FORT RIVER ECOSYSTEM:
PRODUCTIVITY OF THE PERIPHYTON COMPONENT

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ABSTRACT

The primary production and general ecology of the periphyton community of a New England, lowland stream were studied over a seventeen month period. Temperature, discharge, stream bed light, periphyton chlorophyll, and community structure data were monitored regularly. Mean stream bed chlorophyll concentrations ranged from 10 to 136 mg/m^2 (annual mean = 44 mg/m^2). Seasonally distinct chlorophyll peaks coincided with stream bed light maxima occurring in early May, just prior to leaf out, and again in autumn after leaf fall. However, during midwinter, despite low light levels and high stream discharge, mean chlorophyll concentrations remained higher than summer values. At any given time of the year, stream bed rock-size better accounted for the variation of chlorophyll concentrations between different stream sites than either light or current velocity.

Productivity chambers were used to measure productivity and respiration rates of stream periphyton communities in situ. Periphyton colonized on natural substrates were incubated within these chambers at various temperatures, light intensities and periphyton densities throughout an annual period. A mean photosynthetic I_k of 6.25 ly/hr was determined. Photoinhibition was not significant for stream bed populations of periphyton. Light saturation rates of photosynthesis per unit chlorophyll were related to both temperature and periphyton density. Periphyton density was inversely related to periphyton production per unit chlorophyll. This relationship was found to be particularly acute at higher temperatures, causing the maximum estimated rate of production of dense stands of periphyton to occur at a temperature lower than that occurring during mid-summer. Periphyton community

respiration was found to be a function of temperature and benthic chlorophyll densities.

Fort River temperature, light, and chlorophyll data were employed in the empirical equations to estimate weekly periphyton production and respiration. Weekly mean daily estimates of periphyton production ranged from < 0.1 g O_2/m^2, during midwinter, to 6.5 g O_2/m^2 during early May. Estimated annual periphyton gross production was 0.58 Kg O_2/m^2, corroborating the assertion that periphyton contribute about 90% of the Fort River ecosystem gross production of 0.650 Kg O_2/m^2 (Fisher and Carpenter, 1976). Annual periphyton photosynthetic efficiency was estimated to be 1.47%. Estimated annual periphyton community respiration was 1.27 Kg O_2/m^2 with an annual P/R of 0.49.

The summer decline in periphyton standing crop, characteristic of many small streams, is discussed. In Fort River, light, discharge, and grazing factors were not sufficient to explain this phenomenon. Although seasonal patterns of stream nutrient concentrations are not associated with seasonal variations in periphyton standing crop, at higher temperatures when increased rates of metabolism and nutrient uptake occur, nutrient limitation becomes more important. This effect is especially important for dense stands of periphyton where much of the population is sheltered from the current, and accounts for both the temperature dependence of the periphyton density to P_G/chlor relationship and the low summer periphyton standing crop.

INTRODUCTION

Periphyton is the diverse assemblage of algae growing attached to the solid substrates of aquatic environments. This community generally accounts for much or most of the total photosynthetic production in lower order streams. Periphyton production, however, is often minor compared to allochthonous organic matter inputs, derived from the watershed and made available to consumers in these headwater stream ecosystems. At greater distances from the stream's source, where the water flow becomes more stable and less turbulent, other primary producers such as macrophytes, mosses, and bladderworts frequently play increasingly more important roles in autotrophic production (Wetzel, 1975). True phytoplankton populations may only become established in those lowland rivers where the water is moving slowly enough so that a population may be maintained. Odum (1957), after having studied several Florida Springs, suggested that "streams are among the most productive biological environments." A survey of more recent studies, though, tends to disclaim this notion as an unwarranted generalization. Streams and rivers, at least in temperate latitudes, are often much less productive than the watersheds through which they flow (Fisher and Carpenter, 1976).

Numerous estimates of annual and seasonal total community primary production of rivers and streams have been made with upstream-downstream diurnal O_2 methods (Odum, 1956; Kelley, et al., 1974; Duffer and Dorris, 1966). Although satisfactory for many streams, this method becomes less reliable for streams with turbulent sections where reaeration rates at the air water interface are high. Fewer studies have investigated the production and trophic dynamics of stream periphyton as an isolated component of river ecology.

Almost all of these studies were hampered by the difficulties inherent in achieving reliable estimates of rates of metabolic processes in flowing waters.

Techniques measuring increments of periphyton biomass or chlorophyll on artificial substrates in streams over a short period of time, have been employed by several workers as an index of periphyton production. These estimates, however, probably only measure the rate of colonization of a certain component of the algal population (Douglas, 1958) and do not account for turnover (Wetzel, 1965). Furthermore, an intimate chemical association or nutrient dependence occur between the attached algae and the substrate on which it grows (Jorgenson, 1957; Allen, 1971; Parker, et al., 1973). The chemical composition of natural stream bed substrates are clearly quite different from those of plexiglass, glass, and most other artificial substrates.

Primary production estimates attained with light-dark bottles containing periphyton suspensions or with bell jars inverted directly over the stream benthos must also be viewed with reservation. The restriction of water flow depresses both respiration and photosynthesis of rheophilic algae, probably by decreasing the concentration gradient of nutrients and gases between the algae and the "shell" of water surrounding them; (Whitford and Schumacher, 1961; McIntire, 1966). Recently artificial streams have also been used to better understand energy relationships and periphyton production ecology in natural stream environments.

Some investigators (Bqmbowna, 1972; Hansmann, et al., 1971; Pfeifer and McDiffett, 1975) have designed and utilized portable closed photosynthesis-respiration chambers which may incubate small intact portions of the stream benthos and its periphyton community. These chambers circulate the enclosed water so as to simulate natural current conditions, and may be submerged directly in the stream during incubation periods. Results obtained with

these chambers have provided reliable estimates of periphyton production for different stream sites on those days tested. No one study, however, has used the chambers frequently enough through an annual period or at an adequate number of sites to make a satisfactory estimate of the seasonal variations in periphyton productivity (Wetzel, 1975). In addition, the type of rigorous analysis of the effects of such factors as light, temperature, and nutrients on periphyton metabolism such as that carried out in laboratory streams (McIntire and Phinney, 1965), has been neglected in the few chamber studies thus far conducted.

The present study utilized the advantages of both field and laboratory techniques. Enclosed, self-circulating productivity chambers, similar to those used by Bombowna (1972) and Pfeifer and McDiffett (1975), were designed to measure periphyton community primary production and respiration. Over an annual period, these chambers were utilized at several sites in a section of the Fort River in Massachusetts with the intention of developing quantitative models relating periphyton production chlorophyll a concentration, light and temperature. Throughout a seventeen month period of study, light, temperature, stream discharge, chlorophyll a concentration, and community structure data were regularly collected at these same sites. The quantitative relationships derived from the chamber studies were applied to weekly survey data to approximate weekly periphyton primary production over the seventeen month period of study.

Although this study presents a reliable estimate of Fort River periphyton production and respiration and delineates some of the factors which influence these processes, it represents only a first step in developing a production model with predictive value for other streams. Such factors as nutrient concentrations, which undoubtedly are important to the production rates of

many stream ecosystems, have not been incorporated into the model. Furthermore, although a portion of this study was devoted to analyzing the influence of environmental factors on periphyton standing crop, chlorophyll, as an index of biomass, was treated as an independent variable in the model. It is ultimately desirable to express standing crop as a function of environmental or biological factors, thus removing the need to frequently sample periphyton chlorophyll or biomass.

A periphyton production model with this degree of sophistication has recently been developed by McIntire (1973) for eastern Oregon streams Despite the leap of faith which must be made from the mathematical premises of McIntire's model (largely derived from laboratory stream studies) to the natural system, this approach appears to be extremely valuable. A model of this sort has the added value of making quantitative predictions about the effects of certain environmental disturbances on periphyton community metabolism; a goal which is certainly important in enhancing our understanding of the effects of man's activities on streams and rivers.

SITE DESCRIPTION

General

The Fort River rises in the Pelham hills (365 MSL) of central Massachusetts and flows westward to the Connecticut River (30m MSL). Land use in the 155 km^2 watershed is predominantly agricultural, residental, and woodland; the headwater regions of the watershed are nearly intact mixed-hardwood forests. The section selected for this study is a 1.6 km stretch located 16 km upstream from the Connecticut River. In the past, macrophyte primary production and organic carbon metabolism studies have been conducted on this same stretch of the Fort River (Fisher & Carpenter, 1976). A USA gauging station which continuously records discharge from 105 km^2 of the total watershed is located immediately above the study section. Land use in the immediate vicinity is largely grazing. Riparian vegetation consists of mature alder, oak, elm, and maple trees and is nearly continuous through the reach on both banks.

Mean discharge at the gauging station is 1.4m^3/sec (50 cfs) but ranges widely from summer base flow near 0.28m^3/sec (10 cfs) to annual maxima near 28m^3/sec (1000 cfs). There is essentially no floodplain in the study section. Stream width averages 14 m and summer mean depth is 0.3 m. Mean current velocity is 0.12 to 0.18 m/sec.

Water quality of the Fort River is relatively good. Oxygen is always above 5 ppm, pH varies diurnally between 6.9 and 8.1 units and conductivity ranges between 60 and 120 umhos/cm, depending upon discharge. Dissolved PO_4-P averages 25 µg/l and is often < 10 µg/l. NO_3-N is usually < 0.2 mg/l and Cl is 10 mg/l. The only parameter that ever poses a quality problem is turbidity which, although usually < 15 JTU, rises to nearly 100 JTU during

spring runoff and during intense storms at other times of the year. Water temperature ranges from 0 to 27.5 C with summer means near 20 C. In sum, the Fort River is typical of medium size unpolluted streams in this area of New England.

Substrate

The 1.6 km reach of the Fort River was initially divided into 50 meter segments. Streambed substrate observed in each 50 m section was classified as percent area cover for each of three general substrate categories; cobble, mixed cobble on sand, and sand-silt. Cobble was used to describe streambed areas where stones with diameters > 10 cm covered at least 80% of the streambed. Areas where rocks and pebbles covered between 20% and 80% of a sandy substrate were designated as mixed cobble on sand. Sand-silt areas were generally those found in more slowly moving areas of the stream where rocks < 4 cm diameter covered less than 20% of the streambed. The categories, cobble, mixed cobble on sand and sand-silt, comprised 40%, 38%, and 22% respectively of the streambed.

Primary Producer Species Composition

During summer, up to 20% of the stream bed is colonized by macrophytes, including Potamogeton crispus L., P. epihydrus Raf., Callitriche heterophylla Pursh., Ranunculus trichophyllus Chaix, Vallisneria americana Michx. and Eleocharis acicularis R. & S. (Fisher and Carpenter, 1976). Smaller amounts of aquatic mosses are also present, especially in shaded riffle areas of the stream.

Several filamentous forms of Chlorophyceae colonized the stream bed, and were generally represented by one conspicuous dominant after another over an annual period. Hydrus foetidus, an alga characteristic of cold alpine streams (Parker, et al., 1973), was common during the winter months but as

the water warmed in May was replaced by Cladophera glomerata. By mid-July C. glomerata became rare and Microspora stagnorum was clearly the dominant filamentous form. The next filamentous alga to appear on the stream bed was Spirogyra fluvialatus which became common during late August. In September as the water cooled, Stigeoclonium tenue was evident, especially in riffle areas, and remained present until midwinter. Vaucheria sp. was the most common filamentous alga during the winter months before disappearing in the spring. Although filamentous algae were conspicuous throughout much of the year, they constituted, at the most, only 20% of the periphyton biomass.

Microalgae, which formed a greenish-brown slime on the rocks of the stream bed, comprised the major component of the periphyton. In the Fort River, as has been noted in many other streams (Whitton, 1975), the relative abundance of Chlorophyceae (as compared to diatoms) was highest during summer and reached an annual low during mid-winter. An approximated percent composition of Chlorophyceae, Cyanophyceae and Bacillariophyceae was 10%, 15%, and 75% respectively during summer and 1%, 13%, and 86% during winter. Unicellular algae, however, did not appear to exhibit the same type of defined seasonal succession pattern demonstrated by the filamentous algae. Navicula spp., Synedra ulna, Phormidium sp., Frustularia rhomboides, and especially Achnanthes lanceolata, remained the most common algae from late fall to early spring. Late spring and early summer algal populations were most often represented by Navicula spp., Cocconeis placentula, Cymbella tumida, Protococcos sp., Oscillatoria spp., Gomphonema sphaerophorum, and Ankistrodesmus The dominant alga, from mid-summer to early fall, was Melosira varians, a colonial diatom. Other abundant microalgae species during this period were Fragilaria crontonensis, Navicula sp., Cymbella tumida, Oscillatoria sp., and Gomphonema spherophorum.

METHODS AND MATERIALS

Sampling Stations and Colonization Trays

Seven different stream sites (A-H), each representing a different stream habitat type in terms of light, substrate, and current, were chosen as sampling stations. Environmental characteristics of each sampling station are summarized in Table 1.

Six aluminum trays (12 cm X 19 cm X 3 cm) were embedded within the stream bed at each of the seven sampling stations. Each set of trays was filled with natural substrate materials typical of the immediate vicinity and were allowed to stabilize in the river for at least four weeks before chlorophyll or productivity determinations were made. Waters (1961) found four weeks to be sufficient for clean artificial substrates to become maximally colonized by periphyton.

Periphyton Pigment Determination

Periphyton tray chlorophyll a was determined at approximately two week intervals over the 17 month period of study. On each sampling date, the contents of one tray from each sampling station was placed in a one-liter polyethylene container, sealed, and returned to the laboratory for analysis. Prior to pigment extraction, periphyton samples were frozen in order to disrupt the algal cell walls (King and Ball, 1966). After freezing, 250 to 400 ml of 95% basic aqueous acetone was added to the periphyton samples. The containers were again sealed, shaken vigorously, and allowed to remain undisturbed for three hours at 22° C. Extraction periods of more than three hours did not significantly increase the concentrations of pigments in the acetone solution. Following extraction, 10 ml aliquots were drawn from each container and centrifuged for from 5 to 10 minutes to remove particulates.

The following equation, converting optical densities at two wave lenths to chlorophyll "a" concentration, was adapted from Lorenzen (1967) and utilized in this study:

$$\frac{\text{mg chl}}{\text{sample}} = (663_{nmB} - 750_{nmB}) - (663_{nmA} - 750_{nm_A}) \times \frac{V}{1000} \times 26.7$$

where subscripts B and A stand for absorbance before and after acidification and V is the volume of acetone (ml) used for chlorophyll elution. Data were then converted to mg chl/m^2

Spectrophometric analyses were made with a Beckman model DU spectrophotometer. Optical density readings at 750nm corrected for general turbidity while readings at 663mn, before and after acidification within the cuvette with one drop of 4 N HCL, made it possible to quantitatively differentiate chl a from the various chlorophyll degradation products.

Light Measurements

Estimates of average light reaching the river were made by a method based on the property of anthracene ($C_{14}H_{10}$) in a benzene solution, to polymerize into insoluble dianthracene on exposure to visible light (Dore, 1959). Anthracene polymerization in 10 ml glass vials was calibrated against insolar radiation measured by a Weather measure model R401 mechanical pyranograph for several time periods.

Estimates of the average light reaching the stream surface over a 24 hour period were made on three dates: July 20, October 10, and November 7. On each of these test dates, between forty-five and fifty-five 10 ml glass vials were filled with anthracene and were then attached with rubberbands to the surfaces of separate styrofoam "rafts," measuring 10 cm X 10 cm X 3 cm. The rafts, each carrying an anthracene vial, were distributed throughout the study section of the stream at 150 m intervals and were allowed to remain for 24 hr. Over the same 24 hour period, solar radiation was measured with

pyranograph at an open site, at Amherst College, 1.5 km from the stream.

Stream light for each of the three days tested was expressed as total available light (pyranograph) to the stream surface. It was assumed that one stream light reduction factor was approximately constant during the shaded leaf canopy period, while another was constant during the relatively non-shaded period. Weekly averages of roof light were translated into weekly mean insolar radiation reaching the stream surface by applying the empirically defined "canopy" and "no canopy" light reduction factors during the appropriate seasonal periods.

Light extinction between the stream surface and benthos, as a result of surface reflection or attenuation through the 0.5 m depth of water, was determined with a photocel on several occasions. Despite occasional periods of high turbidity (100 JTU) the stream water usually remained fairly clear (15 JTU). Therefore, a single light extinction coefficient, corresponding to relatively low turbidity conditions, was used for the entire study period.

Chamber Design and Utilization

A pair of light-dark chambers was designed to measure production and respiration rates of the periphyton communities established in the colonization trays. The chambers, 38 cmX 23cm X 8 cm,were constructed largely of 3/4" marine plywood coated with polyurethane. Each chamber, when containing a per iphyton tray, held approximately 6.71 of water, which was circulated from one end of the chamber to the other by means of a 1 cm diameter polyethylene tubing. The turbulence created within the chambers was roughly comparable to that found throughout the river. The dark chamber was fitted with an opaque top while the light chamber was fitted with a clear plexiglass top.

Production and respiration rates were measured by monitoring the change

in dissolved O_2 within the chambers, over the incubation periods (1-3 hr). At the beginning and the end of incubation periods, water samples were collected from both chambers, through chamber outflow tubes, and were immediately fixed for O_2 Winkler analysis. Winkler analyses were conducted on the day of collection.

In order to determine cumulative light levels, two vials of anthracene were uncovered and placed directly in the light chamber for the duration of each incubation period. Two more vials of anthracene, wrapped in tin foil, were left in the water at the test site to be used as "zero light" references for spectrophotometric analyses of the exposed anthracene solutions. Due to the relatively high freezing point of benzene (5.5 °C) light determinations in cold water conditions (< 8° C) were conducted with an underwater photometer calibrated against a pyranograph.

Periphyton production and respiration data were organized from six seasonal periods of incubation tests, each of which required about one week of intensive testing. Periphyton trays, over the study period, were incubated at temperatures ranging from 1 °C to 23 °C, and at light intensities ranging from < 1 to 60 ly (g $cal \cdot cm^{-2} \cdot hr^{-1}$). A total of 59 light-dark pairs were run.

The possible significance of nutrient exhaustion within the chambers was investigated briefly. Losses of dissolved nitrate and phosphate were determined after six summer chamber incubations of particularly dense standing crops of periphyton. Despite initially low levels of both NO_3 ($\bar{x}$ = .17 mg/l.) and PO_4 ($\bar{x}$ = 10 µg/l.), both nutrients were reduced by an average of only about 10% after one hour of incubation. The mean volume of overlying water per square meter area of stream benthos was only about 1.6 times greater than the water volume to colonization tray area within the

chambers. This, coupled with short incubation periods, suggested that nutrient depletion was probably not significantly greater in the chambers than in the stream. It is likely that in the stream benthos (largely dominated by heterotrophs) nutrients are rapidly regenerated.

RESULTS AND DISCUSSION

Physical Characteristics

Daily light, recorded at an exposed site near the Fort River, ranged from a monthly mean of 97.3 ly/day during December to 448.0 ly/day during May. Light reaching the stream surface of the study section averaged 38.5%, 31.9% and 63% of roof light readings on July 20, October 10, and November 7 respectively. On the midsummer test date, one stream site which was shaded by an especially dense growth of streamside red maple and white oak trees received only about 12% of the potentially available light, while a relatively exposed site nearby received close to 70%. By November 7th, after litter fall, percent light penetration was roughly 1.8 times greater than that during the summer. As an average of the two summer stream light measurements, it was assumed that approximately 35% of open sunlight reached the stream surface during the leaf-out period (May 10th to October 20th). During the remainder of the year a transmittance factor of 63% was assumed. Edwards and Owens (1960) reported similar seasonal variations of light reaching the surface of a seasonally shaded river (82% during the early spring and 47% in midsummer).

In the Fort River, approximately 55% of the stream surface light penetrated to the stream bed. This further reduced "canopy" and "no canopy" light to 19% and 35%. The annual light regime of the river streambed was characterized by a major peak just before the establishment of the leaf canopy in May, and a minor peak just after leaf fall in late October and early November. Figure 1 illustrates the variations of stream bed light over the study period, which ranged in weekly means from nearly 175 ly/day

in early May to about 25 ly/day in late December and early January. Mean summer streambed light was near 75 ly/day.

Photoperiods ranged from 16 hours of light in June to 9 hours of light in late December. Daytime stream temperatures ranged from 0° C in mid-winter to 24° C in midsummer (Figure 2). Stream discharge was extremely variable, and fluctuated widely from week to week and day to day, depending upon the weather. Stream discharge was lowest during August and highest during March, due to the combined effects of snow melt and heavy rain.

Chlorophyll Standing Crop

Benthic chlorophyll a concentrations were used as an index of periphton standing crop and photosynthetic potential. Total stream chlorophyll estimates were made by weighting colonization tray chlorophyll concentrations, according to the fraction of the streambed substrate type represented by each tray.

Average concentrations of chlorophyll a on the benthos of the stream study section varied from 10 to 136 mg/m^2, with a mean annual concentration of 44 mg/m^2. These values are comparable to those reported in other studies of shaded, unpolluted streams. Reese (1966) reports a similar mean annual chlorophyll concentration of 34 mg/m^2 for a shaded riffle portion of a western Oregon stream. Somewhat higher concentrations of chlorophyll have been reported in many larger less shaded streams and rivers; e.g., 20-390 mg/m^2 in a southern Great Plains stream (Duffer and Dorris, 1966), 70 mg/m^2 in the lower Arakawa River in Japan (Kobayski, 1961), and 300 mg/m^2 in the Logan River located in Northern Utah (McConnell and Sigler, 1959). Odum et al. (1958) found 2.5 g $chlorophyll/m^2$ on the benthos of a polluted Texas river covered with a blue-green algal mat. None of these listed studies corrected for chlorophyll degradation products during spectrophometric

analysis, and probably are overestimates of benthic chlorophyll concentrations. Chlorophyll concentrations in the Fort River were comparable to those that are most often found in eutrophic lakes (30-120 mg/m^2). However, in comparison to terrestrial systems, these values were notably less than for deciduous trees and shrubs (2-6 g/m^2) and grasses and herbs (1.7 - 4.7 g/m^2) and only resembled chlorophyll concentrations found in volcanic steppes or deserts (86 - 300 mg/m^2) (Aruga and Monsi, 1963).

Variations in average chlorophyll concentrations in the Fort River followed a seasonal pattern similar in some respects to the seasonal light regime of the stream bed (Figure 3). Two distinct peaks, a minor one just after leaf fall and a major one just prior to canopy development were apparent. Chlorophyll concentrations during the May and autumn peaks were respectively 3.9 and 1.7 times greater than mean summer chlorophyll concentrations. December through February chlorophyll concentrations averaged 36.0 mg/m^2, slightly higher than the June through August average of 33.2 mg/m^2. However, average stream bed light during the summer period, despite shading, was 1.5 times greater than stream bed light during the winter period, suggesting the influence of other factors aside from light.

A small but significant linear coorelation, $r = .41$ ($P < 0.01$, 70 DF) was found between weekly stream light and stream chlorophyll concentrations. After withholding the effects of temperature and photoperiod, through partial correlation analysis, the correlation between light and chlorophyll still remained significant, $r = .32$ ($p < 0.05$, 67 DF). Except during midwinter, long term increases of stream light were generally associated with increases of average stream chlorophyll. However, sampling stations receiving more light than others did not tend to have more chlorophyll. The correlation coefficient defining this relationship was actually negative,

though insignificant r = -.123 (7 DF). Other factors in addition to light were assumed to be influencing chlorophyll density. By approaching this problem in a slightly different manner, the relative importance of light at each sampling station becomes more evident. For each sampling station, the ratio of light penetration before and after leaf fall was compared to the ratio of chlorophyll before and after leaf fall. This mode of comparison eliminated the effects of variations between stations in other environmental factors. The regression yielded a linear expression having a highly significant correlation coefficient of .81 ($p < .01$, 7DF) and t test value of 3.06 ($p < .025$, 7 DF).

Regressions of chlorophyll against light, generated correlation coefficients of .673 ($p < .01$), .653 ($p < .01$), and .694 ($p < .01$, 14 DF) for the three most heavily shaded sampling stations (B, C, E). Data from the other four sampling stations, when subjected to the same analysis, did not generate significant correlation coefficients. This implies that, at sites which are heavily shaded, light is a more important factor in determining periphyton chlorophyll concentrations than at more open sites. The correlation coefficient between weekly temperature and chlorophyll concentrations was insignificant (r = 0.07, 68 DF).

Fort River periphyton populations were periodically subject to scouring during periods of high discharge. However, standing crop levels appear to recover rapidly. As an example, an intense rainstorm on July 19th reduced streambed chlorphyll from 32 mg/m^2 to 10.1 mg/m^2. Yet by the following week the chlorophyll concentration was back up to 40 mg/m^2.

Chlorophyll concentrations and the maximum stream gauge height occurring within ten days before each chlorophyll sampling date showed a small but significant negative partial correlation when the effects of light and

temperature were withheld ($r = -.297$, $p < .05$, DF 126). Using average instead of maximum gauge heights in the same analysis did not yield a significant correlation coefficient. This may be taken as further evidence of storm discharges in temporarily reducing the standing crop.

Periphyton Production Rates within Chambers

Chamber periphyton production, at six temperature intervals associated with the six seasonal test periods, was mathematically related to light intensity and periphyton density. Characteristically, at low light levels, plant photosynthesis is linearly related to light. However, as light intensity reaches a certain level, photosynthesis becomes rate limited by enzymatic processes, and further increases in light do not cause further increases in photosynthesis. At this point, photosynthesis is said to be light saturated (Rabinowitch, 1945). A commonly used mathematical formula describing this generalized relation between light and photosynthesis is:

$$P = PMAX \quad \frac{A \times I}{\sqrt{1 + (AI)^2}} \qquad (1)$$

where PMAX is the rate of photosynthesis at light saturation, I is the incident light intensity, A is an empirically derived constant situating the curve with respect to light, and P = photosynthetic rate (Vollenweider, 1965). This formula will henceforth be referred to as the Smith equation.

Chamber PMAX determination

It was first necessary to establish the influence of periphyton density on primary production rates before the Smith equation could be employed to describe chamber production data. Light saturation assimilation numbers (mg O_2/mg chlorophyll-hr) determined for dense periphyton populations were consistently lower than the assimilation numbers determined for relatively

sparse periphyton populations. This was especially apparent during mid-summer (22 °C) and late spring (15 °C) chamber test periods. For each temperature period, colonization tray production rates at light saturation were plotted against corresponding colonization tray chlorophyll concentrations. Theoretically, this relationship should be linear and pass through the origin, i.e., for each increase in chlorophyll, a proportionate increase in primary production should occur. Yet as colonization tray chlorophyll concentrations increased past a certain density, light saturation gross production per unit chlorophyll fell off logarithmically as described by the following general equation:

$$PMAS = X \cdot chl^{\hat{}} \qquad (2)$$

where chl - mg chlorophyll/$m^{\hat{}}$, PMAS = mg $O_2/m^2.hr$; and empirically derived R and D values at corresponding temperatures appear below;

(Temp)=	22°C	15°C	10 °C	8.6 °C	3.0 °C	1.0 °C
D =	.27	0.29	0.88	0.54	0.64	1.10
X =	.1730	.0450	.0170	.0250	.0210	.0018

The chlorophyll density exponent, D, was found to be linearly related to temperature as expressed by the following equation:

$$D = ((-.031) \times T) + .909 \qquad (3)$$

$$< .05 \ (+ = -2.66, \ 5 \ DF)]$$

Substitution of equation (3) into equation (2) yields:

$$PMAX = X \cdot chl \ ((-.031 \times T) + .909) \qquad (4)$$

The slope coefficient, X, when plotted against temperature was best approximated by the following exponential function:

$$X = (3.8 \times 10^{-5}) \times T^{2.77}$$

$$P < .001 \ (t = 13.78, 5 \ DF) \qquad (5)$$

By substituting equation (5) into equation (4) an equation was arrived at which expresses PMAX as a function of temperature and chlorophyll density:

$$PMAX = ((3.8 \times 10^{-5}) \times T^{2.77}) \times chl \ ((^{-.031 \times T + .909}) \qquad (6)$$

In Figure 4, actual PMAX rates as measured with the chambers are plotted against PMAX rates as predicted from eeuation (6). The fit of equation (6) to the chamber data was highly significant, $p < .001$ ($t = 7.59$, 46 DF).

Effect of Temperature and Periphyton Density on Production

The ratio of primary production to chlorophyll appears to hold constant for most species of phytoplankton studied under comparable favorable conditions (Edmondson, 1955). However, it has often been noted that as phytoplankton populations become increasingly crowded, this ratio decreases, possibly as a result of nutrient depletion, accumulation of wastes, or limitation of light (Findenegg, 1965; Nalwajko, 1966; Bermann and Pollingher, 1974). Similarly, Fraleigh and Wiegart (1975) and McIntire (1973) found that periphyton populations in artificial streams reach a maximum rate of primary production at relatively low levels of biomass. Recent in situ stream studies have shown that an inverse relationship between chlorophyll density and primary production /unit chlorophyll applies to natural streams as well (Pfeifer and Mcdiffett, 1975; Marker, 1976a, 1976b). In the Fort River this relationship was found to be temperature dependent. Figure 5 shows the relationship between temperature, chlorophyll density, and PMAS primary production. As predicted from the empirical regression, at 10^{o} C,

a five-fold increase of chlorophyll, from 20 to 100 mg chlorophyll/m^2, would generate a 2.63-fold increase of primary production. However, at 20° C, the same increase of chlorophyll would only produce a 1.6-fold increase.

At low densities of chlorophyll (< 40 mg/m^2) PMAX was logarithmically related to temperature. A Q_{10} of 2.6 was calculated for the temperature range from 10 to 20 C at a chlorophyll density of 20 mg/m^2. Above this temperature range, between 20 and 25 C, the Q_{10} declined to about 1.2. Other investigators (McIntire and Phinney, 1965; Kevern and Ball, 1965) have also found a logarithmic relationship between temperature and periphyton PMAX rates with little increase of primary production occurring about 20° C. Due to the interrelationship of temperature, periphyton density, and PMAX, Q_{10} calculations were only meaningful if periphyton densities were specified. As Fort River chlorophyll density increased, the calculated Q_{10}'s decreased, especially at higher temperatures. At unusually high periphyton densities, predicted primary production at lower temperatures actually exceeds predicted primary production at higher temperatures. At a chlorophyll concentration of 200 mg/m^2, for example, predicted primary production at both 15 and 20° are about 20% greater than predicted primary production at 25° C.

PMAX assimilation numbers (gO_2/g chl.hr) at 20° C were 17.75 and 4.64 at chlorophyll concentrations of 20 and 100 mg/m^2 respectively. An assimilation number of 12.5 was calculated for the average summer chlorophyll density of 33 mg chl/m^2. Ryther (1956) compiled several assimilation numbers determined for marine phytoplankton, and suggested an overall value of 12.33 (3.7g C/g chl.hr) to be used at ocean temperatures between 15 and 20° C. Bermann and Pollinger (1975) found a similar average assimilation number for phytoplankton in a warm water lake; however, extreme values ranged from

1.1 during a phytoplankton bloom, to 20.8 under low standing crop conditions.

Average assimilation numbers notably lower than those reported in this study, were published in the only two studies of stream production found which related primary production to chlorophyll. McConnell and Sigler (1959) estimated a periphyton assimilation number of 1-2 (15°C) in the Logan River, where chlorophyll concentrations averaged 300 mg/m^2. By employing 300 mg chlorophyll and 15°C in equation (6) a PMAX of 0.67 corresponding to an assimilation number of 2.23 is predicted. Similarly, McIntire and Phinney's (1965) assimilation numbers of 0.23 and 0.85 at 1.5 and 0.5 g $chlorophyll/m^2$ may be compared with the predicted assimilation numbers of .46 and 1.85. Clearly no one assimilation number, with predictive value for stream periphyton in general, as Ryther has proposed for marine phytoplankton, is adequate. The model proposed in this paper, however, comes somewhat closer to estimating the productive potential of periphyton communities by the use of both chlorophyll and temperature data.

The Effects of Light on Production

Equation (6), which defines PMAX as a function of chlorophyll density and temperature was substituted into the Smith equation to yield the following expression:

$$Pg = [3.8 \times 10^{-5} \times T^{2.77} \times Chl ((^{-}.031 \times T) + .909)] \times \frac{A \cdot I}{\sqrt{1 + (A \cdot I)^2}} \quad (7)$$

where Pg = g O_2/m^2-hr, T = temperature (C), Chl = mg $chlorophyll/m^2$, I = light (ly/hr), and A = an empirically defined constant which situates the curve with respect to light. The inverse of A, of the I_k point as it is commonly called, denotes the approximate light intensity at which the onset of light saturation occurs.

Modified Smith equations (Equation 7) were fitted to each of the six

sets of chamber data. Deviations were minimized by adjusting A to the following constant values at each temperature: 0.13 at 22°, 0.17 at 15° C, 0.20 at 10° C, 0.12 at 8°C, 0.16 at 3° C, 0.05 at 1° C. Commonly, I_k values increase with temperature (Tailing, 1957). Between 10°C and 22°C estimated I_k's increased from 5.0 ly/hr to 7.7 ly/hr. Below 10° C, however, I_k values tended to gradually increase as well. It was concluded that data were too sparse at low light intensities to significantly define resolutions of such minimal changes in the I_k with respect to light. An averaged I_k of 6.25 ly/hr corresponding to an A value of .16 was employed for all temperatures in the stream production model. Ryther (1956) determined average I_k values for several representative phytoplankton species of three taxa and found that Chlorophyceae have relatively low I_k, of about 1 ly/hr, while higher I_k's of about 3 and 4.3 ly/hr were characteristic of diatoms and dinoflagellates. The greater ratio of Chlorophyceae to diatoms observed during the summer in the Fort River could have been partially responsible for the apparent lack of a significant increase in I_k with respect to summer temperatures. Algae have been shown to adapt to high or low light conditions by shifting the I_k to correspondingly higher or lower light levels (Steeman Nielson et al., 1962; Jorgenson, 1968). Although McIntire and Phinney (1965) found little difference between the I_k's of shade adapted and light adapted periphyton communities, the variation of light conditions between sampling stations was probably another factor causing poorly resolved I_k values.

Respiration

Losses of O_2 inthe dark chamber, during incubation periods, resulted from the combined respiration of microbes, fungi, macroinvertebrates, and periphyton. A highly significant linear regression of temperature against

periphyton community respiration was determined. $P < .001$ ($t = 6.44$, 58 OF); however, it was expected that by expressing respiration as a function of both temperature and chlorophyll, deviations between the model and actual respiration rates could be further minimized. Chamber respiration rates were plotted against corresponding chlorophyll concentrations at each of the six temperatures. The six derived equations were expressed in the following general form:

$$R = S \times Chl + b \qquad (8)$$

where R = respiration in g O_2/m^2 and Chl = chlorophyll in mg/m^2. Statistical significance for the 22, 15, 10, 8, 6, 3, and 1 C R/Chl regression were, respectively, $P < 0.05$, 0.20, 0.50, 0.10, 0.20, 0.20, and 0.40. By expressing both the slopes (s) and intercepts (b) from equation (8) in terms of temperature, a new equation was ultimately defined. S and B were approximately related to temperature as follows:

$$S = .00124 \times (T^{.095}) \qquad (9)$$

$$B = (.00769 \times T) + .01031$$

where T = temperature °C. Equations (9) and (10) were then substituted into equation (8) to yield:

$$R = (.00124 \times T^{.095}) \times Chl + (.00769 \times \quad + .01031 \qquad (11)$$

In Figure 6, measured respiration rates are plotted against respiration rates predicted from chlorophyll and temperature data. The fit of the model (eq (11)) to measured respiration was highly significant:

$P < .001$ ($t = 8.17$, 58 DF).

No accurate estimate of periphyyton (algal) respiration alone was possible in this study. Although community respiration was estimated as a partial function of periphyton standing crop (chlorophyll), respiration

correlated with chlorophyll was not necessarily totally attributable to living algae. It is probable that increased densities of viable periphyton were associated with increased densities of decomposing organic material. Nevertheless, the temperature dependence of the slope (S) probably reflected, to some degree, the change of algal respiration with regard to temperature. The slope (R/Chl) was not significantly different at 1, 3, 15, and 22° C but was notably higher at 8.6 and 10° C. Ryther and Guillard (1962) demonstrated that for several species of diatoms, tested at temperatures at which they were conditioned, no regular relationship existed between temperature and respiratory coefficients (g C respired/hr g chl). The same investigators concluded that "chlorophyll and temperature alone do not provide a constant or even predictable index of phytoplankton respiration." The results from this study appear to corroborate their conclusion. Algae from various communities have been found to respire from about 4% (Talling, 1957) to 50% (Bermann and Pollingher 1974) of daily gross production. Intermediate values have been reported by McConnell and Sigler (1959), Pomeroy (1959), Hargrave (1969) and Ryther (1956). Utilizing Odum's algal Pg/estimate of 0.3 algal respiration accounted for 15-20% of the summer periphyton community respiration. Macroinvertebrates accounted for only another 1.1% of the benthic respiration in the Fort River (Fisher, unpubl. data) suggesting that bacterial oxidation played the dominant role in periphyton community respiration.

Community respiration plotted against temperature alone resulted in a Q_{10} of 2.1 for the 5-15° C temperature range, and a Q_{10} of 1.6 for 10-20° C.

Definition of the Annual PG and R Model

Weekly values from July 15, 1974, to December 7, 1975, of Fort River

light, temperature, photoperiod, and chlorophyll were assembled. Estimates of variables were made where any given week's measurements for one or (rarely) two of these variables were missing by averaging measurements from adjoining weeks. This seemed justified since a production estimate made from two, or even one, of these variables, was more reliable than an estimate made simply by averaging production rates of adjacent weeks. A computer program was written so that light, temperature, chlorophyll, and photoperiod were analyzed one week at a time to generate weekly averages of daily gross primary production. Because of the curvilinear nature of the Smith equation, it was necessary to break down each week's average daily light into time segments of intensiy; i.e., light/hr during midday is greater than during early morning. Given the length of the photoperiod (hrs) and the week's daily average of light in langleys, light/hr for each hour occurring during the photoperiod was estimated. These data in addition to the corresponding temperature and chlorophyll figures were employed in the modified Smith equation (7) to generate weekly averages of daily gross primary production. Weekly respiration for this same period was simulated as a function of chlorophyll and temperature data as described in equation (11). The two general equations reappear below:

$$Pg = (3.8 \times 10^{-E} \times 1^{2.72}) \times Chl\left((-.031 \times T) + .909) \times \frac{.16 \times I}{1 + (.16 \times 1)^2}\right) \quad (7)$$

$$R = (.00124 \times T^{.068} \times Chl) + (.06768 \times T) + .0103 \quad (11)$$

In addition, a general cross production model was established utilizing light and temperature values as expressed by the following smooth sine wave functions:

$$T = 12 + 11 \sin\left(\frac{48}{2\pi}\right)$$

$$Lt = 52 + 33 \sin\left(\frac{48}{2\pi}\right)$$ - (Between Oct. 30 and May 1, Lt is multiplied by 1.85)

By reducing short term variations of these variables, seasonal trends in gross primary production became clearer, despite the model's relatively increased inaccuracy.

MODEL OUTPUT AND CONCLUSION

Computer printouts of the seasonal variation of periphyton community respiration and gross primary production in the Fort River are provided in Figures 29 and 30 and in Table 2. Annual periphyton gross primary production and respiration were estimated to be 0.584 and 1.274 Kg O_2/m^2, respectively. Corresponding estimates of average daily periphyton primary production and respiration were 1.6 and 3.49 g O_2/m^2. Other annual periphyton production studies, with which to compare these values, estimated net primary production rates from biomass changes over time (Minshall, 1967; Coffman et al., 1971). In the Red Cedar River in Michigan, Vannote (1963) estimated an annual net periphyton production rate of about 0.58g O_2/m^2 day. Assuming a daily periphyton Pg/R ratio of 0.3, Red Cedar River net primary production corresponds to about 2.1 g O_2/m^2 · day gross primary production which compares well with the value of 1.6 estimated for the Fort River. Periphyton gross primary production in streams has also been estimated indirectly as the difference between stream ecosystem gross primary production, and macrophyte gross primary production (Fisher and Carpenter, 1976; Westlake et al., 1970). Fisher and Carpenter determined macrophyte gross production in the Fort River to account for 9.2% of the annual (1972-3) community primary production. Assuming that the percent macrophyte production was again approximately 9.2% during this study period, an annual ecosystem primary production of 642 g O_2/m^2 was estimated. This value compares favorably to the ecosystem production of 650 g O_2/m^2 estimated by Fisher and Carpenter (1976), thus corroborating the assertion that periphyton account for about 90% of the Fort River ecosystem production. However, in the Red Cedar River

where periphyton accounted for about 87% of annual stream primary production on the average, great variability from year to year in periphyton/macrophyte production has been demonstrated (Ball and Bahr, 1975). Changes in runoff, turbidity, and pollution were the probable causes for this variability.

Macrophytes at peak standing crop during midsummer cover approximately 20% of the Fort River stream bed and reach a standing crop of 10.7 g AFDW/m^2 (Fisher and Carpenter, 1976). Assuming an average periphyton chlorophyll/AFDW biomass ratio of 0.02 as determined from the experiments (Sumner, 1976) periphyton standing crop remains throughout the summer at about 1.65 g biomass/m^2. During the summer, macrophyte standing crop biomass is about 6.5 times greater than periphyton standing crop biomass; yet, macrophyte gross primary production is only about 15% of periphyton gross primary production. Thus macrophytes, in relation to periphyton, were generally more conspicuous than productive. Plant size is generally inversely related to Pg/biomass. Findenegg (1965) and Laws (1975) attributed this phenomenon to the relation of cell size to surface to volume ratios; i.e., small plants have a relatively greater surface area to absorb nutrients and exchange gases. Periphyton appeared to be a fast growing but vulnerable component of the Fort River stream ecosystem. Periphyton standing crop, even during the spring bloom, did not amount to even 1% of the estimated annual periphyton net primary production.

Wetzel (1975) has noted that "as the size of a river increases the extent of autotrophic production by attached benthic algae often decreases in proportion to that contributed by other producers." While headwater streams generally are dominated by heterotrophic metabolism, the primary production that does occur generally is attributable to attached algae (Fisher and Likens, 1973). As rivers become more highly insolated and stable,

macrophytes tend to play increasingly dominant roles (Fisher and Carpenter, 1976). However, as upper order rivers become sluggish, deep, and turbid, the production of both macrophytes and periphyton is often less significant than that of phytoplankton. In the River Thames, in England, average phytoplankton gross primary production is about 4.6 g O_2/m^2 day while periphyton and macrophyte production combined is only 2.28 g/m^2.day (Berrie, 1972). In large rivers light is probably an important factor, limiting benthic primary production (Fisher and Carpenter, 1976).

Annual primary production of the Fort River ecosystem is relatively low compared to other streams of temperate North America. Fort River production rates are comparable to those most often found in mesotrophic lakes (Wetzel, 1975) and somewht lower than those of temperate forests (Odum, 1956).

Annual periphyton Pg/R was estimated to be 0.46 (Figure 33). Compared with Fisher and Carpenter's Fort River ecosystem Pg/R of 0.49, this again suggested the dominant role of the periphyton community in ecosystem metabolism. Similarly low stream Pg/R estimates have been reported for a shaded riffle area of an Oregon Stream, 0.47 (Reese, 1966), and for nine North Carolina streams ($\overline{X}$) = .05 (Hoskin, 1959). Generally, ecosystem primary production exceeds respiration only in larger more highly productive streams (Edwards and Owens, 1962; Duffer and Dorris, 1966) or in special situations such as thermal streams where allochthonous organic matter input is minimal (Stockner, 1967; Naiman, 1976).

As another index to the productive capacity of the Fort River periphyton community, annual photosynthetic efficiency values were determined. Photosynthic efficiency is defined as the percent transformation of light energy into organic energy (calories). Oxygen data in this study were converted to kilocalories. by using the relationship: 3.5 Kcal/g O_2 (Odum

and Hoskin, 1957). Stream bed light data were converted into photosynthetically available radiation, by assuming that 47% of the light spectrum is utilizable for photosynthesis (Vollenweider, 1965). An annual photosynthetic efficiency of 1.47% was determined. Weekly efficiencies ranged from 4.1% during spring and summer, to less than 0.01% during winter (Fig. 32). Although Chlorella cultures under optimum conditions may achieve photosynthetic efficiencies of up to 20% (Wassink et al., 1953), that of natural algal populations is generally much lower, e.g., 0.85% in the River Ivel, England (Edwards and Owens, 1960), 5.1% in Silver Springs, Florida (Odum, 1957), 0.4-3.1% on the benthos of an arctic lake (Hargrave, 1969), and an average of about 0.2% for the oceans of the world (Vallentyne, 1965). Notably higher photosynthetic efficiencies of 10.8% (Kevern and Ball, 1965) and 15.1% (McIntire and Phinney, 1965) have been reported for artificial stream periphyton communities, implying at least one difference between artificial stream ecosystems and natural stream ecosystems.

Computer estimates of weekly periphyton Pg followed approximately the same binodal annual pattern as both light and chlorophyll (Fig. 7). A maximum average daily periphyton primary production of 6.51 g O_2/m^2 was estimated to have occurred during the first week in May, coincident with maximum stream light and chlorophyll values. Although P/Rreached an annual weekly maximum during this period (0.79), respiration also was estimated to have peaked at 8.25 during this week. With the reduction of light and chlorophyll, and the increase of temperature, summer Pg only averaged 3.24 g O_2/m^2/day. Respiration, although directly related to temperature, decreased, somewhat, to a summer average of 5.58 g O_2/m^2/day due to the decrease in periphyton standing crop. As a result of low water temperatures, the prominent post-leaf fall peaks of both light and chlorophyll were associated with

relatively minor peaks in estimated Pg and respiration. Temperatures approaching 0° C during the winter months reduced Pg to insignificant levels (< 0.1), despite the presence of chlorophyll concentrations that actually exceeded summer values. Respiration, however, remained at about 1.5 g O_2/m^2 day through the winter causing P/R to reach an annual low during this period (< 0.06).

The strong correlation between the seasonal patterns of stream bed light, and predicted primary production, indicated that light was an important factor influencing Pg during at least certain periods of the year. The relationship between annual averages of chlorophyll at each sampling station, and the annual averages of light received at each sampling station, also supports this conclusion. McIntire (1973) has also asserted the relative importance of shading by dense, deciduous leaf canopies in reducing primary production in western Oregon streams. However, there are certain puzzling seasonal periphyton characteristics which remain unaccounted for, simply by the influence of light. Although summer light is roughly only half of that received during the early spring, it still is about 1.7 x greater than mid-winter light. Nonetheless, periphyton standing crop is actually greater during midwinter than midsummer. The heavily shaded sampling stations evidenced larger seasonal variations of chlorophyll in association with canopy development and leaffall than unshaded sampling stations. However, it is important to note that even unshaded sampling stations reached annual lows of chlorophyll concentrations by late summer and early fall. McIntire (1973) and Douglas (1958) have pointed out the importance of high discharge rates, associated with high silt loads, in maintaining relatively low standing crops of stream periphyton during certain periods of the year. Water discharge in the Fort River remained especially high during the winter and early spring. The temperatures characteristic of the winter months would normally

inhibit the quick return of a large standing crop of periphyton. Daily primary production rates were at least 25 times greater during the summer months than during the winter. Still, despite both high discharge and low light, standing crop remained relatively high throughout the winter period. Surprisingly high winter standing crops of periphyton have been reported in both streams and lakes (McConnell and Sigler, 1959; Hargrave, 1969; Allen, 1971). Allen suggested that primary production of large winter standing crops is supplemented by chemo-organotrophy or utilization of cellular storage products. Although chemo-organotrophy may occur to some extent, studies have shown that, in general, algae cannot complete effectively with bacteria for available organic substrates (Wright and Hobbie, 1966).

In addition to light limitation and scouring processes, McIntire has asserted that periphyton grazing is of maximum importance in determining periphyton standing crops in western Oregon streams. In the Red Cedar River in Michigan, "the (summer) suppression of periphyton Pg was coincident with the maximum biological demand of the consumer species" (Ball and Bahr, 1975). Grazing of periphyton by pupfish, lamprey eels, and snails has been shown to have at least some impact on the standing crop of stream periphyton (Naiman, 1976; Potter et al., 1975; McIntire, 1973). However, in the Fort River the impact of grazing is probably not large. Macroinvertebrate secondary production in the Fort River is only about 3.3 g/m^2.year (Fisher, unpubl. data). Even if macroinvertebrates selectively consumed only periphyton, and the net production rate of periphyton were conservatively assumed to be 25% of periphyton gross production, less than 10% of the net periphyton production could have been consumed by macroinvertebrates.

Whitton (1975) has compared the spring and fall blooms of stream periphyton to those of lakes, while noting that the factors most often responsible

for summer depressions of lake algal populations are generally not applicable to streams, where nutrients and energy enter from upstream, and carry autotoxic substances downstream, fairly consistently throughout the year (Patrick, 1970). No marked changes in chemical parameters were associated with algal blooms or reductions in an Australian river (Potter et al., 1975) or in a chalk stream in England (Marker, 1976a, 1976b). Similarly, in the Fort River, although NO_3 and PO_4 levels are fairly low, no seasonal pattern in their concentration has been evident in past years. However, the association between primary production and the standing stock of nutrient concentrations may be somewhat misleading. Perhaps the biological availability and demand of nutrients, as well as the concentration, is important. As temperature increases, metabolic rates increase, and the demand for nutrients increases. Duffer and Dorris (1966) explained relatively high rates of primary production in a nutrient poor river with the hypothesis that high current velocities may compensate for low nutrient concentrations. In the Fort River, both Vaucheria sp. and Microspora stagnorum, at the warmest water temperatures at which they were evident, persisted only in fast current areas. Whitton (1975) has noted the same phenomenon in Oedegonium sp. The increasing inhibitory effect of increasing temperatures on primary production, at higher periphyton densities, demonstrated in this study, may be related to this effect. At high densities of periphyton, a significant proportion of the algal population is sheltered from the current. At higher temperatures, when the nutrient demand is greater, this reduction of current and the nutrients it provides might severely limit primary production. Whitford and Schumacher (1961) demonstrated that ^{32}P uptake by Oedegonium kurzii is 10.7 times higher in current than in standing water and inversely proportional to the density of the algal sample. Ball and Bahr (1975) reported that "there

is a strong indication that periphyton (net) production is favored at low temperatures under conditions of maximal enrichment . . . . It would appear that a biotic or abiotic mechanism suppressing (net) productivity may be temperature related." The same authors suggested that bacteria and fungi may be serious competitors for space at higher temperatures. Bott (1975), however, noted that viable benthic bacteria numbers in a similar stream did not fluctuate markedly over the year.

In order to illustrate the possible importance of a temperature dependent Pg/periphyton density relationship, rough theoretical estimates of maximum periphyton standing crops at various temperatures were determined from the model. While assimilation numbers fall off logarithmically with density, respiration is assumed to remain linear (Fraleigh and Wiegart, 1975). This means that at a certain critical density, gross primary production will equal respiration, and the population will no longer be able to maintain itself. Daily periphyton respiration was assumed to be 30% (Odum, 1959) of the gross primary production, at the average Fort River density of 33 mg chlorophyll/ m^2, at all temperatures. Even if the respiratory coefficient, chosen somewhat arbitrarily, is inaccurate, the same general relationship, between temperature and the theoretical limit to chlorophyll density, appears to be valid. The results from this analysis show that at 25, 20, 15, and 10 °C, a rough theoretical maximum standing crop of, respectively, 0.29, 0.47, 0.99, and 3.74 g chlorophyll/m^2 is possible. The highest concentration of chlorophyll measured at any sampling station in the Fort River, 0.492 g chlorophyll/m^2, occurred in early May at 15 °C. This concentration of chlorophyll is above that which could (theoretically) occur at 20 °or 25 °C yet well below the 15 °C limit of 0.99 g chlorophyll/m^2. Before algal density would reach a temperature-dependent theoretical limit, other factors would

undoubtedly become limiting, such as attrition or light. Although self-shading in dense mats of periphyton is probably important, the greater influence of density with increased temperatures is believed to be independent of light factors. Shading is unrealted to temperature.

It may be important to note that the temperature range at which the theoretical standing crop limit rapidly approaches realistically low levels of chlorophyll is the same temperature range at which the May bloom and subsequent decrease of periphyton occurs. During this period, although decreased light due to shading is probably an important limiting factor in periphyton production, the decrease in standing crop and the low level which occurs throughout the summer may be at least partially due to the temperature-density relationship proposed here.

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FIGURE 1. **Insolar radiation reaching the Fort River streambed during the seventeen month study period.**

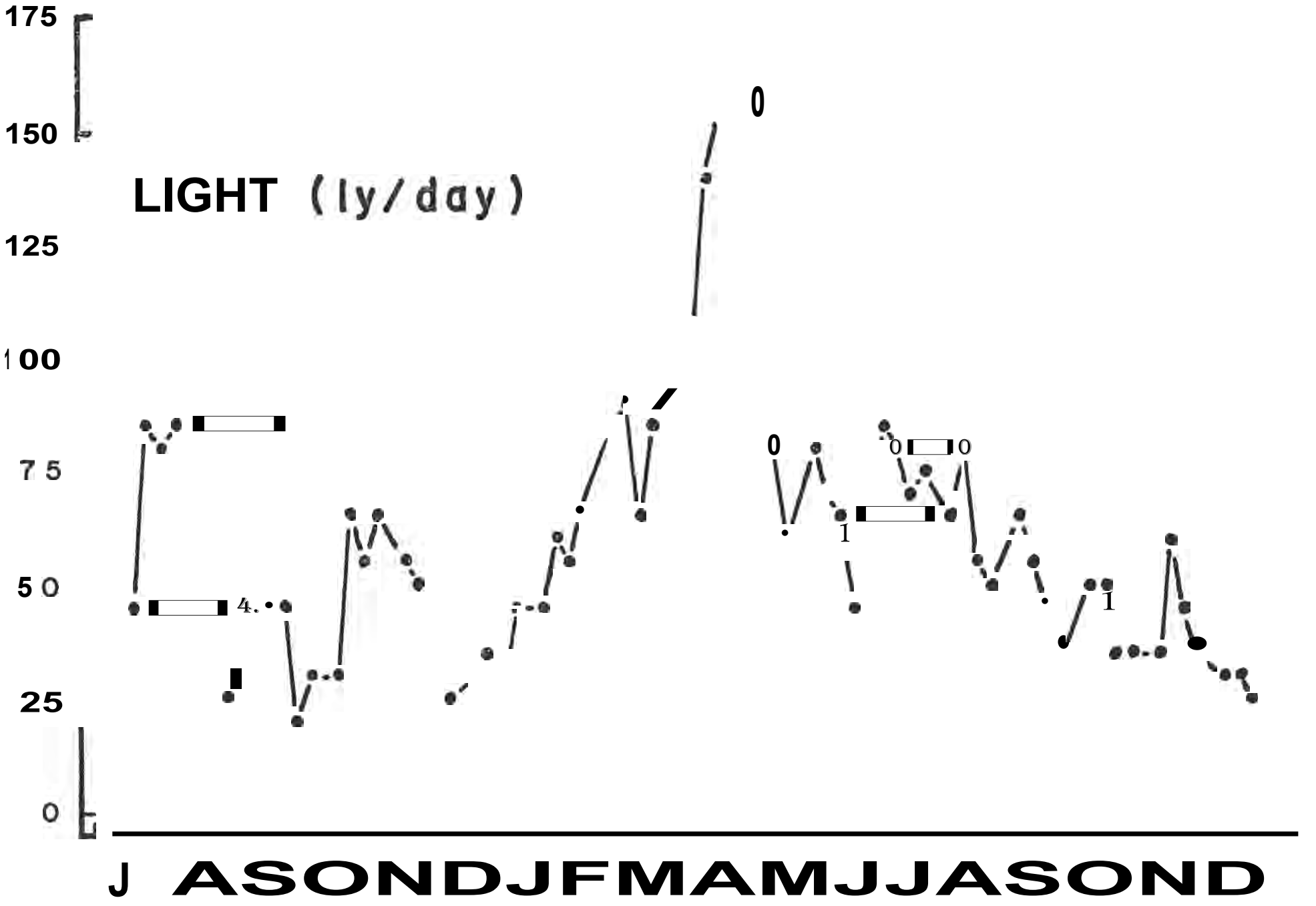
175
150
LIGHT (ly/day)
125
100
75
50
25
0
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FIGURE 2. Fort River stream water temperature during the seventeen month study period (weekly means, °O.

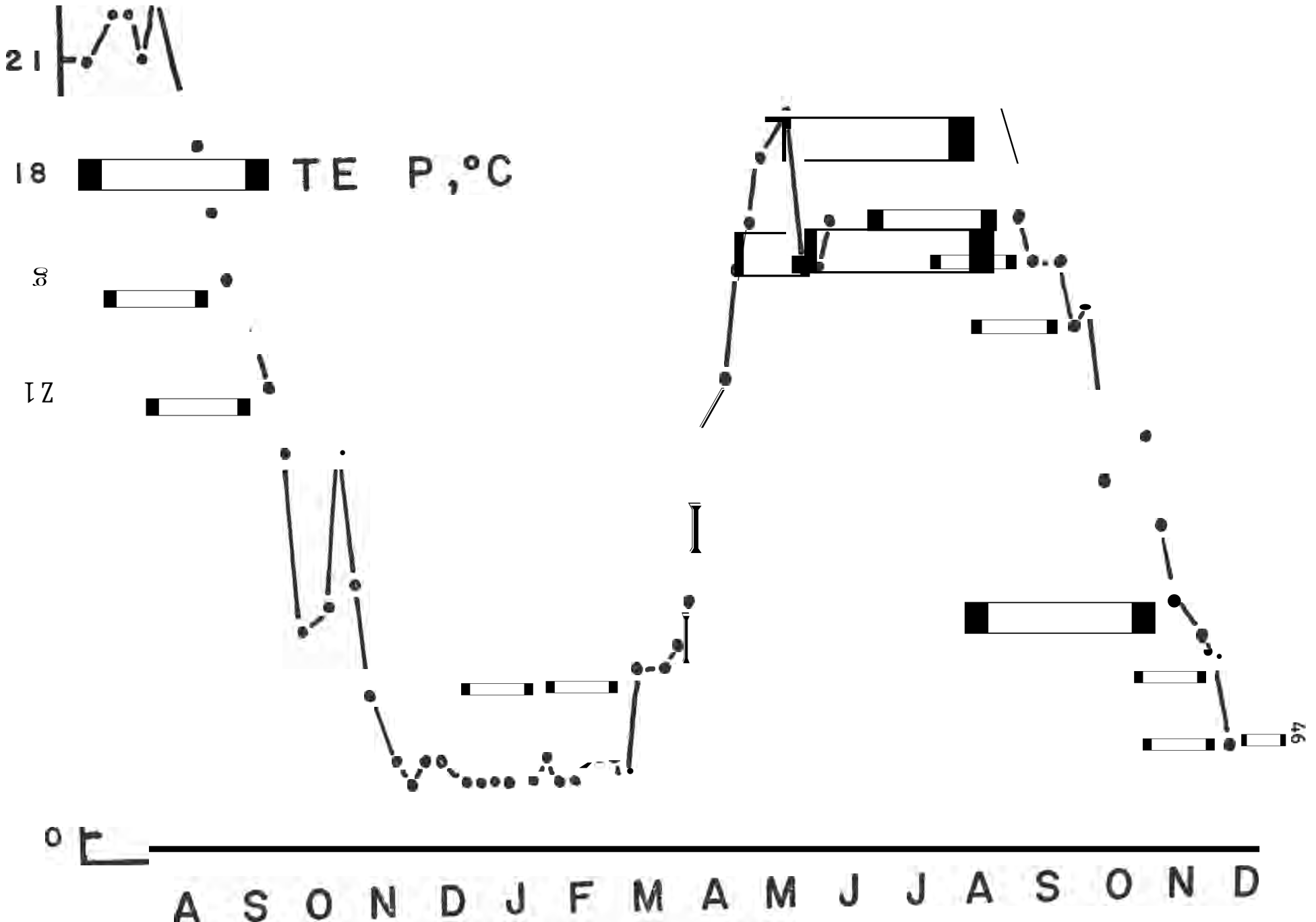
21
18
TE P,°C
0
A S O N D J F M A M J J A S O N D

FIGURE 3. Seasonal variation in chlorophyll a of the Fort River periphyton community.

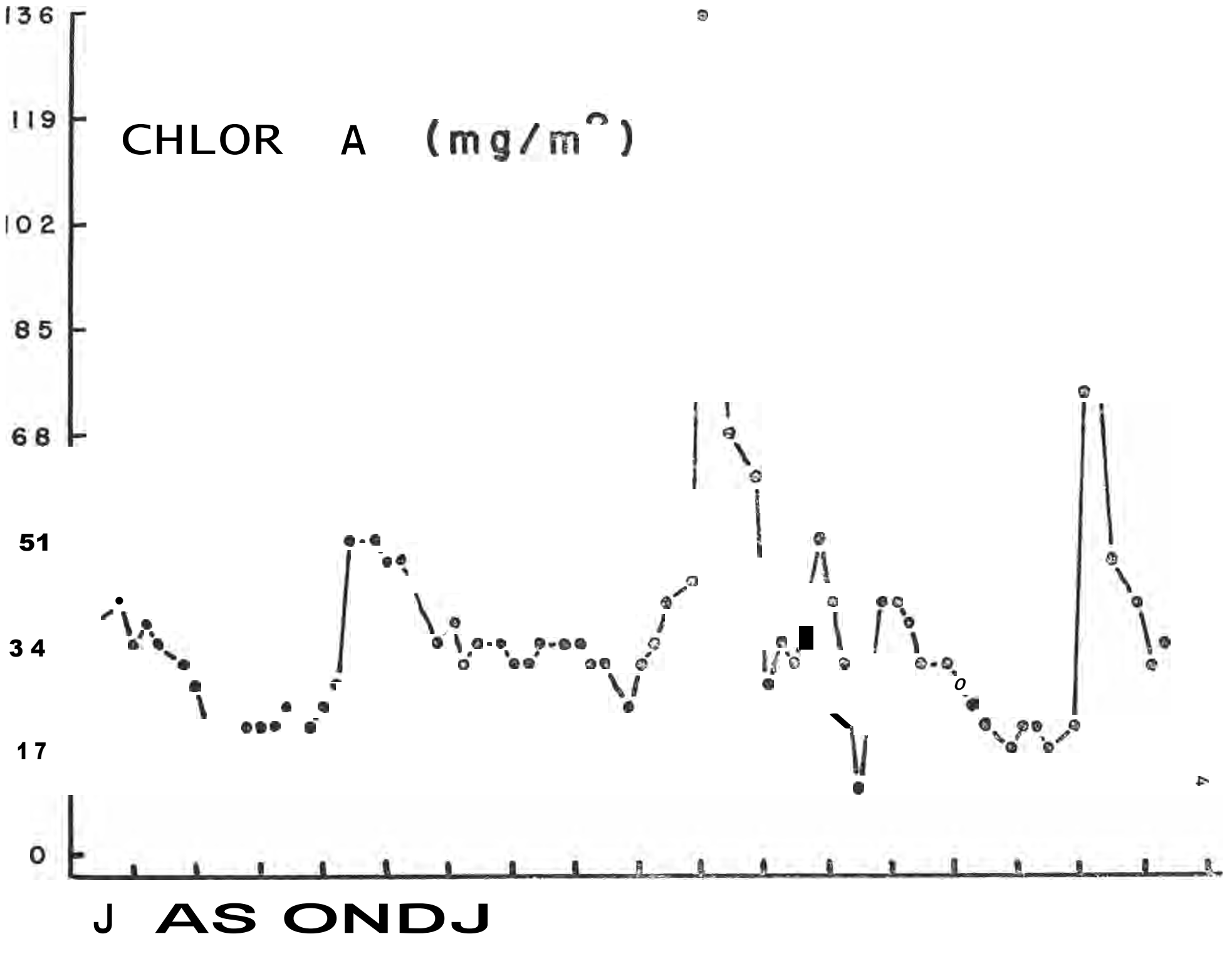
136
119
102
85
68
51
34
17
0
CHLOR A (mg/m³)
J AS ONDJ

Figure 4. Comparison of empirical and predicted PMAX values of Fort River periphy ton.

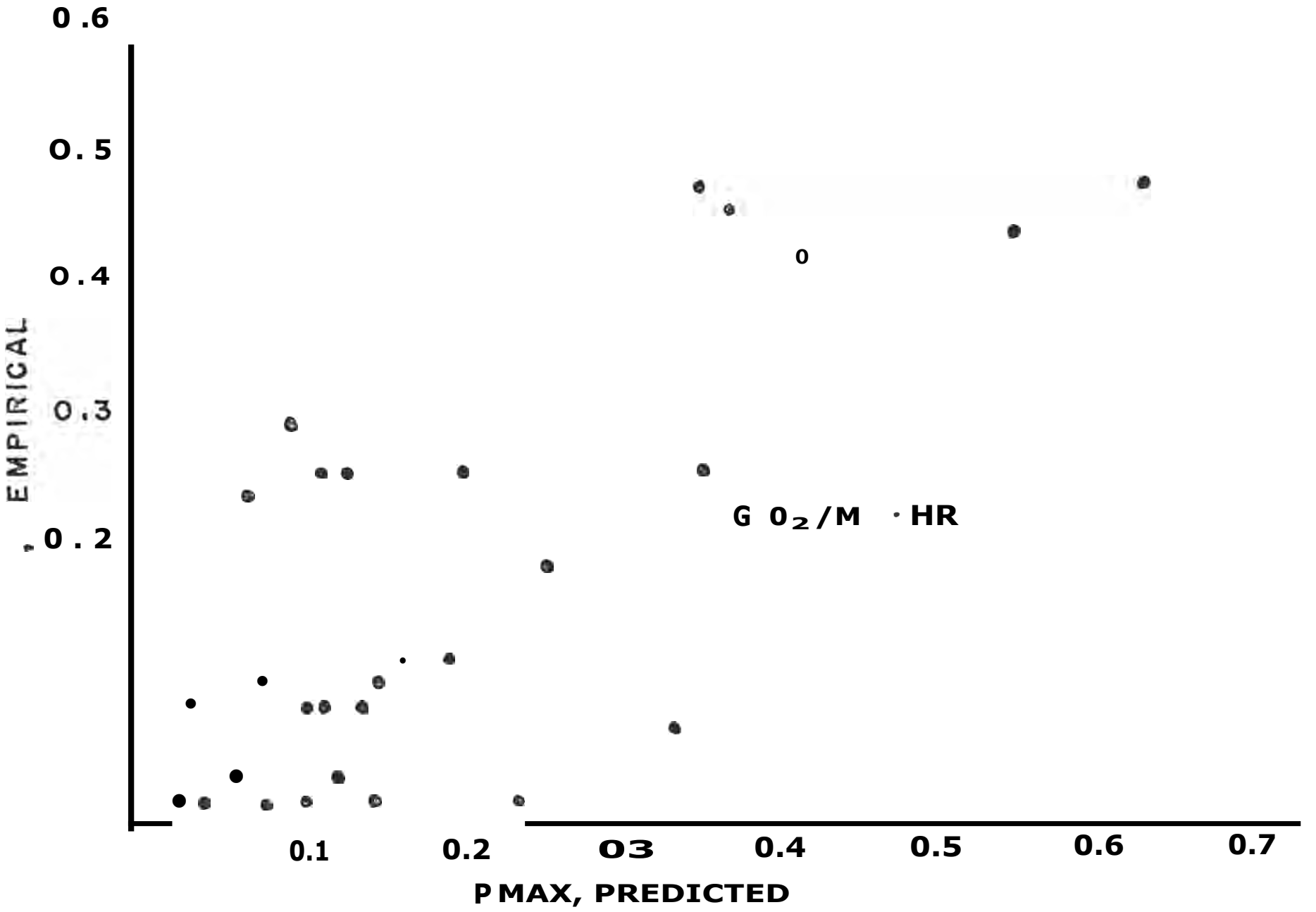
0.6
0.5
0.4
0.3
0.2
EMPIRICAL
0
G O_2/M · HR
0.1
0.2
03
0.4
0.5
0.6
0.7
PMAX, PREDICTED

FIGURE 5. Gross primary production of periphyton as a function of chlorophyll density at six temperature ranges.

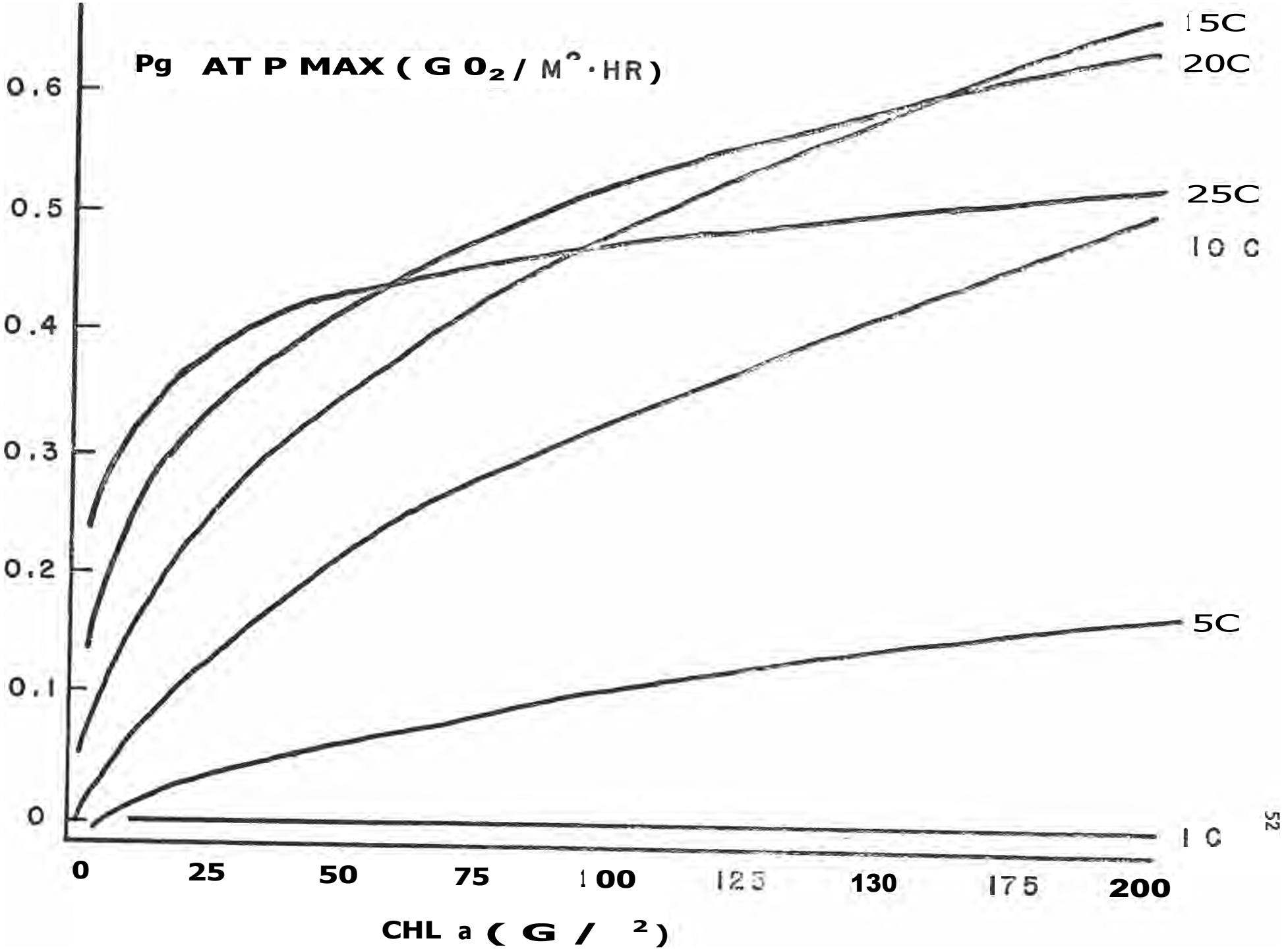
Pg AT P MAX (G O2 / M2 · HR)
0.6
0.5
0.4
0.3
0.2
0.1
0
15C
20C
25C
10 C
5C
1 C
0
25
50
75
100
125
130
175
200
CHL a (G / 2)

FIGURE 6. Comparison of empirical and predicted community respiration of Fort River periphyton community.

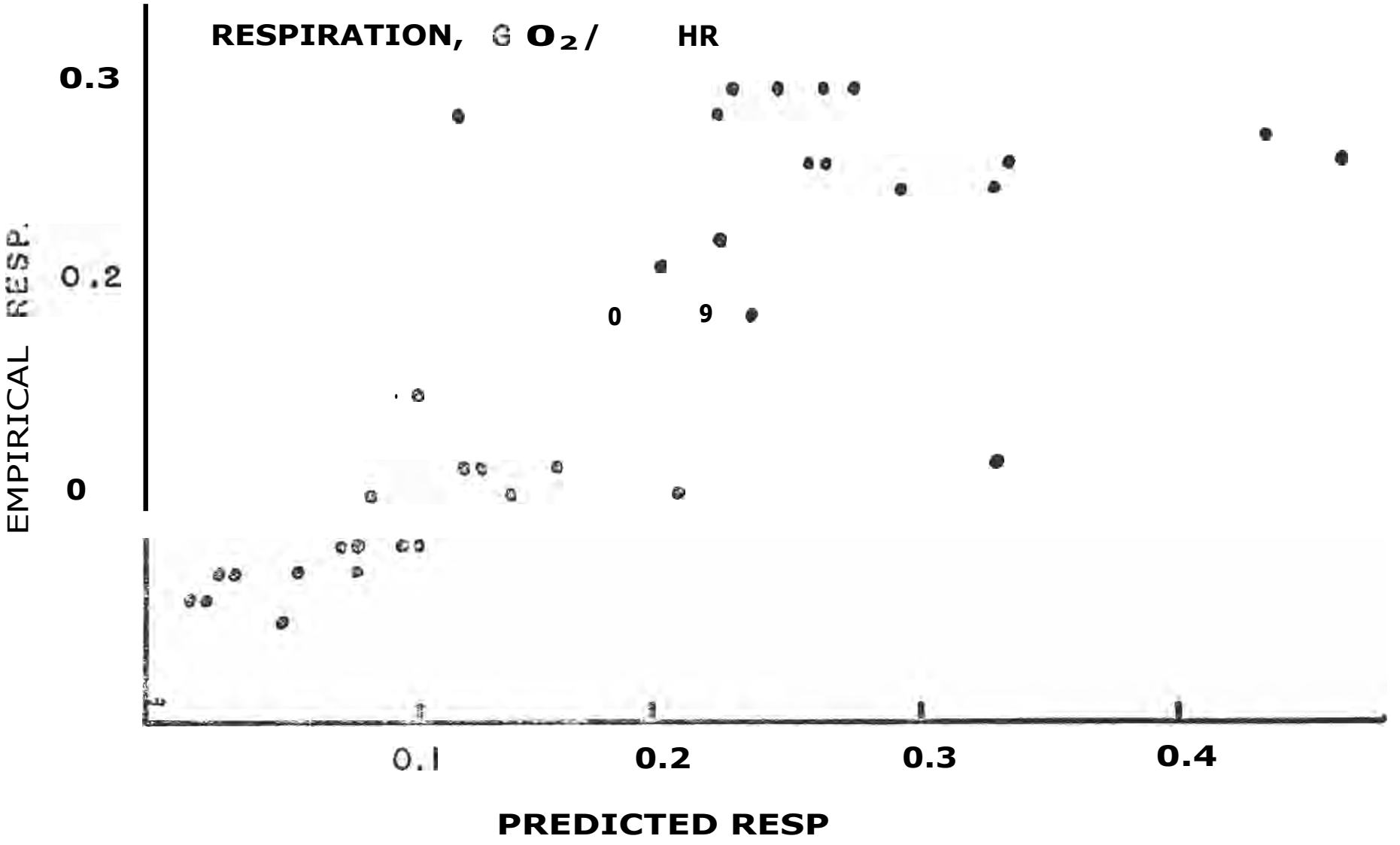
RESPIRATION, G O2/ HR
0.3
0.2
0
EMPIRICAL RESP.
0 9
0.1
0.2
0.3
0.4
PREDICTED RESP

FIGURE 7. Periphyton gross primary production during the seventeen month study period.

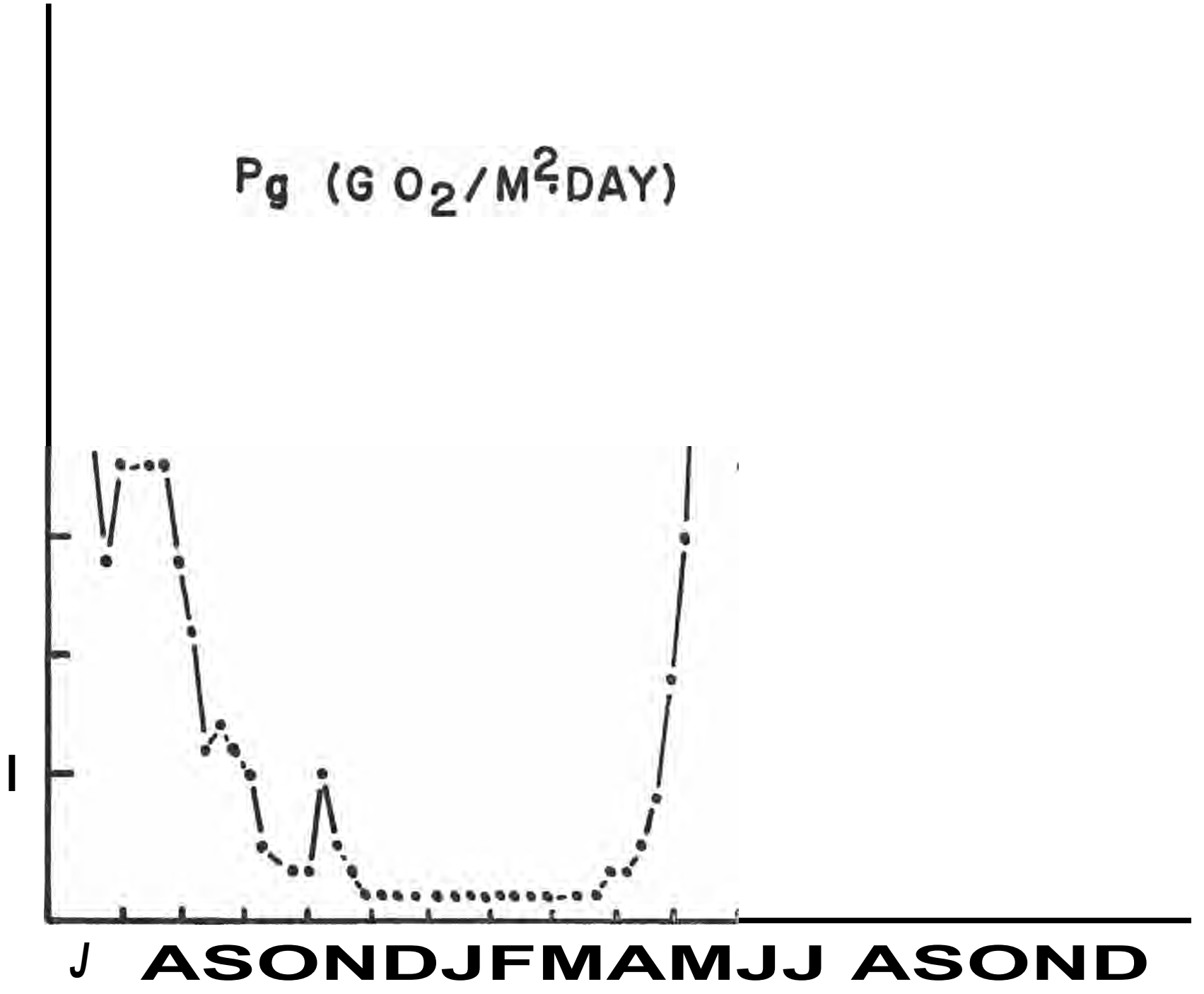
Pg (G O2/M2.DAY)
I
J ASONDJFMAMJJ ASOND

TABLE 1. Physical characteristics and chlorophyll densities at each of the eight Fort River sampling stations (A - H). C = cobble, MC = mixed cobble and sand, S = sand and silt.

	SAMPLING STATION							
	A	B	C	D	E	F	G	H
Annual light penetration, %	34	13	16	21	29	30	28	32
Leaf-out light penetration, %	32	10	12	21	21	23	22	28
No canopy, light penetration, %	37	15	20	21	37	38	34	37
Substrate type	C	C	MC	S	C	S	MC	MC
Maximum substrate diameter, cm	11	13	9	1	12	1	10	9
Current velocity cm/sec	42	15	10	5	20	2	21	10
Mean depth, cm	15	60	63	71	30	58	22	20
Chlorophyll, mean annual mg/m^2	32.1	80.8	27	11.4	101.7	-	47.2	43.2
Chl, leaf-out period	32.2	48.1	20.4	11.6	56.2	6.5	26.7	33.4
Chl, no canopy	32.0	107.0	32.4	11.0	138.1	-	63.6	51.1

TABLE 2. Estimated mean annual and monthly respiration, gross production, photosynthetic efficiency, and P/R values for the periphyton community of the Fort River, Massachusetts.

MONTH	TEMP °C	LIGHT Ly/day	CHLOR mg/m²	PHOTOSYN. EFF. %	PERCENT OF ANNUAL R	PERCENT OF ANNUAL Pg	P/R	RESP g O_2/m²·day	Pg g O_2/m²·day
JAN	1.0	42	34	0.08	3.0	0.1	0.01	1.46	0.02
FEB	1.5	74	32	0.02	4.0	0.1	0.01	1.5	0.02
MAR	2.8	98	30.2	0.08	4.0	0.1	0.07	1.73	0.12
APR	8.0	160	37	0.65	7.0	7.8	0.5	3.06	1.5
MAY	17	106	90.8	3.57	17	24.9	0.68	7.0	4.79
JUNE	17.3	75	36	2.91	12	15.2	0.6	4.92	2.93
JULY	21.5	68	30.5	3.67	14	17.6	0.56	5.84	3.26
AUG	21.6	88	33.5	2.93	13	16.9	0.57	5.6	3.43
SEP	15.8	47	22.6	1.0	4.0	8.5	0.39	4.1	1.53
OCT	8.4	34	21.2	0.95	6.0	3.3	0.17	2.59	0.45
NOV	5.4	68	38.4	0.53	6.0	3.4	0.16	2.57	0.41
DEC	1.4	36	44.5	0.03	4.0	0.2	0.01	1.63	0.04
YEAR	10.1	74	44	1.47			0.46	3.49	1.60