2	Period (days)[2]	Cross-spectral estimates of series 1 and 2	Coherence Squared (r^2)
Zeu/Zm	5.00	-0.12594	2.40	-0.06763*	0.4490
-1 vs.	7.00	+0.06605	2.67	-0.05905	0.2978
Pmax	0.00	-0.06432	4.81	-0.05022	0.2712
	12.00	+0.05517	4.00	-0.03472	0.3033
	8.00	-0.04970	6.00	-0.01144	0.2273
Zeu/Zm	6.00	+0.09248	∞	-0.06414*	0.1394
-2 vs.	4.00	-0.07615	4.00	-0.06230	0.2974
Pmax	8.00	-0.06985	4.81	-0.03518	0.2469
	11.00	+0.06922	2.67	-0.02335	0.6556
	0.00	-0.06604	2.40	-0.02033	0.4577
Zeu/Zm	3.00	-0.12026	∞	-0.09850*	0.1826
-3 vs.	8.00	-0.06550	4.00	-0.04541	0.3975
Pmax	4.00	-0.06415	2.40	-0.01836	0.3520
	6.00	+0.05925	2.67	-0.01102	0.3839
	0.00	-0.05504	4.81	-0.00979	0.03433

* Denotes maximum cross-spectral estimate

1. Number of day lags for the cross-covariance estimates.

2. Period of the cross-spectral estimates.

lagged behind increases or decreases in the value of the Zeu/Zm ratio by 6.0 days.

The maximum cross covariance estimate and a high coherence squared value occurred between ΔZeu/Zm -1 and in situ Pmax with a lag of 2.40 days and a second, strong periodicity was noted at 4.81 days. Cross-spectral estimates between ΔZeu/Zm -2 and ΔZeu/Zm -3 and Pmax were highest at long temporal scales (∞), but the correlation coefficients were low. Periods in the 2.40 - 2.67 and 4.00 - 4.81 day range were highly significant. In situ Pmax responded to changes in the magnitude of the Zeu/Zm ratio over one or two average generation times for ΔZeu/Zm -1, over one, two or three average generation times for ΔZeu/Zm -2 and over two or three generation times for ΔZeu/Zm -3.

III. 6.4 Environmental variability; The Zeu/Zm ratio and variability in photosynthetic efficiency; Pe.

The average cellular generation time of the phytoplankton (or some multiple) represented an important lag period between Pe, the in situ photosynthetic efficiency of the cells and the value of the Zeu/Zm ratio, when Zm was compared on the same day, one and two days before (Table VII). Autocovariance and power spectral analysis of the $\frac{\text{Zeu same day}}{\text{Zm same day}}$ ratio, $\frac{\text{Zeu same day}}{\text{Zm day before}}$ ratio and the $\frac{\text{Zeu same day}}{\text{Zm two days before}}$ ratio time series indicated high variance and statistically significant periodicities at scales of 24 days. Pe, not unlike the in situ Pmax time series, showed high variance and highest power spectral estimates at long term (24 day)

Table VII. Results of cross-spectral analysis between the daily in situ photosynthetic efficiency; Po (series 1) and the $\frac{Zeu}{Zm}$ ratio on the same day, the $\frac{Zeu\ same\ day}{Zm\ day\ before}$ ratio and the $\frac{Zeu\ same\ day}{Zm\ two\ days\ before}$ ratio (series 2), Hamilton Harbour, Lake Ontario, June 25 - August 18, 1979.

Variables	Number of lags (days)[1]	Cross-covariance estimates of series 1 and 2	Period (days)[2]	Cross-spectral estimates of series 1 and 2	Coherence Squared (r^2)
Po vs.	7.00	-0.26109	2.40	-0.08199*	0.1793
$\frac{Zeu\ same\ day}{Zm}$	8.00	-0.20878	4.81	+0.06184	0.4917
	3.00	-0.16042	23.81	+0.06126	0.4042
	12.00	+0.12919	6.00	+0.04006	0.4935
	1.00	+0.08682	2.00	+0.03039	0.6282
Po vs.	6.00	-0.26992	2.40	+0.12261*	0.6293
$\frac{Zeu\ same\ day}{Zm\ 2\ before}$	4.00	-0.19710	6.00	+0.09591	0.6520
	7.00	-0.17149	2.67	+0.08866	0.4689
	9.00	-0.16693	4.81	+0.07941	0.3381
	0.00	+0.16002	4.00	+0.06163	0.1584
Po vs.	5.00	-0.23206	3.42	+0.09768*	0.1688
$\frac{Zeu\ same\ day}{Zm\ 3\ before}$	3.00	-0.19184	6.00	+0.09034	0.4617
	6.00	-0.18397	2.00	+0.02854	0.4378
	8.00	-0.17110	23.81	-0.07616	0.4279
	12.00	+0.16238	∞	-0.03055	0.4180

* Denotes maximum cross-spectral estimate

1. Number of day lags for the cross-covariance estimates.

2. Period of the cross-spectral estimates.

periodicities, with a statistically significant short term period of 2.00 - 3.42 days.

Cross covariance analysis indicated that the variance was highest between the time series when in situ Pe lagged the value of $\frac{Zeu \text{ same day}}{Zm \text{ same day}}$ by 7.0 days, the $\frac{Zeu \text{ same day}}{Zm \text{ day before}}$ by 6.0 days and the $\frac{Zeu \text{ same day}}{Zm \text{ two days before}}$ by 5.0 days. In situ Pe responded negatively to high values of the Zeu/Zm ratio with a 7.0 day lag, since the daily variation in Zeu (Fig. 11a) was not high and the determining variable in the analysis was the value of Zm. The highest cross-spectral estimates for the time series occurred at scales of 2.40, 2.40 and 3.42 days for the three respective analyses (Table VII). The coherence squared value was high at the 2.40 day period for the in situ Pe and the $\frac{Zeu \text{ same day}}{Zm \text{ day before}}$ time series. High coherence squared and cross-spectral estimates indicated that the 2.00 - 2.67, 4.81 and 6.00 day periods were statistically significant in relating changes in the value of Zm and its effect on the Zeu/Zm ratio, to changes in in situ Pe. The 6.00 day lag period showed high correlation coefficients between the two series in all three analyses, suggesting that roughly three generation times are needed for the full expression of environmental change in the value of in situ Pe.

The average cellular generation time in Hamilton Harbour clearly represented a fundamental lag period between the value or magnitude of change for the Zeu/Zm ratio over short temporal scales and changes in the values of in situ Pmax and Pe.

III. 7.0 The Phytoplankton Community

III. 7.1 Chlorophyll a Biomass

Algal biomass (mg chlorophyll a m^{-3}) was primarily distributed in the top 8 m (epilimnion) of the water column (Fig. 20, Appendix I). The vertical distribution of chlorophyll a was patchy, with subsurface and deep hypolimnial patches, the result of erratic mixing and sinking of heavy cells during stable periods. The mean surface biomass ranged from 20 - 90 mg chlorophyll a m^{-3}, with a major bloom occurring in mid July (40 - 90 mg chlorophyll a m^{-3}), followed by a slight decline in biomass and a second bloom in mid August (50 - 60 mg chlorophyll a m^{-3}). Both blooms occurred during periods of thermal stability. Hypolimnial chlorophyll a was low (10 - 30 mg chlorophyll a m^{-3}), representing the presence of sinking algal cells or chlorophyll degradation products.

III. 7.2 Seasonal Species Succession

A total of forty-three previously recorded species were sampled from the harbour during the summer of 1979 (Appendix V). Late spring species (*Asterionella* sp., *Ankistrodesmus* sp., *Dictyosphaerium* sp. and *Stephanodiscus* spp.) were present at the onset of sampling, along with members of the Desmidaceae (*Closterium* sp., *Staurastrum* sp. and *Cosmarium* sp.), some flagellates (*Cryptomonas erosa*, *Rhodomonas* sp. and *Chlamydomonas* sp.) and members of the Chlorophyta (Fig. 21, Appendix I). With increasing epilimnial temperatures and the onset of thermal stratification in July, the

spring species were displaced by increasing numbers of large, green algae, such as Coelsatrum sp., Planktosphaeria sp., Oocystis borgeii and Pediastrum spp. (Fig. 21, Appendix I). Scenedesmus quadricauda and Lagerheimia sp. also increased in abundance during this period, while heavier, larger species such as the diatom Stephanodiscus sp., members of the Desmidaceae and Cryptomonas erosa, were found in decreasing numbers (Fig. 21, Appendix I). With the onset of active vertical mixing at the end of July and decreasing water temperatures in early August, early fall species such as Cyclotella sp., Melosira italica and Cryptomonas erosa increased in abundance (Fig. 21, Appendix I).

The expected relationship was observed between integral (0 - 8 m) chlorophyll concentrations, the surface chlorophyll a values (Fig. 22, Appendix I), and the total abundance of algal cells (cells ml^{-1}) (Fig. 23, Appendix I). Both integral and surface chlorophyll a values showed daily variation and similar vertical distribution patterns, with integral values consistently lower than the mean surface values. Variation in cellular numerical abundance with time (Fig. 23, Appendix I) showed a similar pattern, increasing to a peak in mid July, falling off late in July and rising again to a second peak in mid August. Futhermore, the increase in algal biomass in mid-July was due to an increase in the colonial green species such as Coelastrum sp. and Pediastrum spp. (Fig. 21, Appendix I).

III. 7.3 The Phytoplankton Community and Environmental Variability

Cross-spectral analysis between the numerical abundance time series for the eight major phytoplankton species in the harbour (Chlamydomonas sp., Coelastrum spp., Oocystis borgeii, Scenedesmus quadricauda, Stephanodiscus spp., Cyclotella spp., Cryptomonas spp., and Rhodomonas sp.) and the N^2 stability numbers time series indicated several statistically significant temporal scales of response by the cells to environmental change. The maximum value of the autocovariance function occurred at 0 day lags for the eight species and the maximum power spectral estimates indicated that the most significant internal periodicity in the abundance data occurred in the 23.8 day range. A second internal period was noted for the major species (except Stephanodiscus spp.) in the 2.0 - 6.0 day range, a period representative of the individual generation times of the cells. The N^2 time series also exhibited maximum power spectral estimates and the strongest internal period in the 23.8 day range.

The maximum value of the cross covariance function between N^2 and the numerical abundance data of the major species showed a range of different response patterns as the number of day lags between the two series increased (Fig. 15). Coelastrum spp. and Oocystis borgeii responded positively to increases in the value of N^2 from the previous day, while Chlamydomonas spp. responded positively to changes in N^2 from the previous 4.0 and 6.0 days and Scenedesmus quadricauda responded postively with lags of 2.0 and 5.0 days (Fig. 15; Table VIII). Stephanodiscus spp. and

Fig. 15. Cross covariance function (X 10^5) of the abundance in cells ml^{-1} of the eight dominant Hamilton Harbour phytoplankton species and the N^2 stability numbers (sec^{-2}) plotted against the number of day lags.

Coelastrum spp.

Oocystis borgeii

Scenedesmus quadricauda

Chlamydomonas sp.

Rhodomonas sp.

Cyclotella sp.

Stephanodiscus spp.

Cryptomonas spp.

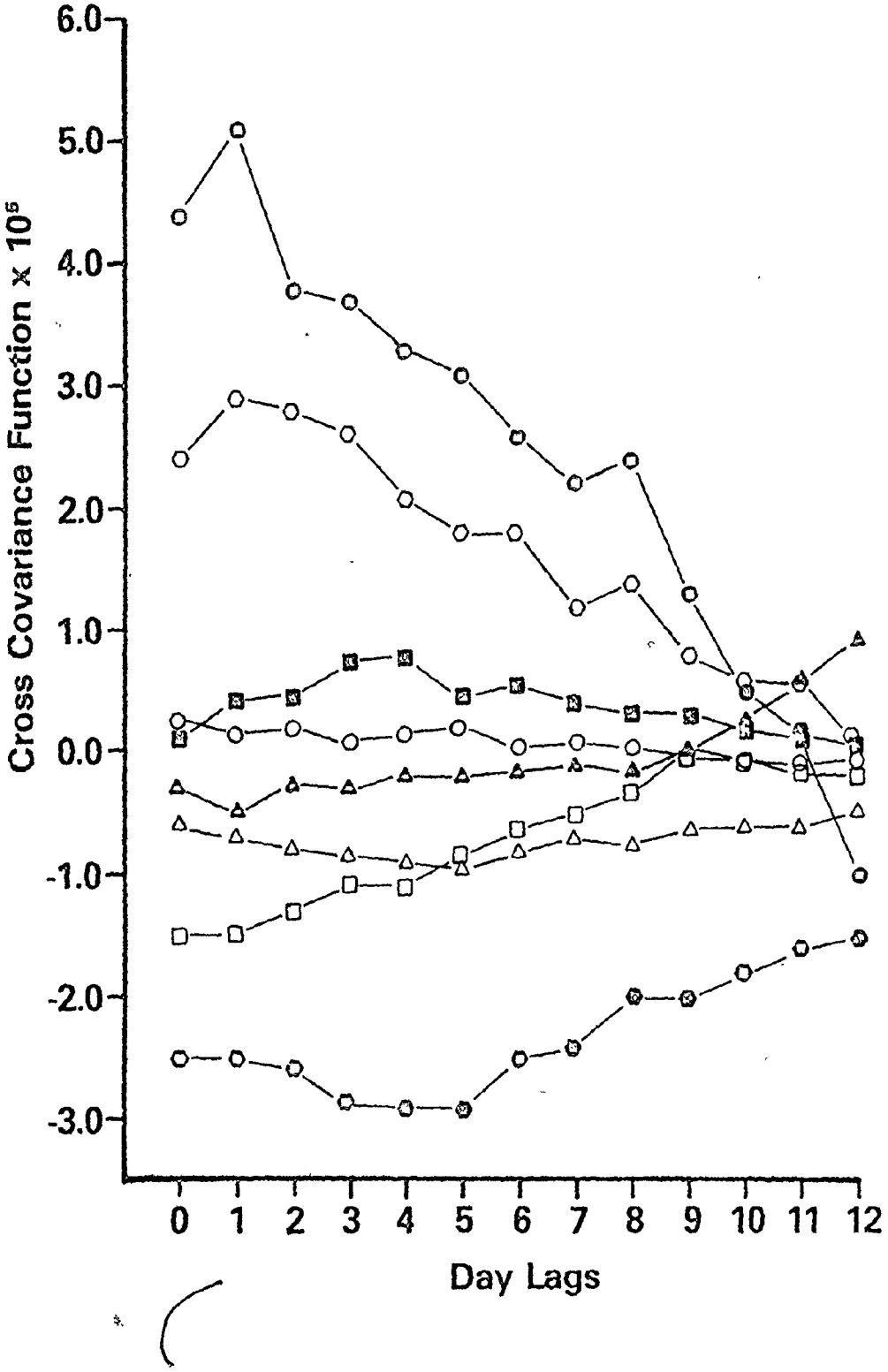

Cross Covariance Function x 10⁶
6.0
5.0
4.0
3.0
2.0
1.0
0.0
-1.0
-2.0
-3.0
0 1 2 3 4 5 6 7 8 9 10 11 12
Day Lags

Table VIII. Results of cross-spectral analysis between the numerical abundance time series for the eight dominant phytoplankton species (series 2) and the J^2 stability numbers (series 1), Hamilton Harbour, June 25 - August 13, 1979.

Species	Number of lags (days) of the highest cross-covariance estimates	Period (days) of the cross-spectral estimates	Cross-spectral estimates	Cross-spectral coherence squared (r^2)	Phase angle of series 1 and 2 (°)
Chlamydomonas sp.	+4.00	23.81	+52845.16	0.4968	62.25
	+6.00	∞	+43609.60	0.3148	63.95
		12.05	+19031.67	0.4651	69.46
		6.00	-15613.57	0.3413	192.39
Coelastrum spp.	+1.00	23.81	+924752.67	0.3308	332.42
	+8.00	8.00	-54700.87	0.7675	194.47
		6.00	-46792.34	0.5161	136.76
		2.00	-46120.92	0.9062	199.69
Oocystis borgei	+1.00	∞	+817081.53	0.8745	5.35
	+6.00	23.81	+552983.62	0.8634	6.05
	+8.00	12.05	+134821.30	0.8001	350.50
		4.81	-45260.24	0.4222	160.96
Scenedesmus quadricauda	+2.00	∞	+66667.71	00.3754	347.76
	+5.00	23.81	+34968.23	0.2292	342.43
	-12.00	6.00	+5747.18	0.1116	2.34
		4.81	+5433.29	0.2177	337.32
Stephanodiscus spp.	-1.00	∞	∞	0.8357	173.05
	-4.00	23.81	∞	0.7874	169.24
	+12.00	12.05	-47384.19	0.3777	163.30
		2.67	+8567.95	0.4410	12.20
Cyclotella sp.	-5.00	∞	∞	0.3500	197.75
	-8.00	23.81	∞	0.3436	210.46
		12.05	-14090.91	0.2124	234.72
		3.42	+7208.89	0.2699	18.58
Cryptomonas spp.	-5.00	∞	∞	0.4628	192.49
	-4.00	23.31	∞	0.4297	201.73
	-3.00	12.05	-50162.74	0.1673	223.78
		4.81	-19468.41	0.1514	160.27
Rhodomonas sp.	-1.00	∞	-68943.47	0.5714	199.51
	-3.00	23.81	-62358.37	0.2973	200.16
	-8.00	12.05	-28268.74	0.1564	178.02
		2.00	+12605.13	0.5704	21.20

Rhodomonas spp. exhibited negative cross-covariance estimates with increases in the value of N^2 with a lag of 1.0 days, while Cyclotella spp. and Cryptomonas spp. showed maximum negative cross-covariance estimates with a lag of 5.0 days.

The value of the cross-spectral estimates between N^2 and the numerical abundance data time series indicated that the most variance and the highest correlation coefficients between the data series occurred with temporal lags in the ∞- 12.0 day region (Table VIII). The high, long term variance estimates of both data series could have accounted for this observation, which may also have represented a seasonal change in species abundance in response to long term environmental changes. Significant short temporal periods with high coherence squared values were also evident and related changes in the value of N^2 to increases and decreases in numerical abundance of the eight species with lags of 2.00 - 8.00 days (Table VIII). Coelastrum spp. and Rhodomonas sp. exhibited strong 2.00 day lag periods to changes in N^2; Stephanodiscus spp. showed a lag of 2.67 days; Cyclotella spp., a lag of 3.42 days; Oocystis borgeii and Scenedesmus quadricauda both showed lags of 4.81 days and Chlamydomonas sp. and Cryptomonas spp. exhbitied lags of 6.00 and 8.00 days respectiviely. These lag periods represented the generation times of the individual species or some multiple of the generation time in the event that one generation time did not enable the majority of the population to respond to the environmental change.

Cells exhibiting the same number of day lags in

response to changes in the value of N^2 responded differently to the nature of the change. Coelastrum spp. responded positively to an increase in N^2, while Rhodomonas sp. responded negatively with a 2.00 day lag (Fig. 15; Table VIII). The phase angles (the distance by which one wave is out of phase with respect to the second wave at the specified frequency) were also different (Table VIII), thus Coelastrum spp. and Rhodomonas sp. did not compete for the same environmental resource in the same manner. Scenedesmus quadricauda and Oocystis borgeii both responded positively to increases in the value of N^2 with a 4.81 day lag, however the phase angles separated them, with Scenedesmus quadricauda closer in phase with N^2 (Table VIII).

Numerical changes in the phytoplankton populations in response to environmental changes occurred with temporal lags of one or more cellular generation times. The greatest changes in abundance occurred about twenty-four days after an environmental change. Different species which responded to environmental changes with similar temporal lags, utilized the environmental change as a resource by optimizing different strategies so that direct competition was avoided.

IV. DISCUSSION

IV. 1.0 General Limnology of Hamilton Harbour, June - August, 1979

The thermal structure (Fig. 2, Appendix I), the concentrations with depth and time of dissolved oxygen (Fig. 3, Appendix I), and the major nutrients (Figs. 4 - 10, Appendix I) recorded in Hamilton Harbour during the summer of 1979, were comparable to previous summers (Harris, 1976; Harris et. al., 1980a; Piccinin, 1977,1979). The temporal and spatial patchiness of the thermal regime and the distribution of dissolved oxygen and nutrients emphasized the importance of the internal physical motions of the harbour itself, the vertical exchange across a somewhat "leaky" thermocline (Harris et. al., 1980a) and the exchange with Lake Ontario waters through the ship canal (Polak and Haffner, 1978).

Hamilton Harbour, like most eutrophic bodies of water, is subject to depletion of hypolimnial oxygen following the onset of stratification in the spring (Polak and Haffner, 1978). Due to the vertical instability in the harbour and the exchange across the thermocline, reduction in epilimnial oxygen concentrations also occur (Palmer and Poulton, 1976). Hypolimnial oxygen depletion proceeded rapidly in July of 1979 (Fig. 3, Appendix I) and epilimnial oxygen reduction was evident by late July. Reoxygenation of the deep hypolimnion occurred around August 1, as a mass of anoxic water was displaced upward, possibly by a mass of cold, oxygen rich Lake Ontario water. Such incursions of Lake Ontario water through the ship canal account for 6 - 19 % of the incoming

oxygen supply to the hypolimnion during the summer months (Polak and Haffner, 1978). The incursions of cold, oxygen rich water coupled with the vertical exchange of lenses of water across the thermocline ensured that complete epilimnial anoxia did not occur, and resulted in irregular oxygen profiles.

The distributions with depth and time of TP (Fig. 4, Appendix I) and SRP (Fig. 5, Appendix I) were patchy and exhibited extreme daily fluctuations. Epilimnial depletion of SRP in 1979, due to algal uptake, was neither extensive or rapid, evidence of the importance of vertical exchange across the thermocline in the maintainance of epilimnial SRP concentrations. Nitrate (Fig. 6, Appendix I) and nitrite (Fig. 7, Appendix I) concentrations exhibited spatial patchiness, and nitrate generally decreased with depth and time while nitrite increased gradually through the season. The extensive depletion of ammonia (Fig. 8, Appendix I) with depth and time indicated the importance of vertical exchange in the water column. Si (Fig. 10, Appendix I) concentrations remained fairly stable despite diatom utilization, indicative of the fact that vertical mixing processes in the harbour served to distribute nutrients to the epilimnion.

Phytoplankton utilize free CO_2 or bicarbonate, HCO_3^- ions in the water as sources of inorganic carbon and extensive photosynthetic activity may deplete inorganic carbon reserves and result in upward shifts in pH (Talling, 1976). pH values (Fig. 11, Appendix I) showed daily variation and increased slightly in surface waters in July, when primary productivity rates were high.

Daily fluctuation in the individual carbon species (free CO_2, HCO_3^- and CO_3^{-2}) were large enough to obscure any trend toward higher HCO_3^- concentrations evident during periods of increasing pH and photosynthetic activity (Appendix II). Total CO_2 alkalinity (Appendix II) was also extremely variable. Mixing processes in the harbour thus contributed to the extreme variation in inorganic carbon concentrations during the study period to such an extent that no meaningful trends between fluctuations in the carbon species, pH and total CO_2 alkalinity could be related to fluctuations in photosynthetic activity.

Nutrient concentrations in the harbour were slightly lower in 1979 as compared to previous summers. SRP concentrations fell to levels of 5 $\mu g\ l^{-1}$, due to increased algal uptake and growth in July. A maximum algal biomass estimate for 1979 of 93 mg chlorophyll a m^{-3} was higher that that recorded in previous summers (Piccinin, 1979). External nutrient loadings were also lower. The concentration of TP in the water column was significantly lower than concentrations observed in 1978, when sewage plant loadings were high (Harris, unpublished data). The concentrations of nitrate in 1979 did not decline to levels limiting to algal growth and productivity. The gradual decreases in the concentrations of free CO_2 and total CO_2 alkalinity with time did not represent extensive depletion of CO_2 that might limit algal growth. Although phosphorus, nitrogen and carbon source available to the algae were patchily distributed, their concentrations were not limiting.

The mean surface biomass estimate in 1979 showed a

standing phytoplankton biomass of 20 - 93 mg chlorophyll a m^{-3} (Fig. 20, Appendix I). Based on Dillon's (1974) significant regression between log total phosphorus and log summer chlorophyll a, the highest predicted chlorophyll a value in Hamilton Harbour would be in excess of 200 mg m^{-3}. Biomass estimates for 1979 summer chlorophyll a would have been in excess of 100 mg m^{-3}. Since the algal biomass did not reach predicted levels, the phytoplankton did not utilize all of the available phosphorus (Harris et. al., 1980a) or the physical variability in the water column placed constraints on algal productivity and growth.

The spatial and temporal distribution of the algae in the water column provided yet another example of the role of vertical mixing. Integral chlorophyll a and surface chlorophyll a concentrations (Fig. 22, Appendix I) exhibited similar temporal patterns, indicating that although the individual depth samples (Fig. 20, Appendix I) showed considerable patchiness, the degree of vertical mixing was regular enough to distribute the algal biomass fairly evenly in the water column.

The complex nature of mixing processes in Hamilton Harbour served to patchily distribute oxygen, nutrients and the algae themselves in the water column. Extensive depletion of the nutrients essential to algal productivity and growth did not occur and the algae did not appear to utilize all of the available nutrients. The low algal biomass observed in the harbour resulted from the physical constraints that the spectrum of environmental variability placed on the phytoplankton population.

IV. 2.0 Environmental Variability and Periodicities

In the absence of nutrient limitation in Hamilton Harbour, the spectrum of short and long term fluctuations in mixing depth (Zm) and water column stability (N^2), as well as the duration and intensity of underwater light and the euphotic zone depth (Zeu), were important in the determination of algal responses to those fluctuations. The periodic nature of these fluctuations, as illustrated by the fluctuation in the daily noon Zeu/Zm ratios, revealed significant temporal periods of phytoplankton response.

IV. 2.1 Thermal Periodicities and Water Column Stability

High frequency variability in temperature and oxygen structures are common in Hamilton Harbour and similar periodic fluctuations evident in the chemical concentrations and water movements (Palmer and Poulton, 1976). The results of the time series analyses of the three temperature data sets (Tem 1, 2 and 3) and their corresponding stability numbers (N^2) revealed the existance of statistically significant physical periods comparable to previously cited values (Table I, Figs. 3 - 8). Time series analysis indicated that the strongest periodic motions occurred at scales of 24.0 - 500.0 h (Table I). The high frequency, short periodic motions (0.36 - 24.0 h) present were important to short temporal variability, but the most important physical events to which the algae responded were in excess of 24.0 h. In terms of water column stability, time series analysis on the daily noon N^2 time series indicated that the strongest periods occurred at 24.0 h.

The wide range of short term thermal periodicities below the 24.0 h range were the result of mixing events dependent on the morphometric parameters of the harbour. Palmer and Poulton (1976) observed periodic motions in the 0.10 - 0.20 h range. Boyce (1974) states that the fundamental periods of wind driven, short standing gravitational waves or seiches lie in the range of seconds to minutes. Periodicities in the 0.35 - 0.40 h range represented the first mode of oscillation of an east-west longitudinal surface seiche (8 km) in the harbour (Palmer and Poulton, 1976; Rao and Schwab, 1974). Periodicities in the 0.40 - 0.70 h range represented longitudinal surface oscillations (Palmer and Poulton, 1976). Horizontal and vertical thermocline displacements occur with periods of seconds to minutes, while internal free waves occur at scales of five minutes (Boyce, 1974). Short term oscillations with periods less than one hour were prevalent in Hamilton Harbour, altered by Lake Ontario periodicities (Harris et. al., 1980a) and interference with each other.

Langmuir circulations; organized helical vertical motions, operate with periods in the range of 1.0 h (Boyce, 1974) and accounted for the periods observed in the 0.90 - 1.20 h range. The 2.30 - 2.50 h periodicity was likely the third free mode of oscillation of Lake Ontario, the Helmholtz or pumping mode (dependent on the width of the harbour opening and the exchange with Lake Ontario) or the resonant co-oscillation involving both modes (Palmer and Poulton, 1976). Long standing surface gravitational waves or seiches operate with periods in the 2.0 - 10.0 h range (Boyce, 1974) and accounted for some of

the harbour periods (Table I). Vertical upwellings and downwellings operate over 1.0 - 24.0 h periods and were important in the harbour (Boyce, 1974). Periodicities typical of Lake Ontario oscillation effects (5.0, 3.2, 2.4 and 2.0 h) were noted in the harbour, again indicating the strong influence of the lake-harbour exchange on periodicities in the harbour (Palmer and Poulton, 1976). Periods in the 10.0 - 12.0 h range represented semidiurnal motions due either to periodic discharges of wastewater or tidal processes in the harbour (Palmer and Poulton, 1976). Periods of mixing in the 16.0 - 20.0 h range were caused by internal standing waves or seiches (Boyce, 1974) and the 21.8 h period may have represented the internal east-west seiche in the thermocline (6 m) region of the harbour.

The physical variability in the thermal structure of the harbour was subject to a broad spectrum of long and short temporal periods. Physical motions with periods below 24.0 h effectively represented random motions or physical periodicities in mixing events which were relatively weak in comparison to the daily and weekly periodicities. Day to day physical variability represented the shortest effective period in terms of algal response.

IV. 2.2 The Light Climate

Short term fluctuations of the type described by Dera and Gordon (1968) were evident in $\sum Io$, the surface integrated irradiance in the water column (Fig. 12, Appendix I). Solar irradiance fluctuations were rapid and so extreme that an accurate estimate of average daily solar irradiance was often difficult to obtain. As the nature of the light field fluctuations influences the duration

and total irradiance received by the phytoplankton (Talling, 1971), the fluctuations may be as important as the daily variability in the integrated irradiance value, ΣIo (Fig. 12, Appendix I).

Short temporal fluctuations in solar irradiance also caused variability in the value of Zeu and ξPAR, however significant changes in both Zeu and ξPAR occurred over temporal scales in excess of several days. The euphotic zone depth followed changes in the algal biomass, the first indication that the algae were influencing their own light climate (Fig. 12, Appendix I; Table II). ξPAR followed a pattern of variability opposite to the pattern observed for Zeu with time (Fig. 12, Appendix I, Table II). ξPAR in the harbour was high due to the fact that a large portion of ξPAR was due to color caused by organic matter. ξmin; the minimum extinction coefficient of ξPAR varied daily and occurred between the 525 - 625 nm spectral band (Table II). No consistent pattern for the spectral band occurrence of ξmin was observed, despite the fact that ξmin shifts toward the red end of the spectrum in waters highly colored by organic matter (Kirk, 1977; Jewson, 1977; Jewson and Taylor, 1978; Jones, 1977b). The contribution of the background extinction to the total PAR was estimated at 0.797 in units m^{-1} for the summer of 1979 (Fig. 9), comparable to previous estimates (Harris et. al., 1980a; Morgan, 1979; Piccinin, 1979).

A significant regression between ξmin and the chlorophyll a biomass occurs only when the algal population is self-shaded, indicating that the background attenuation of light is relatively constant and is only important at low biomass (Harris et. al., 1980b). The

scatter of points about the εmin verses chlorophyll a biomass plot result from daily changes in εDOM and differences in light extinction per unit chlorophyll a in different algal populations (Bindloss, 1976). Light extinction is affected by cell size and geometry (Kirk, 1974,1975a,b; Steel, 1972; Talling, 1971) and by the pigment content, composition and the nature of the pigment packages in the cells (Harris et. al., 1980b; Kirk, 1975a,b, 1976; Steemann-Nielsen, 1962). Changes in the species composition of the phytoplankton community thus affect the absorptive properties of the population.

The slope of the εmin verses chlorophyll a biomass plot (Fig. 9) gave an average estimate of εs, the self-shading parameter of the algal population as 0.0108 ln units m^2 mg chlorophyll a^{-1}, comparable to previous estimates in the harbour (Harris et. al., 1980b). Talling (1960) quotes an average value of 0.020 ln units m^{-2} mg chlorophyll a^{-1}, however the value varies with the species composition of the populations (Harris, 1978; Harris et. al., 1980b; Kirk, 1976, 1975a,b; Steel, 1972; Talling,1971). εs decreases as cell size increases and is small for very small and very large cells (Harris, 1978; Kirk, 1974, 1975a,b). Harris et. al. (1980b) found that εs was correlated with changes in a measure of the mean chlorophyll package size; Cp (10^7 cells mg chlorophyll a^{-1}) and that the scatter about the εs verses chlorophyll a plot was due in part to fluctuations in Cp. The 1979 estimates of εs were significantly correlated with Cp (Fig. 10). In Hamilton Harbour, larger cells had lower εs values. The harbour population was dominated by large, green colonial algae

and diatoms for most of the study period (Fig. 20, Appendix I) explaining the low average ξs value.

The maximum theoretical integral biomass in the euphotic zone; ΣB, derived from the average ξs value of 0.0108 in units m^2 mg chlorophyll a, observed during the study was 343 mg chlorophyll a m^{-2}. The maximum observed biomass was 216.15 mg chlorophyll a m^{-2}. These values, which were comparable to previous estimates (Harris et. al., 1980b) were misleading as they suggested that the effect of DOM was great and that the algal population was not self-shaded. Due to the daily variability in ξs, ξDOM and ξmin, the use of a single ξs value for all chlorophyll a concentrations implies that self-shading does not change as biomass increases, an assumption that is often false. Comparison of the daily observed ξs values with the daily theoretical ξs values, corrected for the small contribution of DOM at the wavelength of ξmin (Table II) revealed that the algae were strongly self-shaded. The maximum theoretical biomass, ΣB was thus 279.85 mg chlorophyll a m^{-2} and the observed ΣB was 255.52 mg chlorophyll a m^{-2} (Table II), indicating that the algae alone were the most important determinant of their own light climate.

The light climate fluctuations were thus strongly influenced by the phytoplankton population. Zeu and ξPAR fluctuated with variability in solar irradiance, but were generally stable over short temporal scales and followed fluctuations in algal biomass.

IV. 2.3 The Zeu/Zm Ratio

Daily variation in the Zeu/Zm ratio was influenced by rapid fluctuations in the values of Zeu and Zm (Fig. 11). Variability

in Zm was greater over short temporal scales than variability in Zeu and changes in the Zeu/Zm ratio were driven by fluctuations in Zm. Periodicities in the thermal structure representing physical mixing processes and seiche effects accounted for the rapid fluctuations in Zm (Table I). Regular periodicities were not evident in ΣIo and fluctuations were random (Table II). The fact that Zeu was influenced to such an extent by the algal biomass and that the background extinction of light was constant suggested that significant changes in Zeu occurred over longer temporal scales and did not contribute to hourly and daily variation in Zeu/Zm.

Time series analysis showed that the Zeu/Zm ratio did not exhibit short term periodicities and the daily fluctuations were random in nature. The strongest periodicities in the Zeu/Zm ratio occurred in the range of 24 days, approaching seasonal time scales.

IV. 3.0 Phytoplankton Response to Environmental Variability

The algal populations exposed to the short and long term fluctuations in the light regime and mixing events in Hamilton Harbour responded to the spectrum of environmental change by utilizing a hierarchy of physiological response mechanisms. Cells responded to random, short temporal fluctuations in Zm and the light field by physiological regulation of the photosynthetic apparatus through the in vivo fluorescence response. Daily fluctuations in the value of ΣIo, the Zeu/Zm ratio and water column stability were reflected in the variable rates of photosynthesis and the reduced, fluctuating values of the photosynthetic parameters Pmax, Pe and Ik. Phytoplankton responded to daily environmental fluctuations with temporal lags

reflecting their generation times. Community change occurred in response to long term environmental periodicities, with lag periods representing the number of generation times appropriate for adaptation by the entire population.

IV. 3.1 In Vivo Fluorescence

The in vivo fluorescence (IVF, F + DCMU and the F ratio) response by the Hamilton Harbour phytoplankton was extremely variable over short temporal scales and established the link between rapid physiological response and short term environmental fluctuations. The F ratio was generally lower in surface and aphotic waters (Fig. 14, Appendix I), decreasing with increasing irradiance in stable water columns (Fig. 12, Appendix I) under conditions of decreasing wind speed, high N^2 values and high Zeu/Zm ratios. F ratios increased as vertical mixing in the water column increased under conditions of low N^2 numbers and Zeu/Zm ratios. The difference between the surface and maximal F ratios decreased with increasing wind speeds (Fig. 12).

Extensive photoinhibition of fluorescence was not evident in the harbour during the study (Fig. 14, Appendix I). During the summer of 1979, phytoplankton were exposed to periods of high surface irradiance (Fig. 12, Appendix I; Fig. 13) and exhibited high Ik values indicative of adaptation to or growth in bright light (Fig. 14). Extensive surface photoinhibiton of photosynthesis was not evident in 1979 (Appendix III), physiological evidence linking the photoinhibition of photosynthesis with the photoinhibition of fluorescence (c.f. Harris and Piccinin, 1977). Harris (1980b) suggested that the measurement technique might also account for the lack of photoinhibition

of fluorescence. The time spent in the dark ($\angle$ 1 min) before measurments of fluorescence of the discrete cell samples may have allowed recovery of the photosynthetic apparatus (Harris, 1980b). Samples pumped directly into fluorometers would not show the effects of such a recovery period (Heaney, 1978; Kiefer, 1973a,b; Loftus and Seliger, 1975). Given the amount of environmental variability present in Hamilton Harbour, it was evident that phytoplankton regulate their fluorescence properties (Harris, 1980b) so rapidly that little pattern of fluorescence yield was observed.

Loftus and Seliger (1975) suggested that the extremely variable R ratio; the in vivo fluorescence yield per unit chlorophyll a, was a good indicator of the physiological state of the photosynthetic apparatus. Slovacek and Hannon (1977) postulated that the F + DCMU per unit chlorophyll a value was constant, the addition of DCMU eliminating the effect of internal and external variability on fluorescence. The 1978 (Harris, 1980b) and 1979 Hamilton Harbour data exhibited variable R ratios and F + DCMU ratios. The value of the R ratio (Fig. 13) changed in response to fluctuations in water column stability and the Zeu/Zm ratio. High R ratios corresponded to periods of low N^2 and Zeu/Zm ratios, conditions of active vertical mixing when the photosynthetic ability of the cells was diminished by the effects of circulation through deep light gradients. The data indicated that rapid regulation of fluorescence occurred in response to environmental fluctuations (see Harris, 1980b).

IV. 3.2 In Situ ΣP, Pmax, Pe and Ik

The 1979 rates of ΣP and max Pv (Appendix III) recorded in the harbour were comparable to previous values (Harris et. al., 1980b) but were much lower than values recorded in water bodies with similar nutrient loadings and algal biomass (Glooschenko et. al., 1974; Stadelmann et. al., 1974; Vollenweider et. al., 1974). ΣP varied daily as did max Pv (Fig. 14; Appendix III). Pmax, the photosynthetic capacity , P_e; the photosynthetic efficiency and Ik (Fig. 14) were comparable to previous estimates in the harbour (Harris et. al., 1980b) and exhibited extreme daily variability.

The relative importance of fluctuations in max Pv, Pmax and Ik to rates of ΣP were assessed using a modified form of Talling's (1957a,b) model : $\Sigma P = \frac{B\ Pmax}{\mathcal{E}PAR} \times \ln \frac{Io'}{0.5\ Ik}$, where B is equal to the algal biomass (mg chlorophyll a m^{-3}); Pmax, $\mathcal{E}$PAR and Ik are as previously defined and Io' is equal to the surface light intensity in the water column (Harris et. al., 1980b). The least squares linear regression between ΣP and max Pv was highly significant ($\Sigma P = 0.542$ max Pv + 45.211, $n = 55$, $r = +0.832$, $p < 0.001$), indicating that the variability in ΣP was strongly influenced by the variability in max Pv. In situ Pmax was also important in determining the variability in ΣP, since the regression between the two parameters was also significant ($\Sigma P = 16.516$ Pmax + 64.480, $n = 55$, $r = +0.533$, $p < 0.01$). For the relationship between ΣP and Pmax to be significant, variations in $\mathcal{E}$PAR and B must be minimal in influencing ΣP (Harris et. al., 1980b). The plot of ΣP versus $\frac{B\ Pmax}{\mathcal{E}PAR}$, whose slope is

theoretically ln $\frac{Io'}{0.5\ Ik}$ was also highly significant ($\Sigma P = 0.658 \frac{B\ Pmax}{\Sigma PAR} + 69.790$, $n = 55$, $r = +0.521$, $p < 0.01$) indicating that changes in Io' and Ik did not influence ΣP to any great extent. Pe was also important in determining ΣP, as the ability of a population to assimilate carbon efficiently at the prevailing environmental conditions determines the maximum rate of photosynthesis, Pm and ΣP. The observed rates of max Pv and Pm are dependent on the values of gross photosynthesis and respiration in the water column, which are controlled by the variability in light, temperature and mixing events (Harris and Piccinin, 1977). Pmax in turn, is determined by Pm and the chlorophyll a biomass. In Hamilton Harbour, environmental variability strongly affects the rate of ΣP, through variation in max Pv, Pe and Pmax.

In situ Pmax was positively correlated with temperature during the study (Fig. 16, Appendix I) and rose above the average temperature trend line during periods of stability in the Zeu/Zm ratio (Harris et. al., 1980b). In 1976, the weekly variation in the Zeu/Zm ratio destroyed the relationship between Pmax and temperature in the harbour (Harris and Piccinin, 1977; Harris et.al., 1980b) but this did not occur in 1979. Nutrient availability is important in controlling Pmax (Curl and Small, 1965; Glooschenko et. al., 1974) but temperature is a more important factor in eutrophic waters where nutrients are not limiting (Harris and Piccinin, 1977).

The overall Pmax values recorded in 1979, were low in comparison to others cited in the literature (Jones, 1977b; Platt

and Jassby, 1976; Williams and Murdoch, 1966), due mainly to the rapid fluctuations in the Zeu/Zm ratio. Low Zeu/Zm ratios corresponded with low Pmax values, and Pmax increased slightly as the Zeu/Zm ratio increased. The daily fluctuations in the Zeu/Zm ratio showed the strongest periodicities over long temporal scales, and the same applied to in situ Pmax values, although a weak 2.0 - 4.0 day periodicity was evident in the in situ data as well. Cross-spectral analysis revealed that in situ Pmax responded to the daily fluctuations in the Zeu/Zm ratio with lag periods in the 5.0 - 6.0 day range. Lag periods in the 2.00 - 2.67, 4.00 - 4.81 and 6.00 day range represented multiples of the average generation time of the cells (Harris, 1980a) (Tables V, VI).

Curl and Small (1965) found that assimilation numbers exhibited by marine phytoplankton populations varied with day time, season and the photic zone depth, as well as with changes in the species composition of the phytoplankton community. Glooschenko et. al.(1974) observed that the highest assimilation numbers occurred in late summer in Lake Erie, when Cyanophyta and Chlorophyta dominated the algal community and assimilation numbers were lowest when diatom populations were dominant. Assimilation numbers were highest in 1979 in the harbour in mid to late July, when the phytoplankton community was dominated by members of the phylum Chlorophyta, noteably Oocystis borgeii and Coelastrum sp. (Fig. 21, Appendix I).

Photosynthetic efficiency; Pe, varied daily in response to environmental fluctuations (Fig. 14). Pe was not temperature

dependent but was significantly correlated with $\ln \frac{Io'}{0.5\ Ik}$, a function of the light climate ($Pe = -0.389 \ln \frac{Io'}{0.5\ Ik} + 2.872$, $n = 55$, $r = +0.450$, $p < 0.01$). Since Pe was negatively correlated with Ik in 1979 (Fig. 18, Appendix I), this relationship was anticipated. Platt and Jassby (1976) correlated Pe with Io, the daily solar irradiance over the three days prior to its measurement in a natural phytoplankton community. Io was extremely variable in the harbour (Fig. 12a, Appendix I) and there was no clear pattern of fluctuation that resembled the day to day fluctuations in Pe (Fig. 14c). At similar ΣIo values however, harbour populations with low Ik values had correspondingly high Pe values (Appendix III). Growth at low light produces phytoplankton cells with higher cellular pigment contents and higher photosynthetic efficiencies at those light intensities (Heron and Mauzerall, 1972).

In situ Pe time series data showed strong periodicities in the 24 day range and weaker periods in the 2.00 - 3.42 day range, representing the average cellular generation time in the harbour. Pe responded negatively to high values of the Zeu/Zm ratio with a lag of 7.0 days (Table VII). Cross-spectral analysis showed that Pe responded to changes in the Zeu/Zm ratio with periods in the 2.00 - 2.67, 4.81 and 6.00 day range, however the most significant period was the 6.00 - 7.00 day one (Table VII). It appears then, that roughly three cellular generation times must elapse for the full expression of a change in the Zeu/Zm ratio in the value of Pe.

Low Zeu/Zm ratios in the harbour result from increases in mixing depth, distributing the phytoplankton deeper in the water

column and altering their exposures to the proportions of light and dark gradients in the water (Jewson and Wood, 1975). Algal cells must offset increases in their respiration rates under these conditions, with more efficient rates of photosynthesis, hence their ability to utilize the available light is enhanced. Through their temporal dependence on changes in the Zeu/Zm ratio, Pe and Pmax were positively correlated in the harbour during the summer of 1979 (Fig. 17, Appendix I). The average cellular generation time, or its multiple, represented an integral period of algal response to environmental variability in Hamilton Harbour.

Ik varied daily during the summer of 1979 and closely followed fluctuations in ΣIo over the previous two days (Fig. 19, Appendix I). Harris et. al. (1980b) found that Ik in the harbour varied weekly and was correlated with the thermal stability in the top five meters. Harris and Piccinin (1977) noted that Ik is a function of a number of physical factors, such as light intensity and exposure time and temperature (Talling, 1957a,b) as well as a function of the physiological state of the algae.

Jones (1978) found that the relative susceptibility of different algae to photoinhibition at high light intensities possibly provided an indication of the physiological state of the algae. At any value of Io, algae with low Ik values were more susceptible to surface photoinhibition (Jones, 1978). An extensive review of the physiological literature (Harris, 1978) points out that the thresholds for Ik values of algal cells; 50. - 120 $\mu E\ m^{-2} sec^{-1}$ correspond to the threshold values for the photoinhibition of

fluorescence and for changes in the cellular contents of photosynthetic and accessory pigments. Ik values for the summer of 1979 were higher than these threshold values; 44 - 830 μ E m^{-2} sec^{-1}. Ik correlated negatively with Pe in 1979 (Fig. 18, Appendix I); high Ik values corresponding to low Pe values observed under conditions of high light and thermal stability. Ik values were highest in mid July, the result of high light adaptation or seasonal changes in species compositions (Harris and Piccinin, 1977).

Ik was not correlated with temperature during the summer of 1979, despite its dependence on Pmax. Under the physically variable conditions dominant in the harbour, daily variability in Pmax and Ik, as well as the instability in the thermal structure, might have masked this relationship. It was evident again, that the cellular generation time represented an integral period for changes in the value of Ik in response to environmental change.

IV. 3.3 Tank Photosynthesis

The rates of photosynthesis observed in the tank for the four sampled populations were lower than the maximum in situ rates of photosynthesis and photoinhibition was not observed due to the light limitation in the tank and the low incidence of in situ photoinhibition. The rates of photosynthesis obtained from the tank incubations were highly variable between populations and from day to day. Time series analysis was not performed on the data however, as the aim of the experiment was not to detect periods in the data, but to establish whether or not the rates of photosynthesis were significantly different with depth and time.

Analysis of variance performed on the tank Pmax data revealed that Pmax values varied significantly from day to day and with depth (Table IV). The significant day-depth interaction suggested that the effect of depth varied slightly as the effect of day did, in other words, small increases and decreases in the value of Pmax from day to day resulted because Pmax varied slightly with depth in the water column. Snedecor and Cochran (1967) state that when the effect of an AB interaction is significant but small in comparison to the individual A and B effects, it is valid to state the individual effects separately. Thus, tank Pmax varied significantly on a daily basis and the variability between populations was not as important as the daily variability. The experiment was not successful in revealing the presence or absence of distinct depth populations in the water column. A probable reason for this was the fact that the entire data set was used in the analysis, representing days of stability and instability in the water column.

Pmax varied daily in response to changes in the value of the Zeu/Zm ratio in the same way that in situ Pmax did. Tank Pmax values lagged changes in the value of the Zeu/Zm ratio at scales of 2.00 - 2.67, 4.00 - 4.81 and 6.00 days (Table V). Pmax was significantly different from day to day in the four populations due to the fact that the phytoplankton populations in the harbour was patchily distributed with depth and time and populations sampled from different depths had been exposed to slightly different niches in the water column.

IV. 4.0 The Phytoplankton Community and Environmental Variability

In the absence of nutrient limitation, major changes in the temporal and spatial structure of phytoplankton communities are largely dependent on the physical variability in the water column (Haffner et. al., 1980; Harris, 1978, 1980a; Harris and Piccinin, 1977; Jones, 1977a). Round (1971) stated that the seasonal succession of species and population growth were determined by shock events in the water column associated with changes in temperature or overturn conditions. Major (seasonal) changes in populations occur in response to variation in the euphotic zone (Zeu) depth and the mixing (Zm) depth, however the dynamics of the thermal barrier is also important (Haffner et. al., 1980). Harris and Piccinin (1980) identified a critical Zeu/Zm ratio of 0.35 in Hamilton Harbour which determined the existence of specific algal groups. Increases above the critical ratio favored dominance by populations of coccoid and colonial green algae, while decreases in the critical ratio favored dominance by diatom populations. Different algal groups respond to the spectrum of turbulence in the mixed layer in different ways, some species utilize turbulent motions to maintain position in the euphotic zone, while others grow best under stratified conditions (Marra, 1978).

In Hamilton Harbour, changes in the Zeu/Zm ratio provided a good indication of the degree and nature of environmental change in terms of cellular physiological response, productivity and species change (Haffner et. al., 1980; Harris et. al., 1980; Harris and Piccinin, 1980). A second measure of environmental variability,

the N^2 stability number indicated the degree of thermal stability in the water column. Of the eight dominant algal species present during the study period, Coelastrum spp., Oocystis borgeii, Chlamydomonas sp. and Scenedesmus quadricauda increased in abundance as the value of N^2 increased, while Stephanodiscus spp., Rhodomonas spp., Cyclotella spp. and Cryptomonas spp. increased in abundance as N^2 decreased (Fig. 15; Table VIII). Harris and Piccinin (1980) found that the short term changes in species composition and abundance within the community tended to "average" the environmental variability over short temporal scales and that such shifts in numerical abundance reflected environmental change much better than the presence or absence of certain groups. A similar relationship was observed for the eight dominant species in 1979.

Allen et. al. (1977) state that simple correlations between changes in environmental parameters and the composition or size of the phytoplankton community might not always be evident, because phytoplankton communities tend to track environmental changes with slight temporal lags. The lag period between environmental and species or community change is dependent on the population composition and its range of long and short term adaptive strategies, as well as the magnitude and periodicitiy of the physical variation (Haffner et. al., 1980; Harris, 1980a; Richerson et. al., 1970). Harris (1980a) linked the generation time of the algal cells in Hamilton Harbour with the principle lag period of physiological and numerical abundance changes in response to environmental fluctuations. Cells which fail to track environmental changes

within their generation times (1 - 7 days in the field) may be eliminated, while cells which can optimize short term variability will regenerate and grow (Harris, 1980a; Richerson et. al.,1970).

The eight dominant species present during the study period responded to environmental flucutations over temporal scales which reflected their generation times. The strongest periods in species abundance change occurred in the range of 24.0 days or longer, representing seasonal time scales (Table VIII). Coelastrum spp. and Rhodomonas sp. exhibited numerical changes in response to changes in N^2 with a 2.00 day lag, while Stephanodiscus spp. responded with a 2.67 day lag. Cyclotella sp. exhibited a lag of 3.42 days, while of 4.81 days were evident for Cryptomonas spp, Scenedesmus quadricauda and Oocystis borgeii. The shortest temporal lag evident for Chlamydomonas sp. was one of 6.00 days (Table VIII). The average in situ generation time of 2.50 days (Harris, 1978, 1980a) or some multiple of the doubling time thus represented a fundamental response period for the expression of environmental variability in the algal population.

The role of short and long term environmental fluctuations in terms of the response of species in a natural community depends upon the full complement of the fluctuation; its mean level, amplitude, phase, period and duration (Grenney et. al.;1973; Harris, 1980a), as well as the scale of phytoplankton response (Allen, 1977). Natural communities consist of mixed species assemblages , exhibiting a variety of growth and division rates and an entire spectrum of physiological response mechanisms (Slobodkin and Rapoport, 1974).

Different species coexist in a physically variable environment by optimizing the spatial and temporal scales of environmental variability as a resource, and respond to and partition that resource in terms of their own endogenous scaling strategies (Allen, 1977; Harris, 1980a; Levins, 1979). In physically variable environments, only a fraction of the total population will be optimally adapted to the set of environmental fluctuations at any one point in time and at that point in time those species will exert a certain degree of competitive adavantage over other species (Richerson et. al.,1970). With rapid fluctuations in the water column, the competitive advantage quickly shifts to another fraction in the population, thus temporal fluctuations which create many separate "patches" of water aid in the maintenance of community diversity and the coexistance of species (Richerson et. al., 1970). Because of the different scales of environmental fluctuation and species response, two coexisting species may never compete for the same environmental resource.

The eight dominant species observed during the summer of 1979 responded to environmental variability over different temporal scales (Table VIII). Cells exhibiting the same temporal periodicity in response to changes in the value of N^2, responded differently to the nature of the change. Species responding positively or negatively to increases in the value of N^2 were not in direct competition because their response mechanisms were different in their phasing. By utilizing different periods and phasing strategies, as well as responding differently to the mean, maximum and minimum levels of N^2, the algal species coexisted successfully in the harbour (c.f. Levins,1979).

IV. 5.0 General Discussion

In Hamilton Harbour, physical periodicities (Fig. 1) appeared to be more important determinants of algal productivity and growth than non-limiting nutrient concentrations. The rates of ΣP and max Pv recorded were generally lower than values cited for bodies of water with similar nutrient loadings and biomasses. Variability in max Pv accounted for the low and variable rates of ΣP. The low algal biomass present and variability in the photosynthetic potential (Pmax, Pe and Ik) of the population also contributed to the reduced rates of primary productivity. Physical variability thus limited the growth of the algal populations and reduced photosynthetic potential.

Knowledge of the physical variability is important for understanding how the algae cope with different temporal cycles in the environment. The thermal structure in the harbour was subject to a wide range of periodicities (Fig. 1; Table I). Short term periods (< 24 h) were caused by horizontal and vertical water movements, Lake Ontario periodicities and random wastewater inputs (Fig. 2). Long term periods (> 24 h) were much stronger and were influenced by daily variability in Zm, the result of the combination of short term mixing events (Fig. 1; Table I). The light climate was subject to solar irradiance and cloud cover fluctuations over various temporal scales (Fig. 1). Zeu and ΣPAR were stable in the harbour and followed fluctuations in algal biomass over temporal scales approaching a number of generation times. Consequently, daily variability in Zm strongly influenced changes in the Zeu/Zm

ratio. N^2, the stability number was dependent on short and long term fluctuations in the thermal structure and mixing events (Fig. 1).

The phytoplankton coped with short temporal fluctuations in Zeu and Zm by regulating photosynthesis and with longer term fluctuations by true adaptation, interfacing various environmental time scales via a hierarchy of response mechanisms (Fig. 1). In vivo fluorescence transients represented the most rapid scale of response and regulation by the phytoplankton to short term environmental fluctuations. Longer periodicities in the physical data were statistically more significant, suggesting that the algae might respond to daily and weekly environmental changes over periods of one or more generation times. Physiological adaptation in terms of changes in Pmax, Pc and Ik values of the phytoplankton were accomplished within the range of one (2.0 days for Ik) or more (5.0 - 6.0 days for Pmax, 6.0 - 7.0 days for Pc) generation times.

Major trends in species composition over longer temporal scales (Fig. 1) occur when physiological adaptation by the cells cannot cope with environmental change over several generation times and species are eliminated (Harris and Piccinin, 1980). An initial decline in numerical abundance of a particular species is the response of that species to the short term environmental change and the final loss of that species from the community may not occur until weeks after the initial change (Harris and Piccinin, 1980). The composition and structure of a phytoplankton community over temporal scales in excess of a few generation times may reflect the most frequent environmental state to which each of the species

responds according to its endogenous scaling strategies, but not necessarily the average environmental condition (Haffner et. al., 1980). Certain combinations of environmental fluctuations may reduce or increase the apparent fitness of algae in a community, thus affecting community diversity (Richerson et. al., 1970). The eight dominant Hamilton Harbour phytoplankton species responded to the spectrum of environmental fluctuation over different temporal lags, and in different ways, exploiting environmental variability as a resource permitting coexistance and enhancing community diversity.

V. CONCLUSIONS

1. The thermal regime, dissolved oxygen and nutrient distributions in Hamilton Harbour were subject to a large degree of spatial and temporal patchiness. The concentrations of the major nutrients essential to algal growth (P, N and C) were consistantly high and did not limit algal growth and productivity. Algal biomass and the rates of primary production were low as compared to similar bodies of water. This study concluded that spatial and temporal heterogeneity in Hamilton Harbour are the key factors limiting cell and population growth and productivity.

2. Variability in the thermal structure and underwater light field, two important determinants of algal growth and productivity, encompassed a broad temporal spectrum. Short periods (<24 h) in the thermal structure resulted from physical mixing, interaction with Lake Ontario, seiche effects and random wastewater discharges. The strongest periods in Zm occurred at scales in excess of 24 h, and both short and long term periodicities in the harbour compared well with previously cited values. Light varied with short term fluctuations and daily cycles of solar irradiance. Zeu and ξPAR were stable over short temporal periods and varied with fluctuations in algal biomass. ξDOM was high, but had little influence on ξmin and the algal cells were strongly self-shaded. ξ_s correlated positively with Cp and self-shading decreases with increasing cell size. The phytoplankton community was successful in controlling their own light climate, but

strongly influenced by variability in mixing depth and water column stability, which they could not control.

3. The Zeu/Zm ratio showed wide daily variability, mainly related to rapid fluctuations in Zm. The maximum power spectral estimates for the Zeu/Zm ratio occurred at scales greater than 24 h, with the strongest periods at 24 days. Variation in the stability number; N^2, was similar to that of the Zeu/Zm ratio. Daily or weekly environmental fluctuations represented the strongest temporal scale to which the algae responded.

4. Variation in light over short periods (<24 h) was associated with rapid physiological regulation by the phytoplankton. In vivo fluorescence varied with previous light history and stability in the water column and represented the most rapid cellular response to short term environmental variation. IVF, F + DCMU and the F ratio varied widely over short periods. Low F ratios corresponded to periods of stability (high N^2 and Zeu/Zm) in the water column. As wind speed and vertical mixing increased, the depth dependent effect on the F ratio diminished. R values were variable, representing rapid regulation of the photosynthetic apparatus in response to changes in N^2 and the Zeu/Zm ratio. R values were high under mixed conditions (low N^2 and Zeu/Zm) in the water column.

5. ΣP and max Pv showed daily variation, the result of short term environmental fluctuations. Pmax, Pe and Ik values were also variable and low, contributing to the reduced rates of production. Pmax, Pe and Ik responded to the spectrum of environmental variability over one or more cellular generation times. Pmax was temperature

dependent, low under deep mixed conditions and responded positively to increases in the value of the Zeu/Zm ratio from the previous 5.0 to 6.0 days. Pmax also responded to the magnitude of the change in the value of the Zeu/Zm ratio from day to day, with a lag of one or more generation times. Tank Pmax values showed significant variation with depth and day and also a significant interaction between day and depth effects. Pe was negatively dependent on the value of Ik. High Pe values lagged low Zeu/Zm ratios by 6.0 or 7.0 days. Pe and Pmax were positively correlated with each other through their dependence on the value of the Zeu/Zm ratio. Ik correlated with fluctuations in ΣIo over the previous two days and due to its variability, was not temperature dependent. Low Zeu/Zm ratios and N^2 estimates in the water column were reflected in algal populations which exhibited high values of Pmax and Pe and low Ik values. The in situ generation time of the algal cells, or its multiple, represented a fundamental integration period between cellular response and change in the physical environment.

6. The eight dominant algal species present in the harbour during the study period responded to variability in water column stability over temporal scales representing one or more generation times. The lag period between environmental and numerical abundance changes varied among the species, as did the pattern of response. Coelastrum spp. and Oocystis borgoii responded positively to increases in the value of N^2 and the Zeu/Zm ratio, as did Scenedesmus sp. and Chlamydomonas sp. Stephanodiscus spp., Cyclotella sp., Rhodomonas sp. and Cryptomonas spp. responded negatively to increases in N^2 and the Zeu/Zm ratio.

Different species exhibiting the same temporal lag to environmental change responded with different phasing strategies to avoid direct competition. Species utilized the spectrum of environmental variability as a resource permitting coexistance and enhancing community diversity.

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APPENDIX I

Fig. 1. Variation in daily morning mixing depth, average wind speed and morning air temperature; June 25 - August 18, 1979.

A. Morning mixing depth, Zm (m)

B. Average daily wind speed, μ, (m sec^{-1})

C. Morning air temperature, C^{o}

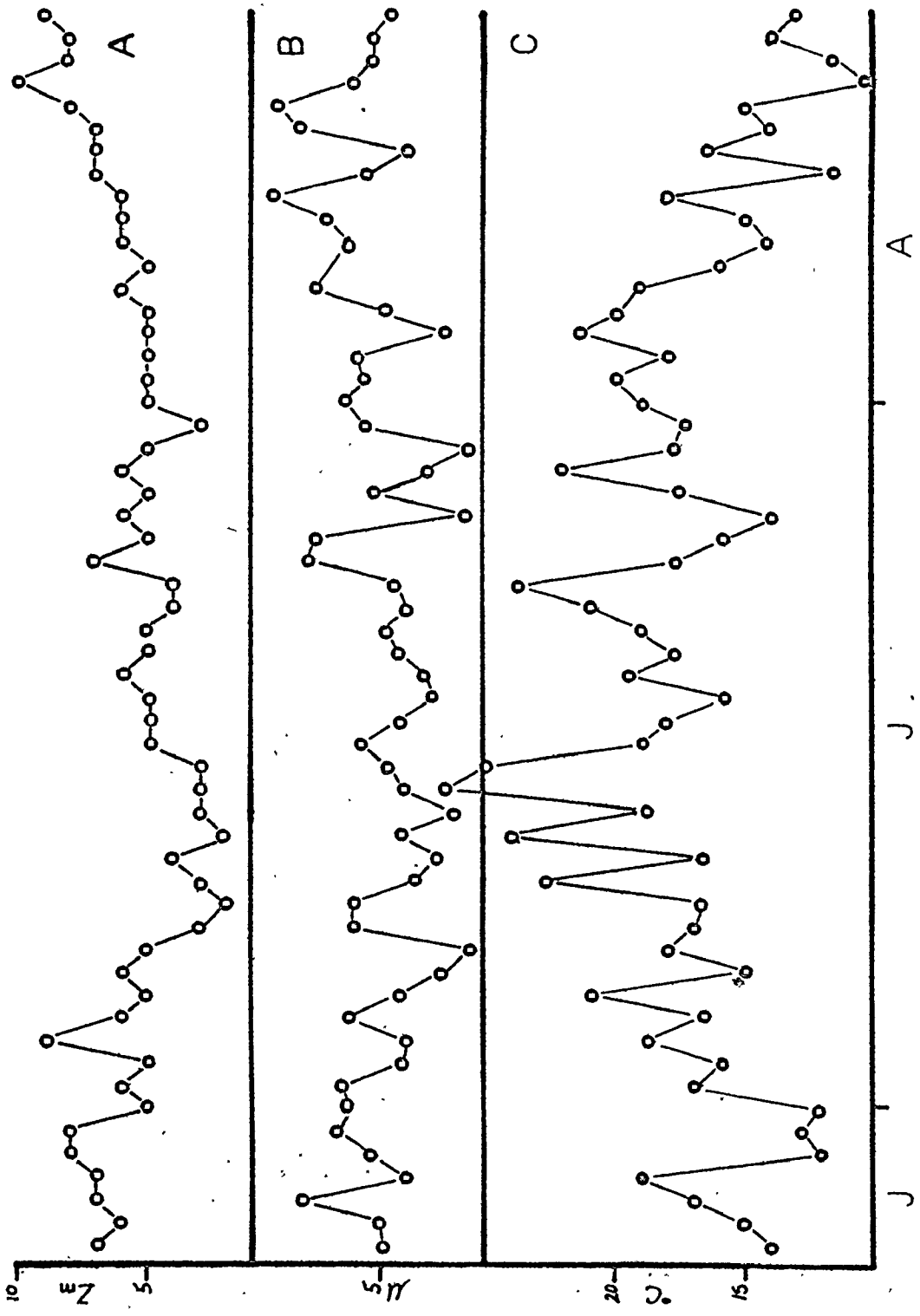

A
B
C
J
J
A
10
5
Zm
5
μs
20
15
°C

Fig. 2. Time-depth isopleth plot of daily morning water temperature (C^{o}); June 25 - August 18, 1979.

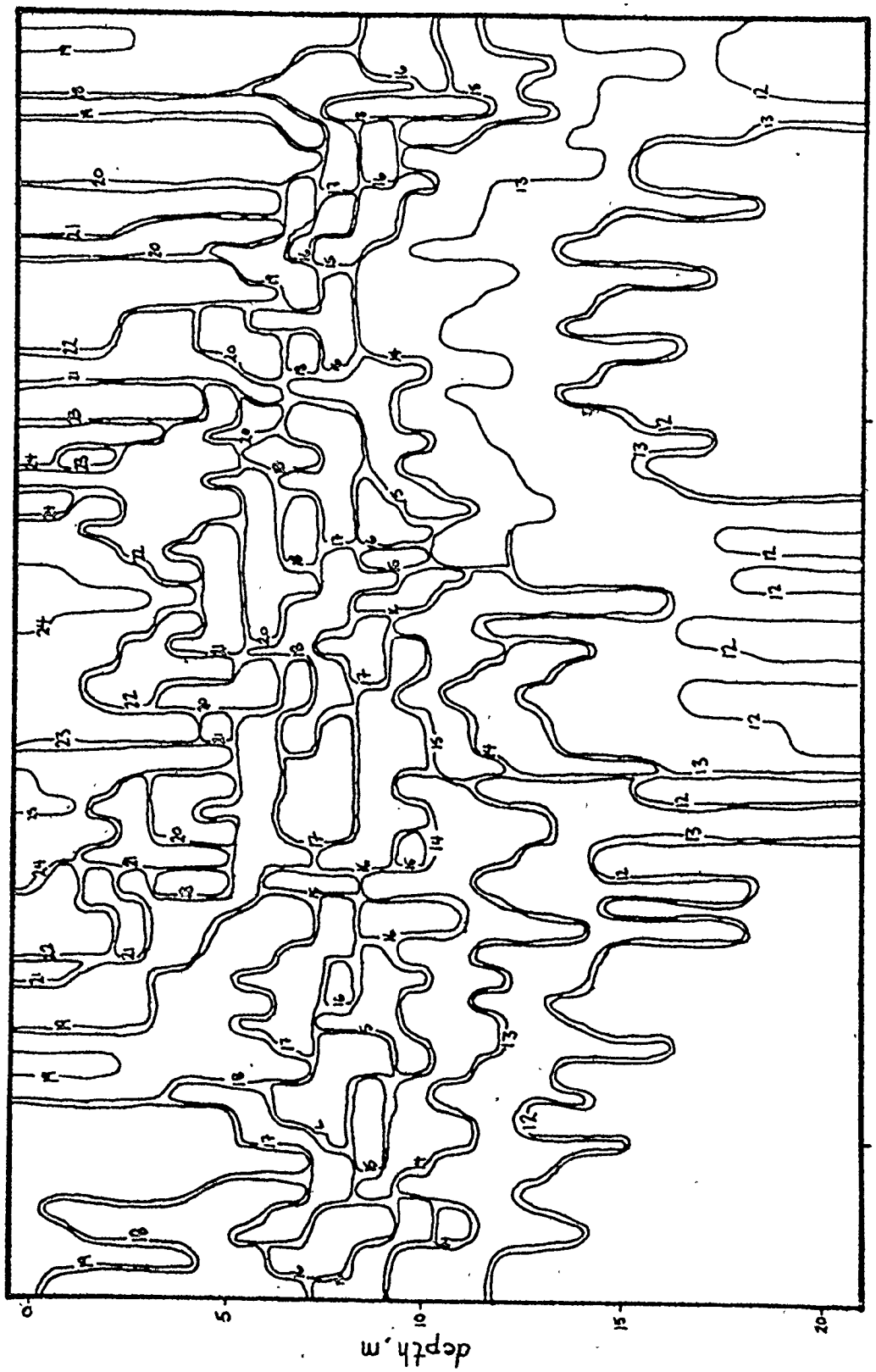

depth, m
0
5
10
15
20
J
J
A
°C

Fig. 3. Time-depth isopleth plot of daily morning dissolved oxygen concentration (mg l^{-1}) in the water column; June 25 - August 18, 1979.

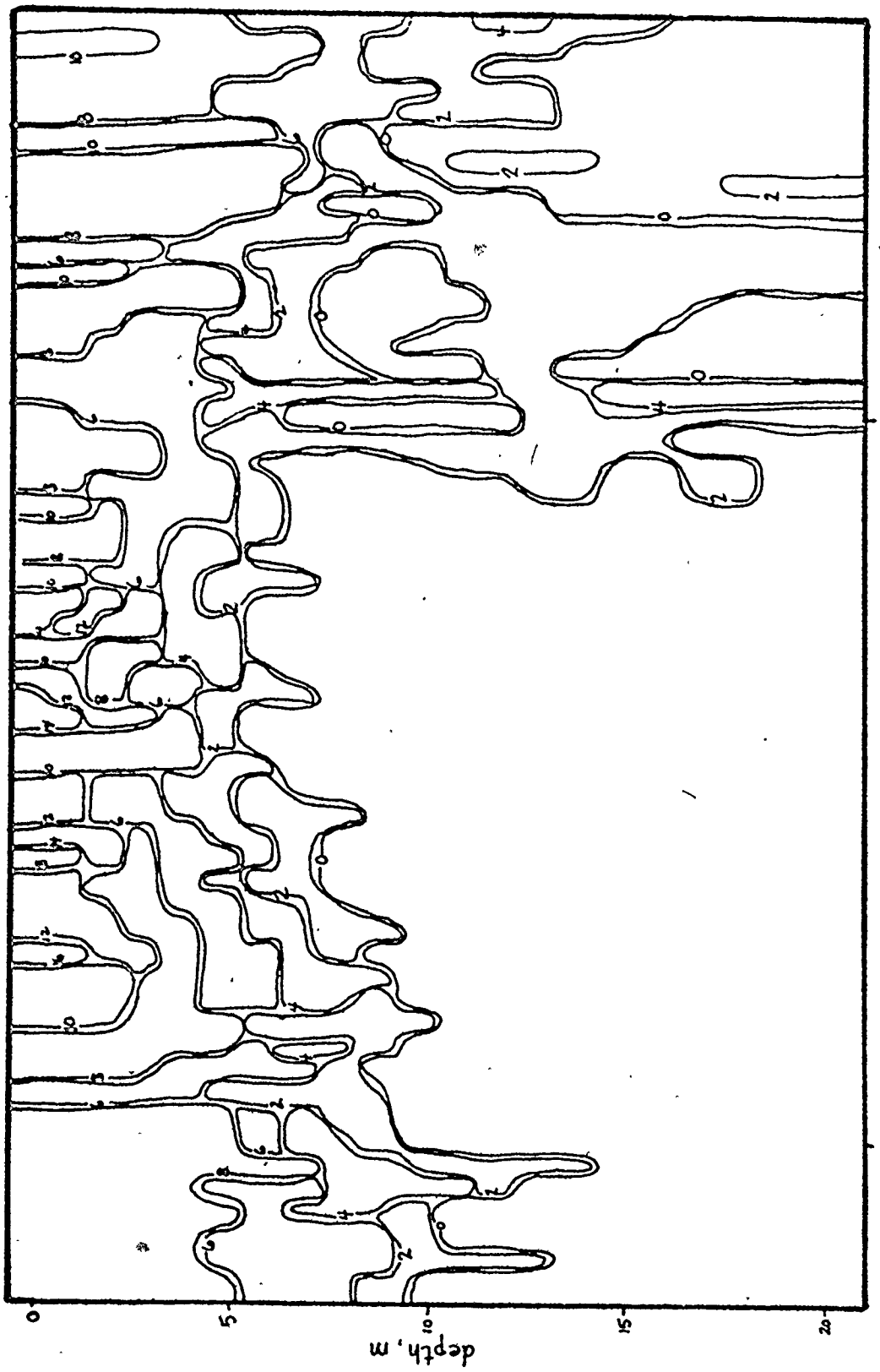

J
A
J
O2, mg l-1
depth, m
0
5
10
15
20

Fig. 4. Variation in total phosphorus (TP) concentration ($\mu g\ l^{-1}$) with depth and time; June 25 - August 18, 1979.

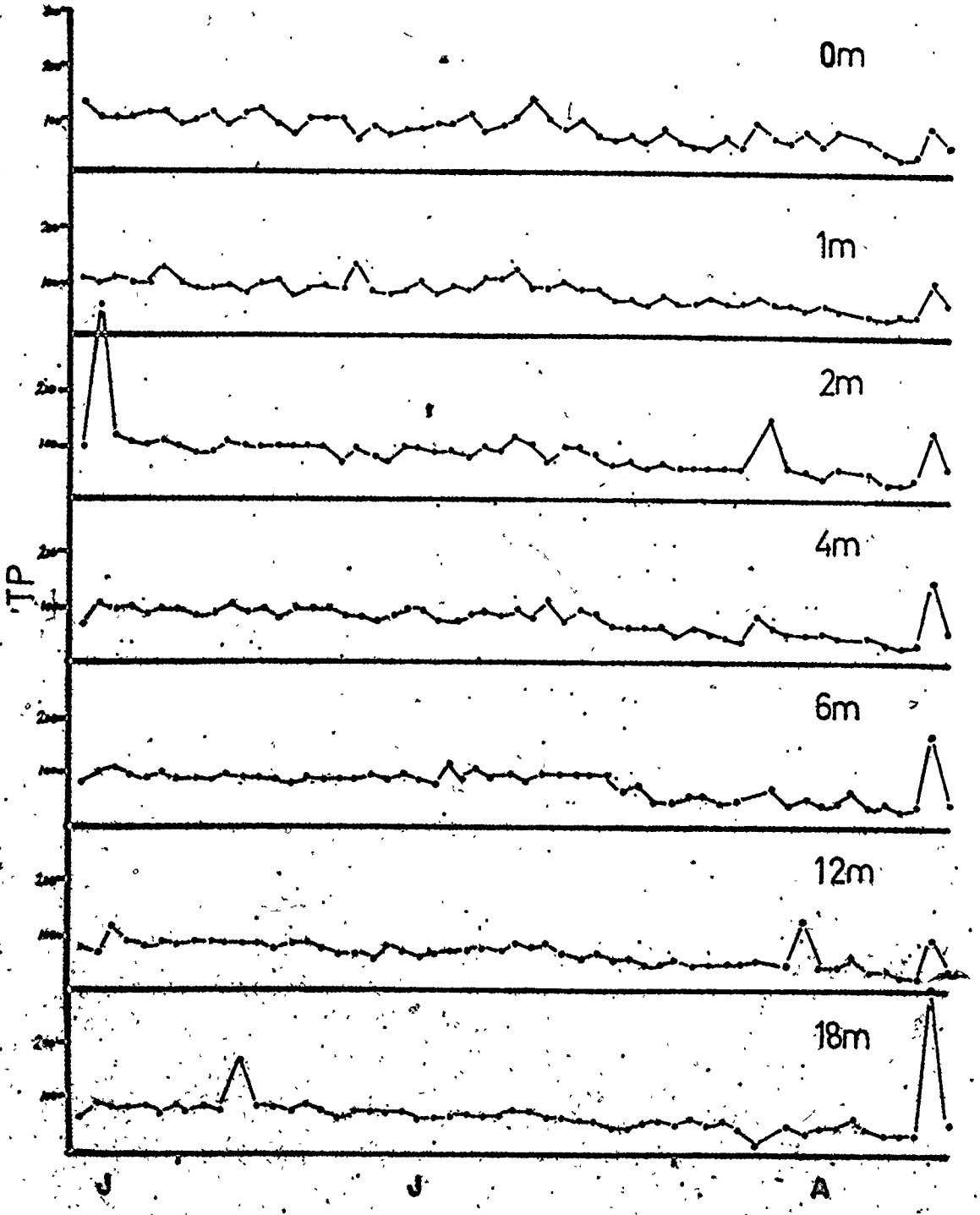

0m
1m
2m
4m
6m
12m
18m
TP
J
J
A

Fig. 5. Variation in soluble reactive phosphorus (SRP) concentration ($\mu g\ l^{-1}$) with depth and time; June 25-August 18, 1979.

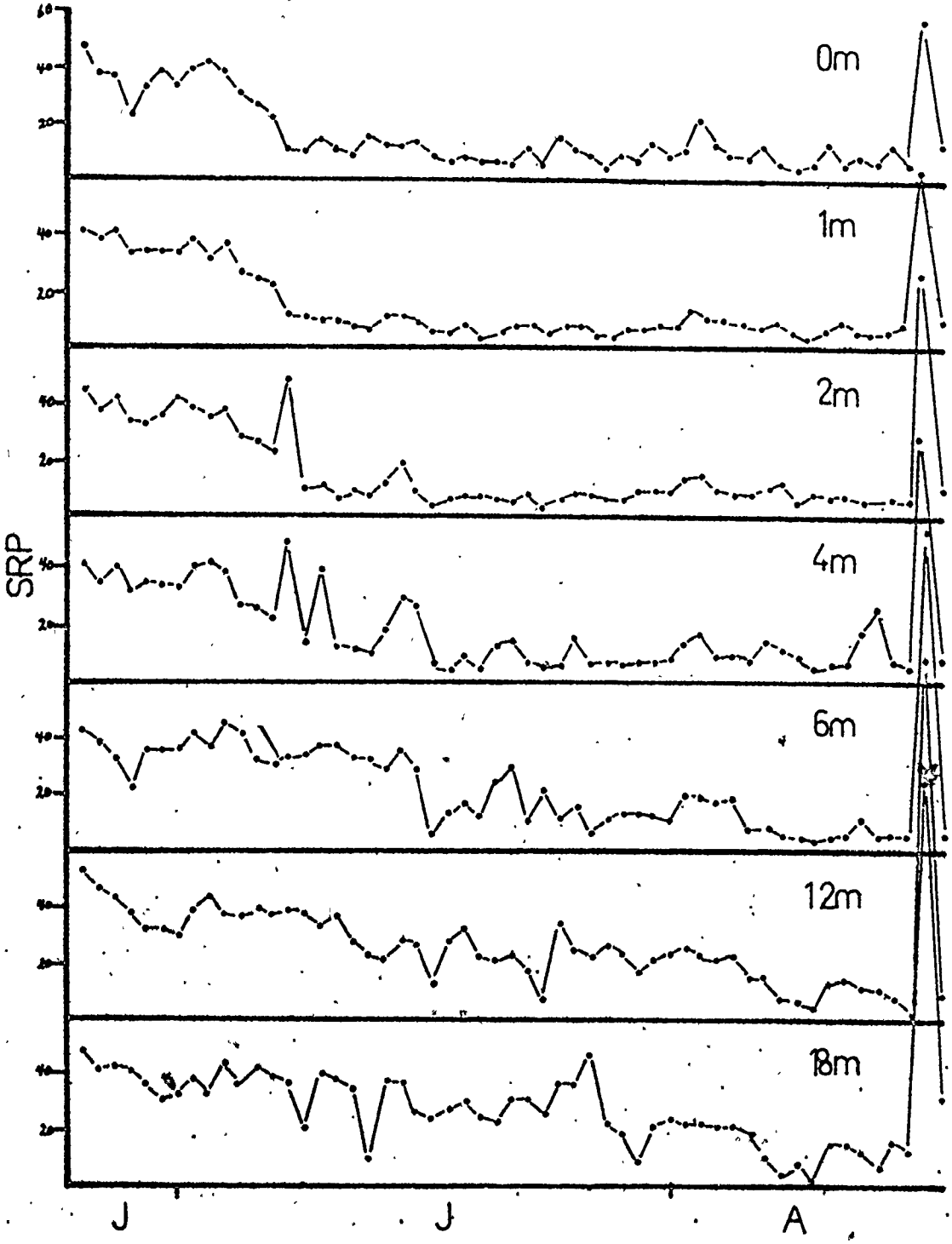

SRP
0m
1m
2m
4m
6m
12m
18m
J
J
A

Fig. 6. Variation in nitrate-nitrogen (NO_3N) concentration (mg l^{-1}) with depth and time; June 25 - August 18, 1979.

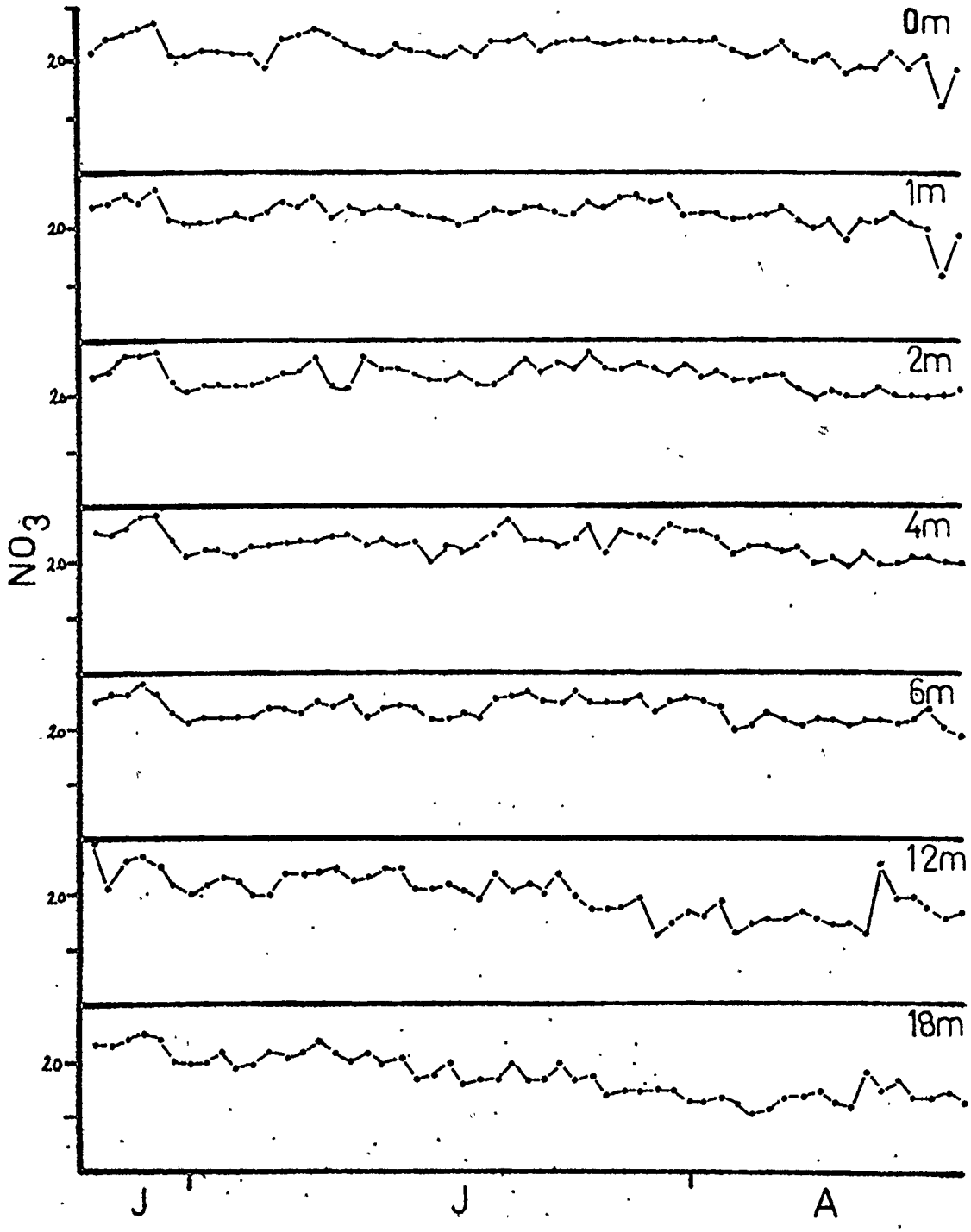

0m
1m
2m
4m
6m
12m
18m
20
NO3
J
J
A

Fig. 7. Variation in nitrite-nitrogen (NO_2N) concentration (mg l^{-1}) with depth and time; June 25 - August 18, 1979.

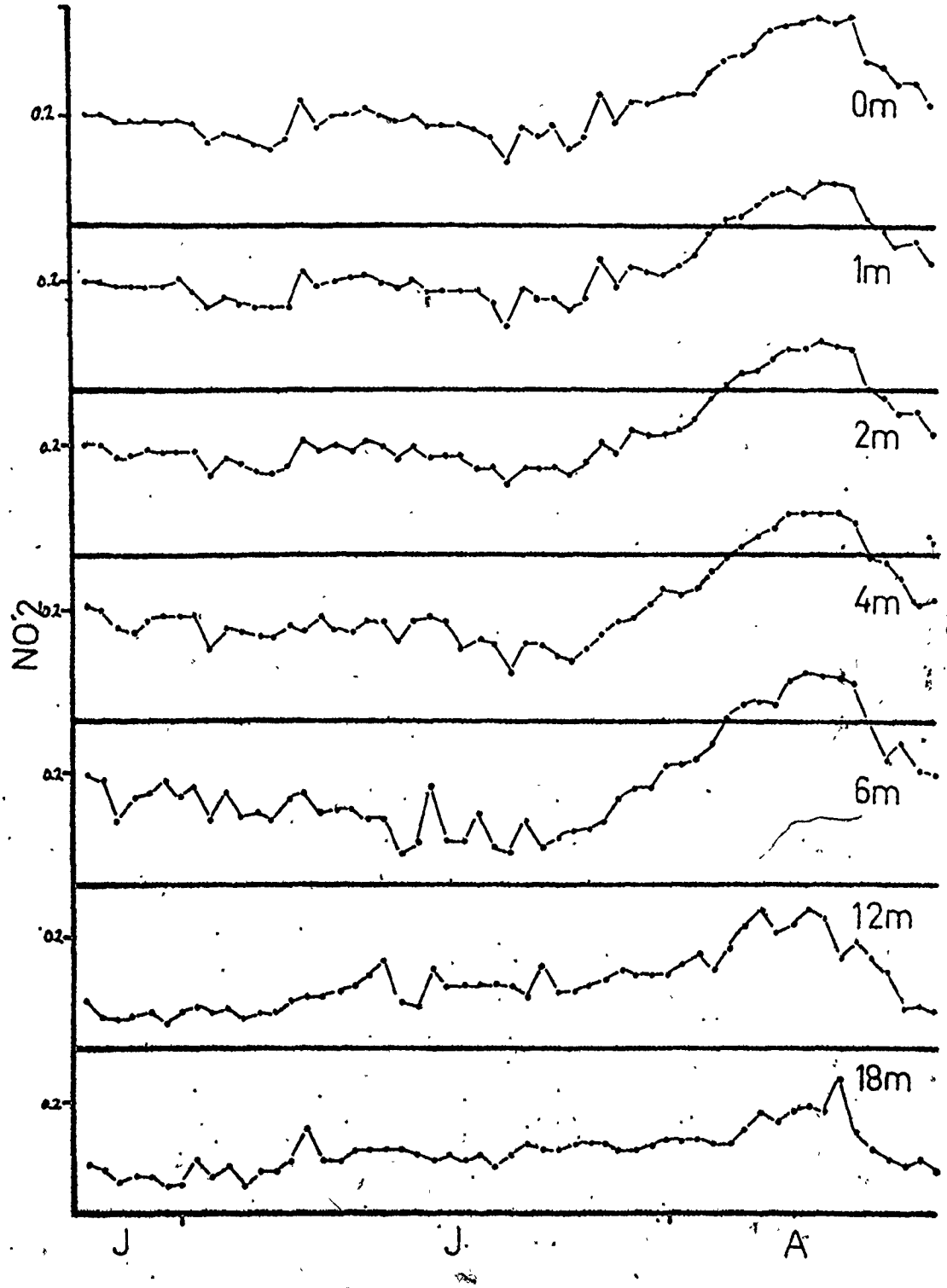

0m
1m
2m
4m
6m
12m
18m
0.2
NO2
J
J
A

Fig. 8. Variation in ammonia (NH_4^+) concentration (mg l^{-1}) with depth and time; June 25 - August 18, 1979.

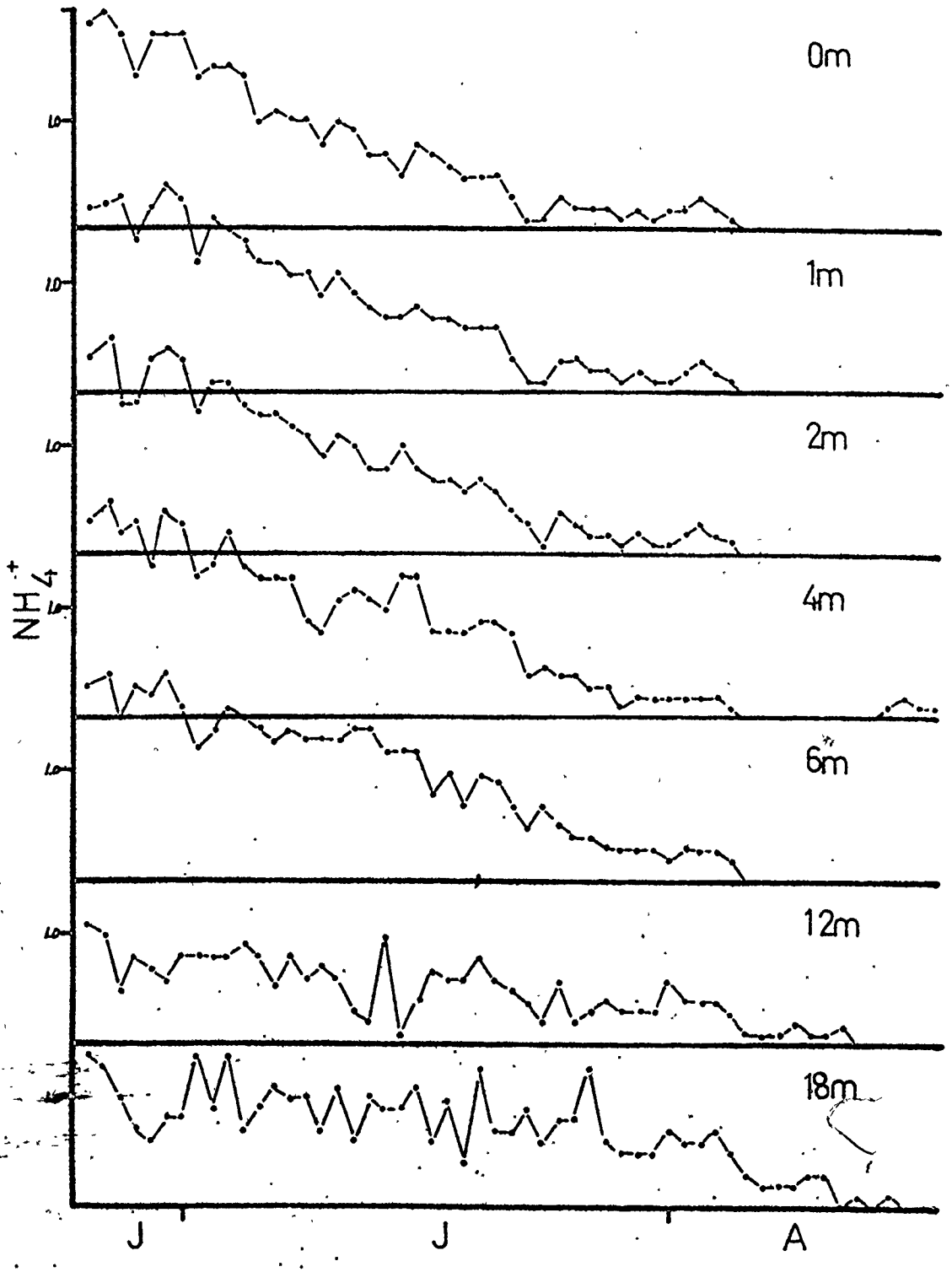

0m
1m
2m
4m
6m
12m
18m
NH_4^+
J
J
A

Fig. 9. Variation in total nitrogen ($NO_3N + NO_2N + NH_4^+$) concentration (mg l^{-1}) with depth and time; June 25 - August 18, 1979.

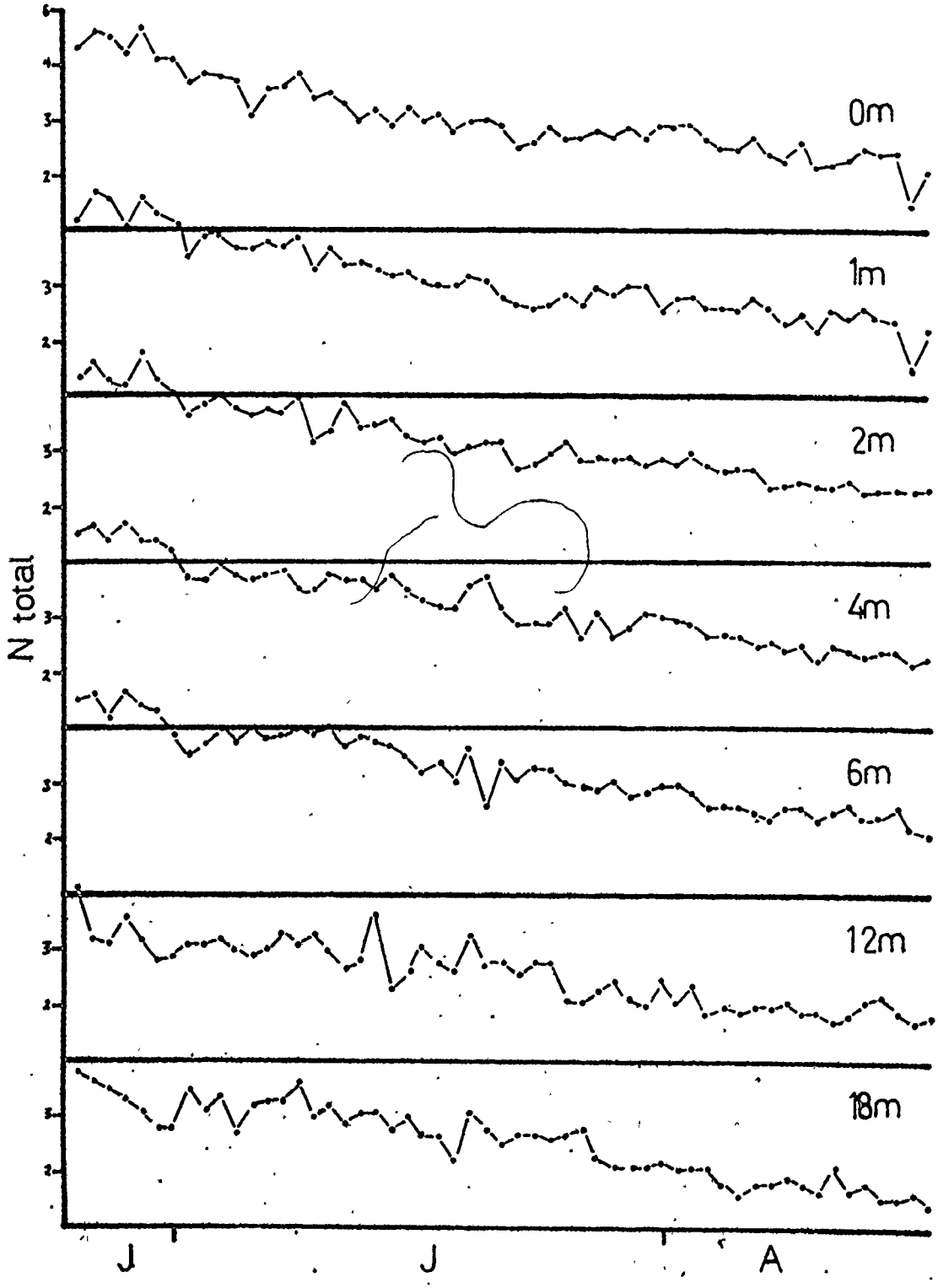

N total
0m
1m
2m
4m
6m
12m
18m
J
J
A

Fig. 10. Variation in soluble silica (Si) concentration (mg l^{-1}) with depth and time; June 25 - August 18, 1979.

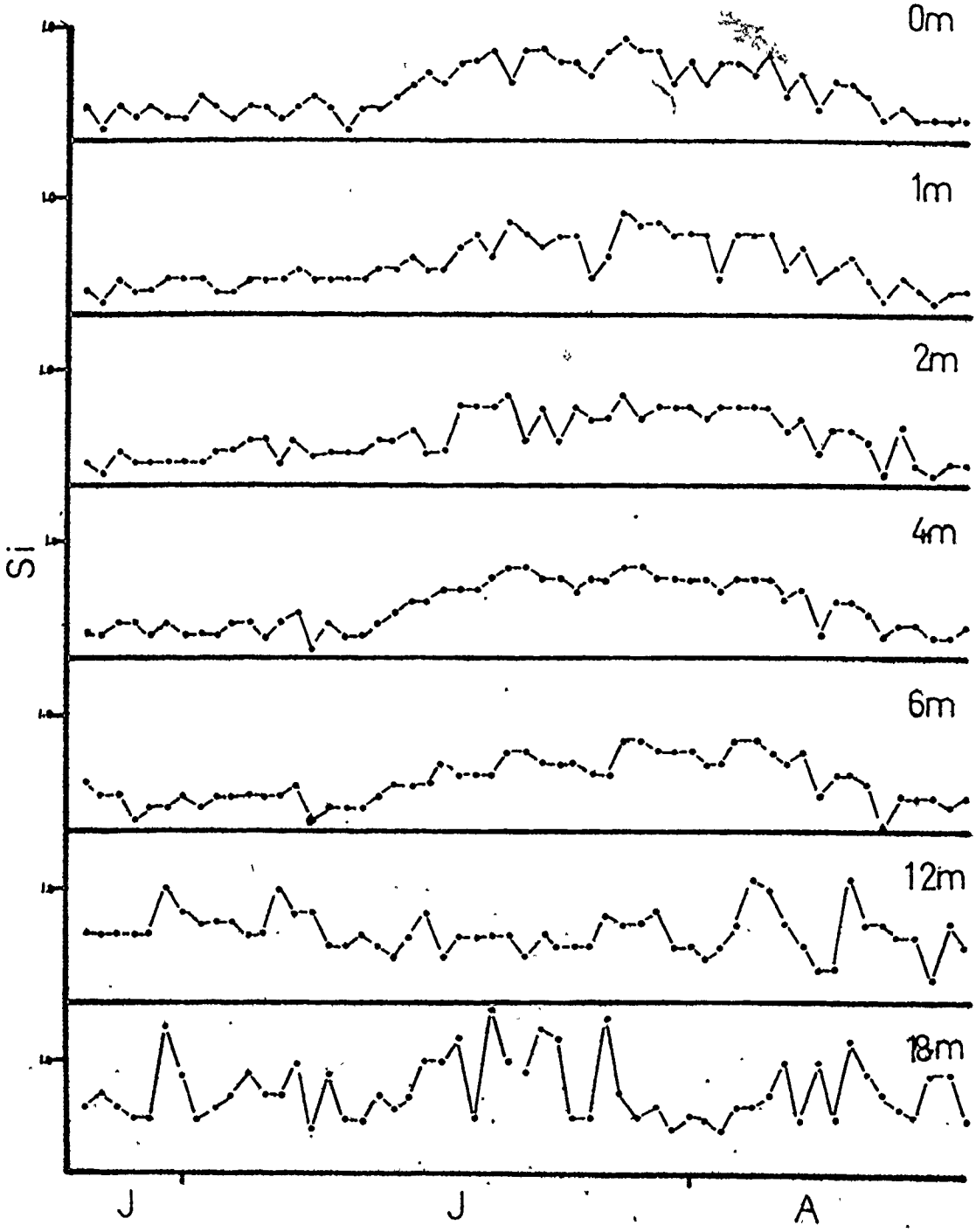

0m
1m
2m
4m
6m
12m
18m
Si
J
J
A

Fig. 11. Variation in pH with depth and time; June 25 - August 18, 1979.

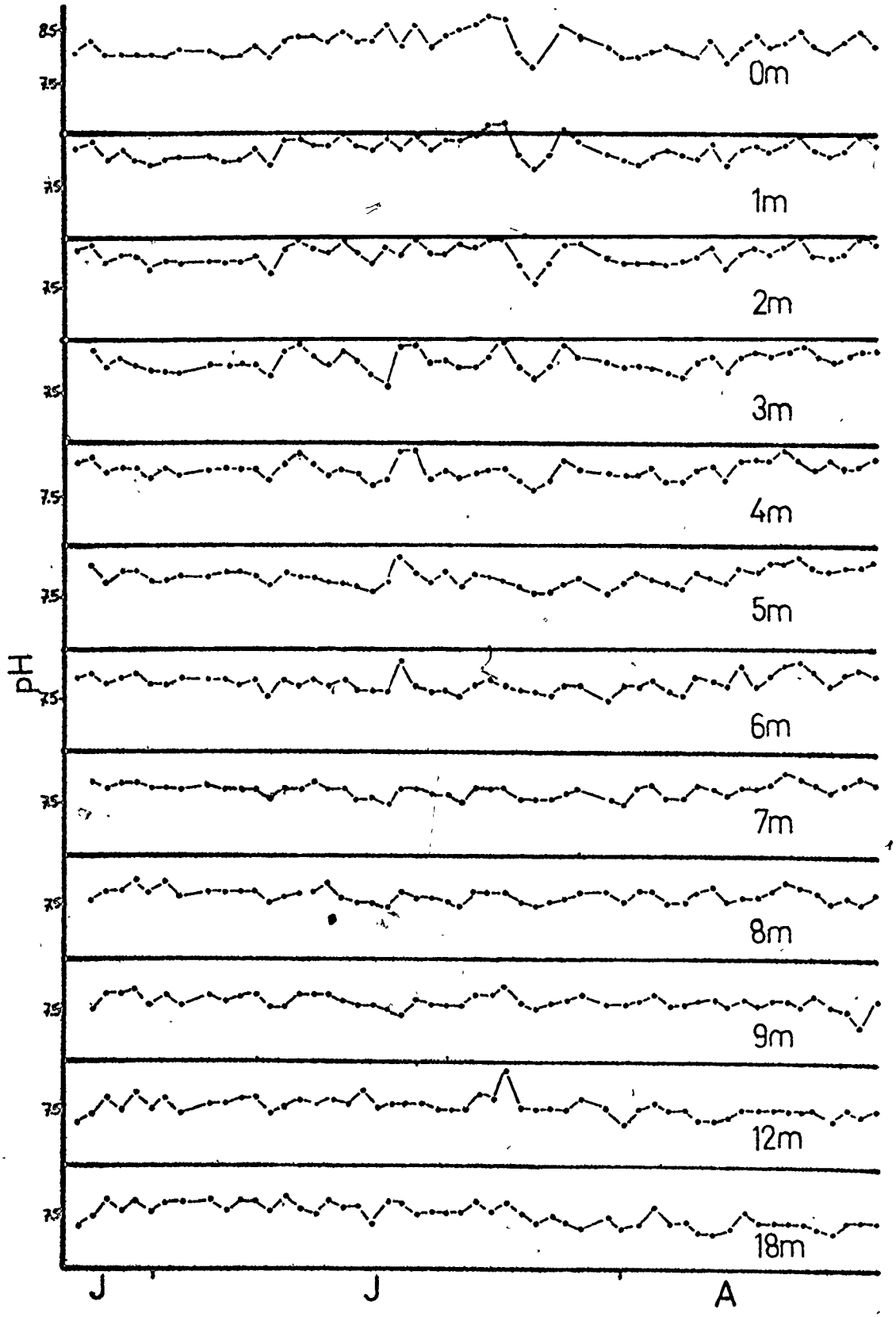

pH
8.5
7.5
0m
1m
2m
3m
4m
5m
6m
7m
8m
9m
12m
18m
J
J
A

Fig. 12. Variation in daily integrated solar irradiance, morning euphotic zone depth and morning extinction coefficients of PAR with depth; June 25 - August 18, 1979.

A. Daily integrated solar irradiance, ΣIo at 0.5 m ($\mu E\ m^{-2} sec^{-1}$, 1000 - 1400 hrs EDT)

B. Morning euphotic zone depth, Zeu (m)

C. Morning extinction coefficient of PAR, ε PAR (In units m^{-1})

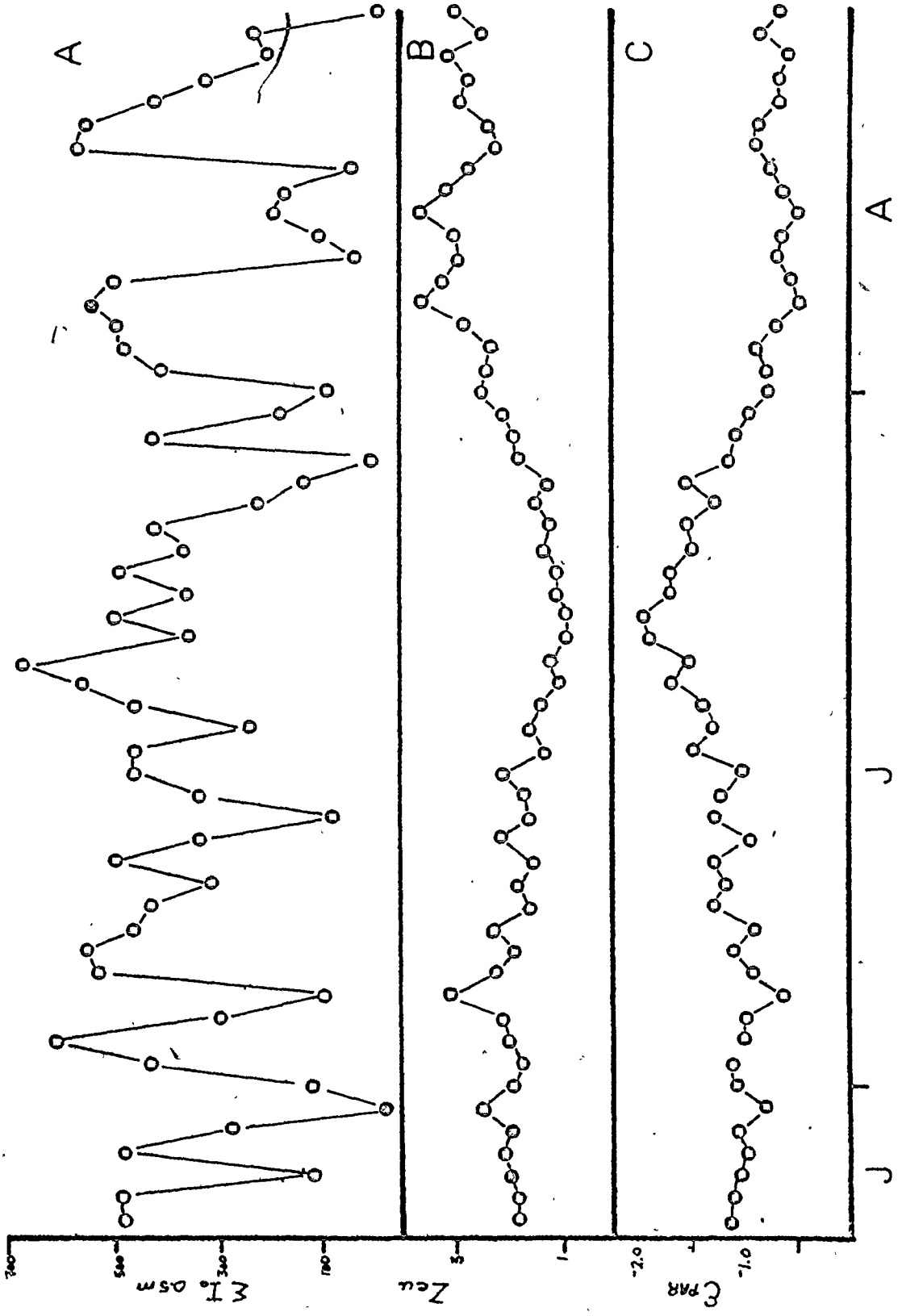

A
B
C
εI_o osm
Z_{eu}
ε_{PAR}
J
J
A

Fig. 13. Relationship between ε_{PAR} (in units m^{-1}) and ε_{min} (in units m^{-1}); June 25 - August 18, 1979.

$$\varepsilon_{PAR} = 1.448\ \varepsilon_{min},\ n = 55.$$

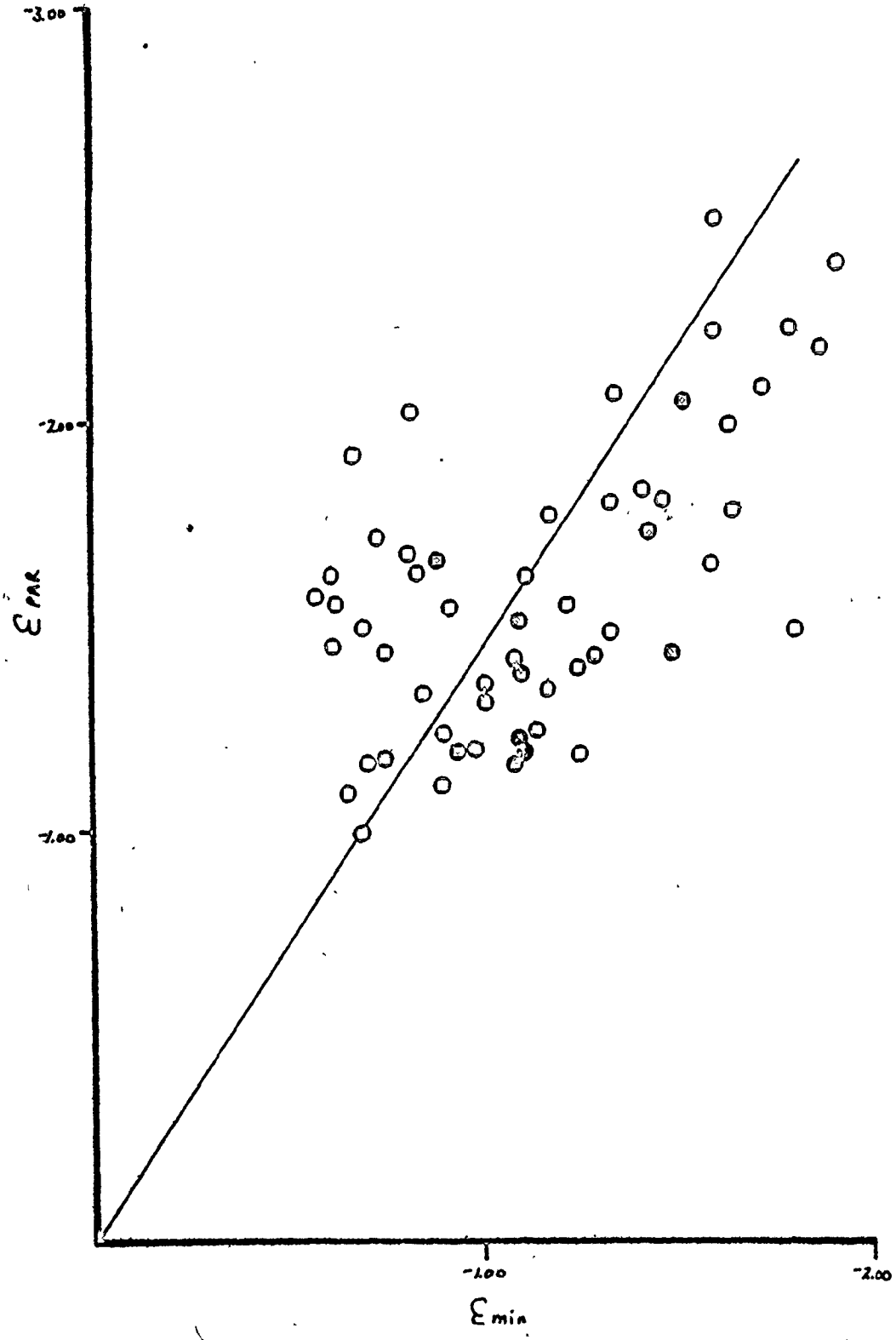

-3.00
-2.00
-1.00
ε_{PNR}
-1.00
-2.00
ε_{min}

Fig. 14. Daily F ratio (F + DCMU/IVF) profiles with depth (0 - 6m) in arbitrary units; June 25 - August 18, 1979. The average daily wind speed (μ, m sec^{-1}) is included for each profile. $\rightarrow$ represents the daily 1% Io light level depth (m).

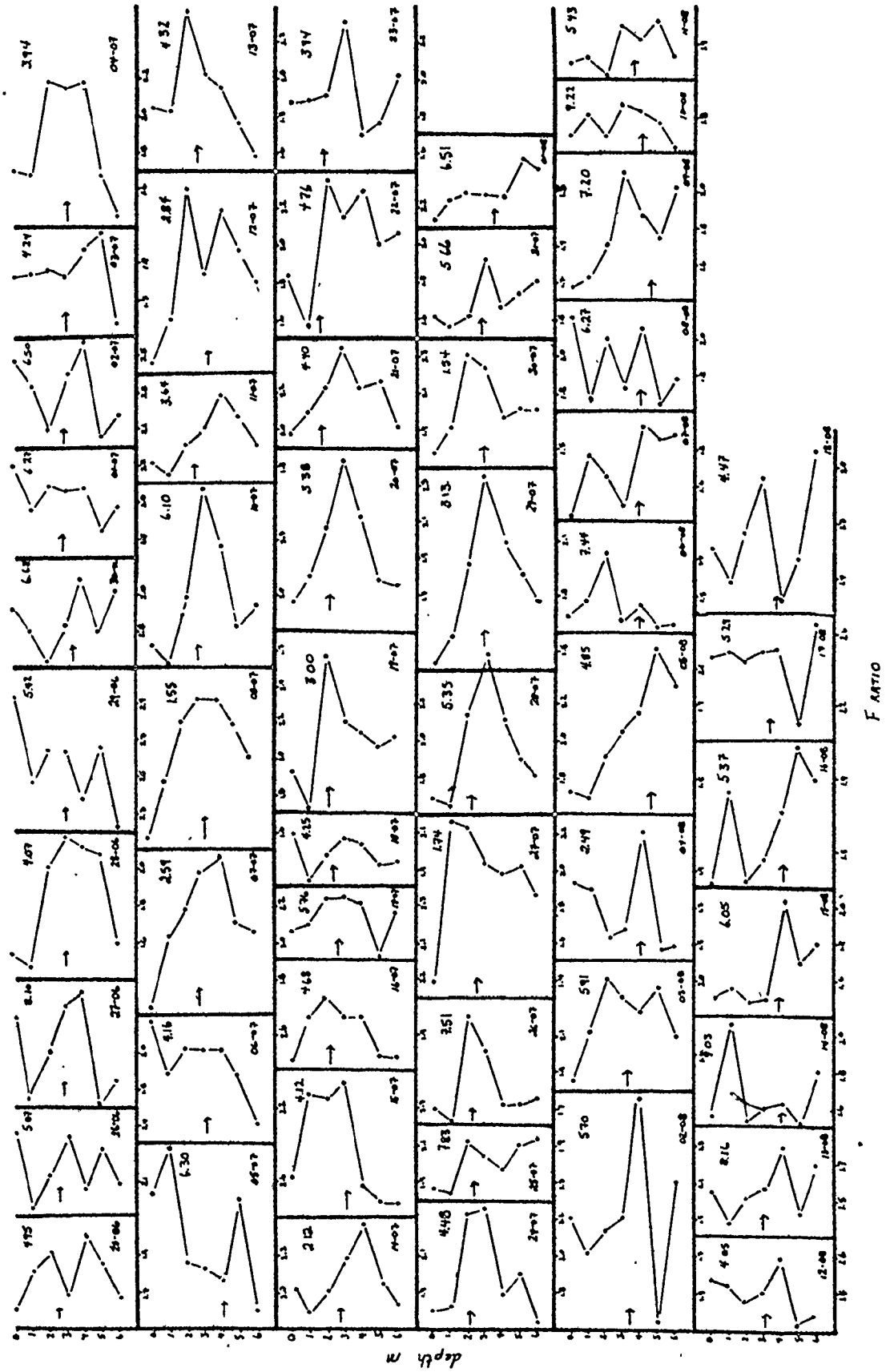

depth m
F RATIO

Fig. 15. Three F ratio-depth profiles (0 - 6m) obtained on occasions of similar integrated surface irradiance ($\sum$ Io, 1000 - 1400 hrs $\simeq$ 310 uE $m^{-2}sec^{-1}$) and different average daily wind speeds (μ, m sec^{-1}).

A. July 27, 1979; = 1.7 m sec^{-1}

B. July 17, 1979; = 5.8 m sec^{-1}

C. August 10, 1979; = 9.2 m sec^{-1}

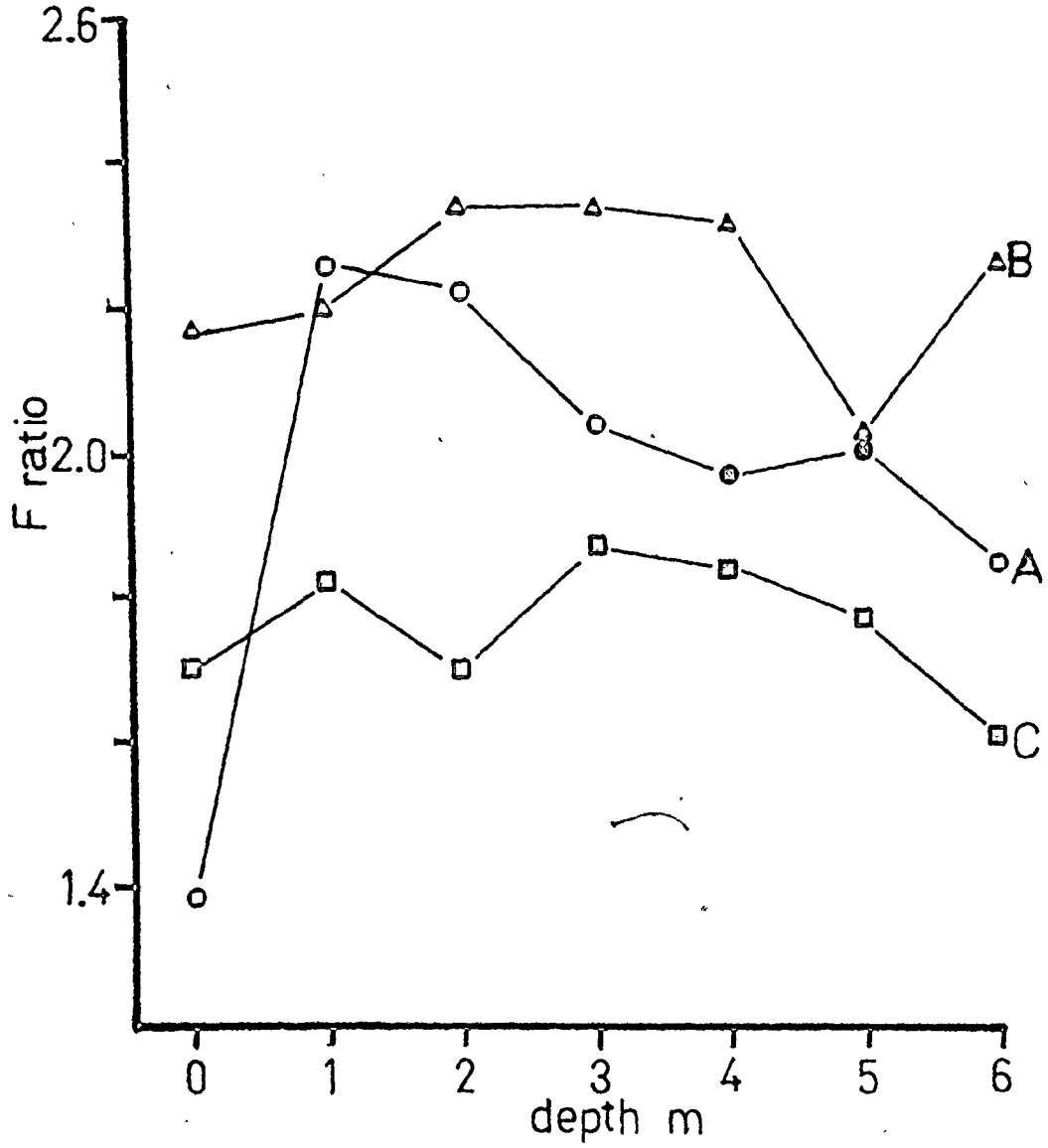

2.6
2.0
1.4
F ratio
0
1
2
3
4
5
6
depth m
A
B
C

Fig. 16. Relationship between Pmax (photosynthetic capacity; mg C mg chlorophyll $a^{-1}h^{-1}$) and the noon, surface water temperature (C^{o}).

$$Pmax = 0.232 \times temperature - 2.047,\ n = 55$$

$$r = +0.346,\ p < 0.01$$

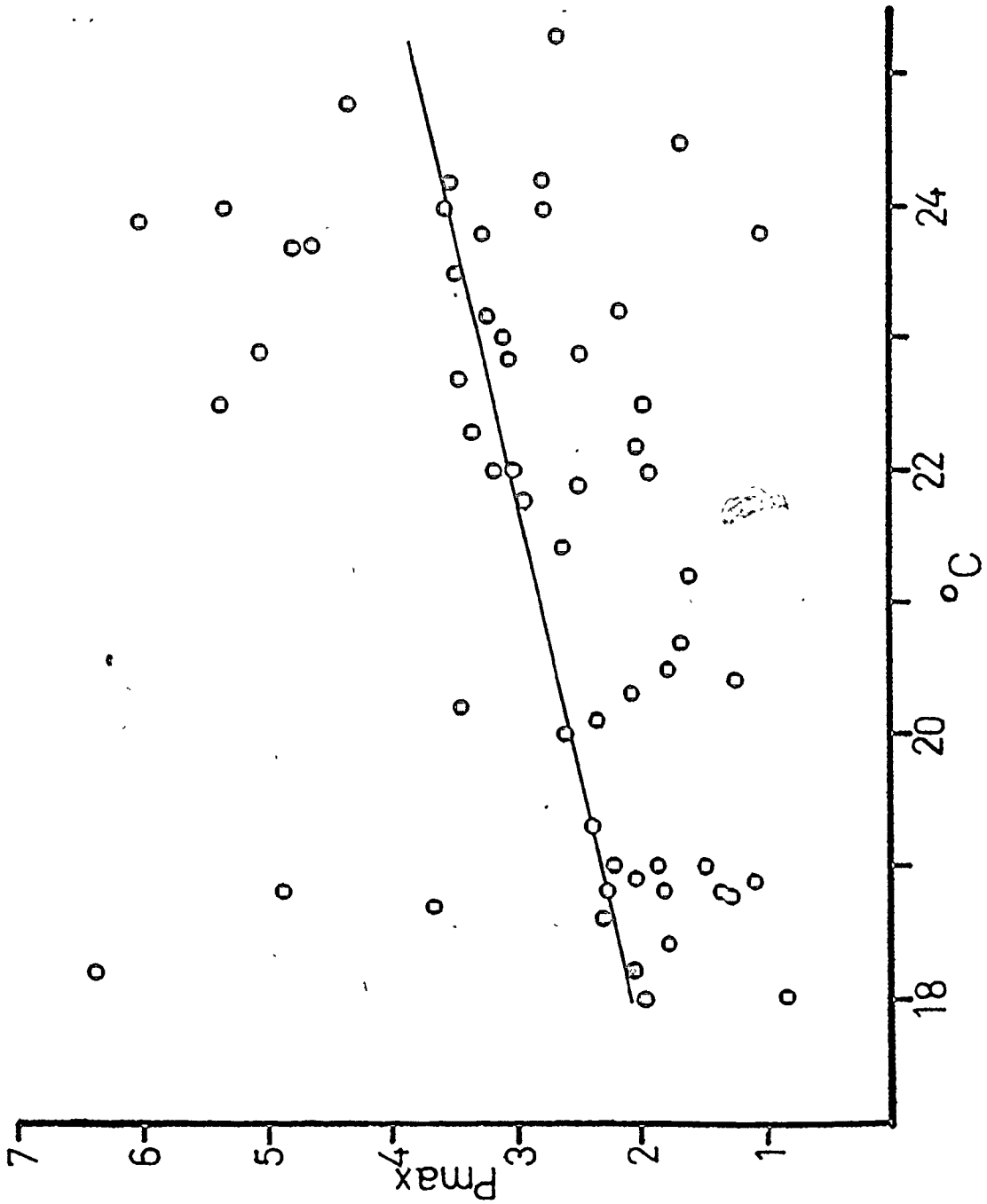

Pmax
7
6
5
4
3
2
1
18
20
22
24
°C

Fig. 17. Relationship between Pmax (photosynthetic capacity; mg C mg chlorophyll $a^{-1}h^{-1}$) and Po (photosynthetic efficiency; mg C mg chlorophyll $a^{-1}E^{-1}m^2$).

$$Pmax = 0.166\ Po + 2.148,\ n = 55$$

$$r = +0.370,\ p < 0.01$$

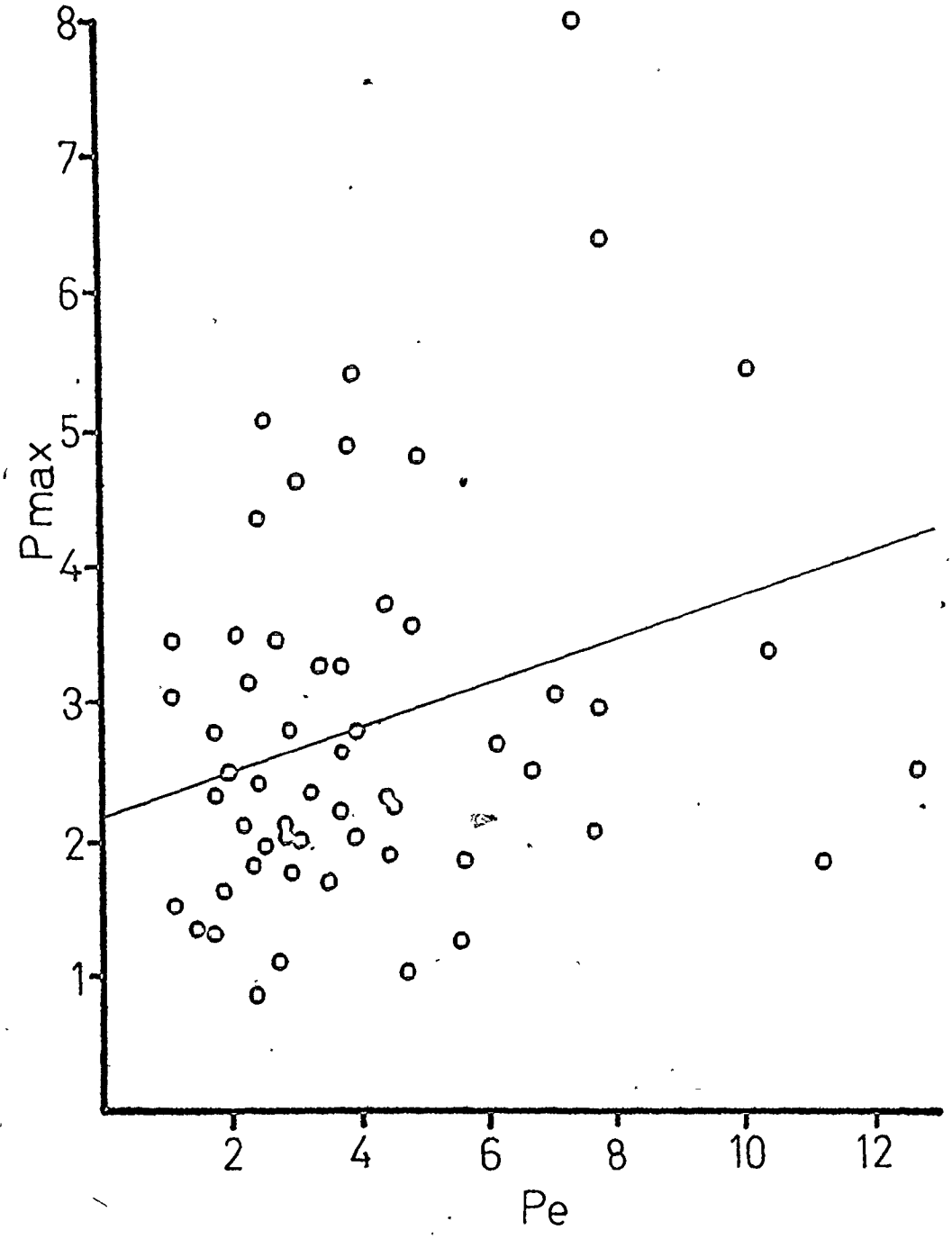

8
7
6
5
4
3
2
1
Pmax
2
4
6
8
10
12
Pe

Fig. 18. Relationship between Pe (photosynthetic efficiency; mg C mg chlorophyll $a^{-1}E^{-1}m^2$) and Ik (uE $m^{-2}sec^{-1}$).

$$Pe = 6.253^{e^{-0.0023\ Ik}}$$

$$r = +0.540,\ p < 0.01$$

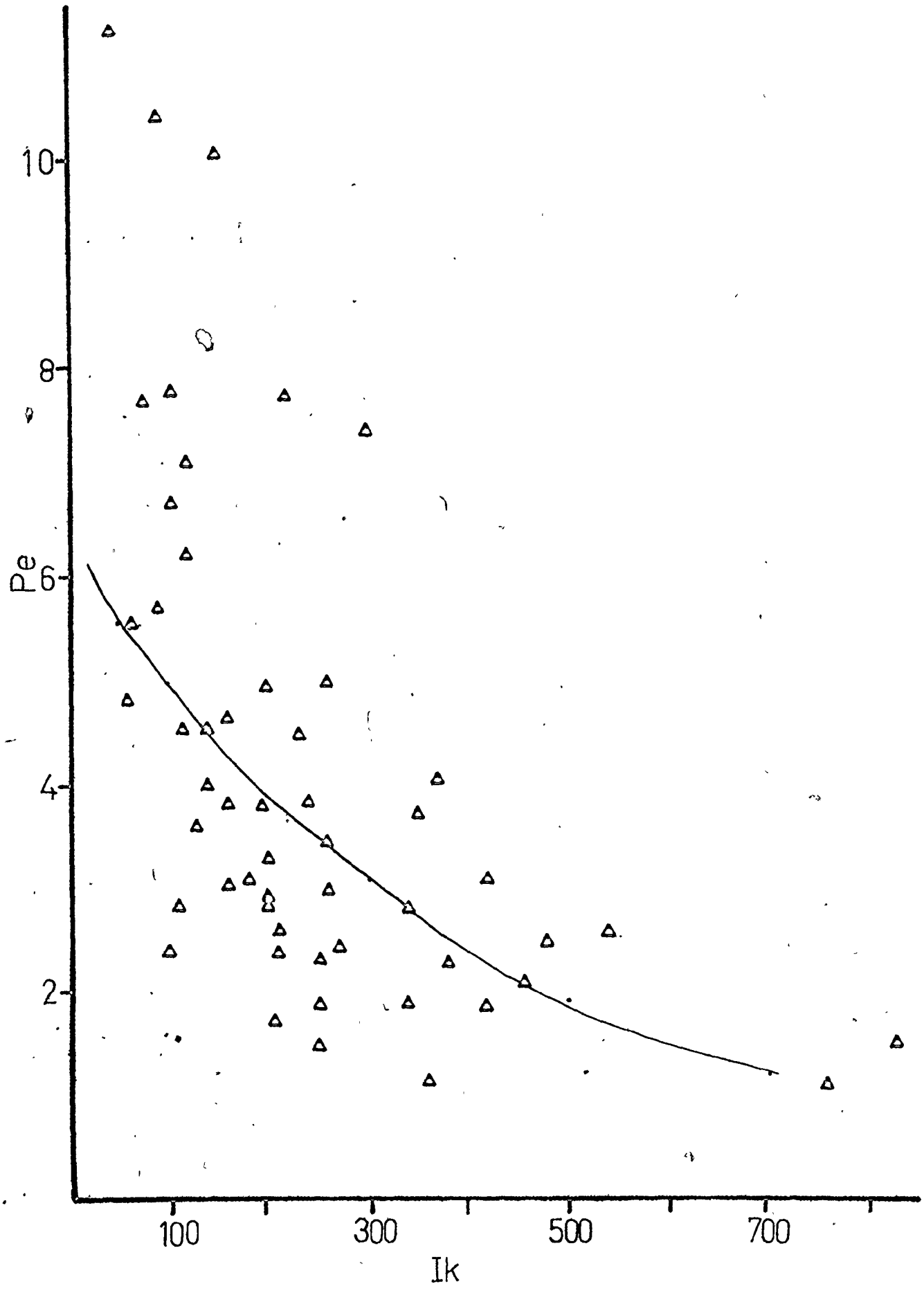

10
8
6
4
2
Pe
100
300
500
700
Ik

Fig. 19. Relationship between daily Ik values ($\mu E\ m^{-2}sec^{-1}$) and daily integrated usrface irradiance, $\sum Io$ ($\mu E\ m^{-2}sec^{-1}$) integrated over the previous two day period.

$\sum Io$.

Ik.

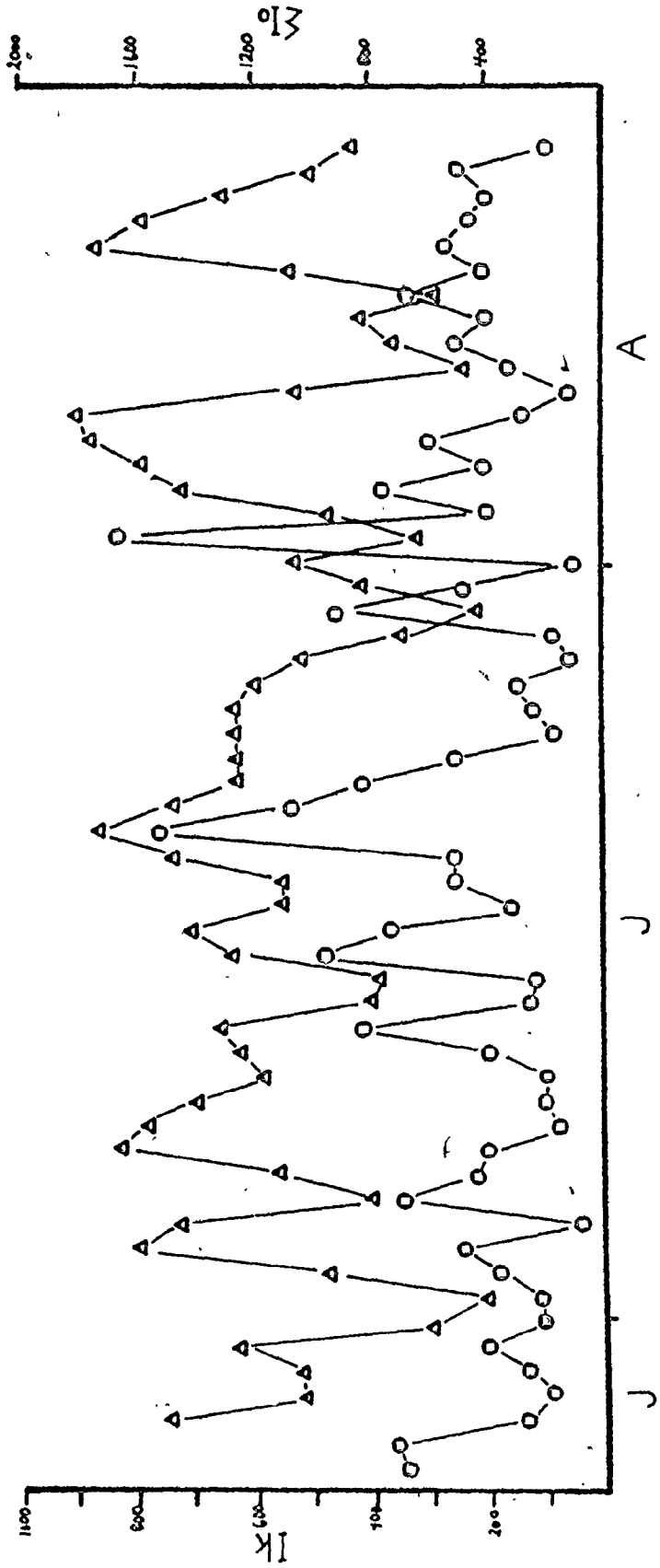

1000
1100
1200
800
400
ε_{10}
A
J
J
1100
600
400
200
1K

Fig. 20. Variation in algal biomass (mg chlorophyll a m^{-3}) with depth and time; June 25 - August 18, 1979.

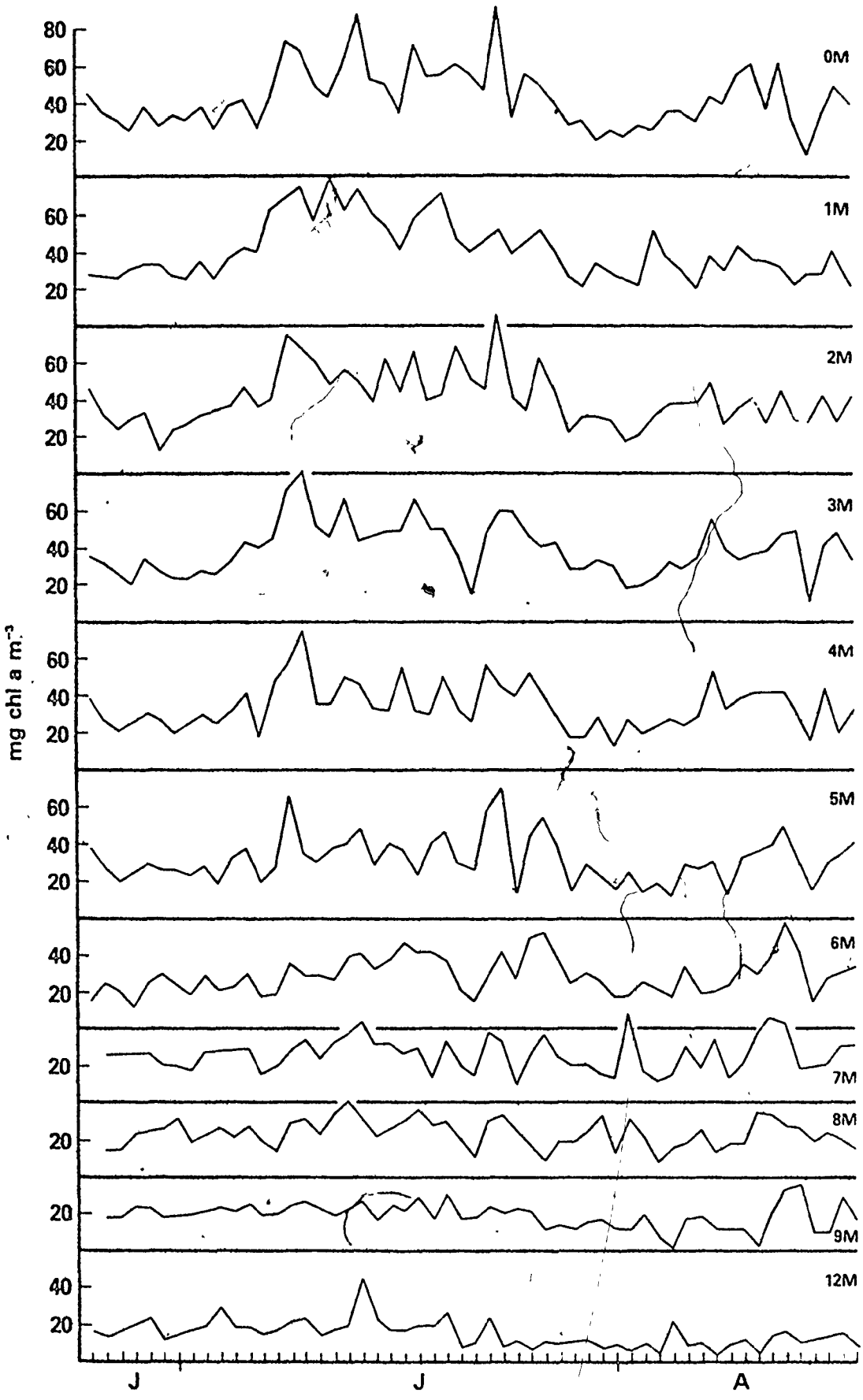

mg chl a m⁻³
0M
1M
2M
3M
4M
5M
6M
7M
8M
9M
12M
J
J
A

Fig. 21 Changes in the numerical abundance (cells ml^{-1}) of sixteen Hamilton Harbour phytoplankton species with time; June 25 - August 18, 1979.

A. *Asterionella* sp.

B. *Ankistrodesmus* sp.

C. *Planktosphaeria* sp.

D. Desmids (*Closterium* sp., *Staurastrum* sp. and *Cosmarium* sp.)

E. *Lagerheimia* sp.

F. *Dictyosphaerium* sp.

G. *Pediastrum* sp.

H. *Melosira* sp.

I. *Scenedesmus quadricauda*

J. *Oocystis borgeii*

K. *Coelastrum* spp.

L. *Cyclotella* sp.

M. *Stephanodiscus* sp.

N. *Cryptomonas* sp.

O. *Rhodomonas* sp.

P. *Chlamydomonas* sp.

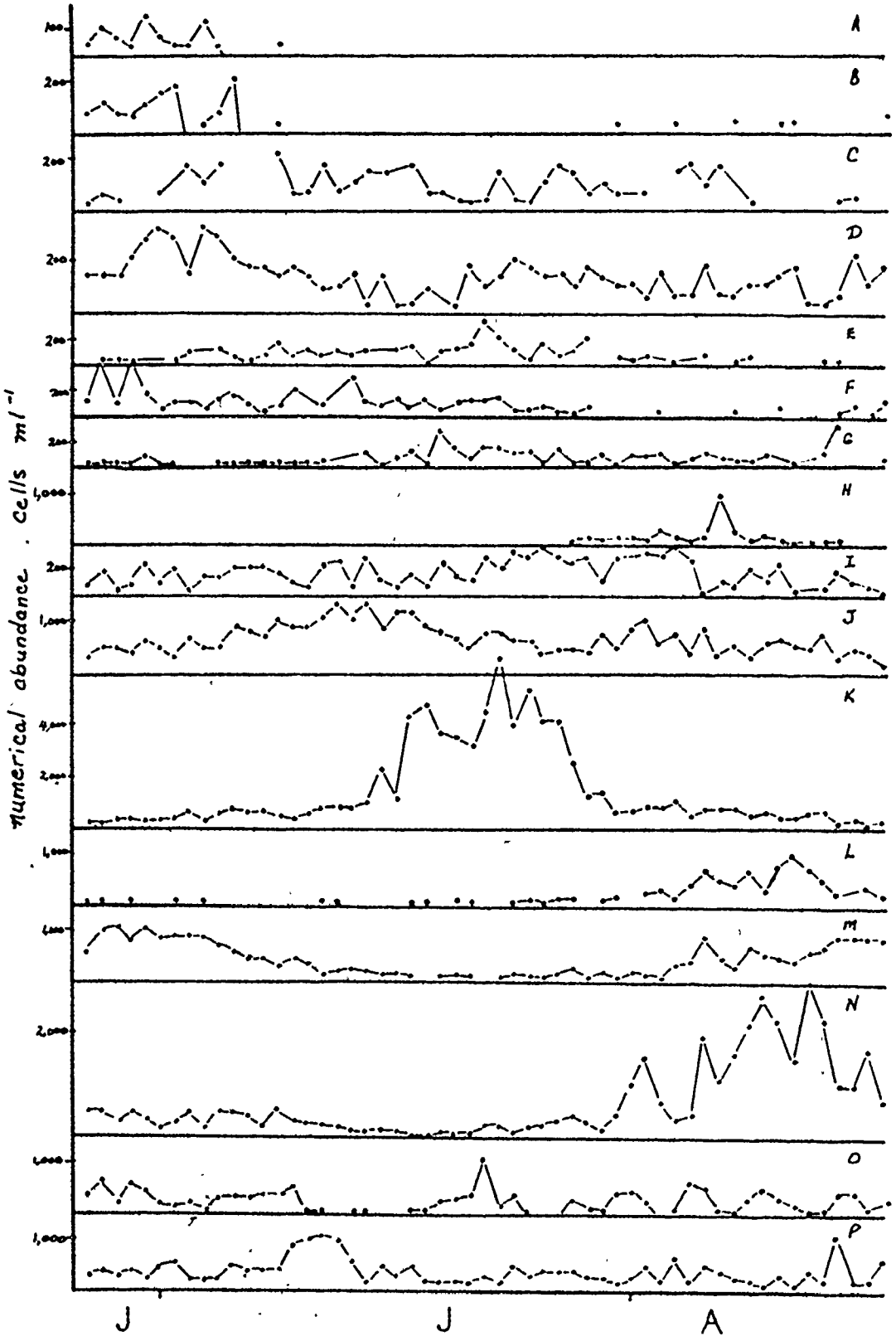

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Numerical abundance . cells ml⁻¹
J
J
A

Fig. 22. Variation in surface chlorophyll a biomass (A; mg chl a m^{-3}) and integral chlorophyll a biomass (B; mg chl a m^{-3}) with time; June 25 - August 18, 1979.

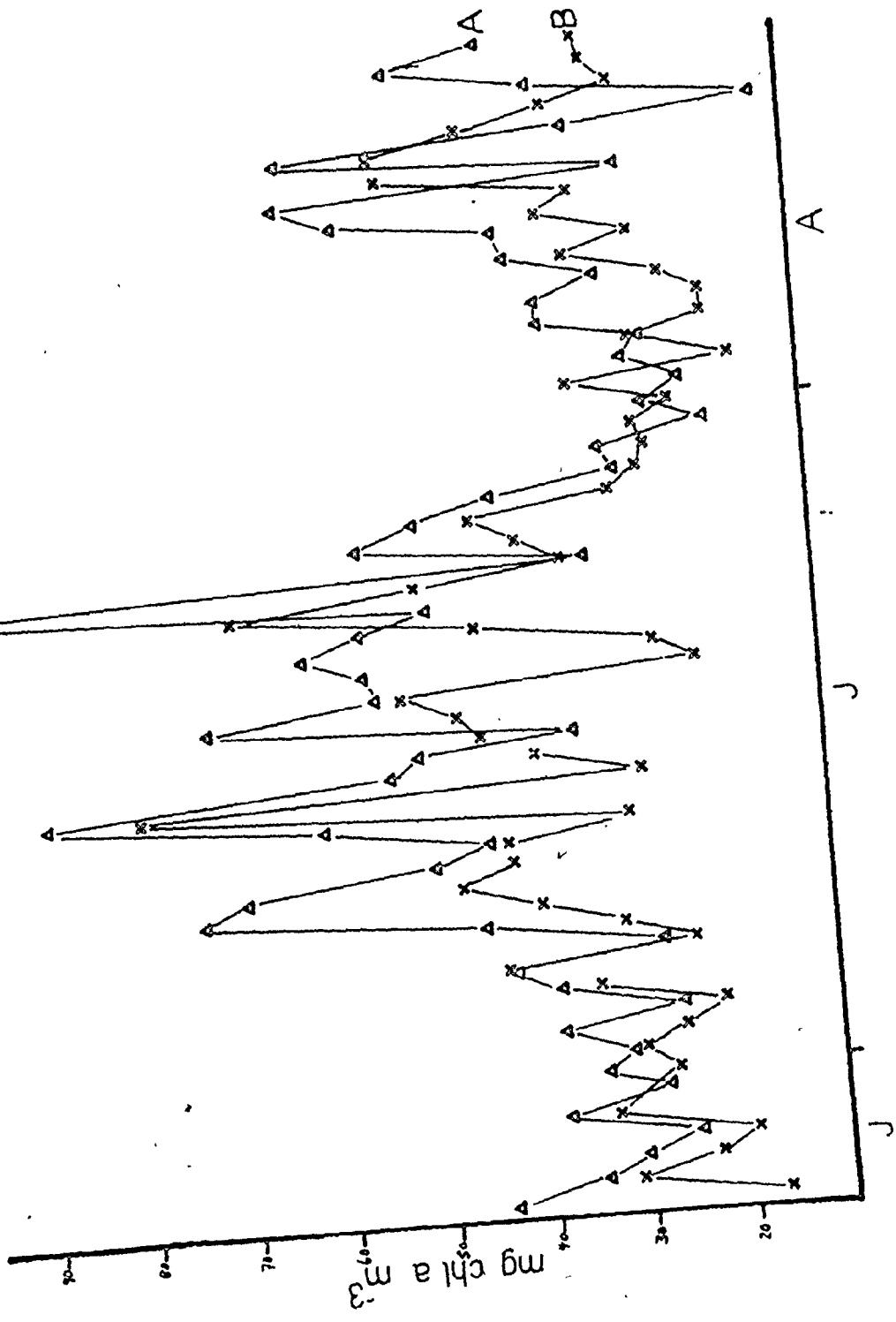
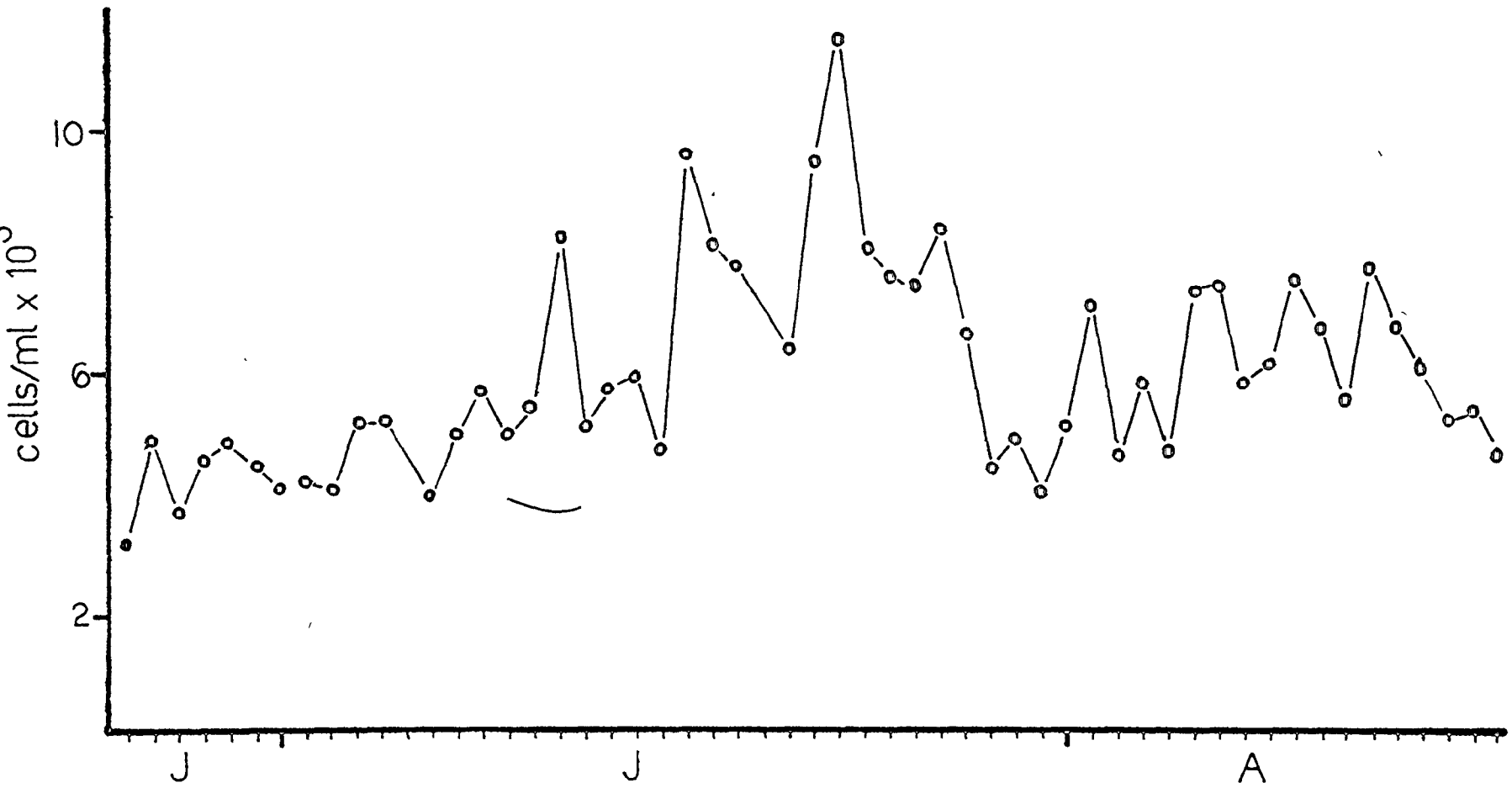

mg chl a m⁻³
80
60
50
40
30
20
A
B
J
F
A
J

Fig. 23. Variation in the total algal cell number (cells ml^{-1}) with time; June 25 - August 18, 1979.


cells/ml x 10^3
10
6
2
J
J
A

Appendix II. Variation with time in the concentrations of the total carbonate alkalinity and the carbon species; HCO_3^-, CO_3^{-2} and free CO_2 (mg CO_2 l^{-1}), the integral in situ productivity; ΣP (mg CO_2 l^{-1}) and surface ph, in Hamilton Harbour, June 25 - August 18, 1979.

Date	Total CO_2	Free CO_2	HCO_3^-	CO_3^{-2}	ΣP	Ph
25/06	86.11	1.38	84.10	0.62	0.422	8.1
26/06	77.36	0.92	75.66	0.78	0.433	8.3
27/06	93.54	5.27	88.08	0.18	0.283	8.0
28/06	83.21	1.70	81.02	0.48	0.298	8.0
29/06	81.09	0.49	79.06	1.52	0.242	8.0
30/06	80.19	1.85	77.93	0.40	0.140	8.0
01/07	86.92	3.99	82.73	0.19	0.095	8.0
02/07	73.75	1.15	72.05	0.54	0.260	8.1
03/07	85.76	2.36	83.04	0.35	0.494	8.1
04/07	82.49	1.35	80.56	0.58	0.256	8.1
05/07	81.02	1.99	78.65	0.37	0.326	8.0
06/07	78.41	1.15	76.63	0.62	0.079	8.0
07/07	76.80	1.07	75.09	0.63	0.402	8.2
08/07	81.09	0.72	79.30	1.06	0.404	8.0
09/07	74.16	0.65	72.53	0.97	0.486	8.3
10/07	74.65	0.77	73.00	0.86	0.466	8.4
11/07	76.95	0.54	75.14	1.26	0.430	8.4
12/07	75.49	0.58	73.77	1.13	0.525	8.3
13/07	69.72	0.42	67.95	1.34	0.535	8.5
14/07	66.04	0.43	64.45	1.16	0.482	8.3
15/07	73.43	0.82	71.80	0.79	0.415	8.3
16/07	75.71	0.89	74.12	0.68	0.790	8.6
17/07	72.81	0.65	71.18	0.97	0.469	8.2
18/07	72.00	0.76	70.46	0.78	0.456	8.6
19/07	69.10	0.51	67.50	1.08	0.852	8.2
20/07	67.13	0.58	65.65	0.90	0.507	8.4
21/07	65.49	0.46	60.57	0.93	0.450	8.5
22/07	67.23	0.68	65.79	0.76	0.689	8.6
23/07	57.25	0.45	55.96	0.84	0.481	8.7
24/07	59.42	0.36	57.93	1.12	0.647	8.7
25/07	65.24	1.38	63.50	0.36	0.542	8.1
26/07	70.95	2.19	68.49	0.25	0.398	7.8
27/07	66.54	0.67	65.11	0.75	0.507	
28/07	60.50	0.61	69.21	0.68	0.156	8.6
29/07	74.79	2.10	72.38	0.31	0.380	8.4
30/07	66.80	1.03	65.29	0.48	0.388	
31/07	68.09	1.36	66.35	0.38	0.184	8.2
01/08	101.58	2.05	98.94	0.58	0.316	8.0
02/08	69.59	4.70	64.78	0.11	0.218	8.0
03/08	72.82	2.37	70.19	0.25	0.405	8.1
04/08	72.72	2.09	70.34	0.28	0.476	8.2
05/08	72.32	2.60	69.49	0.22	0.427	8.1
06/08	78.38	2.05	72.49	0.30	0.780	8.0
07/08	70.51	1.44	68.69	0.39	0.148	8.3
08/08	70.62	10.02	60.56	0.04	0.171	7.9
09/08	72.11	1.54	70.19	0.36	0.421	8.2
10/08	69.14	1.77	67.06	0.30	0.245	8.3
11/08	72.83	1.71	70.77	0.34	0.544	8.2
12/08	69.10	1.04	67.55	0.50	0.506	8.3
13/08	72.99	0.93	71.41	0.65	0.462	8.5
14/08	76.87	2.49	74.11	0.26	0.320	8.2
15/08	74.95	1.73	72.36	0.36	0.327	8.1
16/08	74.80	1.39	72.98	0.44	0.391	8.3
17/08	70.45	1.16	68.82	0.46	0.224	8.5
18/08	74.85	1.47	72.96	0.42	0.085	8.2

Appendix III. Variation of the rates of in situ photosynthesis; ΣP and max Pv, the photosynthetic parameters; Pmax, Pe and Ik, the depth of max Pv and the integral in situ light intensity ΣIo (1000-1400 hrs EDT, 0.1 m) with time in Hamilton Harbour, June 25 - August 18, 1979.

Date	ΣP[1]	max Pv[2]	z[3]	Pmax[4]	Pe[5]	Ik[6]	ΣIo[7]
25/06	115.00	82.12	0.0	2.296	1.88	340	745.0
26/06	118.14	81.99	0.5	1.490	1.15	360	743.3
27/06	77.23	69.81	0.0	2.286	4.54	140	287.0
28/06	81.26	51.81	0.5	1.846	5.70	90	762.7
29/06	65.94	34.90	0.0	2.245	4.63	135	491.3
30/06	38.15	36.12	0.0	1.294	1.75	205	110.7
01/07	25.97	38.15	0.0	1.115	2.82	110	289.9
02/07	70.80	58.11	0.0	1.874	4.53	115	670.0
03/07	134.36	72.13	0.5	1.994	3.08	180	930.5
04/07	69.85	53.68	0.0	2.099	2.33	250	519.1
05/07	88,79	68.49	0.0	1.178	11.25	44	235.6
06/07	184.90	204.55	0.5	1.870	3.86	350	836.7
07/07	109.56	101.29	0.0	3.705	4.47	230	828.1
08/07	110.02	113.25	0.5	2.086	2.90	200	742.5
09/07	132.50	152.74	0.0	2.072	7.67	75	659.4
10/07	126.94	172.70	0.0	2.503	6.69	104	521.2
11/07	117.26	147.55	0.0	2.945	7.79	105	745.0
12/07	142.99	156.08	0.0	3.556	4.94	200	578.3
13/07	145,83	169.24	0.0	2.732	1.84	420	225.9
14/07	131.26	151.18	0.0	1.693	3.62	130	554.2
15/07	110.36	143.72	0.0	2.678	6.22	120	734.8
16/07	215.25	224.14	0.0	4.357	2.52	480	698.0
17/07	127.88	190.80	0.0	5.379	4.04	370	420.3
18/07	124.25	158.37	0.0	2.204	3.82	160	689.3
19/07	232.20	252.99	0.0	4.795	4.99	260	786.4
20/07	138.24	180.30	0.0	3.237	3.45	260	940.5
21/07	122.67	191.17	0.0	3.099	1.13	760	541.6
22/07	187.76	285.37	0.0	5.050	2.60	540	705.8
23/07	131.22	224.78	0.0	4.639	3.07	420	551.1
24/07	176.41	251.49	0.0	2.784	2.97	260	700.3
25/07	147.79	200.47	0.0	6.055	18.69	90	568.3
26/07	108.33	172.67	0.0	3.065	7.09	120	634.2
27/07	138.02	272.80	0.0	5.438	10.07	150	404.1
28/07	42.36	34.69	0.5	1.033	4.78	60	291.0
29/07	103.55	94.57	0.5	3.376	10.42	90	143.1
30/07	105.83	108.64	0.0	3.498	2.11	460	684.0
31/07	49.99	65.52	0.0	3.272	3.79	240	373.6
01/08	86.15	66.84	0.5	2.520	12.72	55	256.5
02/08	59.28	76.68	0.0	3.442	1.15	830	681.3
03/08	110.39	66.25	0.5	2.650	3.78	195	765.7
04/08	129.75	82.86	0.0	3.141	2.29	380	826.2
05/08	116.43	70.07	0.5	1.936	2.56	210	948.0
06/08	212.55	289.92	0.0	7.993	7.40	300	855.5
07/08	40.34	50.22	0.0	2.005	3.98	140	195.9
08/08	46.47	56.16	0.0	1.263	5.56	63	277.6
09/08	114.74	69.18	0.0	1.739	3.02	160	443.1
10/08	66.65	82.47	0.0	1.673	1.86	250	389.1
11/08	148.21	116.20	0.0	2.363	3.28	200	190.2
12/08	137.74	137.74	0.5	3.449	2.82	340	879.8
13/08	125.71	84.03	0.0	1.804	2.39	210	859.5
14/08	87.22	64.50	0.5	2.391	2.46	270	724.6
15/08	89.08	82.32	0.0	6.416	7.75	230	577.1
16/08	106.55	66.46	0.5	2.055	2.85	200	423.7
17/08	60.98	67.29	0.0	1.353	1.50	250	436.5
18/08	23.25	34.22	0.0	0.864	2.40	100	127.0

1. Integral productivity, mg C $m^{-2}h^{-1}$.
2. Maximum volumetric rate of productivity, mg C $m^{-3}h^{-1}$.
3. Z, the depth of max Pv, m.
4. Photosynthetic capacity, mg C mg chlorophyll $a^{-1}H^{-1}=1$ 2
5. Photosynthetic efficiency, mg C mg chlorophyll $a^{-1}E^{-1}$ m^2.
6. Ik, uE $m^{-2}sec^{-1}$
7. ΣIo, uE $m^{-2}sec^{-1}$.

Appendix IV. Variation in the values of photosynthetic capacity; Pmax (mg C mg chlorophyll $a^{-1}h^{-1}$) from phytoplankton populations at depths of 0.2, 1.0, 2.0 and 4.0 m in Hamilton Harbour with time, June 25 - August 18, 1979.

Date	0.2m		1.0m		2.0m		4.0m	
25/06	1.035	1.242	1.708	1.764	0.831	0.979	0.992	1.034
26/06	1.315	1.443	1.499	1.595	1.307	1.337	1.687	0.910
27/06	1.365	1.315	1.590	1.630	1.740	1.604	2.746	2.360
28/06	1.081	2.283	2.036	1.912	1.701	1.819	1.920	2.093
29/06	1.282	1.450	1.445	1.343	1.654	1.522	1.284	0.998
30/06	0.582	1.150	1.098	0.972	2.215	1.356	1.535	0.637
01/07	1.670	1.340	1.650	1.424	2.154	1.820	2.940	1.211
02/07	1.837	1.899	2.480	2.651	1.546	1.824	1.809	1.739
03/07	0.921	0.977	1.022	0.924	1.476	1.608	1.563	1.445
04/07	1.634	1.498	2.074	1.926	1.162	1.276	1.323	1.531
05/07	1.622	1.696	1.689	1.733	1.071	1.159	0.804	0.781
06/07	2.732	2.810	2.992	2.954	2.216	2.306	2.570	2.104
07/07	1.621	1.673	1.560	1.030	0.406	1.700	1.146	1.496
08/07	1.124	0.636	0.698	0.446	1.067	1.361	0.889	0.921
09/07	1.458	1.878	1.475	1.857	0.616	1.256	0.837	0.799
10/07	0.808	1.212	1.309	0.587	0.902	1.346	1.018	0.896
11/07	2.262	2.272	1.893	1.821	0.775	1.349	1.397	1.005
12/07	2.178	2.208	1.116	1.192	1.601	1.387	1.455	1.349
13/07	1.490	1.436	1.493	1.449	1.068	1.180	1.064	1.052
14/07	0.997	1.027	1.345	1.097	1.876	1.997	0.783	1.421
15/07	1.873	2.053	1.779	1.485	1.953	1.823	0.908	0.578
16/07	1.616	0.810	1.855	2.043	1.308	1.554	1.346	1.420
17/07	3.695	3.353	4.009	2.651	2.552	2.712	2.431	2.169
18/07	1.507	1.541	2.136	2.184	1.534	1.594	2.201	2.053
19/07	2.575	2.395	1.431	1.733	2.603	2.621	3.631	3.978
20/07	2.787	3.039	1.797	2.355	2.337	2.355	1.039	1.228
21/07	0.680	1.770	1.231	2.365	1.485	0.855	1.874	1.572
22/07	2.555	2.612	3.057	3.695	1.013	1.633	1.190	1.490
23/07	3.309	3.267	3.426	3.280	3.343	3.327	1.385	1.361
24/07	1.893	1.944	4.300	3.970	2.006	1.466	3.276	3.196
25/07	4.192	4.992	3.438	3.942	2.562	2.762	2.265	2.569
26/07	2.244	2.322	2.702	2.436	3.618	3.198	1.494	1.680
27/07	1.817	1.843	1.799	1.727	1.620	1.776	2.398	2.068
28/07	1.809	1.539	2.112	1.986	1.196	1.354	2.846	2.824
29/07	2.344	1.638	2.330	2.990	2.822	3.026	3.323	3.387
30/07	1.694	1.944	2.865	2.279	1.835	1.907	2.365	2.573
31/07	3.507	3.127	1.789	1.657	2.170	1.510	2.065	1.430
01/08	2.524	1.518	1.854	1.438	1.334	1.136	3.148	3.274
02/08	2.476	4.050	2.178	3.078	2.478	3.512	2.151	0.899
03/08	1.855	1.923	3.178	3.332	2.785	2.577	2.696	3.032
04/08	2.042	2.366	1.196	1.068	1.095	2.029	1.586	1.896
05/08	1.561	1.237	1.502	1.272	1.486	1.480	1.422	0.922
06/08	6.536	6.024	9.703	8.963	5.845	4.311	7.461	8.081
07/08	2.858	3.274	4.350	5.370	2.385	2.081	2.341	2.505
08/08	1.946	1.798	1.357	1.989	1.372	1.338	1.198	1.358
09/08	1.353	2.639	1.559	1.977	1.859	2.735	1.716	1.540
10/08	1.779	1.387	1.560	1.520	2.021	0.505	0.753	1.821
11/08	1.209	1.289	2.172	1.786	1.783	1.577	1.764	1.774
12/08	3.015	2.573	1.895	2.029	2.434	2.452	1.274	0.888
13/08	1.372	1.152	2.450	2.194	1.729	1.543	1.723	1.851
14/08	2.380	2.022	1.922	2.876	2.035	2.145	2.122	1.634
15/08	4.862	5.718	1.239	2.133	2.110	2.258	3.820	3.576
16/08	1.508	1.724	1.737	2.212	1.242	1.168	1.145	1.227
17/08	1.056	0.932	1.625	1.521	1.452	1.178	2.552	2.352
18/08	1.681	1.707	2.639	2.537	1.401	1.561	1.917	1.929

Appendix V. Species List of the phytoplankton sampled in Hamilton Harbour, June 25 - August 18, 1979.

Division Chlorophyta

Chlamydomonas sphagnicola (Fritsch and Takeda)

Pandorina sp.

Eudorina sp.

Golenkinia sp.

Lagerheimia sp.

Franceia sp.

Tetraedron sp.

Pediastrum spp.

Echinosphaerella sp.

Dictyosphaerium sp.

Oocystis borgeii Snow (4-celled, 1-2-celled)

Planktosphaeria sp.

Ankistrodesmus sp.

Closteriopsis sp.

Kirchneriella sp.

Solenastrum sp.

Quadrigula sp.

Scenedesmus quadricauda (Turp.) de Brebisson

Scenedesmus bijuga (Turp.) Lagerheim

Scenedesmus acuminatus (Lag.) Chodat

Scenedesmus denticulatus Lagerheim

Scenedesmus obliqus

Actinastrum sp.

Appendix V (continued)

Tetradesmus sp.

Micractinium sp.

Mougeoutia sp.

Division Euglenophyta

Euglena sp.

Phacus sp.

Division Cyanophyta

Chroococcus sp.

Morismopodia sp.

Division Chlorophyta - Family Desmidiaceae

Closterium sp.

Cosmarium sp.

Staurastrum sp.

Division Crysophyta

Cyclotella sp.

Stephanodiscus spp.

Melosira spp.

Asterionella sp.

Division Chloromonadophyta

Cryptomonas erosa

Cryptomonas ovata Ehrenberg

Rhodomonas sp.