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Simulating the Effects of Increased Temperature in a Plankton Ecosystem

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Prepared for
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FORWARD

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ABSTRACT

The effects of increased temperature on phytoplankton and zooplankton seasonal dynamics were examined using a simulation model. A literature review indicated possible changes to be explored with the model. A simulation "library" of hypotheses from various models was used to examine state variables and process effects on a daily basis, and this output was compared to data collected in Lake Ontario. Comparisons of plankton dynamics in thermally unloaded and loaded runs of the model showed differences in the two situations. Under thermal loading the spring phytoplankton peak occurs earlier and is limited by grazing whereas phosphorous limits the bloom in the unloaded environment. Also, more phytoplankton blooms occur in the model with increased temperature, and light becomes more limiting during the late summer. These comparisons led to hypotheses about adaptations favorable to phytoplankton in a thermally loaded environment including (1) a lower phosphorous and a greater nitrogen tolerance, and (2) lower optimum light intensity. Tests of these hypotheses with the simulator indicated that phytoplankton with these theoretically favored adaptations have increased productivity in the warmer waters. As a group, blue-green algae are known for the physiological characteristics found to be favorable in the thermally loaded environment.

TABLE OF CONTENTS

1355 145

LIST OF FIGURES

FIGURE NO. TITLE

LIST OF TABLES

1355 147

Since chemical reactions are temperature dependent, the thermal environment has a considerable effect on organisms and their competitive abilities. Increasing the water temperature of lakes is one of the by-products of many modern industries, specifically power plants. Hence, thermal loading is important to environmental managers who need an understanding of its impact. Perturbation studies are one of the classical methods of studying community dynamics, and thus thermal loading is of interest to ecologists trying to learn more about the interactions of natural systems. Temperature directly affects phytoplankton growth and zooplankton grazing and respiration, and one would expect that different patterns of responses would be more favorable to organisms living in warmer than normal waters. In this manner thermal loading may actually be a form of selection for certain patterns of population interactions or for those organisms having the types of responses to temperature changes favored in the warmer water. Thus, this study of thermal loading has management, ecological and evolutionary implications.

The effects of increased temperature on plankton can be studied by field, laboratory or simulation experiments. By recording detailed biological and physical information, field and laboratory studies can detect sudden and/or slight changes in the ecosystem. Simulations are useful in cases in which it is not possible or advisable to actually manipulate the ecosystem. One of these is the subjection of aquatic ecosystems to high water temperatures. Studies of the effect of previous high water temperatures carried out at the Savannah River Plant show that the return of the ecosystem to its natural state is greatly determined by the presence of a natural habitat in close proximity (Gibbons and

Sharitz, 1974). The nearer such an area is, the quicker the propagules or individuals can reach the disturbed site. In any case, there can be quite a long time before the disturbed system returns to its natural state. This indicates that care must be maintained in the initial perturbation of such systems if any value is placed on the undisturbed habitats. Computer models of ecosystems offer a means in lieu of manipulation of the natural ecosystem by which possible interactions of the system can be examined. Simulation study can provide an initial characterization of those types of processes which may be more advantageous in warmer than normal waters, and these will suggest laboratory experiments to provide further evidence for the types of organisms and interactions likely to exist in thermal plumes. The simulation experiments may also call attention to critical periods of the organisms and critical levels of nutrients, light or temperature. The importance and difficulty of knowing what details of the system to study in the field have been a major obstacle to biologists (Strickland, 1969). Understanding the nature of temperature induced changes will lead to a greater accuracy in the prediction of the effects of thermal loading in lakes.

Field and simulation studies can both be used to explore the effects of increased temperature on plankton. These approaches are similar in that each must consider the physical and chemical environment in order to understand the biological interactions and each gives some measure of the seasonal dynamics. The primary difference between the two is that field experiments tend to focus on changes in the community structure whereas simulation studies concentrate on processes and their effects on the organisms. Furthermore, field studies are restricted by the manner in which the data is obtained (for instance, plankton net size), but collection allow for later re-examination of the material. A simulation study is relatively easy to run (once the program is created) and, in a deterministic model, is repeatable; however, it represents only the modeler's best understanding of the ecosystem. Since an ecosystem model is dependent upon field and laboratory studies for parameter estimation, its validity is a function of appropriate sampling of the physical and biological system.

The study of the effect of high temperature on organisms has received much attention in recent years [e.g. Brock and Brock (1966), Coutant and Pfuderer (1973 and 1974), and Gibbons and Sharitz (1974)]. Since most enzyme reactions are temperature dependent, a change in the thermal environment can drastically affect organisms. Investigations of phytoplankton indicate that water temperature increases can cause a change in the species composition and diversity, average cell size, biomass, primary production, respiration, chlorophyll a and a number of cell divisions per day. Some species may be more adept physiologically or competitively at the warmer than normal temperatures, and thus species composition and diversity may change. The rate of metabolism is increased in warm waters according to the van't Hoff principle that the rate of chemical reaction increases with rising temperatures. Thus one would expect a decrease in the average cell size, but an increase in biomass, primary production, respiration, chlorophyll a content and the cell division rate. A number of studies of the effect of increased temperature on phytoplankton is summarized in Table 1. Each of these studies had a control consisting of organisms in the normal environment to which characteristics of organisms in the warm waters were compared. In general, the effects of increased temperature on plankton did not differ from those predicted. The interaction of the effects of temperature with those of light intensity and nutrients is apparent from the table.

The plankton model simulator is a "library" of programs using different biological hypotheses translated into equations. To facilitate the readers' understanding of the simulator, this section includes a discussion of the library, its assumptions and restrictions, the comparison methodology and the way thermal loading was simulated.

The simulator library consists of a number of models drawn from the plankton literature and incorporating the biological framework given in Figure 1. The major state variables of the system represent phytoplankton (chlorophyll a/M^3), herbivorous and carnivorous zooplankton (MgC/M^3), detritus (MgC/M^2), nitrogen (organic, ammonia, and nitrate), phosphorous (organic and phosphate) and silicon (Mg/M^3). The variables interact by means of the major processes considered by the model: photosynthesis, respiration, grazing and predation. Photosynthesis is broken down into the subprocesses of light, nutrient and temperature effect on growth. There are a variety of equation forms representing the hypothesized effects of each process, and incorporating a number of these formulations in the simulator allows us to compare them and to determine how appropriate the different biological hypotheses are. The basis for the simulator is the model of Thomann et al. (1975)--chosen since it includes most of the processes we wished to examine. Figure 2 gives the simulator output for this model run under the environmental conditions of Lake Ontario. Other process formulations for the effect of a physical parameter upon plankton were selected from the literature. All equations and parameter values used are listed and discussed in Swartzman and Bentley (1978). Examples of particular processes will be examined in a later section. The library of models can be evaluated under one set of environmental conditions so that a comparison of the effects of different process assumptions can be made in terms of the total ecosystem.

By its very formulation, the simulator is based on a number of assumptions about the ecosystem which can restrict its interpretation. (1) In the model, phytoplankton growth is equal to the multiplicative effects of light, temperature, and nutrients from which grazing and respiration have been subtracted. Although the effects of light, nutrients and temperature are related, it is possible to separate their effects in the biological systems (Hutchinson, 1967). (2) Since most of the models reviewed discuss phytoplankton fluctuations in terms of chlorophyll a, the simulator also uses this unit. Epply (1972) has pointed out the errors in assuming a constant chlorophyll a to carbon ratio, and the simulator is subject to these problems. (3) The simulator includes the functional groups of phytoplankton, herbivorous and carnivorous zooplankton, and detritus. Physiological responses are frequently species specific and some level of realism is lost by considering only large groups of organisms. Nevertheless, characteristics of general groups (e.g. blue-green algae) were considered to ascertain how that group might respond to specific conditions. (4) A deterministic model such as the simulator can only be used to predict average year behavior. Particular seasonal dynamics are frequently due to environmental conditions specific to that year. (5) Model interpretation must be wary of the time scale used. For this discussion, the model was run with a time step of 12 hours for one year. (6) There are some effects associated with the increase in temperatures which have not been included in the computer models. In some cases, parasites or pathogens may do better at increased temperatures (Holl, 1971), but these organisms are not included in the model. Evidence has been found that the distribution of plankton throughout the water body determines the nature of temperature effects (Voronina, 1972)--although Speechi (1969) found no such relationship--and the model allows us to examine this only in terms of a vertical column of water. In her review article, Patrick (1968) discussed the fact that an increase in temperature can cause an increase in the amount of bacteria mineralized organic material (a source of nutrients) and thus increase the nutritive value of the water. Increased temperature and/or bacterial activity may also reduce oxygen levels, and this may cause the release of trace nutritive elements or toxic substances previously held by the oxidized microzone. The distance and velocity of vertical movement of diatoms may also be affected by the thermal environment (Hopkins, 1963), and the diatoms are very important for oxygen production. At least one organism [*Closterium leibleinii*, Munda (1960)] becomes more resistant to hypertonic solutions such as higher chloride concentrations at increased temperatures. Although interesting, none of these effects of increased temperature can be examined with the simulator.

The comparison methodology for plankton models has been discussed in a previous paper (Swartzman and Bentley, 1978). How to compare the output of two model runs is another question. Since seasonal dynamics of plankton and nutrients are the major areas of interest, the simulator output includes a graph of the fluctuations of these variables over one year (Figure 2). To compare these time series, the computer produces a table of average and total production and the timing and values of the critical periods of each of the stable variables (Table 2). These criteria were chosen since they are believed to represent the major components of the dynamics of the plankton system. Critical periods in the system frequently precede changes in the community structure, and these periods are usually correlated to a peak or trough of nutrients or biological activity. The timing and the value of the critical level of each state variable are representative of seasonal dynamics. Total production over the year for each plankton group as well as average standing crop of each variable provides information on the importance of each of these compartments. These factors are most useful for comparisons between model runs since they represent the planktonic system behavior. The reasonableness of model output is determined by placing overlays of the mean enveloped by one standard deviation of data of the state variables obtained from the ecosystem being studied (i.e. with identical hydrodynamic and initial conditions as the model). Comparisons between simulator runs were performed using multivariate analysis of the attributes given in Table 2. Model runs which went outside the bounds of this envelope were examined more closely to determine the cause of this aberrance. In most cases, the biological assumptions--the form of the process equations, the parameter values, or the combination of process equations used--were not representative of the natural system being modeled. This comparison between the model output and the timing of seasonal dynamics of the plankton allowed us to obtain knowledge of those types of processes characteristic of certain lakes.

The general model simulator was used to analyze the effects of temperature by comparing model output run under the thermally loaded and unloaded environments of Lake Ontario. The increased temperature of 8.33°C was obtained from the Ashbury-Frigo model (1971) which predicts areas affected by thermal plumes based on a correlation of surface area data from six power plants having discharges into large northern lakes. The figure of 8.33°C is found from studying 23 thermal plumes and is applicable to a surface area of 1.3 km^2. Although this is a major increase in the water temperature, we believe that by changing the temperature so drastically yet within the bounds of past thermal plumes we will be more likely to observe differences which might occur in the warmer than normal waters.

Since temperature effects are the major emphasis in this paper, only those processes directly involving temperature will be discussed. All other process equations are reviewed in Swartzman and Bentley (1978). In the plankton models considered, temperature was hypothesized to have a direct effect on phytoplankton growth through photosynthesis, on zooplankton grazing through the assimilation efficiency and on zooplankton respiration. Although it is generally agreed that the process effects are positively correlated with increasing temperature, there is no agreement as to the exact nature of the curves.

An increase in temperature causes an increase in phytoplankton growth up to a certain point in most plankton systems. There are three types of curve forms hypothesized for this effect that are used in the simulator (Figure 3 graphs these). Thomann et al. (1975) used a linear effect of temperature on growth although they cited no biological rationale for their choice. The "skewed normal" formulation proposed by Lehman et al. (1975) is identical to that presented by Lassiter and Kearns (1974) under certain conditions. The equations are derived from the general form of the curve for temperature effect on growth. Epply (1972) seems to have done the most perceptive study of the effect of temperature on phytoplankton growth. He points out that when a functional group is being considered a Q10 formulation is the most biologically reasonable choice for the thermal effect since this curve accounts for a change in species composition. Those species with a higher optimal temperature also tend to have a higher rate of photosynthesis at that temperature. Since the simulator lumps all phytoplankton into one group, the Q10 relation is probably the best equation for the effect of temperature upon growth in the simulator. Nevertheless, the lake may be dominated by a few species at a time so we also tested the thermally loaded environment with the simulator using Lehman's "skewed normal" with an optimal temperature for growth of 25°C. The Q10 curve has additional advantages in its smaller number of parameter values and the fact that the change in the rate of response of organisms to each increase of 10°C is frequently measured.

Experimental evidence indicates that grazing is positively correlated with temperature. In the simulator, temperature affects grazing by altering the maximum ration available to the zooplankton for consumption (maximum grazing rate). Using a gamma function for the relationship between temperature and grazing, MacCormick et al. (1972) predict low grazing at most temperatures, particularly those less than 15°C. Kremer's (1975) use of Q10 formulation for this interaction and the linear relationship of Thomann et al. (1975) are similar although the linear equation predicts higher grazing at temperatures between 7 and 25°C. In the thermal loading studies, high, medium and low temperature effects on grazing were simulated by using the linear formulation with different slopes (see Figure 4). The lowest level of grazing resulted in an inability of the zooplankton to graze and thus their elimination. This low level is probably not representative of the true nature of the system, and it was not considered in detail.

The predicted effects of temperature on respiration are similar to those for grazing. MacCormick et al. (1972) use a gamma function, Kremer (1975) proposed a Q10 relation and Thomann et al. (1975) a linear effect of temperature on zooplankton respiration. Although respiration rates are influenced by organism size, physiological state, feeding rate and seasonal acclimation, these factors are not considered in the models. A low, medium and high effect of temperature on respiration is modeled in the simulator by using each of the three predicted process equations (see Figure 5). The higher respiration curve (the Q10 formulation) usually results in rapid elimination of the zooplankton in the system and thus was not considered as an appropriate model.

In order to ascertain the reasonableness of model output, it was compared to data collected on Lake Ontario during 1973 and 1974 (Stoemer et al., 1975). Although Lake Ontario is not a typical lake due to the abundance of phytoplankton species either tolerant of or requiring eutrophic conditions, the availability of data for a number of years and the fact that the "default" model (that of Thomann et al., 1975) was written as a description of this system made it appropriate to use Lake Ontario as the comparison ecosystem for this study. In all simulations discussed, environmental conditions and initial conditions for the state variables are those of Lake Ontario.

Lake Ontario is one of the large northern lakes (latitude 43°55") in the United States making up the Great Lakes system. Its surface area of 19,477 km^2 represents a watershed drainage area of 90,132 km^2. The volume is 1,669 km^3, and the lake has a maximum depth of 244 m. Situated at 74.01 m above sea level, the cryptodepression has a depth of 170 m. The maximum length and width of Lake Ontario are 307 km and 87 km respectively, and the shoreline length is 1,380 km. The major source of inflow into the lake is due to the Niagara River which has an average flow of 195,000 cfs (84% of the total discharge). Average annual precipitation in the area is 83.23 cm and the average annual evaporation is 71 cm. The thermocline begins in late April to early May and dissipates in late September with the average depth being 17 m. The hypolimnetic depth is 73.3 m. Being such a large lake, the hypolimnetic retention time is 8.1 years. The principle zooplankton in the lake (91%) are *Cyclops bicuspidatus*, *Tropocyclops prasinus*, *Daphnia retrocurva* and *Bosmina longirostris* (Thomann et al., 1975).

SIMULATION COMPARISONS

In runs of the simulator without thermal loading, phytoplankton usually increase during April; a rapid drop follows, and a smaller peak in phytoplankton occurs in mid-September which is succeeded by a decrease (see Figure 2). Using the general model simulator, we determined that the height of the first peak is caused by phosphorous limitation and the following decrease is due to zooplankton grazing. Predation by carnivorous zooplankton reduces herbivorous zooplankton in mid-summer and allows phytoplankton to have a second bloom in August. This phytoplankton bloom is enhanced by late summer turnover in the lake which causes an upward mixing of nutrients. Early winter reduction of plankton is due to the falling temperature levels having constraints on respiration and growth.

As Epply (1972) points out, temperature is rarely a limiting factor in phytoplankton growth; instead it sets the upper limit for maximum growth. The simulation runs of the normal lake versus the one increased in temperature seem to demonstrate this. When reasonable sets of parameter values are used (for instance, cases with high respiration and low grazing are excluded since these are physiologically unrealistic), the thermally loaded runs as compared to the nonloaded cases result in an increase in average phytoplankton production. At the higher temperatures, phytoplankton can grow more early in the year, and thus the spring bloom occurs sooner (see Figure 6). Since more food is available during the first months of the year, herbivorous zooplankton are able to increase their biomass during this time. By increasing the temperature effect on grazing, zooplankton are able to track changes in their food abundance more quickly and thus can take advantage of the later bloom. This results in a greater production of zooplankton. Thermal laodings seem to cause oscillations in the plankton but none are very extreme--eliminating the possibility of extinction of entire groups. This has an impact on the total ecosystem in terms of the type of food available. The phytoplankton surviving the warmer temperatures and the periods of heavy grazing are probably able to respond fairly quickly to these extreme conditions since the heavy grazing does not last very long. Nutrients also play an important role in the plankton oscillations.

Less phytoplankton production results when the Q10 relationship between temperature is used for the temperature effect on grazing instead of the linear formulation. Since the Q10 function has higher grazing at high temperatures and lower grazing at medium temperatures, in the thermally loaded environment, the grazing is increased as compared to cooler waters. When the "skewed" normal curve is used for the temperature effect on phytoplankton growth in the loaded run, the phytoplankton increase at a faster rate, the herbivorous zooplankton respond more quickly to the phytoplankton and so the phytoplankton peak earlier in the year. These results are a function of the parameter values as well as the particular curve forms.

In contrast to the unloaded runs, phosphorous is not the important factor limiting the first phytoplankton peak in the warmer waters. Since phytoplankton grow more quickly, the herbivorous zooplankton begin to graze them and thus decrease their biomass before phosphorous limitation occurs. The minimum nutrient effect on growth during this period of growth is twice the minimum during the similar period in the default run. This may result in more favorable conditions for those phytoplankton species which are normally phosphorous limited and so do not do well in ordinary conditions. This drop in phytoplankton biomass caused by grazing is followed by a period of growth as the herbivorous zooplankton are eaten by the rapidly increasing carnivorous zooplankton. The height of this second peak is directly related to nitrogen availability. The subsequent decrease in phytoplankton is due to decreasing light and nutrients. The effect upon growth of temperature, light and nutrients is decreasing during July to mid-August. This interaction between light and phytoplankton growth does not play such a prominent role in the non-thermally loaded cases. Thus, those organisms which are not so limited by medium light intensities may have higher productivity in the thermally loaded waters of a large northern lake.

The mid-August turnover in Lake Ontario causes a mixing of the water layers and results in an increase of nutrient supply in the euphotic zone. Incorporation of this phenomenon into the model allows for an increase in phytoplankton biomass shortly thereafer. Grazing characteristics of zooplankton determine whether phytoplankton can actually grow during this period of increasing nutrients. For example, the model with a medium temperature effect on herbivorous zooplankton grazing and a low respiration effect (Figure 7a) has a higher grazing ration during this critical period than the model with a high temperature effect on grazing and a medium effect on respiration (Figure 7b). Although both these models are run in the thermally loaded environment, only the second case has a significant phytoplankton bloom in mid-August.

In order to ascertain the differences between the model runs under normal conditions and those in which the environment was increased in temperature, a number of model outputs were compared. The runs were made under varying temperature effects on phytoplankton growth and on zooplankton grazing and respiration as is indicated in Figure 8.

Due to the difficulties of comparing time series, multivariate techniques were used to help determine major differences between model outputs run under a variety of hypothesized conditions. The attributes used in this comparison were total production, average standing crop, maximum and minimum value and timing of these events for each of the major compartments (see Table 2). Since the phytoplankton usually have two blooms over the year, the value and timing of the second bloom was also included as an attribute. Using three techniques, the model runs were grouped according to the values of these attributes.

A dendrogram (Figure 9) was produced by MINFO (Goldstein and Grigal, 1971)--an agglomerative, hierarchical, polythetic clustering method (Williams, 1976). Two major groupings seemed to occur with the normal runs and those with increased temperature being subdivisions within the major groups. The coherence and meaning of these groups were examined by discriminant analysis and indirect ordination.

Since discriminant analysis assumes the data are linear, additive and normally distributed, the statistical tests should be used with caution; the technique is appropriate as an advisory tool, however. When the two groups defined *a priori* were normal and thermally loaded runs of the model, total discrimination of the groupings was obtained on the basis of one variable--the timing of the herbivorous zooplankton maximum. The second variable to enter the discriminant equation was timing of the organic phosphorous maximum. When the four groups predicted by the dendrogram were considered by the discriminant analysis routine, 83.3% correct classification of the runs into groups was obtained by considering timing of herbivorous zooplankton maximum and the organic nitrogen maximum value. All runs were correctly classified when timing of the ammonia maximum and of the detritus maximum were also included. Thus, this analysis gives greater confidence in the importance of nutrients and timing of herbivore to the plankton system under normal and stressed conditions.

Ordination techniques were also used to ascertain what the major differences between the runs were. Reciprocal averaging, polar ordination and principal components analysis (PCA) were all used; however, the last procedure gave the best separation so only it will be discussed. The ordination produced by PCA (Figure 10) separated the runs in accordance with those groupings predicted by the dendrogram. By examining those runs at the ends of the axes and the attributes at the end of the axes in that ordination (Figure 11) causal factors of the differences between groups of runs can be determined. Such an indirect ordination assumes that the run order produced reflects some ecological gradient. The primary axis is related to the effect of thermal loading and explains 26% of the overall variation. Comparison of the end runs on the axis indicate that timing of the first phytoplankton peak and of the herbivorous zooplankton maximum are the major determinants of this axis.

The second axis explains an additional 20% of the variation in the model runs. Separation along this axis is related to nutrients. Organic nitrogen, nitrate and phosphate average standing crop as well as the nitrate maximum value and the phytoplankton average standing crop contribute the most information to separation along this axis.

Examination of the ordination results indicates that in some cases thermal loading can produce greater changes in the timing and extreme values of critical events than in others. Pairs of runs (those under normal and increased temperature conditions) closer together in the ordination space (Figure 10) would be expected to represent ecosystems less susceptible to increased temperature. For instance, a strong effect of increased temperature occurs in communities in which the zooplankton are characterized by a medium temperature effect on respiration and a high effect on grazing and the phytoplankton have a temperature effect on growth which can be represented by the "skewed" normal curve (T24 versus T23; see Figure 12). Although the only difference in these two runs of the model is an increase in the water temperature, the simulations results are very different as indicated by their separation in the dendrogram and the ordinations. Other pairs of runs (e.g. T16 and T22) exhibit relatively few differences (Figure 13). Such analysis points out those types of plankton groups which are more susceptible to alterations in water temperatures.

The three outstanding differences in limiting factors between the thermally loaded and unloaded runs observed from examining more than forty combinations of the simulator are summarized in Figure 14. In the warmer waters, phosphorous limitation does not cause the first phytoplankton peak, nitrogen is in short supply in mid-June, and the light effect upon growth is a limiting factor in late summer. These differences suggest characteristics of organisms which may have higher productivity in the thermally loaded environment around a nuclear power plant or other discharge. These differences lead to hypotheses of characteristics of organisms which can survive better in the warm waters. These proposed relations can be tested by means of the general model simulator, and those that support predictions lead to hypotheses to be examined in a laboratory or field experiments.

The major differences between the model outputs from the thermally loaded and the unloaded runs are an increase in total chlorophyll a and zooplankton carbon over the year and a change in the timing of phytoplankton blooms. The first is a measure of total productivity for the plankton system. Experimental and field results from thermal plumes usually show an increase in chlorophyll a, primary production and biomass (refer to Table 1) giving some confidence in the models' ability to successfully predict the outcome of thermal perturbations. These changes may in part be due to alterations in species diversity and/or composition. To determine the degree to which different species groups cause a change in productivity, the nature of environmental pressures at the different times of the year in the thermally loaded case was explored.

CAUSAL DIFFERENCES OF PLANKTON DYNAMICS UNDER INCREASED TEMPERATURE

Organisms which survive and reproduce in the thermally loaded waters of a large northern lake will be a subset of those species which exist in the lake. These will probably be different species from those which are found in the normally warmer waters of a more southern lake due to genetic variability. Freshwater species are often able to avoid adverse conditions by ceasing divisions or forming resting stages. Cairns (1956) demonstrates this in an interesting experiment in which he shows that the temperature range for diatoms is 20-30°C, for green algae is 30-35°C and for blue greens is greater than 35°C. Outside the temperature ranges for each group, those algae were not found in the water although readjustment to the range of that group would allow the species to reappear and grow. This implies that species are not able to compete successfully at some temperatures. The simulator permits examination of the temperature effect in terms of the whole ecosystem. The comparisons of the thermally loaded versus nonloaded runs point out some of the differences in limitations which organisms may experience. Thus, one would predict that those species which have a lower phosphorous tolerance and a higher nitrogen tolerance would have greater productivity in the thermal plumes. This was tested by running the general model simulator in the thermally loaded environment with the half-saturation constant for nitrogen increased and for phosphorous decreased. In all combinations considered, phytoplankton and zooplankton productivity increased.

Similarly, the thermal loading comparisons indicate that in the warmer than normal waters light becomes limiting in August; whereas it is never the most limiting factor in the runs under normal environmental conditions. This leads to the prediction that those algae species with a lower light limitation would produce more. To test this prediction, the light effect on growth was changed as indicated in Figure 15. The optimal light intensity was decreased and the coefficient was lowered so that growth is greater up to 500 langleys per day of surface light intensity. Since this is the intensity at which the second bloom occurs in the thermally loaded case, and since light was shown to be limiting during this time, this is equivalent to reducing the light limitation. Although average productivity does not increase, the amount of chlorophyll a in the second bloom is greater. Because the first bloom is not related to light limitation, it is not altered and it has the greater contribution to average productivity.

The simulator has demonstrated that those species with a lower phosphorous tolerance, a greater tolerance for nitrogen, and a lower optimal light intensity for growth will survive the warmer temperatures better. These characteristics are typical of blue-green algae (Garnier, 1962; Patrick, 1968). Thus, based on physiological considerations, the simulation model predicts that blue greens have a better ability to survive thermally loaded conditions. Numerous experiments have demonstrated that this is the group of algae usually found in warm waters (e.g. Cairns, 1956; Patrick, 1974).

Identification of limiting conditions in thermally loaded waters and of physiological characteristics of phytoplankton able to live in warm waters is a preliminary step for further experimentation in the laboratory and field. The simulation study indicates that lab experiments would be helpful to expore such questions as:

(1) What species in particular have these physiological characteristics?

(2) What blue-green algae do not?

(3) Are there any costs associated with increased ability to live in the warmer waters?

(4) If warm temperatures create nuisance plankton blooms, are there manageable ways to avoid these outbreaks of algae?

Furthermore, being aware of conditions allowing particular algae to occur gives us a better understanding of the aquatic community structure. Species diversity and trophic structure are directly related to the composition of algae species.

CONCLUSIONS

The simulator comparisons of unloaded and thermally loaded aquatic ecosystems indicate that blue-green algae have the physiological capabilities to survive in the warm waters. This fact was known from observations and sampling of thermal plumes; however those components of the physiology of blue greens enabling them to live in warm waters can not be explored in this manner. The simulations show that the major changes occurring in the warmer waters are alterations of the timing and number of blooms of algae. Thus the phytoplankton are under different kinds of stresses in the warmer waters. In both situations, the algae are subject to herbivory by zooplankton; however the trophic dynamics are more critical in the thermally loaded case because the herbivorous zooplankton grow more rapidly earlier in the year. Those phytoplankton which are immune from grazing have a strong competitive advantage in the warmer waters. Also, phosphorous does not become limiting in the warmer waters although nitrogen is. Later in the summer, light limitation occurs in the warmer waters. Those algae not susceptible to herbivory, not limited by phosphorous, and with a lower optimal light intensity for growth have a definite advantage in warmer waters since heavy grazing, nitrogen limitation and light limitation occur. Most blue-green algae have these characteristics. Thus, this study demonstrates that physiological tolerance to the limiting conditions plays a major part in determining species composition.

The value of simulation studies of perturbations has also been considered. Computer models allow for examination of changes to the physical component of the ecosystem without actual (and permanent) manipulation of that system. Processes can be explored with a simulation model which is not always the case with laboratory or field experiments. Also changes of a dynamic seasonal nature can be investigated rather than just averages. Behavior during critical periods of the year can be examined closely. Finally, formulation of hypotheses for lab experiments can be made, thus reducing their costs and frustrations.

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FIGURES

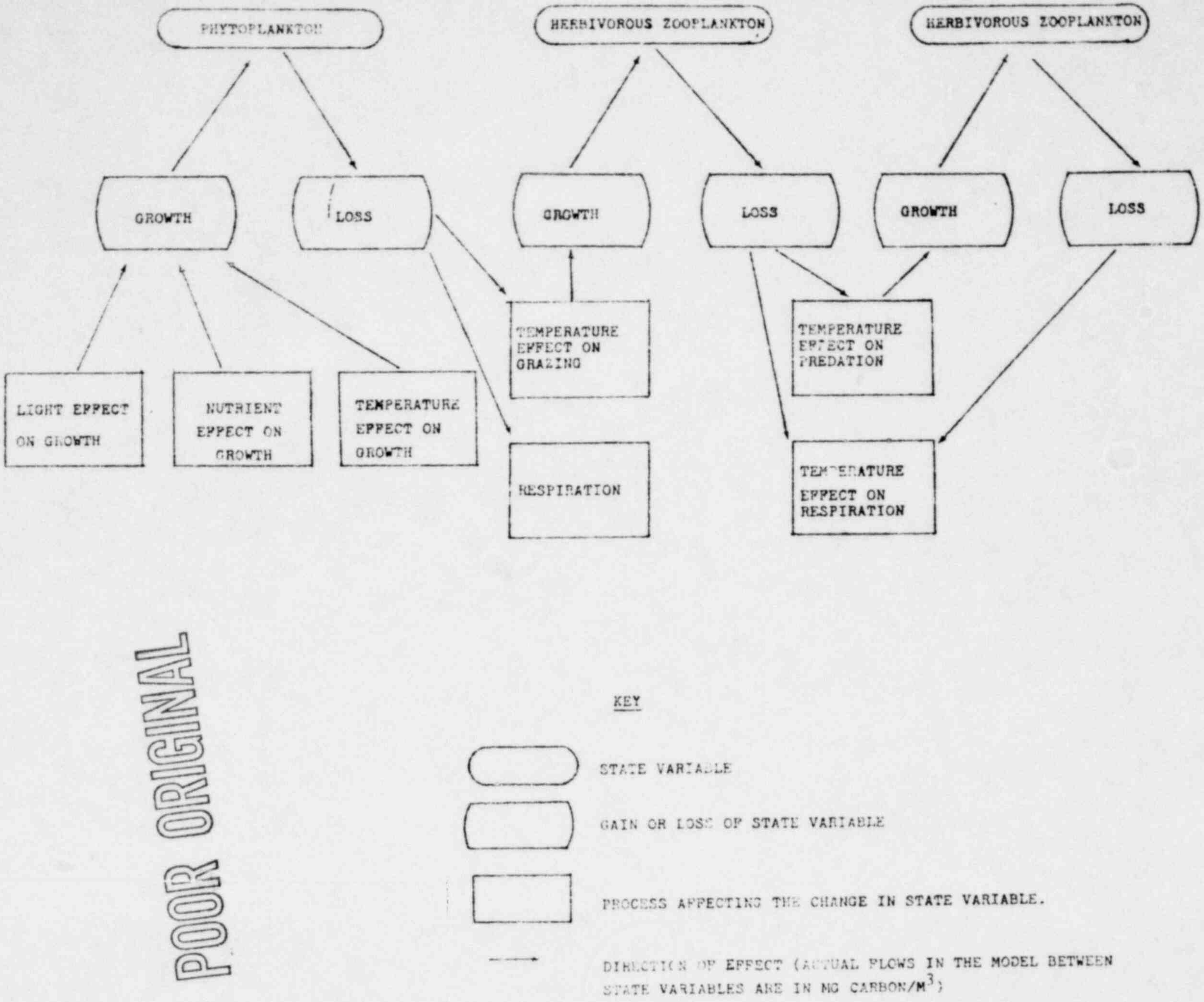

Figure 1.
Systems Flow Diagram

POOR ORIGINAL

"Default" Model Output Run Under Environmental Conditions of Lake Ontario

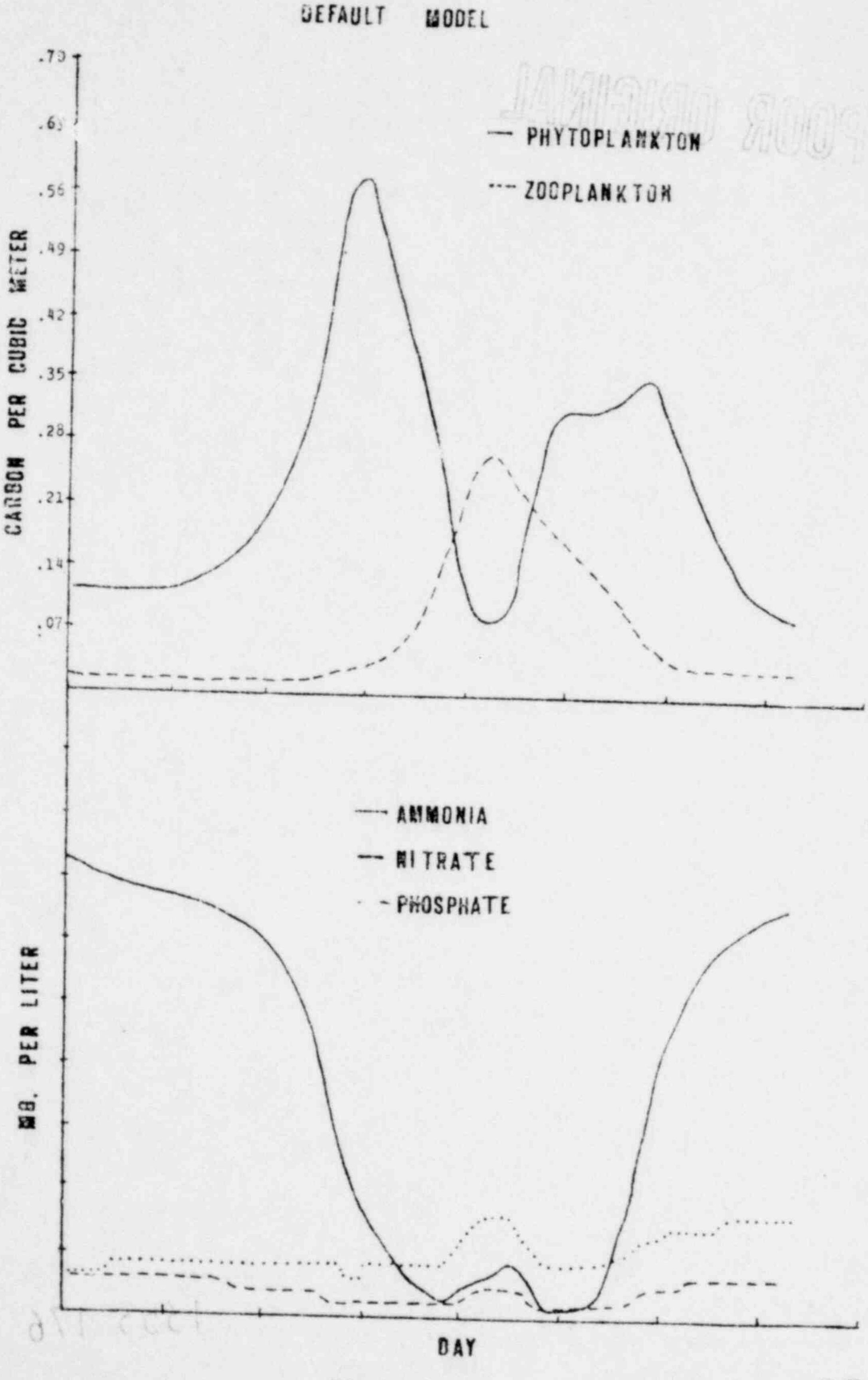

Figure 2.

POOR ORIGINAL

Temperature Effect on Phytoplankton Growth

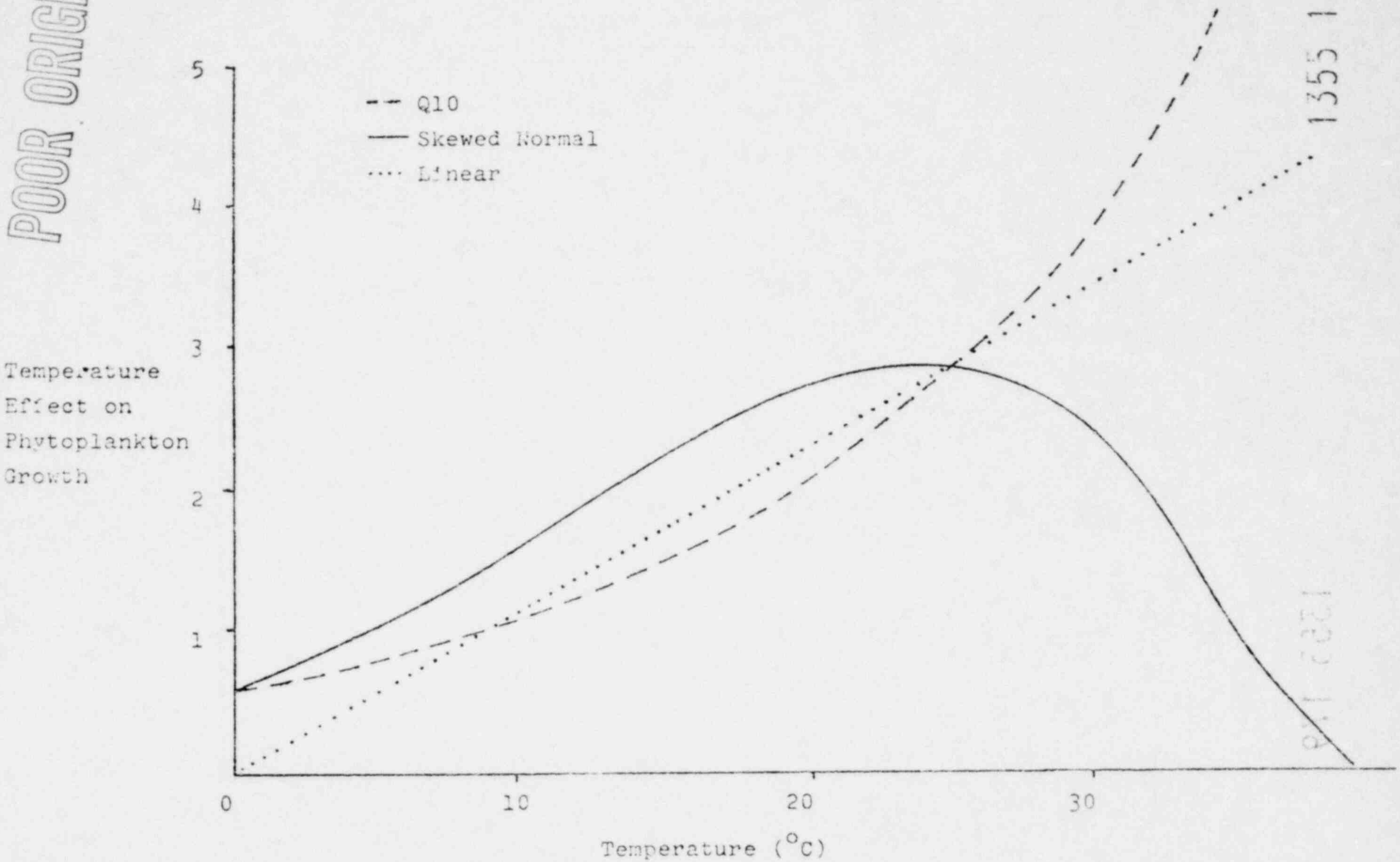

Figure 3.

Temperature Effect on Zooplankton Grazing

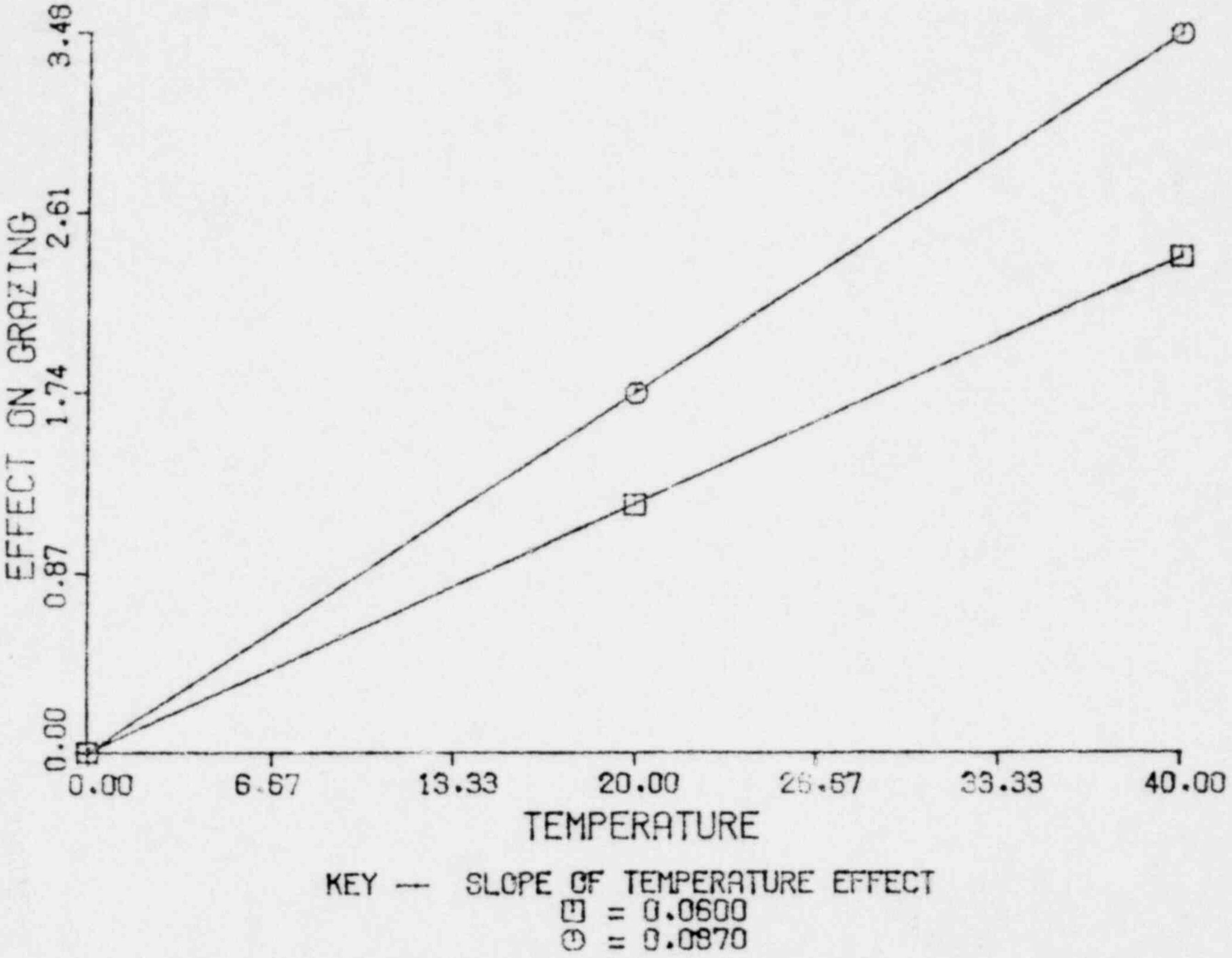

Figure 4.

Temperature Effect on Zooplankton Respiration

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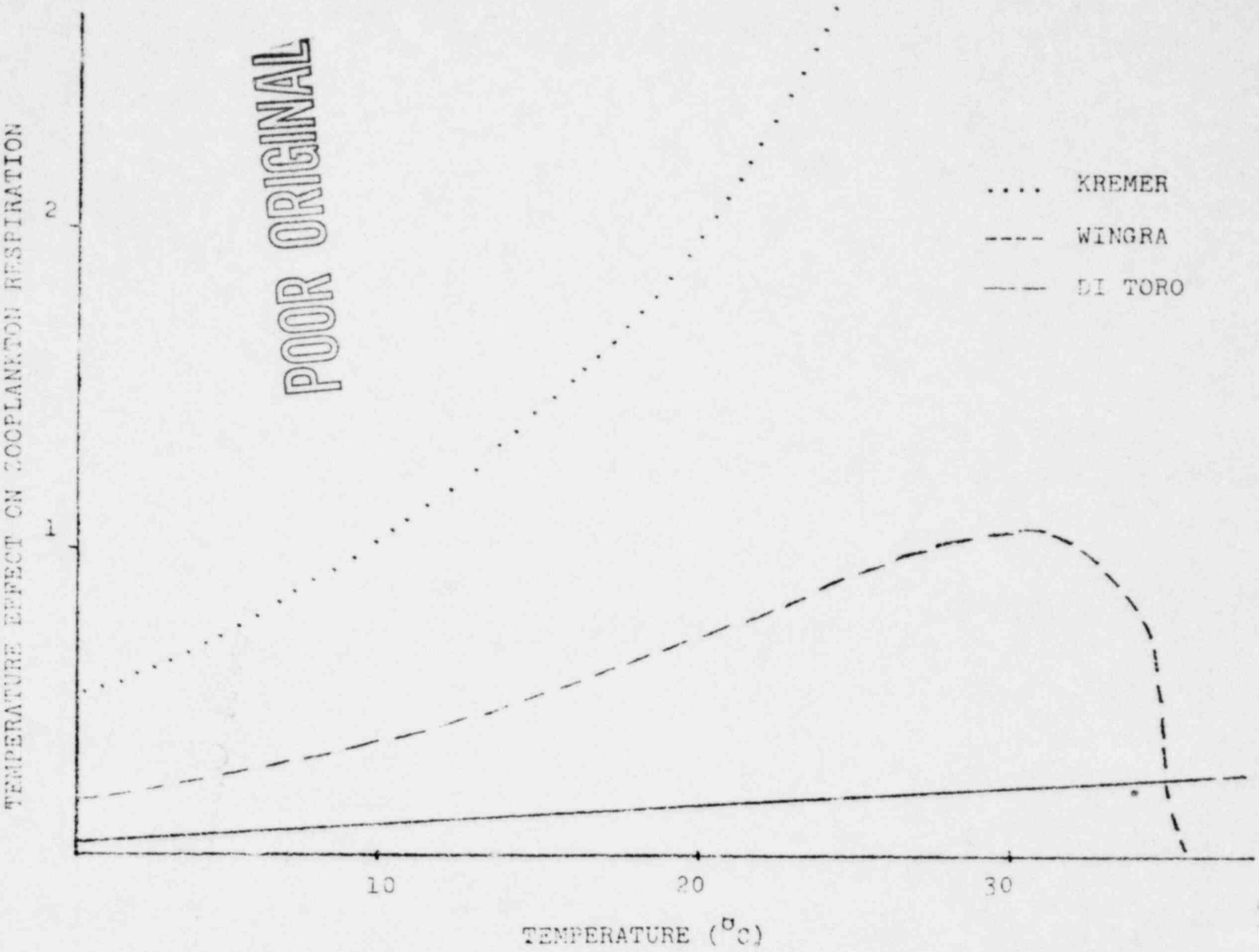

Figure 5.

"Default" Model Run Under Increased Temperature

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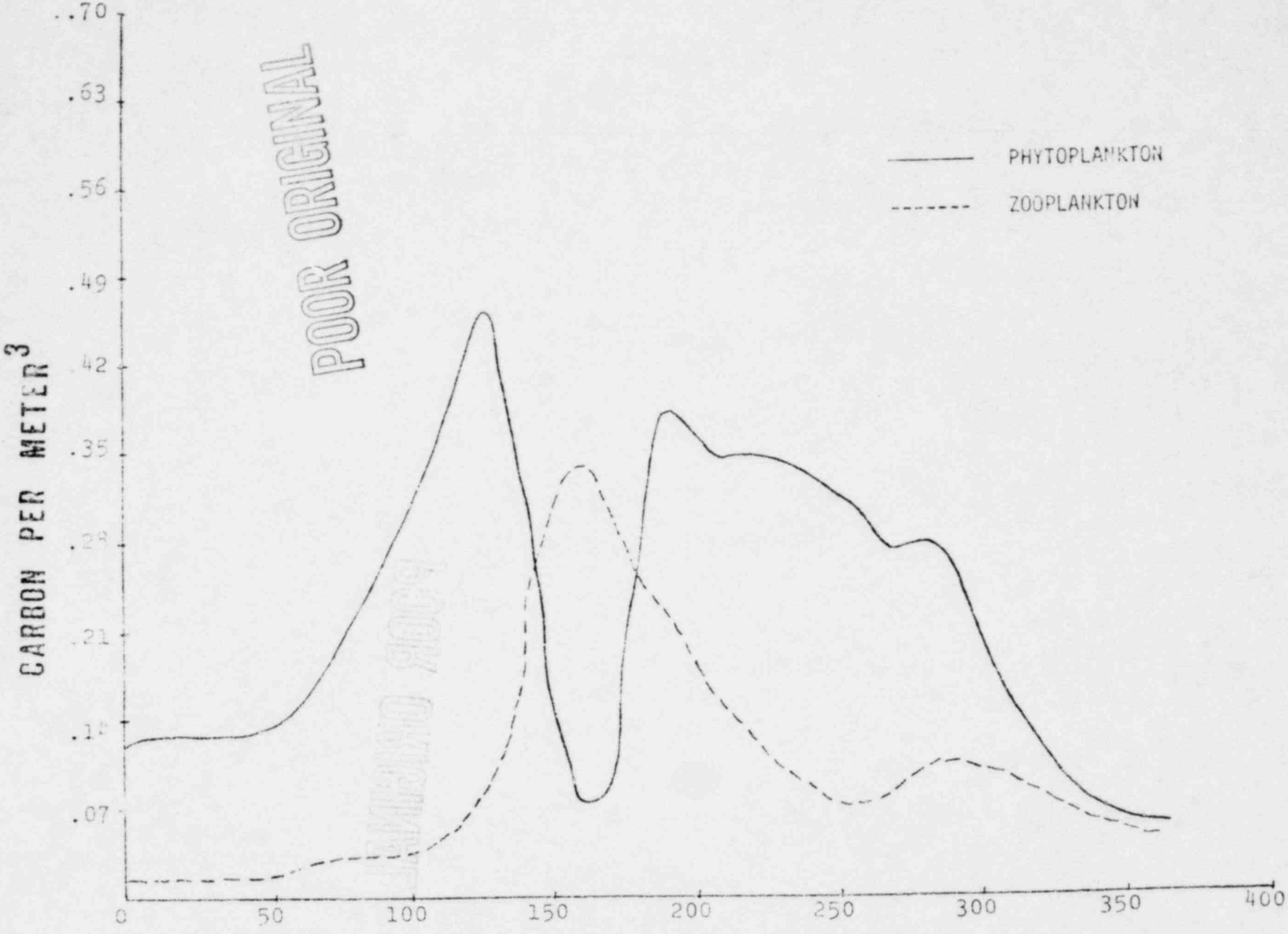

Figure 6.

POOR ORIGINAL

Effects of Grazing Characteristics on Phytoplankton dynamics
THERMALLLY LOADED MODEL RUN WITH "SKEWED NORMAL" TEMPERATURE EFFECT ON PHYTOPLANKTON

GROWTH AND LOW EFFECT ON RESPIRATION

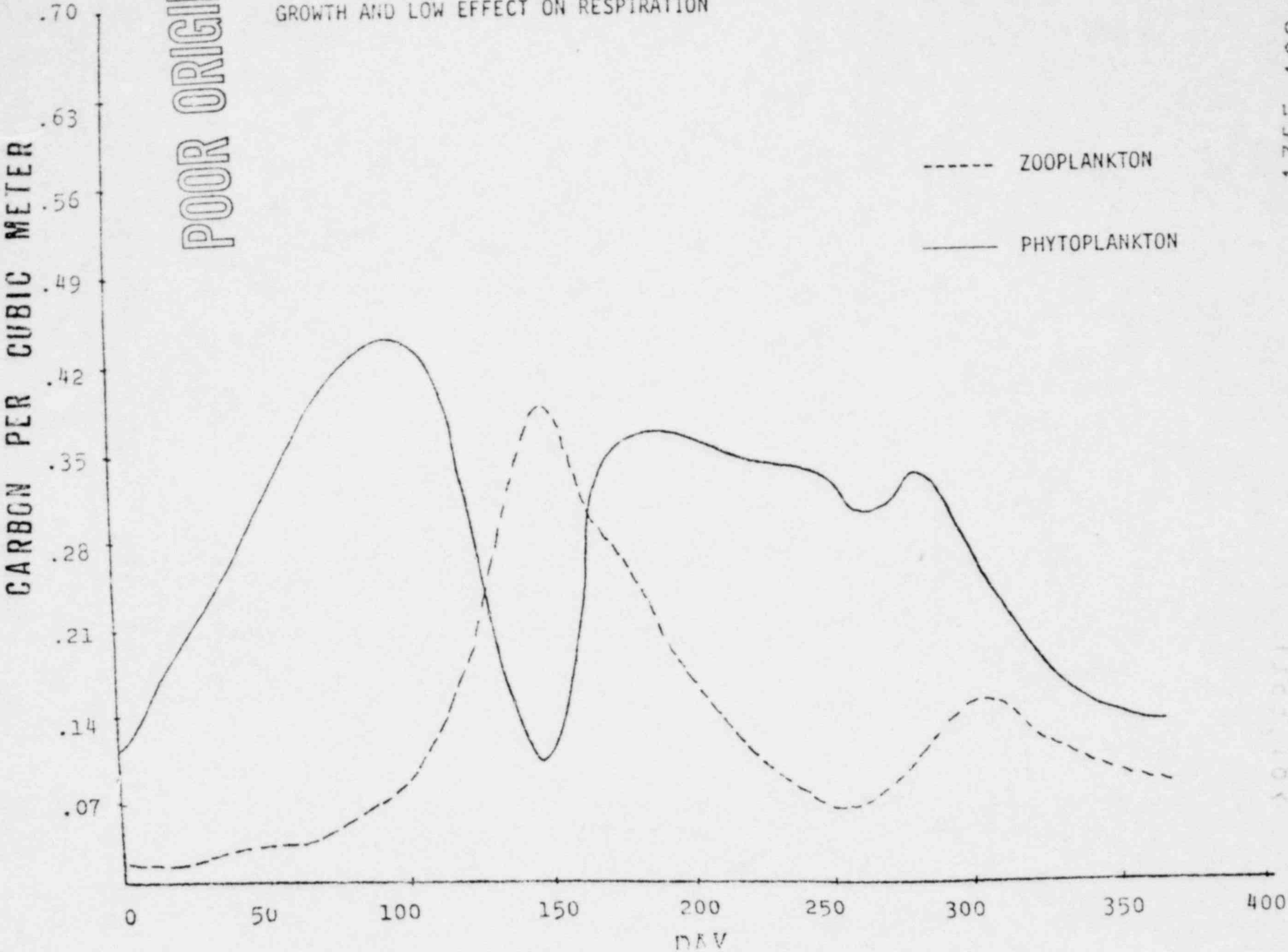

Figure 7a.

Effect of Grazing Characteristics on Phytoplankton Dynamics

T23 -- THERMALLY LOADED MODEL WITH 'SKEWED NORMAL' TEMPERATURE EFFECT ON PHYTOPLANKTON GROWTH, HIGH EFFECT ON GRAZING AND MEDIUM EFFECT ON RESPIRATION.

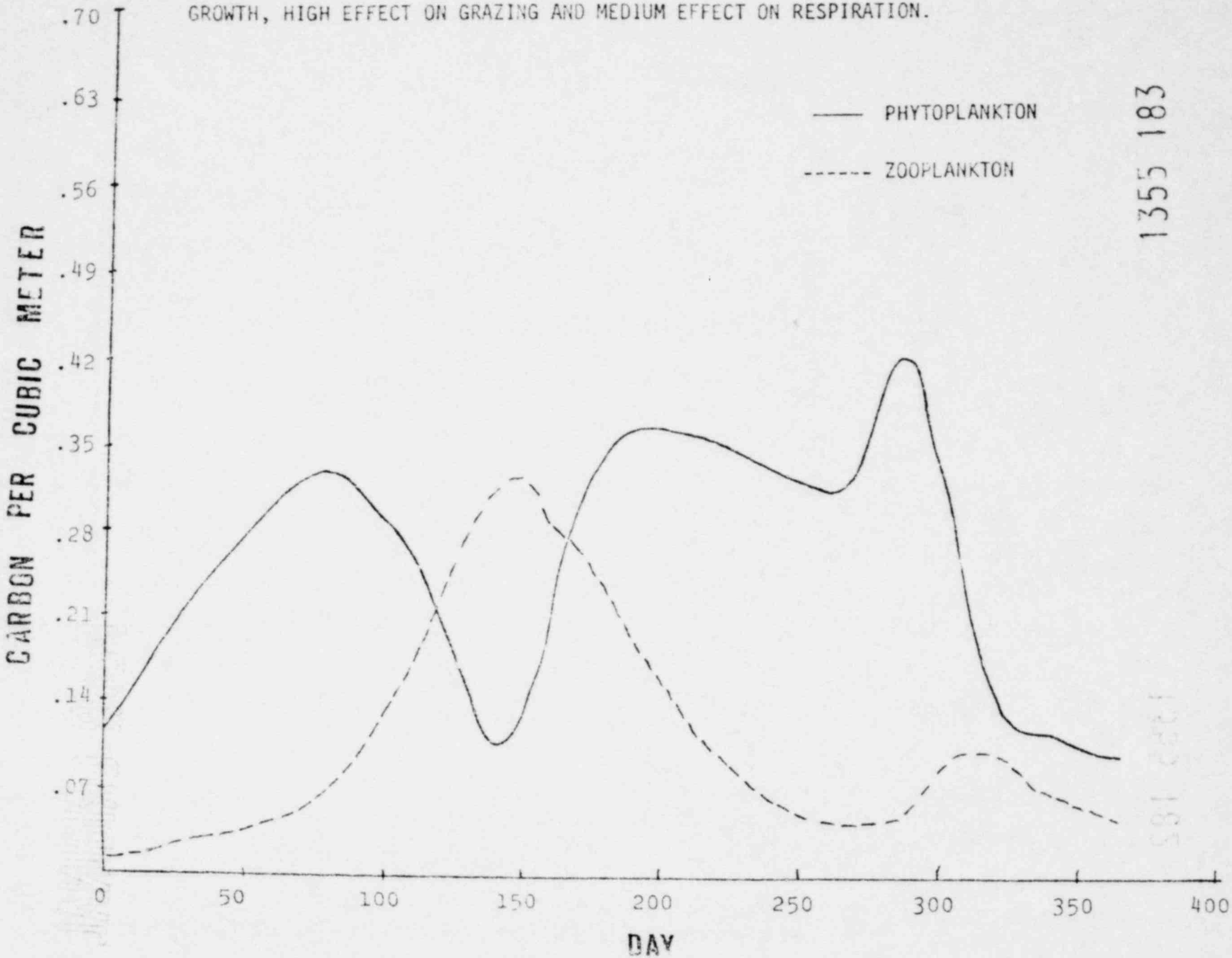

Figure 7b.

1355 183

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Temperature Effect on Grazing

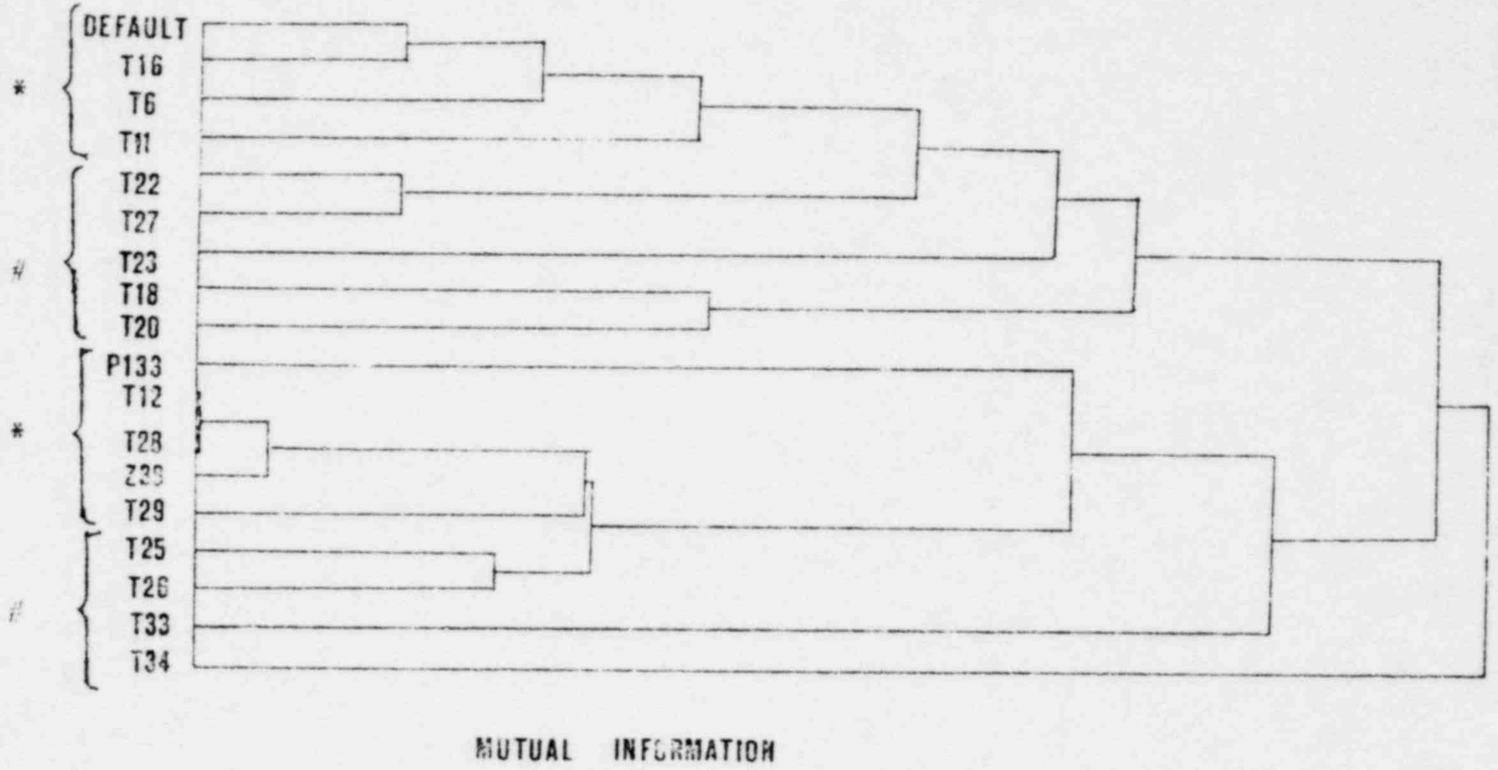
On Phytoplankton Growth		Medium	High	On Respiration
Q10	High	T12 \ T26		Medium
				Low
	Medium	Z38 \ T27	T4 \ T21	Medium
		Z1 \ T18	T6 \ T34	Low
	Low	T16 \ T22		Medium
			T11 \ T20	Low
	Medium "Skewed Normal"	T28 \ T25	T24 \ T23	Medium
		P133 \ T33		Low

Normal conditions \ Temperature increased by 8.33°C

Figure 8.

Model Runs With Different Temperature Effects

Clustering of Model Runs



*Normal Temperature Conditions

#Temperature Increased by 8.33°C

Refer to Figure 8 for conditions of each run

Figure 9.

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Ordination of Mod 1 Runs

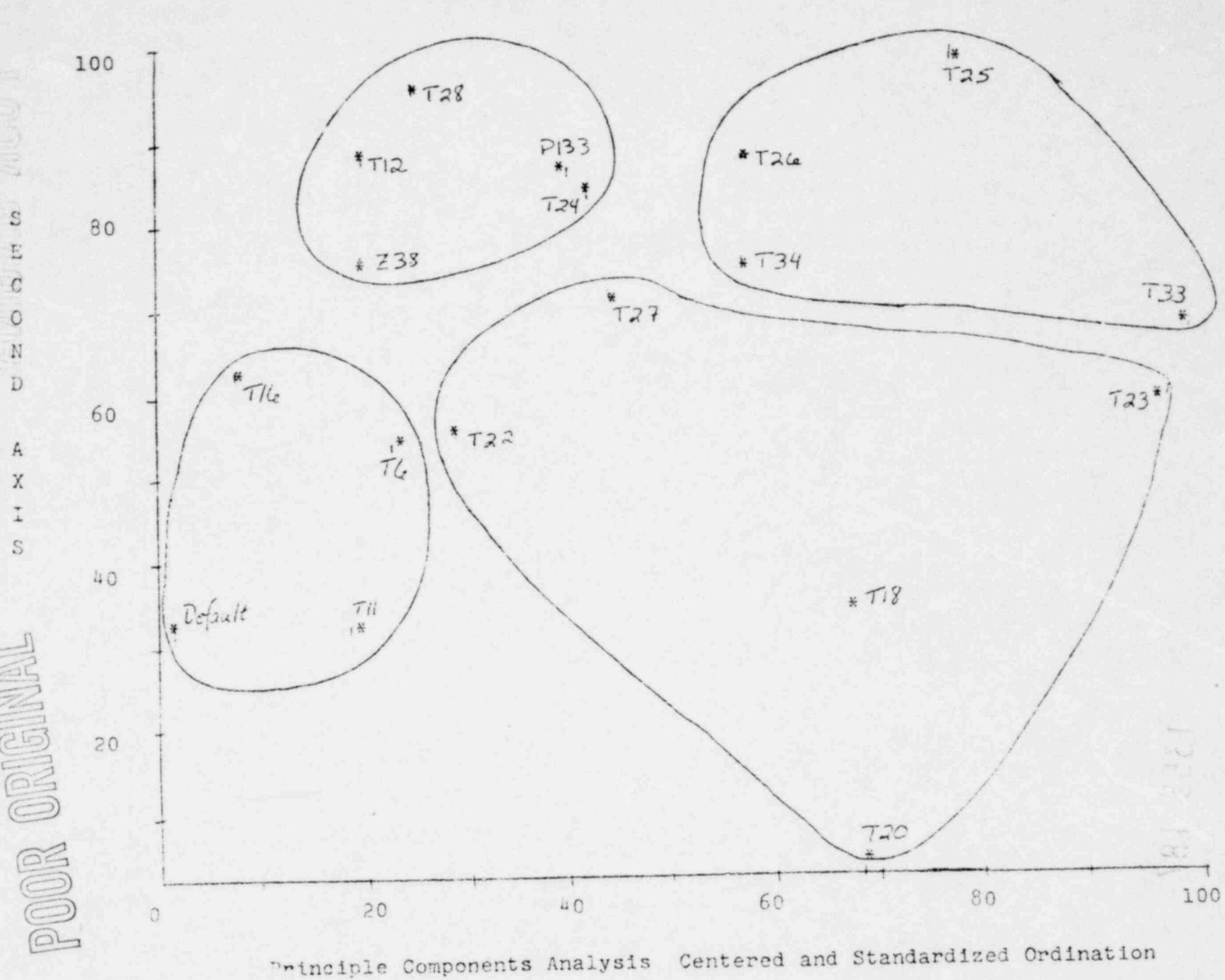

Figure 10.

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Ordination of Attributes

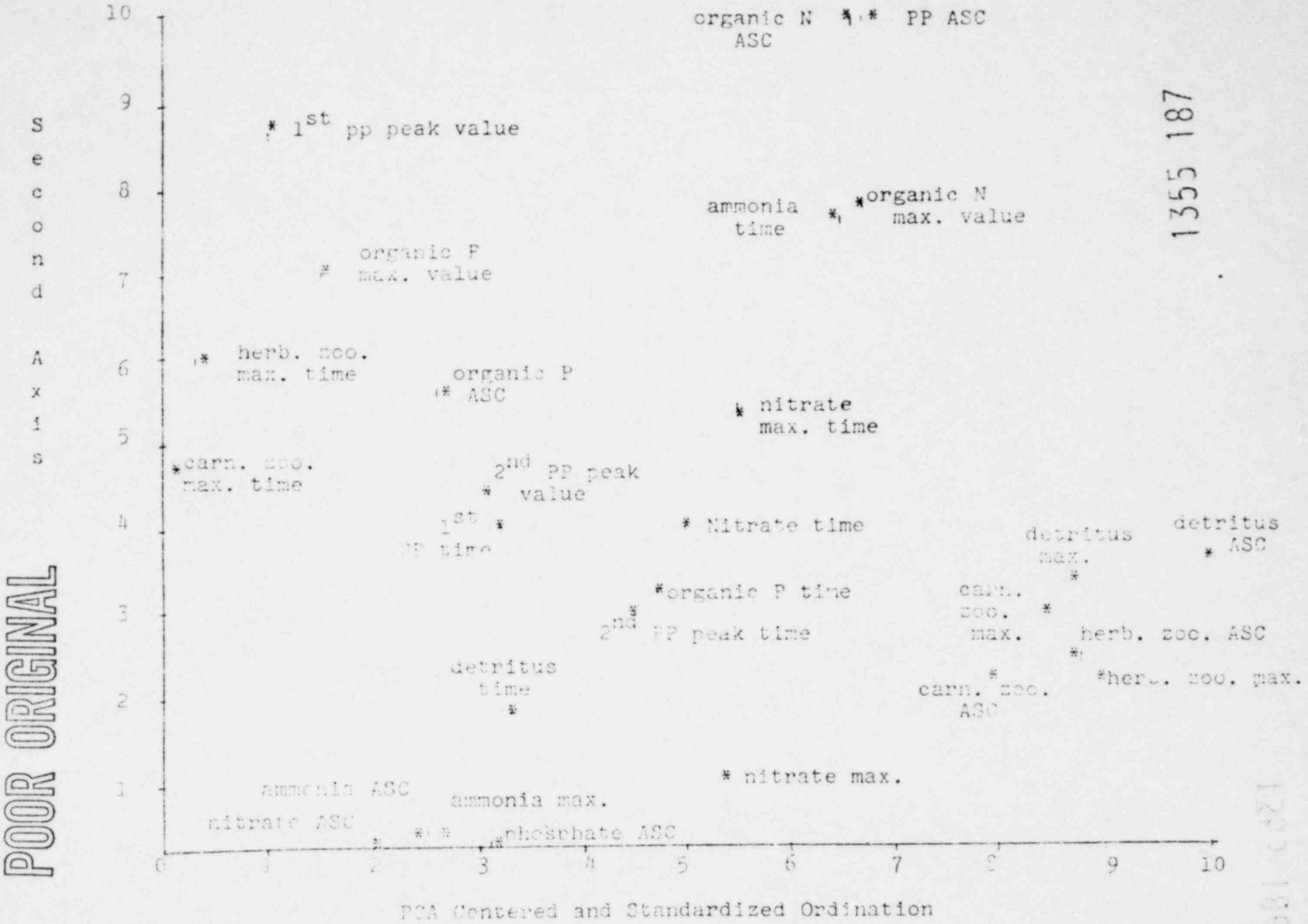

Figure 11.

1355 187

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Model Runs With Major Differences in the Normal and Thermally Loaded Conditions

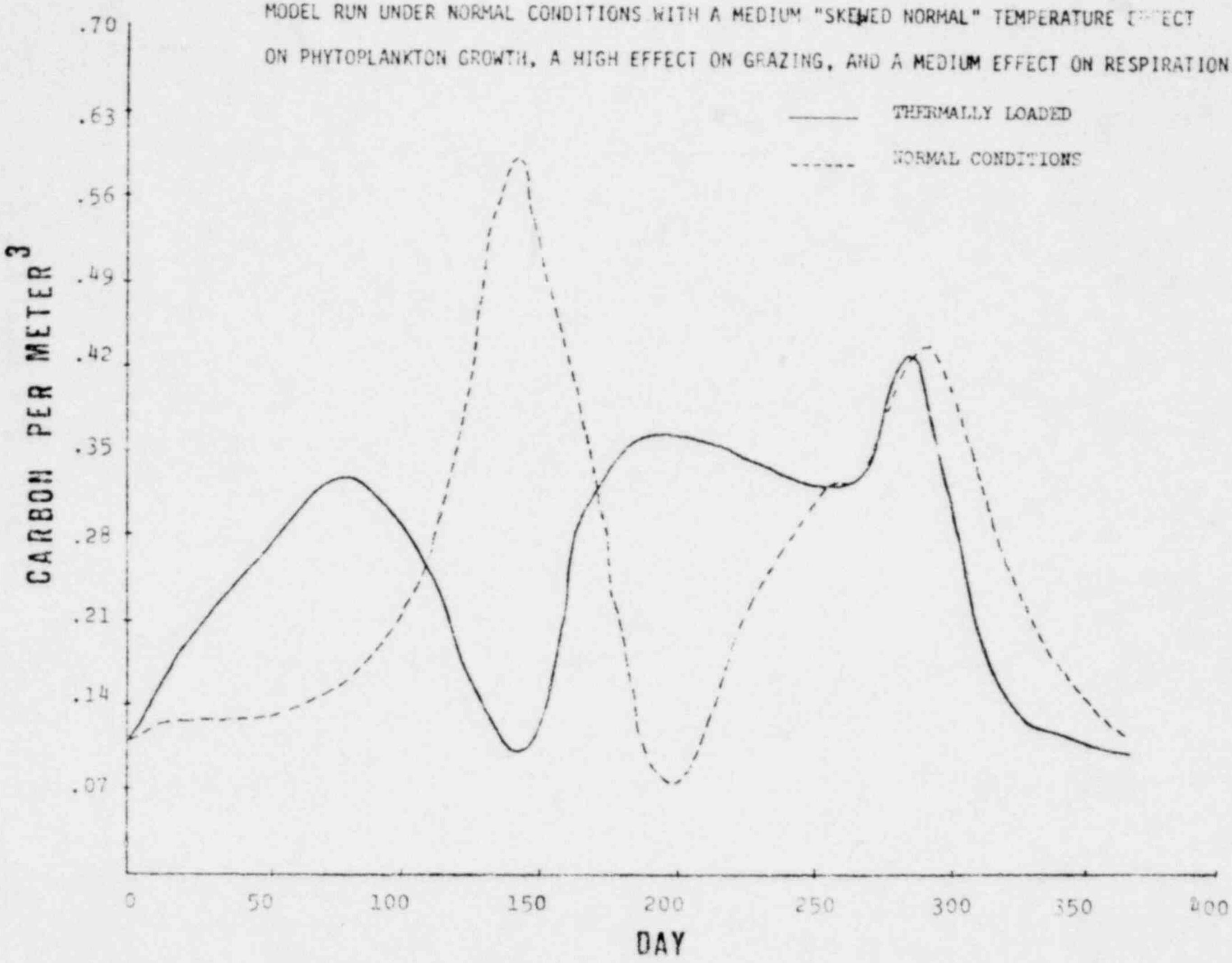
MODEL RUN UNDER NORMAL CONDITIONS WITH A MEDIUM "SKEWED NORMAL" TEMPERATURE EFFECT ON PHYTOPLANKTON GROWTH, A HIGH EFFECT ON GRAZING, AND A MEDIUM EFFECT ON RESPIRATION.

Figure 12.

Model Runs Which Are Similar Under Different Temperature Conditions

MODEL OUTPUT WITH LOW TEMPERATURE EFFECT ON PHYTOPLANKTON GROWTH AND MEDIUM

EFFFECT ON ZOOPLANKTON GRAZING AND RESPIRATION

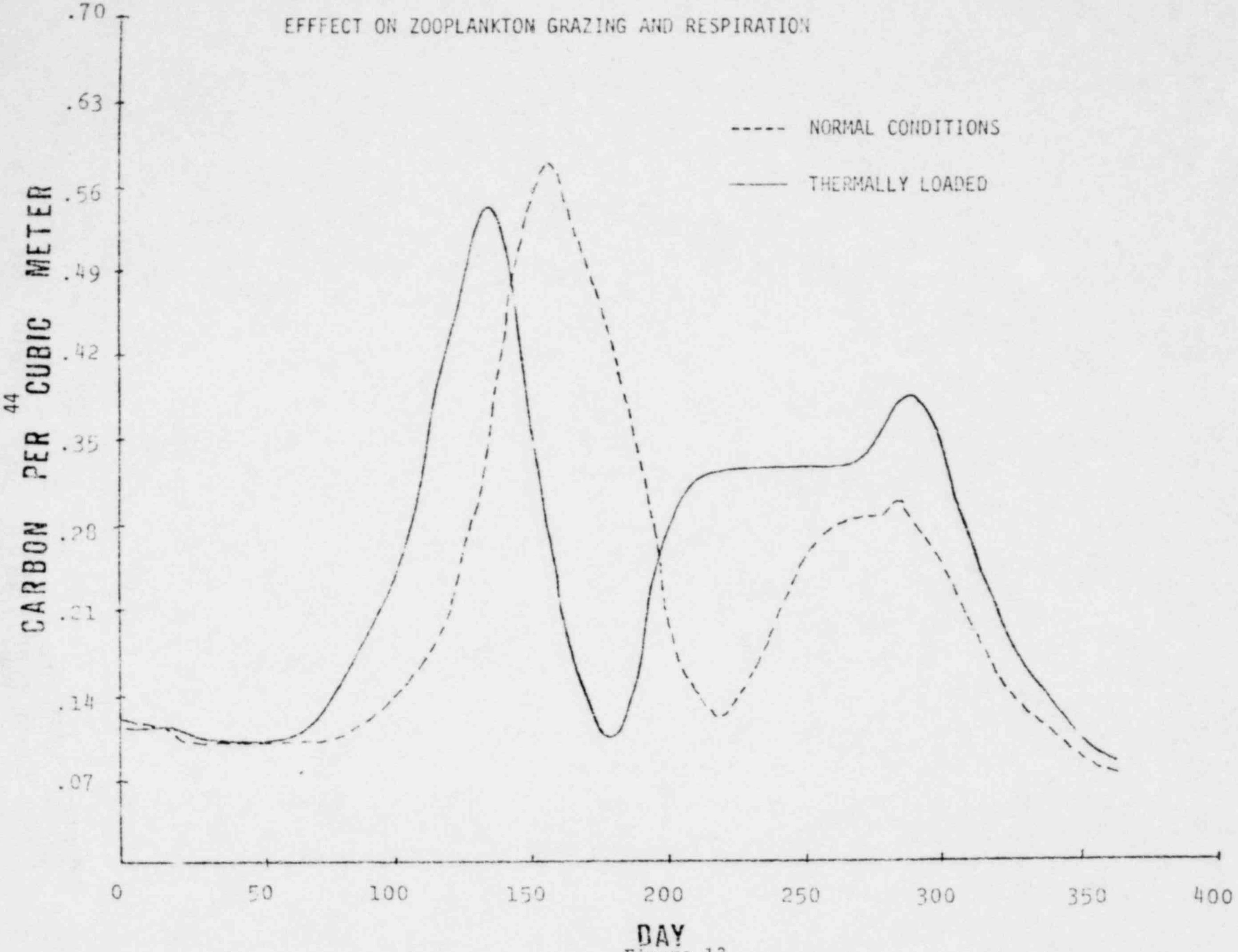

Figure 13.

1355 189

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COMPARISON OF THE CAUSES AND TIMING OF THRESHOLD VALUES IN A NONLOADED VERSUS THERMALLY LOADED SIMULATION RUN.

OCCURANCE	NORMAL TEMPERATURE		TEMPERATURE INCREASED	
	CAUSE	DAY	CAUSE	DAY
FIRST PEAK	LIGHT AND PHOSPHOROUS LIMITATIONS	143	GRAZING	122
FOLLOWING DECREASE	GRAZING	144-208	GRAZING	123
SECOND PEAK	HIGH RESPIRATION AND DECREASING TEMPERATURE EFFECT ON GROWTH	250	NUTRIENT LIMITATIONS	190
FOLLOWING DECREASE		250-365		191-220
THIRD PEAK	NUTRIENT MIXING	285	NUTRIENTS NOT LIMITING	225
FOLLOWING DECREASE	DECREASING TEMPERATURE	290-365	HIGH RESPIRATION AND LOW LIGHT EFFECT ON GROWTH	230-280
FOURTH PEAK			NUTRIENT MIXING	285
FOLLOWING DECREASE			DECREASING TEMPERATURE	290-365

Figure 14.

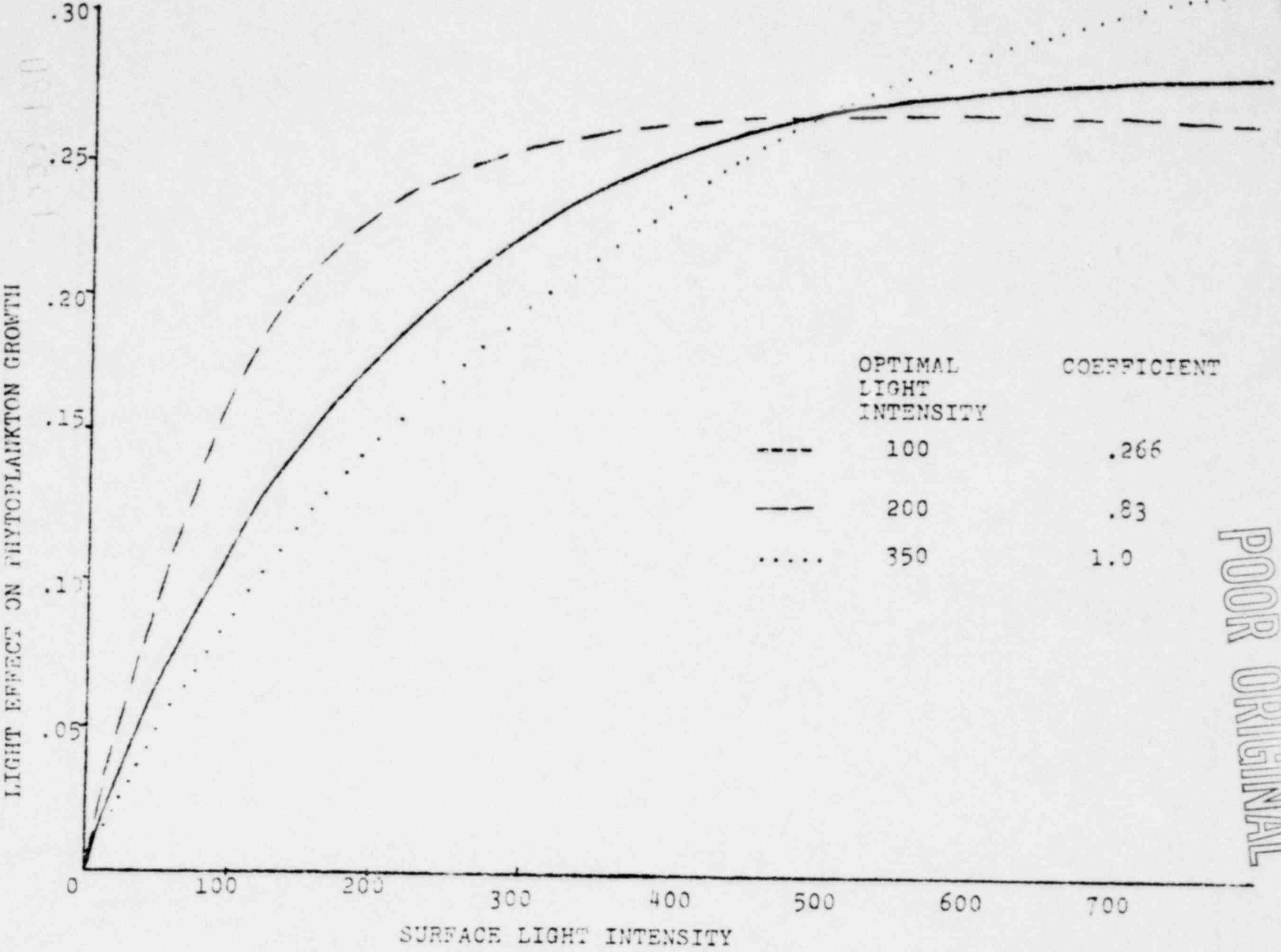

Figure 15.

Different Patterns of Light Effect on Phytoplankton Growth

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TABLES

Summary of Studies of the Effect of Increased Temperature on Phytoplankton

			TEMPERATURE INCREASE CAUSES CHANGES IN							
REFERENCE	PHYTOPLANKTON STUDIED	SITE	SPECIES COMPOSITION	AVERAGE CELL SIZE	BIOMASS	SPECIES DIVERSITY	PRIMARY PRODUCTION	RESPIRATION	CHLOROPHYLL A	CELL DIVISION PER DAY
Stockner (1967)	diatoms	runoff water from hotsprings Wyoming	✓							
Cairnes (1956)	community	Sabine River, Pennsylvania	✓							
Daletskaya and Chulanovskaya (1964)	*Chlorella*	laboratory		↓						↓
Margelef (1954)	*Scenedesmus obliquus*	laboratory		↓						
Garnier (1958 & 1962)	*Oscillatoria brevis*	laboratory							↑h	
Patrick (1966)	diatoms	simulated Pennsylvania river			↓	✓●				↑
	community	Potomac R.				↓▲				
	community	Green R., Pennsylvania	✓			↑				
Stangenberg & Pawlaczyk (1961)	community	power station in Poland				↓†				
Trembley (1960 & 1965)	community	Delaware R.				↑				
Kreh (1973)	community	W. Lake Erie	—		↓		↓s ↓w			
Sorokin (1959 & 1967)	*Chlorella*						↓			
Steidinger & von Breedveld (1969 & 1970)	benthic marine algae	Crystal R. estuary, Florida			↓	↓				
Brooks (1972)	community	Indian R., Delaware					↓w			
Kelly (1971)	community	microcosms			↓		↓		↓	
Werner (1971)	*Coscinodiscus asteromphalus*	laboratory								↓
Schone (1974)	*Thalassiosira rotula*	laboratory								↓
Copeland and Davis (1972)	community	South Creek estuary, N.C.			↓		↓▲	↓▲		
Sangar & Dugan (1972)	*Anacystis nidulans*	culture								↑
Davis (1972)	community	Pamlico R., N.C.					↓			
Specchi (1972)	community	Gulf of Trieste, Italy			—					
Fairchild (1971)	*Achnanthes exigua*	hot springs						↑	↓	↓
Meeks & Castenholz (1971)	*Synechococcus lividus*	laboratory								↑

KEY
✓ change observed
— no change
↓ decrease
↑ increase

NOTES
● difficult to separate from nutient increase
† for greater than 30°C
▲ greatest at 24°C
h at high light intensities
l at low light intensities
s summer
w winter

Table 1.

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TABLE 2.

SUMMARY TABLE OF MODEL "DEFAULT" RUN

	PHYTOPLANKTON	HERBIVOROUS ZOOPLANKTON	CARNIVOROUS ZOOPLANKTON	DETRITUS	AMMONIA	NITRATE	PHOSPHATE
TOTAL PRODUCTION	84.1970	12.3385	12.7242	98.6440			
AVERAGE STANDING CROP	.2308	.0338	.0349	.2704	.0316	.1282	.0102
MAXIMUM VALUE	.5697	.2256	.1635	.9415	.0545	.2495	.0203
TIME OF MAXIMUM	142.7500	202.2500	236.2500	262.7500	216.7500	.2500	364.7500
MINIMUM VALUE	.0702	.0050	.0043	.0000	.0152	.0035	.0009
TIME OF MINIMUM	208.7500	.2500	153.2500	.2500	.2500	259.2500	149.7500

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16. ABSTRACT *(200 words or less)*

The effects of increased temperature on phytoplankton and zooplankton seasonal dynamics were examined using a simulation model. A literature review indicated possible changes to be explored with the model. A simulation "library" of hypotheses from various models was used to examine state variables and process effects on a daily basis, and this output was compared to data collected in Lake Ontario. Comparisons of plankton dynamics in thermally unloaded and loaded runs of the model showed differences in the two situations. Under thermal loading the spring phytoplankton peak occurs earlier and is limited by grazing whereas phosphorous limits the bloom in the unloaded environment. Also, more phytoplankton blooms occur in the model with increased temperature, and light becomes more limiting during the late summer. These comparisons led to hypotheses about adaptations favorable to phytoplankton in a thermally loaded environment including (1) a lower phosphorous and a greater nitrogen tolerance, and (2) lower optimum light intensity. Tests of these hypotheses with the simulator indicated that phytoplankton with these theoretically favored adaptations have increased productivity in the warmer waters. As a group, blue-green algae are known for the physiological characteristics found to be favorable in the thermally loaded environment.

17. KEY WORDS AND DOCUMENT ANALYSIS

17a. DESCRIPTORS

phytoplankton
zooplankton
simulation model
thermally unloaded run
thermally loaded run
grazing

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17b. IDENTIFIERS/OPEN-ENDED TERMS

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