Structure and Photosynthetic Response to Abrupt Thermal Stress of a Periphyton Algal Community Colonized in a Power Plant Discharge Canal

A Thesis Submitted to the Faculty of

Baylor University

in Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

By

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August 1976

ABSTRACT

Tremendous increases in energy needs have led to construction of many new power plants. Effects of heated power plant effluents on aquatic organisms have not been clearly established. Periphyton community structure was used to assess these effects. Species diversity (H") was used to monitor changes in periphyton algal community structure in the discharge canal of a fossil fuel power plant near Waco, Texas. Diversity decreased closer to the power plant discharge. Minimum diversity was 0.96 in June at the sampling station closest the power plant and maximum diversity was 2.89 at the station farthest from the discharge in March.

Diatoms dominated the attached algal flora at all stations in the January and March samples. By May diatoms were being replaced by bluegreens at the sampling station closest the power plant, yet diatoms were still the major group at all stations. By June bluegreens were dominant at the station closest the power plant and were increasing at the other stations but were not dominant.

Primary periphyton production per unit biomass was measured following exposure to abrupt thermal change as encountered during shutdown and startup of a power plant. Production was greatest for samples colonized near the power plant discharge for both 10 C and 30 C experimental temperatures. Maximum primary periphyton production using ^{14}C methods was 0.61 ug C organic matter^{-1} hr^{-1}.

ACKNOWLEDGEMENTS

The contributions of many people contributed to the completion of this thesis. Only some of which will be mentioned here.

I would first of all like to thank Dr. O. T. Lind for directing the research and for his encourage, patience and careful editing. I would also like to thank my other committee members Drs. Floyd Davidson and David Pennington for their respective contributions.

I wish to acknowledge the grant support from O. W. R. to Dr. O. T. Lind.

Texas Power and Light Company aided the research in many ways, especially in the building of booms at the respective stations. Without their cooperation the research could not have been done.

My thanks goes to several who helped in the typing of the thesis including my wife, Judy, Nancy Morgan, Carol Clayton and Linda Brown.

My family, especially my wife, Judy have given me constant support and encouragement as well as contributing to the thesis in ways too numerous to mention.

I wish to thank my God for the strength and energy to finish this thesis and for being a light unto my paths.

DEDICATION

This thesis is dedicated to Judy. Without her help I could not have finished this thesis. Without her to share it this life would have much less meaning.

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I INTRODUCTION

The purpose of this study was to assess the effects of power plant thermal additions on the periphyton community structure as indicated by changes in diversity. In addition, effects of abrupt thermal changes on photosynthetic capabilities of periphyton algae were to be assessed.

There has been growing concern over possible detrimental effects of heated effluents from power plants on aquatic communities. In the discussion of Patrick (1968) Gloos-Chenko pointed out that temperature of subtropical and tropical aquatic systems are much nearer the critical thermal maximum of most organisms than are systems in temperate regions. Natural temperature regimes in Central Texas and elsewhere in the Southern United States approach these critical temperature maxima without further heat additions by power plants. Studies of effects of heated effluents from power plants on aquatic communities in the Southern United States is sorely needed in determining future power plant sites and what measures may or may not be taken to preserve the aquatic ecosystems. Jaske, et al. (1970) pointed out the dilemma, "The press for increased power requirements can be expected to occur at a rate which may exceed the ability of the ecological investigators to quantify the area of interest."

Lind (1975) found thermal effluents to have detrimental effects on phytoplankton photosynthesis in Tradinghouse Creek Reservoir, McClennan County, Texas. Planktonic organisms are usually exposed to a short term thermal stress as they are sucked into the intake structure of power plants but they

may be resistant to such short term thermal stresses. Fish and other motile organisms may move into and out of the discharge area and create uncertainty as to the amount of exposure received (Cairns, Dickson, and Crossman, 1972). Periphyton, in contrast cannot quickly avoid environmental stresses and there is no uncertainty as to the location of the organisms. The attached biota near a power plant discharge are exposed to the harsh conditions for a longer period of time, not just the immediate time the sample is taken (Patrick, 1950).

Another reason for using periphyton is the importance it has to the ecosystem. In flowing waters such as a power plant discharge canal, periphytic organisms are the major primary producers. As Wetzel (1972) pointed out the majority of lakes (or a reservoir in this case) of continental regions are small and the littoral metabolism frequently dominates the system and can materially influence or entirely regulate that of the phytoplankton. Methods have been developed by Patrick, Hohn and Wallace (1954), McIntire (1968a), and others to readily utilize the periphyton community as an indicator of the health of the system.

Biological effects of thermal discharges on aquatic ecosystems are many and diverse. They may range from direct lethal effects of high temperatures to subtle changes in behavior, metabolism, performance, community structure, food-chain relationships, and genetic selection (Coutant, 1970). Several investigators have found community function to be integrally dependent upon community structure. Margalef (1965) linked productivity to community structure. McIntire (1968a) stated community properties such as photosynthetic and respiratory rates, biomass, and pigment concentrations are manifestations of the species composition and the summation of the autecologies of the community constituents. My study combined periphyton community struc-

ture and metabolism to assess any alterations caused by the heated power plant effluent.

To more fully acquaint the reader with meanings of essential terminology and clear up various uses of certain terms in the literature, the following are defined:

Periphyton Community- the assemblage of microorganisms (consisting primarily of algae, protozoans, and bacteria) with associated small microscopic animals (mostly chironomid larvae) which grow attached to the glass substrata used in this study (modified from McIntire, 1966b).

Primary Production- the weight of new organic material created by photosynthesis, or the energy which this represents. It is the increase observed in the biomass of green plants over a period, plus any losses (e.g., excretion, respiration, damage, death, or grazing) (Westlake, 1965).

Standing crop- the actual concentration of different species forming the community expressed in numbers of individuals per a definite area regardless of the factor of time (Sladecek and Sladekova, 1964).

Biomass- if the standing crop is expressed in weight units (wet weight, air-dry weight, dry-weight, ash-free dry weight, organic matter loss on ignition), or in the amount of oxygen needed for its oxidation, or further in calories, the term biomass is applied (Sladecek and Sladekova, 1964).

II Literature Review

Community Structure

Sladekova (1962) concluded her review of methods for investigating periphyton communities, "Finally all the quantitative data obtained by any of the methods discussed and expressed either numerically or in other units are more valuable when supplemented with precise and detailed qualitative analysis of the community." Earlier in the same review she said, "The quantitative determination of periphyton by means of counting methods is laborious and time consuming but in comparison with other methods most precise especially if the results can be proved statistically." Szczpanska (1970) concluded that species composition determined the factors influencing the processes taking place in the periphytic biocenosis. It may be concluded that taxonomic limnological investigations of periphytic and other communities are essential in more fully understanding and evaluating these communities.

Early periphyton investigations were confined primarily to systematic accounts of the organisms present. Reviews of the literature have been done by Cooke (1956), Sladekova (1962), and Wetzel (1964). Most of the important work will be discussed in the methods portion of this review.

While taxonomic studies are necessary to give a more complete picture of the community structure there is a need to transform the traditional species list to quantitative and comparative terms and as Margalef (1965) has pointed out, the eventual interest in diversity should act as a stimulus to not neglect careful taxonomic studies of communities. Patrick (1950) proposed use

of community structure rather than individual species as a means to evaluate the health of the community. Under healthy conditions, many and various species should be present, each being represented by only a few individuals. Even so, biological indicators have distinct advantages over physical and chemical indicators of water quality. Physical and chemical differences don't necessarily indicate the health of one body of water and the polluted status of another; both may be healthy yet different.

Patrick (1964) explained why we are unable to use indicator organisms. "The complex pollution which we encounter today is of recent origin, and time has not been sufficiently long for specific taxa to evolve which are characteristic of its many components. Rather, we have certain species which are tolerant to one or more of a wide variety of chemical and physical conditions commonly associated with pollution. Thus, any one species is not equally tolerant to all the conditions we class as pollution. For these reasons we must be more concerned with a more general type of change to indicate the many aspects of pollution, such as the number of species present and the relative sizes of the populations rather than to the specific species present and the sizes of the populations of specific species." Thus, the presence or absence of major taxonomic groups should be used as an indicator of conditions. So, while we have in the past used indicator species or dominant species as an indicator of the health of the community (Kolkwitz and Marsson 1908; Thienemann 1939; Fjerdingstad 1950, 1960), at present the value of the use of specific indicator associations or species is in indicating the characteristics of the water at the particular time that you find them (Patrick and Strawbridge, 1963a). Furthermore, it is for this reason that when criteria are sought which can be widely used to indicate pollution, one of the most valuable is the structure of the diatom community.

Williams (1964) also supported the community approach in study of water quality. He proposed measuring the degree of change in aquatic communities and comparing and recording the variety of species and number of organisms in these communities, as a basis for indicating environmental conditions. At present, the ecological requirements of each species are not known so attempts to use the mere presence of organisms or a qualitative indicator-organisms principle have been unsuccessful. The species-number principles affords a method that may be used to show differences and fluctuations among stations.

Hohn (1959) has demonstrated clearly the feasability of using random diatom populations as a measure of water quality; he pointed out that there is a direct relationship between the changes in structure of the diatom flora and pollution. Patrick, Roberts and Davis (1968) illustrated this point. Their results indicated that there were no particular species which indicated pH changes of the magnitudes used in the study in a circumneutral stream, but rather these pH changes could be discerned by examining many aspects of the diatom community, such as number of species and biomass produced.

Gause (1936 in McIntosh 1966) commented that the most important structural property of a community is a definite quantitative relationship between abundant and rare species. The significance of this statement is apparent when examining the species diversity indices, for they express just such a relationship. "Diversity should rise in a successional sequence to a maximum at climax. It enhances community stability, relates to community productivity, integration, evolution, niche structure, and competition." (McIntosh, 1966). Margalef (1965) expressed diversity as an expression of the maturity or historical development and thus related to time. Margalef (1969) said diversity could be applied to the distribution of any set in subsets. In a biological sense it results from the function of the ecoystem.

Changes in diversity reflect changes in the community structure as a result of naturally occurring phenomena or because of destructive man-induced changes in the environment. Diversity has been used in several studies to measure effects of various kinds of pollution on aquatic communities. Coutant (1962) observed an increase in both variety and number of organisms as he progressed from hot to cool water, demonstrating the effect of temperature as the primary limiting factor. A tolerance limit near 90° F for a normal population structure with extensive loss in numbers and diversity of organisms accompanying further rise. Cairns, Dickson, and Crossman (1972) used diversity as a means of evaluating changes in community structure with regard to hazardous spills. Patten (1962) used the species diversity principle to indicate degrees of pollution in Raritan Bay: diversity increased away from the polluted Raritan River. Staub, Appling, Hafstetter, and Haas (1970) used diversity to measure effects of industrial wastes on plankton of the Mississippi River near Memphis.

Since the species diversity concept was introduced by Gleason (1922), its usage and meaning have evolved to its present state. Margalef (1965) described biotic diversity as any suitable function which has a minimum when all cells belong to the same species, and a maximum when every individual belongs to a different species.

Gleason (1922) and several subsequent authors (Fisher, Corbet, and Williams, 1943; Williams, 1950; Goodall, 1952; Odum and Hoskins, 1957; Margalef, 1957; Odum, Cantlon, and Kornicker, 1960) used a logarithmic function to describe the relationship between number of species and number of individuals in the sample. Margalef (1957) was the first to recognize the fact that the logarithmic species diversity index has the mathematical form of negentropy (information). He first used a variation of an answer to the question, "How

difficult would it be to predict correctly the species of the next individual collected? If successive individuals in our census are independent of previous ones." (MacArthur 1965). Margalef used: $I/M \log M!/ (M_1!M_2!...M_i!)$

M_i is actual abundance of ith species

M = total of all individuals

By using Stirling's theorem of approximation we are able to measure diversity from species abundances (MacArthur, 1965).

Odum, Cantlon, and Kornicker (1960) reviewed previous workers who used a logarithmic function in describing community structure. They recognized the slope of the graph of cumulative species versus logarithm of individuals as a measure of community species diversity.

$$\frac{\text{increment in cumulative species}}{\text{increment in logarithm of individuals counted}} = \frac{S}{\log I}$$

The patterns of logarithmic relationships between species-individual distributions are derived from postulated of a high degree of organization in nature, the very antithesis of random functions. Thus, it is perhaps prudent to assume that several kinds of phenomena may contribute to this logarithmic relationship including patterns which serve to regulate interaction (Odum, Cantlon, and Kornicker, 1960). They propose a hierarchy postulate to explain this relationship. If the rarer occupations are related to the commoner occupations in constant per cent ratios, the relationships of occupations to individuals is by definition logarithmic. "Rothstein (1952) and others have shown that a hierarchy such as in a military organization could be described in units of information. An ecological hierarchy may be similarly described. Negentropy of informations and organization of species are all measured by the same quantity." (Odum, Cantlon, and Kornicker, 1960) "...it must be concluded that to a considerable extent, communities tend to be organized into

heirarchies in their relationships of species." (Odum, Cantlon, and Kornicker, 1960).

In its present context we more often think of species diversity as dominance diversity, the evenness of distribution of individuals of a community or sample among the species present (Whittaker, 1965). Whittaker included indices by MacArthur (1957), Preston (1948), and Simpson (1949) among those which are a measure of dominance diversity. The "broken stick" model of MacArthur (1957) has been suggested as a measure of diversity by Lloyd and Ghelardi (1964). The calculated diversity is compared to the number of species on an equitability table which would provide the value for maximum equitability using the Shannon-Wiener formula. The hypothetical number of species is then divided by the number of species actually found in the sample and the ratio is found in the form of a decimal equivalent. This value is a measure of the equitability component of diversity (Lloyd and Ghelardi, 1964). Preston (1948) plotted the number of species of a particular abundance versus the logarithm of the abundances. He concluded that the abundance distribution of all species in a habitat would follow a lognormal curve. The shape of the curve allows one to approximate the number of species in a particular habitat including those undiscovered ones. Patrick, Hohn, and Wallace (1954) used the lognormal curve to describe attached diatom populations. Preston continued to use this distribution in later works (Preston 1960, 1962) as did Patrick (Patrick and Strawbridge, 1963; Patrick, 1963). Simpson's (1949) index gives the probability that two individuals selected at random will be of the same species. Fager (1972) suggested use of a modification of the Simpson index (1.0-SI). Hendrickson and Ehrlich (1971) rewrote Simpson's (1949) index to overcome difficulties inherent in diversity indices, namely uncertainty as to identity of individuals within a species and the inequality of difference

among all pairs of species. They suggest setting up criteria for determining how much difference exists between any two organisms.

Since Margalef (1957) first recognized biotic distributions as negentropy, the use of the information theory in describing community structure has greatly increased. Pielou (1966b) reviewed the use of the information theory. She defined diversity in connection with the information theory as the degree of uncertainty attached to the specific identity of any randomly selected individual. "A collection may consist of organisms that naturally occur together; or else it may be an assemblage of organisms gathered by an ecologist that is to be studied as a unit (e.g. the plankton in a water sample, a catch of insects from a light trap). For all such collections the information content as defined by Shannon and Weaver (1963) or by Brillouin (1960) provides a convenient measure of diversity." Sager and Hasler (1969) describe the two components of diversity as:

a) richness of species- increase in richness, increases diversity

b) equitability or relative abundance of species- a tendency toward more equal distribution of individuals among species can result in higher diversity (H').

They found that phytoplankton species in excess of the 10-15 most abundant ones have little effect on the index. "The main effect being measured in Shannon's index seems to arise from the component of relative abundance as expressed in those species with a higher rank of abundance." (Sager and Hasler, 1969) Preston (1962, p. 199) pointed out one of the difficulties in accurately measuring diversity, "...the ratio of species to individuals is vastly higher in a sample than in the universe. We accumulate species at first as rapidly as we accumulate individuals. As we continue collecting this situation ceases to remain, and after a time the addition of new indi-

viduals piles up indefinitely, while the addition of new species is a rare event. We have reached the point of diminishing returns." Williams (1964) has shown that nearly all collections contain several species represented by only a small number of individuals. He used the abundances of the four most common species as an indicator of conditions. Pielou (1966a) concluded that $H(\frac{1}{N} \log \frac{N!}{N_i!})$ depends on three factors --- the number of individuals, the number of species and the comparative abundances of each species. Wilhm (1967) showed that biomass may be a better indicator of abundance than numbers in some cases. He proposed a modification of the Shannon (1963) formula to include biomass. Dickman (1968a) found that planktonic diversity was swamped using the Shannon-Weaver formula. Bacteria and nanoplankton numbers swamped the index. Ten to fifteen species made up the significant 95% of the sample diversity. A biomass index was swamped by zooplankton in the sample. He proposed use of H_p in terms of productivity. A species' mean sample density and biomass times the turnover rate for the species gave him a measure of productivity.

$$-\sum_{i}^{N} P_i \log_2 P_i$$

P_i was defined as pr/PR where pr was productivity of a particular species in the sample and PR was equal to the total sample productivity.

For treating alga samples, either phytoplankton or attached samples, one of the best indices is Margalef's d' (Margalef, 1968). This index gives an estimate of conditions present in a water body. The information theory is utilized in this index and it is easy to calculate. The major drawback of this index is the possible bias by sample size. This can be nearly eliminated by counting a relatively large number of individuals.

Margalef (1969) stated that diversity is insufficient as a measure of

organization and needs to be complemented by some expression of persistence in time, or order. "A more diverse system, once studied, is usually also a more predictable system. The predictability depends on how the community functions; it may be a well organized community able to sustain itself indefinitely in a given environment, or a haphazard assemblage of drifters. It seems necessary to add the measure of the stability or persistance (S) equal to the inverse of the deterioration of information during its transmission" (Margalef, 1969). The notion of stability includes something linked to the fact that, although a system is passing through a series of changes, some aspect of it is unchanging (Ashby in Margalef, 1969). MacArthur (1955) theoretically proved increased diversity leads to increased stability. If a species has many predators, each with alternate prey, then if it decreases in numbers, the predator pressure will shift elsewhere, whereas if it increases in numbers, many species are available to harvest the increase, so that maximizing the number of links in the food web thus maximizes this "structural" stability of the community (Leigh, 1965). Preston (1969) said, "Thus, whatever stability there is in the ecological world is not a static equilibrium, but a fluctuating or dynamic one, and normally a highly fluctuating one. Stability lies in the ability to bounce back, not in the ability to hold tenaciously to ground once taken or numbers once achieved." As Margalef (1969) has proposed, a function called stability is needed which could be compared with diversity and together with it, could provide a complete measure of "organization." Hairston, Allan, Colwell and Futuyma (1968) tried to demonstrate the relationship between diversity and stability in a laboratory experiment with bacteria and protozoa. They found the relationship to hold if the lower trophic level was more diverse but not if the predator level was increased.

Community structure as indicated by species diversity varies widely in

similar types of communities. There have been several distinct hypotheses formulated to identify and explain the controlling influences. Lack (1947) and Vaurie (1951) first noted the limiting similarity of coexisting species. MacArthur (1965) discussed two ways that there can be limiting similarity of species or competition:

(1) resource limited- there is a limiting similarity in the species of coexisting, resource-limited species,

(2) predator-limited- there are advantages for predator limited species being somewhat rare.

"The number of species expected is the usable range of resources divided by the limiting similarity of resources which can be used by co-existing species." (MacArthur, 1965)

The importance of predators in determining species diversity has been stressed by several other investigators. Paine (1966) found that the removal of the top predator of a subweb, or group of organisms topped by a terminal carnivore, allowed the presence of a "winner" in the competition for space. Predation would tend toward an increase in local diversity. Spight (1967) criticized the predation hypothesis of Paine (1966). He related that predators do not necessarily affect the utilization of resources other than space, as an immediate effect of controlling density. His criticisms were founded on the ideas that:

(1) the fact that there are fewer individuals in a population in a more diverse community, than in another in a less diverse community does not allow prediction of relative densities of the predators, and

(2) higher density of the population in the less diverse community does not imply that that population is obtaining a greater

quantity of any of the resources of its community, other than space. Density is thus a poor estimator of competition. Patrick and Strawbridge (1963) listed several reasons why populations stay relatively small and thus allow a higher diversity. They list competition among species, fluctuating nutrient supplies and predation as factors contributing a major influence on communities of diatoms.

"It is possible that owing to fewer climatic hazards, species can be rarer in the tropics without running great danger of extinction." (MacArthur 1965). Although there seems to be a trend favoring higher diversity closer to the tropics, there are exceptions, Patrick (1964) has not found this trend true for diatoms. Protozoans and fresh-water insects also have not consistently shown this pattern. Pianka (1966) reviewed six hypotheses which may be the controlling influence on this diversity gradient:

1) time theory- all communities diversify with time. The temperature regions have been exposed to major disturbances due to glaciation.
    a) ecologically- species exist which can fill a particular niche, but have not had time to disperse.
    b) evolutionarily- a newly opened habitat is not utilized but will be if enough time is given to evolve an organism.
2) theory of spatial heterogeneity- an increase in environmental complexity as one proceeds toward the tropics. On the local scale the size of the environmental elements correponds roughly to the size of the organisms populating the region, i. e. the pattern and complexity of vegetation. It is the component of diversity due to topographic relief and since the number of habitats increases toward the tropics, it is a possible explanation. It does

not, however, explain the diversity gradients within a given habitat type.

3) Competition hypothesis- natural selection in the temperate zone is controlled more by the physical environment; toward the tropics biological competion becomes a more important component of evolution. Tropical species will be more highly evolved and possess finer adaptations than will temperate species. More species can coexist in the unit habitat space.

4) predation hypothesis- it has been claimed that there are more predators in the tropics thus limiting prey populations and lessening competition thus allowing coexistance of more species.

5) theory of climatic stability- regions with stable climates allow the evolution of finer specializations and adaptations than do areas with more erratic climatic regimes, because of the relative constance of resources. A unit of habitat will support the same number of individuals in the tropics and temperate regions, but since each of the species may be rarer without becoming extinct in the topics, there can be more of them.

6) productivity hypothesis- diversity increases with productivity. There may often be an inverse relation between species diversity and abundance or standing crop. A reduction in energy requirements allows the existence of more species.

Sanders (1968) hypothesized that there are two extreme types of communities; those which are totally physically controlled and those which are biologically accomodated. In the physically controlled community, the adaptations are primarily to the physical environment. Examples of this type of community are found in areas which place extreme physiological stress on the

individuals. Small numbers of species are usually found in these areas. Communities such as this are also found in places where there is a recent history, such as most freshwater lakes. A biologically accomodated community is one in which the physical environment is rather constant and remains uniform for long periods. Biological accomodations are evolved and there is a stable compex with large numbers of stenotopic species. Theoretically each community is found somewhere along the gradient between the two extremes.

Slobodkin and Sanders (1969) classified low diversity environments as falling into three general categories:

(1) "new" environments

(2) "severe" environments

(3) "unpredictable" environments

Severity and unpredictability combine in their effects so that a severe, unpredictable environment tends to be poorer in species than either a less severe or a more predictable environment (Slobodkin and Sanders, 1969). They asserted that animals from low diversity, physically controlled environments, were poor competitors but could invade higher diversity areas when competitors were absent.

Sanders (1968) illustrated the importance of the time factor using Lake Baikal as the example. Lake Baikal has a zone of very high diversity in the very stable environment of the lake depths. There are other lakes such as Great Slave Lake in Canada which also have a zone of relatively changeless environment. In the depths of these lakes are found only a fraction of the species found in Lake Baikal. The major difference seems to be the much greater period of time which has passed since any major disturbance has effected Lake Baikal. The glaciers of North America have given Great Slave Lake a relatively short time for evolution of endemic species in the nearly

changeless environment,

McIntosh (1966) stated that diversity should rise in a successional sequence to a maximum at climax. Johnson (1970) also correlated succession with diversity. He pointed out that pioneering communities can be characterized by low species diversity." Instability of the external environment may hold a community at a particular stage of succession indefinitely." (Johnson, 1970). He further stated that periods of disturbance or relative stability would determine the direction of the succession. It seems very likely that the interaction of these controlling factors, rather than any particular factor, is responsible for the observed community structures and diversities found in communities,

The preceeding section of this review which was devoted to the more theoretical papers explained the evolution of diversity indices to their present state and also reviewed some possible explanations hypothesized as controlling factors in determining diversity. The following portion is devoted to brief mention of investigations which utilized a particular index and, in some cases, the reasons given for use of the index. The purpose is to acquaint the reader with practical application of the diversity concept.

Hulbert (1963) used the index proposed by Fisher, Corbet, and Williams (1943) to calculate the diversity of phytoplankton in three different marine habitats. The lower diversity in the estuarine regions depended upon a much smaller number of rare species and a much greater degree of dominance. Sager and Hasler (1969) used Shannon's formula to measure diversity in lacustrine phytoplankton. "The main effect being measured in Shannon's index seems to arise from the component of relative abundance as expressed in those species with a higher rank of abundance." (Sager and Hasler, 1969). Zooplankton diversity in Oklahoma was measured using Shannon's formula by Kochsiek, Wilhm,

and Morrison (1971). Patrick, Roberts, and Davis (1968) followed methods outlined by MacArthur (1965) in comparison of diatom communities of normal and altered pH range. Johnson (1970) used Brillouin's diversity formula to measure diversity in benthic marine organisms. Pielou (1966a) pointed out its usefulness in dealing with small collections. Reiners, Worley, and Lawrence (1970) also used Brillouin's 1962 diversity index because of the difficulty of achieving a truly random sample from patchy vegetation at Glacier Bay, Alaska. They also followed Pielou (1966a) for proper use of diversity indices. Kohn (1967) used Shannon's formula for species diversity in the Gastropod genus Conus. He felt that habitat complexity was an important determinant of species diversity. Cody (1970) used the Shannon-Weaver index to determine within and between habitat bird species diversity in Chile and Kricher (1971) used Shannon-Weaver H' to measure bird species diversity and find the effect of species richness and equitability on diversity. Mackay and Kalff (1968) used Margalef's d(Margalef, 1958) to measure diversity of insect communities in a small Quebec stream. Cameron (1971) used both the Shannon-Weaver and the Brillouin indices to measure insect trophic diversity in salt marshes. He found seasonality to be an important aspect of the relationship of species diversity to community organization. Poulson and Culver (1968) used Brillouin's formula as described by Pielou (1966a) to measure diversity in terrestrial cave communities.

Systematic Studies

As mentioned previously taxonomic studies are irreplaceable in combination with metabolic studies and they have value in their addition to taxonomy. Some notable, relatively recent systematic studies, not specifically related to physical and chemical parameters have been reviewed here.

Round has done a series of taxonomic studies of algae in the English Lakes District (1957a, 1957b, 1960a, 1960b, 1961). He found diatoms to be best suited to epipelic habitats and each lake had a distinct epipelic flora. He also found distinct seasonal cycles for both the epipelic diatoms and blue-green algae.

An epipsammic diatom flora was characterized by Round (1965). The epipsammic flora is composed of minute diatoms, many of which require electron microscopic study for positive identification. Because they are non-motile they often belong to the monoraphidineae and araphidineae. This has been scarcely recognized as a discrete association in freshwaters. He gives two plausbile explanations: the relative scarcity of sandy substrata and the fact that they are normally silt covered.

Castenholz (1967) observed seasonal patterns of non-planktonic diatoms on the coast of Norway. He classified members of the species complement as "winter-early spring," "spring," "summer," and "year-round" types. He found diatom species of Norway to be very similar to those of the west coast of the United States, but the seasonal patterns and degrees of dominance of many species differed considerably.

A taxonomic study was combined with a larger scape investigation on the Red Cedar River, Michigan (Grzenda and Ball, 1968). They found a seasonal variation in the taxonomic composition of the periphyton colonizing plexiglass plates. Algae on the plates were similar to those found on the stream

bottom. There was a differentiation between the clean-water zones and those with organic pollution in the ratios of autotrophic to heterotrophic algae found in these areas. The heterotrophs formed a larger part of the community in the zone of organic wastes.

Kawecka (1970) did a taxonomic study of algae which colonized glass slides mounted in styrofoam. Algae were abundant on the styrofoarm. She used a 6-grade scale of abundance from + to - 5 designed in previous studies (Kawecka, 1965, 1966).

These few taxonomic studies have indicated a distinct seasonality in periphyton algae. Castenholz (1960a) indicated, "It may be seen that the seasonal fluctuations of overall diatom production curves is generally a function of the combined independent variations of several species." Most modern taxonomic studies are combined or correlated with physical or chemical parameters. A correlation of this type adds ecological data on algal species. Wulff and McIntire (1972) stated that if enough is known about the ecological properties of the diatom taxa in the species pool and about the physical environment of a habitat of interest, it is often possible to predict the spatial and temporal distribution of the more abundant taxa. However, from season to season and from year to year the kinds of species found in any one area vary greatly. This is probably due to the fact that we have such a large species pool available, each species with slightly different preferences for this variable yet stable environment (Patrick, 1964). She added that it was evident when considering the natural environment that there are many associations of species which are reliable indicators of general ecological conditions such as temperature, salinity and nutrient level of the water.

Patrick (1948) reviewed factors effecting the distribution of diatoms in both fresh and salt water habitats as well as terrestrial forms. When

speaking of bottom forms, distribution was governed by the amount of O_2, H_2S, CH_4, CO_2, light, and temperature. She brought forth that the type of waterbody makes a big difference in the floral composition. Factors such as turbidity have been found to influence blooms in the Great Lakes. Wind and precipitation also play a role in determining species composition and abundance. Patrick concluded that chemical factors coupled with light and temperature would determine if a species would be found.

Douglas (1958) studied the ecology of the attached diatoms and other algae in a small stony stream in England. She found no evidence that differences in light intensity or temperature had any effect on the attached community; except possibly the algae attached to the moss. The major factor determining community structure and population densities appeared to be the flooding and subsiding of the stream waters. She also found predation inversely affected the density of Achnanthes.

Castenholz (1961) also demonstrated the importance of grazers in maintaining the anomolous summer situation in littoral marind diatoms of high production rate and low standing crop. The large diatom population was held in check by littorines and limpets in the favorable parts of the zone. Castenholz (1961) found few studies on the subject of grazing effects on sessile microvegetation. He cites Brook (1952, 1954, 1955) as well as Douglas (1958) as having worked previously on the problem.

More recently Dickman (1968b) reported on the effects of grazing by tadpoles on the structure of a periphyton community. He concluded that tadpoles can greatly reduce the standing crop of periphyton, especially filamentous green algae such as Mougeotia. He further hypothesized that tadpoles may trigger an annual succession in the periphyton community of the lake he studied. He felt this could have widespread consequences for both the fauna sup-

ported directly by the epiphytic algae as well as for higher trophic levels.

Stockner and Armstrong (1971) noted the importance of grazing on the periphyton of the experimental lakes area of northwestern Ontario although it was not one of the areas of concentration in their investigation. The major part of their study was a taxonomic anlaysis of periphyton from several lakes. They found a definite periphyton seasonal periodicity. The diatoms predominated in April and May followed by filamentous greens and desmids and then blue greens from mid-August to mid-September followed by an autumn diatom peak. Certain diatom species exhibited a clear vertical zonation in the littoral, while others were not restricted to a particular zone.

Four different physical environments were employed by Lyford and Phinney (1968) in assessing the patterns of community structure in a salinity gradient. Distinct benthic plant communities developed in each of these environments. The Enteromorpha-Melosira community developed in the saline environment accounted for the highest metabolic rates of the entire study. The two brackish water communities were a Melosira-Enteromorpha community and one dominated by a Rhizoclonium-Melosira-Synedra association. A Melosira-Spirogyra community developed in fresh water.

Shepherd and Womersley (1970) found water movement and light to be the two most important ecological factors in the sublittoral zone of West Island, South Australia. Horizontally, the species distribution was largely determined by water movement, but vertically, light was the most important factor.

McIntire (1968a) in his work with laboratory streams found "Light intensity, temperature, supply of nutrients and dissolved gasses, and current velocity of the water in the laboratory streams interacted to determine the species composition of a particular association of organisms, and in addition, regulated the increments of gain and loss to the community unit." He also

found the abundance of the more numerous species was related to light intensity, current velocity, and the collective influences of seasonal change.

In another paper McIntire (1968b) outlined the three major algal groups as:

a) the diatoms

b) the blue-green algae

c) the filamentous green and yellow-green algae

He found that in his laboratory streams, regardless of experimental conditions, diatoms were present in significant numbers in all communities. The relative abundance of the three groups of algae was dependent upon seasonal variations in the physical and chemical conditions of the water (primarily temperature).

The vertical distribution of the epipelic algae of Marion Lake, British Columbia was partially influenced by light intensity reaching the sediment, but also strongly influenced by grazing and erosion by wave action (Gruendling, 1971). Temperature, light, and grazing each appear to influence seasonal fluctuations in algal standing crop. Wave action was a significant factor influencing the seasonal distribution of at least the filamentous green algae.

Ecological data have been collected not only for common algal communities, but also for algal communities at the extreme range of physical or chemical tolerance.

Brock and Brock (1970) recently studies the distribution of algae of Waimangu Cauldron (New Zealand) in relation to pH, and found pH 4.8 - 5.0 as the lower limit for blue-green algae, Cyanidium cauldarium.

Castenholz (1969) studied the thermophilic cyanophytes of Iceland in regard to the upper temperature limit. The upper limit for growth was 63-64 C both in the field and in laboratory studies. Mastigocladus laminosus was tol-

erant of the highest temperature. Several species of the narrow-cell-form of Synechococcus which almost exclusively inhabit North American and other springs above 62C and up to 74C were not found in Iceland.

The effects of physical and chemical parameters on communities and individual populations have been shown to be directly related to diversity and the aim of several studies.

Hulbert (1963) found that phytoplankton concentrations of less than 3 X 10^8 liter^{-1} could not limit other species by nutrient depletion. Thus open ocean and coastal regions do not force species out of existance and the diversity is not lowered even in a bloom condition. In estuaries, where plankton concentration may exceed 3 X 10^8 liter^{-1}, dominance by some forms may force others out of existance and lower the diversity.

Stream flow may drastically alter potamoplankton populations. In periods of high flow the numbers of species and individuals were drastically reduced, thus reducing the diversity, but in the period immediately following heavy flow, the plankton community experienced peak diversity (Williams, 1964).

Patrick, Roberts, and Davis (1968) found great diversity deviations from controls at low pH ranges. They found fewer species usually present in the tests than in the controls. Lind and Campbell (1970) also found reduced biotic diversity in areas of low pH as related to acidity in stripmine lakes.

McIntire and Overton (1971) found the diversity of attached diatom communities closely related to environmental gradients. In general, differences were related to the salinity gradient and to the desiccation and insolation gradients. They felt that certain biological factors were also important, primarily interactions between diatoms and macro-algae.

Cairns, Dickson, and Crossman (1972) found that long term stresses from toxicity caused immediate reduction in both diversity and density. An interim

community structure of lower diversity was formed which lasted as long as toxicity persisted.

Temperature plays an important role in determining species distribution and abundances in natural and laboratory communities. Hargraves and Wood (1967) studied periphyton in selected habitats. They found, "The closest correlation between periphyton changes and physiochemical factors was with temperature, with 15-20 C seemingly critical in terms of growth of many species." Diatoms predominated in the river in all seasons. In the eutrophic pond diatoms, greens and blue-greens increased throughout the season, while in the oligotrophic pond the green algae predominated in spring and blue-green in fall.

Patrick, Roberts, and Davis (1968) also found that temperature was an extremely important factor in determining the population size in studies of diatom community structure. "When temperature is in the range for optimum growth, other deleterious sublethal factors in the environment will not have as severe an effect as they do under suboptimal temperature and/or light ranges."

Dillard (1969), in a primarily taxonomic work on the benthic algal communities of a North Carolina Piedmont stream (Barton Creek), found water temperature as the primary factor in initiating seasonal changes in dominance. Temperature fluctuations about 15C seemed of critical importance to numerous species.

Comparative temperature hardiness of marine algae along the Pacific coast of North America was studied by Bieble (1970). Temperature hardiness was directly related to the zone from which the algae were collected. Shallow water forms were more temperature resistant than deep water forms.

The algal distribution in six thermal spring effluents in western Montana

was observed by Kullberg (1971). Blue-green algae was the only group at the sources of the streams. The mean maximum temperature endured by diatoms was 43.2 C, and by the green algae 40.9 C, yet no upper limit was determined for the blue-greens.

There have been some investigations of the effect of temperature on species diversity. Staub, Appling, Hafstetter, and Haas (1970) correlated generic diversity of Mississippi River plankton with several physical and chemical parameters. "Correlation studies have indicated that water temperature is the major controlling influence in regulating both kinds and numbers of individuals in a thriving planktonic community." Wulff and McIntire (1972) studied the effects of heat on the attached diatoms in a laboratory model ecosystem. "...it was obvious that the heated water had a pronounced effect on the structure and productivity of the diatom assemblages." They also felt that it was important to recognize the fact that the distribution of diatoms was undoubtedly regulated by biological factors as well as physical factors. Stockner (1968) studied the ecology of a diatom community in a thermal stream at Mt. Rainer National Park. He found species diversity and redundancy to be quite uniform. This fact suggested community stability despite shifts in species composition.

The use of natural waters for cooling power generating plants has initiated studies of the effects of the artificially added heat on the algal communities. Kyselowa and Kysela (1966) reported an increase in the amount of attached algae below the outfall of the water used for cooling the turbines in a power plant at Skawina, Poland.

In a review of thermal pollution, Patrick (1969) reviewed effects of temperature on freshwater algae. She said that under natural conditions, one of the major factors in seasonal succession of species is the different tem-

perature optima and, as a result, as the temperature increases or decreases, replacement takes place. All the organisms of a group may not be killed, but many species are not able to compete successfully with other, better adapted species. "In general, the effects of thermal discharges are to alter the current pattern in the receiving body of water and to cause a change in the natural existing temperature regimes." She indicated that increases in temperature within the tolerance limits of existing species may increase productivity. If the natural tolerance ranges are exceeded, species composition will change, and if the temperature shifts are great enough, shifts in algal groups may occur. Above 35 C blue-green algae often become dominant, especially if the high temperature is maintained for long periods of time. This may severely damage the ecosystem since blue-green algae are considered a poor food souce.

Hatfield et al. (1966) found higher diatom counts on artificial substrates in the discharge canal than at the other stations when the river water temperature was below 93 F in the Susquehanna River.

Studies of the effects of thermal discharges on the Illinois River by Beer and Pipes (1969) revealed a shift in dominance from diatoms to unicellular green algae in the effluent canal of the Dresden Station. They also found an overall reduction in algae in the effluent canal as compared to the intake area during April when the water in the inlet was 8.9 C and the discharge was 15.6 C.

Williams, et al. (1971) summarized investigations of effects of thermal discharges from Northport power plant. Preliminary studies of periphyton revealed live diatoms in large numbers in the discharge channel.

"Total numbers of algae and total algal species may be reduced in the heated waters near a power plant discharge. This reduction is dependent on

temperature and is most likely to be found during the summer months while actual increases in numbers may be found in late fall and winter". (Gurtz and Weiss, 1972). Aquatic organisms as a whole have the following protective responses to heat discharges:

a) have a broad heat tolerance range

b) have the ability to acclimate to changes in the ambient environment

c) exhibit an avoidance reaction

Heat discharges into the aquatic environment becomes a problem only when these protective mechanisms are overwhelmed!

Tremblay (1960, 1965) was one of the first investigators to conduct an in situ investigation of plankton above and below a power plant discharge. He found that increased temperature or some other aspect of plant operation resulted in lower species variety below the power plant outfall as compared to controls upstream on the Delaware River. He concluded that there was a return to normal condition by 4500 feet downstream.

Wurtz and Dolan (1960) found that when heated water was added to the Schuylkill River, the hot water reduced the diversity of the prevailing biological structure of the river. Warm water from a power station in Poland also decreased the number of species when the temperature exceeded 30 C. Several diatoms were favored by these relatively high temperatures (Strangeberg and Pawlaczyk, 1961).

Another study done on Polish lakes (Poltoracka, 1968) showed that warming a lake from 5.9 to 9.6 C above normal seasonal temperatures by power plant discharge increased the number of algal taxa, especially among the Chlorophyta, compared to other nearby lakes.

Investigations of the Upper Potomac River by Cairns, Kaesler, and Patrick (1970) indicated similar conditions before and after power plant operations

began. There was no evidence from the diversity or kinds of species of adverse effects due to power plant discharge.

Sieman (1970) found the number of algal species and species diversity were depressed by temperatures 5 C above the intake temperatures. Hetchel (1970) likewise found species diversity of algae, calculated by several methods, to be consistantly low in the thermal plume. The plume area appeared as an impoverished habitat with low intertidal benthic biomass.

Carpenter (1971) found algal diversity to be lowest in Cape Fear Estuary in January and February at 4.5 C. His investigations showed an apparent antithesis to the findings of most researchers working with power plant discharges.

Patrick (1968) concluded, "We know that the natural systems are characterized by a high diversity of species and that raising the temperature beyond the optimum for these species reduced diversity. The question is, how much and in what way can this diversity be altered and not reduce the energy flow and productivity of the system, and more important, the stability of the system through time?"

A change in community structure, in space or time, is linked to a change in the rate of production (Margalef, 1965). "Any expression aiming to give an indirect estimate of primary production on the basis of present properties of an ecosystem has to include some quantitative term reflecting the structure of the community (biotic diversity, pigment ratio D_{480}/D_{665})" (Margalef, 1965). He showed that production is a function of the structure of the community in a mathematical sense as well. Production is a derivative relative to time and since diversity is an expression of the maturity and historical development and thus time, the two are inseperable. As previously mentioned, Dickman (1968a) proposed a diversity index Hp with productivity as the measure of relative abundances. Community structure and function are inseperable. Margalef

(1969) gave the relationship between community structure, as indicated by diversity, and the components of community function or metabolism. He stated that in general, diversity was negatively correlated with productivity, but that it was not possible to understand the relationship without understanding the dynamics of the system. Margalef also stated that if primary production keeps increasing, and if it increasingly outdistances respiration, diversity is expected to crop. If biomass decreases, when production is inadequate to maintain the equilibrium the diversity gradient is expected to parallel the biomass gradient; if biomass is increasing the diversity gradient is in opposition to the biomass gradient. With these general relationships in mind, I have reviewed the community function aspect of the periphyton community.

II Literature Review

B. Photosynthetic Response to Abrupt Thermal Changes

Biomass and primary production were reviewed separately, while they are in nature inseparable. A brief introductory section will establish the interrelationships of these components.

In recent years there has been a resurgence of attempts by aquatic ecologists to unravel the questions of growth, production, distribution and upper temperature limits of thermophilic algae (Stockner, 1968). These efforts have been primarily centered around hot springs and the runoff streams. These studies are helpful to ecological studies such as mine, in which the periphyton of power station thermal effluents are examined. They will be included here, when appropriate.

Odum (1956) established the relationship of the metabolic processes for flowing waters as: import rate plus production rate is equal to community respiration plus export rate. Thus the production and respiration of a community will determine the net gain or loss of biomass which will in turn be exported or accumulate as organic detritus.

McIntire (1968a) reiterated, "Any change in the biomass of a community is equal to the photosynthetic production of material minus the losses from respiratory processes and export of material from the system."

Cory and Nauman (1971) stated that if respiration constantly exceeded oxygen production there would be a net loss of organic material from the community. To maintain a steady state community, organic matter would have to be

imported or conversely if photosynthesis consistently exceeded respiration the net gain may be stored or exported from the system.

The productive capacity of the environment is another term depicting the excess of the production over the respiration. McIntire and Phinney (1965) said that study of the rates of energy fixation by autotrophic constituents of an aquatic community along with assessment of energy losses from the community help provide fundamental understanding of this "productive capacity" of the environment.

More recently the emphasis has focused on the cycling of organic matter, Lind (1971) stated that organic matter in aquatic ecosystems arises from two sources. Primary production by phytoplankton is generally the major means of organic matter production in large bodies of water. In smaller bodies of water and many reservoirs, the allochthonous imput may be quantitatively significant.

Brock (1967a) found that for the complete cycling of organic matter bacteria were insufficient. The bacteria are able to take up the organic carbon but it is released to the system only if animal grazers are present.

Beyers (1965) pointed out a factor which should be considered in all respiration and photosynthesis studies and that is diurnal variation. He found that both net photosynthesis and nighttime respiration are maximal in the first half of the light or dark periods. Almost complete cessation of respiration was found in the second half of the dark period. A balanced ecosystem might compensate for cloudy days or long periods of darkness by decreasing respiration before metabolizing to the point that structural damage was done to the organism. This would be a built in mechanism to avoid catastrophic effects of periods of bad weather.

Since Wetzel first called attention to the major role played by periphy-

ton and macrophytes as producers in shallow lakes, ponds or rivers (Wetzel, 1963), several authors have lent support to his findings (Kevern, Wilhm, and Van Dyne, 1966; Wetzel, 1964; Wetzel and Allen, 1970; Allen, 1971). Wetzel and Allen(1970) felt that the allochthonous imput of a lake basin was largely in the form of humic compounds refractory to decomposition. They felt that the littoral flora has the potential of being a major producer of the lake and regulates, at least in part, the entire metabolism of the lake. Allen (1971) found that the littoral vegetation and attached periphytic communities were capable of significant contributions to the total dissolved organic matter (D. O. M.) "pool". He also cited Khailov and Gorbenko (1967) as saying that in systems where there are significant amounts of allochthonous and autochthonous materials and dissolved and particulate organic matter are available for pelagial metabolism and where they may result in increased carbon fixation rates, the epiphytic component may be capable of indirectly affecting population dynamics and community metabolic patterns of the phytoplankton.

The importance of periphytic communities to many lakes, streams, ponds, and other relatively small and shallow bodies of water has been supported here. Some of the basic energy relationships have also been reported. Several authors have attempted to establish the role of increased temperature on periphytic community function. Stockner (1968) found primary production and respiration values of cyanophycean algae growing in the run-off stream of a hot spring (37 C) to be slightly higher than published values from other aquatic ecosystems but not as high as comparable thermal stream run-offs using ^{14}C methods. Brook (1967a) found that the extremely high temperatures found at some of his stations restricted the standing crop of organisms. These organisms were found to photosynthesize better than they do at lower temperatures. His impression was that photosynthesis was not the growth limiting

factor, but rather some other physiological process such as protein or nucleic acid synthesis.

Laboratory studies have been carried out in addition to the field studies with some valuable information additions. Jorgensen and Steemann-Nielsen (1965) studied temperature adaptation in the photosynthetic process with cultured planktonic algae. They found an increase in all enzymes at lower temperatures and thus greater organic content per cell at low temperatures. In order to double the number of cells a much greater amount of organic matter must be produced at lower temperatures. They found that the physiological behavior of a species will vary to a considerable degree. If changes are too pronounced, they may damage or kill the organisms. Adaptations must be gradual. Photosynthesis requires a certain degree of equilibrium between the photochemical and the enzymatic parts of the mechanism. If the enzymatic part is unable to keep pace with the photochemical, damage may take place in the cells. The enzymatic portion of the process thus, is the temperature dependent portion. Steemann-Nielsen and Jorgensen (1968a) illustrate this in the Artic where they found the I_K, light intensity which measures the onset of light saturation for photosynthesis, of surface plankton to be high despite the low temperatures present.

The preceeding introductory remarks have established some basic energy relationships in aquatic ecosystems, established the importance of periphyton to many aquatic ecosystems and set forth some basic algal temperature responses. Since some of the earliest workers with periphyton established biomass as an important measure of periphyton growth capacity, it has been used as a means of quantitatively describing periphyton. The next section will concentrate on this relatively simple periphyton function.

Biomass

Orson Whitney Young (1945) was one of the first to work with periphyton in this country and his work on Douglas Lake, Michigan has remained as a work of value to periphyton investigators. He measured periphyton on bullrush stems both qualitatively and quantitatively. He used volume, dry weight and number of organisms per area sampled as measures of biomass. Diatoms were the most abundant type of organisms. The largest fluctuations in number of organisms was found in the surface to 40 cm depth zone where wave action was most intense. The 40-60 cm depth zone was the most stable against severe wave action in comparison to other strata. Young concluded that the average number of organisms was the best measure of productivity at all levels. He found that dead culms supported a greater average volume and dry weight of periphyton than live culms. His results further indicated the formation of a characteristic mat on all substrata. Various substrata differed only in their per cent composition of characteristic fauna and flora. Biomass accumulation followed a successional pattern. Within three days substrata were colonized by diatoms and a few threads of filamentous green and blue-green algae and fungi. By the end of the first week the Chironomids were able to build tubes in the tangle and by the end of the second week the familiar growth was present. Biomass accumulation on artificial glass substrata was found to be two or three times that of natural substrata. He concluded that the periphyton colonization of lithic substrata was dependent upon marl deposition which cemented periphyton to the stones. Young found biomass values as high as 358 mg dm^{-2} with a mean of 39.9 mg dm^{-2} on living culms and 96.0 on dead culms.

Newcombe (1949) studied the biomass accumulation of periphyton on glass slides in Sodom Lake, Michigan. He felt that a direct potential index of production such as the amount of periphyton accumulation on a uniform substrata

would be the most meaningful. Mean biomass was 3.82 mg ash-free dry wt dm^{-2}.

Castenholz (1960a, 1961) has worked in both fresh and salt water. He found periphyton biomass to be 32.4 mg dm^{-2} in Falls Lake, Washington and 29.4 mg dm^{-2} in Alkali Lake, Washington on the average (Castenholz, 1960a). He concluded from his studies of marine littoral diatom populations that the heavy summer growth was checked by heavy grazer activity. He also felt that regular seasonal fluctuations and successional activities may have been involved in determination of standing crops and total diatom biomass.

Sladecek and Sladekova (1964) reviewed the work of several authors who have studied periphyton biomass. Waters (1961) used concrete cylinders as periphyton substrata in Valley Creek, Minnesota. He used cholorophyll a content as an estimate of biomass and found a 200% increase between the second and fourth weeks and little change for the fourth through tenth weeks of colonization. He concluded that between 3 and 8 weeks were required for a relatively constant biomass to be attained, dependent upon environmental conditions during the colonization period.

Another study reported by Sladecek and Sladekova was the study by Sladekova (1962) who found a mean value of 158.7 mg dm^{-2} of periphyton biomass with a range of 0-614 mg dm^{-2} within the time of her experiments (313 days). They used a value from the literature (20%) to estimate the percent ash in the periphyton samples.

Several other studies briefly cited by Sladecek and Sladekova (1964) and the periphyton biomass values found in each follow. Assman (1951, 1953) found mean periphyton biomass on Equisitum as 77.1 mg dm^{-2} with a range of 25-180 mg dm^{-2} in his summer. Odum (1957) recorded the extremely high figure of 1880 mg dm^{-2} for periphyton biomass in Silver Springs, Florida. McConnell and Sigler (1959) found dry weight of periphyton to be 250 mg dm^{-2} in the Logan River,

Utah, Felfoldy (1961) found mean periphyton biomasses in Lake Balaton of 1820 and 1190 mg dm^{-2} for Gomphonema and Diatoma elongatum, respectively.

Sladecek and Sladekova (1964) attributed the relatively lower values found in their studies of the Sedlice Reservoir to the following:

(a) slower currents in the reservoir increased the time needed for colonization.

(b) some blue-green periphyton constituents which are found on rocks are found very scarcely or not at all on glass.

(c) while vertical positioning of slides is good for keeping from having a heavy deposition of silt on the slides it may reduce values up to 6.6 times compared to horizontally positioned substrata (Newcombe, 1949).

(d) two summer months of probable high biomass accumulation were not included in the study.

They concluded that seasonal cycles of periphytic organisms occur both qualitatively and quantitatively.

Wetzel (1964) also reviewed much of the work done with periphyton and he concluded the chlorophyll concentrations varied seasonally and spatially with population dominance and succession. Also because of enzyme changes and the presence of senescent, yet chlorophyll containing cells that there was a poor correlation between chlorophyll content and photosynthetic rates. Chlorophyll concentrations have been correlated with periphyton cell numbers and volumes in a saline lake in Washington (Anderson, 1958 and Anderson, Comita, and Engstrom-Heg, 1955). Barnes (1962) found contradictory results. Pigments and numbers were not proportional in a large California reservoir, while a correlation was found for another lake. A poor correlation between particulate carbon and chlorophyll, particularly in the log phase of growth was found by

Steele and Baird (1961, 1962).

Williams (1964) compiled extensive plankton data from the major waterways of the United States. He made some astute observations concerning algal biomass in general. He stated that in many circumstances where algal mass reaches nuisance levels, the standing crop is in far greater supply than the substance or nutrient responsible for the bloom (Renn, 1954). If pollution may be defined as too much of any ingredient, the algal mass can frequently be considered a pollutant. Williams (1964) also found a direct correlation between pigment extracts and diatom standing crop.

Burkholder, Repak and Sibert (1965) studied the littoral microorganisms on Long Island Sound. They quantified their finding with both actual number or organisms and biomass measurements using pigment extracts. They found abundances of as many as one million euglenoids or thirteen million diatoms $gram^{-1}$ of mud. Chlorophyll values varied with algal community type. Blue-green algal communities had values ranging up to 532 mg Chlorophyll a kg^{-1} of wet mud, while mixtures of flagellates and diatoms had up to 542 mg Chlorophyll a kg^{-1} of mud. They cited the lack of distinction between Chlorophyll a and degradation products as a major difficulty in using pigments to assess algal biomass. They concluded that the significance of chlorophyll in benthic communities could only be fully meaningful when combined with relative rates of photosynthesis.

Steele (1965) likewise studied a marine littoral area. He found Chlorophyll a content to be low at the low water mark and increased to a depth of 15 m below the low water area. He also studied the depth distribution of chlorophyll in the sand and found it to be constant through the top 3-10 cm at 15 m, with intermediate values in between. Good correlation was established between Chlorophyll a and attached organic matter.

Wetzel (1965) described major problems of estimating periphyton biomass as placement of colonization substrata, heterogeneity of distribution and rates of population turnover. He found poor correlation between chlorophyll biomass and in situ production rates in epilithic periphyton populations (Wetzel, 1963).

Kyselowa and Kysela (1966) determined biomass fractions by estimation. They used the index of coverage of periphyton, seston, and microbenthos in the Vistula between Oswiecemia and Cracow, Poland. Diatoms were most numerous and green algae was an insignificant fration of the biomass. Heated water from the power plant effluent was found to increase growth of attached algae at the banks of the Skawinka and Vistula below the mouth of the Skawinka.

McIntire (1966a) found greater biomasses in faster currents in laboratory streams after an initial period when the faster current velocity seemed to retard early colonization. Slower velocity seemed to favor the green algae with a higher organic fraction. The faster currents favored the diatoms and a lower organic fraction. In a more general study of water movements Findenegg (1965a) noted losses in biomass due to fast flushing water. Neal, Patten, and DePoe (1967) concluded from their study of a radioactively contaminated lake that sloughing of biomass from a substrate was most important where biomass and turbulence were highest. It may be a prime factor which placed an upper limit on the amount of biomass which could develop on a submerged surface.

Another area of concentration in the study by Neal et al. (1967) was the biomass accumlation curve. They found biomass accumulation to be nearly complete on the upper polyethylene tape sections after two weeks of incubation. Full development in the deeper sections took longer. Blue-greens were found to be the initial dominant periphyton, followed by diatoms and filamentous

green algae. Blue-green algae remained dominant in the lower zones with filamentous green algae taking over in the upper zones. They concluded that uniform vertical distributions of periphyton mass do not tend to develop. They cited a study by Butcher (1946) which concluded that biomass development was essentially complete in twenty days, except in winter. Kevern, Wilhm, and Van Dyne (1966) found an increase in periphyton standing crop with time using an ash-free basis for estimates.

Vertical distribution of periphyton in the form of epipelic algae was also studied by Gruendling (1971). He concluded that vertical distribution was partially influenced by light intensity, but also strongly by wave action and grazing. He found the highest standing crop consistently at 2.0 m. Stocker and Armstrong (1971) attributed vertical distribution of periphyton in lakes of northwestern Ontario to be mainly influenced by light.

McIntire (1968a,b) concluded that 2 to 3 months were necessary for communities to approach a constant standing crop in laboratory streams. After that losses due to sloughing, respiration and grazing equals gains. At this point biomass fluctuates around some mean value. Cooper and Wilhm (1970) in their studies of Skeleton Creek, Oklahoma, constructed a growth curve from biomass accumulation rates. Ash-free dry weight leveled off after approximately 4 weeks of incubation.

Several authors have related biomass of periphyton to illumination. McIntire (1968a,b) found highest biomass and standing crop in streams of highest illumination. He found that changes in temperature and CO_2 were significant only at light intensities of greater than 1000 ft.-c. Steemann Nielsen and Jorgensen (1968b) found great variations in pigment biomass with light intensity. The algae grown at lower light intensity had much greater amounts of chlorophyll per cell than those grown at high light intensities. McIntire

and Wulff (1969) found biomass of marine benthic diatoms accumulated more rapidly at high light intensities and no exposure to dessication in the laboratory than with the opposite conditions present. In his studies of Marion Lake, British Columbia, Gruendling (1971) found that temperature, light and grazing all appeared to influence seasonal fluctuations in algal standing crop. Light and temperature were the most important variables influencing total standing crop.

McIntire (1968a, 1968b) found significantly higher biomass in streams with velocities of 15 or 35 cm sec^{-1} than streams with 0 cm sec^{-1} velocity. Although the streams with velocities of 35 sec^{-1} had higher biomass than streams with 14 cm sec^{-1} velocity, the difference was not significant. Studies of the Red Cedar River, Michigan (Ball, Kevern, and Linton, 1969) substantiate those findings. Rates of colonization were slower in riffle areas but with a higher maxima. The highest velocity, more than 91 cm sec^{-1}, was inhibitory with intermediate velocity 30.5-61 and 61-91 cm sec^{-1} supporting greater biomass accummulation. The 30.5-61 cm sec^{-1} velocity was the best for biomass. Szczepanska (1970) stated that in general there was greater biomass at stations of free water exchange in some Polish lakes.

Several authors have investigated the seasonality of periphyton biomass accumulation. Among those, Szczepanska (1970) in his study of several Polish Lakes of the Mazurian lakeland found a general picture of seasonal changes in lakes of similar trophy using dry weight, organic matter and chlorophyll as indicators of biomass. He found a low in spring, a high in early summer and a decline in late summer with another maximum in the fall. Gruendling (1971) further divided seasonal effects on periphyton into seasonal effects on each major algal group. He found that wave action was a significant factor influencing the seasonal distribution of at least the filamentous green algae.

Total solar radiation, temperature, and magnesium were most important to the seasonality of green algae in general. Light and chemical factors were most important for the diatoms with grazing also an important factor. Desmids were influenced by temperature and light in that order. Blue green algae was found consistantly more abundant at shallow depths. Temperature and light were the most important factors influencing their standing crop.

In their studies of the experimental lakes region of northwestern Ontario, Stockner and Armstrong (1971) found that diatoms comprised between 60 and 90% of the epilithic assemblage of algae. The green and blue green fraction increased in importance in July and August, but several comprised over 40% of the volume of the total algal biomass. Seasonal periodicity was similar on both natural rock substrata and glass slides at 1 m. Mean organic content exhibited little seasonal variation.

The importance of temperature to periphyton biomass has already been mentioned in the study by Gruendling (1971) and Kyselowa and Kysela (1966). Steemann Nielsen and Jorgensen (1968b) investigated the chlorophyll biomass and temperature relationship in the laboratory. While chlorophyll biomass was considerably higher per cell at the lower temperatures, there was very little difference in photosynthetic rates. More protein was needed to merely maintain the normal cell functions at lower temperature. Brock (1967a) used chlorophyll anf RNA per unit area of algal mats in a thermal spring runoff to indicate standing crop. He found the thickest mats at 58 C and low standing crop at temperatures near the upper limit for algal growth. He also found low standing crops at temperatures below 50 C but this may have been due to animal grazing activity. He felt that primary productivity as affected directly by temperature was not the limiting factor for algal standing crop. His hypothesis was that the very high standing crops at relatively high tem-

peratures was due to unfavorable conditions for grazers and relatively favorable conditions for growth. McIntire (1968a,b) summed the sentiments of several authors as he concluded that normal variations in temperature probably had no direct effect on periphyton biomass. Total community breakdown and subsequent recolonization were noticed particularly during periods of rapid temperature changes or silt load changes.

Gurtz and Weiss (1972) reviewed responses of phytoplankton to thermal stress. Their conclusions substantiate the findings of the aforementioned authors. Reduction in algal numbers near a power plant discharge was dependent upon temperature and was found predominantly during summer months. They felt differences in composition of the algae was due to higher temperatures favoring groups such as the blue green algae.

The two algal components of a body of water are the plankton and the attached or periphyton group. Little attention has been given to the relationship these groups have to each other. Hickman (1971) compared the epipelon of two ponds of different trophic status using both standing crops and primary productivity. Algal groups other than diatoms were found to be insignificant because of the good correlation between chlorophyll a content and total diatom counts. He found that periods of increased standing crop of epipelon coincided with decreased phytoplankton standing crop as did Moss (1969).

Several authors have reviewed the literature for periphyton biomass comparisons. Nelson, Kevern, Wilhm and Griffith (1969) compared standing crops of stream periphyton. McConnell and Sigler (1959) found 25 $g\ m^{-2}$ of dry weight from rocks in the Logan River, Utah. McIntire et al. (1964) found 187 $g\ m^{-2}$ dry weight on rocks in a laboratory stream. Kobayasi (1961) found 2.5-7.0 $g\ m^{-2}$ dry weight of periphyton biomass on rocks in the Arakawa River, Japan. Cushing (1967) found 4.2 $g\ m^{-2}$ of dry weight periphyton and 1.8 $g\ m^{-2}$ ash-free

dry weight on glass slides incubated 14 days in the Columbia River, Washington. Drum (1963) reported 210 g m^{-2} ash-free dry weight of periphyton on flat rocks in the Des Moines River, Iowa. Kevern et al. found 12 g m^{-2} ash-free dry weight of periphyton colonized for 34 days on plexiglass in laboratory streams and 5.2 g m^{-2} on a 35 day exposure of plexiglass plates in a Tennessee spring. They found 15.6 g m^{-2} dry weight of periphyton and 3.0 g m^{-2} ash-free dry weight on glass slides in White Oak Creek, Tennessee. The same authors found 2.7 g m^{-2} of ash-free dry weight on the stream bottom at one place and 11.2 g m^{-2} ash-free dry weight at another in White Oak Creek. Stockner and Armstrong (1971) reported 0.68-1.25 mg organic matter cm^{-2} from Ontario lakes. Diatom counts ranged from 300,000 to 1,300,000 cm^{-2} on rock substrata in lake 240. They reported similar numbers in Lake Superior by Fox et al. (1969). They cited another study which found 5-7 X 10^6 cm^{-2} at the mouth of the Red River by Stockner and Evans (unpublished data). Allen (1971) reported some of the highest standing crops in the literature found in winter under the ice. Maximum Chlorophyll a values were 7.3 g m^{-2}.

While biomass is a useful measure of conditions at a particular time period, several authors have reported poor correlation between standing crop and photosynthesis. Brock (1967a) was one of those authors and he found primary productivity and standing crop correlated well only at higher and lower temperature ranges. At 41.6 and 48.3 C primary productivity was much higher than would be predicted from the chlorophyll a content. Already reported upon was the study by Steemann Nielsen and Jorgensen which inferred a poor correlation between chlorophyll and photosynthesis. A relatively recent study by Wetzel, Rich, Miller, and Allen (1972) also indicated that changes in attached algal biomass was not proportional to changes in photosynthetic activity, except during periods of intense growth.

Periphyton Primary Production

The following section is directed toward periphyton production. Many authors have addressed the subject either directly or indirectly. Included here are those deemed most pertinent to this study.

Several definitions of production have been used in a variety of ways. Wetzel (1964) defined production as the static product of biomass, usually without any reference to the processes involved. He differentiated it from production rate which was defined by Tansley (1929) as the rate of consumption, including that matter consumed in metabolism. Wetzel seemed to support the view of MacFayden (1948,1950) who stated that energy measurements should be defined as simply "productivity," leaving "production" and "yield" to signify food intake rates and the quantity of food accumulated by food groups or organisms. Westlake (1965) reported suitable terminology suggested by the International Biological Program. Primary production was defined as the weight of new organic material created by photosynthesis, or the energy which this represents. It is the increased observed in the biomass of green plants over a period, plus any losses (e.g., excretion, respiration, damage, death, or grazing). Margalef (1965) defined production of a derivative relative to time. Production is a function of the structure of the community in a mathematical sense. Accelerations and decelerations in the rate of production are reflected by a decrease or an increase, respectively, of the diversity of the community. Instantaneous growth rates were deemed a better estimate of productivity than average growth rate by Kevern, Wilhm, and Van Dyne (1966) in their studies of periphyton production. The instantaneous growth rate was taken during the linear growth phase following a colonization and lag period.

1. Ecological Factors Influencing Production

To understand ecological factors affecting production, a basic understanding of photosynthetic processes is mandatory. Gargas (1971) gave a simple explanation in which he divided photosynthesis into photochemical and enzymatic processes. The photochemical portion depends on light absorption by pigments. Rates of enzymatic processes depend on temperature and enzyme concentration. Algae are thus able to adapt to prevailing conditions of illumination and temperature by changing relative proportions of enzymes and pigments.

Many investigators have addressed themselves to ecological factors affecting periphyton production. A review slanted toward diatoms specifically by Patrick (1948) reported the importance of light or illumination as a growth factor. In addition to light, Brandt (1899) was cited as the first to demonstrate the importance of nutrients in diatom growth. The kind and abundance of nutrient salts were deemed very important to diatom growth. Patrick listed predation, excessive turbulence, intolerable accumulation of wastes, and epidemics of diseases in addition to light and nutrients as factors which may limit diatom growth.

Several other authors have investigated effects of more than one parameter on production. Phinney and McIntire (1966) studied effects of short term temperature variations on periphyton metabolism. Temperature increases from 11.9 to 20.0 C raised oxygen production from 335 to 447 mg O_2 m^{-2} hr^{-1} with light saturation. When light and CO_2 concentrations are not limiting, the rate of photosynthesis is increased by increased temperature, as are many chemical reactions. Periphyton photosynthesis was found to be dependent upon nutrients, floral composition and light (Neal, Patten, and DePoe, 1967). Their study of vertical distribution of periphyton lent support to the concept of photoinhibition at or near the surface. Within the zone of optimum illumi-

nation, warm water temperatures may decrease net production. The investigators felt that cooler zones would favor higher production because of the lower respiration rates. McIntire (1968b) commented that production at any one time of the year is regulated primarily by light intensity, current velocity, and the species composition of the community that develops with existing conditions. He reported light quality, carbon dioxide supply, temperature, and degree of circulation and mixing as the most important external factors found to influence photosynthesis (McIntire, 1968b). He also reported that changes in temperature within a physiologically tolerable range had little or no effect on photosynthetic rates when carbon dioxide was the rate-limiting factor. At light intensities below 500 ft.-c, temperature increases of 10 C had no significant effect on photosynthetic rates, but at light intensities above 1000 ft.-c the Q_{10} value varied between 1.3 and 1.6. In Marion Lake, British Columbia, gross epibenthic algal production was measured using oxygen evolution over undisturbed core samples (Hargraves, 1969). Production was directly related to temperature, light, and community respiration and inversely related to day length. Net production by epibenthic algae equaled 85% of gross production during the summer. Leach (1970) found seasonal epibenthic algal production in an intertidal mudflat was correlated with solar radiation, temperature, and standing crop of functional chlorophyll, but not with the amount of organic carbon. Production of epipelon in two small pond in north Somerest, UK, was compared by Hickman (1971). Production resulted from an interrelationship among light intensity, standing crop size and other viable environmental factors in both ponds, however light in Abbott's Pond appeared to be the most important factor in limiting production in lower depth categories. Where light conditions were similar, the more eutrophic nature of Abbott's Pond increased production. Elster (1965) found no strong correlation

between light intensity, water temperature and assimilation rates for lake phytoplankton. He postulated that the wavelength of light might be of greater importance than the quantity of light.

In addition to those studies involving several ecological parameters and their relation to production, several other studies concentrated on one factor affecting periphyton production. Odum (1956) stated that the production curve of a stream showed a seasonal trend which correlated with the course of sunlight. He concluded that light was the main cause of seasonal patterns in stream periphyton production. Illumination was determined to be the major variable affecting growth at various locations in a lake at fall overturn (Maciolek and Kennedy, 1962). Pamatmat (1968) also reported a high correlation between gross primary production of benthic algae on a tidal sand flat and incident radiation at all stations. In areas of good light penetration, such as the experimental lakes area of northwestern Ontario, attached algal production has been exhibited as deep as 10 meters (Stockner and Armstong, 1971).

Several authors have related periphyton production to illumination curves. In laboratory streams Phinney and McIntire (1965) found that curves relating illumination to periphyton production were characterized by approximately linear range from 100-200 foot candles, and a saturating intensity between 1000-2000 foot candles. Light intensity production curves for shade adapted communities exhibited a steep initial slope, a short linear range up to 100 foot candles and a long, gradual inflection from the linear segment toward the horizontal, and saturating intensity of slightly less than for the light-adapted community. Molecular carbon dioxide concentrations up to 45 mg l^{-1} enhanced production of light adapted communities at light saturation. Enhancement was not found in the shade-adapted communities. Gargas (1971) also

plotted photosynthesis as a function of light intensity and estimated the state of algal adaptation from it. The slope of the initial part of the curve was found to be a function of the photochemical part, while the light saturated rate represented the enzymatic maximum at the prevailing temperature. The light intensity where these two portions intersect was named I_k by Talling (1957) and has been used as a means of describing the physiological state of the algae. Gargas found no significant difference in the adaptation change between the psueudobenthic and the psammophytic algae. He stated that high resistance of benthic algae to strong illumination had previously been demonstrated (e.g. McMillan and Verduin, 1953; Odum, 1957; Pamatmat, 1968). Microbenthic algae were found more resistant to high light intensities than planktonic algae (Braarud, 1935; Burkholder et al., 1965). The previously mentioned studies by Steemann Nielsen and Hansen (1959) established light adaptation in algae at the cellular level. Their studies indicated a lack of correlation between light intensity and algal production within certain limits.

2. Nutrient Limitations of Primary Production

Nutrients of various types both inorganic and organic have stimulated algal production. Wetzel and Allen (1970) discussed interactions and functions of dissolved organic matter. They indicated that cycling and utilization rates of energy sources, e.g., organic matter, as well as nutritional factors of photosynthesis that are directly or indirectly coupled to the dynamics of organic matter in particulate and dissolved phases, are intimately related to these regulatory interactions. Organic matter in a lake is both labile and refractory compounds. Refractory compounds form 75% and are functionally insignificant. The labile compounds, on the other hand, are highly utilized and quickly turned over and are thus of major functional significance to the metabolism of the system. Epiphytic algae and microflora are able to utilize

CO_2 as well as dissolved organic carbon released from macrophytes. Epiphytic algae appeared able to compete effectively with sessile bacteria for the D.O.M. (dissolved organic matter) of the macrophytes within the muco-organocarbonate complex at rates significantly greater than those of the planktonic algae. An investigation of the organic matter budget of a central Texas reservoir by Lind (1971) indicated that reservoirs may tend to accumulate or utilize in some way within the reservoir excess allochthonous as well as autochthonous organic matter. These excess nutrient substances may act to stimulate algal production in reservoirs. Phytoplankton production in the same reservoir was limited by phosphate in the main body of the reservoir, but no nutrient limitations were detected at points of tributary inflow (Kimmel and Lind, 1972). The importance of $CaCO_3$ in inactivating and precipitating nutrients in marl lakes was noted by Wetzel (1972). No production increase was realized with additions of iron alone, due to the rapid precipitation. A combination of iron and chelating compounds enhanced phytoplankton production.

Ruttner (1953) called attention to the accelerating effect that flow has on community metabolism by increasing diffusion rates. Odum (1956) stated that this in turn increased production efficiency in stream periphyton. In lakes a very rapid renewal rate for water such as floods or vertical displacement by a tilted thermocline depressed production; but slowly upwelling water rather favors production by replenishing nutrient supplies (Findenegg, 1965a). In explanation he stated that flushing depopulates the lake and diminishes production for some time. Fresh water contains high amounts of phosphate and nitrates but may be devoid of organic compounds. Old water has large amounts of phosphorus and nitrogen in the form of suspended or dissolved organic matter. A continuous mineralization of these compounds replenishes old water uninterruptedly. McIntire (1966a) found initial attachment retar-

dation by current velocity of laboratory streams. After that, initial phase production was stimulated with increased current velocity. After a sufficient time organic matter accumulation was about equal. Sloughing and productivity were both greater in streams with higher velocity. Gargas (1972) felt that microalgal production in a shallow-water area in southern Denmark was depressed by ineffective water exchange in the fjord.

3. Other Variables Influencing Primary Production

Several other factors have been correlated with periphyton production changes. Inverse correlations between algal biomass and production per unit of weight and between plankton size and assimilation rates were reported by Findennegg (1965b). Foerster and Schlichting (1965) reported on the importance of substrata in algal production. Their data showed that Myriophyllum supported a much higher production than other plants in an oligotrophic Canadian lake. They proposed a hundred fold production increase if periphyton on logs and rocks was calculated. Hargraves (1970) found that natural densities of amphipods stimulated epibenthic algal production. Higher amphipod densities caused a decline in production.

Several investigators have differentiated periphyton into autotrophic and heterotrophic fractions. Thus segregating factors affecting the separate components. King and Ball (1966) used plexiglass slides to investigate aufwuchs production in the Red Cedar River, Michigan. They developed methods for separating the two components. The autorophic community was primarily diatoms and the heterotrophic fraction was composed of bacteria, fungi, and protozoans. Ball, Kevern and Linton (1969) reported remarkable uniformity in total aufwuchs production in grossly different environments. Greatest differences were found in relative contributions of various components of aufwuchs production. Surprisingly small heterotrophic production was found in one zone

and a surprisingly small contribution in a zone of abundant nutrients. Heterotrophic production was highest in the area receiving domestic wastes. Total production was highest in the reservoir, intermediate in a zone which received metal plating plant wastes and in a recovery zone from the domestic wastes and lowest in the farthest downstream station, an area of urban development. Hobbie (1965) described the competition between heterotrophic algae and bacteria for organic solutes in water. Two modes of uptake were recognizable. A transport system appeared to be utilized by bacteria which was very effective at substrate concentrations below 100 ug liter^{-1}. The algal uptake mode seemed to be simply diffusion kinetics and was effective only at higher substrate concentrations (above 500 ug liter^{-1}). In natural water the highly efficient bacteria kept substrate concentrations below 20 ug liter^{-1} and thus drastically limited algal heterotrophy.

4. Temperature Effects on Periphyton Production

The major focus of this study is effects of temperature on periphyton communities. In addition to those studies previously mentioned, the following studies have focused primarily on the effects of temperature on algal production. An ecological investigation of periphyton by Hargraves and Wood (1967) showed the closet correlation was between temperatyre and periphyton changes. The 15-20 C temperature range was a seemingly critical range in terms of growth. Gargas (1970) cited several works (Grontved, 1960; Steemann Nielsen, 1964) which indicated that benthic diatom production as well as plankton production in shallow areas closely followed the temperature curve. The phenomenon was caused by the accelerating influence of temperature on the liberation of nutrients as phosphates and nitrates from sediments, partly by bacterial activity and partly by a biochemical process. Mosser and Brock (1971) found the runoff from a thermal geyser to be a highly fluctuating habitat.

The geyser errupted only periodically. The attached algae experienced optimal production temperatures for only a small fraction of the time. The factor which favored the particular bluegreen algae found by Mosser and Brock was their tolerance to temperature fluctuations. In a series of experiments conducted on algae with similar optimal growth temperatures, it was discovered that the algae grown at non-fluctuating temperatures were more sensitive to temperature fluctuations.

To control the variables involved in ecological studies, many investigators have conducted closely controlled laboratory studies with temperature as the prime variable. McCombie (1960) found that specific growth of planktonic algae at any temperature within the growth range depended not only on the controlling effect of the temperature, but also the level of the limiting nutrients. Nutrient concentration limited growth at 200 ft-c illumination. Lyutova, Zavasskaya, Luknitskaya, and Feldman (1967) established the concept that higher cultivation temperatures led to greater cell resistance in algae. They concluded that the higher the incubation temperature, the more rapid the shift of heat resistance as evidenced by higher photosynthetic rates. Culture experiments with the filamentous green algae, Cladophora glomerata (L) Kutz. had maximum production rates between 15 and 30 C (Bellis, 1968). Effects of near lethal temperatures were dependent upon duration of exposure in addition to temperature attained. In his review of thermal pollution-biological effects, Coutant (1970) cited two laboratory investigation which will be noted in passing. The laboratory Chlorella study by Turkin and Mikryakova indicated that dry weight produced was independent of temperature at the test temperatures of 25, 32, and 39 C. Keller et al. found a strong dependence for algal growth in bacteria-free cultures with no salinity, but little dependence in other cultures of differing bacteria and salinity content. Another culture

experiment in which ten minute exposures to high temperatures (42 and 37 C) were used, found photosynthetic activity inhibited completely by the end of the ten minute period. The investigators concluded that the high temperature of effluents from power plants into the open sea should not cause great damage to marine phytoplankton (Hirayama and Hirano, 1970). Bieble and McRoy (1971) compared two forms of the marine phytoplanktonic algae, Zostera marina for production with varying salinity and temperature. Normal seawater salinity had maximum production with depressed production either zero or twice normal salinity. Production increased with temperature in the tidepool form up to 35 C, but only up to 30 C with the subtidal form. Higher temperatures produced a sharp decline in both forms.

One application of these laboratory studies and other ecologically oriented studies is the possible effects thermal effluents from power plants have on periphyton algae and other organisms of the community. Many investigators have addressed themselves to this purplexing and controversial topic as it was related to production. Tremblay (1960) found that chlorination of the cooling water from a power plant drastically limited periphyton growth in the immediate area and also may have stimulated blue-green algal growth below the power plant. Hatfield et al (1966) studied effects of hot water discharges from the Brunner Island Steam Electric Station on the Susquehanna River. Water temperature had the greatest effect on diatom growth. As temperatures increased above 90 F, diatom growth was progressively retarded. Churchill and Wojtalik (1969) reported on effects of heated power plant discharges at several power stations. On the Tennessee River at the Widow's Creek Station no consistant differences in periphyton growth on glass slides were observed in August to September 1967, above and below the discharge area. Periphyton growth was enhanced slightly in the heated discharge area of the Colbert

Stream Plant site on the Tennessee River during September 1967. At the Paradise Power Plant on the Green River periphyton growth rates were reduced in the plant vicinity in summer, but moderately stimulated in late fall and early winter during 1965-66. Cory and Nauman (1971) found that production of phytoplankton was unrelated to thermal discharge of a steam electric station located 6.5 km upstream of the Patuxent River Bridge, Maryland in 1968-9. A detectable temperature rise in the area was observable only during latter ebb tide.

5. Indirect Temperature Effects on Periphyton Production

Several ecological studies relating production to seasonal changes are closely related to any study of temperature effects. Seasonal changes are caused by changes in temperature and light. In his investigation of production of freshwater and saline lakes in Washington, Castenholz (1960a) used glass plates to determine periphyton production rates. He concluded that a bimodal production curve was evident in freshwater lakes with the spring peak being higher than the fall peak. Lowest production was in late summer. In the saline lakes the fall diatom pulse was at least as high as the highest pulse in the freshwater lakes and in addition a winter pulse reached a level twice that of the fall pulse. This very high production pulse was followed by a distinct spring pulse. Another variable which Castenholz considered was the partial selectivity against blue-green algae by the glass plates. He also reported widely different temperature-light values at the initiation of major diatom pulses even though some of the same species might have been involved. In summary he stated, "It may be seen that the seasonal fluctuations of overall diatom production curves is generally a function of the combined independent variations of several species." Round (1961) discussed growth patterns of benthic blue-green algae. He found a pronounced spring early summer growth

period. Ocassionally a fall growth period was also pbserved. The author felt that this autumn growth peak may have been linked with the decay of aquatic angiosperms. Growth maxima coincided with those of epipelic diatoms. Round suspected a direct relationship between nitrogen content and the Cyanophycean algal group. Talling (1965) reported diatom maxima which developed seasonally in both Lake Victoria and Lake Windermere. Production was higher in the tropical Lake Victoria probably due to temperature dependent photosynthetic rates at light saturation. Periphyton production on plexiglass plates in a warm-water stream was highest in June and lowest when the river was ice-covered. A sharp drop was observed in late August followed by a gradual increase (Grzenda and Ball, 1968). Gross primary production rates were highest in May and June in both years of a study by Stockner (1968). A negligable production was recorded during winter months in the run-off of the hot spring (37 C) studied. The author attributed significant differences in growth between years to harvest methods and autoinhibitory toxins produced by layers of senscent cells in the "natural" algal mat. Production studies in central Texas reservoir, Lake Waco, were completed by Kimmel and Lind (1972). They recorded phytoplankton production maxima in June, July, and August which corresponded with annual surface-water temperature maxima. Seasonal patterns of short term thermal stratification insterspersed with periods of mixing may have contributed to the high production levels.

In concluding this section some of the pertinent production values will be recorded. Castenholz (1960b) found maximum values for his freshwater lake of 500 mg biomass m^{-2} day^{-1} and as high as 1000 mg m^{-2} day^{-1} in a saline lake. In the Sedlice Reservoir Sladecek and Sladekova (1964) found a mean value of 158.7 mg dm^{-2} for 313 days and a mean net production rate for all four depths of 0.213g ash-free dry matter m^{-2} day^{-1}. Newcombe (1950) had mean periphyton

production values of 11.8 and 37.5 mg dry matter m^{-2} day^{-1}. Odum (1957) found 12,300 mg biomass m^{-2} day^{-1} in Silver Springs, Florida, the highest recorded periphyton production values. Assman found a net production rate of 128.8 g m^{-2} 150 $days^{-1}$ for periphyton. McConnell and Sigler(1959) estimated the annual gross production rate for the Logan River in Utah to equal to about 1.2 kg O_2 m^{-2}. Felfoldy (1961) listed hourly production rates for periphyton ranging grom 1.4-2.1 mg O_2 dm^{-2}. Working in laboratory streams Kevern and Ball (1965) recorded net periphyton production values which varied from 2815-5565 cal m^{-2} day^{-1} with efficiencies from 3.8-9.8%. Efficiencies for gross productivity varied from 6.4 to 16.6%. McIntire and Phinney (1965) found gross periphyton production values of 1.7-4.1 and 2.5-6.4 g O_2 m^{-2} day^{-1} for shade and light adapted communities, respectively. These were roughly equivalent to the least productive of flowing waters. Gross production for the same streams was estimated at 1.344 kg O_2 m^{-2} day^{-1} for light and shade adapted communities for 343 days. Efficiency of available light usage was 15.1 and 18.3% for light and dark grown communities respectively. Steele (1965) reported 10 g C m^{-2} $year^{-1}$ for sandy beach communities on the west coast of Scotland. By using a combination of methods in laboratory streams, Kevern, Wilhm, and Van Dyne (1966) assertained the periphyton growth rate as 0.51 g biomass m^{-2} day^{-1} and the average growth rate was 0.31 g m^{-2} day^{-1}. Average aufwuchs production for the entire Red Cedar River, Michigan, during summer months of 1961 was 281.18 mg organic matter m^{-2} day^{-1} (King and Ball, 1966). Autotrophic production was 212.8 mg of that total. Grzenda and Ball (1968) found mean production rates for periphyton in a warm-water stream ranging from 0.01-2.28 g ash-free dry weight m^{-2} day^{-1}. They calculated the weighted mean annual rate of net production from gravimetric estimates as 0.4 g m^{-2} day^{-1}. By using a conversion factor of 2 to convert

net production to gross production as suggested by Odum (1957) and Riley (1957), the weighted mean annual gross production rate of the Red Cedar River was approximately 0.8 g m^{-2} day^{-1}. Pamatmat reported gross annual production for a tidal sandflat in a range from 210-297 liters $O_2 m^{-2}$. By using chlorophyll estimates, a value of 333 liters O_2 m^{-2} was derived. He reported photosynthetic efficiency of only 0.10% of total incident radiation. Gross primary production for blue-green algae in a 37 C hot spring run-off in spring ranged from 5.8-11.3g O_2 m^{-2} day^{-1}. Net production was 1150g O_2 m^{-2} $year^{-1}$. Hargrave (1969) reported average gross epibenthic algal production in an intertidal mudflat by Leach (1970) yielded an annual production of 31 gC m^{-2}. Algal epiphytes on Scirpus and Najas-Chara dominated sites yielded total annual productions of 2.86 and 35.00 g C m^{-2}, respectively and mean daily productivity per unit area of the littoral zone for all the macrophytic surface area colonized was 195 and 1807 mg C m^{-2} day^{-1} in the Scirpus and Najas-Chara dominated sites, respectively (Allen, 1971). Average daily gross production of phytoplankton at the Patuxent River Bridge, Maryland in 1968 and 1969 was 5.2 and 6.1 g O_2 m^{-2} day^{-1}, respectively (Cory and Nauman, 1971). Periphyton growth in lakes of northwestern Ontario was 27 mg organic matter m^{-2} day^{-1} during initial colonization and 250 mg organic matter m^{-2} day^{-1} during maximum growth (Stockner and Armstrong, 1971). Average phytoplankton production in a Central Texas reservoir was 857 mg C m^{-2} day^{-1} or 390 mg C m^{-3} day^{-1} as reported by Kimmel and Lind (1972).

Primary production values which were listed as productivity in the literature are presented in the following prargraphs.

Average productivity was 0.56 mg C mg Chlorophyll a^{-1} hr^{-1} at one klux light intensity (Jorgensen, 1970). Wetzel recorded annual means of

phytoplankton, periphyton and macrophyte productivities as 249.3, 731.5, and 76.5 mg C m^{-2} day^{-1}, respectively. The total annual productivity resulted in 101.0, 75.5 and 1.36 kg C $lake^{-1}$ day^{-1} for phytoplankton, periphyton and macrophytes, respectively (Wetzel, 1964). ^{14}C productivity averaged 4.45 mg C m^{-2} day^{-1} for blue-green algae, 4.05 mg C m^{-2} day^{-1} for diatoms and 5.03 mg C m^{-2} day^{-1} for mixed flagellates and diatoms in a study of macroorganisms of the littoral zone of Long Island Sound (Burkholder, Repak, and Sibert, 1965). Lenn (MS, 1966) estimated blue-green algal productivity in Drakesbad Hot Springs, Mount Lassen National Park, California. He obtained summer values of 7-12 g C m^{-2} day^{-1}. Hargrave (1969) listed the following values from the literature for ^{14}C productivity studies in g C m^{-2} yr^{-1}:

Borax Lake periphyton	267	Wetzel (1964)
Borax Lake phytoplankton	91	Wetzel (1964)
Borax Lake macrophytes	28	Wetzel (1964)
Marion Lake phytoplankton	8	Efford (1967)
Marion Lake macrophytes	18	Davies (MS, 1968)
Intertidal marine sediments	115-178	Grontved (1962)

Flemer (1970) found that gross productivity in the Raritan River, New Jersey, at station I from May to September was 4.7 g O_2 m^{-2} day^{-1}, at station II it was 9.9 and at station III it was 11.6. He also calculated that the productivity of the attached algal microflora for the entire water column above 1.0 m^2 of benthic area on the calcareous bench averaged 0.962 g C assimilated m^{-2} day^{-1}. The lowest rate was 0.506 mg C m^{-2} day^{-1} under ice in February. Hickman (1961) calculated mean primary productivity for the epipelon of each pond at 5.29 and 1.71 mg C $hr.^{-1}$ m^{-2} for Abbott's Pond and Priddy Pool respectively.

6. Productivity

Wetzel (1965) stated that rates of periphyton growth, especially those in situ measurements of photosynthetic productivity, were far superior to

biomass estimated and calculated productivities. He cited a study of Bervald (1939) as probably the first quantitative estimate of epipelic periphyton productivity. This pioneering study was accomplished in an aquarium inverted over the sediments of small, shallow (0.4m), dystrophic Lake Piavochnoye. This preliminary study indicated a productivity which twice exceeded that of the plankton per square meter. Several others noted by Wetzel (1965) who pioneered periphyton productivity studies were Odum (1957); Park, Hood, and Odum (1958); Pomeroy (1959a, 1959b); Felfoldy (1961a, 1961b).

As early studies gave way to more sophisticated work from different parts of the world, discrepencies in terminology have emerged until there was a need to set forth acceptable definitions and standard units for the sake of comparison among the findings of several authors. The International Biological Programme has aimed to produce comparable biological parameters for the productivity of many different types of communities. Considerations have been given to facilitate comparisons of data which normally were not comparable because of different terminologies, units, criteria, or methods (Westlake, 1965). At that conference it was recommended that productivity should be given as metric tons of organic matter ha^{-1} $year^{-1}$ or g organic matter m^{-2} day^{-1}. Primary productivity was defined as the production, Q, divided by the period of time, T., i. e., the rate of production. Gross productivity was defined as the rate of production of new organic matter, or fixation of energy, including that subsequently used by the plant and lost as carbon diozide and heat; that is, the observed change in biomass plus all losses, including respiration, divided by the time interval. The net productivity was defined as the rate of accumulation of new organic matter, or stored energy; that is the observed change in biomass plus all losses except respiration, divided by the time interval.

Several authors have demonstrated the importance of periphyton to the total productivity of lakes, reservoirs and streams. Since many of the studies have already been referred to in previous section of this review, they will receive only passing consideration here. Allen (1971) found epiphytic algal communities to be among the most productive for both freshwater and marine environments. Gruendling (1971) noted that his data supported the idea that epipelic algal growth was high in shallow, low nutrient lakes and that productivity of this group was extremely important to the total energy budget of the lake. Burkholder, Repak, and Sibert (1965) determined the contributions of different algal groups to the total productivity of the littoral zone of Long Island Sound. They found that in the benthic photosynthetic communities, diatoms were an important group because of the large number of species and their significant contributions to primary productivity.

Several authors have compared the productivity of periphyton with the productivity of macrophytes and, phytoplankton in assessing the importance of periphyton to the system. Wetzel (1964) compared the three components of the littoral zone of a lake; namely phytoplankton, periphyton, and higher aquatic plants. He demonstrated the importance of macrophytes and periphyton to many lakes. Wetzel found the productivity of the periphyton of the large, shallow lake was greater than that of the phytoplankton. On an annual basis phytoplankton productivity was somewhat greater than that of the periphyton. This phenomenon resulted from a continuous although lower, phytoplanktonic growth during the later fall and winter periods of low light and temperature. In contrast, periphytic productivity was absent during these periods. Responce to more favorable conditions by the periphytic community was also slower than similar phytoplanktonic responses.

As with other measures of growth, many periphyton productivity studies are aimed at drawing correlations between some physical or chemical parameter and productivity values. Several other investigators have examined the relationship between periphyton productivity and another measure of productivity such as the standing crop of the periphytic community. Among physical and chemical factors affecting periphyton productivity, light or incident radiation is among the most important. Steemann Nielson (1960) generalized concerning the rate of dark fixation of $^{14}CO_2$ as a percentage of light saturated fixation. He felt that 1-3% was normal for experiments of a four hour duration. Higher percentages might be found in polluted water or when production rates were very low, particularly in samples collected at the lower photic zone boundary. In a study of attached marine diatoms along the coast of Norway, Castenholz (1967) concluded that in general, attached diatom productivity decreased with decreasing light in the autumn to January. In addition several investigators combined light and temperature in drawing conclusions from their productivity studies. Leach (1970) studied epibenthic algal populations in an intertidal mudflat in situ with ^{14}C. Significant correlations were drawn between light and temperature and the mean rate of ^{14}C fixation. Low light and temperature in winter were also the limiting factors for algal productivity in two diatom dominated ponds studied by Hickman (1971). Gruendling (1971) determined the most important variables influencing epipelic community primary productivity to be temperature, algal standing crop, and light. Taylor and Palmer (1963) used the ^{14}C method for measuring diatom productivity at Barnstable, Massachusettes. Maximum productivity was measured at a light intensity of 12 langlys hr^{-1}. The ratio of carbon fixed per biomass, measured by chlorophyll determinations, varied over a considerable range with variable light and number of organisms. Standing

crop was highly correlated to periphyton productivity in several investigations. At low light intensity productivity of Skeletonema costatum was distinctly correlated with chlorophyll a content per unit of cells (Jorgensen, 1970). Hickman (1971) examined two ponds of differing nutrient status and concluded that primary productivity corresponded closely with chlorophyll in the diatom dominated algal flora. Findenegg (1965b) concluded that the correlation between standing crop and productivity rates was not a static relationship but varied from lake to lake. He found that nannoplankton were more active in relative assimilation than larger species and also that increased population density diminished relative assimilation rates. The more favorable surface to volume ratio of the smaller cells facilitated uptake of nutrients. On the other hand a poor correlation between standing crop and ^{14}C primary productivity was determined by Brock (1967a). Allen (1971) used ^{14}C techniques to monitor macrophyte-epiphyte interactions in a small temperate lake. Changes in biomass were not proportional to changes in photosynthetic activity except during periods of intense productivity. The same conclusion was drawn by Wetzel, Rich, Miller and Allen (1972).

The major crux of my investigation was the relationship between the periphytic productivity and the temperature fluctuations found within a power plant discharge area. Other investigators have delved into this relationship between periphytic productivity and temperature variations caused naturally or by some source other than power plants. A small, but insignificant, increase in productivity in recirculating artificial streams was related to temperature in studies by Kevern and Ball (1965). Wariner and Brehmer (1966) conducted experiments to determine effects of thermal effluents on marine organisms. Included were some ^{14}C primary productivity studies which showed an enhancement of relative carbon assimilation rates with a 3 C temperature

rise but a decrease with larger temperature rises (more than 5.5 C). The heating of river water already above 15 C always depressed primary productivity significantly with temperature rises more than 5.5 C. At the maximum temperatues normally encountered in the river a 3.5 C temperature rise was sifficient to depress production. Brock (1967) investigated the algal productivity in the natural thermal gradient from a hot spring runoff. He detected no obvious nutrient depletion and thus concluded that productivity was probably not the factor limiting standing crop. In a study published in 1968, Lyford and Phinney investigated a unique aquatic ecosystem which developed in an impoundment constructed in a natural tidal estuary. Water control structures made it possible to control to a great degree the salinities present. In this situation the relationship of primary productivity to salinity was studied. Their findings reinforced the notion that the amount of energy fixed within stabilized shallow ecosystems is due primarily to the benthic communities. The saline environment accounted for the highest metabolic rates of the study. In a review, Patrick (1969) stated that in general, the effects of thermal discharges, if the temperature increase is in the range of tolerance of existing species and light and nutrients are sufficient, may be to increase productivity. Allen (1971) reported that uptake of carbon was stongly influenced by temperature, except at low temperatures where transport and diffusion mechanisms seemed to be inactivated.

Other factors affecting periphyton primary productivity include latitudinal differences, current velocity, surface to volume ratios in different algal species, different nutrient levels and the presence or absence of bacteria. Each of these have been addressed by at least one author. Talling (1965) addressed himself to the question of whether latitudinal differences produced differences in phytoplankton productivity. He concluded

that productivity was much higher during the diatom maximum in Lake Victoria than in Lake Windermere, due chiefly to high and probably temperature dependent rates of photosynthesis at light saturation per unit population (Pmax). Kevern and Ball (1965) recorded significant increases in net productivity in comparing riffle vs. pool communities. No significant difference was found between fast and slow streams. A study by Odum, Kuentzler, and Blunt (1958), which was among the first to use the isotope ^{32}P in productivity studies of benthic algae in sea water, indicated uptake rate and gross productivity were both proportional to the surface to volume ratio of the algal species involved. Thus higher surface-per-volume ratios increased the uptake rate as well as increased the ability of a given biomass of plant to fix energy under favorable conditions. In a periphyton productivity investigation undertaken by Williams and Mount (1965) to assess the effects of zinc on periphyton communities, they found productivity to be low with zinc additions for the first two week period. For the following two week incubation periods they recorded the lowest productivity for the highest zinc concentration producing 6 times as much respectively. Except for the time when there were high phytoplankton populations the autotrophic components dominated the periphyton on the glass slides. Productivity of epipelon in two nutrient dissimilar ponds reflected the richer nutrient status of the eutrophic Abbott's Pond compared with the oligotrophic Priddy Pool (Hickman, 1971). Allen (1971) reported that epiphytic algal uptake increased in the presence of bacteria, suggesting uptake of $^{14}CO_2$ previously respired by the bacteria.

II LITERATURE REVIEW

C. Methods

1. Community Structure

The following section is devoted to methods used by previous investigators to sample, identify, quantify or work up in some other manner periphyton communities. Several very good and complete reviews of methods for periphyton have already been compiled by Cooke (1956), Sladekova (1962), and Wetzel (1964). Portions of these reviews have been used in preparation of this section and are cited as such.

The first portion of this review deals specifically with periphyton community structure methods. It does not include diversity, which has been previously addressed.

Young (1945) reviewed early literature on sampling techniques for periphyton. Hentschel (1916, 1917) made limnological studies of periphyton on glass slides, in aquaria, and on floating marine plants. Wesenberg-Lund (1908) studied periphyton on beach stones. Willer (1920, 1923) studied periphyton on natural substrata which were living. Naumann (1925) investigated colonial algae attached to various substratum types. Other early investigations of periphyton noted by Young were Borner (1921), Brehm and Ruttner (1926), and Hentschel (1925).

Several authors have described methods for removing periphyton from natural substrates and using naturally occurring substrates as sites for periphyton colonization and growth. Margalef (1949) described a method for

periphyton removal from natural rock substrates using a colloidal film to cover the rocks. After the film was allowed to dry, it was peeled from the rock and mounted in suitable media. Douglas (1958) was one of the first investigators who used some sort of a brush to scrape periphyton from natural substrata. She sampled rock substrata using a brush inside a polyethylene bottle which was pressed against the rock surface. She used a brush inside a metal cylinder for larger rocks. McIntire (1968a) scrubbed the gravel incubated in artificial streams and homogenized the algae for species composition studies. Stockner and Armstrong (1971) sampled rocks of 10-20 cm size with a stiff nylon brush attached to the piston of a 50 cc disposable plastic syringe. Using this method they detected no discernable damage to algal cells. One investigation for taxonomic purposes utilized a simple rubber tube pushed along the mud-water interface, stopped at one end and poured into a collection vial (Round, 1960b). Other naturally occurring periphyton substrates include the stems and other parts of aquatic macrophytes. Young (1945) scraped live and dead bullrush culms of measured surface area for attached algae in Douglas Lake, Michigan. Foerster and Schlichting (1965) studied periphyton attached to Vallisneria americana, Myriophyllum farwellii, and Sagittaria sp. They loosened the algae from a cut section of the stem by agitation.

Many investigators have found it more convenient and practical to use one or more types of artificial substrates placed in the sampling area for the purpose of periphyton colonization. Glass microscope slides have been used far more than other substrate types because of their ready availability and easy examination. Cooke (1956) reviewed literature on the subject. He stated that Naumann (1916) was the first to introduce a foreign solid substrance onto which organisms could adhere. A paper by Heron-Allen (1930)

concerning the slide exposure method stated that he did not think it was an original idea. Hentschel (1916) used slides mounted in pontoons one or two meters below the surface. Lloyd (1930) described a technique where two cover glasses were tied together with string and suspended in a pool with their bottom edges touching the bottom. In 1930, Bissonnette described a device for collecting marine invertebrates. The device was described as a rectangular formation of wood with twenty saw cuts in the long sides designed to hold 20 3" x 1" slides. The two open sides were covered with 0.8 cm mesh zinc wire and one was hinged for ready access. This has been subsequently used in various modifications by several workers. Newcombe (1949, 1950) used a Bissonnette type sampler in Sodom Lake, Michigan and found that four slides should be adequate for study purposes.

Cooke (1956) told of several methods used specifically for diatoms. Wilson (1925) used a slide technique to study diatoms on the California coast. Clements made suggestions about the use of slides for community and successional studies of diatoms as early as 1905. Patrick, Hohn, and Wallace (1954) developed the Catherwood diatometer to collect stream diatoms. This device and modifications of it have been used in a number of studies. Trembley (1960) used a modified diatometer called a pralgometer above and below a power plant discharge. Cooke (1959) also noted that glass slides have been used in the study of fouling organisms and sewage organisms. Cooke (1956) concluded, "This summary indicated that glass slides and plates and other materials such as pieces of wood and cement blocks have been used to advantage as bare areas in the study of the initiation and development of communities of organisms which grow attached to surfaces of many types in aquatic environments as well as for the study of organisms occurring in the soil. ... It is apparent that the techniques are highly adaptable, and

that from them can be gained information concerning types of organisms capable of adhering to a surface, their quality, density, rate of development, succession of communities and the component members of communities in aquatic environments."

Subsequent to Cooke's summary, glass substrates have been used in a variety of ways. Castenholz (1960a) reported that 75-85% of the naturally occurring species and 95% of the species that had either or more specimens on the slides were found on 2 to 4 week slides. Castenholz (1960a) also reported on comparison of horizontal and vertical surfaces. He found differences in the percent ash on materials from the top of horizontally placed slides in comparison to material taken from the slide bottoms. He concluded that replicate plates were not necessary with a single plate reliable within 25%.

Sladekova (1962) reviewed periphyton methods and also stated that glass was the most common artificial substrate. She noted that in most comparisons of substrata the differences in periphyton composition have been negligable. In the majority of cases only the total periphyton quantity varied. Sladekova stated, "Where exact examination of these organisms is needed, the only practicabel plates are those made of glass and transparent plastics. Periphyton grown on their surfaces can be observed in an undamaged state in its natural position directly under the microscope." She credited Hentschel (1916) as the first to use glass slides and other artifical substrates for qualitative and quantitative determination of periphyton and then went on to describe devices designed by several authors for the suspension of glass slides in water. These included Geitler (1927), Butcher (1928-1949), Hentschel (1916, 1925), Wysocka (1952, 1957a, 1957b, 1959), Welch (1948), Brown and McDaniel (1952), Burbanck and Allen (1947), Newcombe (1949, 1950),

Yount (1956), Godward (1937), Smaragdova (1937) and Budde (1942).

Wetzel (1964) cited several of the studies already noted and commented on the use of glass slides as follows: "The immersion of glass plates for varying periods of time, with very little modification from the original methods of Hentschel (1916) is a generally common technique of quantitatively estimating dominant groups of periphyton and succession rates of colonization." He also cited the study by Butcher (1949) who used glass slides for 15 years to study river conditions, especially relating the distribution of periphyton algae to the degree of eutrophication and to seasonal variations in meteorology and current. Wetzel felt glass was at least partly selective for diatoms and could introduce grazing problems but concluded that within the limitations of the technique, the glass slide technique provides a meaningful tool for the estimation of standing crop of a majority of the periphyton organisms (Castenholz, 1961).

Williams and Mount (1965), who studied influences of zinc on periphyton, cited a study by Hohn and Hellerman (1963) that compared diatoms growing on glass and styrofoam substrates. They concluded that styrofoam supported a diatom sample regardless of temperature or current velocity, while glass was less reliable at relatively low temperatures and fast current. Glass was, however, reported to be as good as styrofoam at summer temperatures and comparatively slow current velocities. Williams and Mount further commented that the glass slide technique affords a method of starting with a clean substrate each week to sample the development and compositon of the periphyton communities at many different periods. Furthermore, this technique allows a comparison of short-term development on glass slides with the relative long-term accumulative changes on the submerged walls of the canals.

Artificial substrates have been used to monitor a variety of ecological conditions as well as population dynamics. Several examples have been cited in the following portion of this review. Hatfield et al. (1966) used glass microscope slides to monitor diatom numbers at 10 stations above and below the Brunner Island Stream Electric Station. Castenholz (1967) examined the species complement on the coast of Norway using submerged glass substrates and found that the results using slides divided the species complement into "winter-early spring", "spring", "summer" and "year-round" types. Patrick, Roberts and Davis (1968) and Patrick (1969) used diatometers to monitor diatom population dynamics. Dillard (1969) used glass slides in a North Carolina stream, and stated that glass slides were used for simplicity and repeatability. He found slides to provide a good measurement technique for comparative purposes. Flemer (1970) used slides and cement blocks as artifical substrates in the Raritan River, New Jersey. After two weeks of exposure, total number and relative abundance of periphyton organisms were determined. Kawecka (1970) used glass slides as well as styrofoam bricks to collect attached algal forms in five Polish lakes. Slides were transported to the laboratory and the styrofoam was scraped. She found algae more abundant on the styrofoam. McIntire and Overton (1971) noted that presumably, the colonization of a clean substrate is some kind of a short-term successional process that probably begins with a bacterial film and is followed by a more or less predictable sequence of invasions by diatoms and other micro-organisms, the exact nature of which depends on the season and the location of the substrate in the estuary. They used glass substrates to determine diatom assemblages in Yaquina Estuary, Oregon. Lanza and Cairns (1972) used glass slides in determining physiomorphological effects of abrupt thermal stress on diatoms. One portion of this study was to use diatometers with glass slides

colonized 7-21 days. These slides were brought to the lab, maintained in continuous flow cultures and then exposed to thermal stresses.

In addition to glass slides, several other forms of artificial substrates have been used in determining community structure in periphyton communities. Styrofoam, as previously mentioned, has been used by at least two investigators. Hohn and Hellerman (1963) and Kawecka (1970) both compared styrofoam with glass as substrates for periphyton. Their findings were similar, indicating styrofoam was superior for supporting representative diatom samples regardless of temperature and current velocity, while glass was as good under specific conditons of relatively slow current velocity and summer temperatures.

Three more types of artificial substrates used in periphyton studies to determine community structure include parafin (Beers and Neuhold, 1968), cement blocks (Flemer, 1970) and plexiglass (Lanza and Cairns, 1972). The parafin method was advantageous in that it made possible the removal of different portions of the surface and its attached biota without special instruments. The cement blocks were more like a natural substrate than glass. The plexiglass trough was used in a laboratory stream situation.

Once the method for collection of periphyton has been determined, the representative samples must be examined. Again several methods have been devised for examination and counting of periphyton. The two major devices for examination are the conventional compound microscope and the inverted scope. At least one author has used the inverted microscope. Knudson (1957) used the inverted microscope to determine population densities of one species of diatom attached to macrophyte stems.

Among the investigators who have used a conventional compound microscope to examine periphyton collections, several have counted the organisms while

they remain attached to the slides and other have first scraped the periphyton from the slides. Sladekova (1962) stated that periphyton grown on transparent glass or plastic plates is usually examined and counted directly under the microscope. The whole or a portion of the slides may be examined. The portion counted is usually delimited by a certain number of fields of view, selected systematically or at random. She also noted that the majority of periphytic organisms fall off the substratum after preservation, others become completely damaged. Therefore, the examination of periphyton samples in a living state is extremely important, especially when precise quantitative analyses are needed. Sladecek and Sladekova (1964) marked an area of 13 cm^2 on each side of each slide. Material outside the marked areas was scraped off and the slides were transported in an empty wide-mouth jar to the field laboratory. Williams and Mount (1965) counted 3 horizontal strips on each slide comprising 118,800 mm^2 for each proportional census.

Investigators have used various means of scraping periphyton from slides and remounting it for examination. Young (1945) pulled apart the fibrous mass of periphyton scraped off the culms. Diatoms and other small organisms were counted in a Sedgwick-Rafter counting cell, using low power. Diatoms and desmids were counted in square units of one cubic millimeter each. Counts were made from bottom sediment organisms collected to a depth of 3 to 4 mm on Long Island Sound (Burkholder et al., 1965). Williams (1964) counted 250-300 individuals per sample of plankton diatoms using Hyrax mounts to determine the dominants. McIntire (1968a) scrubbed the attached algae from rocks in the bottom of artifical laboratory streams and homogenized the samples. One set of samples was cleaned and Hyrax mounts were made and others were examined as wet mounts for identification purposes. Other wet mounts were made in the same manner but the cover glasses were sealed

with parafin oil. Sager and Hasler (1969) used a method slightly modified from McNabb (1960) where plankton were enumerated by filtering through a membrane filter and then clearing the gridded membrane filter for enumeration. Flemer (1970) scraped glass slides and policed them with a rubber probe. Hyrax mounts were made for diatom identifications. Diatoms were prepared on permanent mounts by Stockner and Armstrong (1971).

In addition to the direct methods of counting the community constituents, several indirect methods were used. McIntire, Tinsley and Lowry (1969) measured the fatty acid spectra of 6 periphyton communities without any appreciable correlation between some of the fatty acids and community structure. The use of proportions of myristic, palmitoleic, oleic, linoleic and linolenic acid were, however, closely related to taxonomic differences. Wulff and McIntire (1972) used a laboratory model ecosystem to study changes in community structure of attached diatoms at different light, temperature and salinity.

2. Photosynthetic Response to Abrupt Thermal Stress

a. Biomass

Methods for community function include methods for determining biomass, primary production, and productivity. Two major methods for determining periphyton biomass include using artifical substrates by weighing accumulated biomass and, more recently, pigment analysis. Newcombe (1949) reported using glass slides to measure biomass. He stated, "It seems reasonable, therefore, to consider a more direct potential index of productivity; namely, the actual amount of organic substance produced on a uniform substratum per unit area of surface per unit of time." He suggested a 25-day incubation period. Sladekova (1962), in her review of the literature, related several quantitative mass methods. Volume, wet weight, dry weught, ash-free, standard

amount of nitrogen in the sample and pigment extractions were mentioned. Sladekova concluded that glass is the most common of the artifical substrates. She cited several methods for suspending slides which were mentioned previously in this section. Sladecek and Sladekova (1964) used glass slides for determining periphyton mass and production in the Sedlice Reservoir. Sladececk and Sladekova also cited several studies using glass slides for determining periphyton biomass. In addition to the study of Newcombe previously mentioned. Assman (1951, 1953) used glass slides to determine periphyton biomass and turnover rates. Odum (1957) determined periphyton biomass by using a combination of glass slide colonization and chlorophyll content in Silver Springs, Florida. Castenholz (1960, 1961) was cited as having used glass slides in the Lower Grand Coulee, Washington. He presented his data as ash-free dry weight. Waters (1961) used concrete cylinders as substrata for periphyton on which he subsequently determined mass chlorophyll content. The Chlorophyll a content per substrate increased to 200% between the 2nd and 4th week and remained essentially unchanged for another 6 weeks. Other experiments of this nature carried out by Waters showed 3 and 8 weeks of exposure, in separate experiments, necessary to reach a relatively constant community. He concluded from these experiments that 3-8 weeks were necessary for colonization depending on the prevailing environmental conditions at the time. Sladecek and Sladekova (1964) used a series of corks with glass glides suspended at different depths. They removed one slide at 4-6 week intervals from each depth. The slides had a given area marked off and periphyton outside that area were scraped off. The slides were dried at room temperature for 3-5 hours, weighed, then dried at 105 C for 2-3 hours, cooled in a desiccator and reweighed. Very small differences were found between the two weights and they concluded that it was unnecessary to

dry at 105 C if the samples had been air-dried.

Wetzel (1964) cited Castenholz when he spoke of using glass slides. He said, "However, within the limitations of the technique, the glass slide technique provides a meaningful tool for the estimation of standing crop of a majority of the periphytic organisms (Castenholz, 1961)." Rabe (1965) used the glass slide techniques to determine the organic content of periphyton. Wetzel (1965) reviewed techniques and problems of periphyton quantification. He cited two major problems with using glass slides. Firstly, in a great majority of the studies on periphyton, the substrata are suspended in the pelagic regions of standing bodies of water or the main flow areas in lotic situations. Natural periphytic substrates are primarily benthic and macrophytic in nature. Only rarely are natural substrata studied or are artificial substrata placed in an ecologically realistic position (e.g., Castengolz 1960a, 1960b). The other major difficulty lies with the rate of population turnover, since the rates of turnover vary markedly with several factors such as season, extent of colonization of the substrate, type and position of the substrate, environmental parameters and other factors.

Neal, Patten, and Depoe (1967) suspended polyethylene tape vertically for up to 9 weeks in a radioactively contaminated lake. After 2 weeks periphyton biomass colonization was nearly complete on the upper tape sections but the deeper sections took longer for complete colonization. They cited a study by Butcher (1946) who indicated that biomass development on glass slides was generally complete by 20 days, except in winter.

McIntire (1968a) used laboratory streams with gravel. The gravel was scrubbed and the periphyton was dried at 70 C. The biomass was expressed as grams per square meter. Ball, Kevern and Linton (1969) used the methods of Grzenda and Brehmer (1960) with some slight modifications. It involved use

of both vertical and horizontal plexiglass plates with their long axis parallel to the direction of flow and at 0.6 of the depth of the stream. Upon removal from the stream, samples were placed in plastic bags and frozen after return to the laboratory. They determined biomass both on the basis of pigment extracts and then drying at 55 C, weighing, combusting at 550 C and then reweighing. Churchill and Wojtalik (1969) reported on use of glass slides to determine differences in growth of periphyton between stations above and below the thermal discharge of the Widows Creek Station on the Tennessee River. The same method was used for the Colbert Steam Plant (Tennessee River) and at the Paradise Power Plant (Green River). Cooper and Wilhm (1970) used artificial substrates and reported biomass as ash-free dry weight. They determined 4 weeks to be the optimal colonization period.

Szczepanska (1970) cited a study by Pieczynska and Spodniewska (1963) who concluded from their work with artifical substrates that when different substrata are located at one place in a reservoir then the occurrence of periphyton organisms is similar (species composition, dominance structure, abundance). The existing differences, even considerable ones, do not distinguish a certain substratum or group of substrates (e.g. live, dead or experimentally introduced into the reservoir) and are of the same order as the differentiations in time and space observed on one kind of substratum. Considerable differences of periphyton were, however, observed on the same substrata from different lakes or even places within one lake. On the other hand Szczepanska (1970) also cited Rehbronn (1937) who found the existence of an obvious dependence of periphyton on the kind of substratum, especially in initial colonization stages. Szczepanski and Szczepanska (1966) found that the initial 14-day colonization period in periphyton development is

followed by a four week period of stabilization. This allowed the authors to compare periphyton samples from artificial substrata having an exposure time of 2-6 weeks.

Allen (1971) pointed out some shortcomings of using artificial substrates. He concluded that much of the productivity work using artificial substrata was of little relevance in determining the importance of in situ metabolism by attached communities. This might be especially true when slides or other substrata have been suspended in reservoirs and deeper waters, since attachment during prolonged stratification might yield periphytic communities which are representative of natural plankton. In order to overcome difficulties involved with contamination of periphyton by parts of the macrophyte stems previously used as substrata, he used artificial substrates.

Stockner and Armstrong (1971) obtained samples from natural rocks with a stiff nylon brush attached to a piston and also used glass slides placed at 1 m depth on a rock shelf. After preservation material was filtered on a preweighed millipore filter (0.45 μ), oven dried at 105 C and weighed. A duplicate was treated the same but combusted at 500 C to get organic matter.

The other frequently used method of determining periphyton biomass, pigment extraction, has come into broad usage in recent investigations. Castenholz used the absorbance of a methanol extract at 665 nm to estimate the standing crop of Achnanthes sp. Samples were frozen with no observable effects. Absolute menthanol with 0.5% dimethylamiline was used as the solvent (Strain and Manning, 1942). Samples were extracted for 24-30 hours in darkness. He determined a chlorophyll absorbance value of 1.0 to be equal to about 30 mg of diatom "organic matter". Sladekova (1962) cited a study by Kurasawa (1959) who measured pigments of algae attached to tile

plates. She also cited McConnel and Sigler (1959) who used artificial as well as natural substrates in a river to determine chlorophyll concentrations. Grzenda and Brehmer proposed that chlorophyll-extraction methods were the most convenient quantitative method for determining periphyton in streams. Wetzel (1963) criticized estimates of littoral periphyton standing crop using pigment analyses because of the interference of the absorption spectra of chlorophyll degradation products. Sladecek and Sladekova (1964) cited Yount (1956) who determined the chlorophyll content of periphyton on glass slides from Silver Springs, Florida. Odum (1957) also noted by Sladecek and Sladekova, determined chlorophyll for Silver Springs, Florida. They cited yet another chlorophyll study by Jorgensen (1957) who counted diatoms and measured chlorophyll in periphyton on Phragmites sp. stems in two Danish lakes. Another study cited in this work was Margalef (1960) who worked on pigment extractions on benthic plants in a natural park in Spain. Papers by Grzenda and Brehmer (1960), who used plexiglass plates in the Red Cedar River, Michigan, in determination of pigments and Felfoldy (1961a) who determined pigment, nitrogen and dry matter of natural diatom communities under laboratory conditions were also reviewed by Sladecek and Sladekova (1964). A study by Waters (1961) was mentioned in which concrete cylinders were placed in Valley Creek, Minnesota, as substrates to be used for periphyton colonization and subsequent pigment analysis.

Burkholder et al. (1965) determined chlorophyll of Long Island Sound littoral organisms by taking 100-300 mg of wet substrate and suspending in 10 ml of 90% acetone in screw-cap centrifuge tubes. A small amount of $MgCO_3$ was added to each tube and extraction was accomplished for 24-hours in a refrigerator at 10 C. Chlorophyll was determined using the methods of

Creitz and Richards (1955) and the formula of Parsons and Strickland (1963). Results were calculated as mg Chlorophyll a kg of wet mud^{-1}. He concluded that although the ratio of carbon fixed $chlorophyll^{-1}$ appears to vary over a considerable range in different kinds of organisms under conditions of light saturation, nevertheless the Chlorophyll a content of planktonic and benthonic communities has considerable significance. In response to criticism of chlorophyll degradation products, he believed that extraction of living flora in sand and in the upper thin layer of euglenoid and diatom mixtures on the mud surface yielded chiefly cellular pigments.

Wetzel (1965) cited several studies in which measures of biomass such as chlorophyll were poorly correlated with photosynthetic rates. He stated that similar findings between chlorophyll biomass and in situ production rates were evident in epilithic periphyton populations (Wetzel, 1963). The importance of estimating "functional chlorophyll" is emphasized (Wetzel, 1964).

King and Ball (1966) employed an expansion of the technique used by Garzenda and Brehmer (1960) in which phytopigment extracts were taken from material which colonized plexiglass plates. Samples were frozen to aid in rupturing of cells and then scraped from substrates and rinsed with 95% ethanol. Extraction was carried out for 48 hours. Grzenda and Brehmer (1950) found that samples could be stored for at least 30 days without decompositon of phytopigment.

Brock (1967a) and Brock and Brock (1967) determined the chlorophyll content of algal mat cores from the thermal spring effluents. The cores were removed from the algal mat with a #3 brass cork borer and homogenized. The homogenate was centrifuged, and supernatent discarded, the pellet again homogenized in 100% acetone and the absorbance measured at 665 nm using a

Spectronic 20 with a red filter. He used the equation of Odom, McConnell and Abbott (1958) to estimate Chlorophyll a.

Castenholz (1967) did pigment analyses on attached algal samples from the coast of Norway by extracting dry material with methanol and using 665, 645, 630 and 477 nm as the wavelengths measured. Beers and Neuhold (1968) reported on use of paraffin-coated substrates for use with periphyton in running waters. The paraffin was placed in widemouth bottles filled with acetone and stored. The acetone-water-acetone extraction procedure of McConnell and Sigler (1959) was used with two additions: filtration of the acetone-paraffin mixture through Nitex cloth after extraction to remove larger particles and then clearing of the filtrate of smaller particles by centrifugation. The revised equations of Strickland and Parsons (1965) were used to calculate quantities of Chlorophyll a.

McIntire (1968a) in one of his studies using laboratory streams, scrubbed gravel from pans on the bottom of the streams and then homogenized the samples. He used a portion of the samples for pigment analysis. Allen (1971) used methods outlined by Strickland and Parson (1965) to analyse algal samples taken from macrophyte stems. The macrophyte stems were sampled with a cork borer, samples were removed from the macrophytic disks with small pads of precombusted flass-fiber ultrafilters and then analyzed for chlorophyll.

Hickman (1971) stated that the tissue trapping technique of Eaton and Moss (1966) has enabled quantitative measurements of epipelic algal standing crops to be made, either indirectly through cell counts or directly through Chlorophyll a content, since the spectrophotometric methods of Moss (1967 a, b) correct for the amount of Phaeophytin a present. Hickman continued to say that this technique has been used to measure the standing crops of the

epipelon in a wide range of field conditions.

In addition to the two most common methods for estimating periphyton biomass, several other methods have been used in a limited capacity. Nelson, Kevern, Wilhm and Griffith (1969) described a rapid method for determining periphyton biomass on the bottom of a small rocky stream using ^{32}P. ^{32}P was released in a small section of stream in a known quantity. Activity of the water after passing over a section of stream was measured for both the particulate and dissolved fractions. Periphyton from both natural and artificial substrates which had been incubated at the site of ^{32}P release for 35 days prior were also measured for mass and radioactivity. The standing crop was calculated using the following:

$$\frac{Pr\ (dis\ min^{-1})}{Pw\ (dis\ min^{-1}\ mg^{-1})} = \text{standing crop of periphyton in stream section (mg),}$$

where Pw is the activity (unit wt in periphyton on natural or artificial substrates. Also,

$$\frac{Pr\ (dis\ min^{-1})}{Pa\ (dis\ min^{-1}\ cm^{-2})} = \text{total bottom area } (cm^2), \text{ where Pa is activity/unit area of periphyton.}$$

Evans and McGill (1970) used a Model A Industrial Coulter Counter for determining the biomass of freshwater phytoplankton and which might be applied to periphyton suspended in solution. When correlated with other parallel determinations, good agreement was found. They concluded that for unialgal samples the Coulter counter does not necessarily give a quicker result than other methods. However, for at least two reasons the Coulter counter adds a most useful new dimension to the realm of plankton analysis. For assemblages of algae whether or not certain species are dominant or co-dominant a more rapid determination of a result which can be taken to represent the biomass is possible than by other methods. Such results,

expressed as total particulate volume (T.P.V.) can be accepted as accurate as those obtained by any other method and are probably better than some.

Armstrong, Goldman and Fugita (1971) measured microgram amounts of organic carbon in seston and periphyton using an infrared analyser after combustion with an induction furnace. Replicates gave results within 3% for seston and 20% for periphyton.

B. Primary Production

Production of periphyton has also been measured using a number of different methods, the most widely used involving changes in oxygen concentrations and use of artificial substrates in calculation of production from biomass estimates. Newcombe (1949) used artificial substrates with 20 to 30 day attachment times. He used this as an index of production when considered through time. Castenholz (1960a) satisfactorily used a glass plate method to quantify periphyton changes. He used a 2-4 week incubation period at various depths. Sladecek and Sladekova (1964) reported their mass determinations on glass slides at different depths in the Sedlice Reservoir as production through time. They used a 4-6 week interval for incubation. Kevern, Wilhm and VanDyne (1966) used increasing exposure times with plexiglass plates to calculate instantaneous growth rates of periphyton. A growth curve was constructed at 2-4 day intervals from which the instantaneous production was calculated. King and Ball (1966) also measured aufwuchs production in a stream from accrual on plexiglass plates. They separated autotrophic and heterotrophic production of aufwuchs and utilized six different exposure periods of 3, 6, 9, 12, 15 and 18 days. Castenholz (1967) made estimates of diatom production using submerged glass substrates at different depths along the coast of Norway. Differences in light, temperature and salinity were correlated with production. Grzenda and Ball (1968)

used plexiglass plates in a warm water stream and then scraped the periphyton from the substrates and made gravimetric estimates of net primary production.

Sladecek and Sladekova (1964) cited at least one study in which light and dark oxygen changes were used to estimate periphyton production. McConnell and Sigler (1959) used light and dark jar experiments to measure gross production of periphyton. Wetzel (1965) cited a study by Pomeroy (1959a, 1959b) who estimated photosynthetic rates of salt marsh algae by light and dark bell jar methods. Pamatmat (1968) studied production on an intertidal sand flat using light and dark bell jars in situ.

Oxygen changes in running water have also been monitored as a method for estimating periphyton production using a method commonly called the upstream-downstream oxygen method. Kevern and Ball (1965) used several methods including upstream-downstream oxygen method described by Odum (1956) to determine periphyton production in artificial streams. The authors were unsuccessful in finding K for diffusion corrections and had to rely on values given by Odum (1956). Stockner (1968) estimated primary production in thermal spring runoffs by monitoring O_2 changes through time at the end of a trough which was inserted into the stream runoff. Both the standard Winkler method with the Pomeroy-Kirschman alkali reagent and an oxygen electrode designed by Kanwisher were used to determine oxygen levels.

Several other methods have been used by investigators in determination of periphyton production. Felfoldy (1961a) was cited by Sladecek and Sladekova (1964) as having used manometric techniques to determine periphyton production. Wetzel (1965) cited a study by Bervald (1939) in which changes in oxygen concentrations were monitored in glass aquaria inverted over the sediments in small, shallow (0.4m) dystrophic Lake Piavochnoye. Hargrave

(1969) measured gross epibenthic algal production in Marion Lake, British Columbia, by following changes in dissolved oxygen over undisturbed sediment cores. Gruendling (1971) used the methods proposed by Hargrave just mentioned.

C. Productivity

Several investigators have referred to certain types of primary production methods as productivity. Productivity measurements have been made more and more commonly in recent studies both with and without isotopes. Kobayasi (1961b) removed sessile macroalgae by hand homogenized and suspended this material in bottles of river water and estimated productivity by the standard light and dark bottle oxygen technique.

Included in the studies using isotopes in measurement of primary productivity are several which were not specific about their technique except that radioactive isotopes were used. Jorgensen and Steemann Nielsen (1965) used ^{14}C in adaptation experiments involving temperature changes. Steele (1965) estimated organic carbon production using ^{14}C on the sublittoral benthic community of a sandy beach. Goldman (1968) warned other investigators specifically against the use of barium carbonate labelled with ^{14}C in calibration of Geiger Muller counting equipment. He concluded that since the radioactivity of algae rather than barium carbonate is being measured, algae are the best radioactive source for determining the efficiency of GM counting. He stated that the absolute activity of any particular thickness of filtered algae as well as that of ^{14}C label could be accurately determined in gas phase. Pugh (1970) reviewed recent literature dealing with liquid scintillation counting of radioactive productivity samples. He cited increased interest since the paper by Wolfe and Schelske (1967). For calibration, Wolfe and Schelske utilized an internal standard which did not take

fully into account the self-absorption. Lind and Campbell (1969) have added information on calibration techniques. Wallen and Green (1968) also concluded that self absorption had no significant effect on counting efficiency. They used a wet membrane filter and dissolved it in a fluor solution of ethylene glycol monomethyl ether. Schindler (1966), who also dissolved membrane filters using a napthalene fluor, joined Wallen and Green in determining counting efficiences by adding a ^{14}C internal standard. Lind and Campbell used an external standard method which, according to Pugh, can only properly be used to determine the degree of quenching within a homogenous fluor and should not be applied to heterogeneous ones. Pugh concluded that the only reliable method for determining the counting efficiencies of this material is by a channel ratio to counting efficiency method which is markedly different from that for homogeneous solutions. Hickman (1971) measured the primary productivity of the epipelon in two small ponds in North Somerset, U. K., using a ^{14}C method devised by Hickman (1969) and activity was determined with a Nuclear-Chicago D-47, thin window, gas flow counter to 5000 counts. Mosser and Brock (1971) used a ^{14}C bicarbonate method for measuring productivity of blue-green algae of Bead Geyser Yellowstone National Park. A study of counting techniques by Ward and Nakanish: (1971) led them to conclude that most of the differences in counting wet liquid scintillation as opposed to desiccated Geiger-Mueller seems to be in the drying. They stated that desiccation should not be used, but rather a dioxane based fluor which will absorb water and dissolve the filter. Wood (1971) examined self-absorption corrections for ^{14}C studies using $BaCO_3$ for primary productivity measurements. He stated that self absorption of ^{14}C beta radiation is shown to follow an exponential relationship under certain conditions. In the modification presented by Wood, it is possible to determine primary

productivity without using the efficiency of the detector in calculations.

Studies specifically using light and dark bottle radioisotope methods are presented in the following paragraphs. Odum, Kuentzler and Blunt (1958) used ^{32}P in light and dark bottle experiments with marine benthic algae. Light and dark bottles containing seven species of large intertidal benthic algae were measured simultaneously in a running seawater aquarium under constand light and temperature.

Wetzel (1964) cited a study by Goldman, Mason and Wood (unpublished manuscript) in which ^{14}C was used as a tracer in net productivity estimates of an algal mat from Antartic ponds. Wetzel noted a possible error in use of bottles because of the lack of current which might cause an underestimate of productivity (Whitford, 1960).

Studies of littoral micro-algae on Long Island Sound by Burkholder, Repak and Sibert (1965) utilized ^{14}C in estimation of productivity. Sand with associated diatoms or flagellates would be weighed wet and then placed in seawater. By gentle agitation and employing several changes of water, the micro-algae were washed out of the sand to obtain a clean suspension. Two-hundred ml of the suspension was dispensed into clear and dark glass stoppered bottles and 1 ml of isotopic $Na_2{}^{14}CO_2$ was pipetted into each bottle. Samples were then incubated in a fluouescent light incubator. Samples were incubated for 5 hours. Methods used by Strickland and Parsons (1960) were employed in filtering through Millipore filters. Small volumes of 10 to 200 ml of each sample were filtered to reduce the self absorption. When mud or larger pads of filametous micro-algae were used in the studies, the samples were assayed by Schoniger oxygen flask combustion and liquid scintillation counting.

Brock (1967a) took cores from a hot spring algal mat with a #3 brass

cork borer. Cores were placed in screw-capped 5 ml clear glass vials previously rinsed and completely filled with spring water taken from the station of origin of the core. Vials were then placed on their sides in the stream at various stations and after 5-10 min to allow for temperature equilibration, isotope was added with a syringe (0.1ml $Na_2{}^{14}CO^3$) gently to the bottom of the vial. The vial was quickly capped, inverted to mix, and returned to the spring for 1 hour. Uptake was stopped by adding 0.5 ml of 40% formalin. Other samples were treated in a like manner but incubated in the dark. Cores were homogenized, a subsample was filtered onto a Millipore filter, the filter was washed with water and glued to a planchet for counting. Brock and Brock (1967) used identical methods as those just described.

Allen (1971), after initial experiments in which macrophyte contamination of epiphyton samples caused problems, used artificial substrates to overcome those problems. Slides attached to rods were incubated at distances of 5 and 10 cm above the sediments. The slides were placed in widemouthed, ground glass stoppered, clear and opaque (with black tape) Pyrex bottles (125 ml). A ^{14}C solution, predominantly as $NaHCO_3$ was injected into each collection bottle. The isotope had previously been analyzed using gas phase techniques. Samples were resuspended for 3-4 hours and immediately transported to the lab in a light free box. Samples were filtered and counted on a gasflow Geiger-Muller counter (Nuclear Chicago, Model 6010) with micromil window D-47. All samples were assayed before and after 10 min exposure to fumes of concentrated HCl. For samples other than the attached community, liquid scintillation counting was used. A fluor consisting of 6:7 (v/v) of toluene plus Fluoralloy R mix was used. He recommended use of that fluor when samples contained considerable amounts of water. Color

quenching required construction of a color quenching series.

Several authors have felt productivity measured in situ was more meaningful than when artificial substrates have been used or when the samples have been removed from their natural surroundings. Wetzel (1964) stressed the importance of in situ studies. He used plexiglass chambers which were inserted into the mud along the shoreline. An innoculum of ^{14}C was added to the chambers and after incubation, the overlying solution was removed and stored frozen under vacuum over silica gel until combustion of the samples.

Vollenweider (1965) emphasized the importance of having in situ experiments using ^{14}C which did not exceed 4-6 hours. This was to avoid excessive losses of ^{14}C. He also pointed out that due to decreasing photosynthetic activity during the course of the day, simple conversion factors for a short time period of exposure to productivity for a whole day are likely to be erroneous.

Wetzel (1965) stated that the only ^{14}C assays of measured productivity of benthic periphyton in situ known to him were the studies done by him (Wetzel, 1963, 1964a) in northern California. He used a 4 hour incubation period. A later study by Baird and Wetzel (1968) utilized moist sand in clear and dark glass jars innoculated with ^{14}C. For in situ measurements, the jars were lowered on trays to the depth from which they were collected. Counting was accomplished using a thin window Geiger-Mueller counter with a correction for zero thickness activity. Leach (1970) also used dark and light perspex cylinders in making in situ ^{14}C productivity measurements on intertidal mudflats.

III METHODS

A. Community Structure

The periphyton community structure in the discharge canal of the Tradinghouse Creek power plant was sampled using in situ glass microscope slides. The Tradinghouse Creek power plant is located on Tradinghouse Creek Reservoir southeast of Waco, Texas.

I used a slide holder of the Bissonette (1930) type, suspended from a boom over the discharge canal by nylon ropes and weighted with cement weights from the bottom of the sampler (Fig. 1). The slide racks were suspended approximately 0.5 m from the surface. Four slides were placed in each rack at each of the three stations. One station was established at the upper end of the discharge canal approximately 200 yards downstream from the outfall. The second station was located at the lower end of the discharge canal just upstream from a retaining fence barring boats from entering the discharge canal. The final station, which acted as a reference, was located in a relatively quiet water area in the reservoir just out from the power plant intake structure (Fig. 2).

Four incubation periods of two weeks were used in this study. The first from January 6 - January 20, the second from March 12- March 26, the third from May 16 - May 30 and the fourth from June 13 - June 27, 1973.

At the conclusion of each incubation period, the slide racks were detached from the booms and placed in ice chests containing ambient reservoir water collected in the vicinity of the corresponding station. Each slide

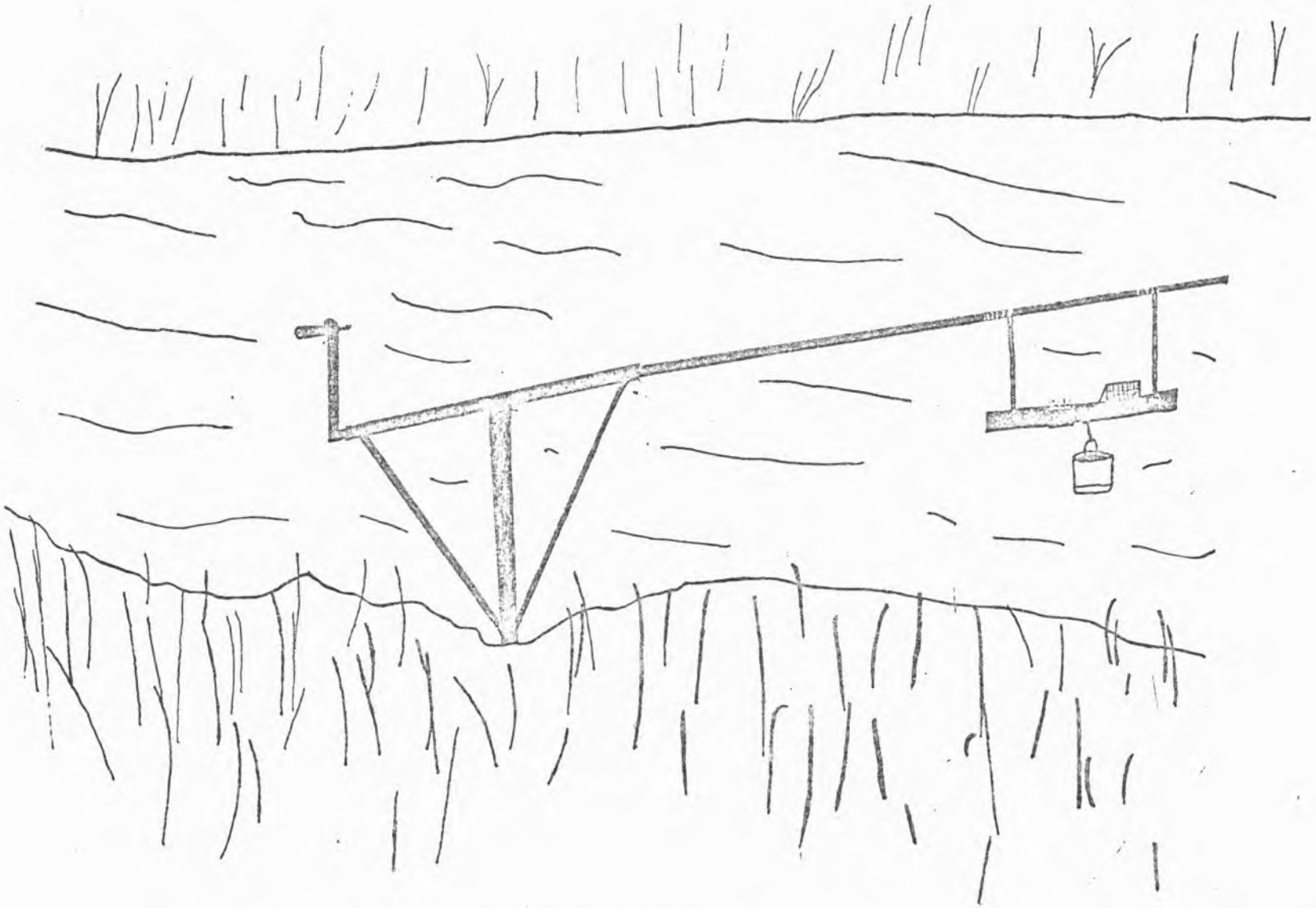

Figure 1. Experimental apparatus for colonization by periphyton on artificial substrates at Tradinghouse Creek Reservoir sampling stations 1-3.

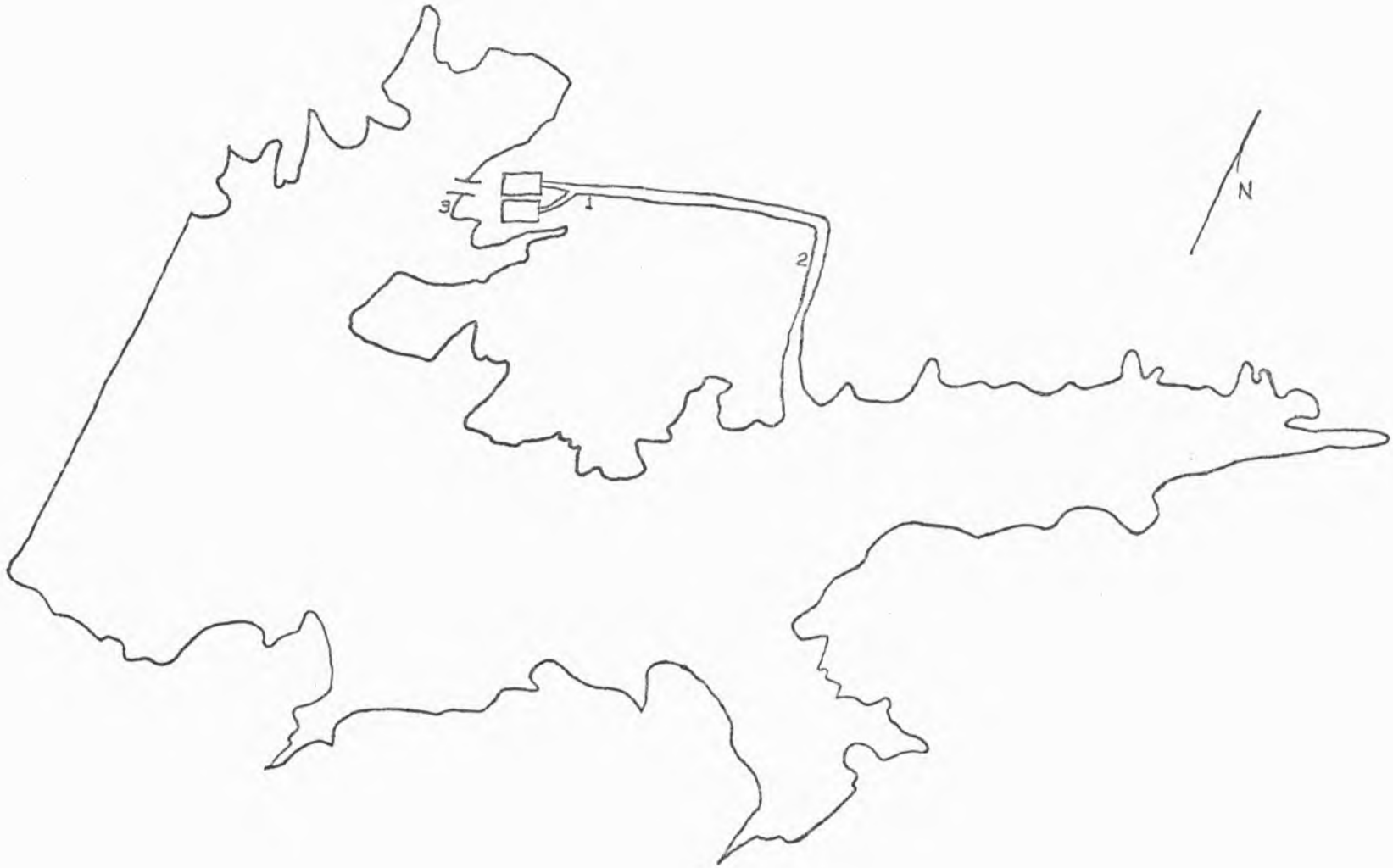

Figure 2. Tradinghouse Creek Reservoir with sampling stations 1-3.

holder was transported in a separate ice chest and held there upon arrival at the laboratory until examined.

Three slides from each slide rack were always examined. A fourth slide was counted in instances of small numbers of individuals to increase statistical validity. The slides were kept alive for examination for reasons outlined by Sladekova (1962). Although the area counted varies drastically from one investigator to another, an area 2 x 2 mm, in the center of each slide was used for counting in this study. Each organism was identified to the greatest degree of specifity to which the author felt competent using Patrick and Reimer (1966), Patrick (unpublished key to diatoms), Prescott (1962) and Prescott (1970) as primary sources. Descriptions of each taxa were presented in a numerical sequence along with a sketch and size dimensions whenever there was any question about identification. The counts and descriptions of each taxa were recorded in bound laboratory notebooks. Examination was done under the oil immersion objective of a compound microscope at 1000X for counting after a preliminary examination under lower magnification. After examination of the live mounts, the attached material from each set of slides was scraped into a beaker. The beaker contents were then cleaned and hyrax mounts were prepared using methods described by Patrick and Reimer (1966). The hyrax mounts were examined under an oil immersion objective at 1000X to better identify the diatom component of the periphyton community.

The final species list from each slide was then used to calculate diversity ($H'' = - \sum \left(\frac{n_i}{N}\right) \log_e \left(\frac{n_i}{N}\right)$ as proposed by Shannon and Weaver (1963) and further explained by Pielou (1966a). The calculations were done using a Wang model 462 programmable calculator. In the diversity formula n_i is the number of individuals in any species and N is the total number of individuals

in the sample. Diversity is in natural bits per individual. Evenness ($J = H''/Hmax = H''/\log_e S$) as described by Pielou (1966b) was calculated in a similar manner also using the Wang model 462 programmable calculator. In the evenness equation $\log_e S$ is the maximum possible value of H''. Species richness ($D' = (S-1)/\log_e N$) (Margalef, 1968) was the final measure of community structure calculated also using the Wang calculator. In the richness index, S is the number of species and N is the number of individuals. The combination of these measures of community structure were used to better describe the components of species diversity.

Each measure of community structure was plotted against the maximum recorded temperature for each sampling period on scatter diagrams. Correlation coefficients (r) and regression lines were calculated using a Wang model 462 programmable calculator and are also presented on the scatter diagrams.

Temperature of the water was measured using a hand held centigrade thermometer at the beginning and end of each incubation period and sometimes during the period.

B. Photosynthetic Response to Abrupt Thermal Change

1. Biomass

Biomass of periphyton from the thermally influenced discharge canal was measured using artificial glass substrates consisting of glass rods (diameter = 0.64 cm (1/4 in.)) which were incubated for use in the productivity studies. As discussed earlier, exposure times for biomass determinations varied among the different investigators. A one month exposure time (Jan. 6 - Feb. 6, 1973) was used for colonizing the glass rods used for both biomass and primary production studies.

Each glass rod was removed from the scintillation cocktail after counting and placed in a clean dry crucible and dried for one hour at about 105 C. The crucibles were removed from the oven, placed in a desiccator cabinet for cooling, weighed using a Mettler analytical balance accurate to 0.1 mg, and data were recorded in bound notebooks. Samples were then combusted in a muffle furnace at 550 C for 20 minutes, recooled in the desiccator cabinet and reweighed on the analytical balance. Losses in weight between the two weighings was recorded as organic matter lost in combustion. Since unequal amounts of residue were left in the scintillation vials after removal of the glass rods, the scintillation fluid was filtered using Gellman glass fiber filters whenever residue was present. The filters and residue were dried at 105 C, again cooled in a desiccator, weighed, combusted at 550 C for 20 minutes, again cooled in the desiccator and reweighed. The results were combined with those previously recorded for the rods above. Results were in grams organic matter and grams organic matter m^{-2} for biomass determinations.

Analyses of variance were performed on biomass values using methods outlined by Bailey (1972). F-ratios were considered significant at the 95% confidence level. Biomass was plotted vs. maximum recorded ambient temperature

during colonization and correlation coefficients (r) and regression lines were calculated and constructed on a scatter diagram.

2. Production

Several investigators have used light and dark chamber ^{14}C methods to measure production of periphyton or related communities.

Primary periphyton production in the discharge canal of the Tradinghouse Creek electric generating plant was measured using a ^{14}C light and dark bottle method. Eight glass rods 0.64 cm (1/4") in diameter and 9.53 cm (3 1/4") long were scored with a file for easy breaking at a point 4.45 cm (1 3/4") from the end to be inserted in the wood, spaced evenly in holes 0.64 cm (1/4")deep drilled in the top of a block of wood and fastened to the sampling boom (Fig. 3). They were lowered to a depth of approximately 0.5 m and allowed to colonize for one month (Jan. 6 - Feb. 6, 1973) at the three stations previously described.

The rods were taken out of the block using a pair of pliers and transported to the laboratory in bottles of reservoir water in ice chests containing ambient reservoir water. Half the rods from each station were put in each of two ice chests for incubation at 10 or 30 C, respectively. Ice was added to one chest during transport to bring the water temperature down to 10 C gradually. When the chests reached the laboratory, each group of bottles were left in the chests and placed in separate light proof constant temperature rooms. The lids were opened to allow temperature equipibration.

The temperature controlled water bath portion of a Warburg respirometer apparatus with two banks of fluorescent lights of two bulbs each mounted over it were used as the experimental incubation chamber. Experimental incubation bottles consisted of light and dark paired 29 ml glass bottles. These were filled with prefiltered lake water and placed in the Warburg apparatus to

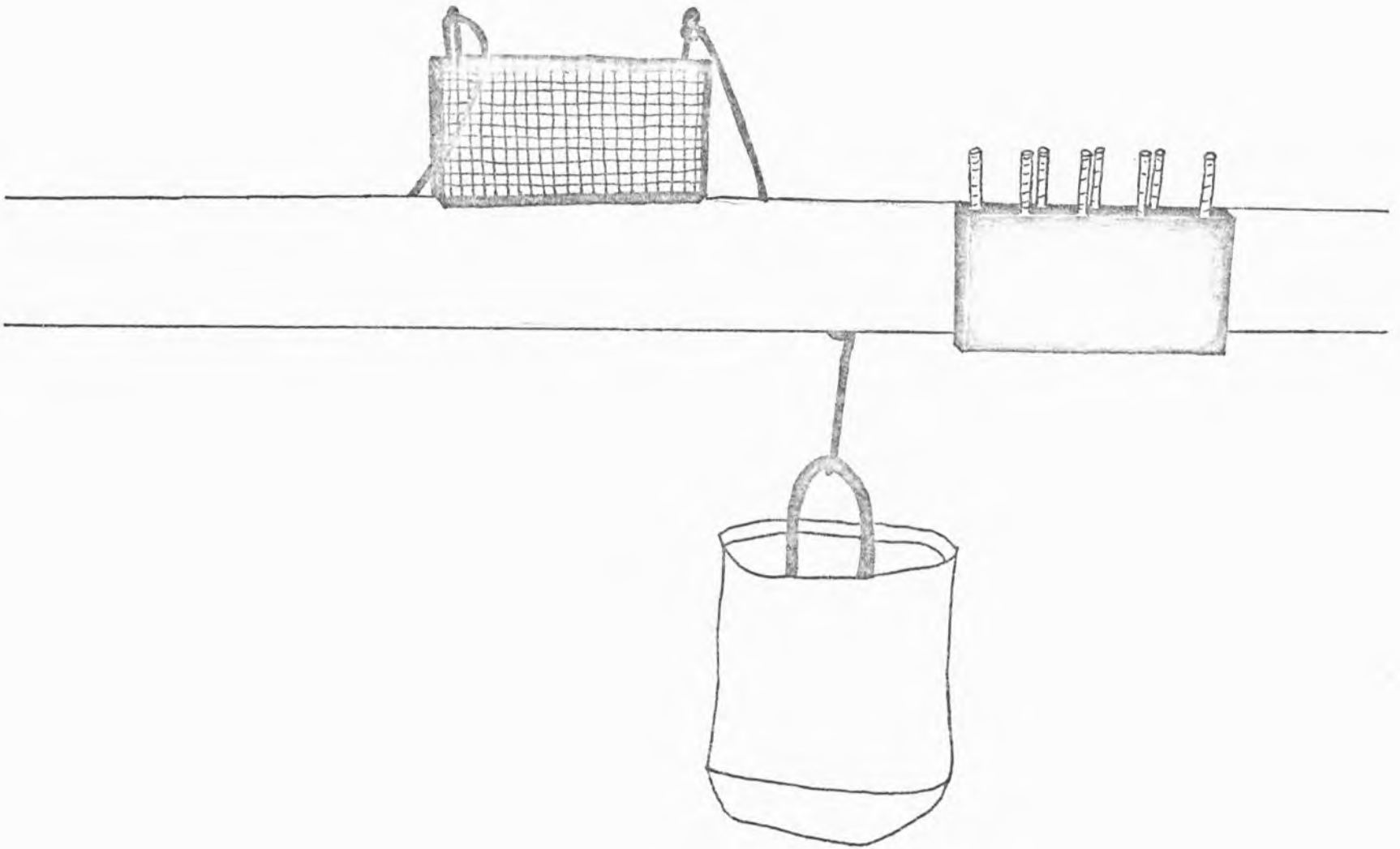

Figure 3. Bissonette type slide rack and glass rods for periphyton colonization.

equilibrate. The colonized rods were taken out of the constant temperature rooms, broken in two at the premarked place and half of each rod was placed in a light bottle and the other half in a dark bottle. One ml of ^{14}C as $NaCO_3$ with an activity of 2.33 microcuries ml^{-1} was added to each incubation bottle. The isotope was added by inserting a syringe tip to a point near the bottom of the bottle and slowly injecting the contents into the bottle. The glass stoppers were quickly replaced and aluminum foil was wrapped around the lid and neck of each dark bottle to prevent light penetration.

The periphyton was incubated for two hours with each bottle being turned 90 deg. every half hour so that a full revolution had been completed by the end of the experimental time. The light intensity at the surface of the water, which just covered the bottles in their vertical position, had a 300 ft-c intensity.

At the end of the two hour incubation period, the rods were removed from the glass stoppered bottles, dipped in a bath of dilute HCl with a pH of 3.0-3.5 and then dipped in a distilled water bath. The rods were transferred to numbered scintillation vials and placed in desiccation cabinet containing a CO_2 absorbant to dry for 24 hours.

The procedure was identical for both incubation temperatures (10 and 30 C) with the exception that the 30 C incubation bottles were placed in an ice bath at the end of the two-hour incubation to slow metabolic activity until each rod could be dipped in the acid solution.

Liquid scintillation counting was used to determine the radioactivity of the dried rods. The scintillation vials were filled with a liquid scintillation cocktail described by Lind and Campbell (1969). It consists of a toluene based fluor for use with previously dried samples. Samples were counted using a Beckman model 100 liquid scintillation counter with automatic

external standard. Each sample was counted for 10 minutes in each of four positions with 90 deg. rotation to check for differences which might occur due to interference from the glass rod. Due to color quenching in some of the samples, a color quench series was made by using periphyton material similar to that on the experimental rods.

Differences among stations for each temperature were tested using analyses of variance as described by Bailey (1972). Analyses of variance were also performed on the counting positions to determine possible differences in counting efficiencies by position of the rods. Correlation coefficients (r) and regression analyses were calculated for production rates versus mean temperatures. Scatter diagrams were plotted and regression lines were calculated using a Wang model 462 programmable calculator. Comparisons for all statistics were deemed significant at the 95% confidence level.

IV Results

A. Community Structure

Mean temperatures during power plant operation for this study were 28.4 C for Station 1 (discharge near power plant), 27.4 C for Station 2 (end of discharge canal), and 23.5 C for Station 3 (intake) (Table 1). These means represent mean ΔTs of 4.9 and 3.9 C for station 1 and 2, respectively. Thus, there is a mean drop of 1.0 C as the water travels down the discharge canal. The second slide incubation period was during a power plant shut down when no heat was produced, but normal water circulation patterns were measured. This provided information concerning possible effects of power plant operation other than heat additions on periphyton community structure.

Colonization of Periphytic Organisms

Following two weeks of colonization algal periphyton communities were highly variable among stations in both taxa and densities (Tables 2-13). Power plant operation was a major factor in determining periphyton densities at Station 1. Mean densities for incubation periods 1, 3, and 4 with power plant operation were 5.56, 14.31, and 9.42 cells mm^{-2}. In contrast mean periphyton algal density for incubation period 2 when the power plant was not generating was 213.83 cells mm^{-2}. At station 2 the trend was reversed with greatest mean periphyton density found for periods of power plant operation. The lowest mean density of 93.75 cells mm^{-2} was found during incubation period 2. Station 3 exhibited the same trend as found for station 2 with mean periphyton density lowest during incubation period 2 (Tables 2 - 13).

Table 1. Surface temperature regimes (deg. C) at sampling stations 1-3 near the Tradinghouse Creek power plant southeast of Waco, Texas.

Date	Incubation Period	Station 1	Station 2	Station 3
1/20/73	1	20.0	16.5	12.0
1/31/73		16.7	15.5	10.2
2/6/73		17.0	15.0	12.0
3/3/73*		14.0	14.5	14.5
3/12/73*	2	17.0	17.0	17.5
3/15/73*	2	18.0	18.0	18.0
3/23/73*	2	17.0	17.0	17.0
3/26/73*	2	16.5	16.5	16.5
3/28/73*		17.0	17.0	17.0
3/29/73*		18.0	18.0	18.0
4/11/73*		15.5	16.0	16.0
5/2/73*		22.0	22.5	-
5/16/73	3	30.0	30.0	24.0
5/17/73	3	30.0	30.0	26.0
5/30/73	3	33.0	33.0	28.0
5/31/73		34.0	33.5	28.0
6/6/73		33.0	33.0	29.0
6/7/73		28.0	28.0	30.0
6/27/73	4	34.0	33.0	29.0
6/29/73		36.5	34.0	30.5
Mean Tem. (deg C) excluding shutdown		28.4	27.4	23.5
Mean deg. C above intake		4.9	3.9	-

* Power plant was shut down for repairs during this time period.

Table 2. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from January 6 - January 20, 1973, at station #1 in the discharge canal of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Slide #4	Total	Total mm^{-2}
Cyclotella sp. #1	2			2	4	0.25
Navicula sp. #1	8		1	1	10	0.63
Navicula sp. #2	1				1	0.06
Fragilaria sp. #1	1				1	0.06
Fragilaria sp. #2	1		4		5	0.31
Fragilaria sp. #3	1				1	0.06
Fragilaria sp. #4	7		22	1	30	1.88
Diploneis sp. #1	1				1	0.06
Synedra rumpens	6	2	2	3	13	0.81
Cymbella sp. #1	1		1		2	0.13
Pinnularia sp. #1	1		1		2	0.13
Pinnularia sp. #2			1		1	0.06
Gomphonema sp. #1			3		3	0.19
Pennate diatom #1	1				1	0.06
Pennate diatom #2	2		1		3	0.19
Pennate diatom #3	1				1	0.06
Pennate diatom #4	1				1	0.06
Pennate diatom #5	1				1	0.06
Tetraedron minimum	1			1	2	0.13
Mougeotia viridis	1		5		6	0.38
Totals	38	2	41	8	89	5.56

Table 3. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from January 6 - January 20, 1973, at station #2 in the discharge canal of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Slide #4	Total	Total mm^{-2}
Cyclotella Meneghiniana	12	6	8	22	48	3.00
Melosira granulata		2	4	5	11	0.69
Stephanodiscus sp. #1				1	1	0.06
Navicula protracta	3		1		4	0.25
Navicula sp. #3	5				5	0.31
Navicula sp. #4	120	24	20	48	212	13.25
Navicula sp. #5		2			2	0.13
Navicula pupula			2		2	0.13
Fragilaria vaucheriae	13	4	12	21	50	3.13
Pleurosigma sp. #1	10	2	4	3	19	1.19
Nitzschia filiformes	41	12	24	32	109	6.81
Nitzschia hungarica			2		2	0.13
Hantzschia sp. #1				2	2	0.13
Cocconeis sp. #1	23	3	6	4	36	2.25
Diploneis puella	1		12	17	30	1.88
Asterionella sp. #1	2				2	0.13
Asterionella formosa	40	37	12	20	109	6.81
Synedra ulna	7	1	6	5	19	1.19
Gomphonema olivaceum	44	4	9	4	61	3.81
Gomphoneis sp. #1		1			1	0.06
Achnanthes sp. #1	15	16			31	1.94
Cymbella ventricosa	3	2	3	7	15	0.94
Cymbella tumida	2		15	2	19	1.19
Amphipleura pellucida	8	1	4	5	18	1.13
Stauroneis sp. #1			1	1	2	0.13
Pinnularia sp. #1				10	10	0.63
Amphora sp. #1				2	2	0.13
Pennate diatom #4		2			2	0.13
Pennate diatom #6			16	44	60	3.75
Pennate diatom #7	18				18	1.13
Pennate diatom #8		1	14	2	17	1.06
Scenedesmus sp. #1	41				41	2.56
Scenedesmus dimorphus	20		6	2	28	1.75
Scenedesmus opoliensis		12	30	30	72	4.50
Closterium sp. #1	2				2	0.13
Staurastrum sp. #1	1			2	3	0.19
Staurastrum limneticum		2	2		4	0.25
Euastrum sp. #1		1			1	0.06
Sorastrum sp. #1		4			4	0.25
Tetradriella gigas		1	3	7	11	0.69
Pediastrum tetras			4		4	0.25
Sphaerocystis sp. #1				1	1	0.06

Table 3 - Cont'd.

Taxa	Slide #1	Slide #2	Slide #3	Slide #4	Total	Total mm^{-2}
Spirogyra sp. #1	31				31	1.94
Mougeotia sp. #1	39	5	20	15	79	4.94
Oocystis nodulosa	3				3	0.19
Micractinium eriense			8		8	0.50
Phacus sp. #1				3	3	0.19
Cyanophycean #1		1			1	0.06
Gymnodinium sp. #1			1		1	0.06
Total	504	146	249	317	1216	76.00

Table 4. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from January 6 - January 20, 1973, at station #3 in Tradinghouse Creek Reservoir.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana	12	12	4	28	2.33
Cyclotella michiganiana	14	2		16	1.33
Stephanodiscus sp. #1	1	1		2	0.17
Melosira granulata		2		2	0.17
Asterionella formosa	45	63	48	156	13.00
Fragilaria sp. #5	22	7	4	33	2.75
Synedra ulna	13	15	14	42	3.50
Gomphonema olivaceum	42	35	41	118	9.83
Achnanthes sp. #1	3		8	11	0.92
Achnanthes clevei	9		1	10	0.83
Cymbella ventricosa	8	7	4	19	1.58
Cymbella tumida		4	4	8	0.67
Nitzschia filiformes	29	9	5	43	3.58
Nitzschia sp. #1	1			1	0.08
Hantzschia sp. #1		2		2	0.17
Mastoglia smithii	2			2	0.17
Amphipleura pellucida	1			1	0.08
Gyrosigma sp. #1		1		1	0.08
Diploneis puella		6	2	8	0.67
Navicula protracta	3	8	4	15	1.25
Navicula sp. #3	1	12	1	14	1.17
Navicula pupula	2	5	18	25	2.08
Pennate diatom sp. #7			3	3	0.25
Pennate diatom sp. #9	3			3	0.25
Staurastrum sp. #2	1			1	0.08
Scenedesmus sp. #2	2			2	0.17
Scenedesmus opoliensis		9	2	11	0.92
Closterium sp. #2			1	1	0.08
Leptosira sp. #1	20			20	1.67
Mougeotia sp. #1	17	58	20	95	7.92
Euglena sp. #1	1			1	0.08
Tetraedron minimum		2	1	3	0.25
Franceia sp. #1			2	2	0.17
Micractinium sp. #1			1	1	0.08
Chlorophyta sp. #1			1	1	0.08
Synura sp. #1			1	1	0.08
Total	252	260	190	702	58.5

Table 5. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from March 12 - March 26, 1973, at station #1 in the discharge canal of Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana		1		1	0.08
Synedra ulna	27		96	123	10.25
Synedra rumpens	8	6	9	23	1.92
Synedra sp. #1	13			13	1.08
Fragilaria virescens	70	11	1	82	6.83
Fragilaria vaucheriae		20	7	27	2.25
Asterionella formosa	503	243	968	1714	142.83
Asterionella sp. #1	7			7	0.58
Diatoma sp. #1	4	5	3	12	1.00
Diatoma sp. #2	6			6	0.50
Tabellaria sp. #1	67			67	5.58
Achnanthes clevei	2	12	11	25	2.08
Achnanthes sp. #1	21	2		23	1.92
Gomphonema olivaceum	25	1	1	27	2.25
Cymbella sp. #2	7	2		9	0.75
Cymbella ventricosa		1	1	2	0.17
Cymbella tumida			2	2	0.17
Nitzschia filiformes	3	123		126	10.50
Mastoglia sp. #1	27			27	2.25
Diploneis puella	1			1	0.08
Navicula protracta	24	4	4	32	2.67
Navicula sabiniana	16	13		29	2.42
Navicula pupula		28	2	30	2.50
Navicula sp. #5		19	7	26	2.17
Pennate diatom #10	9			9	0.75
Mougeotia sp. #1	12			12	1.00
Mougeotia sp. #2		8		8	0.67
Spirogyra sp. #2		84		84	7.00
Spirogyra sp. #3			6	6	0.50
Selenastrum sp. #1	1			1	0.08
Tetraedron sp. #1	1			1	0.08
Chlorella sp. #1	1			1	0.08
Scenedesmus opoliensis		7	2	9	0.75
Phacus sp. #1		1		1	0.08
Total	855	591	1120	2566	213.83

Table 6. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from March 12 - March 26, 1973, at station #2 in the discharge canal of Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana	1	7	1	9	0.75
Melosira sp. #1	25		4	29	2.42
Achnanthes grimmei	3	7		10	0.83
Achnanthes sp. #1	5	16		21	1.75
Gomphonema olivaceum	11	10	6	27	2.25
Cymbella sp. #3	5			5	0.42
Cymbella sp. #1		14		14	1.17
Amphora sp. #1			2	2	0.17
Cocconeis pediculus	1	4		5	0.42
Cocconeis sp. #1		1		1	0.08
Diploneis puella	12	26	5	43	3.58
Synedra rumpens	9		1	10	0.83
Synedra ulna	10	32	5	47	3.92
Synedra sp. #1	6		3	9	0.75
Fragilaria vaucheriae	21			21	1.75
Fragilaria virescens		82	19	101	8.42
Navicula sp. #4	63			63	5.25
Navicula cryptocephala	51			51	4.25
Navicula pupula	4	27	19	50	4.17
Navicula sp. #1	44		39	83	6.92
Navicula gregaria		28	1	29	2.42
Navicula sp. #5		4		4	0.33
Navicula protracta		17	9	26	2.17
Navicula hungarica		5		5	0.42
Nitzschia filiformes	3			3	0.25
Amphipleura pellucida	2	1		3	0.25
Hantzschia sp. #1	1	4	1	6	0.50
Gyrosigma sp. #1	4		2	6	0.50
Surirella sp. #1		4		4	0.33
Mastoglia elliptica		57	17	74	6.13
Stauroneis sp. #1		8		8	0.67
Pleurosigma sp. #1		1		1	0.08
Pennate diatom sp. #7	4			4	0.33
Pennate diatom sp. #1	2			2	0.17
Pennate diatom sp. #10	3			3	0.25
Pennate diatom sp. #11	24	6		30	2.50
Pennate diatom sp. #12		4		4	0.33
Scenedesmus dimorphus	10	6		16	1.33
Scenedesmus opoliensis	8		6	14	1.17
Dictyosphaerium sp. #1	4			4	0.33
Tetraedron sp. #1	4	1		5	0.42

Table 6 - Cont'd.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Selenastrum sp. #1	1			1	0.08
Staurastrum curvatum	1		1	2	0.17
Chlorella sp. #1	2			2	0.17
Spirogyra sp. #1	8		46	54	4.50
Mougeotia viridis	32		8	40	3.33
Oedogonium sp. #1		4		4	0.33
Characium sp. #1		7		7	0.58
Chlorophyta sp. #1	4			4	0.33
Ophiocytium sp. #1			4	4	0.33
Oscillatoria sp. #1	97	39	15	151	12.58
Gomphosphaeria sp. #1	4			4	0.33
Total	489	422	214	1125	93.75

Table 7. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from March 12 - March 26, 1973, at station #3 near the intake structure of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Melosira granulata	3			3	0.25
Cyclotella Meneghiniana	5	4	3	12	1.00
Cymbella affinis	8	4	6	18	1.50
Amphora ovalis			5	5	0.42
Achnanthes sp. #1	9	12	6	27	2.25
Achnanthes grimmei	15	7	35	57	4.75
Gomphonema olivaceum	3	2		5	0.42
Cocconeis placentula	2	2		4	0.33
Surirella sp. #1	2	1		3	0.25
Synedra ulna	9	8	9	26	2.17
Synedra rumpens	10	8	15	33	2.75
Fragilaria vaucheriae	12	5		17	1.42
Fragilaria virescens		11	20	31	2.58
Asterionella formosa	9	12		21	1.75
Diploneis puella	19	11	9	39	3.25
Gyrosigma sp. #1	5	3	2	10	0.83
Diatoma hiemale	3	2	1	6	0.50
Opephora sp. #1	7		1	8	0.67
Hantzschia sp. #1			1	1	0.08
Navicula protracta	8	5	5	18	1.50
Navicula sp. #5	12	4	3	19	1.58
Navicula sp. #1	15	10		25	2.08
Navicula sp. #6	11			11	1.92
Navicula sp. #4		9		9	0.75
Pinnularia sp. #1	2		10	12	1.00
Pennate diatom sp. #13	11			11	0.92
Pennate diatom sp. #11	2			2	0.17
Pennate diatom sp. #10		3		3	0.25
Pennate diatom sp. #7		2		2	0.17
Scenedesmus opoliensis	38	19	25	82	6.83
Staurastrum sp. #2			1	1	0.08
Tetraedron sp. #1	7	1	4	12	1.00
Chlorella sp. #1	2		1	3	0.25
Oedogonium sp. #1	25			25	2.08
Mougeotia sp. #1	4	16		20	1.67
Spirogyra sp. #1		3		3	0.25
Protoderma viride		20		20	1.67
Selenastrum sp. #1		12	8	20	1.67
Ophiocytium sp. #1	8			8	0.67
Total	266	196	170	632	52.67

Table 8. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from May 17-31, 1973, at station #1 in the discharge canal of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Slide #4	Total	Total mm^{-2}
Achnanthes clevei	2	2		2	6	0.38
Achnanthes sp. #1	1	1	3		5	0.31
Cocconeis placentula	1	1			2	0.13
Synedra amphicephala	5	2			7	0.44
Synedra fasciculata	23	7		4	34	2.13
Synedra rumpens				2	2	0.13
Asterionella formosa	4		51	5	60	3.75
Fragilaria vaucheriae	3				3	0.19
Navicula protracta	1	4		1	6	0.38
Navicula pupula		1	2		3	0.19
Navicula sp. #7		1			1	0.06
Diploneis puella				1	1	0.06
Amphora ovalis			1		1	0.06
Pennate diatom sp. #11	1				1	0.06
Pennate diatom sp. #14	1	3			4	0.25
Pennate diatom sp. #15			1		1	0.06
Scenedesmus opoliensis	1			2	3	0.19
Selenastrum sp. #1	4				4	0.25
Cystodinium sp. #1	1	1			2	0.13
Spirogyra sp. #1			3		3	0.19
Dictyosphaerium sp. #1			4	4	8	0.50
Cosmarium circulare				1	1	0.06
Tetraedron regulare	1	2		2	5	0.31
Chlamydomonas sp. #1	1				1	0.06
Englena minuta		1	1		2	0.13
Oscillatoria sp. #1	5	53			58	3.63
Spirulina sp. #1		1			1	0.06
Glaucocystis oocystiformes				4	4	0.25
Total	55	80	66	28	229	14.31

Table 9. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from May 17 - May 31, 1973, at station #2 in the discharge canal of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana	2	2	1	5	0.42
Stephanodiscus sp. #1			1	1	0.17
Synedra pulchella	3			3	0.25
Synedra rumpens	5	12		17	1.42
Achnanthes clevei	10			10	0.83
Achnanthes hauckiana	530	4420	444	5394	449.50
Achnanthes sp. #1	459	1670	50	2179	181.58
Achnanthes sp. #2	1			1	0.08
Cocconeis sp. #1	2	2		4	0.33
Diploneis puella	34	17	16	67	5.58
Diploneis sp. #1	4			4	0.33
Gomphonema olivaceum	56	28	10	94	7.83
Gomphonema parvulum			4	4	0.33
Cymbella ventricosa	24	10	1	35	2.92
Cymbella sp. #1	5	25	1	31	2.58
Opephora martyi	4	1		5	0.42
Navicula sp. #5	12	1		13	1.08
Navicula sp. #7	3	1		4	0.33
Navicula halophila	1		2	3	0.25
Navicula protracta	1			1	0.08
Navicula sp. #6		3		3	0.25
Pinnularia sp. #2	6	25	14	45	3.75
Nitzschia sp. #2	2			2	0.17
Nitzschia fonticula	2			2	0.17
Scenedesmus opoliensis	12		14	26	2.16
Tetraedron regulare	4			4	0.33
Tetraedron caudatum	3		7	10	0.83
Pediastrum obtusum	8			8	0.67
Dictyosphaerium sp. #1	3			3	0.25
Cosmarium sp. #2	2		3	5	0.42
Oocystis nodulosa			1	1	0.08
Euglena sp. #1	2	1		3	0.25
Characiopsis sp. #1			2	2	0.17
Spirulina sp. #1	1		2	3	0.25
Total	1201	6218	573	7992	666.00

Table 10. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from May 17 - May 31, 1973, at station #3 near the intake structure of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana	11	1	2	14	1.17
Cyclotella glomerata			6	6	0.50
Stephanodiscus sp. #1	1	5		6	0.50
Asterionella formosa	29	24	17	70	5.83
Fragillaria vaucheriae	3		6	9	0.75
Synedra rumpens	12			12	1.00
Diatoma sp. #1	4			4	0.33
Diatoma hiemale			1	1	0.08
Achnanthes minutissima	897	239	46	1182	98.50
Achnanthes hauckiana	1072	2615	122	3809	317.42
Cocconeis sp. #1	1		3	4	0.33
Cymbella ventricosa	11	30	11	52	4.33
Cymbella tumida	47	12	41	100	8.33
Gomphonema olivaceum	7			7	0.58
Comphonema sp. #1	2	3		5	0.42
Diploneis puella	16	12	22	50	4.17
Amphipleura pellucida			8	8	0.67
Navicula seminulum	4	12		16	1.33
Navicula pupula	1	2	12	15	1.25
Navicula protracta			4	4	0.33
Pinnularia sp. #1	3			3	0.25
Hantzschia sp. #1			1	1	0.08
Nitzschia linearis	4			4	0.33
Cosmarium sp. #1	4	2	2	8	0.67
Cosmarium sp. #2		9	2	11	0.92
Protoderma viride	15		50	65	5.42
Tetraedron regulare	4	4	1	9	0.75
Scenedesmus opoliensis	4	10	18	32	2.67
Scenedesmus dimorphus			4	4	0.33
Oocystis sp. #1	4			4	0.33
Oocystis nodulosa	2			2	0.17
Chlorella sp. #1	1		4	5	0.42
Pediastrum tetras	4			4	0.33
Spirogyra sp. #1		16	16	32	2.67
Binuclearia sp. #1			2	2	0.17
Euglena sp. #1	2	2	1	5	0.42
Oscillatoria sp. #1	14			14	1.17
Oscillatoria sp. #2	15			15	1.25
Total	2194	2998	402	5594	466.17

Table 11. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from June 13-27, 1973, at station #1 in the discharge canal of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Synedra sp. #1			1	1	0.08
Achnanthes sp. #2		1		1	0.08
Achnanthes sp. #3			2	2	0.17
Cocconeis sp. #1			1	1	0.08
Pennate diatom sp. #16	2	1	1	4	0.33
Cosmarium sp. #1	2			2	0.17
Gonium sp. #1	1			1	0.08
Uronema sp. #1			10	10	0.83
Oscillatoria acutissima	7	33	30	70	5.83
Spirulina sp. #1	1			1	0.08
Merismopedia sp. #1			20	20	1.67
Total	13	35	65	113	9.42

Table 12. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from June 13 - 27, 1973, at station #2 in the discharge canal of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana	5	5	6	16	1.33
Melosira granulata		3		3	0.25
Diatoma hiemale	3			3	0.25
Synedra radians	12			12	1.00
Synedra ulna	4			4	0.33
Fragilaria brevistriata	20		14	34	2.83
Hannaea acus		10	11	21	1.75
Achnanthes sp. #2	154	6	175	335	27.92
Achnanthes minutissima	3			3	0.25
Achnanthes sp. #1	37		24	61	5.08
Achnanthes sp. #3	20		5	25	2.08
Achnanthes sp. #4			1	1	0.08
Cocconeis sp. #1	6		4	10	0.83
Gomphonema parvulum	38	8		46	3.83
Gomphonema olivaceum		3	12	15	1.25
Cymbella affinis	4		2	6	0.50
Amphora ovalis	14	6	1	21	1.75
Diploneis smithii	26	5	8	39	3.25
Stauroneis sp. #1	10		2	12	1.00
Mastoglia smithii			1	1	0.08
Mastoglia sp. #1			2	2	0.17
Navicula salinarum	80			80	6.66
Navicula arenaria	2			2	0.17
Navicula pupula	14	2	1	17	1.42
Nitzschia acicularis	22	3	2	27	2.25
Nitzschia sp. #2	4	1	1	6	0.50
Nitzschia filiformes	16	4	7	27	2.25
Epithemia turgida			1	1	0.08
Pennate diatom sp. #17		13		13	1.08
Pediastrum sp. #1		9		9	0.75
Pediastrum tetras	5			5	0.42
Pediastrum duplex			8	8	0.67
Chlamydomonas sp. #1	1			1	0.08
Scenedesmus dimorphus			4	4	0.33
Scenedesmus opoliensis	8	10	12	30	2.50
Gloeocystis ampla	12	18	9	39	3.25
Oocystis nodulosa	2		5	7	0.58
Chlorella variegatus	1			1	0.08
Chlorella vulgaris	7	1	8	16	1.33
Tetraedron regulare	3		7	10	0.83
Actinastrum Hantzschii	63		29	92	7.67
Spirogyra sp. #1	4	2		6	0.50
Cosmarium sp. #1	2		6	8	0.67

Table 12-Cont'd. Page 2 of 2 Pages

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Mougeotia sp. #1		15		15	1.25
Staurastrum sp. #1			1	1	0.08
Phacus sp. #1		1		1	0.08
Phacus acuminatur			9	9	0.75
Euglena sp. #1			1	1	0.08
Chrysophycean statospore	1			1	0.08
Tribonema sp. #1		13		13	1.08
Oscillatoria acutissima	85	40	159	284	23.67
Oscillatoria sp. #1			40	40	3.33
Anabaena sp. #1		65	25	90	7.50
Chroococcus sp. #1		1		1	0.08
Chroococcus giganteus		4		4	0.33
Merismopedia tenuissima			16	16	1.33
Gomphosphaeria lacustris			8	8	0.67
Spirulina sp. #1	1		5	6	0.50
Total	689	248	632	1569	130.75

Table 13. Periphyton counts on a $4mm^2$ area of replicate glass slides incubated from June 13 - 27, 1973, at station #3 near the intake structure of the Tradinghouse Creek power plant.

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Cyclotella Meneghiniana	3	2		5	0.42
Stephanodiscus sp. #1	1			1	0.08
Hannaea acus	2	1		3	0.25
Fragilaria brevistriata	3	3		6	0.50
Asterionella formosa			3	3	0.25
Synedra ulna		2		2	0.17
Opephora martyi			2	2	0.17
Diatoma vulgare			2	2	0.17
Achnanthes sp. #1	24	25	31	80	6.67
Achnanthes sp. #2	94	39	60	193	16.08
Achnanthes minutissima	89	17	89	195	16.25
Achnanthes sp. #4	7		2	9	0.75
Achnanthes sp. #3			3	3	0.25
Cocconeis placentula	2	4	3	9	0.75
Cymbella ventricosa	2	1	4	7	0.58
Cymbella turgida	3	1	3	7	0.58
Gomphonema parvulum	1		1	2	0.17
Diploneis smithii	6	7	10	23	1.92
Diploneis puella		1		1	0.08
Gyrosigma obscurum	1	2	6	9	0.75
Pinnularia sp. #2	3	1		4	0.33
Frustulia rhomboides	3			3	0.25
Amphipleura pellucida	2	2		4	0.33
Stauroneis sp. #1			1	1	0.08
Navicula pupula	7	3	2	12	1.00
Navicula protracta	1	3	5	9	0.75
Nitzschia acicularis	19		12	31	2.58
Nitzschia filiformes	1		9	10	0.83
Nitzschia sp. #2		8		8	0.67
Pennate diatom sp. #17		1	1	2	0.17
Chlorella vulgaris	2			2	0.17
Scenedesmus opoliensis	9	4	16	29	2.42
Scenedesmus dimorphus	4			4	0.33
Conium sp. #1	6	1	1	8	0.67
Tetrastrum sp. #1	4			4	0.33
Oedogonium sp. #1	21		4	25	2.08
Oocystis nodulosa	2	1	1	4	0.33
Tetraedron regulare	8	3	1	12	1.00
Tetraedron minima		1	1	2	0.17
Gloeocystis ampla	5	4	6	15	1.08
Arthrodesmus sp. #1		2		2	0.17
Cosmarium sp. #1			4	4	0.33
Staurastrum sp. #1			2	2	0.17
Mougeotia sp. #1			7	7	0.58
Phacus sp. #1	1	2		3	0.25
Euglena sp. #1	1			1	0.08
Trachelomonas sp. #1			2	2	0.17

Table 13-Continued

Taxa	Slide #1	Slide #2	Slide #3	Total	Total mm^{-2}
Chrysostephanosphaeria sp. #1	16		70	86	7.17
Oscillatoria acutissima	247	24	110	381	31.75
Glenodinium quadridens	1		1	2	0.17
Spirulina sp. #1	1		2	3	0.25
Anabaena sp. #1			5	5	0.42
Merismopedia tenuissima			36	36	3.00
Total	602	165	518	1285	107.08

The percent composition of the major algal groups changed through time with the blue-greens increasing as the diatoms decreased. The diatoms were the major component at all stations until the June incubation period when they comprised only about one-half of the periphytic algae at stations 2 and 3 and less than 10% at station 1 (Figure 4). The blue-green algae, in contrast, were not in evidence at station 1 until the third incubation period (May) when they formed about one-fourth of the population and by the fourth incubation period (June) were the major periphyton algal component at station 1. At stations 2 and 3, the blue-green algal component did not comprise one-fourth of the population until the fourth incubation period. The green algae were never the dominant group at any of the experimental stations (Figure 4).

Differences were apparent in both trends and actual numbers of taxa present among stations. There was an increase from the first to the second incubation period followed by a decrease at station 1 (Table 14). At stations 2 and 3 the trend was similar through the first three incubation periods with increases in the number of taxa from the first to the second incubation period followed by a decrease during the third period (Figure 5). The main difference in the trends of the three stations was in the fourth incubation period when a rise was found for stations 2 and 3 and a sharp decrease was detected for station 1 (Table 14). The differences among stations were very minimal between stations 2 and 3 for any given incubation period, but consistently higher numbers of taxa were found at stations 2 and 3 than at station 1. The differences became very pronounced during the June incubation period when temperatures reached their maxima for this study. In actual numbers, station 1 had means of 8.6 taxa for incubation periods during power plant generation and 19 when the power plant was not in operation. In

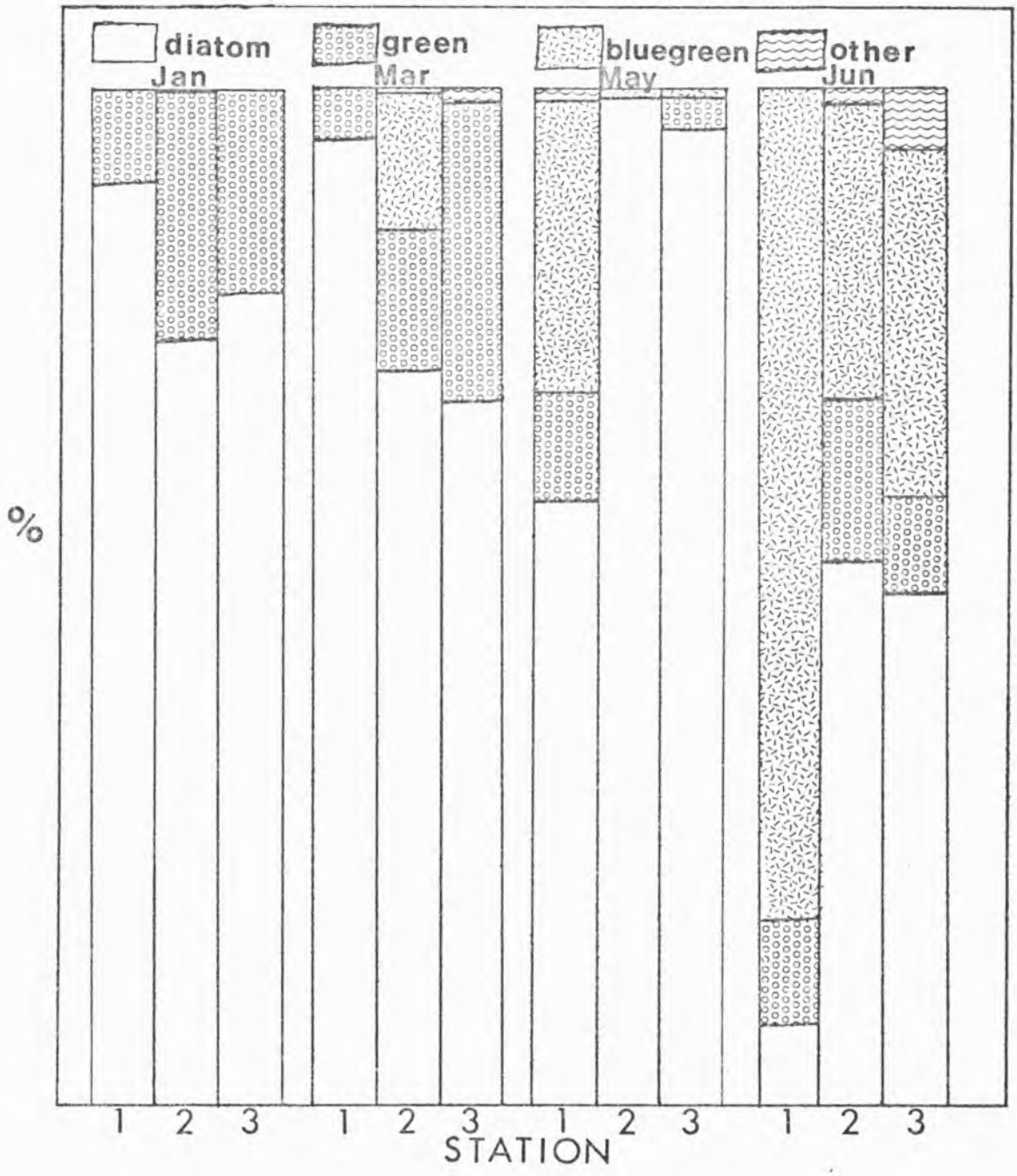

Figure 4. Per cent composition of major algal groups on glass slides colonized at Tradinghouse Creek Reservoir sampling stations 1-3, January-June, 1973.

Table 14. Mean numbers of individuals (taxa) counted per slide for each sampling station and incubation period at Tradinghouse Creek Reservoir

Incubation Period	Station 1	Station 2	Station 3
Jan. 6-20, 1973	22.3(8.5)	304(26.3)	234(22.0)
Mar. 12-26, 1973	855.3(19)	375(28.7)	210.7(25.7)
May 16-30, 1973	57.3(12.3)	2664(20.3)	1864.7(23.7)
June 13-27, 1973	37.7(5.0)	523(32.3)	428.3(33.7)

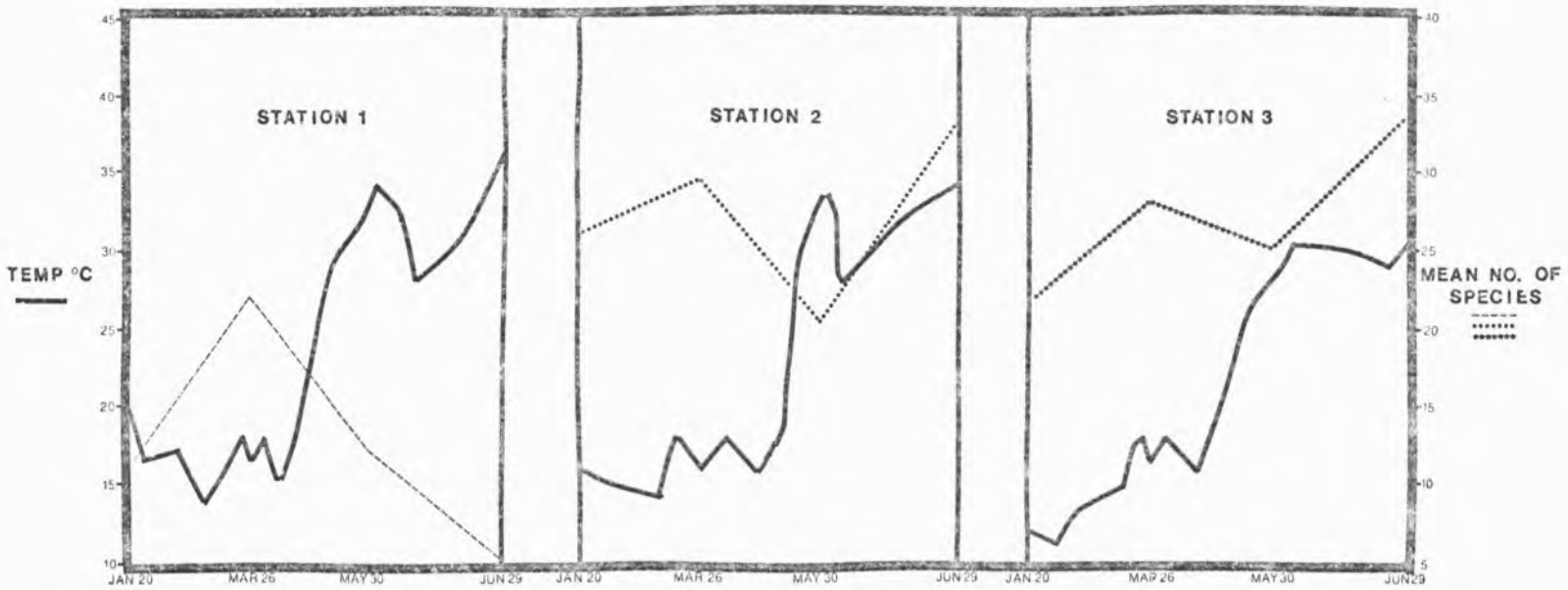

Figure 5. Changes in mean numbers of periphyton species colonized on glass slides at Tradinghouse Creek Reservoir sampling stations 1-3 with temperature.

contrast, stations 2 and 3 had means of 26.3 and 23.1 taxa during times of power plant operation (Table 14).

Diversity of the Periphyton Community

Comparison of diversities among stations show small differences between stations 2 and 3 with station 1 having less diversity than either station 2 or 3, except during the third incubation period when station 1 exhibited a slightly higher diversity than either station 2 or 3 (Table 15). Analyses of variance indicated significant differences among stations for the January and March, and June incubation periods (Table 16). Differences were significant at the 95% confidence level for the January and March samples and at the 99% confidence level for the June sample.

Evenness calculations, for which 1.0 is the case where all species are represented by the same number of individuals, had significant differences only during the time when the power plant was shut down. (Table 17). All the evenness values for stations 2 and 3 ranged between 0.7 and 0.9 with the exception of incubation period 3 when values were about 0.4 (Table 18). The great drop in evenness was the primary reason for the decrease in diversity in May. These samples were dominated by a few species (Tables 9, 10).

Station comparisons in species richness of periphyton algal samples show stations 2 and 3 similar to each other and different from station 1. Stations 2 and 3 had higher richness than station 1 for the first two incubation periods, approximately equal to station 1 for incubation period 3, and much higher than station 1 in the final incubation period (Table 19). Mean richness during power plant operation was 2.10 for station 1, but 4.10 and 4.19 for stations 2 and 3, respectively. Richness was significantly different among stations for incubation period 2 (95% confidence level) and

Table 15. Mean diversity (H") of periphyton algae per slide counted for each sampling station and incubation period at Tradinghouse Creek Reservoir

Incubation Period	Station 1	Station 2	Station 3
Jan. 6-20, 1973	1.40	2.73	2.42
Mar. 12-26, 1973	1.40	2.70	2.89
May 16-30, 1973	1.69	1.07	1.41
Jun. 13-27, 1973	0.96	2.63	2.44

Table 16. Analyses of variance for periphyton diversity (H") on glass slides colonized at Tradinghouse Creek Reservoir sampling station 1-3, January - June, 1973.

January 6 - 20

	SS	DF	MS	F-ratio
Stations	3.83	2	1.92	4.57*
Residual	3.36	8	0.42	
Total	7.19	10	--	

March 12 -26

	SS	DF	MS	F-ratio
Stations	3.95	2	1.98	9.88*
Residual	1.20	6	0.20	
Total	5.15	8	--	

May 12-26

	SS	DF	MS	F-ratio
Stations	0.66	2	0.33	0.73
Residual	3.14	7	0.45	
Total	3.80	9	--	

June 13-27

	SS	DF	MS	F-ratio
Stations	5.03	2	2.52	16.80**
Residual	0.88	6	0.15	
Total	5.91	8	--	

* indicates significance at $\alpha = 0.05$
** indicates significance at $\alpha = 0.01$

Table 17. Analyses of variance for periphyton evenness (J) on glass slides colonized at Tradinghouse Creek Reservoir sampling stations 1-3, January - June, 1973.

January 6-20

	SS	DF	MS	F-ratio
Stations	0.10	2	0.05	0.71
Residual	0.55	8	0.07	
Total	0.65	10	---	

March 12-26

	SS	DF	MS	F-ratio
Stations	0.31	2	0.16	8.00*
Residual	0.10	6	0.02	
Total	0.41	8		

May 17-31

	SS	DF	MS	F-ratio
Stations	0.20	2	0.10	2.00
Residual	0.32	7	0.05	
Total	0.52	9	--	

June 13-27

	SS	DF	MS	F-ratio
Stations	0.05	2	0.03	0.44
Residual	0.20	6	0.07	
Total	0.25	8	--	

* indicates significance at $\alpha = 0.05$

Table 18. Mean evenness (J) of periphyton algae for slides counted at each sampling station and incubation period at Tradinghouse Creek Reservoir.

Incubation Period	Station 1	Station 2	Station 3
Jan. 6-20, 1973	0.62	0.84	0.78
Mar. 12-26, 1973	0.47	0.81	0.89
May 16-30, 1973	0.68	0.35	0.44
Jun. 13-27, 1973	0.57	0.76	0.70

Table 19. Mean richness (D́) of periphyton algae for slides counted at each sampling station and incubation period at Tradinghouse Creek Reservoir

Incubation Period	Station 1	Station 2	Station 3
Jan. 6-20, 1973	2.25	4.52	3.86
Mar. 12-26, 1973	2.84	4.67	4.61
May 16-30, 1973	2.85	2.69	3.21
Jun. 13-27, 1973	1.19	5.10	5.51

4 (99.5% confidence level) (Table 20). Weak negative correlations were calculated for all three measures of community structure and maximum temperature of incubation (Figures 6 - 8).

B. Photosynthetic Response to Abrupt Thermal Change

It has been hypothesized that abrupt thermal changes are more likely to produce detrimental effects on periphyton communities than are high temperatures or large ΔTs (Lind, personal communication). More specifically, the effects of a power plant shut down or start up after a period when heat has not been produced would be expected to be more detrimental to periphyton communities than a continual power plant operation accompanied by a gradual seasonal temperature rise.

Evaluation of possible effects of abrupt thermal changes on periphyton photosynthetic capabilities was best described in terms of primary production per unit biomass (P_2).

Biomass determinations on the glass rods used for primary production experiments showed highest mean biomass at station 2, lower at station 3 and lowest at station 1 for the Jan. 6 - Feb. 6 colonization period (Table 21) (Figure 9). Mean temperatures of colonization for the three stations were 17.9, 14.1, and 11.4 C for stations 1, 2, and 3, respectively. Significant differences in biomass were found among stations (Table 22). An orthogonal comparison showed station 1 to be different from stations 2 and 3 as well as stations 2 and 3 to be different from each other.

Primary periphyton production per unit biomass (P_2) was greatest at station 1 (colonized at about 18 C) and lower at stations 2 (colonized at about 16 C) and 3 (colonized at about 12 C) for the 10° C experimental

Table 20. Analyses of variance for periphyton richness (D') on glass slides colonized at Tradinghouse Creek Reservoir sampling stations 1-3, January - June, 1973.

January 6-20

	SS	DF	MS	F-ratio
Stations	10.74	2	5.37	3.58
Residual	11.99	8	1.50	
Total	22.73	10	--	

March 12-26

	SS	DF	MS	F-ratio
Stations	7.23	2	3.62	6.69*
Residual	3.25	6	0.54	
Total	10.48	8	--	

May 17-31

	SS	DF	MS	F-ratio
Stations	0.44	2	0.22	0.21
Residual	7.30	7	1.04	
Total	7.74	9	--	

June 13-27

	SS	DF	MS	F-ratio
Stations	34.12	2	17.06	60.93 **
Residual	1.69	6	0.28	
Total	35.81	8	--	

* indicates significance at $\alpha = 0.05$
** indicates significance at $\alpha = 0.01$

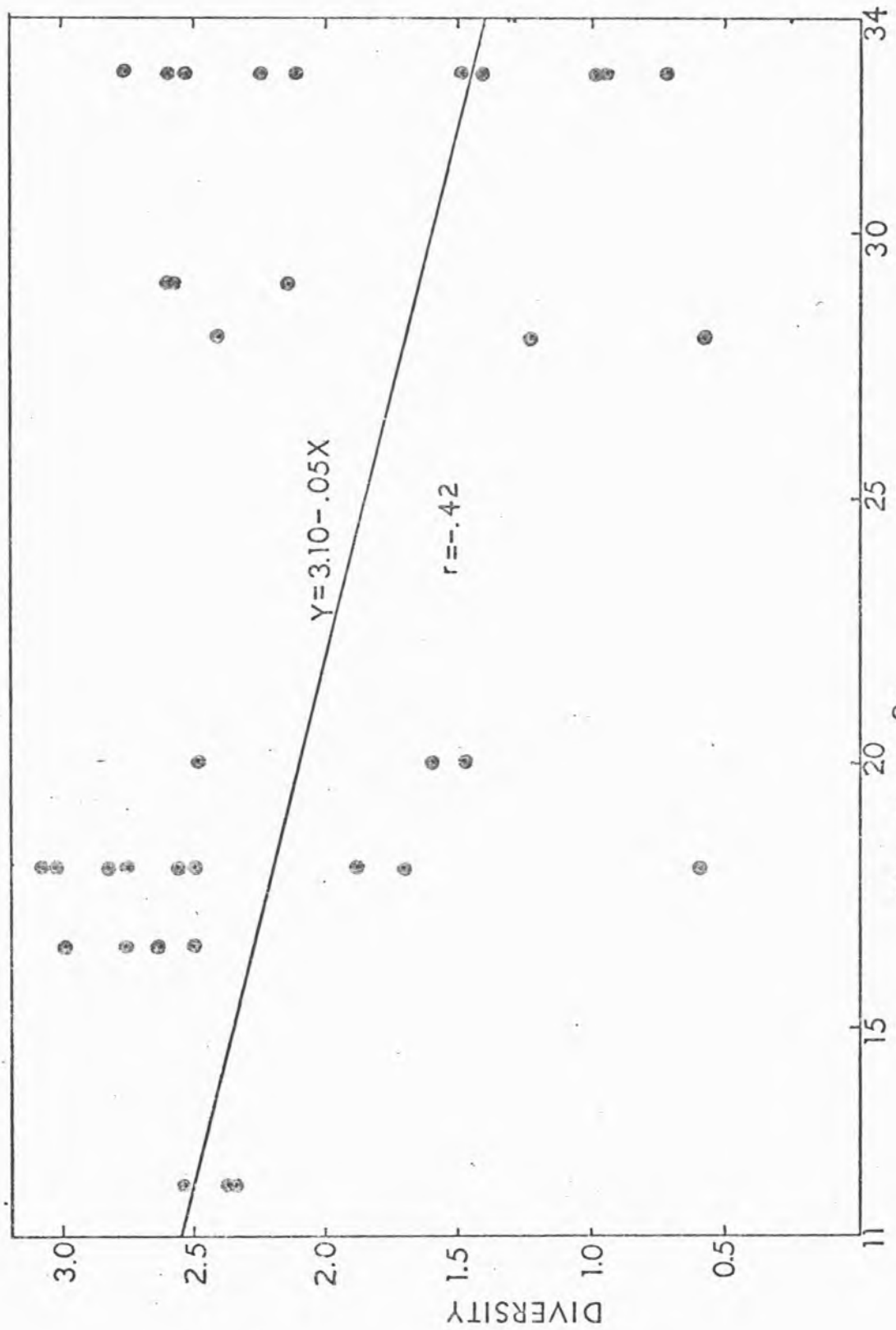

Figure 6. Scatter diagram for Diversity (H') of periphyton from Tradinghouse Creek Reservoir sampling stations 1-3, January - June 1973.

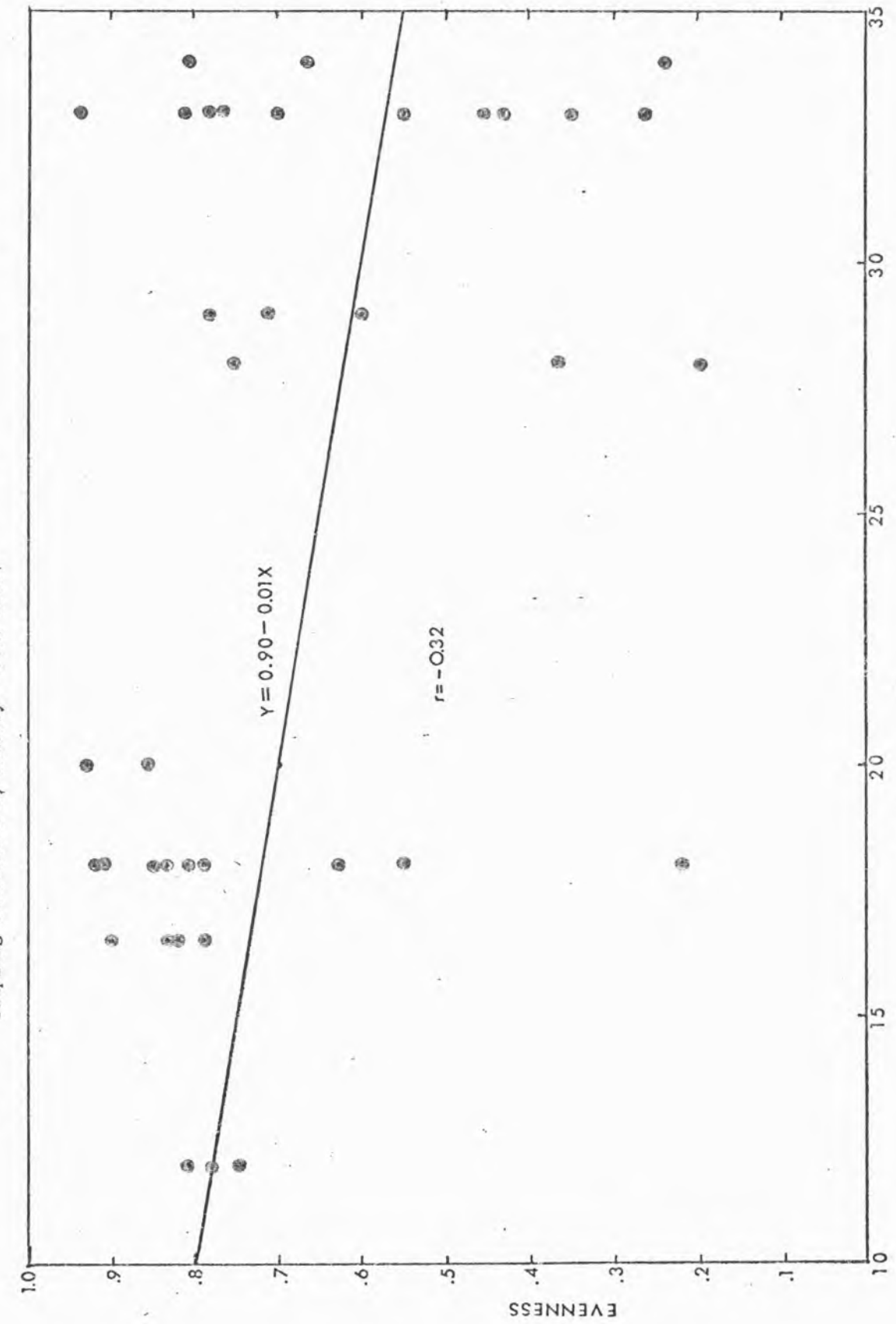

Figure 7. Scatter diagram for Evenness (J) of periphyton from Tradinghouse Creek Reservoir sampling stations 1-3, January - June 1973.

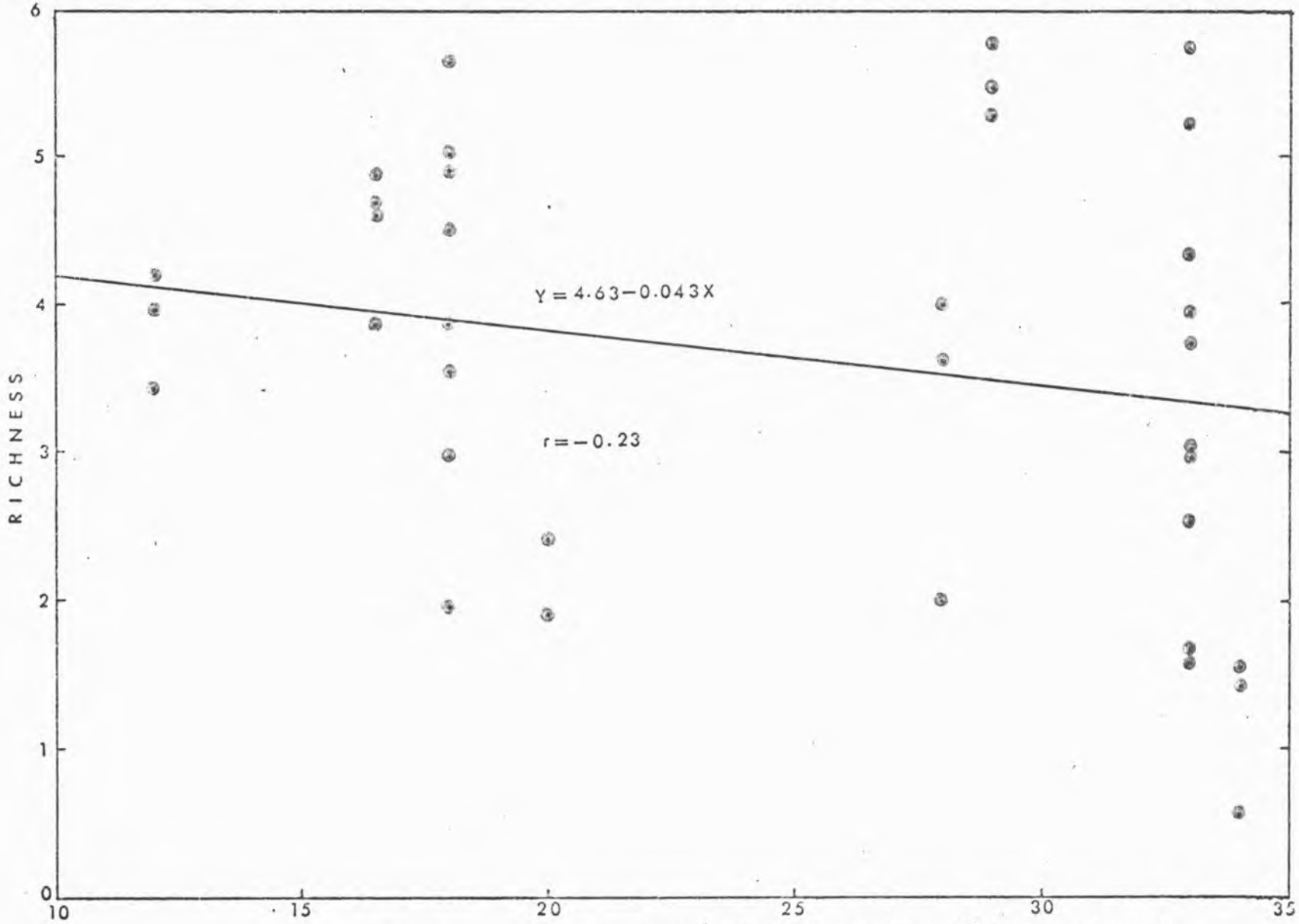

Figure 8. Scatter diagram for Richness (D′) of periphyton from Tradinghouse Creek Reservoir sampling station 1-3, January - June, 1973.

Table 21. Periphyton biomass at Tradinghouse Creek Reservoir sampling stations 1-3, 6 January-6 February, 1973.

Station	Biomass (mg. organic matter m^{-2})	Mean
1	9.275, 1.775, 3.950, 2.213, 0.963, 2.013, 0.688	2.982
2	21.238, 37.750, 30.038, 34.600, 32.838, 43.063, 4.938	29.209
3	12.888, 15.675, 28.775, 25.413, 18.175, 22.700, 10.375	19.144

Figure 9. Periphyton biomass at Tradinghouse Creek Reservoir sampling station 1-3, January 6 - February 6, 1973.

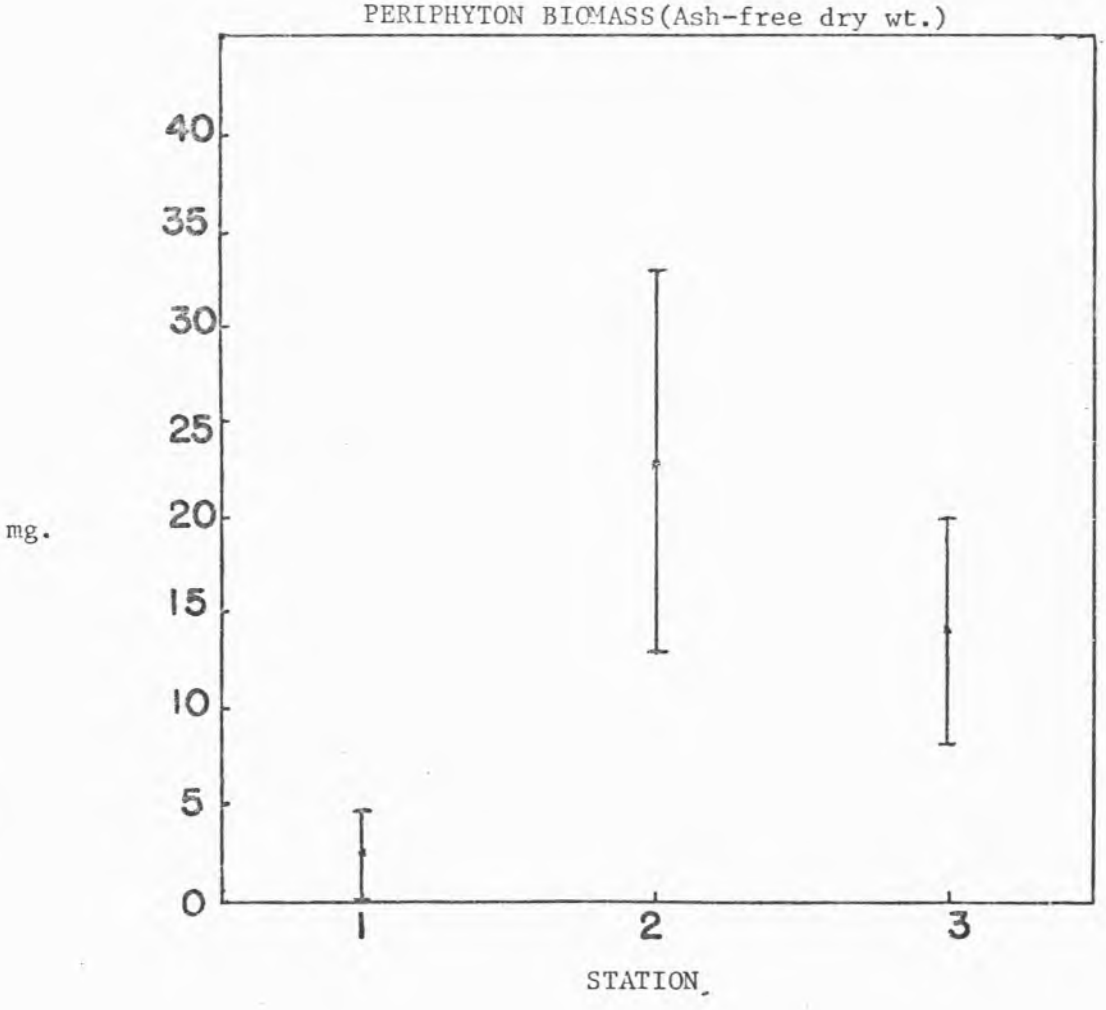

Table 22. Analysis of variance of periphyton Biomass values from Tradinghouse Creek Reservoir sampling stations 1-3, 6 January - 6 February, 1973.

	S.S.	D.F.	M.S.	F-ratio
Stations	2450.71	2	1225.36	17.14*
Residual	1286.94	18	71.50	
Total	3737.65	20		

*Significant at the 95% confidence level.

incubation temperature (Table 23). Significant differences were found among stations for the analysis of variance (Table 24). An orthogonal comparison revealed significant differences between station 1 and the other 2 stations, but no significant difference between stations 2 and 3. The regression analysis for primary periphyton production (P_2) at the 10 C experimental temperature gave a correlation coefficient of 0.59 (Figure 10).

Primary periphyton production was also greatest at station 1 at the 30° C experimental incubation temperature with stations 2 and 3 being lower (Table 23). Analysis of variance for primary periphyton production (P_2) at 30° C experimental temperature indicated no significant differences among stations (Table 25). A regression analysis gave a correlation coefficient of 0.50 for the 30° C experimental temperature (Figure 11).

Primary periphyton production (P_1) on the basis of area was also significantly different among stations for the 10° C experimental temperature (Table 26). An orthogonal comparison indicated significant differences between station 1 and the other two stations, but not between stations 2 and 3. A positive regression was calculated for primary periphyton production (P_1) and incubation temperature for the 10 C experimental temperature (Figure 12).

At the 30 C experimental temperature no significant differences in primary periphyton production (P_1) were found among stations (Table 27). The regression analysis showed no correlation between mean temperature of colonization and primary periphyton production (P_1) (Figure 13).

Table 23. Primary periphyton production, P_2 (ug C mg organic matter^{-1} hr^{-1}), at 10 and 30 C experimental temperatures from Tradinghouse Creek Reservoir sampling stations 1-3.

Incubation Temp. (C)	Colonization Station (Approximate temperature of colonization C)		
	1 (18)	2 (16)	3 (12)
10	0.1610	0.0016	0.0586
10	0.5070	0.0000	0.0557
10	0.5820	0.0125	0.0630
10	1.1900	0.4430	0.0444
mean	0.6100	0.1143	0.0725
30	0.0137	0.0046	0.0312
30	1.1000	0.0251	0.0085
30	0.6690	------	0.0858
30	------	0.1750	0.2570
mean	0.5942	0.0682	0.0956

Table 24. Analysis of variance for periphyton primary production (P_2) from Tradinghouse Creek Reservoir sampling stations 1-3 at 10 deg. C experimental temperature.

	S.S.	D.F.	M.S.	F-ratio
Stations	$7.42X10^{-7}$	2	$3.71X10^{-7}$	4.78 *
Residual	$6.98X10^{-7}$	9	$7.76X10^{-8}$	
Total	$1.44X10^{-6}$	11		

*Significant at the 95% confidence level.

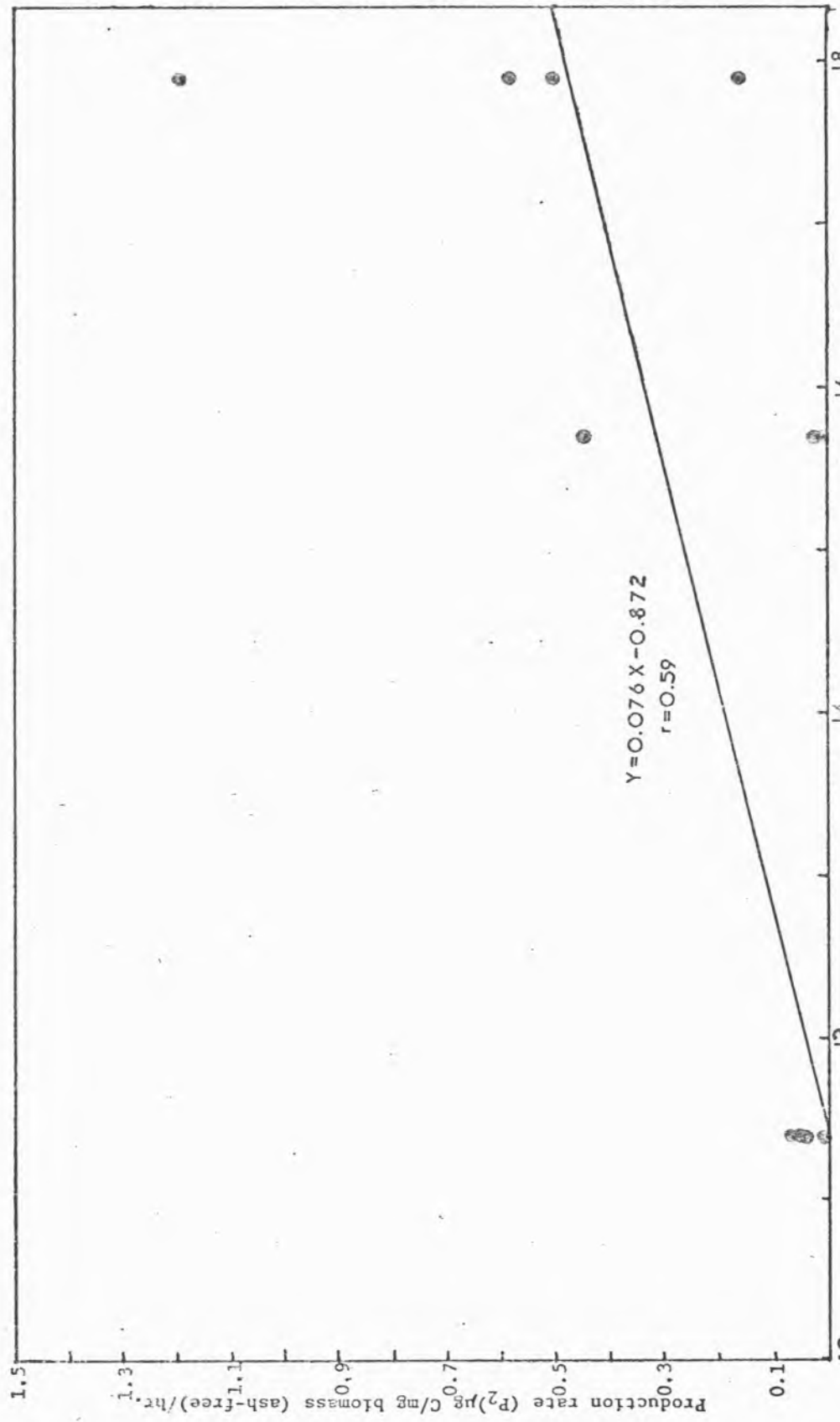

Figure 10. Scatter diagram for production (P_2) and mean temperature of periphyton colonization for 10° C experimental temperature.

Table 25. Analysis of variance for periphyton primary production(P_2) from Tradinghouse Creek Reservoir sampling stations 1-3 at 30 deg. C experimental temperature.

	S.S.	D.F.	M.S.	F-ratio
Stations	$5.69X10^{-7}$	2	$2.85X10^{-7}$	3.02
Residual	$6.61X10^{-7}$	7	$9.44X10^{-8}$	
Total	$1.23X10^{-6}$	9		

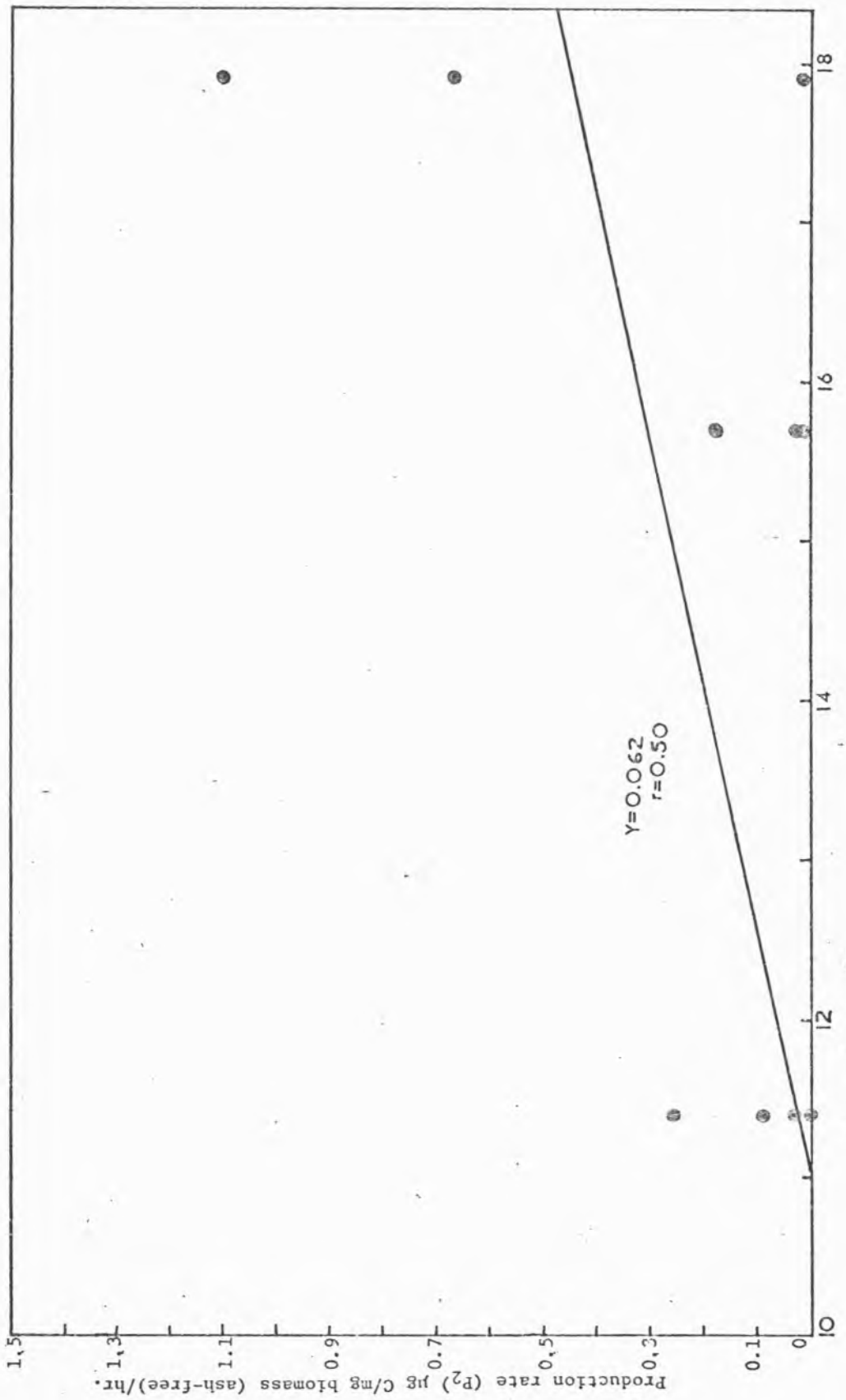

Figure 11. Scatter diagram for production (P_2) and mean temperature of periphyton colonization for 30° C experimental temperature.

Table 26. Analysis of variance for periphyton primary production (P_1) from Tradinghouse Creek Reservoir sampling stations 1-3 at 10 deg. C experimental temperature.

	S.S.	D.F.	M.S.	F-ratio
Stations	6765.30	2	3382.65	7.58 *
Residual	4018.20	9	446.47	
Total	10783.50	11		

*Significant at the 95% confidence level.

Figure 12. Scatter diagram for production (P_1) and mean temperature of periphyton colonization for 10° C experimental temperature.

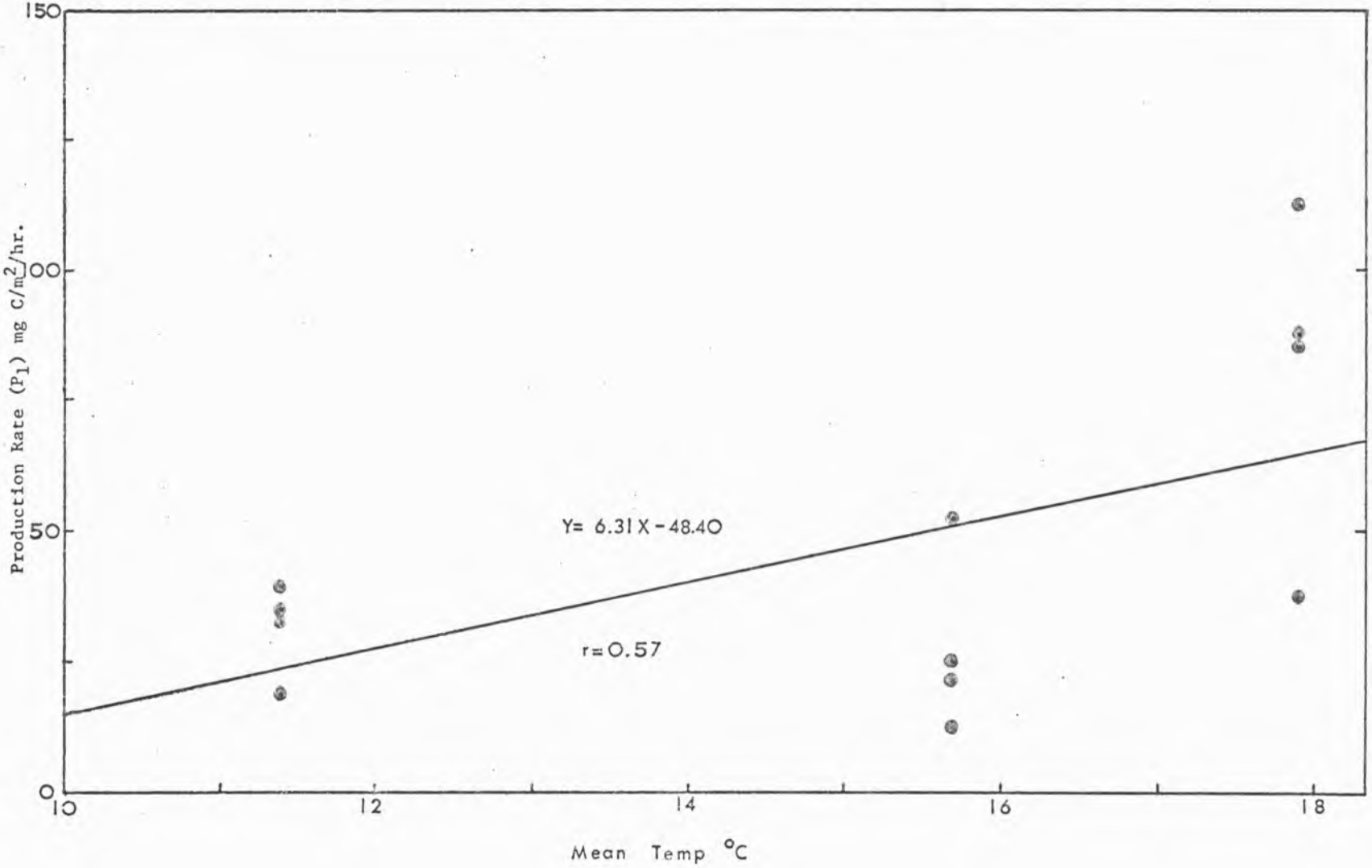

Table 27. Analysis of variance for periphyton primary production (P_1) from Tradinghouse Creek Reservoir sampling stations 1-3 at 30 deg. C experimental temperature.

	S.S.	D.F.	M.S.	F-ratio
Stations	111.63	2	55.82	0.170
Residual	2619.66	8	327.46	
Total	2731.29	10		

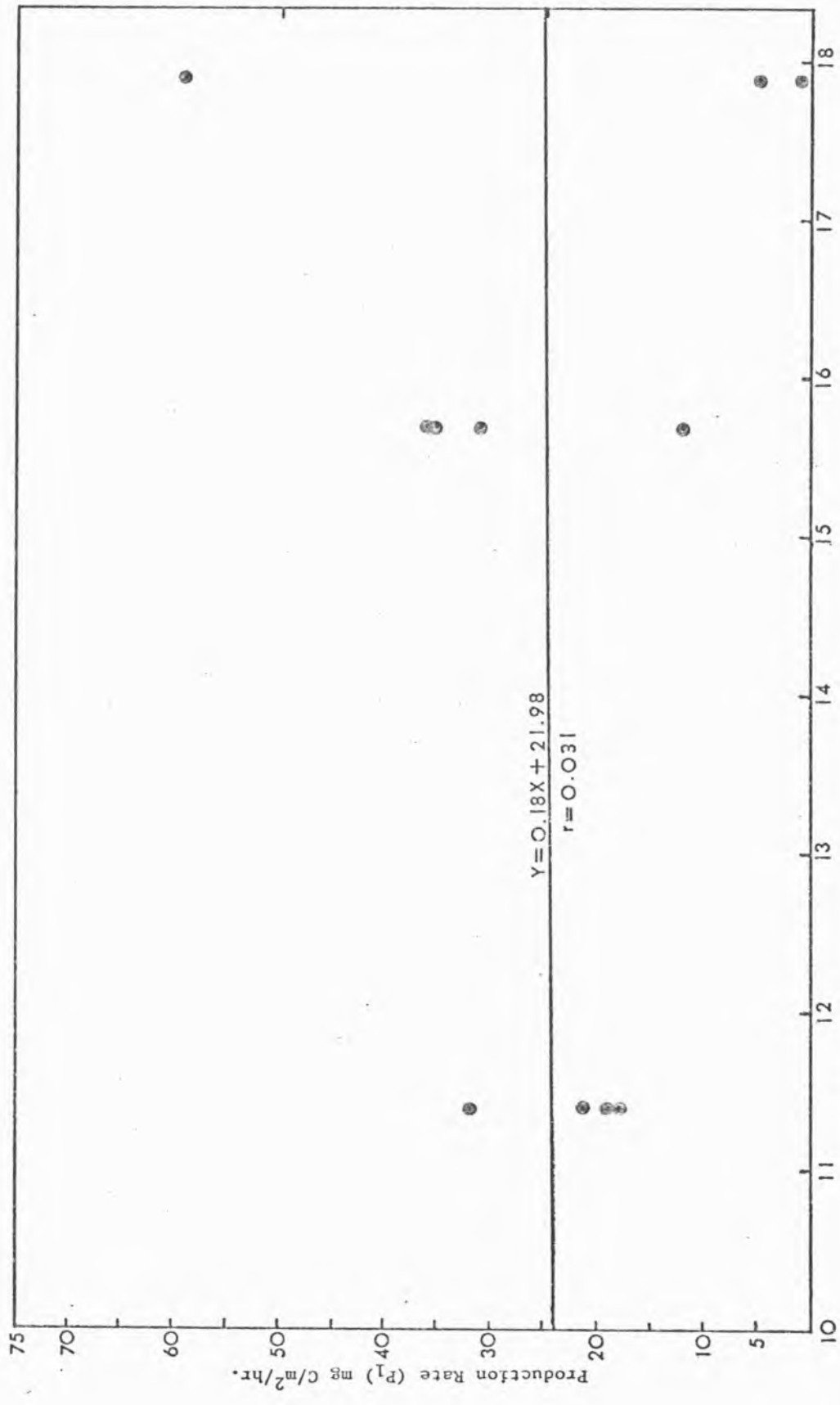

Figure 13. Scatter diagram for production (P_1) and mean temperature of periphyton colonization for 30° C experimental temperature.

V. DISCUSSION

A. Community Structure

The primary question to be answered in the community structure portion of this study was posed by Patrick (1968). She concluded, "We know that the natural systems are characterized by a high diversity of species and that raising the temperature beyond the optimum for these species reduces diversity. The question is, how much and in what way can this diversity be altered and not reduce the energy flow and productivity of the system, and more important, the stability of the system through time?" In this context periphyton diversity was measured at two locations in the discharge canal and one location near the intake of a power plant to determine possible alterations in diversity due to thermal additions from the water circulation by the power plant.

Coutant (1962) observed an increase in both variety and numbers of organisms as he progressed from hot to cool water, demonstrating temperature as the primary limiting factor. A temperature of near 90 F (32.2 C) was the maximum at which a normal population structure could be maintained with extensive loss in numbers and diversity of organisms accompanying further rise. Many others have noted the importance of temperature as a determinant of community structure (Patrick, 1948; Wurtz and Dolan, 1960; McIntire, 1968a; McIntire, 1968b; Patrick, Roberts and Davis, 1968; Patrick, 1969; Gurtz and Weiss, 1972; Wulff and McIntire, 1972). Several investigators do not concur exactly with the temperature tolerance limit set by Coutant.

Patrick (1969) noted that temperatures above 35 C would cause shifts in major algal groups and Kullberg (1971) found the mean maximum temperature endured by diatoms in thermal spring effluents was 43.2 C and 40.9 C for the green algae. A temperature critical in shifting community structure away from diatom dominance in the discharge canal of a Susquehanna River power plant was 93 F (33.9 C) (Hatfield et al., 1966). Other investigators have noted critical temperatures for major shifts in community structure more dependent on the ΔT, the rise above ambient water temperatures. Zieman (1970) found that algal diversity was depressed by temperatures 5 C above the intake structures in the Florida Gulf of Mexico.

Maximum measured temperatures for stations in the discharge canal of the Tradinghouse Creek power plant during the colonization of substrates used for community structure investigations were 34.0 and 33.0 C for stations 1 and 2, respectively. The maximum temperature for the reference station 3, located near the power plant intake structure was 29.0 C (Table 1). The mean ΔT for stations 1 and 2, respectively was 4.9 and 3.9 C. Maximum ΔT was observed when ambient water temperatures were coolest. A ΔT of 8.0 C was observed in January, 1973 (Table 1). Minimum ΔT was observed during the period when the Tradinghouse Creek power plant was shut down for repairs. During the shutdown a maximum ΔT of 0.5 C was measured.

The water temperatures encountered during this study represent winter, spring, and early to mid-summer measurements. Any effects on periphyton due to high temperatures would likely be magnified in late summer and early fall (Gurtz and Weiss, 1972) when temperatures are higher than those recorded in Table 1 (c.f. Table 1, Lind, 1975). While the maximum recorded temperature during any one of the periods of colonization was 34 C at station 1, the temperature had risen to 36.5 by June, 1973 (Table 1).

Colonization of Substrates by Periphyton

As Patrick (1964) stated, "The complex pollution which we encounter today is of recent origin, and time has not been sufficiently long for specific taxa to evolve which are characteristic of its many components. Rather, we have certain species which are tolerant to one or more of a wide variety of chemical and physical conditions commonly associated with pollution." These tolerant species probably are the major community constituents in stressed situations encountered in a power plant discharge canal.

Station 1 generally exhibited much lower densities than did stations 2 and 3 except during the second colonization period when heat was not being produced. Power plant operation apparently had the effect of greatly reducing periphyton density during periods when heat was being produced (Tables 2-13). Since stations 2 and 3 had the least colonization during the second heat-free incubation period, the sharp rise for station 1 during this period was not a seasonal effect. Whitford (1960) and others have indicated a higher production for areas of greater stream velocity. Since station 1 which had the maximum current velocity generally exhibited relatively low densities except during the period when there were no heat additions and at that time exhibited the highest relative density, it thus might be concluded that the heat addition had a repression effect on periphyton density at station 1 over the possible stimulation by current velocity but did not effect station 2, downstream, in the same manner.

Several investigators have concluded that the presence or absence of major taxonomic groups should be used as indicators of environmental conditions (Patrick, 1950; McIntire, 1968b). Both McIntire (1968b) and Patrick (1969) have shown drastic shifts in major taxonomic groups associated with

temperature increases. In the present investigation trends for the major taxonomic groups were shown in Figure 5. Emphasis has been placed on the diatoms and blue-green algae. Patrick (1969) stated that above 35 C blue-green algae often become dominant, especially if the high temperature is maintained for long periods. This trend was graphically illustrated in Figure 4 when the percent composition of diatoms at station 1 was reduced during the third colonization period when the temperature reached 33 C (Table 1) and was further reduced during the fourth colonization period when the temperature reached 34 C. A reciprocal increase in the percent composition of blue-greens was observed for station 1 during the same two colonization periods. These data indicated a critical temperature for the shift from diatoms populations to be expected if the temperature persists. Stations 2 and 3 had a moderate decrease in diatoms accompanied by an increase in blue-greens for the fourth period of colonization when recorded temperatures reached 33 and 29 C respectively (Table 1). While temperature appeared to be the major determinant of shifts in major algal groups, other factors such as a nutrient related algal shift, i.e. nitrogen fixers (blue-greens) come in when nitrogen is low in summer. Patrick, Roberts, and Davis (1968) found that when temperatures were at suboptimal or superoptimal levels, other deleterious sublethal environmental factors will have a greater impact. Chlorination which is sometimes used to rid power plants of boiler buildup may have been a contributing factor in decreasing periphyton densities.

The number of taxa represented in each colonization period was higher at stations 2 and 3 than at station 1. Patrick (1950) described healthy conditions for streams when a large number of taxa are each represented by a small number of individuals. The rise in number of taxa at station 1 between the first colonization period and the second (Figure 5) may represent

a more healthy situation when the power plant was not in operation. Station 1 then showed a rapid decrease in numbers of taxa during the third and fourth colonization periods. In contrast there was a slight decline during the third period of colonization at stations 2 and 3 followed by an increase during the fourth period of colonization. Any possible synergistic effects of heat and other variables would be more likely to be manifested at station 1.

Diversity

Biotic diversity is any suitable function that has its minimum when all individuals belong to the same species and a maximum when every individual belongs to a different species (Margalef, 1965). Changes in diversity reflect changes in the community structure as a result of naturally occurring phenomena or because of destructive man-induced changes in the environment (Coutant, 1962). Sepcifically, decreases in diversity are associated with environmental stress and thus, decreases in diversity may be suitable indicators of stress. Periphyton diversity measurements were designed to measure differences between naturally occurring phenomena at reference station 3 and man-induced changes at stations 1 and 2.

Since great similarities were found for periphyton diversities at stations 2 and 3 (Table 15) and both were higher than station 1, we conclude that the periphyton community at station 1 was adversely affected by the heated water discharge from the Tradinghouse Creek power plant. When the power plant was not in operation the pattern among stations was not appreciably different (Table 15). Lower periphyton diversity at station 1 is indicative of power plant operation thermal stress. Some support is added by the results shown in Figures 6-8 which indicate a weak negative correlation between maximum temperatures of colonization and all three measures of

periphyton diversity.

The significant differences found among stations for the January and June colonization periods when the power plant was producing heat and also for the March period when no heat additions were being produced (Table 16) lend support to the argument concerning abrupt thermal changes which are being tested in the latter section of this investigation. The reason for the lack of a significant difference among stations in the third colonization period was not that staton 1 diversity had an appreciable change, but that periphyton diversity for stations 2 and 3 showed a large decrease. The decrease in diversity corresponded with a period when the power plant had been started up again after a two month shutdown. Specifically, stations 2 and 3 encountered a temperature rise of about 10 C just prior to and including the third incubation period (Table 1). This was the largest monthly rise in temperature at these two stations during this study.

Some general types of environments with low diversities have been described by Slobodkin and Sanders (1969). They listed new environments, severe environments, and unpredictable environments. The periphyton community at station 1 had a combination of the three listed types of environments contributing to this relatively low diversity situation.

Evenness values (J), which give an indication of the apportionment of individuals among the species present (Pielou, 1975), were generally similar between stations 2 and 3 and were both generally higher than at station 1. No significant differences were found among stations during power plant operation (Table 17). The significant difference in evenness calculated for the second incubation period can be attributed to the decrease in evenness at station 1. Because of the extremely small number of individuals present at station 1 during power plant operation (Tables 2,

7, 10), evenness of distribution is more likely. The rise in density of individuals at station 1 during the power plant shutdown was accompanied by a less even distribution among the taxa present. The preceeding discussion for diversity should also be applied here. The major noteworthy deviation from this pattern was observed for colonization period three when the sharp drop occurred in periphyton diversity at stations 2 and 3 and at the same time an increase was observed for station 1 (Table 4). This drastic drop in evenness may be explained through examination of tables 9 and 10. While the number of taxa decreased slightly, densities of a few taxa increased drastically. In natural situations this happens when conditions change such that certain species have a competitive advantage over the others. In this instance the nutrient levels may have been just right, or the water temperature may have risen to a level too high for some of the competitive species, but more likely a combination of several physical and chemical factors led to the dominance of the periphyton community by a few species.

Significant richness (D') differences were found among stations for the March and June colonization periods (Table 20). Richness is indicative of the number of different taxa present. Richness was significantly greater for stations 2 and 3 in June because of the great reduction in numbers of taxa able to survive the high temperatures encountered at station 1. Mean richness was approximately twice as high at stations 2 and 3 than at station 1. Stations 2 and 3 experienced a substantial drop in richness for colonization period three in May, 1973 (Table 19). Richness dropped to a level that approximated richness at station 1. The drop in number of species was not a drastic drop and was followed by an increase during the fourth period of colonization (June, 1973) (Table 19). The decrease from colonization period two to period three was primarily due to losses in numbers of diatom species

(Tables 6, 7, 9, 10). The drop then was probably attributable to temperature increases which approached the upper limits of some diatoms without reaching the temperatures needed to cause a major shift in periphyton community structure. Station 1, at the same colonization periods, had already experienced the shift in major algal groups by the end of the third colonization period (Figure 4) which showed up as no change in species richness (Table 19). Spatially, station 1 slides were not as crowded as slides from stations 2 and 3. By the fourth period of colonization, stations 2 and 3 had shifted major algal groups to include a greater number of blue-greens and greens (Figure 4) and thus experienced a rise in richness. Station 1 periphyton reached a point of stress by colonization period four (June, 1973) which was indicated by a sharp decrease in richness (Table 19).

A constant "reseeding" of communities would be likely at the circulating water stations 1 and 2 without the heat stress. A static water station such as station 3 would require a much greater length of time for "reseeding" under the same stressful conditions.

B. Photosynthetic Response to Abrupt Thermal Changes

Biomass and Primary Production

The hypothesis being tested was whether or not abrupt thermal changes caused by the Tradinghouse Creek power plant significantly increased or decreased primary periphyton production in periphyton previously colonized at two locations in the discharge and one near the intake of a power plant. Brock (1967) found the greatest periphyton standing crop at 58 C in thermal spring runoffs and lower standing crops at temperatures below 50 C. He concluded that the decreases were due to grazing at temperatures below 50 C. Brock noted, however, that total community breakdown and subsequent

recolonization were recorded, particularly during periods of rapid temperature change or silt load. While power plant effluents may not be exactly analogous to thermal spring runoffs, certain community characteristics are the same. The temperatures encountered in the present investigation were not necessarily high enough to limit periphyton production. The rapid changes in temperature, as noted by Brock, were the most deleterious single factor which disrupted attached algal communities. Because of its close proximity to the Tradinghouse Creek power plant, station 1 was most susceptible to rapid temperature changes and thus to greater losses in biomass due to community breakdown. Primary phytoplankton production was reduced by thermal additions in Tradinghouse Creek Reservoir (Lind, 1975).

Current velocity has been found to be a contributing factor in determination of periphyton biomass by several investigators. McIntire (1966a) found greater biomass in faster currents after an initial period when colonization was retarded. Ball, Kevern, and Linton (1969) also found rates of colonization to be slower in faster water but a higher maxima was possible at all but the highest velocity. Findenegg (1965a) noted losses in biomass due to fast flushing water and Neal, Patten, and DePoe (1967) found sloughing of biomass to be most important where biomass and turbulence were highest. At station 1 the current velocity and turbulence were greatest, with station 2 intermediate in these respects, and station 3 the lowest. Consistent with these earlier findings, station 1 was slowest in rate of colonization, most succeptible to sloughing from the turbulence and fast flushing water and probably not able to reach the higher maxima possible for intermediate current velocity locations such as station 2.

Biomass values on an ash-free basis have been compared with values found in the literature for natural and artificial substrates (Tables 28 and

Investigators	Body of Water	Substrate	Incubation Period	Biomass
Young (1945)	Douglas Lake, Michigan	living bullrushes dead bullrushes		39.9mg/dm^2 96.0mg/dm^2
Assman (1951,1953)		Equisetum		77.1mg/dm^2
McConnell and Sigler (1959)	Logan River, Utah	rocks		dry wt. 250 mg/dm^2
Felfoldy (1961)	Lake Balaton			Gomphonema sp. 1820 mg/dm^2 Diatoma elongatum 1190 mg/dm^2
McIntire (1964)	laboratory stream	rocks		1870 mg/dm^2
Kobayasi (1961)	Arakawa River, Japan	rock		25-70 mg/dm^2
Drum (1963)	DesMoines River, Iowa	rocks		ash-free 2100 mg/dm^2
Stockner and Armstrong (1971)	Ontario Lakes	rock		organic matter 68-125 mg/dm^2

Table 28. Periphyton biomass on natural substrates from the literature.

29). The mean values for stations 2 and 3 were higher than most of those determined by other investigators, but mean values for station 1 were lower than for most of those in Tables 28 and 29. In comparison to other biomass values for studies using glass and plexiglass substrates, periphyton biomass was higher at all stations than for Sodom Lake, Michigan (Newcombe, 1949). Production was higher in Tradinghouse Creek Reservoir than for Falls Lake or Alkali Lake, Washington (Castenholz, 1960a, 1961). Tradinghouse Creek Reservoir biomass and production values also exceeded those found by Cushing (1967) in the Columbia River, Washington, although Cushing's incubation period lasted only 14 days. Incubation periods for studies done by Kevern et al. (1965) were comparable to those for this investigation as were his substrates and his values generally were higher than those for station 1, but lower than those for stations 2 and 3 (Table 29). Comparisons to other substrate types would be only partially valid. The study done by McIntire et al. (1964), for instance, utilized pans of rocks in which the exposed surfaces for colonization were much greater than indicated in Table 28, even though they approximated a natural stream bottom.

In conclusion, periphyton biomass values were generally higher for Trandinghouse Creek Reservoir than for those reported in the literature, except at station 1 where biomass was decreased by more rapid temperature fluctuations, higher maximum temperature and higher turbulence and current velocity which slowed colonization rates and increased losses due to sloughing.

The presentation of primary periphyton production values in this paper has been given in two parts; on the basis of area (P_1) and on the basis of biomass (P_2). Conventional production rates have been given as in Table 30 on the basis of mg C $m^{-2}hr^{-1}$ or on an annual basis. Westlake (1965) reported

Table 29. Periphyton biomass on artificial substrates from the literature.

Investigators	Body of Water	Substrate	Incubation Period	Biomass
Newcombe (1949)	Sodon Lake, Michigan	glass slides		ash-free dry wt. 3.82 mg/dm^2
Castenholz (1960a, 1961)	Falls Lake, Wash.			32.4mg/dm^2
	Alkali Lake, Wash.			29.4mg/dm^2
Sladekova (1962)	Sedlice Reservoir	glass slides		158.7mg/dm^2
Odum (1957)	Silver Springs, Fla.			1880 mg/dm^2
Cushing (1967)	Columbia River, Washington	glass slides	14 days	dry wt, 42 mg/dm^2 ash-free 18 mg/dm^2
Kevern et al. (1965)	lab streams	plexiglass	34 days	ash-free 120 mg/dm^2
	a Tennessee spring	plexiglass	35 days	ash-free 52 mg/dm^2
	White Oak Creek, Tenn.	glass slides		dry wt. 156 mg/dm^2
	bottom of White Oak Creek	glass slides		ash-free 27-112 mg/dm^2
Present Study	Tradinghouse Creek Reservoir	glass rods	31 days	organic matter 42-365 mg/dm^2
	Station 1	glass rods	31 days	organic matter 42 mg/dm^2
	Station 2	glass rods	31 days	organic matter 365 mg/dm^2
	Station 3	glass rods	31 days	organic matter 239 mg/dm^2

Table 30. Primary periphyton productivity from the literature and from Tradinghouse Creek Reservoir.

Investigators	Location	Substrate	Productivity
Gruendling (1971)	Marion Lake	pelic	44.2 gC m^{-2} yr^{-1}
McConnell and Sigler (1959)	Logan River, Utah	pelic	as high as 1.0 mg O_2 hr^{-1}mg chlorophyll^{-1}
Wetzel (1964)	Borax Lake	pelic	annual mean=731.5 mgC m^{-2}day^{-1} total annual productivity= 75.5 kgC lake^{-1}day^{-1}
Burkholder, Repak, and Sibert (1965)	Long Island Sound	pelic	blue-green algae 4.45 mgC m^{-2}day^{-1} diatoms 4.05 mgC m^{-2}day^{-1} mixed flagellates and diatoms 5.03 mgC m^{-2}day^{-1}
Lenn (MS, 1966)	hot springs Mt. Lassen Nat. Pk., Calif.		summer values 7-12 gC m^{-2}day^{-1}
Flemer (1970)	Raritan River, N.J.		gross productivity(May-Sept) 4.7-11.6 g O_2 m^{-2}day^{-1}
Allen (1971)	Mich.	macrophytes in the littoral	Scirpus dominated 195 mgC $m^{-2}hr^{-1}$ Najas-Chara dominated 1807 mgC m^{-2}day^{-1}
Hickman (1971)	Abbott's Pond Priddy's Pool	pelic pelic	5.29 mgC $m^{-2}hr^{-1}$ 1.71 mgC $m^{-2}hr^{-1}$
Present Study	Tradinghouse Creek Reservoir	glass	10 C experimental temp. 27.74-79.82 mgC $m^{-2}hr^{-1}$ 30 C experimental temp. 21.72-28.86 mgC $m^{-2}hr^{-1}$

on efforts by the International Biological Programme to standardize terminology to facilitate data comparisons. Primary productivity was defined as production divided by time or production rate. Gross productivity was equal to the rate of production of organic matter including that lost to respiration and other sources. Net productivity was defined as the rate of accumulation of new organic matter or the change in biomass plus all losses except those due to respiration divided by time. Because ^{14}C was used in these primary periphyton production studies and because of the relatively short duration of the experiments, results were in terms of net primary periphyton production. While production values based on area are valuable for comparison with values recorded in the literature, production values per biomass are more useful in evaluation of the ability of a given quantity of periphyton under defined ecological conditions to produce new organic matter.

Primary production values, P_1, at 10 C were significantly higher at station 1 than at stations 2 and 3 (Table 26). Station 1 had a higher mean temperature of colonization than did stations 2 and 3 (Table 1). At 30 C experimental temperature no significant differences were found among stations (Table 27). Simply speaking, periphyton colonized at the highest temperatures maintained higher primary production levels when exposed to a cooler temperature regime (10 C) and periphyton colonized at cooler temperatures maintained lower primary production levels. Periphyton colonized at cooler temperatures and then exposed to abrupt temperature increases (30 C) experienced decreased primary production. Patrick (1969) gave a plausible explanation when she reviewed temperature effects. She noted that if temperature increases were in the range of tolerance of existing species and light, and if nutrients were sufficient, increased primary production might occur. Wariner and Brehmer (1966) found power plant effluents enhanced primary

production of marine phytoplankton with a 3 C rise in temperature, but decreased with rises of more than 5.5 C. The 30 C experimental temperature represented a rise of more than 10 C from the mean temperatures of colonization at any of the Tradinghouse Creek Reservior sampling stations (Table 1). The depressed primary production at all stations for the 30 C experimental temperature might have been expected if the ranges of tolerance for many of the periphyton species had, indeed, been exceeded.

Primary periphyton production on the basis of biomass (P_2) indicated similar trends, as far as significant differences among stations (Tables 24, 25). Examination of means, on the other hand, showed a reversal of trends. On the basis of area (P_1) station had the lowest mean primary production for the 30 C experimental temperature, but on the basis of biomass (P_2) station 1 had the highest mean production. Since station 1 had the least amount of biomass (Figure 9), periphyton was being produced at a faster rate at station 1 but was also being lost faster either through more sloughing, or increased respiration, or both.

Positive correlations were calculated for both 10 and 30° C experimental temperatures between colonization temperature and primary periphyton production (P_2) (Figures 10, 11). A positive correlation was also calculated on a per area basis (P_1) for 10° C, but not for 30° C experimental temperature (Figures 12, 13). Primary periphyton production showed virtually no correlation to mean temperature of colonization on the basis of area (P_1) because of the lower amount of biomass available to produce organic matter at station 1, but a higher production per amount of biomass was found for periphyton colonized at higher temperatures.

In addition to the review by Patrick (1969) previously mentioned, several other investigators have found temperature to be an important

variable in periphyton production (Leach, 1970; Hickman, 1971; Gruendling, 1971). Kevern and Ball (1965) found small, but insignificant differences in productivities at different temperatures in recirculating artificial streams. Allen (1971) reported carbon uptake was strongly influenced by temperature except at low temperatures where transport and diffusion mechanisms seemed to be inactivated. Temperature influenced periphyton productivities in Tradinghouse Creek Reservoir, but exact relationships were difficult to define on the basis of a single experiment. In general, higher experimental temperatures decreased productivity, while increased temperatures of colonization increased productivities at each experimental temperature.

Primary periphyton production found for Tradinghouse Creek Reservoir are not directly comparable to many of the primary periphyton production values found in the literature (Table 30). Most of the values listed in Table 30 were found using natural substrates, rather than the glass rods used in Tradinghouse Creek Reservoir studies. Periphyton production was certainly higher than values recorded by Burkholder et al. (1965) for Long Island Sound. Primary periphyton production for hot spring runoffs were higher than those for Tradinghouse Creek Reservior, but were based on an algal mat which very likely represented a much greater amount of biomass per area (Lenn, MS 1966). Raritan River values for gross productivity during summer represent lower values than those for Tradinghouse Creek Reservoir, but the functional surface area for periphyton colonization on macrophytes was much greater than for the smooth surface of a glass rod. Tradinghouse Creek Reservoir production values were greater than either Abbott's Pond or Priddy's Pool (Hickman, 1971). Taking into account differences in methodology, periphyton production values for

Tradinghouse Creek Reservoir were among the highest in the literature (Table 30).

VI. SUMMARY

A. Community Structure

Effects of a power plant thermal effluent on the periphyton community in the discharge canal were assessed in two ways. Species diversity (H") was used to detect changes in community structure of the periphyton algal community associated with power plant operation. At least three glass slides were examined from each of three stations. Samples were collected in January, March, May and June of 1973. The power plant was not in operation during the March sampling period.

Mean temperatures during power plant operation were 28.4 C for station 1 (near power plant discharge), 27.4 C for station 2 (end of discharge canal), and 23.5 C for station 3 (reference station). Mean ΔT was 4.9 C for station 1 and 3.9 C for station 2.

At station 1, periphyton algal density was much greater during the period when the power plant was shutdown. At station 2 and 3, in contrast, the lowest algal densities were for the March colonization period. Power plant operation had the effect of greatly decreasing periphyton density near the plant during periods of heat production. While heat additions depressed periphyton densities at station 1, station 2 densities, near the entrance of the discharge canal into the reservoir, were not depressed.

Diatoms and bluegreen algae dominated the periphyton algal flora. Diatoms were dominant at all stations during the January, March and May colonization periods. Bluegreens formed a greater portion of the algae from sta-

tion 1 during the May colonization period (28%) and were dominant at station 1 during June (82%). At stations 2 and 3, bluegreens reached their maximum for the study period in June (25%), yet were not the dominant algal group. Diatoms increased as bluegreens increased and temperature increased. While temperature appeared to be the primary determinant for shifts from one major algal group to another, other factors such as nutrients may have contributed.

Periphyton algal diversities were significantly different among stations for the January, March and June colonization periods. The evenness component showed significant differences among stations for only the March colonization period when no heat was being produced. The richness component had significant differences among stations for the March and June colonization periods. Decreases in diversity have been associated with environmental stress and thus may be suitable indicators of stress. Station 1 had the lowest diversity among the stations (1.5) and diversity for stations 2 and 3 were very similar (2.5). Station 1 was adversely affected by heated water discharge from Tradinghouse Creek power plant. The reason for the notable absence of a significant difference in diversity for the May colonization period resulted from a decrease at stations 2 and 3. The decrease paralleled a decrease in evenness due to the domination of the sample by a couple of species. The diversity decrease also corresponded to a large temperature increase following the power plant startup. The significant evenness difference among stations for March resulted from decreased evenness at station 1 during shutdown. The richness component decreased just prior to the beginning of the shift from diatom dominated communities. The June difference among stations mirrored the temperature rise at station 1 in June accompanied by a drastic reduction in the periphyton algal flora.

B. Photosynthetic Response to Abrupt Thermal Changes

The second method of assessing effects of power plant thermal effluents on the periphyton algal community in the discharge canal was the exposure of periphyton colonized in the discharge canal to abrupt thermal change. Glass rods were colonized at two locations in the discharge canal and one reference station near the intake. The colonized rods were put in light and dark bottles and innoculated with ^{14}C. The primary production was measured at both 10 C and 30 C, using rods from each station at both temperatures. Biomass determinations were made on the experimental rods on an ash-free weight basis. Primary periphyton production was calculated using both per area (P_1) and per unit biomass (P_2). Evaluation of possible effects of abrupt thermal changes were best described in terms of primary production per unit biomass (P_2).

Mean temperature of colonization for the three stations were 17.9, 14.1 and 11.4 C for stations 1, 2 and 3, respectively. Station 2 had the greatest biomass accumulation and station 1 the least. Because of its close proximity to the power plant, station 1 was most susceptible to rapid temperature changes and thus to larger biomass losses from community breakdown.

At the 10C experimental temperature, primary production (P_2) was significantly greater at station 1 (0.61 µg C mg organic matter^{-1}hr^{-1}) than at stations 2 (0.11 µg C mg organic matter^{-1}hr^{-1}) or 3 (0.07 µg C mg organic matter^{-1}hr^{-1}). Since station 1 had the smallest amount of biomass, and the largest primary production per unit biomass among the stations, then losses due to sloughing and respiration were also greater at station 1.

At the 30 C experimental temperature highest mean production was at station 1 also (0.59 µg C mg organic matter^{-1}hr^{-1}) with stations 2 (0.07 µg C mg organic matter^{-1}hr^{-1}) and 3 (0.10 µg C mg organic matter^{-1}hr^{-1})

being much lower. At both experimental temperatures primary periphyton production was highest nearest the power plant discharge, yet had the lowest biomass. This was indicative of a more highly tolerant community closest the power plant better able to withstand abrupt thermal changes, yet susceptible to rapid losses of biomass through sloughing and respiration.

VII. CONCLUSIONS

The temperature fluctuations which commonly occur in the discharge canals of power plants can have detrimental effects on the periphyton algal flora near the outfall. A reduction in diversity (H''), primarily in the richness (D') component, was found in the vicinity of a power plant discharge. Fewer species were able to survive in the relatively unstable environment. A reduction in periphyton algal density was also found in the vicinity of the thermal discharge. This phenomenon can be attributed to increased sloughing associated with the turbulence and rapid temperature changes in the vicinity of the power plant outfall.

Naturally occurring seasonal shifts in periphyton algal dominance were affected by temperature. The higher water temperatures near the power plant caused a shift from a diatom-dominated to bluegreen-dominated community in the May and June samples. The shift was just beginning at the other sampling locations in the June samples.

Periphyton biomass was lowest near the power plant, but production per unit biomass was highest. Rapid temperature fluctuation and increased turbulence near the power plant discharge limited colonization to a smaller number of species with lower biomass, but the periphyton present were better able to withstand abrupt thermal change as evidenced by greater primary production per unit biomass.

Detrimental effects on the periphyton algal flora which were evident at station 1 near the power plant outfall, were not in evidence at station 2

near the lower end of the discharge canal. It can be concluded that returning the heated effluent through a relatively long discharge canal alleviated most of the possible detrimental effects associated with heated power plant effluents.

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