THE DYNAMICS OF A PLANKTON COMMUNITY: FEEDBACK ANALYSIS OF A SPECIALIZED PREDATOR-PREY INTERACTION IN A STRESSED ENVIRONMENT

A THESIS
Presented to
The Faculty of the Division of Graduate Studies
By
Clay L. Montague

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in the School of Industrial and Systems Engineering

Georgia Institute of Technology
March, 1977

THE DYNAMICS OF A PLANKTON COMMUNITY: FEEDBACK ANALYSIS OF A SPECIALIZED PREDATOR-PREY INTERACTION IN A STRESSED ENVIRONMENT

Approved:

Willard R. Fey, Chairman

David M. Gillespie

Richard D. Wright

Date approved by Chairman 3/1/1977

Dedicated to the memory of

Dr. George A. Lafitte, Sr.

ACKNOWLEDGMENTS

I wish to thank Professor W. R. Fey of the School of Industrial and Systems Engineering, Georgia Tech for his patient guidance through this modeling effort. Dr. D. M. Gillespie of the School of Biology, Georgia Tech provided many fruitful discussions leading to an understanding of the biology and ecology of the Great Salt Lake. I thank Dr. R. D. Wright of the School of Industrial and Systems Engineering, Georgia Tech for helpful criticisms especially during the completion of this work.

Dr. R. G. Wiegert of the Department of Zoology, University of Georgia provided useful discussions leading to the discovery of some model weaknesses.

Special thanks to Mrs. Mary David of the University of Georgia for typing the manuscript.

Finally, I wish to thank my wife, Wendy, for her encouragement and support throughout my program at Georgia Tech.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

SUMMARY

Time history data describing the interdependent annual population fluctuations of two plankton species in the Great Salt Lake, Utah are analyzed using the concepts and techniques of feedback dynamics. This predator-prey system is found in the highly stressed saltwater environment of the Great Salt Lake's southern basin. *Dunaliella viridis*, a green alga, is preyed upon exclusively by *Artemia salina*, a brine shrimp.

A DYNAMO simulation model of this system attempts to reproduce the observed time histories. The model equations describe a set of five major feedback loops (together with some minor feedback loops) which interact to reproduce the observed time histories. This is the Dynamic Hypothesis to be tested. These feedback loops [1) algal reproduction, 2) algal self shading, 3) algal consumption, 4) brine shrimp reproduction, and 5) brine shrimp starvation] are believed to account for the annual dynamics observed in the Great Salt Lake. Evidence for this is presented through a parametric sensitivity analysis and a new analysis procedure called Dominant Forces Identification. The procedure for performing the Dominant Forces Identification is presented in detail.

The results of these analysis procedures indicate a need for future research in nutrient dynamics, brine shrimp egg dynamics, and additional *Dunaliella* growth studies.

The general conclusions are: 1) that the model adequately tests the feedback loop hypothesis believed to account for the annual dynamics observed, 2) that this hypothesis seems correct in general, 3) that future research at the Great Salt Lake is needed, and 4) that this model can be used as part of an interactive procedure with which to collect future data and better understand the Great Salt Lake as an ecosystem.

CHAPTER I

INTRODUCTION

The plankton community of the southern basin of the Great Salt Lake is an example of an ecosystem existing in a very harsh environment. Salinity in the Great Salt Lake varies around 200 o/oo[1] (Stokes, 1966). This is about seven times the salinity of the open ocean. The Great Salt Lake salinity is second only to that of the Dead Sea at 226 o/oo (Stokes, 1966). This harsh environment is not favorable for many species of flora and fauna and hence the Great Salt Lake's southern basin plankton community is a very simple ecosystem. It consists of a single phytoplankter *Dunaliella viridis*, (a single celled biflagellate green alga similar in appearance to *Chlamydomonas*) which provides the only food for a single zooplankter, *Artemia salina*, a brine shrimp or fairy shrimp (order Anostraca). (Wirick, 1972; Stephens, 1974; Stephens and Gillespie, 1976).

H. T. Odum (1971) and E. P. Odum (1971) define stress in regards to ecosystems as an energy drain on an ecosystem. Harsh environmental conditions are considered a type of stress because they divert energy away from the system (E. P. Odum, 1971). In the Great Salt Lake little of the solar energy influx is actually fixed as organic carbon because the stressful saline conditions both limit the number of species that

---

[1] o/oo = parts per thousand by weight. This is the weight of salt ions in grams per kg of lake water.

can exist and require extra energy for the metabolism of those species that do exist. Hence, in the Great Salt Lake, much more of the available energy is unused and lost as heat than in less stressful environments. Therefore the Great Salt Lake is considered a stressed ecosystem. Understanding such simple, stressed ecosystems is of interest because of the widespread belief that they contain basic principles of all ecosystems.

Data recently published (Stephens and Gillespie, 1976) describe annual standing stock dynamics for each of these plankton species in the Great Salt Lake. The following annual pattern (Figure 1) is believed to recur with some consistency (Wirick, 1972). The algae bloom in the spring (in somewhat of a sigmoid fashion) from densities on the order of a few million cells per liter in January to over 200 million cells per liter by late April. At this point the algae sharply decline to levels of less than one million cells per liter during the summer months. Corresponding to the decreasing algal densities is the increase of the concentration of brine shrimp from none in mid April to around 20 per liter by mid June. From this peak the brine shrimp initially sharply decline, but later continue to decline more slowly and steadily. Only overwintering eggs remain during the winter months, since brine shrimp suffer thermal death when water temperatures reach about 6°C (Vorhies, 1917; Relyea, 1937; Wirick, 1972). A slight increase in algal concentration occurs during the winter months.

Recently there have been several attempts to explain various aspects of this annually recurring pattern in a holistic manner. After extensive field work, Wirick (1972) observes that this community exhibits

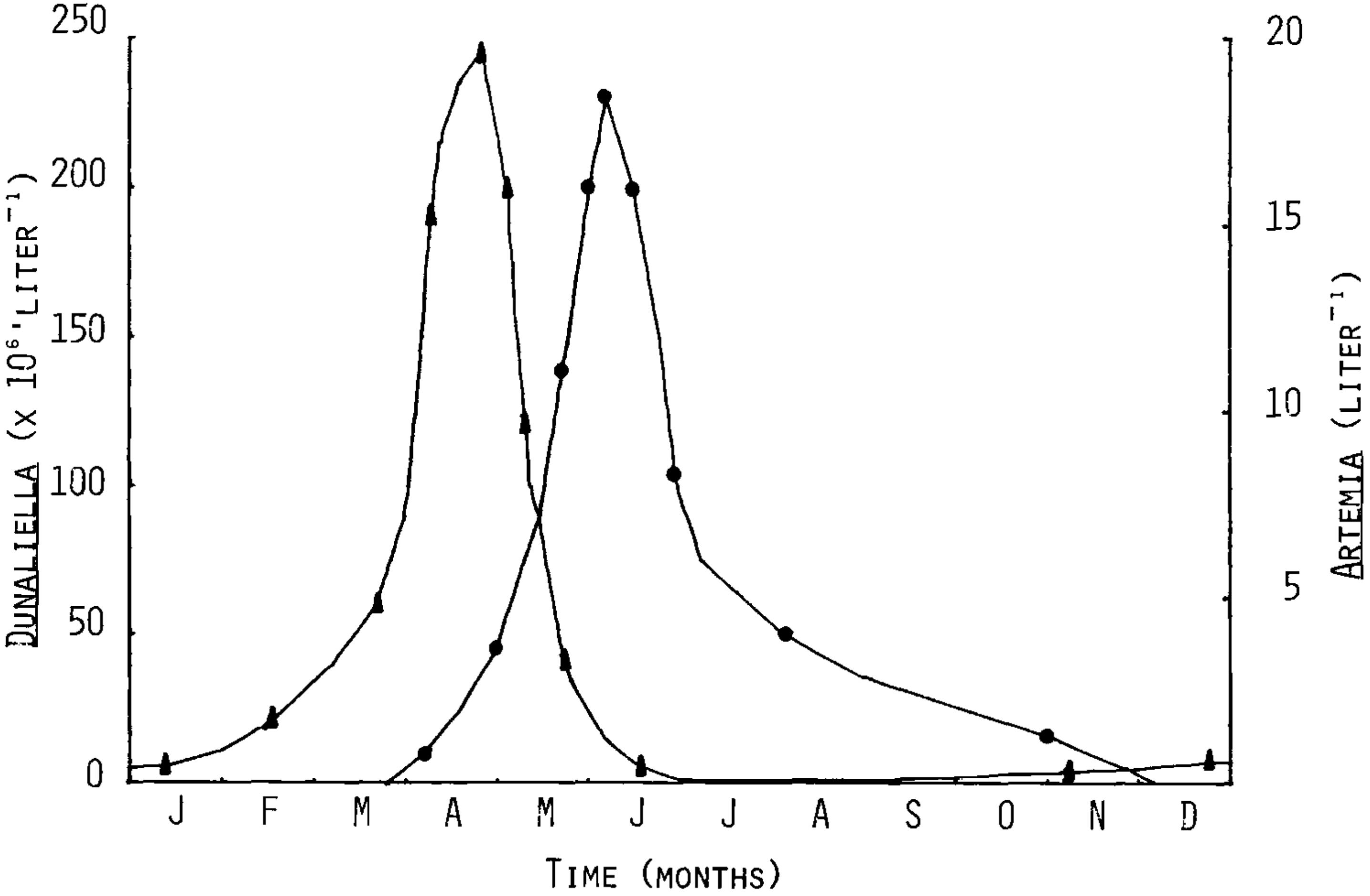

Figure 1. Supposed Recurring Annual Pattern (The Standard Behavior): *Dunaliella viridis*, ▲—▲; *Artemia salina*, ●—●.

predator-prey oscillations, and presents a model which simulates algal growth and grazing by brine shrimp. The model was difficult to control, a tenfold increase of the grazing rate of brine shrimp being unable to decrease the algal standing stock to the real system level. Stephens and Gillespie (1972; 1976) suggest that self shading limits algal growth prior to the onslaught of brine shrimp grazing. Stephens (1974) reviews the previous biological investigations of the Great Salt Lake, describes the system, and assays for nutrients as a possible limiting factor to algal growth. Stephens and Gillespie (1976) assess phytoplankton production and suggest that nitrogen limits algal growth during the summer months.

Feedback interrelationships between the algae and the brine shrimp accumulations in the Great Salt Lake are believed to account for the recurring annual dynamics observed. The strength of the relationships may be constrained by open-loop environmental factors, however the dynamics within these constraints should arise from endogenous feedback loops (Gutierrez and Fey, 1975a; 1975b). The immediate goal of this research is to begin to account for the consistent annual fluctuations observed for the two interacting populations of plankton in the southern basin of the Great Salt Lake. A hypothesis based on interacting positive and negative feedback loops will be developed. This dynamic hypothesis seeks to bring together the present knowledge and theory concerning each of the two populations and their interaction. Using Forrester's "industrial dynamics" methodology (Forrester, 1961) the biological concepts either known or believed about this ecosystem will be translated into a set of algebraic and discretized first order integral equations. When solved, this concrete and easily communicated set of statements may point out areas of needed research required for a thorough understanding of the ecosystem.

The ultimate goal of the research is a better understanding of the dynamics of the described plankton community. With such an understanding it may be possible to predict the effects of changing environmental conditions and human intervention. This understanding may also contribute to the understanding of stressed ecosystems in general. Stressed ecosystems, because of their relative simplicity, are believed to exhibit fundamental processes common to all ecosystems. A thorough understanding of several stressed ecosystems may lead to the discovery of recurring structures which, in turn, may provide support for new unifying theories in ecology. Through continued feedback between the model and the real ecosystem, via experimentation with each, it should be possible to eventually approach complete understanding of the forces producing the dynamics of this plankton community.

CHAPTER II

METHODOLOGIES

Data Collection

The supposed annual pattern presented in Figure 1 (referred to as the standard behavior) is the result of combining data collected under the supervision of D. M. Gillespie during 1970, 1971, and 1973 (Figures 2, 3, and 4, respectively). The midsummer peaks of algae and brine shrimp in the 1973 (Figure 4) data are due to a bloom of an unidentified green flagellate, not *Dunaliella viridis* (Stephens, 1974; Stephens and Gillespie, 1976). This algal species has been observed before by Kirkpatrick in 1934 (Stephens and Gillespie, 1976). The midsummer bloom in 1973, however, is believed to be the result of decreasing salinity in the southern basin of the Great Salt Lake between 1971 and 1973 (Gillespie, personal communication). For the purposes of the present study, salinity is assumed to be constant at the level found in 1970 and 1971 [mean dissolved solids=22% (Wirick, 1972)].

While it is true that the system has evolved away from the standard behavior to some degree, it is believed that the major feedback loops responsible for this behavior are still intact. Therefore, as a convenience so that a preliminary understanding of the ecosystem may be attained, the smaller green flagellate will be ignored in this study.

The collection procedures used for the plankton are given in Wirick (1972) and Stephens and Gillespie (1976). Phytoplankton samples

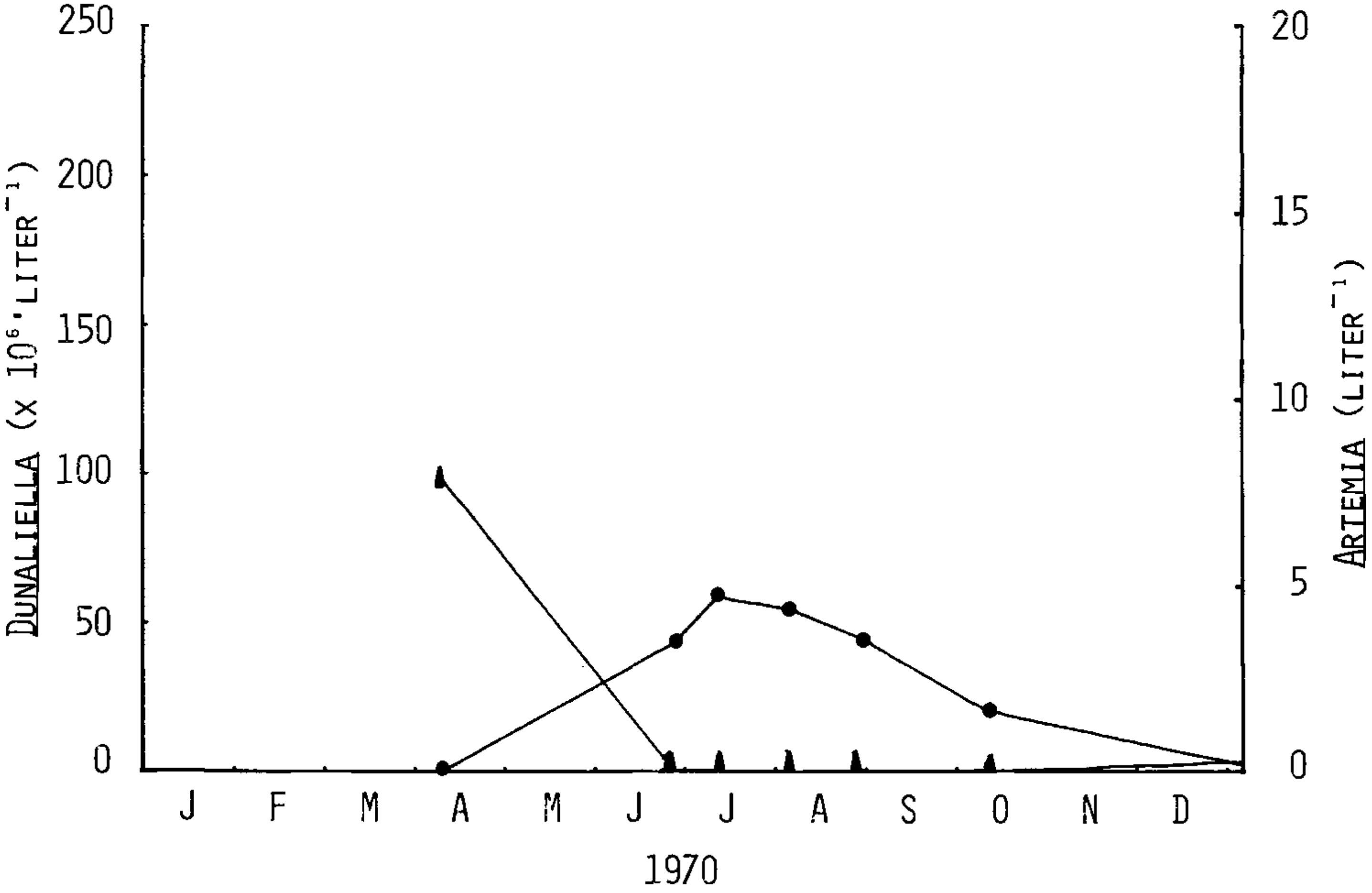

Figure 2. Plankton Data Collected at the Great Salt Lake During 1970: *Dunaliella viridis*, ▲——▲; *Artemia salina*, ●——● (Courtesy of D. M. Gillespie).

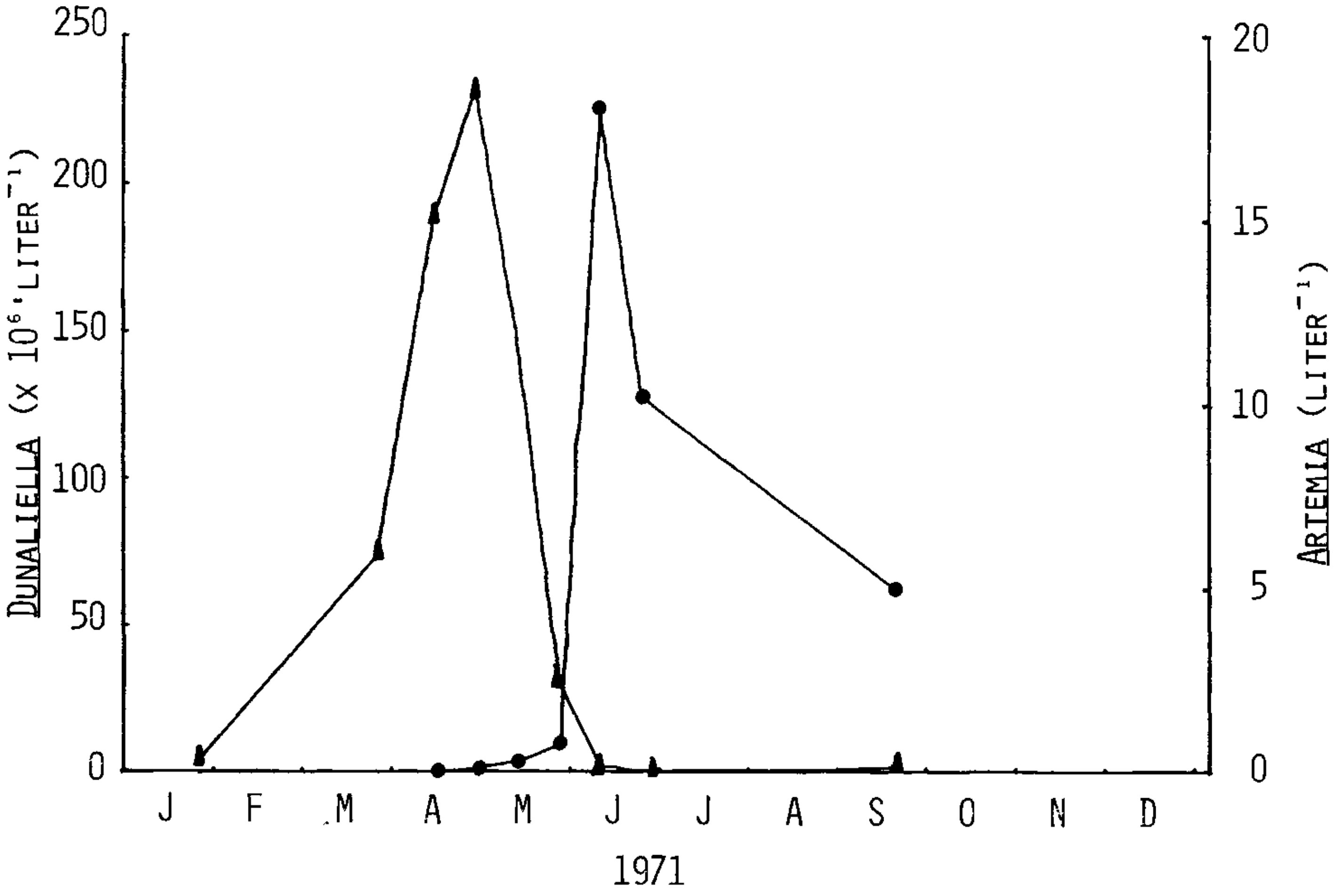

Figure 3. Plankton Data Collected at the Great Salt Lake During 1971: Dunaliella viridis, ▲——▲; Artemia salina, ●——● (Courtesy of D. M. Gillespie).

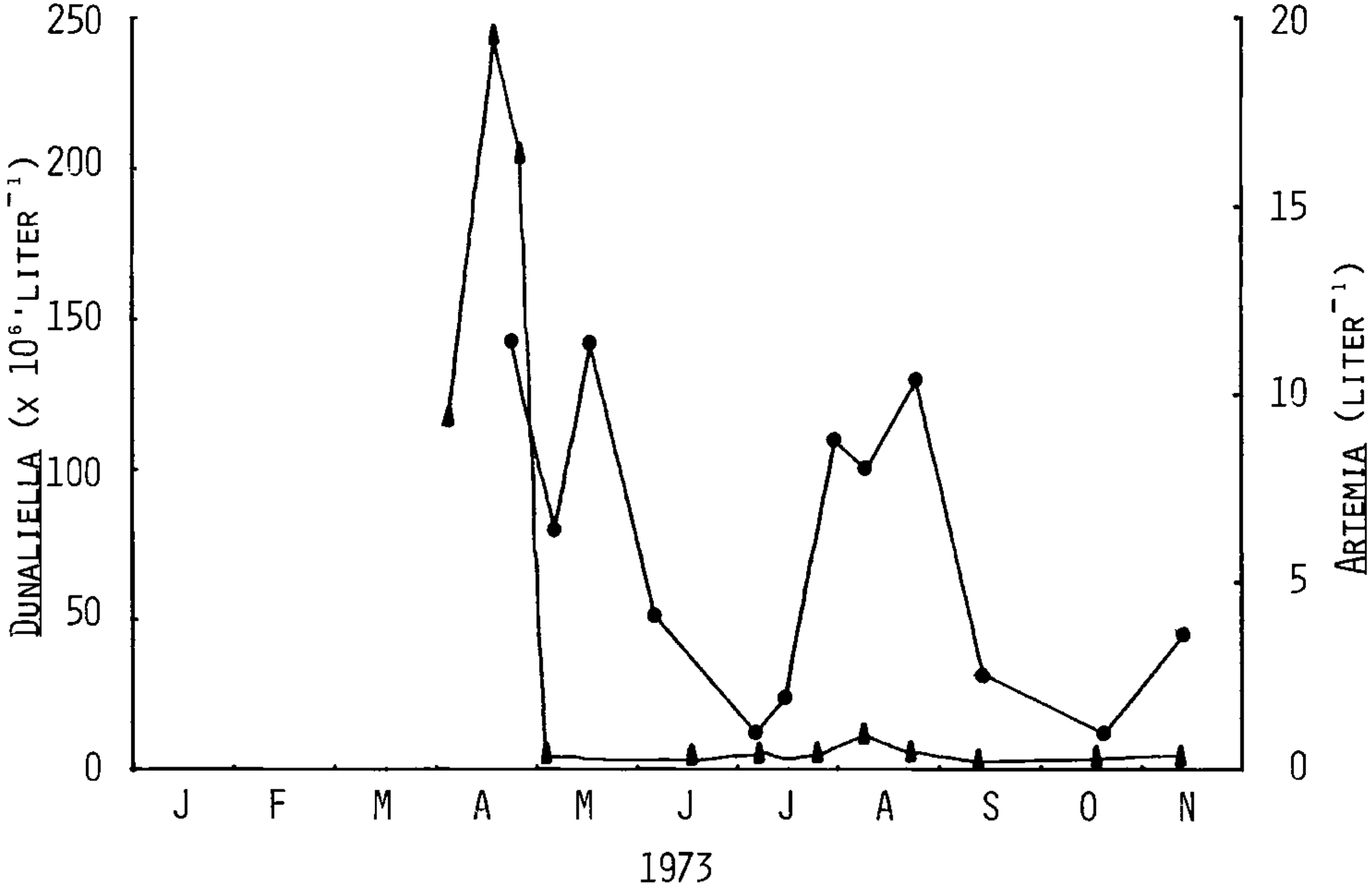

Figure 4. Plankton Data Collected at the Great Salt Lake During 1973: *Dunaliella viridis*, ▲——▲; *Artemia salina*, ●——● (Adapted from Stephens and Gillespie, 1976).

were collected in Kemmerer bottles and fixed with Lugol's solution prior to counting (for 1970 and 1971 data) or were counted live on the day of collection (for 1973 data). Phytoplankton were counted with a haemocytometer. Brine shrimp were collected with a Clarke-Bumpus sampler fitted with a #10 plankton net (175 μm mesh). The number of Artemia given is the sum of all age classes found.

Modeling

A simulation methodology for developing and testing hypotheses which seek to explain the dynamic behavior of systems by their feedback structure was originally named "industrial dynamics" by Forrester (1961). Because of the general applicability of this methodology to many large scale, complex, nonlinear, and unclear systems for which there had previously existed no satisfactory analytical methodologies, the name "systems dynamics" has been used. Since the primary structural form responsible for the dynamic behavior of systems is the endogenous feedback loop, the name "feedback dynamics" will be used here (Gutierrez, 1974).

Feedback dynamics has been used to analyze ecological systems. Gutierrez (1974) developed a theoretical model of the dynamics of secondary succession in a grassland ecosystem. The research has produced an endogenic theory of secondary succession in which open-loop environmental factors are viewed as imposing limits on the successional dynamics arising as a result of closed feedback loops (Gutierrez and Fey, 1975a; 1975b). Knight (1970) and Knight and Hines(1970) developed a feedback model of the social, political and economic factors important in water quality management and control. Included in the model (based on Ohio River data) are ecological deterioration by pollutants, water quality standards and their enforcement and public awareness to pollution. N. B. Forrester (1969) studied general aspects of a predator-prey relationship by simulating a rabbit-coyote system. His paper serves as a concise review of the techniques employed in building a model using the concept of feedback dynamics. In addition to ecological systems, feedback dynamics has been used to analyze social, economic, educational, military and industrial systems. A general outline of this methodology follows.

Through observing a time history (such as the standard behavior of Figure 1) a problem can often be identified and a clear statement of objectives developed. The present problem was identified in the introductory remarks.

Key variables are identified within the framework of a precisely stated system boundary. The key variables are accumulations (levels) and flow rates. In the Great Salt Lake ecosystem the key variables are the accumulations and flow rates involved in each species' life cycle. The inflow of algae (division rate), the accumulation of algae (standing stock), and the consumption rates are key variables involved in the algal dynamics. The laying rates and accumulations of both nondurable brine shrimp eggs (those that hatch within one or two days) and overwintering (winter) eggs are some of the key variables important to the brine shrimp dynamics. Others include the hatching rates and attrition rates of eggs, the accumulation and maturation rate of nauplii, the accumulation of adults, the death rate of adults due to old age, and the death rates of both adults and nauplii due to starvation. Solar energy input is the key exogenous variable.

The nature of the relationships between the key variables is determined through empirical data, expert opinion and a review of pertinent literature. By observing the time history a set of feedback loops can be determined which seem necessary to produce the output observed. With this set in mind, the relationships between key variables are determined and a feedback structure believed responsible for the observed behavior results. This structure becomes the dynamic hypothesis. The dynamic hypothesis for the Great Salt Lake model and accompanying influence diagrams are presented in the next chapter.

With the aid of Forrester's flow diagram (see Forrester, 1961; 1968) a set of algebraic and discretized first order integral equations are written for digital computer simulation. In this case, the DYNAMO II language is the computer simulation language used (Pugh, 1973). The DYNAMO equations constructed for the Great Salt Lake ecosystem are given in Appendix I. The parameter values and the nature of the table functions used in this set of equations were determined from various sources (as indicated in Appendix I). Some were found in the literature, some were based on the observations and empirical data of experts working in the Great Salt Lake (e.g. D. M. Gillespie), and some were estimated within a range of possible values based on accepted ecological theory. The relative importance of accuracy in such estimates is the subject of some of the parametric sensitivity analysis presented in Chapter IV.

Model validation, in this study, includes checking the soundness of the dynamic hypothesis, the equations, and the computer program. Here, this is referred to as structural validation. If the equations have been written properly, the units are correct, and the model consistent with present knowledge and theory concerning the real system, the model is considered structurally valid (Gutierrez, 1974; Forrester, 1961). Also involved is an assessment of the model with respect to its normal output behavior as well as its response to various parametric and input function perturbations (referred to as functional validation in this study). Analysis and validation of the model herein developed is the subject of Chapter IV.

If the validation procedures indicate that a change in the model is necessary, such changes should be performed with caution. Changes other than those involved with model structure should be accompanied by additional literature or experimental evidence that the changes are warranted. To achieve a useful level of understanding of the system such cross-checking between the model and the real system is necessary.

If the real system changes are desired, a set of possible avenues of change are determined and the changes are implemented. The changes are evaluated and the model redesigned appropriately if necessary. Continuing to recycle new information eventually results in a model that accurately evolves with the system. At this point a very high level of system understanding will have been achieved possibly resulting in a reliable predictive model. At its present stage of development, the study of this plankton community can only suggest ways in which new data can be gathered experimentally and what information seems most critical to our understanding of the Great Salt Lake (see Conclusions, Chapter VI).

The methodology of feedback dynamics is largely qualitative, the results often temporary and is as much an art as a science. Like any modeling approach, when performed and interpreted properly, the level of understanding obtained for the whole system may be far greater than that obtained from our mental models (Forrester, 1968).

Dominant Forces Identification

A new sensitivity analysis methodology which allows the assessment of interaction effects between parameters in feedback dynamics models is presented in Chapter V entitled Dominant Forces Identification. This methodology was originally developed by Low (see Low and Cowles, 1975) and is further developed in this study. Details of the methodology will be presented in that chapter.

CHAPTER III

DYNAMIC HYPOTHESIS

A simplified view of the dynamic hypothesis is given in the system influence diagram of Figure 5. This diagram traces the major interactions believed responsible for the standard behavior of Figure 1. The system contains the driving force of solar energy and five major feedback loops. Two of the loops are positive, and three are negative. The two major accumulations pictured here are the algal (Dunaliella viridis) and the brine shrimp (Artemia salina). The exponential growth of algae occurring in the early spring is accounted for by the positive algal reproduction loop. The speed of this growth is modified by the available sunlight and the water temperature. As the division rate of algae increases, more algae are produced which in turn allow a greater reproduction rate. However, as their concentration increases, they shade themselves (Stephens and Gillespie, 1972; 1976) reducing their productivity. This negative self-shading loop is believed responsible for the growth rate reduction observed in late spring for the algae (producing a sigmoid algal growth curve).

When water temperatures reach 10-14°C, overwintering brine shrimp eggs hatch producing free swimming nauplii (Stephens and Gillespie, 1976). Immediately they begin to graze the algal population down, being quite voracious (see Reeve, 1963a, b, c, d; Sushchenya, 1962; Mason, 1963; Wirick, 1972). This large consumption of algae is responsible

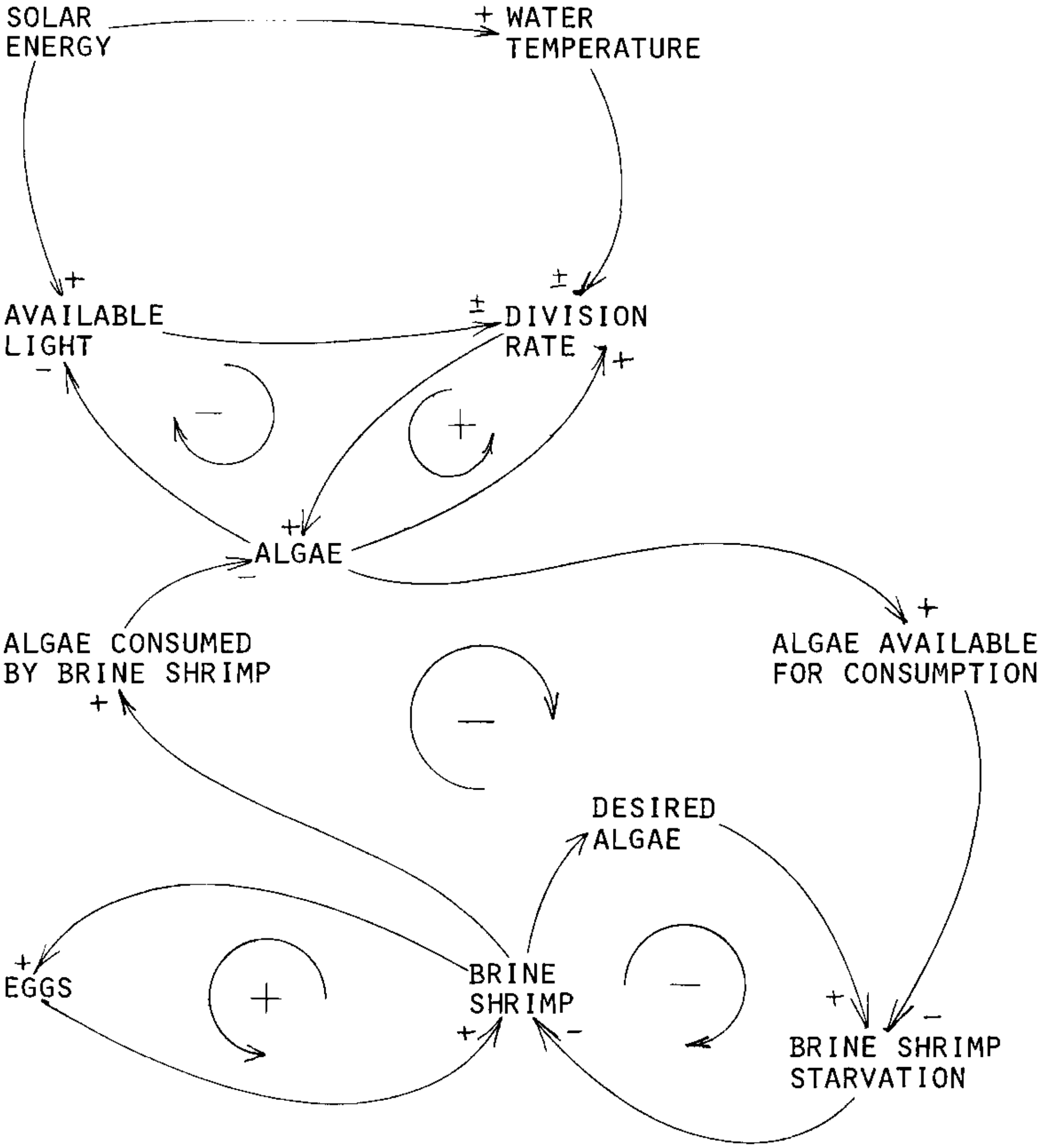

Figure 5. Overall System Influence Diagram Illustrating the Dynamic Hypothesis.

for both the decline of algae and the survival of brine shrimp during the early summer. The feedback loop associated with algal consumption is negative and should tend to balance the system towards some steady state densities for both algae and brine shrimp. As the brine shrimp increase, due to their reproduction (in the form of nondurable eggs that hatch within one day of oviposition), algae are consumed and therefore their concentration decreases. This causes a decrease in algae available for consumption and therefore increases the possibility of brine shrimp starvation. Starvation, of course, reduces the total brine shrimp population, which, in turn, reduces the algae consumed by brine shrimp. This illustrates the control exerted by the negative algal consumption feedback loop.

Starvation is responsible for brine shrimp decline and subsequent control as well. As brine shrimp increase by their reproduction feedback loop, the total algae required to prevent any starvation is increased (referred to as desired algae). As desired algae increase, it may exceed available algae and cause brine shrimp starvation which, in turn, reduces the total shrimp population. Reduced shrimp means reduced total desired algae, less starvation, and therefore more shrimp. In this manner it may be seen how a negative loop is responsible for oscillations in a predator-prey interaction.

The details of each of the five major feedback loops just described will follow. Each loop will be described separately. However, it must be kept in mind that the total behavior observed is a function of properties of all loops taken as a whole, rather than a function of the specifics within any single loop. The relationships within each of these five loops will be constructed with reference to three sources of available information: 1) empirical data, 2) theory, and 3) expert opinion.

The Algae: Logistic Growth

In the southern basin of the Great Salt Lake growth of the alga *Dunaliella viridis* is limited possibly only by sunlight and temperature (as assumed by Wirick, 1972). Nutrients are believed to be plentiful during the spring bloom due to pollution input from the influent rivers of the southern basin (Coburn and Eckhoff, 1972; Stephens and Gillespie, 1972, 1976). However, this point has been argued (Porcella and Holman, 1972) and it may be that nutrients are limiting at some times during the year. It is now believed by Stephens and Gillespie (1976) that the springtime bloom is light limited, due to self shading. This bloom, however, uses available nitrogen, which thus becomes limiting during the remainder of the year. That nitrogen is limiting later in the year has been shown through laboratory bioassays performed by Stephens and Gillespie (1976) and earlier by Porcella and Holman (1972). The present dynamic hypothesis concerning algal limiting factors assumes that self shading and water temperature limit algal growth, and, for now, ignores the possible limiting effect of nitrogen availability. More will be said about this assumption in the section on validation of this model.

The feedback loops responsible for the algal logistic growth in the early spring are given in Figure 6. The primary variables are the accumulation of algae and the total population's division rate. Division

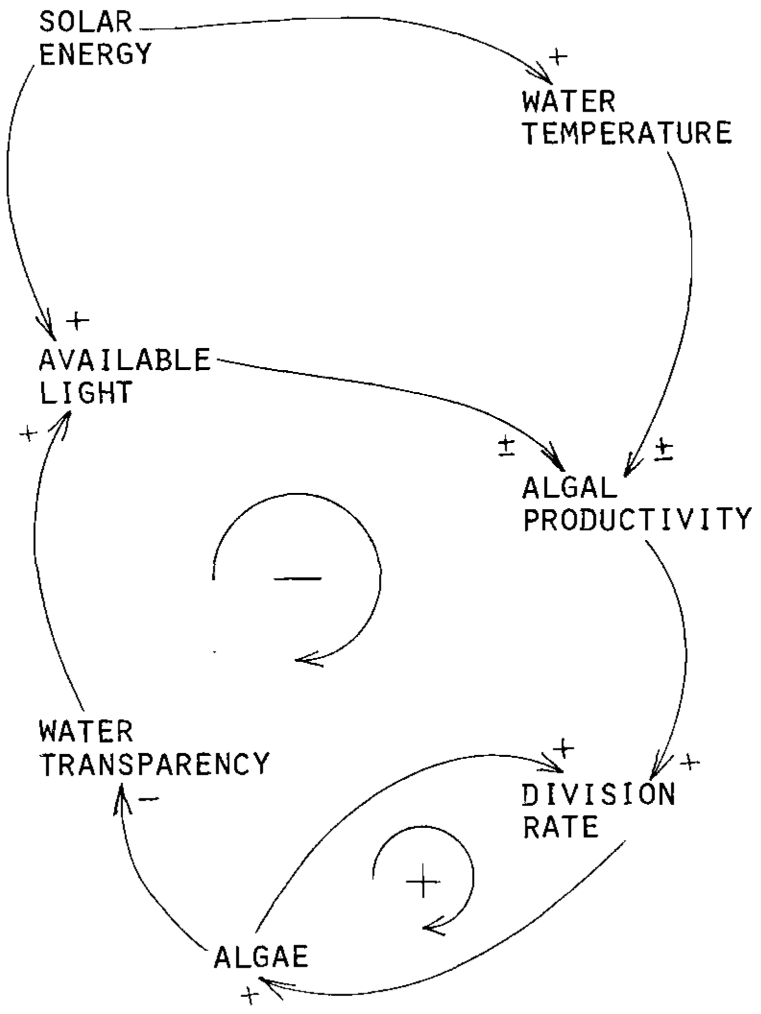

Figure 6. Feedback Loops Believed Responsible for the Algal Growth Dynamics Observed in the Great Salt Lake.

rate is defined here as the number of new algae being added to the accumulation each day. It is the multiple of the average algal productivity (defined as the new algae per old algae per day, or the inverse of the algal doubling time in days[2]) and the number of algae already present. Algal productivity is a function of average daily light and water temperature values. At optimal light and temperature, the productivity value is at some maximum. These functions were empirically determined for the algal species in the southern basin of Great Salt Lake by Van Aukin and McNulty (1973) and are presented here in Figures 7 and 8. Van Aukin and McNulty also demonstrated that algal productivity is a function of salinity, carbon dioxide concentration, and the potassium:sodium ratio. These environmental factors were not seen to change greatly during the 1970, 1971 measurements and therefore have been ignored in the present model.

The average daily values for solar intensity (as measured by an Eppley pyrheliometer in langleys per day) and for average water temperature (as determined from Kemmerer water samples and unpublished data from the Utah Geological and Mineralogical Survey) are given in Figure 9. In the model, solar energy is approximated by a cosine wave with a 365 day period and appropriate amplitude. Water temperature is merely a converted delayed value of solar intensity. Van Aukin and McNulty's (1973) experiments on algal growth versus light intensity used klux as the light units. Therefore, Wirick (1972) calibrated a light

---

[2] This is an incorrect approximation. For a discussion of this problem see section entitled Corrected Algal Productivity of Appendix II.

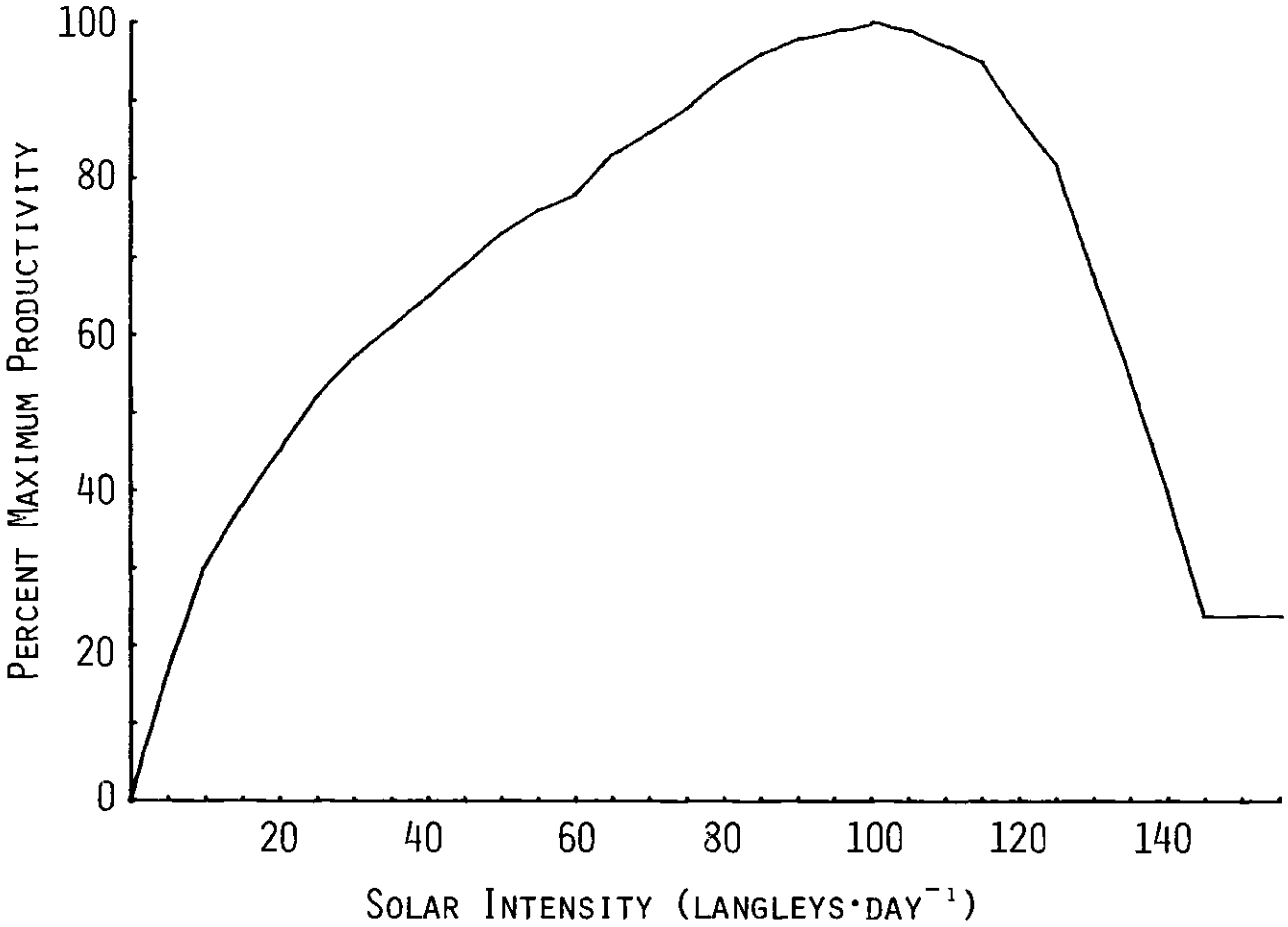

Figure 7. Percent Maximum Productivity as a Function of Sunlight Intensity (Adapted from Van Aukin and McNulty, 1973).

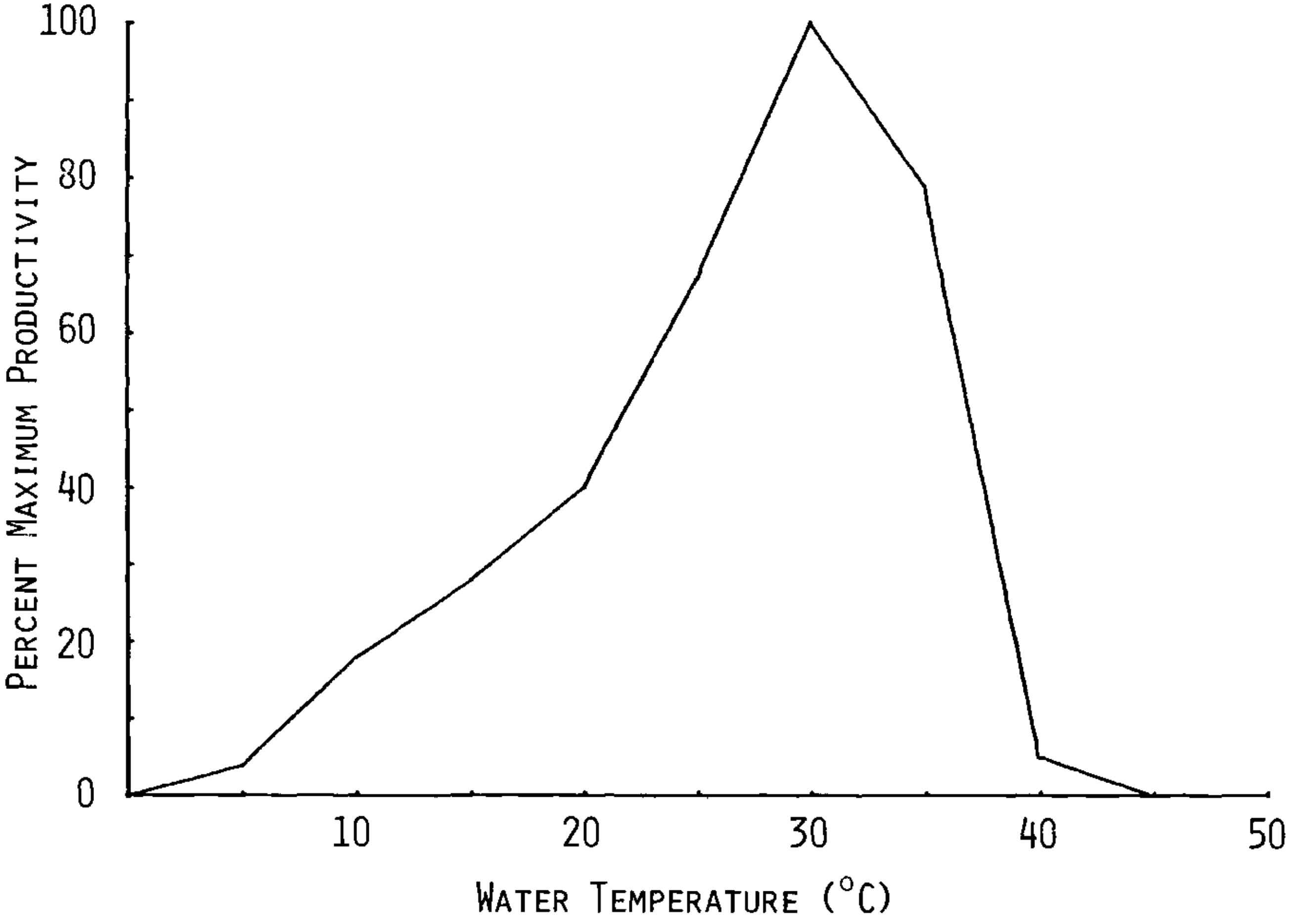

Figure 8. Percent Maximum Productivity as a Function of Water Temperature (Adapted from Van Aukin and McNulty, 1973).

Figure 9. Incident Radiation and Water Temperatures Found at the Great Salt Lake During 1971: Water Temperature, ○—○; Sunlight, △—△.

source similar to the one Van Aukin and McNulty used to obtain a conversion factor in langleys per day. This was done after the method of Stephens and Strickland (1962). The conversion factor obtained was 1 klux = 3.24 langleys per day.

Available light is a function of both solar intensity and water transparency. It is assumed that the water transparency remains at some constant background level in the absence of algae. This appears true except during the winter when sodium sulfate is observed to precipitate, clouding the water (Handy and Hahl, 1966; Handy, 1967; Hahl and Handy, 1969). Otherwise observed changes are due strictly to changes in algal density. Transparency in the model is defined as some percentage of photosynthetically active radiation (PHAR). As the algal density increases, the percentage of photosynthetically active radiation which penetrates the water declines. The function used for this relationship is given in Figure 10. It has been approximated from 1) actual secchi disk data [assuming 95% of the indicated radiation has been absorbed at the indicated depth (Hutchinson, 1957)], 2) Wirick's (1972) simulated secchi disk data, and 3) Stephens and Strickland's (1962) curves for percent transmission of PHAR at around four meters depth, the average depth of the Great Salt Lake (Stokes, 1966). Due to the approximate nature of this function, it will be thoroughly analyzed for sensitivity in the validation of this model.

Thus, the functions presented in Figure 6 document the structure of two feedback loops, a positive reproduction loop, and a negative self shading loop. These are believed responsible for the sigmoid

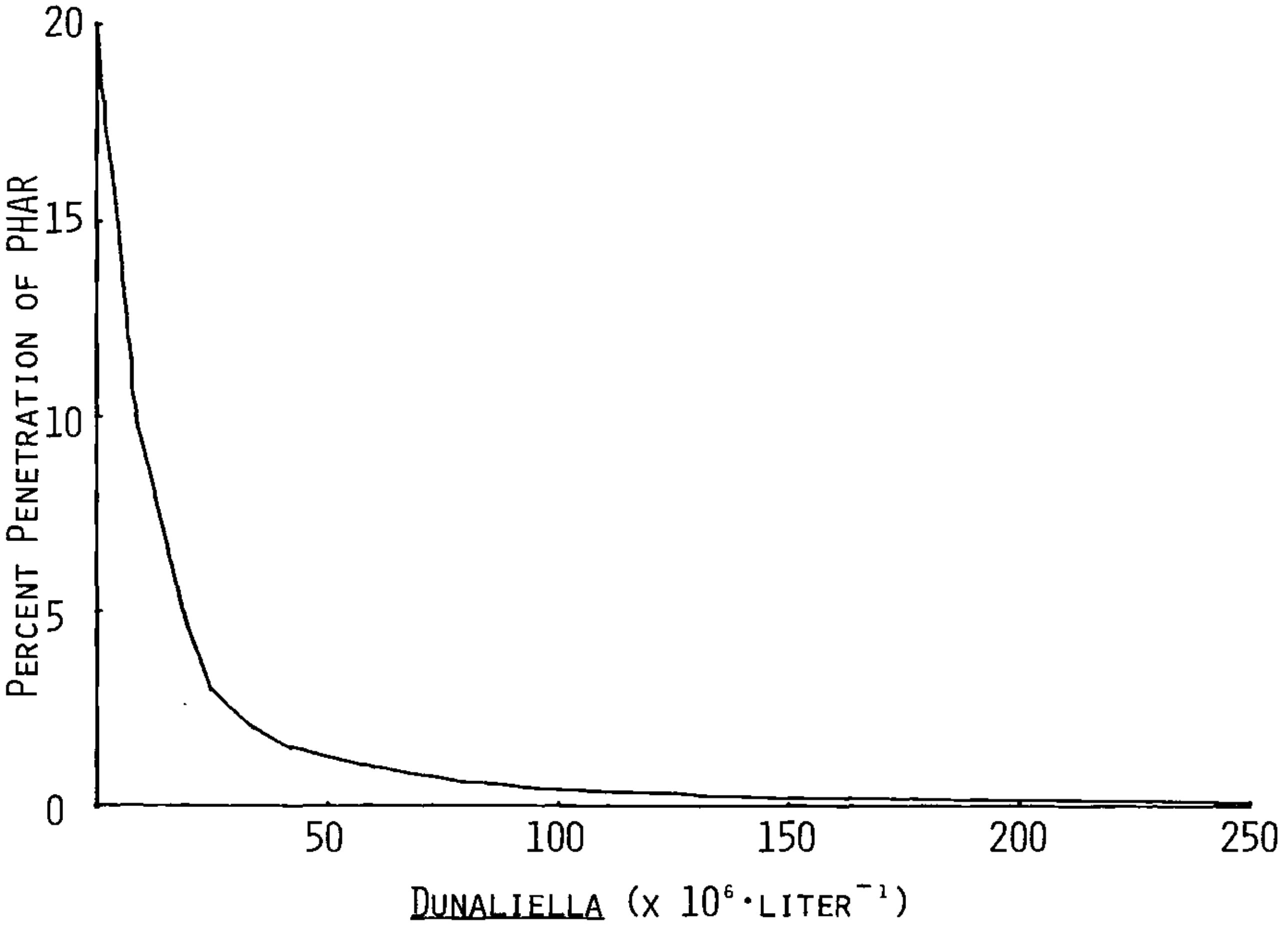

Figure 10. Percent Penetration of Photosynthetically Active Radiation (PHAR) as a Function of Algal Density (An Estimate Based on Secchi Disk Data and Stephens and Strickland's (1962) Curves for Transmission of PHAR at Four Meters Depth.

growth curve of algae seen in the early spring blooms.

Shrimp Life Cycle

Following the algal bloom, a dramatic increase in brine shrimp occurs. Responsible for this increase is the (temporarily) uninhibited operation of the brine shrimp *Artemia salina's* life cycle (Figure 11). A description of this life cycle follows.

Brine shrimp suffer thermal death in late autumn or early winter, when the water temperature falls to about 6-9°C (Vorhies, 1917; Relyea, 1937; Engel and Angelovic, 1968; Wirick, 1972; Stephens, 1974). The population survives as overwintering eggs which do not hatch until they have met an assumed cold requirement, and water temperatures again rise to 9-14°C (Vorhies, 1917; Wirick, 1972; Stephens, 1974). At this temperature, the eggs hatch within a day or two, becoming free swimming nauplii (Jensen, 1918; Relyea, 1937; Wirick, 1972). Nauplii reach maturity within 18-21 days at around 20°C (Jensen, 1918). Of course, both hatching times and maturation times are subject to temperature. A Q_{10}[3] value of two is the assumed response to temperature of all metabolic processes in the model. Adults die after a total lifetime of about 130 days at 25°C (Khmeleva, 1967), assuming that they do not starve beforehand. Birds are seen to prey on *Artemia* in the Great Salt

---

[3] Q_{10} is the factor by which respiratory processes vary with every 10°change in temperature. A value of two has been found for many small poikilotherms (Wiegert, 1976). Thus, from an initial reference temperature, respiration is doubled with a 10°C increase in temperature and halved with a 10° decrease.

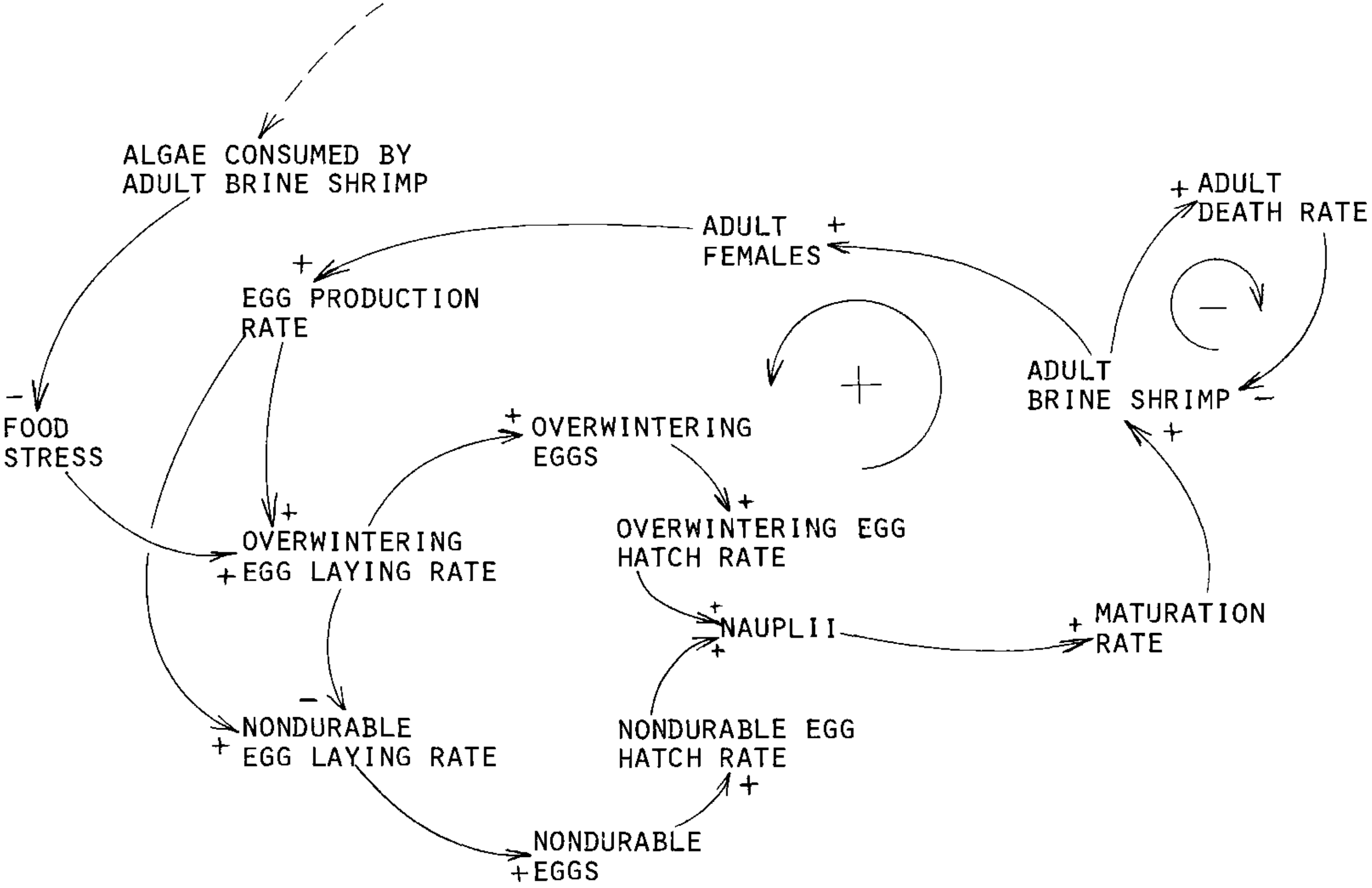

Figure 11. The Life Cycle of *Artemia* in the Great Salt Lake.

Lake (Wetmore, 1917) but their effect is considered negligible (Gillespie, personal communication).

From the data of Wirick (1972) together with personal communications with Gillespie, it appears that about half of all adults are female. Broods of eggs develop about every 5-7 days for each female at 25°C (Khmeleva, 1967) and do not have to be fertilized to produce viable males and females (Relyea, 1937; Woodbury, 1936; Khmeleva, 1967). The average clutch size found for Artemia salina by Wirick (1972) was 30-50 eggs, however, Jensen (1918) found clutch sizes to vary between 16 and 120 eggs per gravid female.

The first eggs produced in the spring are of a nondurable type which hatch within a day. Sometimes they hatch before leaving the ovisac, leading earlier observers to believe nauplii were produced viviparously (see Keunen, 1939). As the summer progresses, overwintering eggs become more apparent. The factors causing the change from production of nondurable to overwintering eggs is presently being argued. Some authors believe that when food concentrations are low, females begin producing winter eggs (Wirick, 1972; Stephens, 1974). However, Holman (1975) has some convincing evidence that day length is responsible. If day length was totally responsible, it might be expected that one would see a sudden increase in winter eggs at some time during the summer or fall. Instead, a gradual increase has been noted (Gillespie, personal communication). Perhaps both mechanisms operate to insure continuation of the species, both in unexpected hard times (that of food stress), and in predictable hard times (cold winter temperatures). The present model operates on the possibly erroneous assumption that food stress is the only factor causing winter egg production, since the model was initially formulated prior to the presentation of Holman's data. Future modification of the model should consider the impact of this new hypothesis.

The hatching rates, maturation rate, adult death rate, and the egg production rate all refer to the total numbers flowing into or out of accumulations during a day. That is why the accumulation of eggs has a positive influence on the hatching rate and the accumulation of nauplii has a positive influence on their maturation rate, etc. These rates have associated with them a value of time, each of which is a function of temperature, as mentioned previously. The times are the average times a member of an accumulation will remain in that accumulation before flowing out through the respective flow rate.

Leakages occur from the egg compartments for a variety of reasons. For example, eggs may be inviable, be blown away, or washed onto the shore. It is estimated that approximately 2.5% of all winter eggs are lost each day, and 8.0% of all nondurable eggs fail to hatch each day. These values are estimated from Wirick (1972), and Gillespie (personal communication). The sensitivity of these estimates have been analyzed and the results are reported in Chapter IV.

The above described life cycle is believed responsible for the shrimp growth observed in the spring. It is interesting to note that shrimp hatching appears to be timed to occur when food is plentiful, allowing the gain around the life cycle loop to be at a maximum until food is grazed to a very low level. How algae are consumed and the effects of starvation on shrimp adults and nauplii will be considered in the sections that follow.

Algal Consumption: The Rapid Springtime Decline of Algae

The only requirement for algal decline is that the daily algal production is less than the daily algal death. Apparently death of *Dunaliella viridis* is caused solely by consumption. When normal environmental factors are severe, these algae merely form cysts which remain viable for extended periods of time as in other Chlamydomonadaceae (Chapman, 1968).

Figure 12 illustrates the dynamic hypothesis concerning the consumption of *Dunaliella viridis* by *Artemia salina* in the southern basin of the Great Salt Lake. Illustrated are two nested loops that are opposite in sign. The dominant loop is the negative control loop. The positive loop is an artifact of the reduction in filtration rate caused by increasing algal density. This effect occurs more slowly than the overall increase in consumption rate upon increases in algal density. The relationship between algal concentration and brine shrimp filtration rate is given in Figure 13. It is approximately a negative exponential curve. This relationship was reconstructed from the data of Reeve (1963 a,b) for *Artemia salina* feeding on a related alga, *Dunaliella tertiolecta*. That the filtration rate decreases with increasing food concentration was also found by Suschenya (1962) for *Artemia salina* feeding on yeast suspensions. The filtration rate maximum of 220

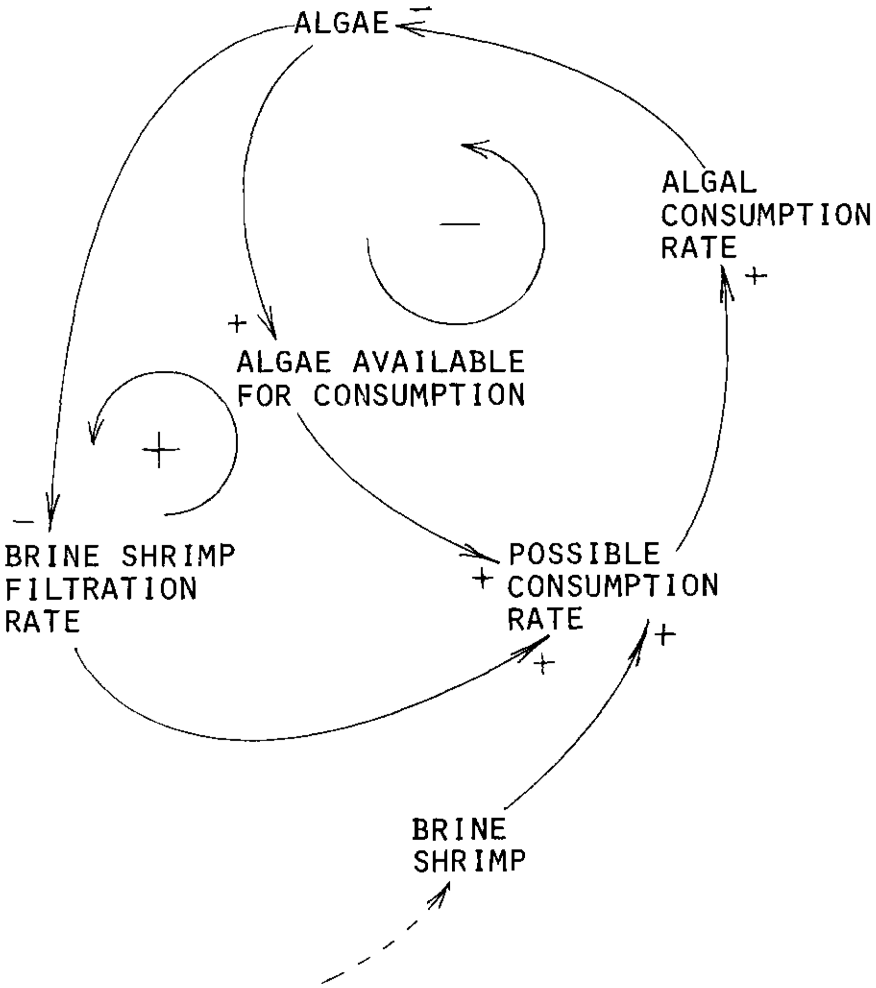

Figure 12. Feedback Loops Believed to Account for Algal Consumption in the Great Salt Lake.

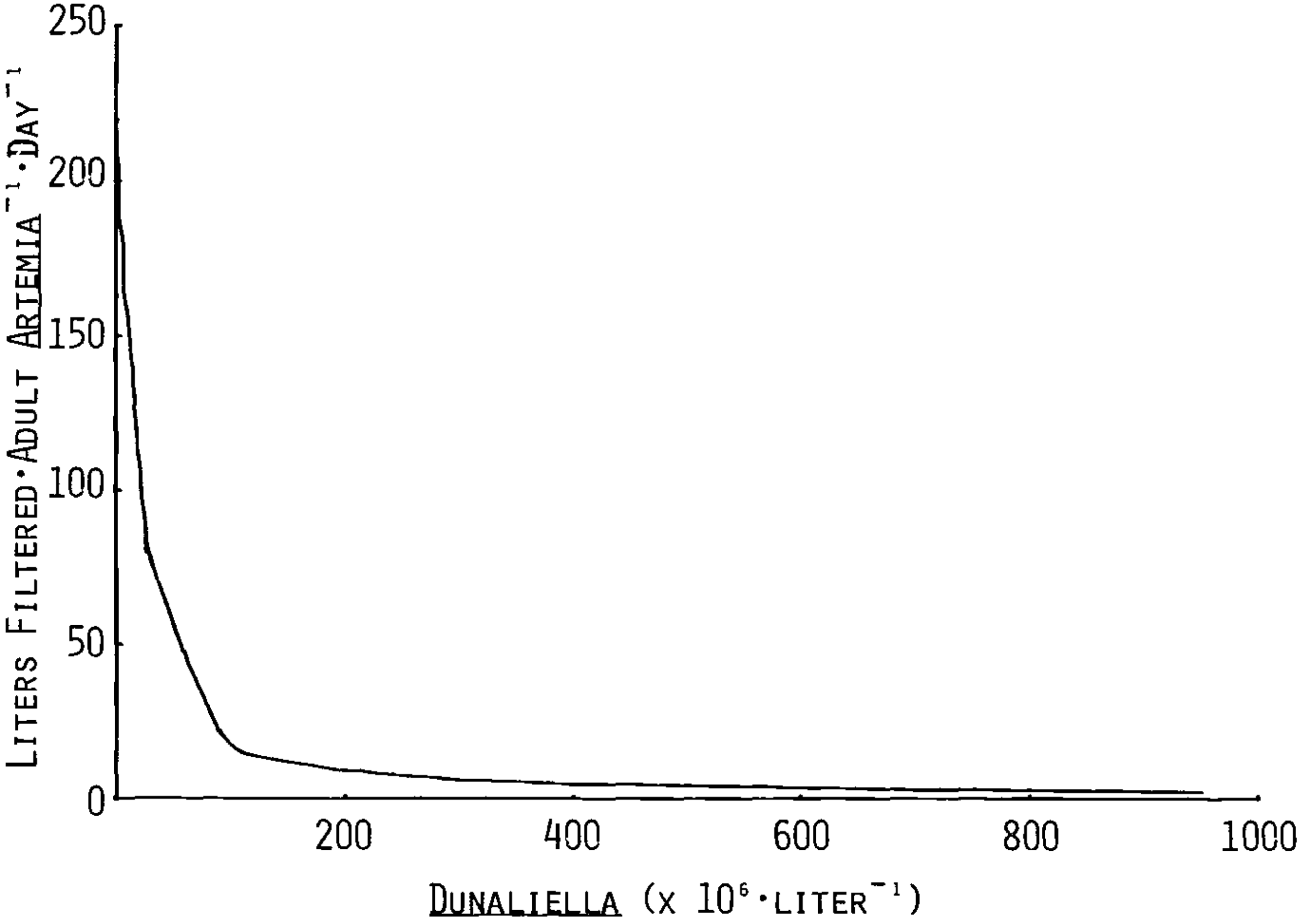

Figure 13. *Artemia* Filtration Rate as a Function of the Concentration of *Dunaliella* (Estimated from Reeve, 1963a; 1963b).

liters[4] of water per shrimp per day may seem a bit large to the reader unfamiliar with brine shrimp rapaciousness. Provasoli and Shiraishi (1959) found Artemia nauplii to be quite vorcious. Mason (1963) writes, "At the highest level, a single shrimp [_Artemia salina_] daily cleared 64 ml. of water of 6,400,000 cells [of _Dunaliella tertiolecta_]; in a preliminary set of experiments not reported here [in his 1963 paper], over 10 million cells/shrimp/day were converted into fecal pellets by adult animals". Mason concludes: "The grazing pressure these animals must exert upon the natural phytoplankton seems to be limited only by the distance any animal can cover".

Thus, it is not hard to imagine that a few shrimp can cause the sharp decline of algae seen in the late spring. The actual algal consumption rate in Figure 12 is often less than the maximum possible consumption rate. In such cases, all available algae are consumed. However, this does not mean complete annihilation of the algae, for below a certain concentration, the brine shrimp are unable to find any algae. Essentially, the data show that the algae are grazed down to a lower limit from which they do not recover. That this lower limit exists is unsubstantiated, but it is logical, both with respect to brine shrimp energetics and ecosystem evolution. Energetically, it is wasteful to try to filter only a few cells. Evolutionarily it is advantageous not

---

[4] Several errors were made in the extraction of Reeve's data which have been recently discovered by the author. Please see the section entitled _Corrected Brine Shrimp Filtration_ in Appendix II for further discussion.

to annihilate one's prey, especially when there is no alternative food source (Slobodkin, 1968). While the function of Figure 13 shows that brine shrimp are filtering at their maximum rate when algal concentration is zero, in reality they slow their rate in the presence of very small food concentrations (Sushchenya, 1962). This fact is treated in the model as though the algae had refuges limiting their availability. Hence, the term "algae available for consumption" is used along with the filtration function of Figure 13 to calculate the filtration rate of brine shrimp. The equations for this relationship are given in Appendix I.

As algae are consumed, fewer are available for consumption. This, in turn, decreases the consumption rate, thereby allowing the algae to again increase; but, in the face of voracious predators. It is by this mechanism that the algae population declines and is believed controlled throughout the remainder of the summer. When the shrimp die in the late autumn, it is then too cold for much algal increase until the spring of the following year (Stephens, 1974).

Finally, it should be mentioned that the set of loops pictured in Figure 12 occurs between the algae and both the nauplii and adult brine shrimp. The major difference is that, on the average, the nauplii filtration rate is about one-tenth that of the adults (from the data of Reeve, 1963a,b). Also, filtration rates are surely a function of temperature, a detail that has been ignored in the present model.

Brine Shrimp Starvation

Brine shrimp may filter many more algae than they actually need. However, if the brine shrimp do not obtain all the algae they are capable of obtaining, they do not necessarily starve. They starve when they do not receive a sustenance ration which is much lower than what they are capable of ingesting (Porcella and Holman, 1972). This starvation mechanism is hypothesized to act through the negative feedback loop illustrated in Figure 14.

Again, shrimp may be adult or nauplii, each with their own average sustenance ration which must be received to prevent starvation. As the number of brine shrimp increase, the total need for algae is increased. The ratio of amount of algae available to the amount needed is given by the "error" seen in Figure 14. This value assumes that the brine shrimp will filter all the algae they need if they are available. The sustenance ration, for purposes of this model, is defined as that amount of shrimp just necessary to thwart the onset of starvation. Hence the "error" ratio expresses the percentage of brine shrimp which survive (a ratio greater than 100% is assumed to mean 100% survival). One minus this value is the percent of brine shrimp that are starving. Hence, the starvation rate is the proportion of brine shrimp starving over some starvation time delay. This value assumes that starvation does not happen immediately, but rather over the course of several days (Gillespie, personal communication). While this starvation time is a function of temperature, this detail is not included in the present model.

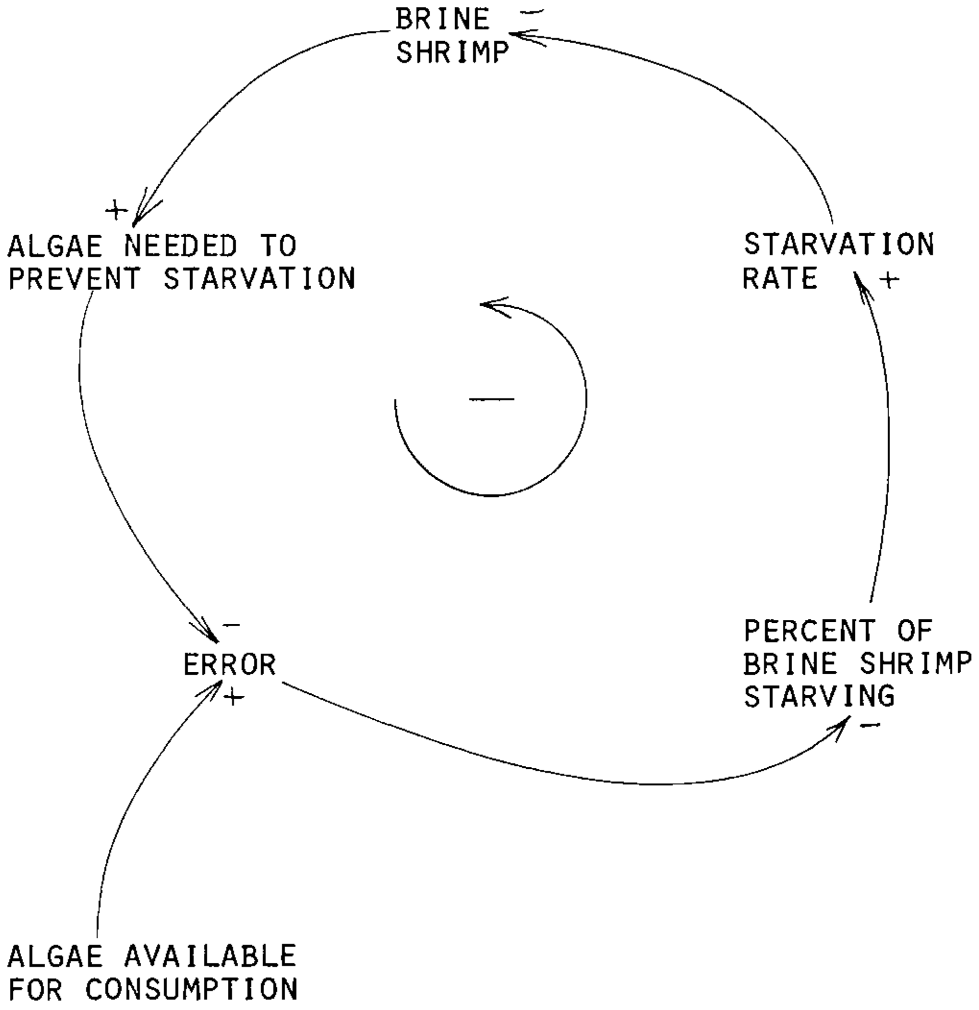

Figure 14. Feedback Loops Believed to Account for Brine Shrimp Starvation in the Great Salt Lake.

It is the negative feedback loop just described that is believed responsible for the brine shrimp decline and subsequent control until thermal death occurs at around 6°C. Now, the total model should be reconsidered.

The Dynamic Hypothesis Reviewed

When all of the feedback loops are connected they form the dynamic hypothesis given originally in Figure 5. The structural relationships are based upon the best available empirical data, theory and expert opinion. Structural validity is established by defending the validity of each relationship contained within each loop (Forrester, 1961). The actual parameter values and variable names are given in the appendix. Also given are the DYNAMO algebraic and discretized first order integral equations used to simulate this plankton community. The results of simulating the above dynamic hypothesis are given in the next chapter. Validation of these models is a complex and difficult subject based primarily on common sense. The validation procedures used, including the sensitivity tests run, are also presented in the following chapter.

CHAPTER IV

MODEL ANALYSIS AND VALIDATION

If a model consists of a mathematically consistent set of equations based on the best available knowledge of the real system, the model is considered to be structurally valid. If the equations, when simulated, interact to represent reality to a degree useful in meeting the stated objectives, the model is considered functionally valid. The preceding chapter, together with the set of equations presented in the appendix, provide the evidence necessary for structural validity.

A variety of formal tests can be performed which will aid in assessing a model's functional validity. For complex nonlinear models, such as the one presented, these tests can indict an egregiously wrong model, but give little evidence to support or condemn others. There is no proof that the model is useful until after it has accomplished its objective (Forrester, 1961). Wright has shown that standard statistical tests are inappropriate for such models and has suggested that model validation is largely judgmental. If the structurally sound model reproduces the observed real system time histories well enough; if all the model variables are judged as behaving properly or within reason; and, if changes in parameter values give reasonable results, then much evidence has been gathered for the model's functional validity (Wright). Additional evidence may be gathered by perturbing the model (e.g.

altering input functions or environmental conditions) and observing the subsequent behavior, especially if real system data are available for comparison. Finally, field testing of the real system may be plausible for controllable experimental sub-systems. Thus, model predictions may be tested empirically to provide additional evidence for the model's functional validity.

Below is presented an output analysis of the model developed in the previous chapter. The standard output of each sector of the model is thoroughly examined for plausibility, being compared with real system data where available. Also the effects of altering model constants one at a time is demonstrated. Through such an analysis model weaknesses can be indicated. Comments are made where appropriate suggesting future research which should improve the present model.

Standard Model Behavior

The equations presented in the appendix when simulated on a digital computer produce the annually repeating pattern given in Figure 15. Each data point represents the value at the week's end. This output may be compared with the standard real system behavior (Figure 1). The two behaviors are quite similar. The level of similarity is strong evidence that a basic understanding of the ecosystem has been attained under the conditions existing at the time of data collection. An important similarity is the phase relationship between the peak of the algae (D's in the model output) and that of the shrimp (*'s in the graph). In the data collected for the Great Salt Lake, the time interval between peaks is five to six weeks. For the model, this interval is around five

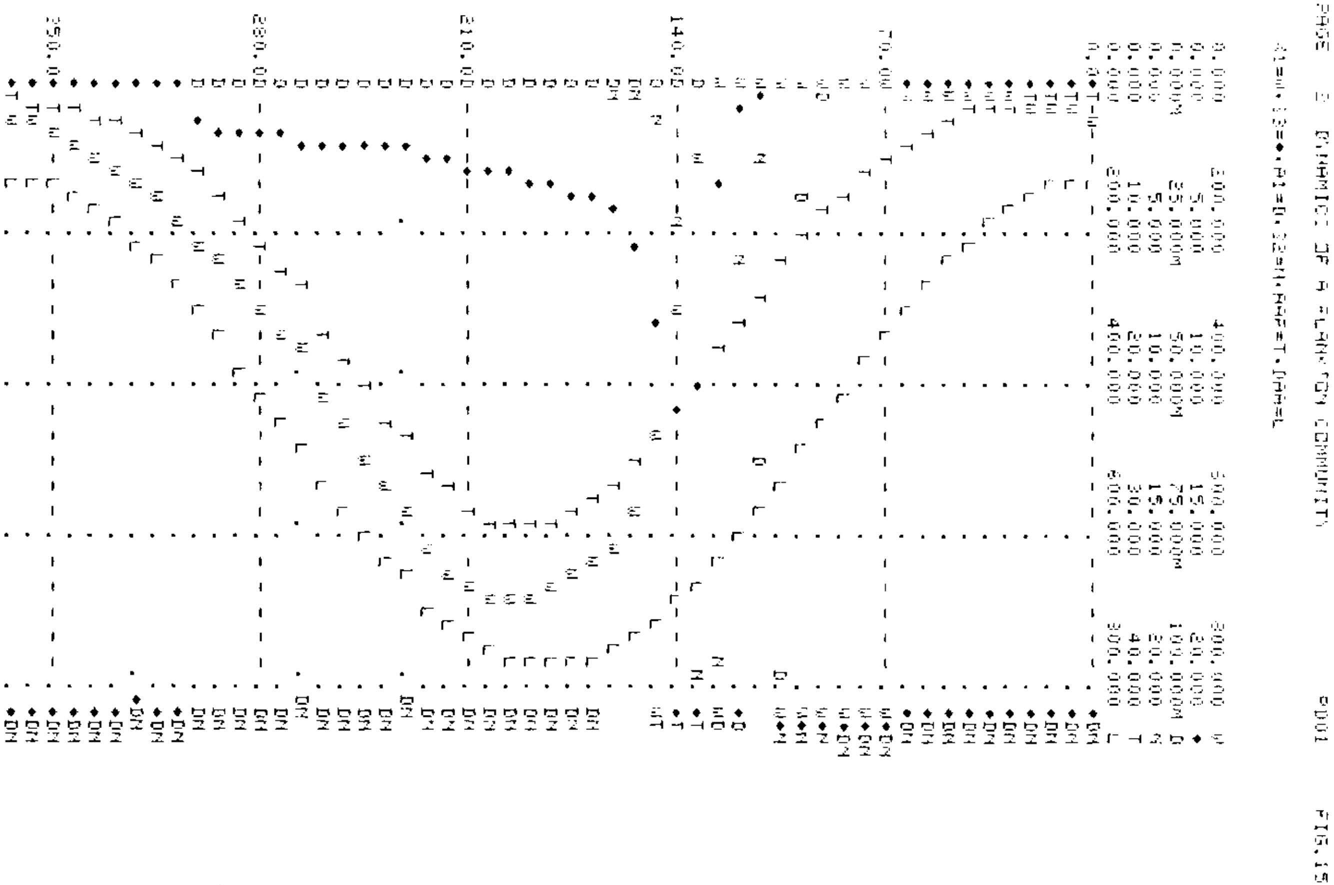

Figure 15. Standard Run Output Illustrating the Annual Dynamics of Dunaliella (D) and Various Stages of the Life Cycle of Artemia: Adults (*), Nauplii (N), Overwintering Eggs (W). Light (L) and Water Temperature (T) are also Illustrated.

weeks. The height of the algae peak is much lower than that measured in the lake itself, and the growth of the algal population occurs much later in the spring and is of much greater slope. These differences may be due to inaccurate selection of parameter values. If this is the case, the parametric sensitivity analysis and dominant forces identification should indicate a better fit. The brine shrimp's growth and decline appear to be quite similar to the real data. It must be pointed out that the lake data for brine shrimp include both adults and those nauplii countable with the naked eye. Many nauplii may have been missed, as admitted by the collectors, since often they are less than one millimeter in length. When considering such data collection errors, the model output for brine shrimp growth, peak, and decline seems accurate enough. The sharp drop of brine shrimp in late autumn is due to cold temperatures (<6°C) which are not tolerated by the shrimp (Vorhies 1917; Relyea, 1937; Wirick, 1972). Samples from the Great Salt Lake were not taken frequently enough to show such a drop in density.

Samples from the lake were taken approximately twice monthly. Such infrequency of collection allows a very great possibility that the true peaks attained by algae and brine shrimp were not measured. Greater confidence may be placed in the peak reached by the algae, however, since it appears that algae concentrations are approaching some asymptote. This is not the case for the brine shrimp. Because no asymptotic growth is perceptible prior to the measured peak, it is possible that the brine shrimp peak concentration may actually have been much higher than measured. This possibility must be considered when interpreting the results presented.

The light and temperature output from the model are very closely correlated to the lake data. This is because the light input cosine function, given in the model equations, was approximated directly from these data (see Appendix I).

No data from the Great Salt Lake are available for comparison with respect to the annual dynamics of the overwintering egg accumulation (represented by W in the model output). Only the approximate number found before hatching in the spring is known. Because of the present argument concerning the cause of winter egg production [day length (Holman, 1975) and/or food stress (Wirick, 1972)] these data would be very useful. Gillespie (personal communication) indicates that eggs are quite abundant throughout most of the summer months (before short days occur). Such information provides support that food stress is at least partly responsible. As mentioned, the present model incorporated food stress, but not day length, as the factor producing overwintering eggs. The results support neither argument.

Standard Run Analysis by Sectors

The output given in Figure 15 describes the behavior of only those lake parameters for which we have some empirical data. The inflows and outflows that interact to produce the patterns given in Figure 15 are presented by functional sectors in Figures 16 through 21. "Functional sector" refers to that group of variables which interact to cause a certain dynamic pattern such as growth and decline. While no empirical data are readily available for comparison, qualitative judgments concerning the plausibility or implausibility of the variables may be made.

Algal Production Sector

The annual dynamics of those variables believed to account for algal production are given in Figure 16. The algal concentration (represented by 0's) has its peak marked. At this point, algal concentration is about 100 million cells per liter (as shown on the vertical axis). The point occurs around April 15 (day 105) as shown on the horizontal axis. The inflow of new algae (represented by 1's peaks shortly after the algae peak.

The inflow of algae increases as the algal concentration declines because more light becomes available for photosynthesis as algal concentration is reduced. Also, at this time of year, water temperatures are more favorable for rapid algal division.

Perhaps the most peculiar behavior represented is algal productivity (2's). Its value is a function both of available photosynthetically active radiation (represented by 4's) through a light factor (3's) and of water temperature (7's) through a temperature factor (6's) (see Dynamic Hypothesis). The light and temperature factors are multipliers of an empirically determined maximum productivity. These multipliers vary between 0 and 1 with light or temperature as determined in laboratory studies (Van Aukin and McNulty, 1973).

Productivity (new algae/old algal cell-day) is shown to begin to rise in the early spring, peak at a relatively low level and drop to a low level during the peak of algal density. This is due to algal self

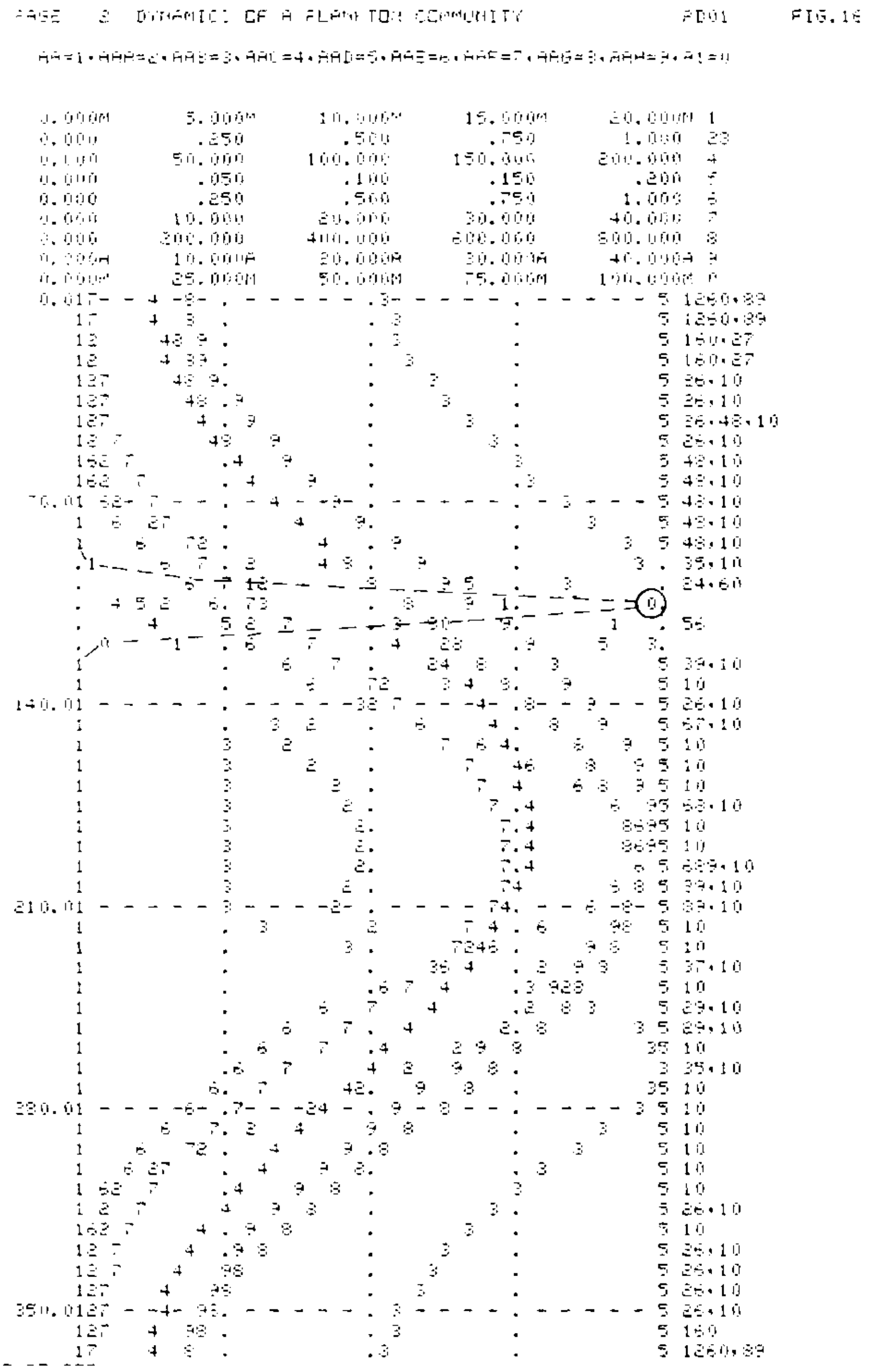

Figure 16. Standard Run Output for Algal Production Sector Variables. (See Text for Symbol Definition).

shading, which decreases available light (4's). As algae are grazed, more photosynthetically active radiation penetrates. Also, by this time (late spring), light intensities are optimal for productivity. This can be observed by the high value for the light factor (3's). Therefore, productivity (2's) increases following grazing. After this increase, solar energy becomes so intense that it actually reduces productivity. This was found to be true in laboratory studies performed by Van Aukin and McNulty (1973). The light factor (3's) abruptly levels off at .25 during the summer months. This value is due to the following assumption. Van Aukin and McNulty report no data for light intensities much beyond optimal, since they were searching only for optimal points. Thus, the values for the light factor were arbitrarily chosen at these intensities. One alternative was to assume that light intensities never are large enough in the Great Salt Lake to completely halt production. Thus, 25% of maximum productivity (at optimal temperature) was chosen as the lower limit to productivity at high solar intensities. The effect of using other light factor values past the optimal point is discussed in the parametric sensitivity analysis section.

While the light factor is at 0.25 during the summer months, productivity (2's) still rises slightly and then falls again. This represents the fact that water temperature (7's) is going through an optimal value (temperature factor represented by 6's).

As light intensities (4's) again fall toward the end of summer, productivity rises. At this time, water temperatures are favorable for high productivity. The productivity thus reaches its highest point in the year in late summer or early fall. However, because of intense grazing pressure, increases in the algae population do not noticeably occur in Figure 16. The potential for a fall bloom is certainly present, however. In fact, model algal concentration increases from 5,000 to 16,000 cells/liter during this time; an increase too small to be detected in Figure 16 due to scaling. If other factors affecting algal productivity had been included in the model, such as nutrients, a fall bloom may not appear so possible.

For the remainder of the year, algal productivity falls with light and temperature in a very regular manner. While not noticeable in Figure 16, after the brine shrimp suffer thermal death in the late fall (day 301), the productivity is sufficient to allow a slight increase in algal standing crop (from 3,000 to 14,000 cells/liter). This is shown by the model daily printout not given in this report. As the following spring approaches, water temperature and light increase to allow a new spring bloom. The annual cycle is repeated, assuming the annual dynamics of nutrients, salinity, water temperature, light, etc., also repeat themselves.

The 8's and 9's of Figure 16 represent a delayed value of sunlight and the value of the conversion factor for solar energy to water temperature. They are the result of the input function approximation procedure and merely track the solar energy cosine wave input.

Algal Consumption Sector (Figure 17)

Algal consumption by adult brine shrimp (1's) and by nauplii (7's) is seen to be quite low except during the spring algal bloom

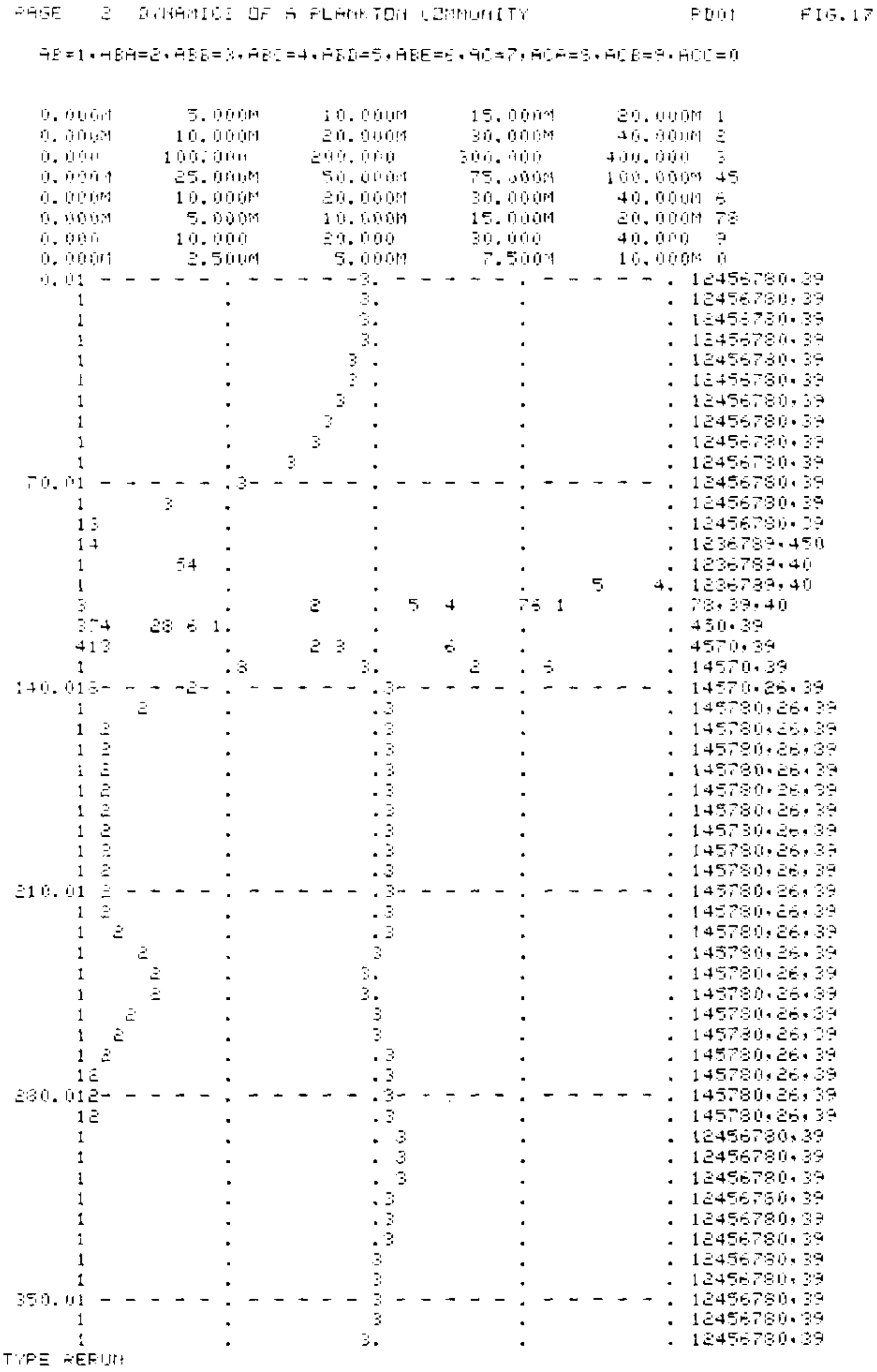

Figure 17. Standard Run Output for Algal Consumption Sector Variables. (See Text for Symbol Definitions).

following initial hatching. This is simply because there are few algae available to be eaten after the initial grazing by brine shrimp.

The number of algal cells that would be consumed by each adult brine shrimp if available (2's) and that for nauplii (8's) are always greater than what is actually consumed (1's and 7's) except for the week around day 112 (the first day of algal consumption on Figure 17). This is difficult if not impossible to see in Figure 17, but is evident in the daily printout. During the rest of the year, when brine shrimp are present, the total population could consume more algae than are available (total population algal consumption = 6's; available algae = 4's). Instead, each age group eats the maximum number of algal cells it can find (5's and 0's respectively, for adults and nauplii). In other words, all available algae are consumed during each iteration of the model. New algae come about through the reproduction of unavailable algae and available algae prior to consumption.

The brine shrimp are capable of consuming much more algae than are present because their water filtration rates are so high and are inversely related to the concentration of algae (Mason, 1967; Reeve, 1963 a,b,c,d). The values for filtration rate per adult and that for nauplii are given in Figure 17 by 3's and 9's respectively. Filtration per brine shrimp is seen to drop off as algal concentration increases in the early spring. This occurs (even though no brine shrimp have yet hatched) because filtration rate per shrimp is formulated in the model as simply a negative exponential of algal concentration (determined through published empirical evidence).

In late summer (between days 210 and 280) filtration rate per shrimp of each age class is seen to drop (3's and 9's) with a corresponding increase in possible algal consumption (2's and 6's). This corresponds to the slight increase in algal concentration noted in the previous section. Possible algal consumption increases even though there is a decrease in filtration rate. Possible algal consumption (algae per liter-day) is a result of multiplying available algae per liter by liters filtered per brine shrimp-day and by brine shrimp per liter (see Figure 12 and Appendix I). While there is around a sixfold increase in algae per liter, there is only a 9% decrease in filtration rate and a 23% decrease in brine shrimp per liter during the period between days 210 and 245. Therefore possible algal consumption increases during this period. However, only available algae are actually consumed, as explained earlier.

Brine Shrimp Production Sector (Figure 18)

The behaviors of the various variables given in Figure 18 are difficult to evaluate, since there is little empirical evidence of relevance. There are no remarkably implausible behaviors. The winter egg laying rate (1's) is the percentage (5's) of the total egg production rate (2's) that are winter eggs. Total egg production rate is calculated by the number of adult females present (3's) times a productivity per female and divided by a brood development delay time, represented by 4's (a function of water temperature by a Q-10 relationship).

The amount of food required to produce a 50:50 mixture of winter and nondurable eggs is given by the 7's. When food consumed by adults

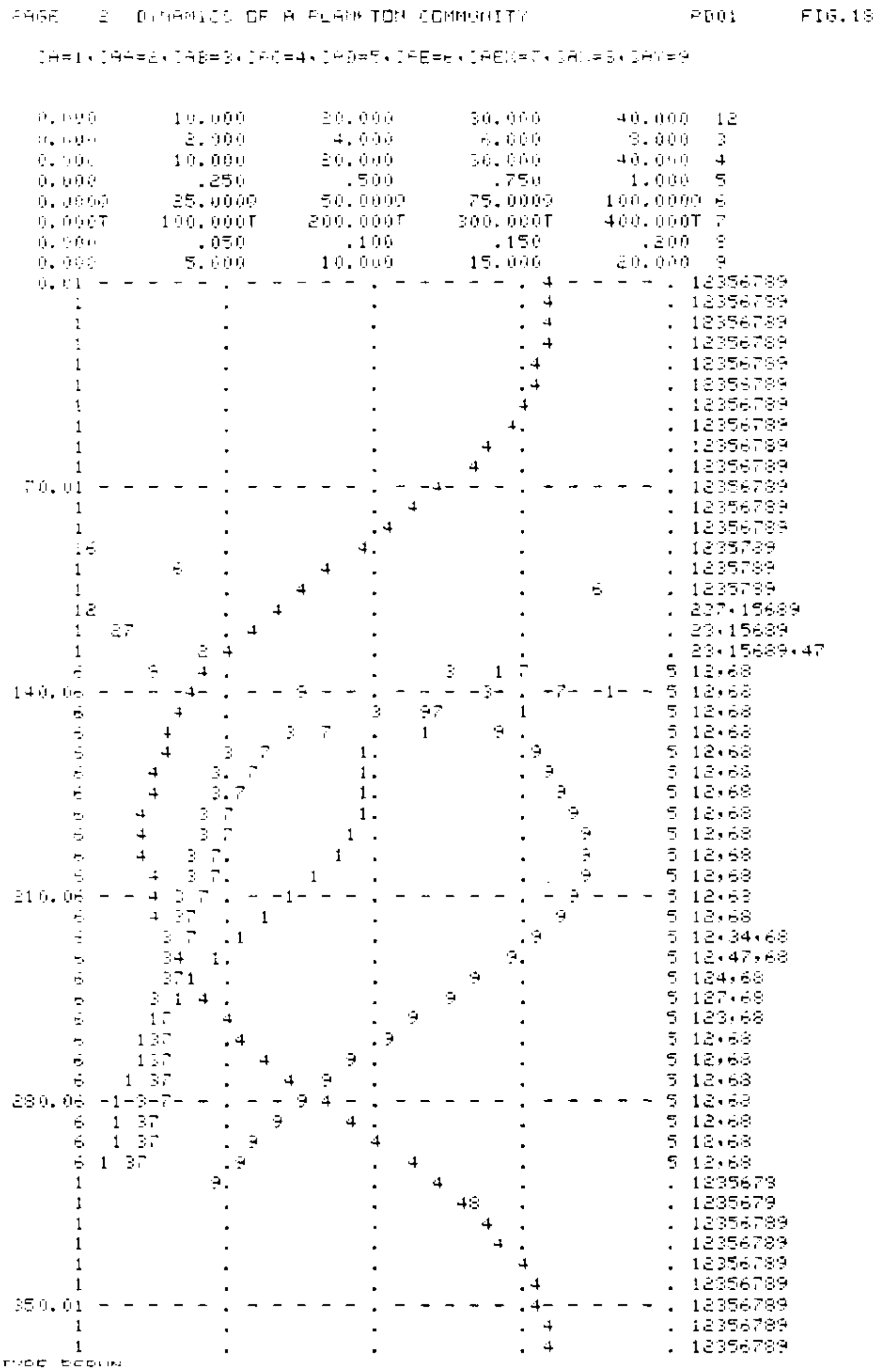

Figure 18. Standard Run Output for Brine Shrimp Production Sector Variables. (See Text for Symbol Definitions).

(represented by 5's in Figure 17) is less than this amount, a proportionate increase in winter egg production results (see Dynamic Hypothesis and Appendix I). The ratio of food consumed to the food required to produce the 50:50 mixture is given by the 6's and is referred to as the egg type allocation ratio.

Possibly peculiar is that except for three weeks following the first appearance of adult females in the spring, only winter eggs are produced. 100% of all egg production is winter eggs except during this three week period. The relationship between the egg type allocation ratio (6's) and the percent winter egg production (5's) is represented by a smooth sigmoid curve (see Appendix I) but acts like a switch. This is because of the sudden drop in available food upon the appearance of brine shrimp (due to the tremendous grazing pressure represented in the model). As mentioned previously, winter egg production may be partially or totally controlled by day length (Holman, 1975), a factor not considered in the present model.

The single 8 which has a nonzero value in Figure 18 (at day 315) represents a temperature switch which indicates that the winter eggs produced are now ready to hatch when the warm temperatures of the following spring arrive. Prior to becoming "ready" winter eggs, there existed a nonready egg attrition rate (9's). Not all of the eggs produced will hatch within the Great Salt Lake due to inviability, being carried away from the lake by wind, tropical fish food collectors, or other reasons. This attrition is represented in the model by having some constant percentage of all remaining "unready" eggs leave the system of interest each day. Corresponding attrition rates for nondurable eggs and for "ready" winter eggs are similarly represented and will be mentioned in subsequent sections.

Brine Shrimp Eggs Sector (Figure 19)

Figure 19 illustrates the behavior of those parameters associated with the inflow and outflow of winter and nondurable eggs. Some of these parameters have been described in preceding sections and are included again to complete the picture of egg dynamics.

The accumulation of unready eggs (1's) peaks in late summer as the result of the winter egg laying rate (5's) described in the previous section. At around day 315, the unready eggs all become ready to hatch (2's) with the return of springtime water temperatures the following year. This flow is represented by the 3's and is the same parameter as the 8's of Figure 18 (discussed in the previous section). The attrition rate for unready eggs (4's) is the same as that described in the preceding sector (see the 9's of Figure 18).

The shape of the curve for this outflow is exactly the same as that of the accumulation from which it flows because it is merely a constant percentage of the unready eggs. There is only a difference of scale.

The attrition rate (7's) for ready eggs follows the same format as that for unready eggs. The same percentage of ready eggs is lost each day as were lost from the unready accumulation. What superficially appears to be a large jump in the number of ready eggs from unready eggs at day 315 is really a continuation of the smooth decline

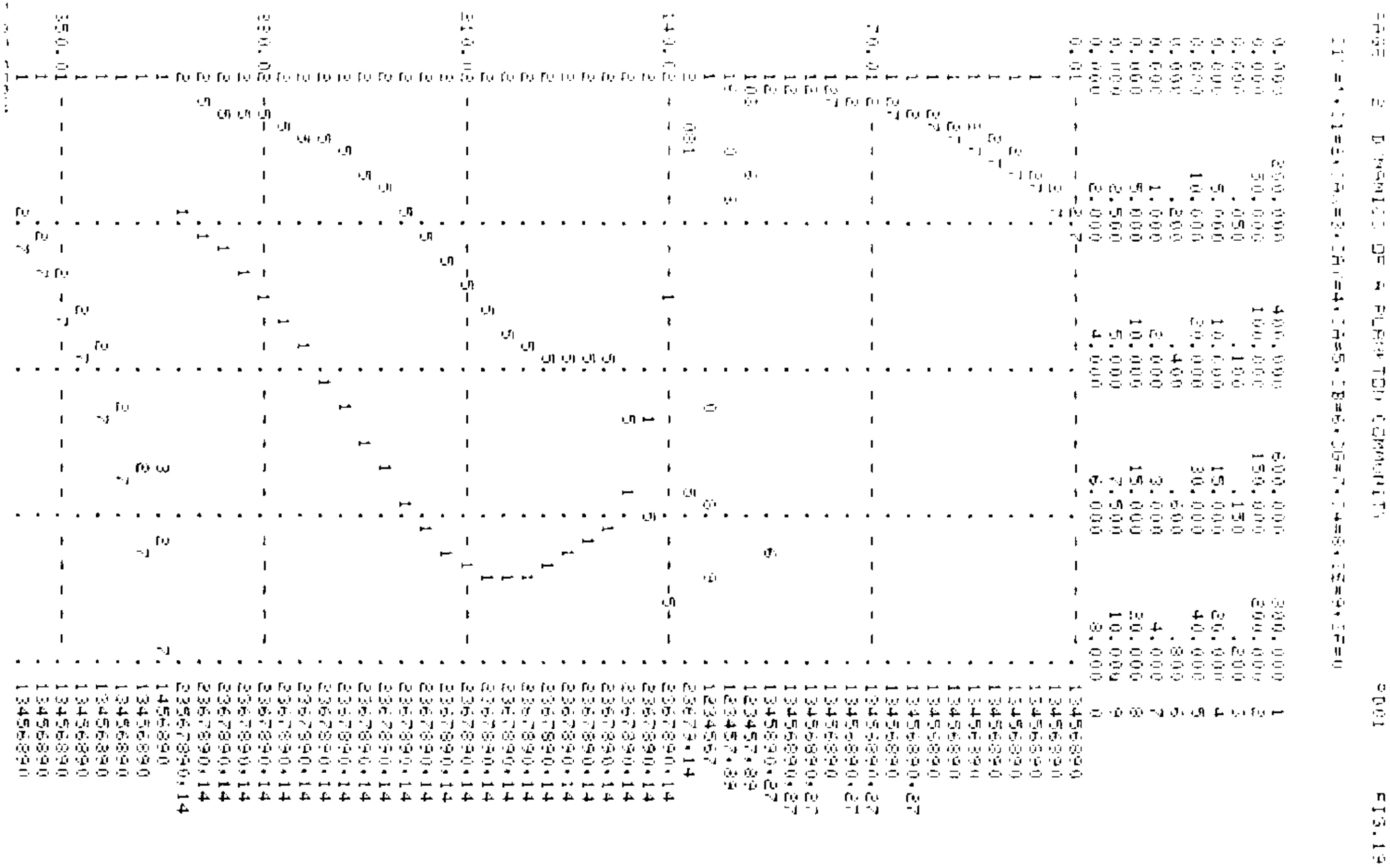

Figure 19. Standard Run Output for Brine Shrimp Eggs Sector Variables. (See Text for Symbol Definitions).

of winter eggs taken as a whole (W's in the standard run; Figure 15). This becomes evident as one takes note of the DYNAMO scaling on the vertical axis of the graph.

At day 105, the overwintering eggs begin to hatch, since at this time the water temperature is sufficiently warm. This hatching takes place conveniently (for the brine shrimp) in the middle of the algal bloom, both in the real system (The Great Salt Lake) and in the model system, as discussed earlier. The hatching rate is represented by 6's. It is a function of the number of ready winter eggs divided by a hatching delay time (a function of temperature). This outflow also represents one inflow into the nauplii accumulation, to be discussed in the next section.

As explained in a previous section, when food is plentiful, nondurable eggs (8's) are produced. The nondurable egg laying rate (9's) is merely that percentage of the total egg production rate (2's in Figure 18) that is not winter egg production rate. The determination of the winter egg proportion was discussed in the previous section. Nondurable eggs and the nondurable egg laying and hatching rates (8's, 9's, and 0's, respectively) are nonzero only during the spring algal bloom when food is very plentiful. As food availability declines, winter eggs are soon produced according to the hypothesis of Gillespie discussed previously.

Nondurable eggs hatch with a rate (0's) which is constructed similarly to that for the winter egg hatching rate. It is the number of nondurable eggs divided by a hatching delay time which is a function of water temperature. The hatched eggs become nauplii as did the winter eggs. Some very few nondurable eggs never hatch. This is expressed in the model similarly to the attrition rates for overwintering eggs. The values for this rate are not included in the figure as they are rather insignificant.

Brine Shrimp Nauplii Sector (Figure 20)

Those parameters involved in nauplii dynamics are presented in Figure 20. Again, some of the parameters mentioned have been previously discussed and are included again to complete the picture of the changing accumulation of nauplii.

Almost all of the significant activity associated with accumulation of nauplii (1's) occurs shortly after initial hatching during the springtime algal bloom (the hatching rate is represented by 2's). This is because no new nauplii are produced after all the winter eggs hatch and after the brief interval of nondurable egg production (nondurable egg hatching rate represented by 3's). Nauplii mature in around three weeks after hatching (depending upon water temperature), so by midsummer, few nauplii are detectable in the model representation. According to Gillespie (personal communication), this is somewhat similar to the real system. The nauplii maturation rate (4's) is the number of nauplii per liter divided by a maturation time (which is a function of water temperature). It peaks and declines in close association with the nauplii accumulation.

The nauplii accumulation is depleted both by maturation into adults (4's) and by death through starvation. The starvation death rate

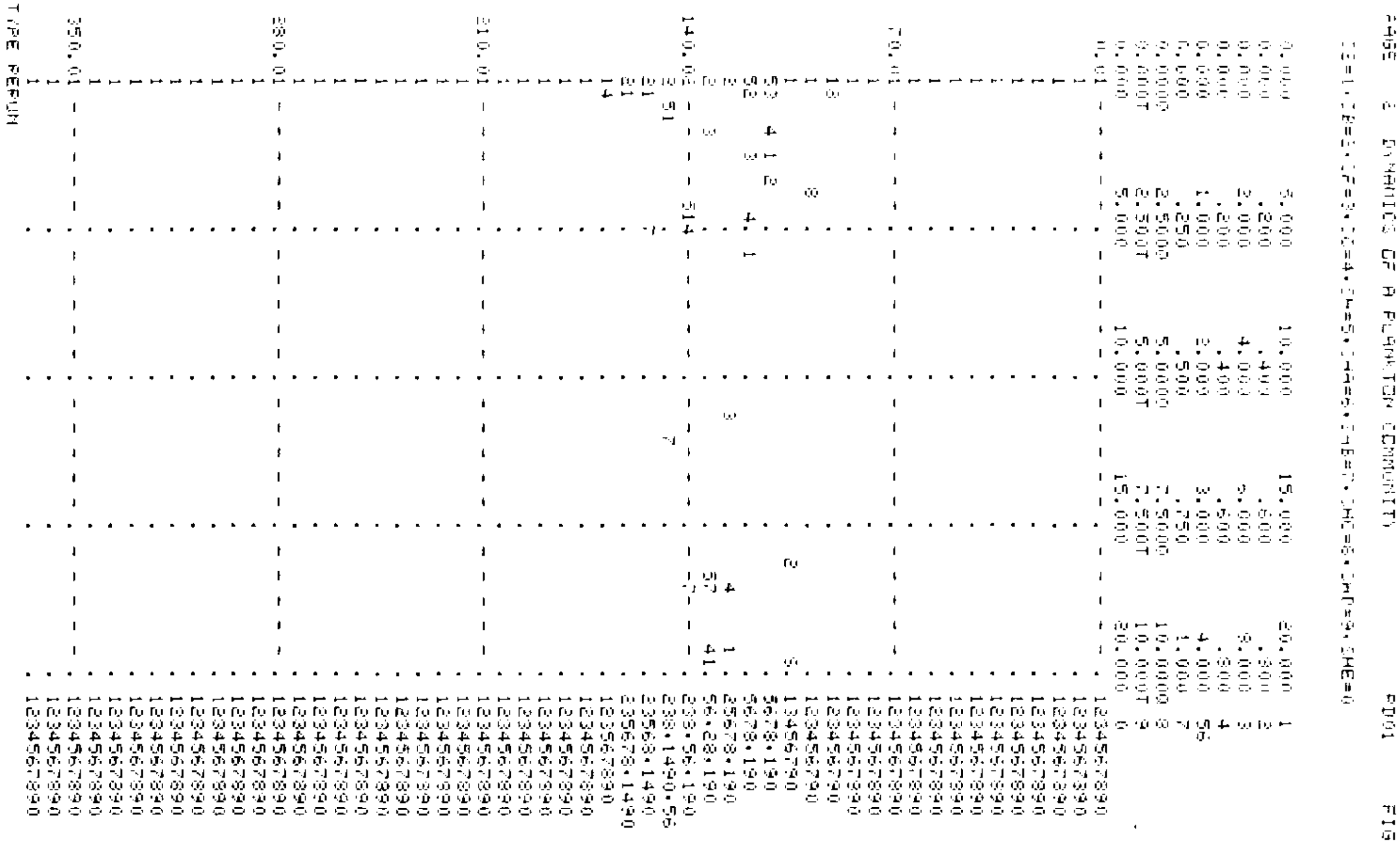

Figure 20. Standard Run Output for Brine Shrimp Nauplii Sector Variables. (See Text for Symbol Definitions).

is represented by 6's. Nauplii death by starvation occurs only between days 133 and 154 in the model output. This is because no nauplii exist after day 154, since all of the winter eggs have hatched and no new nondurable eggs are being produced at this time.

The 5's represent the actual outflow of dead nauplii, which may be due to starvation or to cold temperatures. The 5's and 6's are exactly superimposed on the graph, because no thermal death is occurring. Had there been any nauplii present in late fall, thermal death would occur and the 5's and 6's in the graph may have been different.

The nauplii starvation rate is calculated as some percentage of the total population (7's) divided by a starvation delay time. The percentage of nauplii which starve is the ratio (between 0 and 1) of available algae to algae required to prevent starvation (9's). The algae required to prevent starvation is the number of nauplii per liter times the amount of algae required per nauplius.

The 0's are exactly superimposed on the accumulation of nauplii (1's) and represent the entire population of nauplii which will die upon the occurrence of cold water temperatures. As explained earlier, thermal death does not occur for nauplii in the present model.

Brine Shrimp Adults Sector (Figure 21)

Increases in the adult population of brine shrimp (1's) occur when the number of maturing nauplii exceed the number of dying adults. The inflow of maturing nauplii is represented by 3's. Each of these flows is on the same scale in Figure 21. After the spring hatching during the algal bloom, some of the nauplii mature to adults. Soon

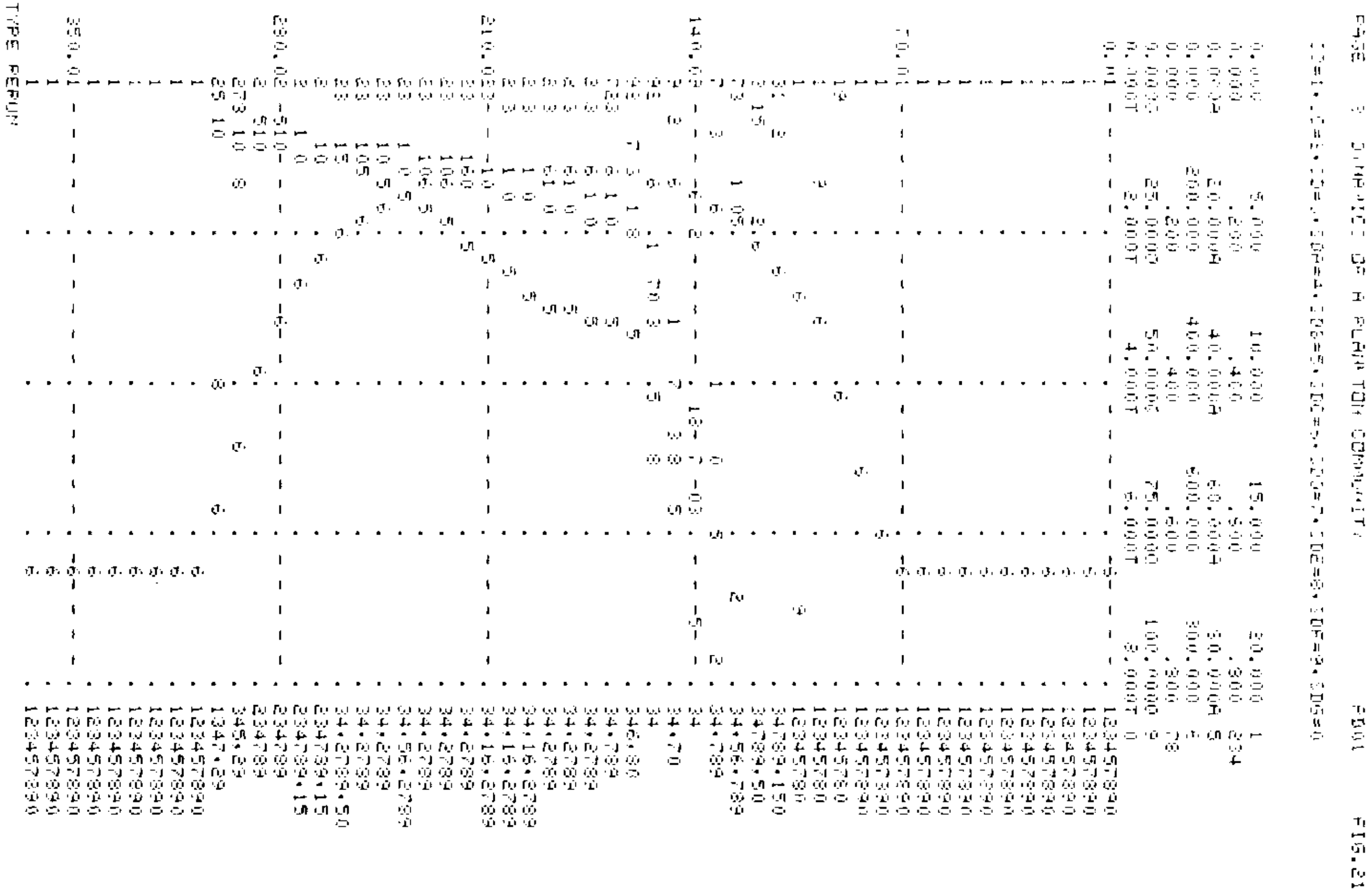

Figure 21. Standard Run Output for Brine Shrimp Adults Sector Variables. (See Text for Symbol Definitions).

thereafter, they begin to starve. Starvation death rate (7's) is the usual mode of death for these brine shrimp. This rate is calculated similarly to that for the nauplii mentioned in the previous section. It consists of the percentage of adults that starve (8's) divided by a starvation delay time. The percentage starving again is the ratio (values between 0.0 and 1.0) of available algae (5's in Figure 17) to the amount of algae required to prevent starvation (9's). The algae required is calculated as the population of adults times the algae required per adult (0's).

Adult brine shrimp may also die of old age. The old age death rate (5's) is calculated as the accumulation of adults divided by their average lifetime. Average lifetime (6's) is figured on a degree-day basis from water temperature. The values are from empirical data (Khmeleva, 1967).

Comments on Standard Run Analysis

While there are areas of the model structure for which there exists no data for comparison and are thus largely not known to be correct, there appear to be no obvious implausibilities in the standard run behavior of the model. The variables associated with algal production seem to be the most active at this point in the analysis. Perhaps the inclusion of algal nutrient dynamics as a factor in algal productivity would increase the level of functional validity with respect to understanding the whole system. There is a need for study in the area of brine shrimp egg dynamics in the Great Salt Lake to resolve much of the guesswork employed in the present model.

Where data are available, the model parameters tend to agree well or at least hold promise, given the present level of model completion. The evidence thus far indicates that a fair level of understanding has been achieved from the analysis of causal feedback loops in this plankton community of the Great Salt Lake. Additional evidence will be presented in describing the results of the model's sensitivity to various parametric adjustments.

Model Response to Parameter Changes

By far the most sensitive sector of the model to parameter changes is the algal productivity sector. The parameters of this sector were therefore chosen as the subject of the rigorous dominant forces identification presented in the next chapter. Because of this, the algae sector parameters are not dealt with in the present chapter, with the exception of the temperature and light factor tables. These are altered here to illustrate how slight changes can cause a greatly increased fit of the model output to that of the real system.

The following series of graphs and the standard run output are presented in order to make general subjective statements about the gross effect of changing 18 parameters. No interaction effects are assessed here. The concern in the present chapter is to determine how sensitive the model is to changes in various parameters. After changing a parameter the model is allowed to run until an annual or biannual repeating pattern is obtained. This pattern is the one reported. The output behavior during the transition period from the standard run behavior to this new repeating pattern is not reported. The behaviors of the accumulations of algae (D), adult brine shrimp (*), nauplii (N), and overwintering eggs (W), will be roughly compared to the standard run output behavior (Figure 15). Fine changes in the actual values at particular points in time are of little interest. Of great concern are changes in, 1) the overall output pattern of each accumulation, 2) phase relationships between the output variables, and 3) large changes in peak heights or growth and decline slopes. Light and water temperature values are also plotted for convenience in orienting the reader to the time of year, as was done in the standard run.

Changes in the Algal Productivity vs. Light Intensity Curve

The function which describes the relationship between algal productivity and light intensity (as adapted from Van Aukin and McNulty, 1973) is given in Figure 22. As was mentioned in the previous chapter, points greater than the optimal light intensity were largely ignored by Van Aukin and McNulty, since they were merely concerned with finding optima. The points on the graph beyond 130 Langleys per day were simply estimated. The standard run employs a graph in which light intensities effect productivity as a straight line decrease from 0.68 of maximum at 130 Ly/day to 0.24 of maximum at 145 Ly/day. Any intensities greater than 145 Ly/day do not decrease productivity below 0.24 of maximum. It seems reasonable that the normal light intensities occurring at the Great Salt Lake in midsummer would not completely inhibit algal production in midsummer by being too intense. However, in reference to Van Aukin and McNulty's paper, some inhibition seems likely. Hence 0.24 of maximum was selected as the lower limit of production at the highest

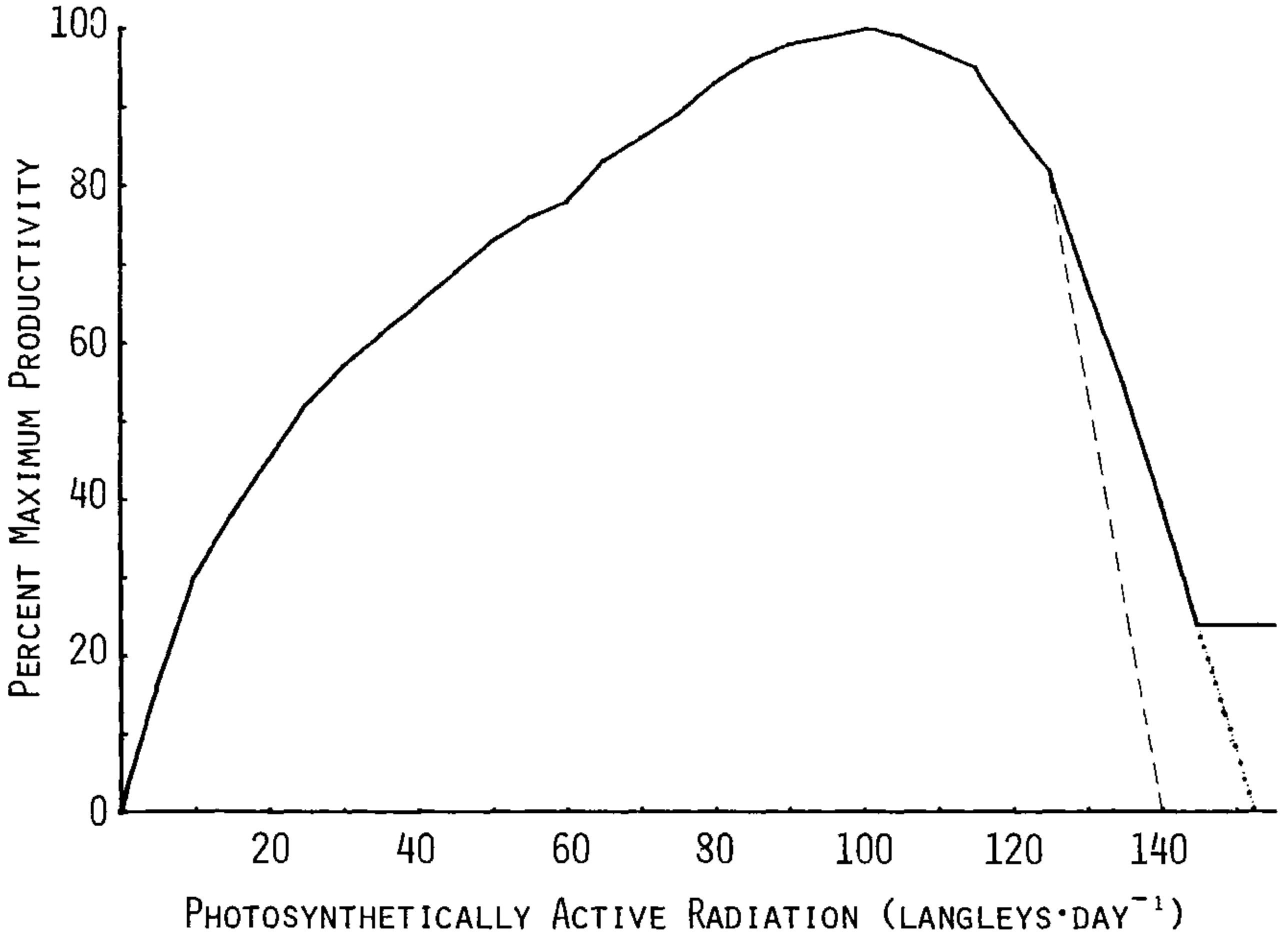

Figure 22. **Light Factor Table Illustrating Sensitivity Tests Performed: First Alteration Represented by Dots; Second Alteration by Dashes.**

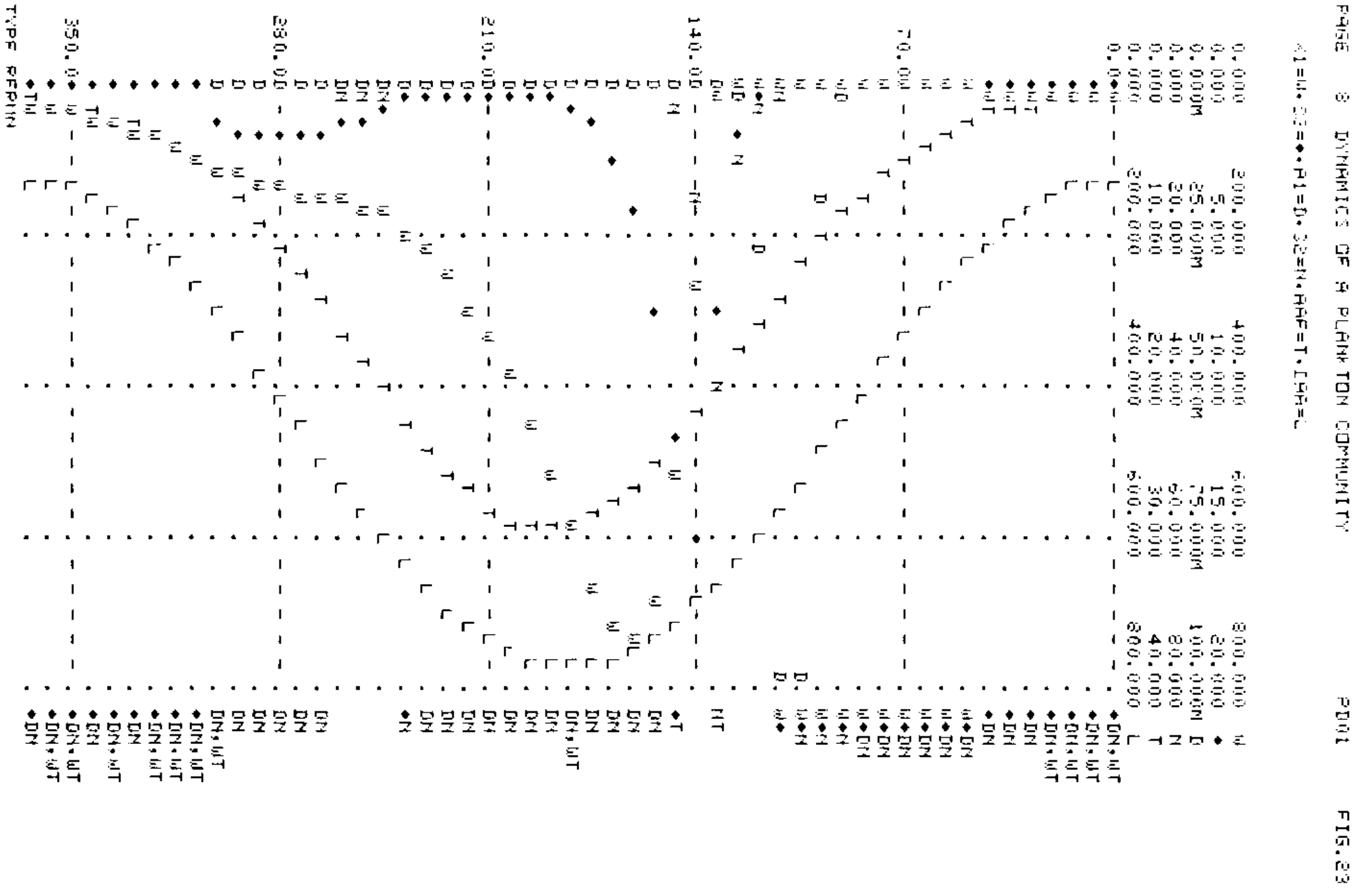

Figure 23. Results of First Light Factor Curve Alteration: Extending the Upper Tail to Zero (See Figure 22).

Great Salt Lake light intensities.

To test the sensitivity of the above reasoning, the upper tail of the productivity vs. intensity curve was altered and additional simulations performed. In the first adjustment, the straight line from 130 Ly/day to 145 Ly/day was continued until it intersected the light axis so that at 155 Ly/day, productivity is 0. The model was allowed to run until a new stable repeating annual pattern occurred. The new initial values thereby indicated were employed to give the output of Figure 23.

The alteration created little difference from the standard behavior with respect to overall pattern and phase relationships. The increased inhibition of algae in midsummer apparently reduces the brine shrimp population drastically during this time. When the potential for a fall algal bloom occurs, the ratio of available algae to shrimp is great enough that some new nauplii are produced. The result is an increase in the population of brine shrimp back to where it is in the standard run just prior to thermal death. Because there are fewer brine shrimp in the midsummer months, fewer overwintering eggs are produced, so fewer nauplii hatch in the spring. Hence algae are not grazed down as fast. This evidently allows more brine shrimp to survive to maturity in the spring, yielding a slightly higher adult peak than is found in the standard run. The surge of brine shrimp causes a rapid decline of algae to its low level by midsummer. Also, a higher peak of overwintering eggs occurs because of the greater number of adult shrimp present at the beginning of the summer decline of algae (when food stress begins, winter eggs are produced).

A second, more drastic alteration of the upper tail of the production vs. intensity curve is illustrated in Figure 22 and the results are given by Figure 24. Here there are even fewer winter eggs hatching in the spring, but many more nauplii survive to adulthood because of reduced grazing pressure after hatching. However, the additional available food allows fewer overwintering eggs to be produced before the algae stop producing in the summer. These interesting observed effects are not unreasonable. They provide evidence that the upper tail of the standard run's production vs intensity curve is relatively insensitive and involves reasonable assumptions.

Changes in the Algal Productivity vs Water Temperature Curve

The productivity vs water temperature curve used in the standard run is given in Figure 25. The curve given by Van Aukin and McNulty for temperature is fairly complete and no test for unknown values is needed. However, the algal growth, as shown by the real system data, begins earlier in the spring than that for the model system's standard run. If algal productivity is very sensitive to changes in the productivity vs temperature curve, slight differences between the laboratory conditions of Van Aukin and McNulty and those of the Great Salt Lake could account for the deviation exhibited by the model in this case. Such differences of conditions might reflect differences in water temperature measurement or variance, or actual differences in physiological response of the algae from lab to field. Differences in microenvironment around the algae may account for a slightly different productivity vs

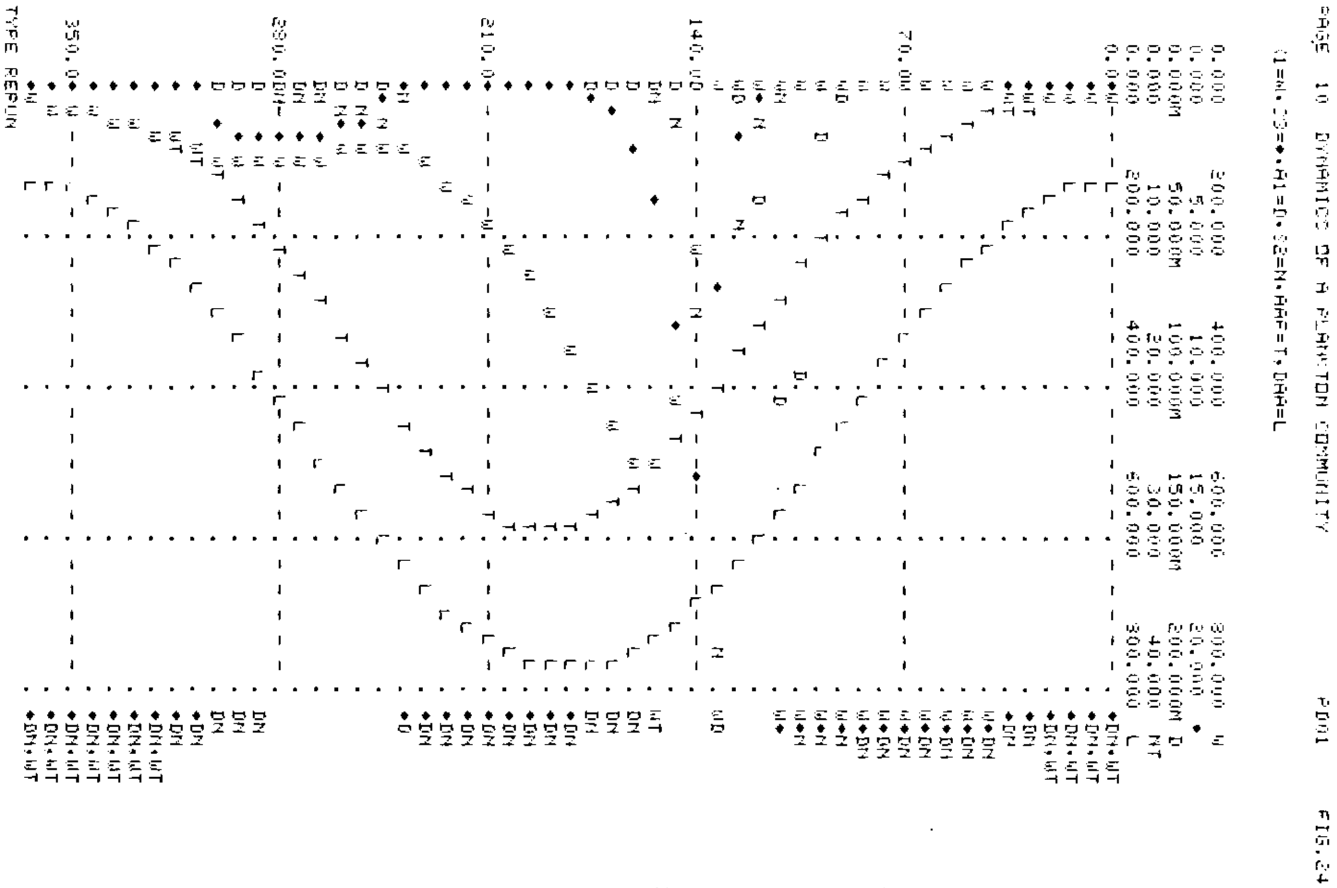

Figure 24. Results of Second Light Factor Curve Alteration: Decreasing the Values of the Upper Tail (See Figure 22).

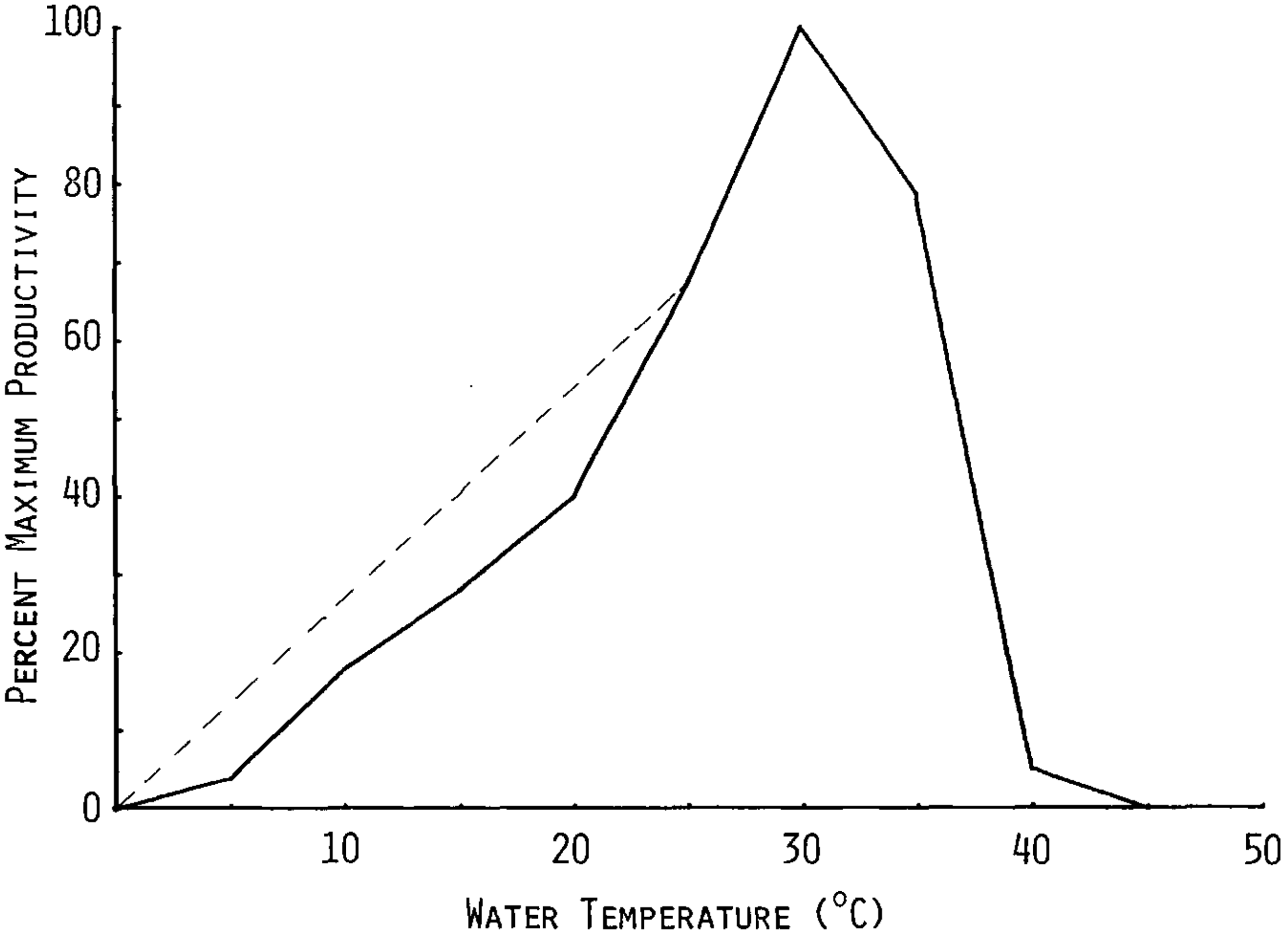

Figure 25. Temperature Factor Table Illustrating Sensitivity Test Performed: Alteration Represented by Dashes.

temperature curve. Hence the change indicated in Figure 25 was made and an additional simulation performed. It was expected that algae would grow earlier and reach a higher peak prior to the onset of grazing by newly hatching brine shrimp.

The results of such a simulation are presented in Figure 26. The slight alteration of the productivity vs temperature curve produced considerable effects on the order of what was expected. The algae plot appears to match the Great Salt Lake data much more closely now, while the general shapes of the curves and the phase relationships are changed very little. The additional algae appear to cause many more brine shrimp to survive than are detected in the real system. It must be remembered however, that the field samples were not taken often enough to insure the detection of the true brine shrimp peak. Winter eggs have increased by an order of magnitude as have nauplii and adults. It is evident that small errors in the estimation of true field water temperature and true physiological temperature response curves may cause great changes in the behavior of the model. This may have implications for the real system as well. Factors that effect the growth response of *Dunaliella viridis* to temperature may have a considerable influence on the variance in annual like primary and secondary production.

Reducing the Filtration Rate of Brine Shrimp

That brine shrimp are very voracious eaters and amazing filterers of water is quite well documented (Woolley and Marsell, 1946; Mason, 1963; Reeve, 1963a, b). The exact quantities of water filtered per brine shrimp are difficult to extract from the literature, but it is evident

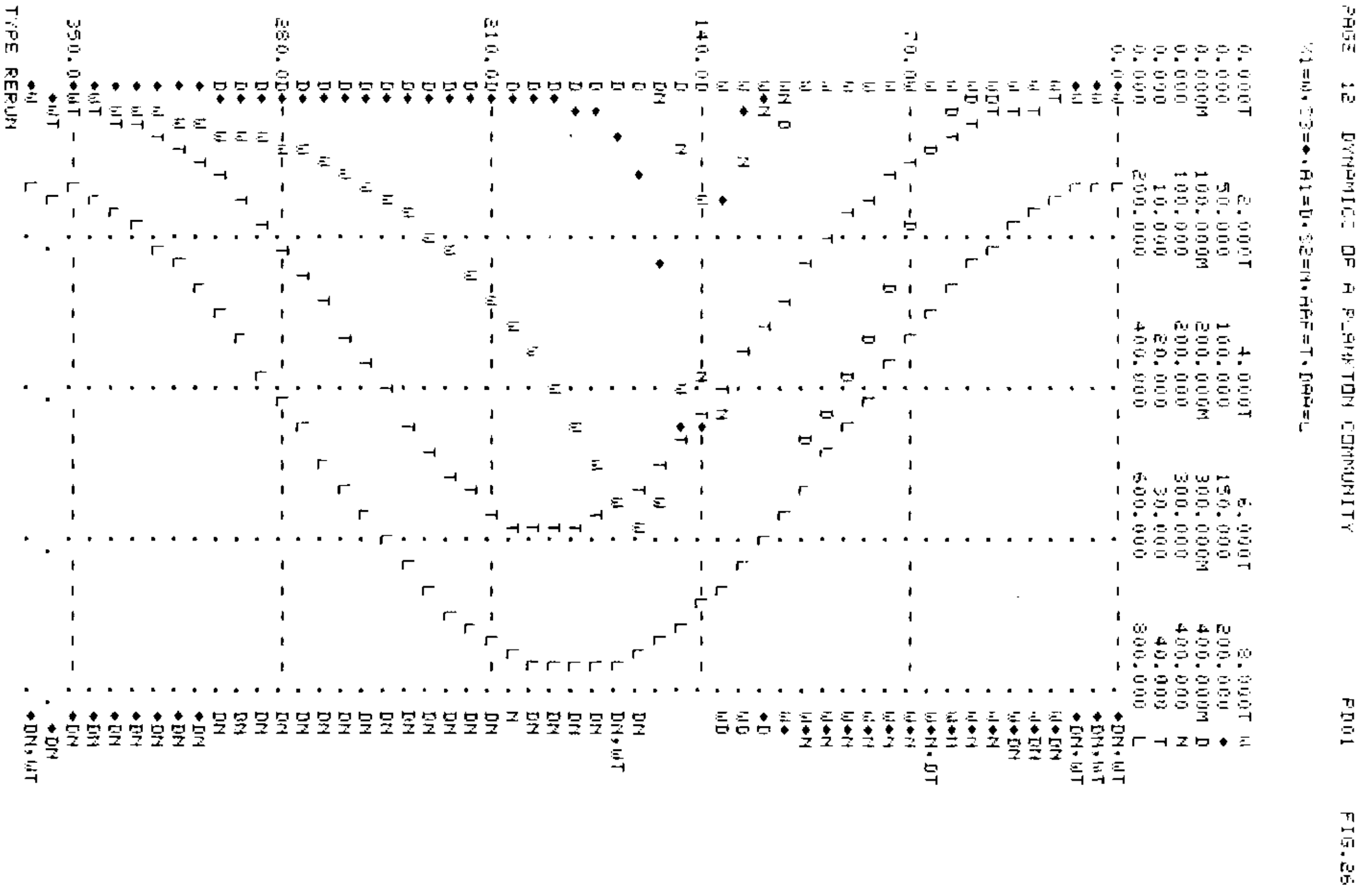

Figure 26. Results of Altering the Water Temperature Curve (Lower Tail, See Figure 25).

that filtration rates approximate a negative exponential function of algal concentration.[5] The maximum filtration rate (when algal density is least) used in the model is 220 liters per shrimp-day. This exponentially decreases to 1 liter per shrimp-day as algal concentration approaches around 600,000 cells/liter. That a brine shrimp is physically able to filter 220 liters of water per day seems remarkable. Therefore, the exponential function described was decreased by an order of magnitude so that 22 liters per shrimp-day was the maximum filtration rate. This decreased to 1 liter per shrimp-day at algal concentrations of around 350,000 cells/liter. The results are given in Figure 27.

The differences are trivial. Close examination of the graph reveals a very minor increase in algal peak height with an order of magnitude reduction in the filtration rate of brine shrimp. The lack of difference is due to the fact that filtration rates in the model do not go below 1 liter per shrimp-day no matter how great the algal concentration. This is a reasonable assumption with respect to the published accounts available[6], and from personal observation in a laboratory microcosm containing brine shrimp. Indeed, upon springtime hatching in the Great Salt Lake, brine shrimp are faced with algal densities of around 240 <u>million</u> cells/liter. In the model, the densities

---

[5] Several errors were made in the estimation of brine shrimp filtration from Reeve's papers. Please see the section of Appendix II entitled <u>Corrected Brine Shrimp Filtration</u>.

[6] In fact this is <u>not</u> a reasonable assumption with respect to Reeve's data. Please see <u>Corrected Brine Shrimp Filtration</u> section of Appendix II.

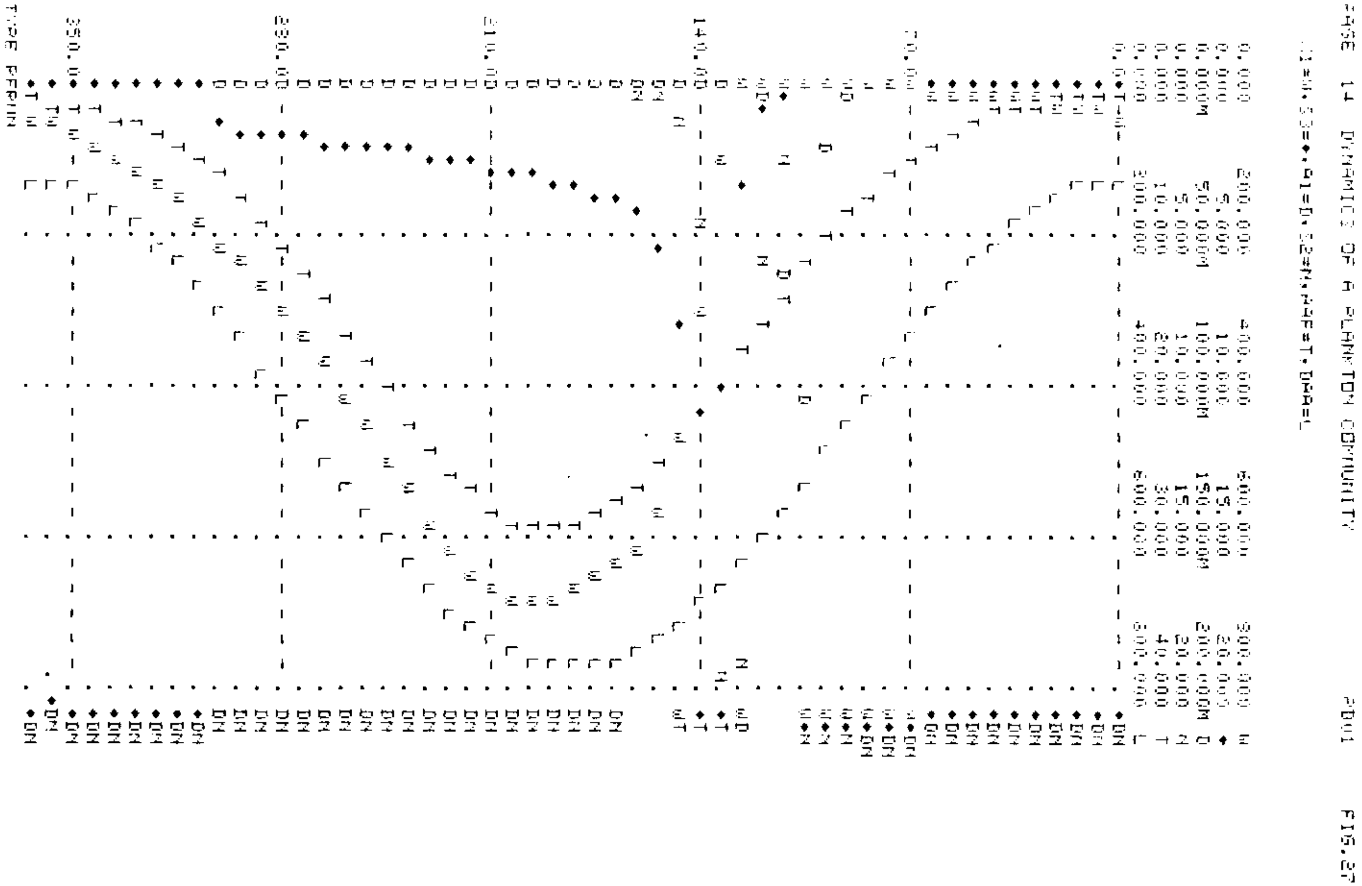

Figure 27. Result of Reducing the Filtration Rate of Brine Shrimp.

are half this, but still are much greater than those required to produce a minimal filtration rate of 1 liter per shrimp-day. Thus, no great differences in the springtime peak and decline of algae would be expected. However, in summer when algal standing crop is low, differences might be expected. The model behavior is not particularly sensitive to an order of magnitude reduction in filtration rate at this point either.

However, even with such a reduction, grazing pressure is sufficient to maintain a low standing crop of algae, and continue the steady starvation of brine shrimp. In conclusion, errors in the estimate of brine shrimp filtration rates appear to be of little importance in understanding the dynamics of this plankton community.

Increasing Overwintering Egg Hatching Temperature

Another factor which may contribute to the low peak height of the model algae accumulation (relative to that observed in the real system) is the temperature of winter egg hatching in the spring. If hatching occurs later, the algae will have additional time in which to increase their concentration before being grazed.

The result of changing the hatching temperature from 12°C to 15°C is given in Figure 28. The expected increase in the algal peak is large. The algae almost double their standard run concentration in only one week of extra growth before grazing by brine shrimp reduces their density. Almost four times as many nauplii are produced when the hatching temperature is 3°C warmer than in the standard run, due to the extra algae. The adult brine shrimp peak is more than twice that in the standard run, and occurs one week later. Because there are more

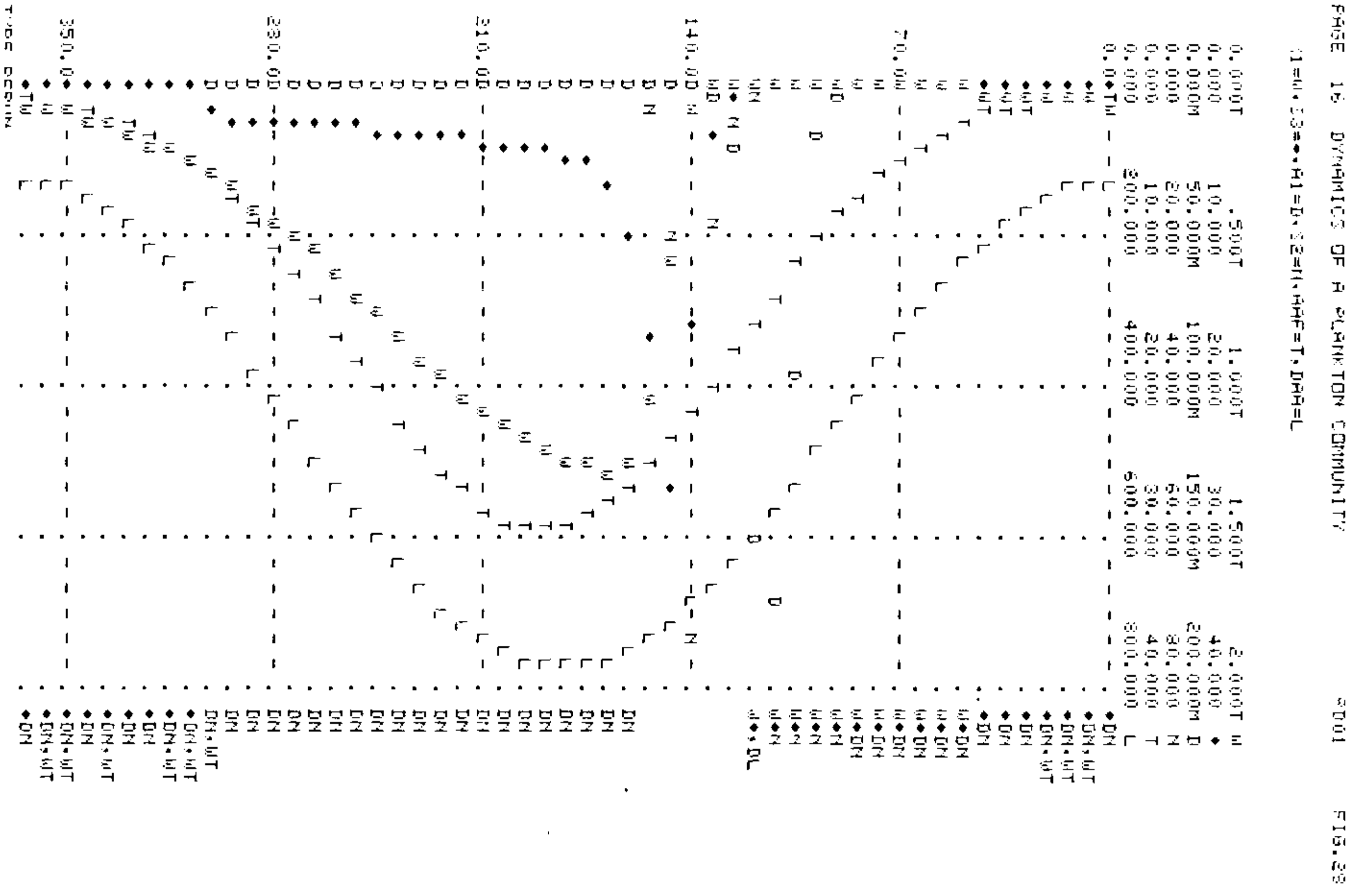

Figure 28. Result of Increasing Overwintering Egg Hatching Temperature from 12°C to 15°C.

adults, about one and one half as many overwintering eggs are produced when food finally becomes so limiting.

Obviously, the hatching temperature is a sensitive model parameter. The value of 12°C used in the standard run was chosen because, according to Wirick (1972), *Artemia* in the Great Salt Lake hatch when water temperatures are between 9 and 14°C. A few degrees of difference, however, has been shown to greatly alter the primary and secondary production in the model system. It would be interesting if observations of this phenomena could be made in the real system. Such data would strongly support the validity of the model.

Changing the Number of Eggs per Female

The number of eggs per female brine shrimp produced is reported to range from 16 to 120 by Jensen (1918), from 50 to 60 by Khmeleva (1967) and from 30 to 50 by Wirick (1972). For the purposes of the model, an average value of 50 eggs per female adult was chosen. No information was found concerning the causes involved in greater or lesser numbers of eggs per female, so a lower value (20 eggs per female) and a higher value (100 eggs per female) were included in two additional simulation tests. The results are given in Figures 29 and 30, respectively.

The result of lowering the production to 20 eggs per female (Figure 29) had little effect except to reduce by approximately half the winter egg accumulation, as expected. Peak heights, growth rates, and decline rates of algae, nauplii, and adults, are all only slightly altered.

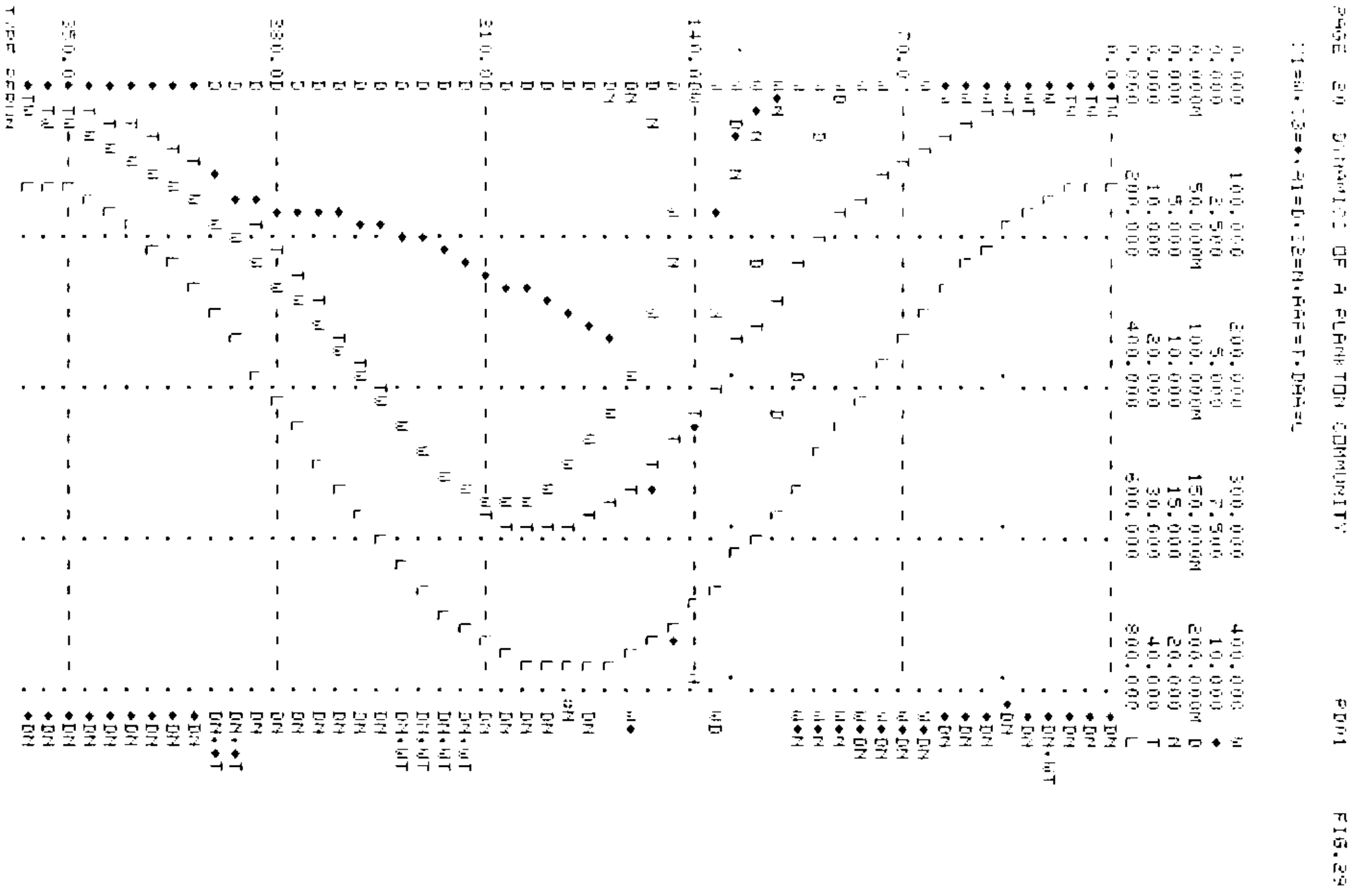

Figure 29. Result of Decreasing the Number of Eggs Per Female Brine Shrimp from 50 to 20.

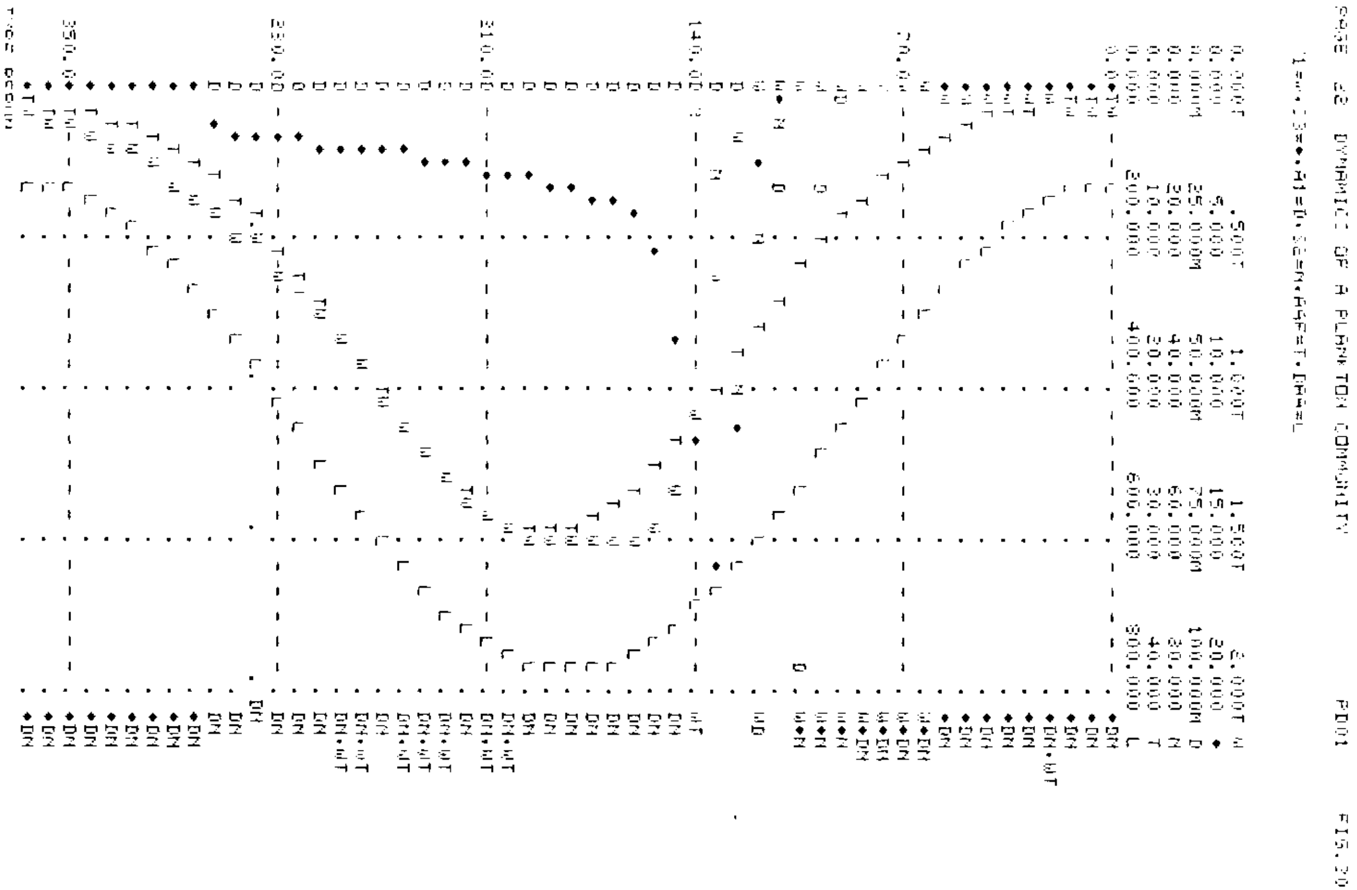

Figure 30. Result of Increasing the Number of Eggs Per Female Brine Shrimp from 50 to 100.

Doubling egg production over that of the standard run (Figure 30) approximately doubled the winter egg accumulation and doubled the nauplii peak height (day 126). However, adult peak height was only slightly increased and algae peak height was relatively unaffected. Algae rate of decline was increased slightly, due to the additional grazing pressure of twice as many nauplii.

In conclusion, the general pattern of model behavior is not believed sensitive to changes in the number of eggs per female within the wide range of possibilities tested, with the exception of the winter egg accumulation. No comparable field data is yet available for winter egg accumulation. Such a refinement may have little impact on understanding the causal forces producing the algae and brine shrimp dynamics measured in the Great Salt Lake.

Increasing the Percentage of Adults That are Female

For the standard run of the model, it was assumed that 50% of the adult brine shrimp population is female. Wirick (1972) found a range of 32 to 73% with a mean of 57.3% in the Great Salt Lake. The variance may have been due to sampling error (Gillespie, personal communication). Because of these data, an additional simulation which employed a 60% female proportion was performed. The results are given in Figure 31.

The change to 60% has very little effect on any of the output variables included. Winter egg accumulation is increased as is the nauplii peak in spring. This is similar to the results found for the increases in egg production mentioned previously. In conclusion,

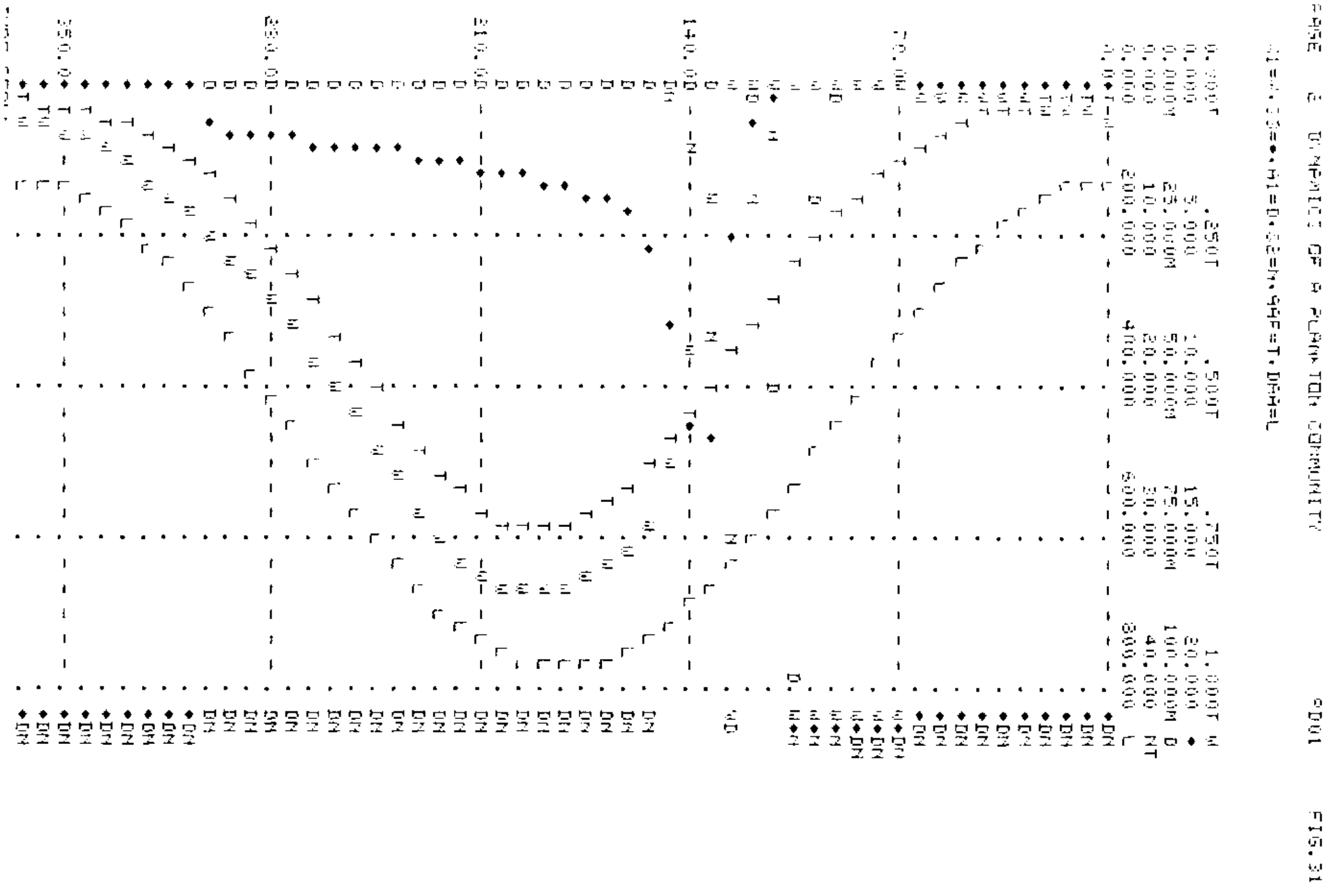

Figure 31. Result of Increasing the Percentage of Adults that are Female from 50% to 60%.

whether the percentage of adult brine shrimp is 50% or 60% appears to have little effect on the model output.

Changing the Algae Required for the 50% Production of Overwintering Eggs

When the food obtained by adult brine shrimp decreases below some level, some of the adult females begin producing overwintering eggs rather than the nondurable eggs which hatch within one or two days. This is the hypothesis of Wirick (1972) based on his reported field observations. The model is so constructed that overwintering egg production follows a sigmoid function of food obtained symmetrical about the 50% winter egg production level (Figure 32). The food level required for the entire population to produce 50% winter eggs and 50% nondurable eggs was arbitrarily chosen at 30,000 algal cells per adult shrimp-day. This represents a plentiful quantity of food per brine shrimp, since the adults have been shown in the laboratory to optimally utilize 1000 *Dunaliella* cells per shrimp-day, with greater growth occurring with 2000 and 3000 algal cells per shrimp-day (Porcella and Holman, 1972). Because the 50% winter egg value of 30,000 cells per shrimp-day is nothing more than a guess, two additional simulation tests were performed; one with a value of 15,000 (Figure 33) and the other with a value of 60,000 (Figure 34).

Very minor changes are evident from these alterations. By causing winter egg production to take place at half the standard run food concentrations (Figure 33), a very few additional nauplii are produced and the adult peak height is only one or two brine shrimp higher. The converse is true of the doubled 50% winter egg production

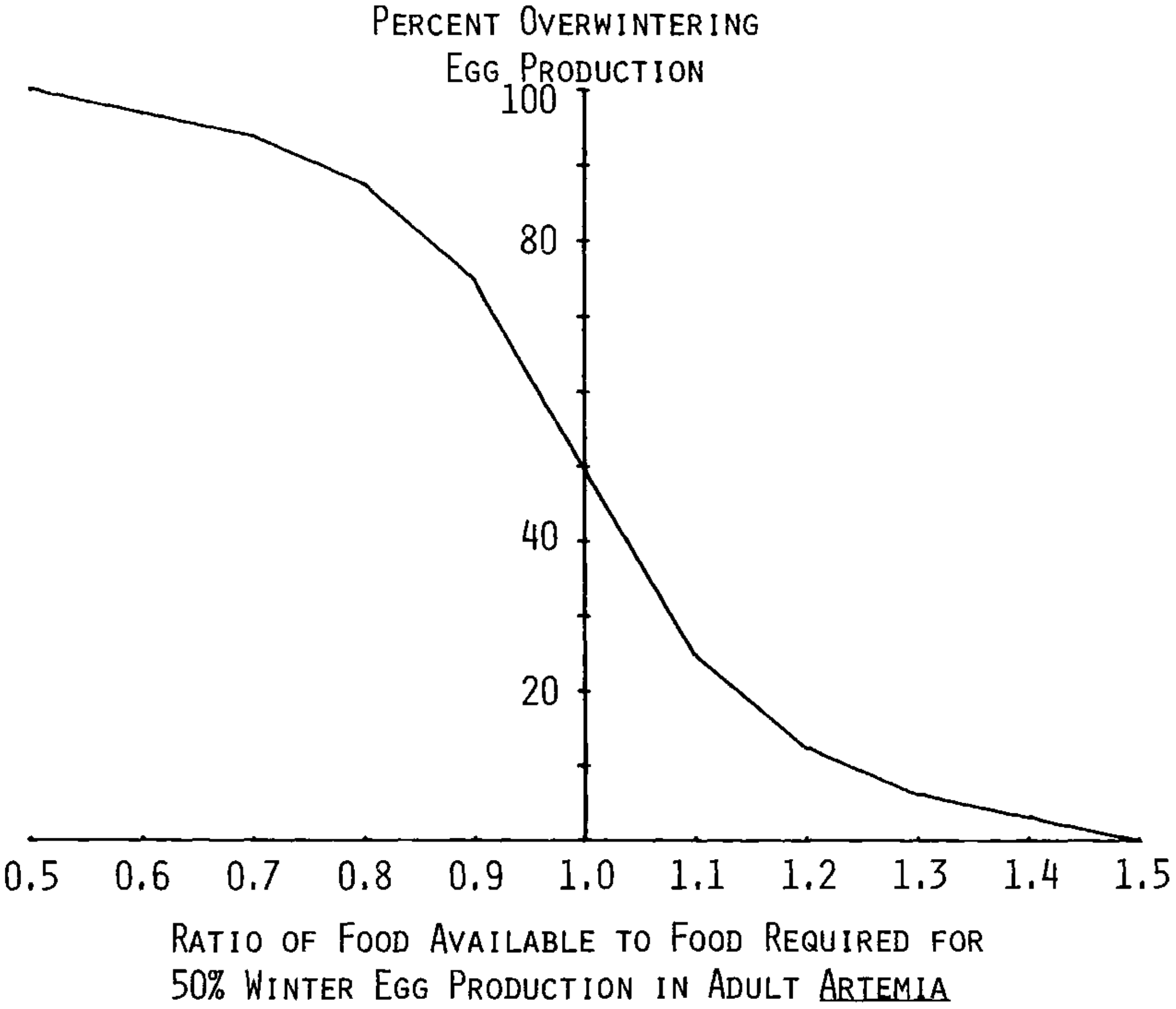

Figure 32. Overwintering Egg Production as a Function of Food Available to Adult Brine Shrimp (After the Food Stress Hypothesis of Overwintering Egg Production).

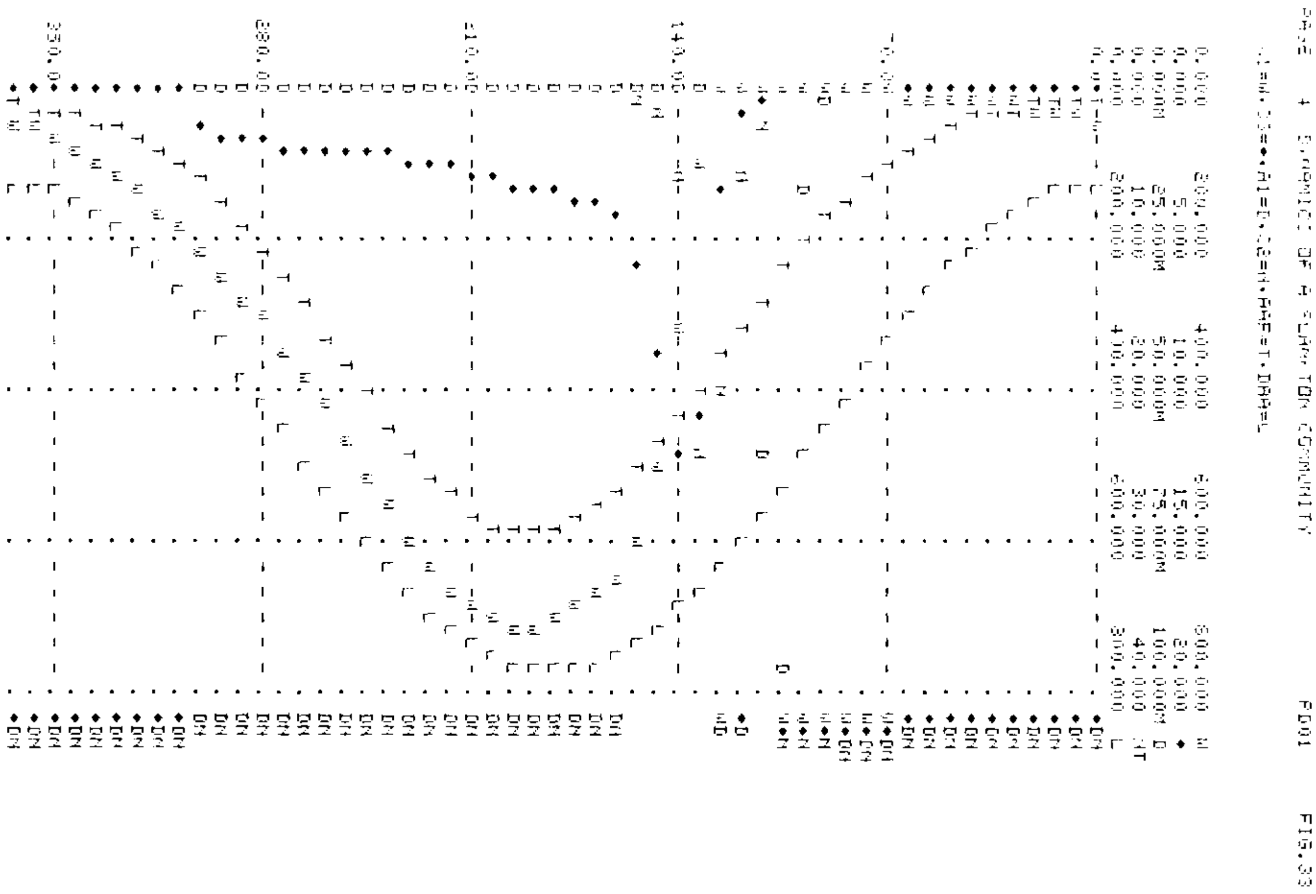

Figure 33. Result of Reducing the Algae Required for the Production of 50% Overwintering Eggs from 30,000 to 15,000 cells·shrimp^{-1}·dy^{-1}.

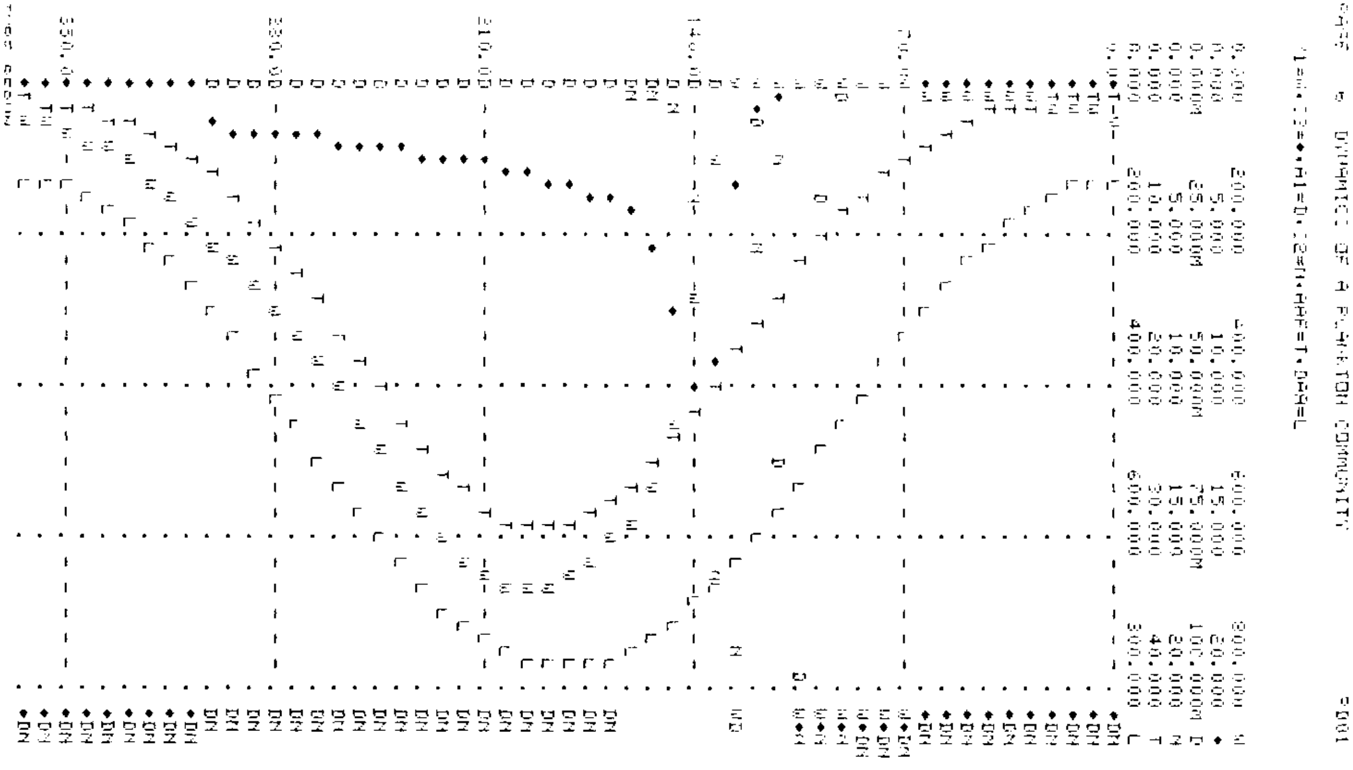

Figure 34. Result of Increasing the Algae Required for the Production of 50% Overwintering Eggs from 30,000 to 60,000 cells$\cdot$shrimp$^{-1}\cdot$dy^{-1}.

level. In conclusion, the model seems quite insensitive to changes in this parameter within the range chosen. Possibly, a great reduction of this value would produce more significant increases. In light of the controversy over the mechanism or mechanisms actually responsible for overwintering egg production, some additional physiological and feeding studies in the laboratory are necessary together with some bimonthly field samples of egg accumulations before adequate evaluation of this area of the model is possible.

Changes in the Time Required for Adult Starvation

The ration required for the onset of starvation was extrapolated from the results of Porcella and Holman (1972) to be around 500 *Dunaliella* cells per shrimp-day. The time for an adult shrimp to actually die from starvation was assumed to be 10 days, for the purposes of this model. This value was tested for model sensitivity by halving (Figure 35) and doubling (Figure 36). Two immediately noticeable changes occur. First, the winter egg accumulation is decreased and increased respectively, since the starving adults remain for less or more time prior to death. Second, the rate of brine shrimp adult decline is faster when the starvation delay is shorter and slower when this delay is longer as expected. The model is not very sensitive to these changes, but the results indicate that the model is behaving as expected.

Changing the Ration Required for the Onset of Adult Starvation

Results similar to those above, but slightly more intense, are obtained when the minimum starvation ration of 500 algal cells per adult shrimp-day is halved (Figure 37) and doubled (Figure 38). The reduction

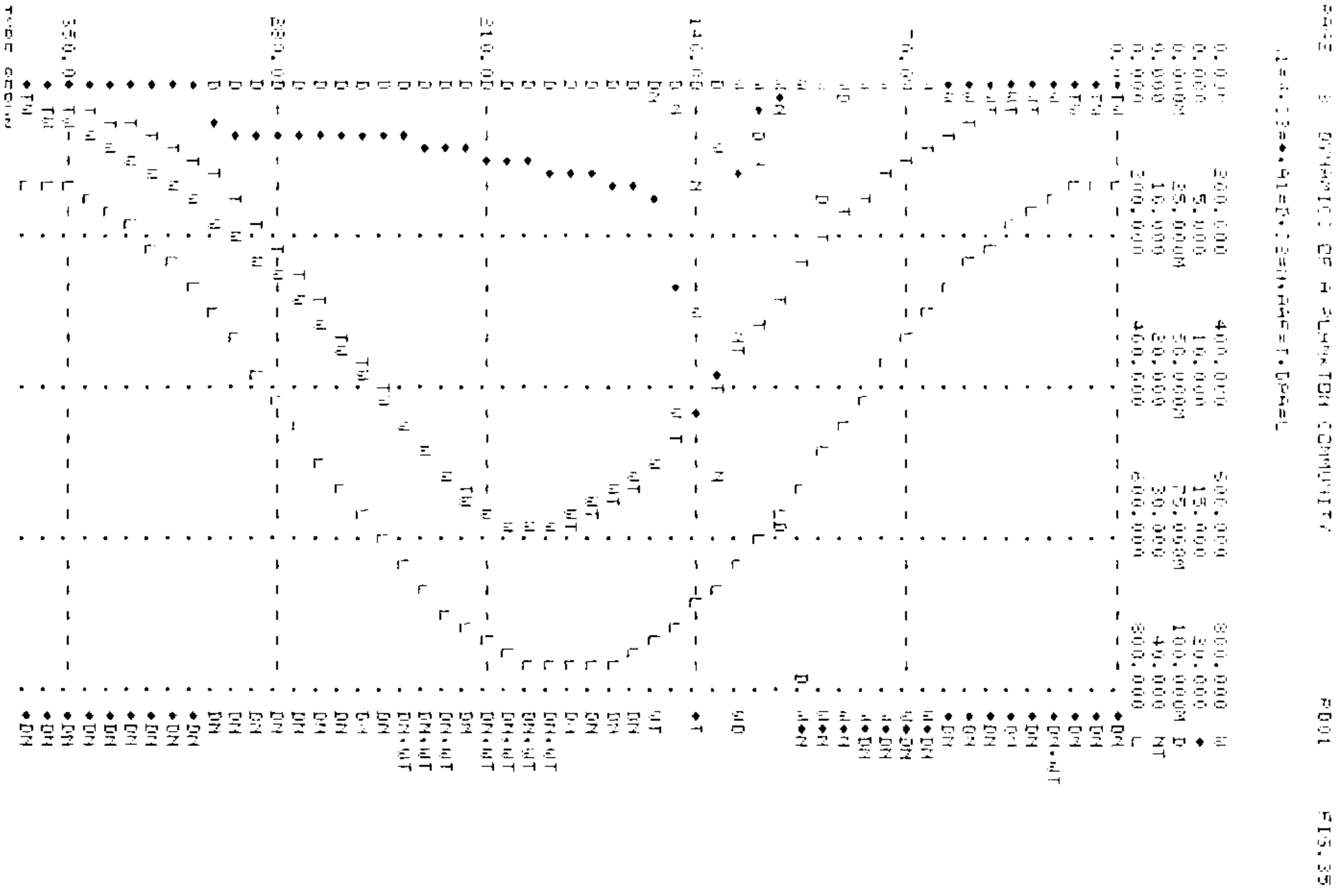

Figure 35. Result of Decreasing the Time Required for Adult Starvation from 10 days to 5 days.

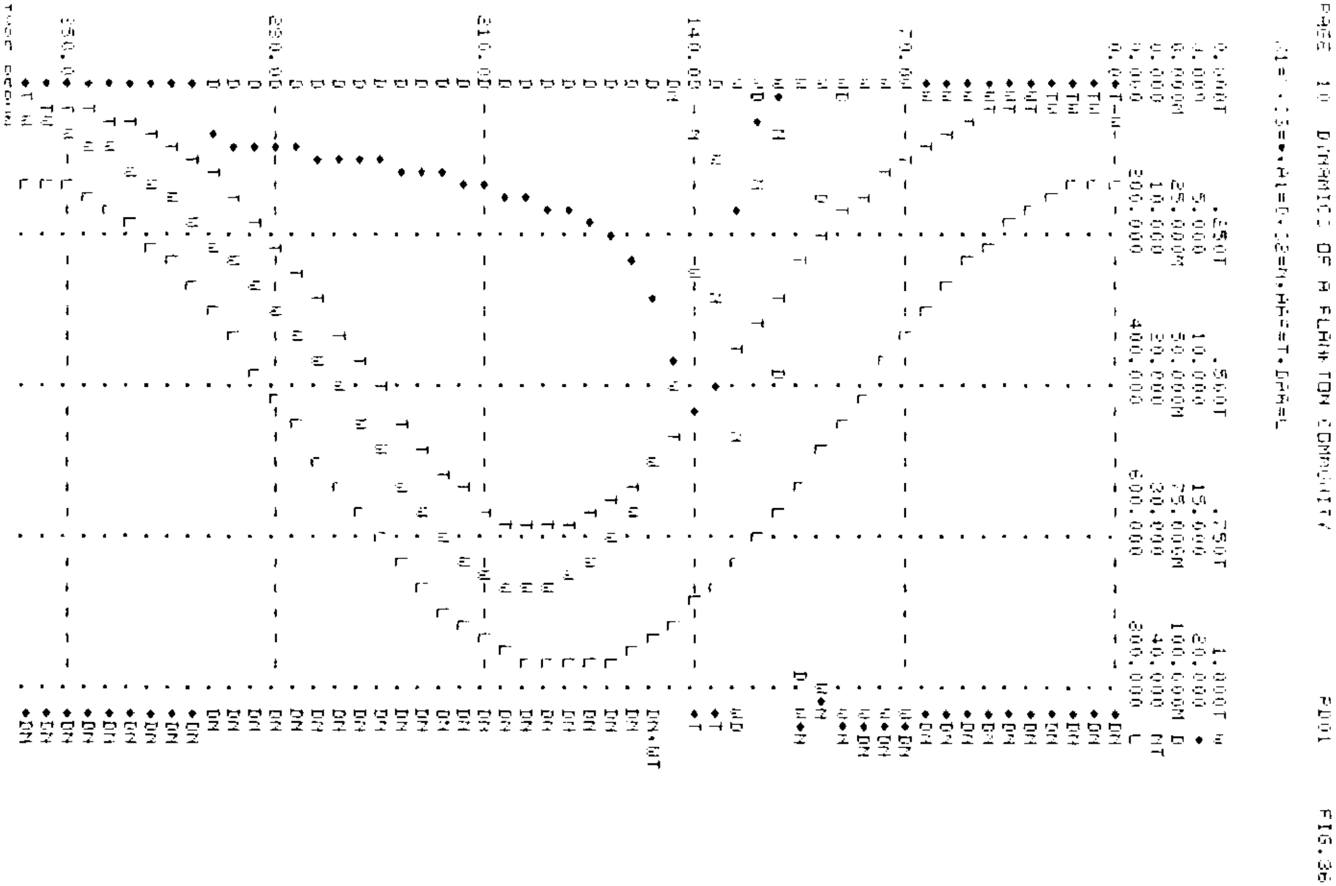

Figure 36. Result of Increasing the Time Required for Adult Starvation from 10 days to 20 days.

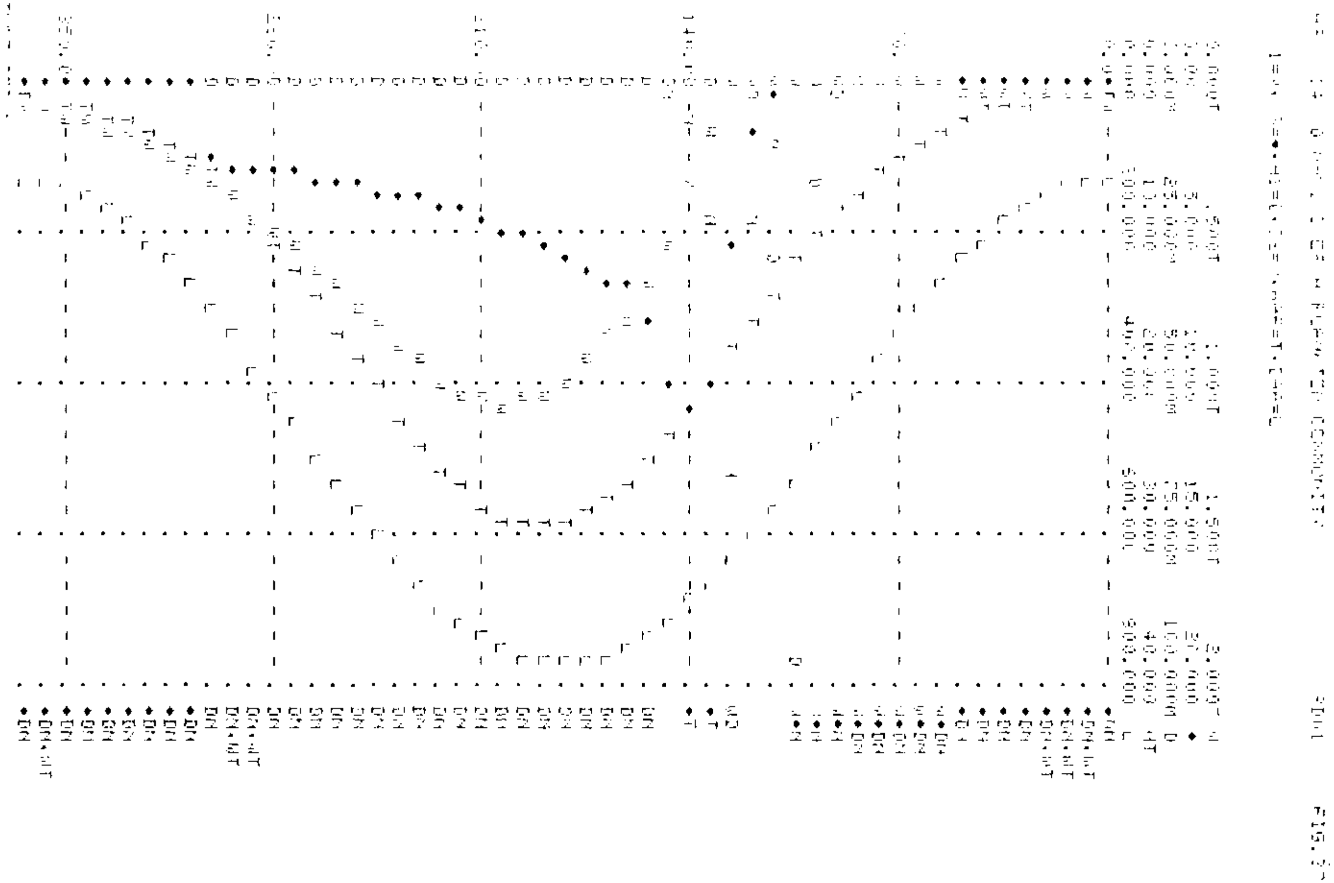

Figure 37. Result of Reducing the Ration Required for the Onset of Adult Starvation from 500 to 250 cells·shrimp^{-1}·dy^{-1}.

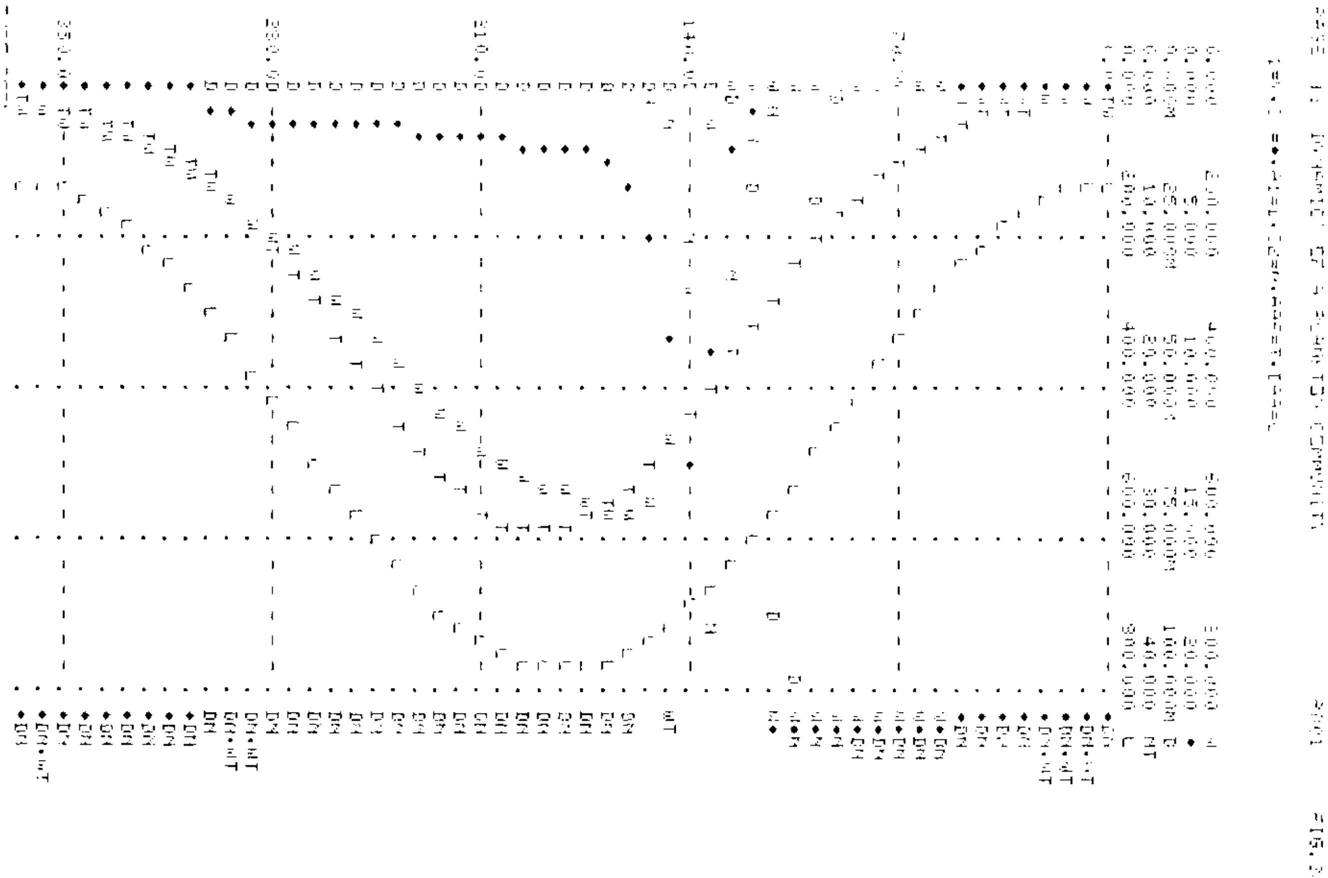

Figure 38. Result of Increasing the Ration Required for the Onset of Adult Starvation from 500 to 1000 cells·shrimp^{-1}·dy^{-1}.

in this ration slows the adult shrimp rate of decline in a similar manner to increasing the time required to starve (Figure 36). Conversely, increasing the density of Dunaliella at which starvation begins increases the rate of brine shrimp decline, and correspondingly lowers the overwintering egg accumulation (because of fewer brine shrimp and therefore fewer eggs). Figures 38 and 35 may be compared in this regard. The sensitivity of the model to such changes evidently is not very great for parameters dealing with adult brine shrimp starvation.

Changing the Percentage of Overwintering Eggs Lost per Day

Not all of the overwintering eggs produced by adult brine shrimp actually hatch. Some are physiologically incapable of hatching for various reasons, some are blown away from the Great Salt Lake, others are washed onto shore, and a considerable number are collected by humans for sale as tropical fish food in home aquaria. The attrition rate for overwintering eggs is expressed in the model as a constant percentage of the egg accumulation lost per day. This causes an accumulation (without inflows) to change approximately as a negative exponential function with time. The value used in the standard run for this percentage is 0.025. This value was chosen using judgments based on Wirick's (1972) scanty information concerning overwintering egg dynamics.

Reducing this value to 0.010 (Figure 39) greatly increases the brine shrimp annual productivity in the model. The algae productivity is relatively unaffected. While more brine shrimp hatch in the early spring and more are producing overwintering eggs at the beginning of their decline, the grazing pressure on algae is about the same as that in the standard run after the initial algal decline. This is because

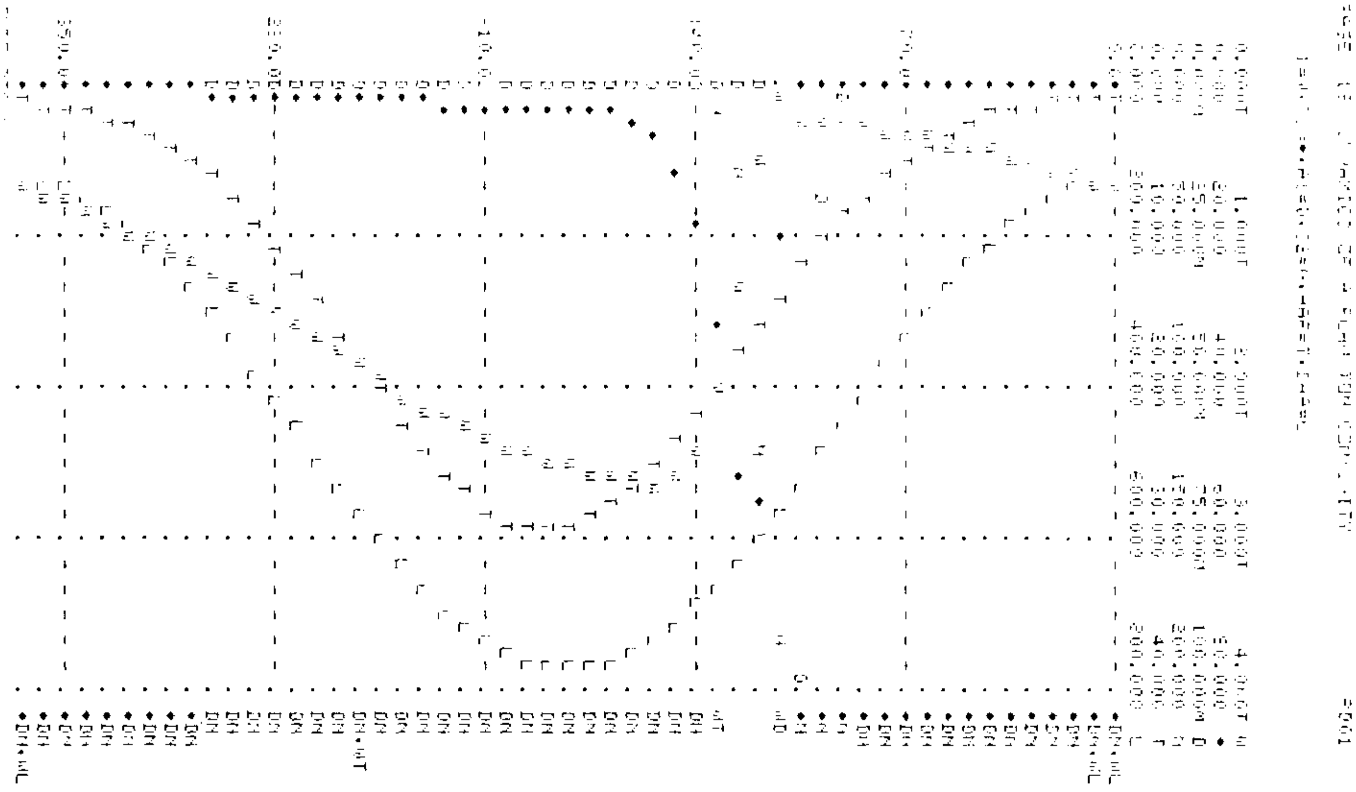

Figure 39. Result of Reducing the Percentage of Overwintering Eggs Lost per Day from 0.025 to 0.010.

standard run grazing is already of maximum intensity. Thus the behavior of the brine shrimp accumulation after the initial sharp decline in spring is much the same as that of the standard run. The brine shrimp accumulation declines slowly until all suffer thermal death in autumn.

Increasing the percentage of the winter eggs lost per day to 0.050 has surprising bimodal results (Figures 40 and 41). Through further experimentation the following explanation was developed. Increasing the attrition rate for overwintering eggs to 5% per day causes very few eggs to be present (<0.3 eggs per liter) when the water reaches hatching temperature. The grazing of so few brine shrimp does not cause a decline in the algae population. The algae continue to grow until self shading causes their division rate to equal the increasing grazing rate of the developing brine shrimp. Subsequently, a slow decline of algae begins, but much later in the year than for the standard run. As the algae decline, self shading decreases until a light intensity that is optimal for algal productivity is achieved. With the warmer summer temperatures, algal division can proceed at an extremely rapid pace. Algal productivity is greater than one new cell per existing cell per day. Because the model brine shrimp can only eat the existing cells (new cells are protected from being eaten during the integration interval by the fact that the model equations are discretized) more algal cells are produced each day than are eaten. Hence, a growth of algae results allowing the continued exponential growth of brine shrimp. At this time, the brine shrimp are obtaining enough algae to produce nondurable eggs which hatch rapidly. Finally, in midsummer when temperatures begin to fall, algal

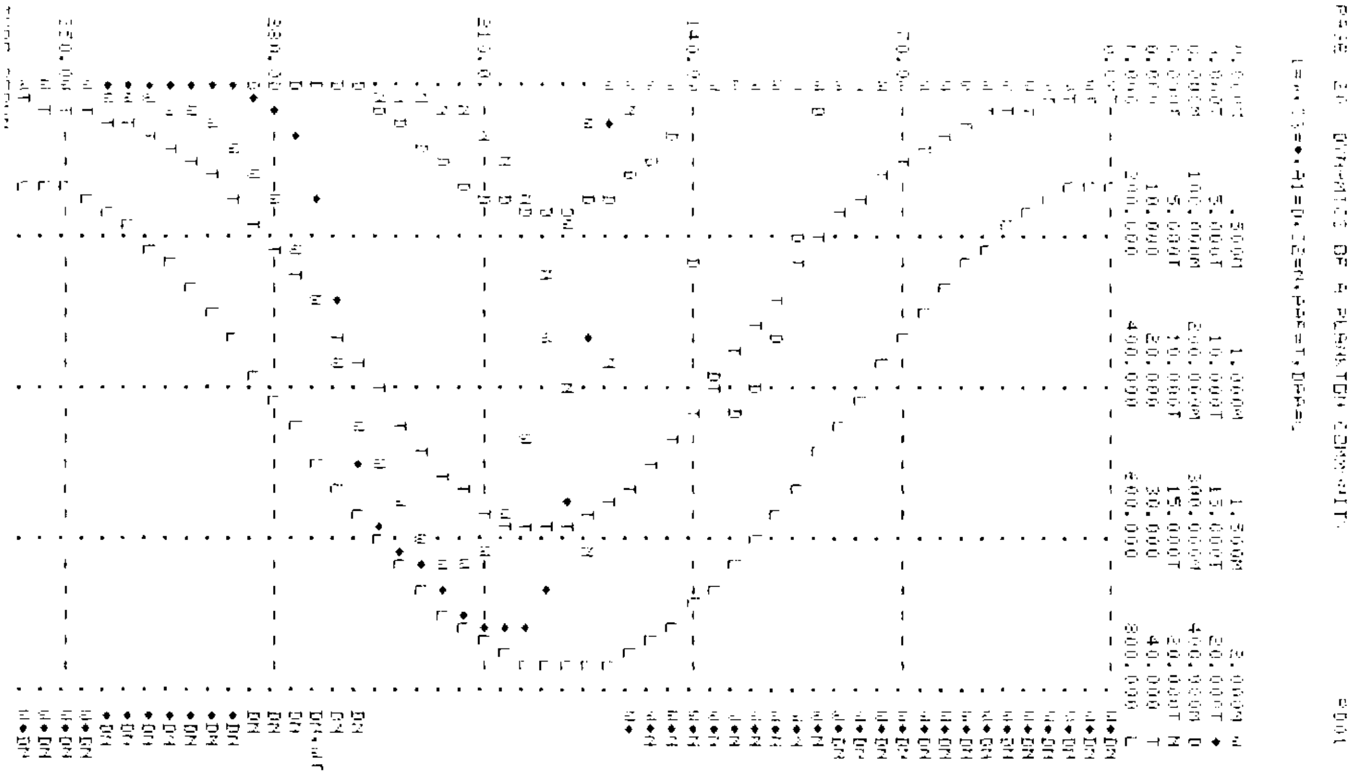

FIG.40

Figure 40. Result of Increasing the Percentage of Overwintering Eggs Lost Each Day from 0.025 to 0.050 (First Annual Mode).

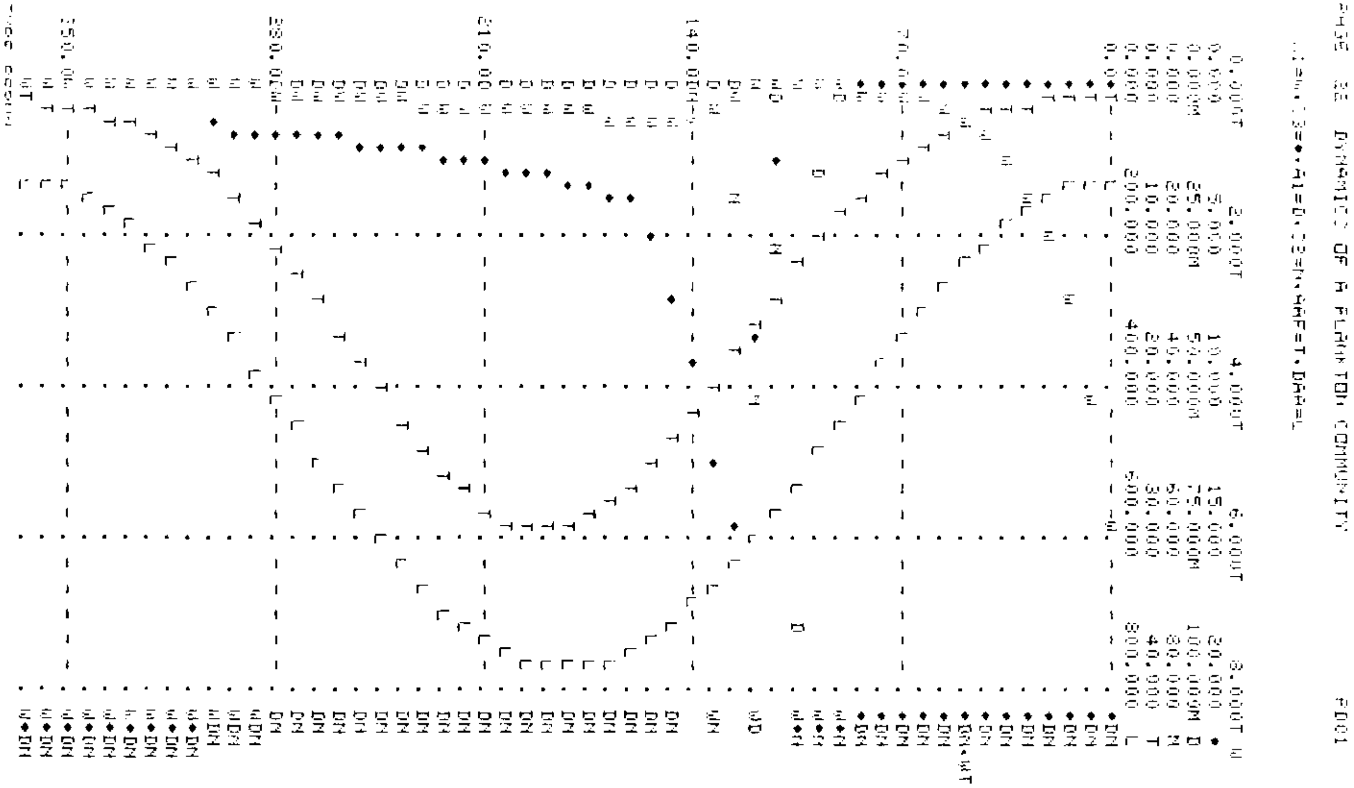

Figure 41. Result of Increasing the Percentage of Overwintering Eggs Lost Each Day from 0.025 to 0.050 (Second Annual Mode).

productivity falls, brine shrimp starvation increases, and winter egg production begins. There are so many brine shrimp that huge quantities of overwintering eggs are produced. The rapid attrition rate, however, causes the overwintering egg accumulation to fall by hatching time to a number (around 40 per liter) which is more characteristic of the standard run number (around 4 per liter). Hence the second annual mode (Figure 41) is not unusual except that the winter egg accumulation falls off rapidly enough to allow less than .3 eggs per liter by the subsequent year's hatching time. Thus the biennial cycle recurs.

Through continued experimentation, it was discovered that the maximum attrition rate allowed by the model without causing the bimodal situation is 0.0365 per day. With this value, there are approximately 0.39 eggs per liter at hatching time. The results are presented in Figure 42. In comparing Figures 39 and 42 with the standard run, a most peculiar result is observed. Both a decrease and an increase in the overwintering egg attrition rate cause an <u>increase</u> in the brine shrimp peak height, but for different reasons. Note that the phase relationship between the algae and shrimp peak heights is also altered. The time between these peaks is decreased by approximately three weeks when the attrition rate is reduced from 0.025 to 0.010 (Figure 39) and is increased by about two weeks when the attrition rate is increased from 0.025 to 0.0365 (Figure 42). Also note that because fewer eggs hatch initially, Figure 42 shows an algal accumulation that rises to 1.5 times the peak of either the standard run or the reduced attrition rate run shown in Figure 39. The delayed but increased peak of adult brine shrimp in Figure 42 is the result of the algae being grazed more slowly (because

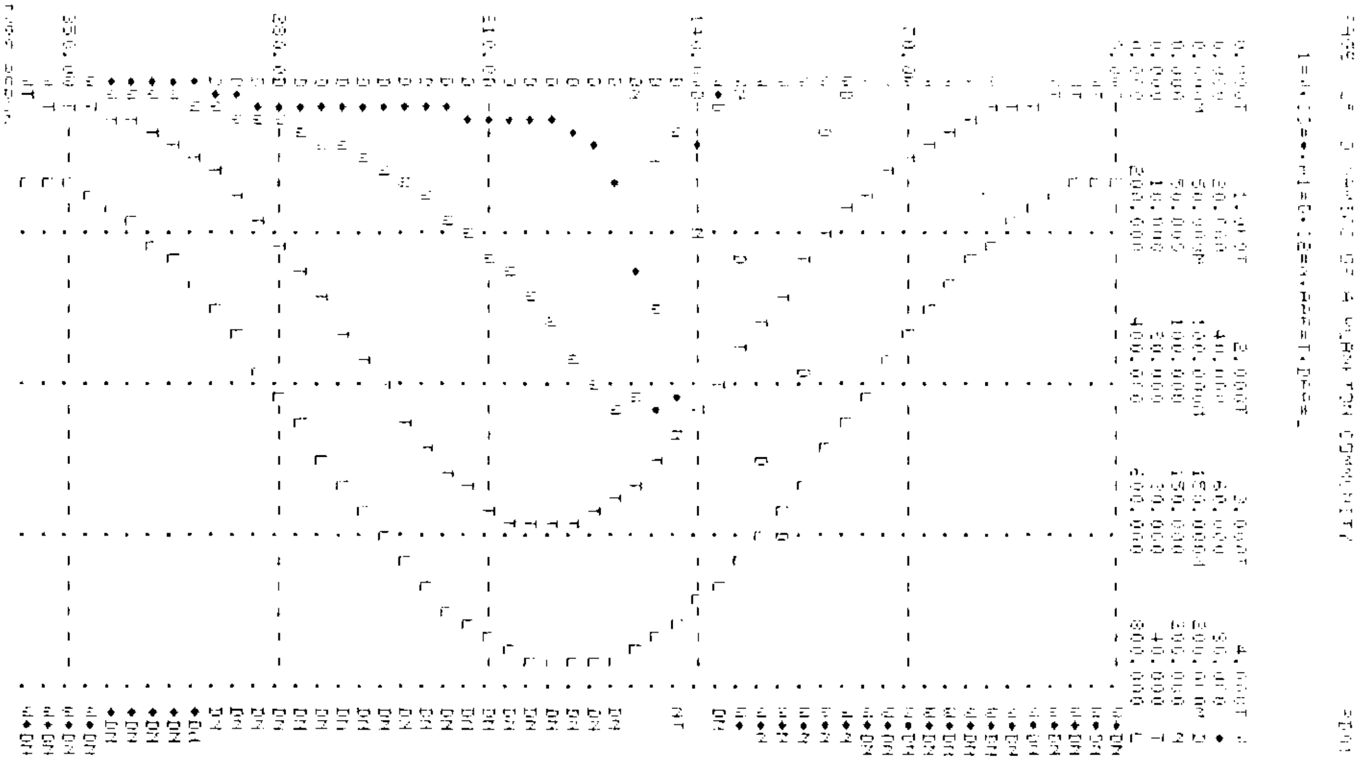

Figure 42. Result of Using 0.0365 as the Maximum Attrition Rate Allowable without Causing a Bimodal Output.

fewer brine shrimp are initially present). This allows the algal productivity to increase (because of more favorable environmental conditions) which in turn supports a shrimp population increase later in the year.

When the attrition rate is reduced as in Figure 39, the large number of brine shrimp which hatch rapidly graze the algae to a density low enough that no self shading is possible. The intense summer sunlight being limiting to some degree prevents a surge of new algal growth. This behavior is similar to that found in the standard run. More concerning the productivity functions of the algae will be discussed in the dominant forces identification (see the next chapter). The time between algae and brine shrimp peaks is reduced in Figure 39 from that of the standard run because the onset of starvation begins earlier. This is due to the increased number of shrimp at hatching which causes an intense grazing pressure earlier in the year.

In conclusion, these runs have illustrated the sensitivity of the model to winter egg dynamics. It seems unlikely that the brine shrimp density could ever attain that allowed by the model in Figure 40. This anomaly demonstrates some weaknesses of the model. Evidence has recently accumulated which indicates that algal nutrients may be limiting during the summer months in the Great Salt Lake (Stephens and Gillespie, 1976). This important factor, the dynamics of which have been ignored in the present model, may correct the anomalous behavior observed if included. If nutrients limit the algae, then the midsummer growth would not occur. Hence, the huge brine shrimp productivity of

Figure 40 would not be possible. The model suggests two areas of future research at this point: 1) overwintering brine shrimp egg dynamics, and 2) nutrient cycling dynamics in the Great Salt Lake.

Changing the Percentage of Nondurable Eggs Lost per Day

An attrition rate similar to that for the overwintering eggs is included in the model for nondurable eggs. The value used in the standard run is 0.08 of the accumulation lost per day. The value is merely an educated guess made in conjunction with the judgment of D. M. Gillespie, who has worked in the Great Salt Lake system. Figures 43 and 44 show the effect of halving and doubling the standard run value. The model is not very sensitive to these changes and no unusual results were obtained. Allowing more nondurable eggs to survive to hatching allows more nauplii, a few more of which survive to maturity (Figure 43) than in the standard run. The converse is true when fewer nondurable eggs are allowed. The alterations are relatively insignificant to the adult accumulation behavior because starvation is so intense at this point.

The Relationship of Development Time to Temperature

All of the development times for the brine shrimp were modeled as functions of temperature assuming a Q-10 of 2. That is, for every 10°C increase (or decrease) in water temperature, the development time in question is halved (or doubled). The egg production delay time, the winter egg and nondurable egg hatch times, and the maturation time for brine shrimp were modeled in this manner. This temperature relationship for the adult brine shrimp lifetime was calculated by assuming a constant number of degree-days of life. As the temperature

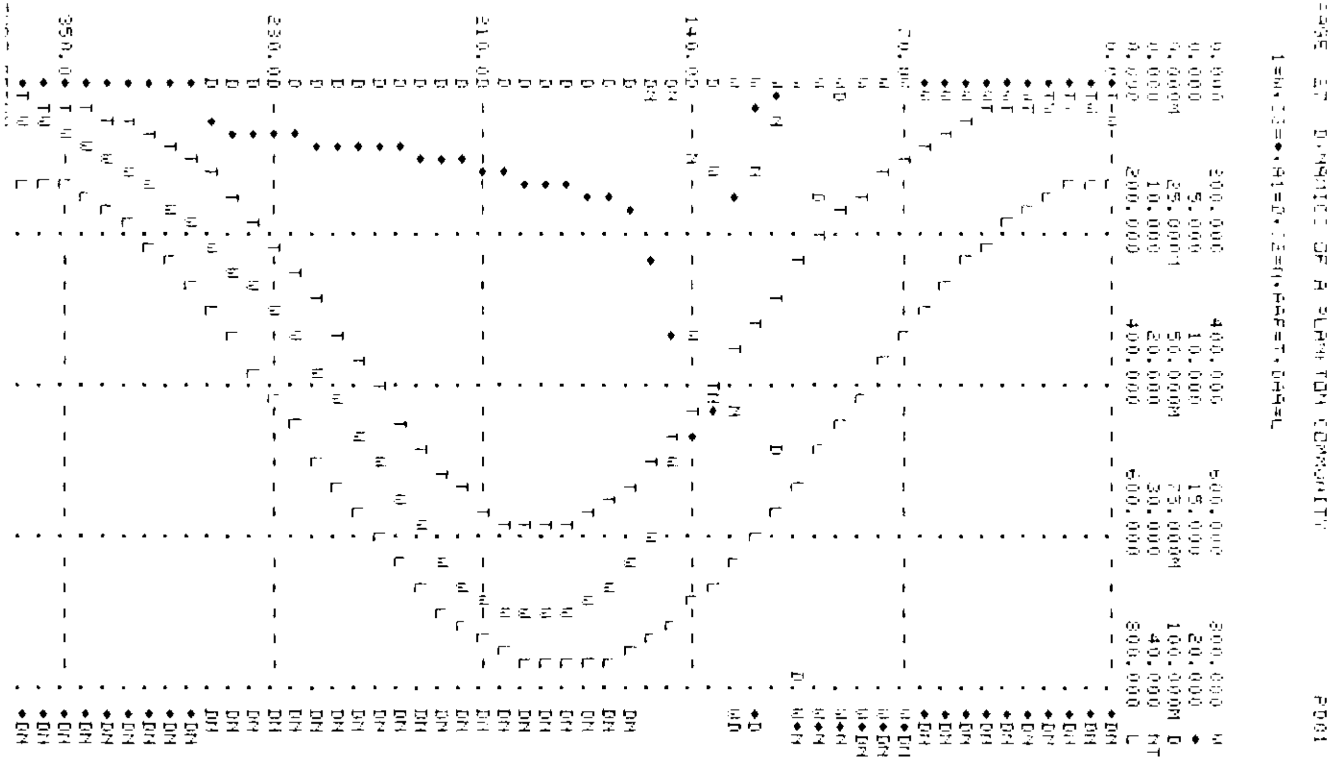

FIG.43

Figure 43. Result of Reducing the Percentage of Nondurable Eggs Lost per Day from 0.08 to 0.04.

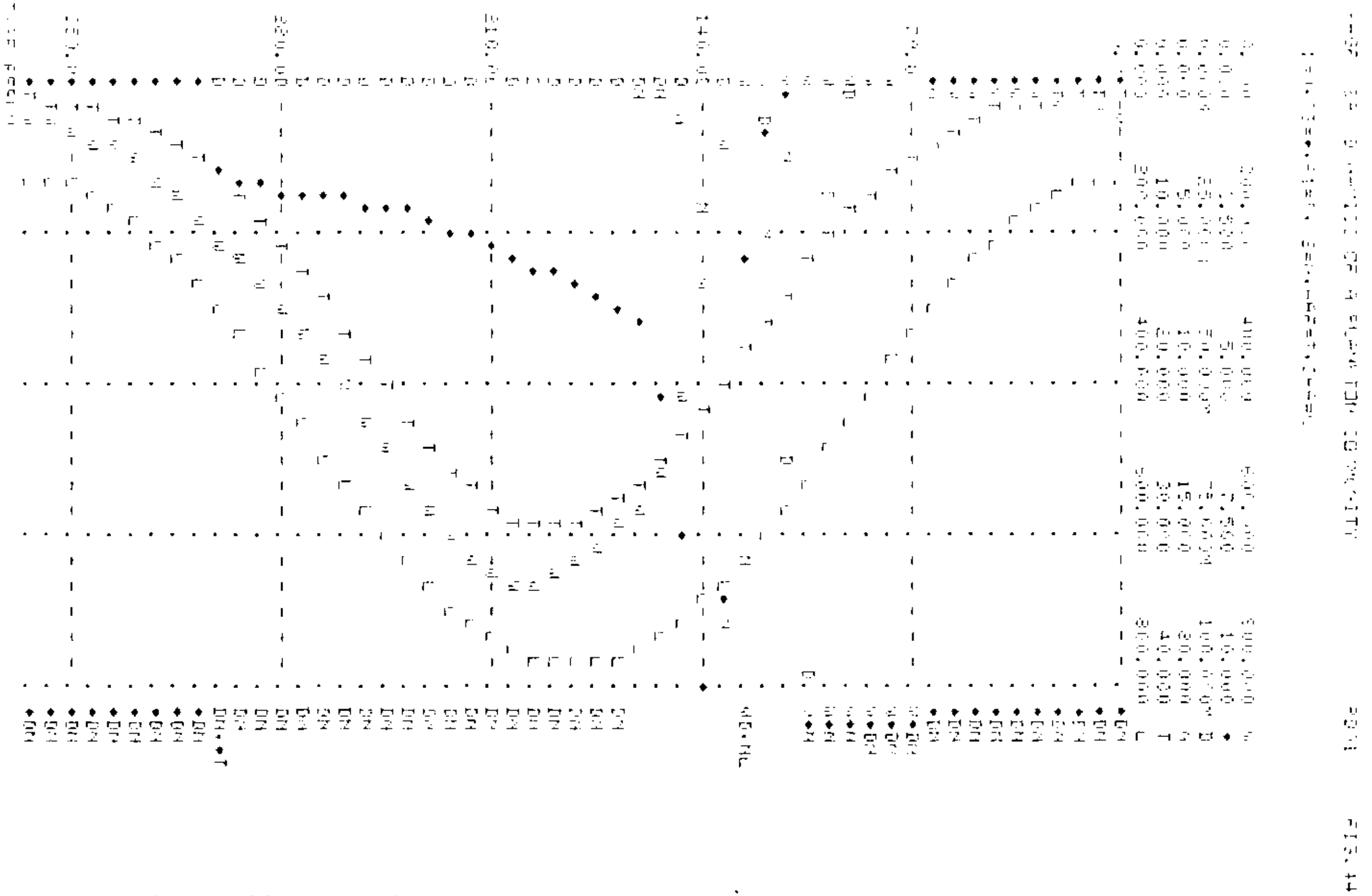

Figure 44. Result of Increasing the Percentage of Nondurable Eggs Lost per Day from 0.08 to 0.16.

increases, the lifetime in days decreases to maintain this constant value. Several experimental runs were performed to determine if the presence of the development times as a function of temperature makes a very large difference in the standard run behavior.

Constant development times were substituted for the temperature dependent functions together in one run and separately in individual runs (the output from these runs is not given). The value chosen for the constant was the respective development time at 25°C. In the run with all constants taken together, the shrimp peak and the overwintering eggs were increased slightly, but no changes in the phase relationship between peaks or in the overall pattern were detected. Individually, the parameter effecting the model most by itself was the egg production delay time. Using the 25°C value rather than expressing it as a function of temperature decreased the algal productivity, increased the shrimp peak height, and the overwintering egg accumulation, all very slightly. In conclusion, it appears that such physiological detail is of little significance to the behavior of the ecosystem model as a whole.

Model Response to Various Input Function Noise Levels

The cosine wave solar energy input function employed in the standard run is a smooth function. Random noise was included in this cosine function via the NOISE() function contained in DYNAMO. NOISE() gives random numbers uniformly distributed between -½ and +½ (Pugh, 1973). The chosen value was multiplied by 10, 20, 40, 80, and 160 on successive experimental runs and the resulting noise amount added to the input function each integration interval. The results from the 10, 40, and 160 level runs are presented in Figures 45, 46, and 47, respectively.

Differences between the standard run and the 10-level noise run (Figure 45) are obviously insignificant. Noise begins to be more obvious in the 40-level run (Figure 46) with the respect to the light and water temperature curves, but the only noticeable effect on the algae or shrimp curves is a slight increase in the nauplii peak height. The noise resulting from the 160-level run (Figure 47) causes great variance in the solar energy input function. However, little alteration of the general pattern can be detected. This run was allowed to continue for four simulated years. During this time the algae peak varied between approximately 75 and 90 million cells per liter and the adult shrimp peak between approximately 8.5 and 9.5 shrimp per liter. The overall pattern and phase relationships were otherwise unchanged from the standard run.

In conclusion, the model insensitivity to input noise means that the output observed in the standard run is not caused by or dependent on a smooth cosine wave input function.

Summary and Conclusions

The model of the plankton community was found to be rather insensitive to changes in: 1) the upper tail of the productivity vs solar intensity function, 2) the brine shrimp water filtration rate, 3) the level of food causing 50% winter egg production, 4) the starvation delay time of adult brine shrimp, 5) the starvation ration of adult brine shrimp, 6) the percentage of nondurable eggs lost per day, 7) the expression of brine shrimp development times as a "Q-10" function of

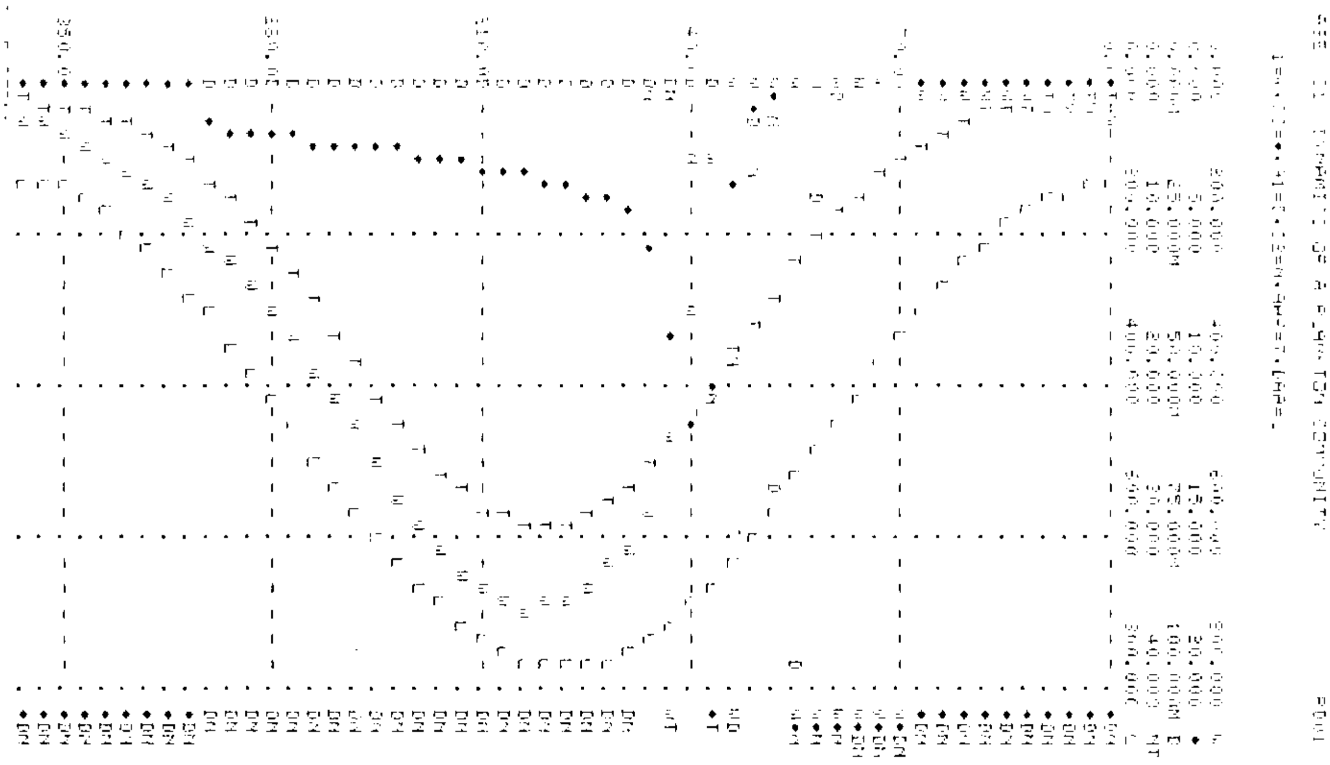

FIG.45

Figure 45. Result of Introducing Noise into the Solar Energy Input Function (Noise Level of 10).

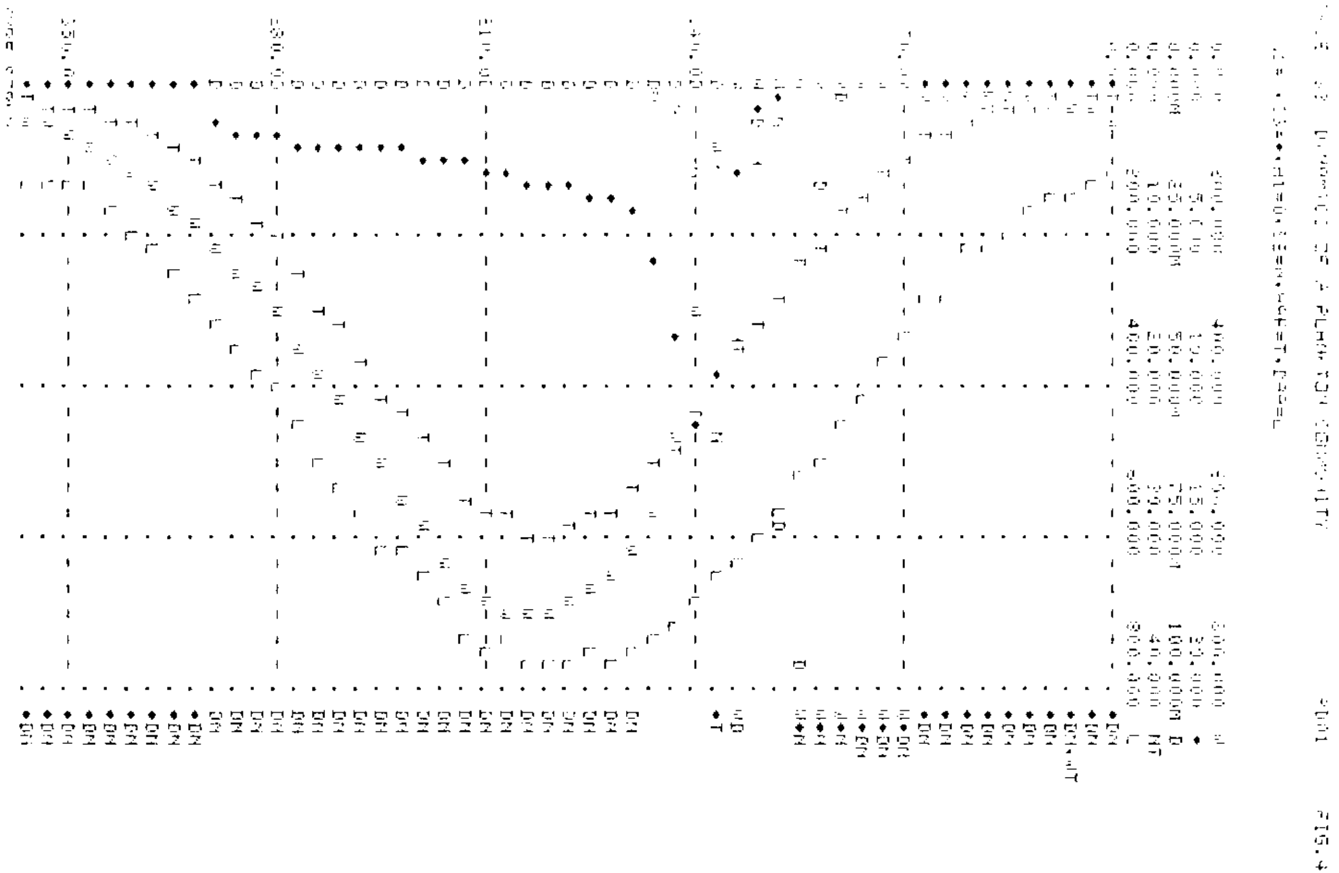

Figure 46. Result of Introducing More Noise into the Solar Energy Input Function (Noise Level of 40).

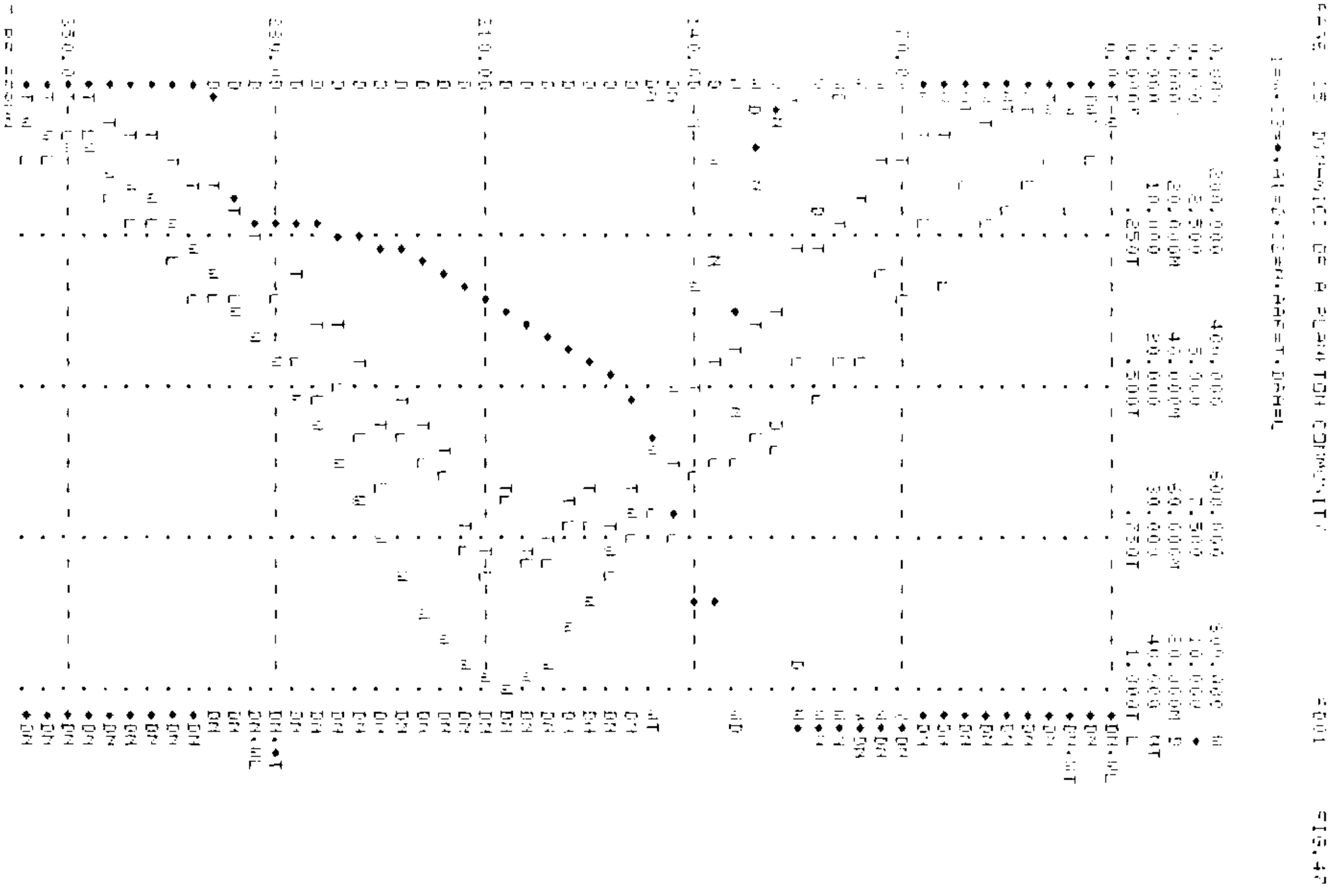

Figure 47. Result of Increasing the Noise Level to 160
(See Text for Further Explanation).

temperature, and 8) random noise in the solar input cosine wave. Given some other set of model parameters or ranges of parameter change the model could become sensitive to any of the above parameters. However, for the purposes of understanding the present system efficiently, the more sensitive parameters are recommended for the primary focus of research on this plankton community in the near future.

The following parameters were found to elicit relatively important alterations in model output upon being changed through the range tested: 1) the lower tail of the productivity vs water temperature curve, 2) the number of eggs per female brine shrimp, 3) the percentage of adult brine shrimp that are female, 4) the overwintering egg hatching temperatures, and 5) the percentage of overwintering eggs lost per day. These are not the only sensitive parameters in the model. The parameters tested in the dominant forces identification (see next chapter) have not been included, and may well be the most sensitive parameters in the model. However, the above sensitive parameters further emphasize two needed areas of research: nutrient dynamics as a factor in algal productivity, and brine shrimp reproduction dynamics. Both seem to have considerable effects on the primary and secondary production in the plankton community of the Great Salt Lake. In general, factors which affect the productivity of algae (e.g. nutrients, temperature, sunlight) as well as the physiological response of algae to such factors seem to be very important in producing the dynamics observed in the model output. Similarly factors affecting brine shrimp reproduction (e.g. the number of females, the number of eggs per female, the overwintering egg inflows and outflows) are important in producing the observed output. The significance of these factors in the real system has not been determined but it is recommended that these be the focus of future research.

In the next chapter an example of a rigorous model sensitivity analysis procedure is given, which employs the parameters of the sensitive algal productivity sector of the model. This will be the final set of data gathered in the present study to help assess the functional validity of the present model.

CHAPTER V

DOMINANT FORCES IDENTIFICATION

A methodology to determine those parameters in a feedback dynamics simulation model most responsible for changes in some chosen characteristic of the model's output (such as amplitude or period, if the output is an oscillation) has been developed by W. C. Low (see Low and Cowles, 1975). The procedure uses statistics generated from a multiple linear regression analysis of data from a set of model simulations to determine the most dominant parameters affecting the output characteristic. Such a procedure is needed due to a lack of a body of mathematics to analyze nonlinear models (as is available for linear models).

This methodology, called dominant forces identification, gives more information than the traditional sensitivity analysis approach to nonlinear models in which only one parameter is varied in each successive rerun of the model. Here more than one parameter is varied in each simulation rerun in such a way that the effect of parameter interactions as well as the order of dominance of parameters may be assessed. This procedure may also be used to locate logical errors in the model structure when coupled with intuition on the part of the modeler.

Methodology: A General Outline

It should be emphasized that in using this method the modeler should not rely only on the rote procedure to be described. Judgment is also required. The effects of noise in the simulation output or its measurement, the fact that errors may be incurred in the transcription of large amounts of data, and incorrect model formulation may cause unexpected or physically suspect information to be generated by the procedure. An awareness of this possibility is necessary for the successful interpretation of results from the dominant forces identification.

The first step in the procedure is to obtain a satisfactory standard simulation run of a system of interest. The modeler should have had enough experience with his model to have some idea of the effect of changing the model parameters, and be reasonably satisfied that the model accomplishes its task, and is logically correct.

From the standard run output the modeler selects certain features of interest. Changes in model parameters will change these output characteristics according to the relative dominance of the parameters, as will be shown. The criteria for selection is up to the modeler; however, consideration should be given to the ability to measure these features. Inability to accurately measure a characteristic may lead to confusing results. As a general rule, concern is with a pattern through time rather than with a particular value at a certain point in time. Usually the models for which this method is useful are sufficiently inaccurate to provide little precise value information. Measurements of this kind are therefore subject to the problems incurred by excessive noise.

Ideally one would like to ascertain the dominant parameter over all the possible parameters in the model including constants, table functions, and various possible logical structures or sets of equations. However, in many larger models it is possible to thoroughly analyze only one sector of the model at a time. Therefore one may select only those model parameters of interest while being aware that parameters not included might possibly be dominant ones. Many models contain sectors or feedback loops which offer a convenient method of parameter selection. For example one may choose to ascertain the order of dominance of all the parameters around a single loop or within a specific sector of a model. Eventually a comparison between sectors or loops may be accomplished.

The selected parameters are grouped into sets of three. Each of the parameters within a set will be increased and decreased by the same percentage of its original value on successive reruns until all combinations of increased and decreased parameters have been run together. With three parameters this yields a total of eight reruns. Notice that this is an orthogonal 2^3 factorial experimental design. Table 1 illustrates the format for the orthogonal set of eight reruns. Deviations from orthogonality are discouraged by Low (personal communication). However, if no interactions are present, Low believes that as many as seven parameters may be tested for dominance in a single set of eight reruns. This is accomplished by adjusting a set of seven parameters in each of the eight reruns as illustrated in Table 2. Table 2 is coded with plus ones and minus ones to indicate increases and

Table 1. Format for an Orthogonal 2^3 Factorial Experimental Design

A	B	C
−	−	−
+	−	−
−	+	−
+	+	−
−	−	+
+	−	+
−	+	+
+	+	+

Table 2. Seven Column Coded Orthogonal Design for Testing up to Seven Parameters, or Testing Three Parameters and their Interactions.

(1)	(2)	(3)	(4)	(5)	(6)	(7)
			AxB	AxC	BxC	AxBxC
A	B	C	D	E	F	G
-1	-1	-1	+1	+1	+1	-1
+1	-1	-1	-1	-1	+1	+1
-1	+1	-1	-1	+1	-1	+1
+1	+1	-1	+1	-1	-1	-1
-1	-1	+1	+1	-1	-1	+1
+1	-1	+1	-1	+1	-1	-1
-1	+1	+1	-1	-1	+1	-1
+1	+1	+1	+1	+1	+1	+1

decreases from each parameter's original value by the same chosen percentage. Entries in columns four through seven in Table 2 are found by considering the cross products of columns one and two (for column four), columns one and three (for column five), columns two and three (for column six), and column one, two and three (for column seven). This gives an orthogonal set for seven parameters in eight simulation runs. Notice that should columns four through seven not be used for parameters, then the coded values may represent the interaction effects of columns one, two and three. Thus any significant interaction effects actually existing in the model will confound the effects of any parameters adjusted in columns four through seven. For this reason it is advised that the more conservative technique of adjusting only three parameters in each set of eight reruns be used until a modeler has had enough experience in using this technique, and in evaluating his model, to be able to draw useful inferences from a more liberal approach. Therefore, in this study columns four through seven will remain open in order to assess the amount of influence that interaction of the three parameters has on the observed changes in the output characteristics selected. This is accomplished by a regression analysis (to be discussed).

To determine by what percentage each of the parameters within a set of three should be increased and decreased, some prior experience with the model, and some knowledge of the physically possible ranges of the parameters in question, are necessary. All of the parameters within a set of three must be adjusted by the same percentage. Between sets the percentage may vary since, in general, sets are not compared directly with one another. Parameters may be adjusted outside of their normal ranges of operation in an analysis of this kind, as long as the model logic has not assumed they would always be within this range. In such a case unusual results may occur. However, some models have several explainable modes of output behavior that may be triggered by certain parameter values or combinations of parameter values. These alternate modes may be perfectly reasonable given these parameter values in the real system. If the goal of the dominant forces analysis is to assess output characteristics in only one of several possible output modes, care must be taken to attempt to select ranges around the standard value of a parameter which will avoid switching to another mode. If the goal is to assess those parameters most responsible for the mode switching behavior, then this problem is insignificant (and in fact very rough output measurements may be used such as an on-off one-zero coding). Should mode switching be unavoidable for one or two runs in a set of eight, the aberrant data may be treated as missing data in the subsequent regression analysis.

Before simulating any of the orthogonal sets of reruns, some hypotheses should be developed about the parameters likely to control each chosen output characteristic. These hypotheses will allow one to notice more easily any unusual model behavior that may need further exploration or explanation should any become apparent during the analysis. In this way these hypotheses serve as a test of the modeler's understanding of his model, and keep his intuition about the model alive. An attempt should be made at the beginning to assess the overall dominant parameter for each output characteristic named, or at least to determine a subset of likely-to-be-dominant parameters from the initially chosen set of parameters.

After running a set of eight reruns each output characteristic of interest in each run is measured. As mentioned previously, to avoid excessive noise in the results, caution must be used to insure that the measurement technique employed actually measures the output characteristic intended. In the case of period or amplitude this problem is trivial, but for other output characteristics such as growth or decline rates of curves the problem may be more acute. For example, a growth rate may be considered a simple slope, or a percentage of a peak height per unit time, or an evaluation of a growth rate constant such as k in the expression $x=e^{kt}$. While it is true that often only rough measurements are necessary to adequately represent some output features, others, especially those which change very little between successive reruns in a set, may require more careful measurement to avoid confusing noise. Other causes of noise will be discussed later.

With a complete set of parameter values and output characteristic values recorded, a regression analysis to find out which of the three parameters has the greatest influence on each output characteristic is employed. However, prior to using a multiple linear regression technique, the modeler should take a few minutes to observe the data. Several advantages are gained by this. First, often it is apparent by looking at the raw data which of the parameters is most responsible for the observed output behavior, thus avoiding a regression analysis altogether (unless a formal report requires this). Second, unusual, unexpected, or even physically impossible (in the real system) results may be evident indicating a need for further model evaluation or simply some additional explanation. In this way this methodology can be a great aid in structural evaluation of the model. Third, the pre-regression overview may very well point out the general principle of Low (unpublished information) that "relationships between parameter values and output characteristics are nonlinear".

Because the regression analysis is linear and the relationships are nonlinear, it is reasonable to suspect that the regression model would be a poor representation of the situation, and that interaction effects may occur frequently. In fact, while it is true that the regression model is probably poor for predictive purposes, the important statistics from the regression analysis of interest in this methodology are relatively unaffected, as shown by experience. Although no hard evidence is available at this time to support this, empirical evidence demonstrates the methodology to be adequate in determining relative dominance. In no way is it implied that this methodology is exact. As will be seen, however, most of the dominant parameters are unquestionably dominant, though determining the second and third place dominants is often difficult.

Should significant interactions occur due to the nonlinearity phenomenon, then according to Low (personal communication) a multiple regression of the logarithms of the parameter and output characteristic data will usually cause these to disappear (the author has not yet been able to demonstrate this, however). Assuming a relatively low noise level, interaction effects will generally appear only occasionally and may be easily explained with experience in this methodology and with a good familiarity with the simulation model.

The multiple linear regressions may be performed by any computerized package that gives the appropriate information. The package used here is the SPSS (Statistical Package for the Social Sciences, Second Edition) REGRESSION procedure. Advantages of this procedure include widespread availability, a complete set of relevant output statistics, ease of use, and the ability to handle missing data (a possible use of this feature was mentioned with respect to mode switching problems). The independent variables of the regression analysis are the three parameters (e.g. A,B, and C) and the four possible interactions (e.g. AxB, AxC, BxC, AxBxC). The response variables are the output characteristics of interest. Nine sets of data are available for each variable in the regression analysis: the eight sets generated by the orthogonal 2^3 factorial design and one set from the standard run. All nine sets are input into the regression program.

The only statistics generated by the regression analysis of importance to the dominant forces identification are: 1) the sign of the partial correlation coefficient for each independent variable (indicating the direction of influence of an independent variable on its response), 2) the change in the square of this coefficient upon the addition of each independent variable into the regression equation, called the percent explained statistic for each independent variable [indicating the proportional increment in the explained variation of the response variable due to each independent variable (Nie, et al, 1975)], 3) the F-ratio and its corresponding level of significance for each independent variable (giving a reliability measure for each percent explained statistic), 4) the total percent explained for the entire regression model [giving the proportion of variation in the response variable explained by all of the independent variables in the regression equation together (Nie, et al, 1975)] and, 5) the overall F-ratio for the regression equations (a reliability measure for the total regression). For further explanation concerning the calculation and use of these statistics see Nie, et al (1975) pages 321-342.

The data for the independent variables may be coded as zero, plus one, or minus one depending on if the parameter value is that of the standard run, the standard run plus some percentage, or the standard run minus that same percentage. The interaction terms are the cross products of the parameter values as previously indicated. Thus the matrix for the independent variables may look exactly like Table 2. The response variables must be input as they are measured. The independent variables may be coded as indicated because coding does not affect the values of the five statistics of interest for the dominant forces identification. If any doubt exists, performing regression analyses with coded and noncoded data should verify this fact. Coding does, however, change the regression model coefficients, but these are of no consequence to the dominant forces identification.

The five statistics are used in the dominant forces identification as follows. The value of the overall model is assessed by observing the total percent explained statistic (called R-SQUARE in SPSS) together with the significance level of the overall F-ratio. If the overall F-ratio is not significant at a 95% confidence level, the information in the model is suspect, and inferences should be made with caution. This may be an indication that the output characteristic is not significantly affected by the independent variables (easily verified by examining the raw data), or that there is a great amount of noise in the data, (possible causes of noise have been discussed). If the total percent explained is below 90%, the above may also be true and caution must again be used in interpretation. However if this is the case but the overall F-ratio indicates high significance, it may be that several of the output characteristics are approximately equivalent in their effect. Experience with the procedure should yield greater ability in explanation and evaluation of borderline cases such as these.

Assuming the overall model to be adequate, an examination of the individual statistics will reveal the dominant independent variables affecting the output characteristic. The individual percent explained statistics (CHANGE R-SQUARE in SPSS) reveal the proportion of the change in the output characteristic for which each independent variable (parameter or interaction) is responsible. Often one of the three parameters will by itself explain over 80% of the total change. Invariably this parameter has a high significance level as indicated by the individual F-ratio. This is the dominant parameter of the set.

Parameters with less than 10% explained are usually considered of little importance. Most interactions will be of this sort.

Before accepting a percent explained statistic the reliability of the statistic must be assessed by determining the individual F-ratio significance. This should be significant at the 95% confidence level. Indeed most of the parameters will be at this level of reliability, but occasionally a parameter with 20% or 30% explained will have poor reliability. Often this situation arises when interactions are shown to account for much of the response variable behavior. This should be explained before additional studies are attempted using the same set of parameters or output characteristic values.

After ranking the dominants within a set of three parameters and their interactions, it is useful to know the direction of influence of the dominants on the output characteristic. These are given by the sign of the partial correlation coefficients (R in SPSS) for each independent variable. If the sign is positive, increases and decreases in the model parameter correspond to increases and decreases in the output characteristics. If negative, the influence is reversed.

Interpretation of the sign associated with an interaction is not as straightforward. Since the interaction codes are found as the cross product results of the parameters, then a positive sign means that the two parameters involved in the interaction move the output characteristic in the same direction. If each parameter involved in the two-way interaction has a positive influence or if each has a negative influence the sign for the interaction will be positive. If the sign is negative, the two parameters involved have opposing influences on the output characteristic. The three-way interaction is the most confusing. A positive sign means that either all parameters have a positive influence, or else only one of the three has a positive and the other two have negative influences. A negative sign means the reverse. Fortunately it is rarely necessary to deal with three-way interactions as their percent explained statistics are almost always small and insignificant. In fact, for many models, significantly important two-way interactions are rare (Low, personal communication).

Occasionally one may find an interaction term that does not have the sign it should, as indicated by the signs of the parameters by themselves. For example, the interaction sign may be negative while the signs of both parameters are either both positive or both negative. This usually is resolved by observing the reliability of the interaction term which should be very low. If all three of the independent variables involved are highly reliable and the interaction percent explained statistic is significant (greater than five or ten percent), excessive noise in the data measurement may exist that must be explained. Again, according to Low (personal communication), this could be an indication of faulty simulation model structure or poor measurement technique and data handling. However, it may simply be the result of a highly non-linear situation.

After determining the dominant parameters in each set of three parameters for each output characteristic, the dominants are then grouped into sets of three for further similar analysis. When the dominant forces are eventually narrowed down to one or two dominant parameters, the rank ordering begins. It is usually of practical interest to attempt to rank order only the top three or four dominant parameters. Below this point the differences in dominance among remaining parameters may have a large random component. In fact, sometimes only one parameter can be said to dominate, all others having substantially less effect.

One rule must be remembered when ranking dominant parameters. The top most dominant factor has been found through several previous runs. The subdominants in each run may be more dominant than the other final dominants if they have not previously been tested together in the same set of three parameters. For example, consider a simple case of nine parameters to test for dominance (A through I). Originally these are put into three sets of three each (ABC, DEF, and GHI). Assume it is found that A is dominant over B and C, D is dominant over E and F, and G over H and I. Assume that all of the statistics are clear and significant and the data is noise free. Let B, E and H be the second place dominants in each set. Assume it is chosen that A be run with D and G to determine which of the three initial dominants is actually having the greatest influence on an output characteristic. Let A be dominant over D, and D over G. One might be tempted to rank the dominant factors as A, then D, then G. However, it might be that B, the second place dominant in the initial run of A, B, and C, is dominant over D and/or G. To be sure, B must be run with D and G. If B is found to be dominant over either D or G we still don't know the proper order for G. Indeed, E could be similarly dominant over G! In cases such as these, which frequently occur, care must be taken to insure the proper ranking of the top several dominant parameters.

In summary, the dominant forces identification consists of eight major steps:

(1) Obtain a satisfactory standard simulation run.

(2) Select output characteristics of interest.

(3) Vary model parameters of interest plus and minus some percentage in an orthogonal 2^3 factorial set of simulation reruns (Table 2).

(4) Develop some preliminary hypotheses about the parameters likely to control the selected output characteristics.

(5) Measure the output characteristics in each of the nine simulation runs available per set of three parameters.

(6) Observe the raw data prior to performing any regression analyses.

(7) Analyze the data with a multiple linear regression program such as SPSS: REGRESSION.

(8) Locate the dominant parameters through additional sets of reruns.

Mastery of the above steps requires experience and intuition. Performing these steps by rote will mislead and confuse the modeler. The dominant forces identification is a new technique which provides some additional information previously unavailable from traditional sensitivity analyses of nonlinear models. It represents a beginning of a set of practical techniques with which to analyze nonlinear models to a greater extent. The following sections will present an application of this technique to an existing feedback dynamics model of a plankton community in the Great Salt Lake, Utah.

An Example of Determining the Dominant Forces of a Simulation Model

Standard Simulation Run

The simulation model[7] used has been described in previous chapters. It is a feedback analysis of the dynamics of two interactive populations of plankton in the southern basin of the Great Salt Lake, Utah. The model contains five major feedback loops and several minor feedback loops. The major loops are the algae (*Dunaliella viridis*) productivity loop, the algae self shading loop, the brine shrimp (*Artemia salina*) productivity loop, the algal consumption loop, and the brine shrimp starvation loop. The two productivity loops are positive loops which create unidirectional trends (e.g. growth) in their respective plankton populations; the other three are negative or control loops for each species which tend to hold the populations at some level. The standard simulation run for this model is illustrated in Figure 15. As can be seen, the model simulates a population of *Dunaliella viridis*

---

[7] The dominant forces identification herein described was completed prior to the discovery of a slight error in the estimation of the algae productivity vs water temperature curve. The alteration used in this analysis is given in Figure 25 (see previous chapter). The outcome of making such an alteration is discussed in the previous chapter.

growing logistically in the early spring, followed by the growth of Artemia salina and simultaneous decline of the algae which are being consumed. Lagging shortly behind the brine shrimp peak is the accumulation of overwintering eggs being produced as a result of food stress. As shown by the actual sample data from the Great Salt Lake (Figure 1) the model simulates the system quite well. While the model does contain limitations (see previous chapter), the modeler is satisfied in general with its logical structure and is aware of its limitations.

Selection of Output Characteristics

Many features of the output illustrated in Figure 15 are of interest and, for a total analysis of the model, all of these might possibly offer some interesting information. However, it is not the intention of this study to perform a complete analysis of the model due to time and expense constraints. Therefore, it was initially decided to study four of the more obvious output characteristics: the springtime growth rate, peak, and rate of decline for the algal population and the brine shrimp peak height. It is felt that these characteristics are of the greatest general interest to ecologists, and others, interested in this Great Salt Lake ecosystem. The goal of this research is to find those parameters in some section of the model most responsible for changes in these output characteristics. To discover those parameters most controlling the growth rates and peak height of the algae is to find the parameters vital to each of the plankton populations' viability. Likewise, parameters controlling the rate of algal decline may give insight into each population's vulnerability. It was felt that the output characteristics chosen could be measured reasonably simply and with a minimum of error. Also, these characteristics were considered to be expressions of broad model trends rather than precise values at specific points in time, following the general spirit of the analysis procedure.

Model Parameter Selection

As was the case for the output behavioral characteristics, it would be beyond the scope of this research to attempt an analysis of all possible parameters in the model with respect to each output characteristic chosen. Therefore, it was necessary to develop a set of criteria for parameter selection. The feedback loop structure of the model offered a convenient separation of sets of parameters. However, all four major loops were very probable factors in the growth rates, peak heights and rates of decline of the two populations. It was decided that only one loop would be analyzed using this methodology in the present study. Previous work with the model indicated the algae population to be the driving factor for the entire system. Stated differently, the rest of the model was very sensitive to changes in the algal population. Therefore, it was decided to analyze only the algal productivity loop since variables in this loop are unaffected by the presence of the brine shrimp, but rather are only functions of the forcing caused by the solar energy input. The dominant forces in the other loops may be ascertained at some future date, and then compared with one another.

The algal productivity loop has been described thoroughly in a previous chapter. It is primarily a positive feedback loop describing the division rate of Dunaliella viridis as a function of light, temperature, and already existing algae. However, a negative loop is included describing how the algae may grow so dense that they shade themselves, cutting off some of their available sunlight. The loop structure is illustrated in Figure 6. The list of equations that describe the algal productivity is given in Table 3. These equations are mathematical expressions of the relationship between variables and constants pictured by the flow diagram given in Figure 48. The parameters to be tested and their standard run values are listed in Table 4. A total of nine parameters are to be tested. These are arbitrarily placed into three sets of three parameters, as indicated in Table 4, each to be varied according to the orthogonal 2^3 factorial design described in the methodology presentation. As previously discussed, the interaction effects (represented by columns four through seven in Table 2) are to be assessed along with the parameters themselves.

The percentage decided upon to vary the parameters (within each set of three) was ± 10% for each of the three sets. This value was chosen because it was discovered in the model evaluation that certain parameters around the algal productivity loops caused the output to change modes if they were adjusted too drastically. Testing prior to the formal dominant forces analysis indicated that changes greater than 25% in the values for theoretical maximum algal productivity (AAAA), maximum light penetration (AADA), and the exponential rate factor for

Table 3. Algal Production Equations (Standard Run).

Equations	Interpretation
A1.K = A1.J + DT * (AA.JK)	Algal Concentration
AA.KL = A1.K * AAA.K	Division Rate
AAA.K = AAAA * AAB.K * AAE.K	Productivity
AAB.K = TABHL (AABT,AAC.K,0,155,5)	P vs I Curve
AAC.K = DAA.K * AAD.K	Available Light
AAD.K = AADA * EXP (-AADB * A1.K)	Water Transparency
AAE.K = TABHL (AAET,AAF.K,0,45,5)	P vs T Curve
AAF.K = AAG.K * AAH.K	Water Temperature
AAG.K = AAG.J + DT * (1/AAGD) * (DAA.J - AAG.J)	Heating & Cooling Delay
AAH.K = TABLE (AAHT,DAA.K,0,850,850)	Water Temp vs Sunlight Curve
DAA.K = COS (6.28318 * TIME.K/365) * (-DABA)	Sunlight in Ly·Dy^{-1}

Tables

AABT = 0,.16,.30,.38,.45,.52,.57,.61, .65,.69,.73,.76,.78,.83,.86,.89, .93,.96,.98,.99,1.00,.99,.97,.95, .88,.82,.68,.55,.40,.24,.24,.24	Light Table
AAET = .032,.14,.22,.34,.48,.75,1.0,.80, .06,0	Temp Table
AAHT = .001343,.04291	Sun to Water Temp Table

Constants

DAAA = 450	Avg. Annual Sunlight
DABA = 320	Input Fcn. Amplitude
AAAA = 2.1	Theoretical Max. Productivity
AADA = .20	Max. Light Penetration
AADB = 2.3E-8	Light Penetration Rate
AAGD = 15	Heating & Cooling Delay Time

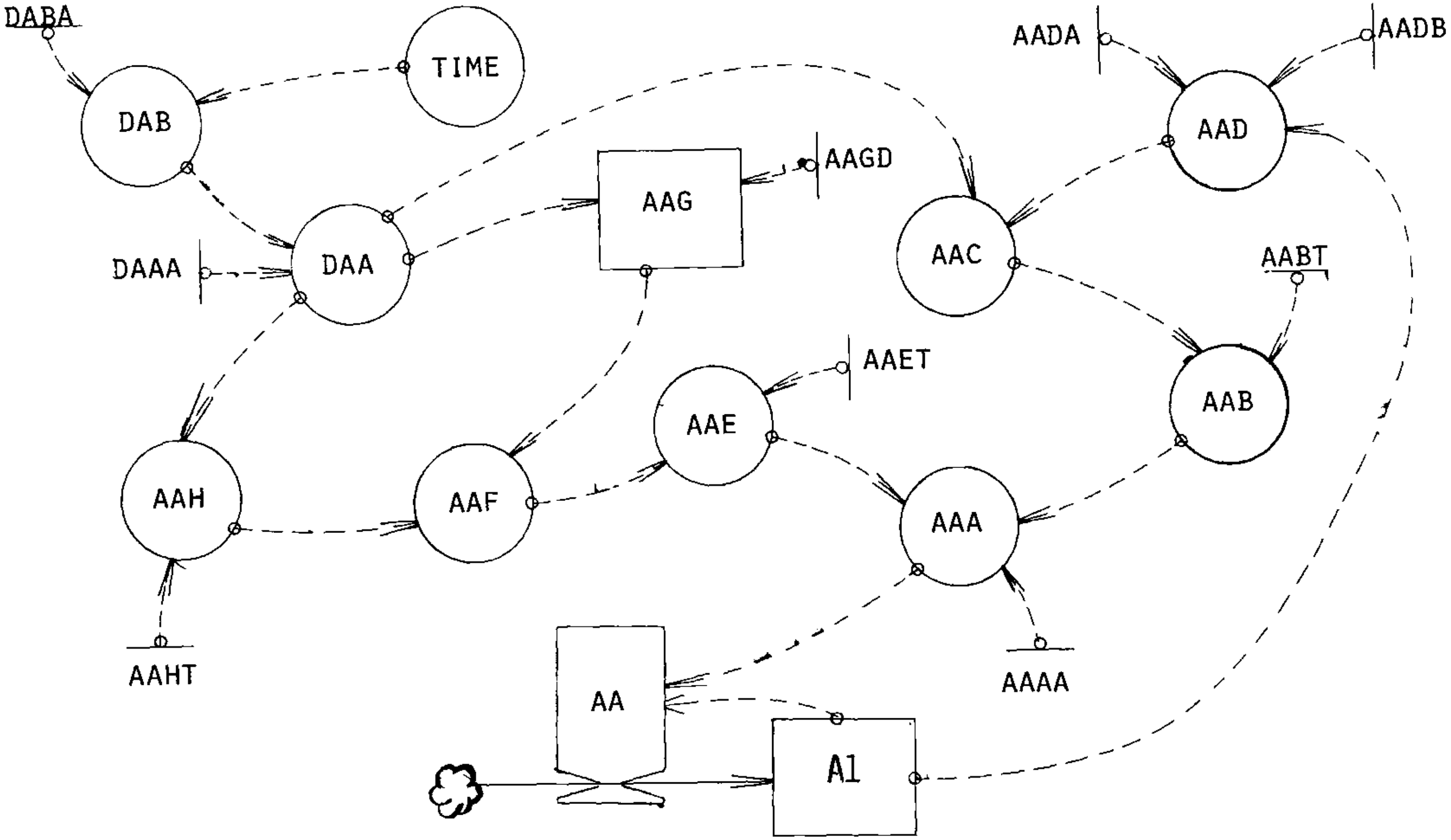

Figure 48. Flow Diagram for Algal Reproduction Sector of Model. Boxes Represent Accumulations, Valves Represent Flow Rates, Circles Represent Auxiliary Variables (See Forrester, 1961).

Table 4. Parameters Tested Using Dominant Forces Identification Procedure.

	Parameter	Value	Units	Interpretation
	AAAA	2.1	$\mathrm{Cells \cdot Cell^{-1} \cdot Dy^{-1}}$	Theoretical Max. Algal Productivity
Set #1	AADA	.20		Max. Light Penetration
	AADB	2.3E-8		Light Penetration Rate Exponent
	DAAA	450	$\mathrm{Ly \cdot Dy^{-1}}$	Average Annual Sunlight Factor
Set #2	DABA	320	$\mathrm{Ly \cdot Dy^{-1}}$	Input Fcn. Wave Amplitude
	AAGD	15	Dy	Heating & Cooling Delay Time
	$\mathrm{AABT_r}$	0,155,5	$\mathrm{Ly \cdot Dy^{-1}}$	Light Factor Table Range of Response
Set #3	$\mathrm{AAET_r}$	0,45,5	°C	Temp Factor Table Range of Response
	AAHT	.001343,.04291		Conversion Table Producing Water Temp

light penetration (AADB), in various combinations, caused the output to have a prominent midsummer algal peak in addition to the usual initial springtime algal peak. This second peak allowed the population of brine shrimp to grow to very large densities before a sufficient number began to starve. (The anomolous behavior has been explained in the previous chapter). Therefore, it was hoped that changes of 10% would avoid the mode switching behavior as much as possible since it is the primary goal of this analysis to assess characteristics within the normal output behavioral mode. It was not known prior to the dominant forces analysis how changes of various percentages affected combinations of the six parameters in the other two sets, but in light of the explanations given for the second peak phenomena, it was decided that the output behavior might be as sensitive to these parameters. Thus, 10% was chosen as their adjustment factor also.

Preliminary Hypotheses

From the modeler's concept of the structure and function of this model, as well as from preliminary experience with many of the model's parameters, some preliminary hypotheses were developed concerning the factors most likely to be dominant for each of the six output characteristics chosen. While the theoretical maximum productivity (AAAA) seems to be an obvious choice in controlling algal growth rate, peak height, and even rate of decline (through controlling daily regenerative power), the structure of the system was such that those areas of the model most closely associated with the driving function (i.e. solar energy cosine wave) seemed to dominate the remainder of the model with respect to algal growth rate, peak height and rate of decline. In fact, this is one reason why the algal productivity loop was initially chosen for this analysis. Following through with this idea, it was decided that those parameters associated with the light factor in the algal productivity would be most dominant. These parameters include AADA, AADB, DAAA, and DABA (see Table 4 for interpretation of symbols). It was felt that AADB would be more dominant than AADA since small changes in AADB affect the light factor variable AAD.K (see Table 3 and Figure 48) much more than the same change in AADA. The dominant among the input wave amplitude (DABA), the average yearly sunlight factor (DAAA) and the light penetration rate factor (AADB) was not hypothesized with respect to algal growth rate, peak height or rate of decline. One factor for consideration which may negate the above hypothesis is that the light factor depends on an optimum amount of light. Increases in the allowed amount of light in the system may be as detrimental as decreases to the factors of interest. This problem may not occur if the adjustment ranges around the parameters are sufficiently small, but a knowledge of this is essential before attempting an interpretation of the results. In summary, for the ranges of parameter values tested, it is believed that the parameters likely to exert the most control over algal growth rate, peak height and rate of decline are AADB, DAAA, DABA, and possibly AADA. All parameters are possible dominants for each of the output characteristics named.

Measuring the Output Characteristics

The simulation output was plotted on a graph, similar to the one shown in Figure 15, every week for ten years (3650 days). The interval of calculation was 1/4 day, all model time units being in days. Values for algae per liter, brine shrimp per liter, and overwintering eggs per liter were printed every day for the ten year simulation. The run length of ten years allowed the output to reach a stable repetitive annual pattern. The output characteristics were measured on the tenth year's pattern for each of the eight runs indicated by the experimental design, and for the standard run: a total of nine runs per set of three parameters.

The algae and brine shrimp springtime peak heights are measured, straightforwardly, as the density of each on the day of its greatest value. Little measurement error is expected. The growth and decline rates were expressed as the simple slope of a straight line between two points on the growth or decline curves. Since the peak heights of the algae population always occur around the same time between simulations containing parameter changes, it might be suspected that a high correlation exists between the growth slopes and the algal peak height. While this is in fact true for large variations in peak height (a large peak would necessarily need a large growth slope if it is to peak at roughly the same time as a smaller peak), experience with the model parameters indicated that the ± 10% changes would not cause such large changes in the algal peak heights. Hence, if separate parameters control growth rate and peak height, it is felt that slope is an adequate measure of significant differences. The slope of decline may also be a function of algal peak height and may cause some difficulty of this nature. It was measured as the slope from peak height to ten days after peak height, as this was representative of the nearly linear decline of algae after the hatching of brine shrimp.

Different parameters might be dominant during different phases of algal growth. To check for this, two growth slopes were measured rather than one. The earlier growth slope was measured as that of the line between fifty days and thirty days prior to the algal peak. A later growth slope was measured from 20 days before the peak to the peak value itself. While such rough measurements increase the error in the data, it was felt that these were accurate enough to predict broad trends of dominance without requiring the extra time involved with using more sophisticated techniques.

The primary goal of the present analysis is to assess the dominant forces of algal productivity on the algae population itself, since the success or failure of this species determines the fate of the entire simulated biological community. In addition, the algal rate of decline measure which is nearly error free (the decline is very close to linear) could be considered a rough indication of shrimp growth rate since the only cause of algal decline in the model is consumption by shrimp (the rate of decline however is also an indirect function of algal regeneration).

The recorded data from the first three sets of three parameters are given in Tables 5, 6, and 7. The parameter values are not coded as may be done for the regression analysis so that the reader may see the actual values used in each rerun. The parameters are adjusted ± 10% in each set. The simulation output plots are not included since

Table 5. Results from the First Set of 8 Runs.

Initial Comparisons Set #1

	Parameters			Response Variables					
Run	AAAA	AADA	AADB	A_{50-30B}	A_{20B}	A_p	A_{10A}	B_p	
Standard	2.1	.20	2.3E-8	4.20M	2.43M	229.9M	-21.29M	26.25	
1	1.89	.18	2.07E-8	4.88M	3.35M	234.4M	-23.35M	195.7	*
2	2.31	.18	2.07E-8	5.12M	2.80M	253.4M	-25.10M	1818.0	*
3	1.89	.22	2.07E-8	5.16M	2.86M	252.7M	-19.82M	8.94	
4	2.31	.22	2.07E-8	3.73M	2.46M	270.5M	-24.34M	19.29	
5	1.89	.18	2.53E-8	4.06M	2.67M	192.6M	-19.18M	178.9	*
6	2.31	.18	2.53E-8	4.03M	2.25M	207.9M	-20.59M	1485.0	*
7	1.89	.22	2.53E-8	4.09M	2.30M	207.3M	-16.19M	8.62	
8	2.31	.22	2.53E-8	2.94M	1.99M	221.6M	-19.89M	18.60	

* Second peak phenomenon occurred.

A_{50-30B} = Algal growth slope measured between 50 days and 30 days prior to the algal peak.

A_{20-B} = Algal growth slope measured between 20 days before the algal peak and the peak itself.

A_p = Algal peak height.

A_{10A} = Algal decline slope measured over the first 10 days after the algal peak.

B_p = Brine shrimp peak height.

M = Million.

Table 6. Results from the Second Set of 8 Runs.

Initial Comparisons Set #2

	Parameters			Response Variables				
Run	DAAA	DABA	AAGD	A_{50-30B}	A_{20B}	A_p	A_{10A}	B_p
Standard	450	320	15	4.20M	2.43M	229.9M	-21.29M	26.25
1	405	288	13.5	3.49M	2.16M	234.3M	-22.27M	21.78
2	495	288	13.5	2.89M	1.93M	237.7M	-22.74M	22.37
3	405	352	13.5	4.01M	3.43M	217.2M	-19.57M	35.16
4	495	352	13.5	4.64M	2.75M	223.9M	-21.39M	26.59
5	405	288	16.5	3.44M	2.12M	236.5M	-22.39M	20.87
6	495	288	16.5	2.83M	1.90M	240.0M	-23.04M	20.75
7	405	352	16.5	3.98M	3.48M	218.2M	-18.62M	30.83
8	495	352	16.5	4.71M	2.69M	226.8M	-22.01M	22.24

Table 7. Results from Third Set of 8 Runs.

Initial Comparisons Set #3

	Parameters			Response Variables					
Run	$AABT_r$	$AAET_r$	AAHT	A_{50-30B}	A_{20B}	A_p	A_{10A}	B_p	
Standard	155,5	45,5	.001343, .04291	4.20M	2.43M	229.9M	-21.29M	26.25M	
1	139.5,4.5	40.5,4.5	.0012087, .038619	3.05M	2.13M	249.1M	-20.31M	16.54	
2	170.5,5.5	40.5,4.5	.0012087, .038619	4.11M	2.37M	234.5M	-23.19M	399	*
3	139.5,4.5	49.5,5.5	.0012087, .038619	3.63M	2.20M	238.3M	-15.38M	6.94	
4	170.5,5.5	49.5,5.5	.0012087, .038619	4.29M	2.39M	224.3M	-21.56M	15.83	
5	139.5,4.5	40.5,4.5	.0014773, .047201	3.95M	2.44M	238.2M	-22.28M	44.98	
6	170.5,5.5	40.5,4.5	.0014773, .047201	4.83M	2.80M	222.5M	-22.02M	1667	*
7	139.5,4.5	49.5,5.5	.0014773, .047201	4.55M	2.58M	226.5M	-19.79M	10.62	
8	170.5,5.5	49.5,5.5	.0014773, .047201	4.28M	3.06M	209.7M	-20.90M	502.6	*

* Second peak phenomenon occurred.

there are eight of these for each set of three parameters.

Pre-regression Overview of Data

On observing the data, the first item of interest is that the ± 10% parameter changes failed to prevent the model from achieving the second peak output mode in some of the reruns. This should be of little consequence to the growth slopes and peak height of the algae since this mode does not disproportionately affect these output characteristics. However, the algal rate of decline and brine shrimp peak height is greatly affected. These points are easily verified upon examination of the data. The fact that the second peak is m-shaped in one of the runs reported in Table 7 needs some further explanation. The peak's existence is due to the same phenomena as for all the second peaks (explained in detail in an earlier chapter) but the depression is caused by water temperatures beyond optimal values causing a temporary reduction in algal regeneration (unlike in the standard run). Therefore brine shrimp are able to graze the algae down until the temperature again approaches its optimal value.

By observing Table 5 the algae peak height can be seen to be affected by all three parameters AAAA, AADA, and AADB. Theoretical maximum productivity (AAAA) has about the same strength of effect and has the same positive direction of influence as the maximum light penetration (AADA). The light penetration rate factor (AADB) appears to have a larger effect however; and an opposite direction of influence. It can be seen that the effect of these three parameters is roughly a linear relationship with algal peak height and also that little interaction is occurring.

In contrast, the same parameters seem to affect algal rate of decline in a nonlinear way. Possibly some interaction will be evident in the regression analysis. These data illustrate the influence of the brine shrimp population (from overwintering eggs) on the algal rate of decline.

It can be seen that low values of AADA are responsible for the presence of the second peak. This is because if less light is made available to the algae, their growth will not be light limited by the highly intense summer sun, as they are in the standard run (see previous chapter for further details). Whether the second peak is large or small is determined by the value of the theoretical maximum productivity of the algae (AAAA).

Finally, in Table 5 it canbe seen that AADB probably dominates the other two parameters in controlling the algal growth rate, in addition to its peak height, as mentioned. The direction of influence here is also negative as it was for peak height. However, unlike peak height, the variation in the response of the middle algal growth rate (the rate measured from 50 to 30 days before peak height) is quite obviously nonlinear. Observe the reductions of the values for runs four and eight. While run two shows an increase over run one (with an increase in AAAA) and run three also shows an increase over run one (with an increase in AADA), when both AAAA and AADA are increased in run four a sharp decrease is evident in the growth rate! It is hypothesized that the interaction of <u>increases</u> <u>only</u> in these two parameters has pushed the model past some optimum point for algal growth.

In Table 6, DABA, the solar wave amplitude, seems to dominate algal peak height control with a negative influence. In other words, as DABA is increased, algal peak height is decreased. This is reasonable biologically. The more extreme environmental conditions produced by increasing the cosine wave amplitude would very likely reduce the overall productivity should this be the case in the real system. The other two parameters have little effect comparatively.

In general there seems to be a stronger nonlinear relationship between parameter values and output characteristics in Table 6. For example, observe the brine shrimp peak height and the algal rate of decline data. It may be possible to pick out the dominant for the other output characteristics prior to the regression analysis if one is careful.

As an aside, another interesting feature of Table 6 is the algal rate of decline data for run number three. While Table 5 illustrates the influence of the brine shrimp population on this decline, Table 6 illustrates the effect of the algal peak height on the decline. Since the decline is measured as a slope (i.e. as the reduction in value per day), then even though there are more shrimp in run three, there are few enough algae to slow the decline slope. It might be expected that because of the additional grazing pressure provided by more shrimp this slope would be steeper as was the case in Table 5, run numbers two and four.

The data of Table 7 once again illustrate the effect of the second peak phenomenon on the algal decline rate (to some extent).

However, the other algal characteristics are unaffected and the strong effect of the light factor table response range ($AABT_r$) on algal peak height is easily observed. It has a negative influence. As the range of available light, over which light factor adjustments take place, is decreased algae peak height is increased. The other two parameters also have noticeable influences on the algal peak height.

With careful examination, the dominant parameters controlling the behavior of the remaining algal output characteristics may possibly be assessed without the aid of the computer. However, the effects of nonlinearity are evident in the data. Any significant interaction effects present would be difficult to ascertain for most analysts without the aid of a regression analysis.

Regression Analysis

Being satisfied from the previous overview that no unexplainable or physically suspect data (indicating logical errors in the simulation model) have occurred, the data is coded as described in the methodology (*response* variables are not coded) and entered into the multiple linear regression program contained in the *Statistical Package for the Social Sciences: Second Edition* (SPSS: REGRESSION). The procedure for the regression analysis and descriptions of the output statistics of interest is given in the methodology section. The SPSS: REGRESSION statements used are listed in Table 8. For information concerning the use of SPSS: REGRESSION see Nie, *et al* (1975).

The regression analysis used for this study is a *stepwise* multiple linear regression. In the first step a complete regression

Table 8. SPSS: REGRESSION Equations Used for the Dominant Forces Analysis

SPSS: Regression Program Statements:

```
RUN NAME                        DFI
VARIABLE LIST                   A,B,C,AxB,AxC,BxC,AxBxC,
                                A1A,A1B,A1C,A1D,S3A
INPUT FORMAT                    FREEFIELD
INPUT MEDIUM                    CARDS
NO. OF CASES                    9
REGRESSION                      VARIABLES = A TO S3A/
                                REGRESSION = A1A WITH A TO AxBxC (1)/
                                REGRESSION = A1B WITH A TO AxBxC (1)/
                                REGRESSION = A1C WITH A TO AxBxC (1)/
                                REGRESSION = A1D WITH A TO AxBxC (1)/
                                REGRESSION = S3A WITH A TO AxBxC (1)/
STATISTICS                      ALL
READ INPUT DATA
```

Note: A1A = A_{50-30B}, A1B = A_{20B}, A1C = A_p, A1D = A_{10A}, S3A = B_p as before.

line is made for the independent variable most responsible for the variation in the response variable. The next step adds the next most responsible variable, making a new regression line with two independent variables. This process continues until all independent variables which have a significance level (as determined by their individual F-ratio) of greater than five percent have been entered. This may be up to seven for the present study (three parameters and four interactions). Hence, there may be as many as seven separate regression models, each with their own overall F-ratios, for each output characteristic tested. For purposes of reporting the overall F-ratio (and individual F-ratios) which may change from model to model, the model with the highest overall F-ratio is chosen. This does not effect the individual percent explained statistics, only their significance. In the event of a tie, the model including the most independent variables is chosen. Therefore the individual statistics for all of the possible independent variables will seldom be reported. The ones omitted are sufficiently insignificant both in percent explained and reliability to be detrimental to the overall reliability of the regression model, so are of no consequence to the outcome of the dominant forces identification.

While the overall total percent explained for the model may approach very near to 100% when all seven of the independent variables are included, it will usually be lower for the model of greatest reliability (since not all of the variables have contributed to the regression model). Even so, most of the models reported will have better than 90% of the variation in the response variable explained.

The algal output characteristics behaved in a manner typical of a successful dominant forces search. The regression analysis results for the four algal response variables, and the brine shrimp peak height, are presented for the data of Tables 5, 6 and 7 in Tables 9, 10 and 11 respectively. As previously explained, the results of the most reliable model for each output characteristic is reported.

A brief glance at the regression results of Tables 9 and 10 shows that AADB, the light penetration rate factor, and DABA, the solar wave input amplitude, are clearly the dominant forces controlling all of the algal output behaviors of interest for their respective data sets. The second place dominants are also clear: AAAA, the theoretical maximum algal productivity for Table 9, and DAAA, the average annual sunlight intensity factor, for Table 10. Notice that the dominant parameters AADB and DABA are parameters which deal with the availability of light to the algae following the preliminary hypothesis developed for all of the algal output characteristics.

The results in Table 11 do not stand out as dramatically. The different output characteristics are dominated alternately by the three parameters. The clearest dominant occurs for the late algal growth rate and is AAHT, the table which converts solar energy to water temperature. The other dominants listed are not greatly dominant over their second place contenders. Indeed, the top two for algal decline rate, $AAET_r$ (the range of response for water temperature factor table values) and $AABT_r$ (the range of response for light factor table values), are

Table 9. Regression Analysis Results Determining the Dominant Forces for Each Output Characteristic: Initial Comparisons Set #1

Output Characteristic	Independent Variable	Sign	% Explained	F-ratio	Reliability % Significance Level	Overall Statistics	
Algal peak height	AADB	-	79.3	334771.8	>99.9	Total % explained :	100%
	AAAA	+	10.7	44955.0	>99.9	Overall F-ratio :	70341.4
	AADA	+	9.8	41277.1	>99.9	Level of significance:	>99.9%
	AAAAxAADB	-	0.1	520.5	99.8	Degrees of freedom :	6/2
	AADAxAADB	-	0.1	472.3	99.8		
	∇AAAAxAADA	-	0.0	51.9	98.1		
Middle algal growth rate	AADB	-	43.5	2003.9	>99.9	Total % explained :	99.9%
	∇AAAAxAADA	-	23.8	1097.5	>99.9	Overall F-ratio :	920.0
	AAAA	-	17.2	791.9	>99.9	Level of significance:	>99.9%
	AADA	-	14.4	663.9	>99.9	Degrees of freedom :	5/3
	∇AAAAxAADAxAADB	+	0.9	42.7	99.3		
Late algal growth rate	AADB	-	49.2	77.8	>99.9	Total % explained :	96.8%
	AAAA	-	27.2	43.0	99.9	Overall F-ratio :	51.1
	AADA	-	20.5	32.4	99.8	Level of significance:	>99.9%
						Degrees of freedom :	3/5
Algal decline rate	AADB	-	56.0	864.5	>99.9	Total % explained :	99.8%
	AAAA	+	25.8	398.6	>99.9	Overall F-ratio :	308.4
	AADA	-	12.7	196.0	99.9	Level of Significance:	>99.9%
	°AAAAxAADA	-	5.1	78.8	99.7	Degrees of freedom :	5/3
	†∇AAAAxAADB	+	0.3	4.1	86.5		
Shrimp peak height	AADA	-	40.9	36.0	99.8	Total % explained :	94.3%
	AAAA	+	27.1	23.8	99.5	Overall F-ratio :	27.7
	°AAAAxAADA	-	26.3	23.2	99.5	Level of Significance:	99.8%
						Degrees of freedom :	3/5

† Unreliable statistics (F-ratio below 95% significance level).

∇ Incongruent sign for interaction: needs further explanation.

° Important interactions.

Table 10. Regression Analysis Results Determining the Dominant Forces for Each Output Characteristic: Initial Comparisons Set #2

				Reliability		
Output Characteristic	Independent Variable	Sign	% Explained	F-ratio	% Significance Level	Overall Statistics
Algal peak height	DABA	-	85.9	2041.6	>99.9	Total % explained : 99.9%
	DAAA	+	10.8	257.6	99.9	Overall F-ratio : 474.5
	∇DAAAxDABA	+	1.5	35.8	99.1	Level of significance: >99.9%
	AAGD	+	1.5	35.5	99.1	Degrees of freedom : 5/3
	†DAAAxAAGD	+	0.1	2.1	76.0	
Middle algal growth rate	DABA	+	73.0	86.9	>99.9	Total % explained : 95.0%
	°DAAAxDABA	+	21.9	26.1	99.8	Overall F-ratio : 56.5
						Level of significance: >99.9%
						Degrees of freedom : 2/6
Late algal growth rate	DABA	+	78.7	530.3	>99.9	Total % explained : 99.4%
	DAAA	-	16.1	108.7	>99.9	Overall F-ratio : 167.5
	DAAAxDABA	-	4.6	30.7	99.5	Level of significance: >99.9%
	†DAAAxDABAxAAGD	-	0.1	0.4	45.0	Degrees of freedom : 4/4
Algal decline rate	DABA	-	55.5	110.8	>99.9	Total % explained : 98.0%
	DAAA	+	28.4	56.7	99.8	Overall F-ratio : 48.9
	°DAAAxDABA	-	11.9	23.7	99.2	Level of significance: 99.9%
	†DAAAxAAGD	-	2.2	4.3	89.4	Degrees of freedom : 4/4
Shrimp peak height	DABA	+	52.5	233.4	99.9	Total % explained : 99.3%
	°DAAAxDABA	-	19.3	86.0	99.7	Overall F-ratio : 68.3
	DAAA	-	17.3	77.0	99.7	Level of significance: 99.8%
	AAGD	-	7.8	34.8	99.0	Degrees of freedom : 5/3
	DABAxAAGD	-	2.4	10.5	95.2	

† Unreliable statistics (F-ratio below 95% significance level).

∇ Incongruent sign for interaction: needs further explanation.

° Important interactions.

Table 11. Regression Analysis Results Determining the Dominant Forces for Each Output Characteristic: Initial Comparisons Set #3

					Reliability	
Output Characteristic	Independent Variable	Sign	% Explained	F-ratio	% Significance Level	Overall Statistics
Algal peak height	$AABT_r$	-	45.1	2071.1	>99.9	Total % explained : 99.9%
	$AAHT$	-	29.4	1348.2	>99.9	Overall F-ratio : 917.4
	$AAET_r$	-	25.1	1152.0	>99.9	Level of significance: >99.9%
	†V$AABT_r$x$AAHT$	-	0.2	8.8	94.1	Degrees of freedom : 5/3
	†V$AAET_r$x$AAHT$	-	0.1	6.7	91.9	
Middle algal growth rate	$AAHT$	+	37.0	10.5	97.7	Total % explained : 82.4%
	$AABT_r$	+	31.4	8.9	96.9	Overall F-ratio : 7.8
	†$AABT_r$x$AAET_r$	-	13.9	3.9	89.6	Level of significance: 97.5%
						Degrees of freedom : 3/5
Late algal growth rate	$AAHT$	+	59.5	33.8	99.9	Total % explained : 89.4%
	$AABT_r$	+	29.9	17.0	99.4	Overall F-ratio : 25.4
						Level of significance: 99.9%
						Degrees of freedom : 2/6
Algal decline rate	$AAET_r$	-	31.7	9.0	97.0	Total % explained : 82.4%
	$AABT_r$	+	30.1	8.5	96.7	Overall F-ratio : 7.8
	†$AABT_r$x$AAHT$	+	20.6	5.9	94.0	Level of significance: 97.5%
						Degrees of freedom : 3/5
Shrimp peak height	†$AABT_r$	+	32.8	10.0	94.9	Total % explained : 90.1%
	†$AAHT$	+	16.7	5.1	89.0	Overall F-ratio : 5.5
	†$AABT_r$x$AAHT$	+	15.5	4.7	88.2	Level of significance: 90.4%
	†$AAET_r$	-	13.2	4.0	86.1	Degrees of freedom : 5/3
	†$AABT_r$x$AAET_r$	-	11.8	3.6	84.5	

† Unreliable statistics (F-ratio below 95% significance level).

V Incongruent sign for interaction: needs further explanation.

o Important interactions.

essentially tied; about 30% explained each. All of the shrimp peak results in Table 11 are unreliable. It is believed that these results, in this case, when compared to those run in Tables 9 and 10, indicate that the parameters tested in this set will not be as dominant in the final analysis as those of Tables 9 and 10. (It is not standard practice to directly compare statistics between sets of parameters; however, intuitive hypotheses are encouraged throughout the analysis. In this manner, the ultimate goals of understanding the model and, through it, the real system, are more readily achieved).

Of the parameters tested, shrimp peak height seems to be most influenced by AADA (the maximum light penetration into the water), and DABA (solar wave amplitude). These will be adjusted together within an orthogonal set of reruns along with $AABT_r$ (light factor response range). $AABT_r$ is being added since, although unreliable, it was indicated as the dominant factor affecting shrimp peak height for the results in Table 11.

For the algae peak height and rate of decline AADB will be adjusted with DABA and $AABT_r$ in an orthogonal set of eight reruns. Both of the algal growth slopes will be represented by AADB together with DABA and AAHT. With these three new sets of three parameters each, the most dominant parameter for each output characteristic should be able to be assessed.

Before going on to this step, however, several items in the regression results of Tables 9, 10 and 11 need further explanation. It may be noticed that many of the interaction terms have the "wrong" sign of influence. In most of the cases either the reliability of the statistic is low (less than 95% confidence) or the value for the percent explained is very low (less than 2%). The incongruency of sign can be explained as the effects of random noise and need not be worried about further as long as one is confident of his accuracy in recording the data. There is one very noticeable exception to the above, however, that of the AAAA x AADA interaction for the middle algal growth rate in Table 9. We see that the signs of both AAAA and AADA are negative which should mean a positive sign of interaction. However, this sign of the partial correlation coefficient for this interaction is also negative. The percent explained of 23.8% is substantial and the reliability is excellent, so some further explanation is in order.

In the pre-regression overview the data of Table 5, with respect to its nonlinear relationship to the middle algal growth rate, was discussed. It was hypothesized that interaction of the increases in AAAA and AADA values pushed the model past some optimum point. This explains the odd decrease in value for middle algal growth rate in runs four and eight of Table 5. Column four of Table 2 shows the pattern of increases and decreases which the output must follow to be highly correlated with the AAAA x AADA interaction. A high positive correlation would produce an output which increased on runs one, four, five, and eight and decreased on runs two, three, six, and seven. In general, we see that the exact opposite is true for the data of Table 5 (for the middle algal growth rate) indicating a high negative correlation with the AAAA x AADA interaction. So, the incongruency seen in Table 9 is merely an artifact of the nonlinear data, rather than some problem in the model structure producing physically impossible results [often suggested as the reason for such incongruencies by Low (personal communications)].

If this is the case an explanation of the physical reality of the nonlinearity is needed. Increases in AAAA (the theoretical maximum algal productivity) produce increases in the rate in which the algae population can grow under ideal conditions. Increasing AADA (the maximum light penetration factor) increases the amount of photosynthetically active radiation (PHAR) which reaches the algae <u>when the water is clear</u> (i.e. before the presence of algae has caused decreased transparency). The effect of both of these factors acting together leads to a great increase in early spring growth of algae. This results in high peak heights as can be seen in the data of Table 5. This result is also evident in the values for algal density at 30 days and 50 days prior to the algal peak given in Table 12. These are the values used to find the middle growth slope. By 50 days prior to the algal peaks (which all occurred on the same day in the eight reruns of Table 5) the density of algae is much greater in runs four and eight (in Table 5) than in the other runs. Therefore, due to the self shading property of the algae (see Figure 6), the growth slows down earlier for these runs than for the others. This gives the drop in growth rate observed between 50 days and 30 days prior to the peak. Thus, the algal growth rate has passed its optimum for this 20 day time period containing increased earlier productivity. The optimal value for growth in this

Table 12. Data Contributing to the Explanation of the Regression Results of Table 9 (see text).

Run	Value of Algae 30 Days Before Peak	Value of Algae 50 Days Before Peak
1	116.57M	19.01M
2	160.75M	58.30M
3	157.29M	54.05M
4	191.72M	117.18M
5	99.67M	18.54M
6	133.84M	53.34M
7	131.19M	49.32M
8	158.11M	99.38M

time period is subject to the constraint of self shading. The incongruency in the sign of interaction for the middle algal growth rate of Table 9 has now been explained.

In digression, it can be seen that most of the reliable interaction effects are of minor importance (account for less than 5% of the explained variation) in Tables 9, 10 and 11. Notable exceptions are the AAAA x AADA interaction for algal decline rate and shrimp peak height (Table 9) and the DAAA x DABA interaction for middle algal growth rate, algal decline rate and shrimp peak height in Table 10.

In light of the preceding discussion it is not hard to visualize how AAAA and AADA could interact to produce significant effects on the output characteristics since both increase algal productivity. Also easily explained is the interaction of DAAA and DABA. Both of these parameters act to adjust the input wave function representing solar energy. DAAA is the value determining overall average annual solar intensity; DABA is the amplitude of the solar intensity around its average. Because of this close physical proximity in the model, interactions are not surprising.

Analyzing the Sets of Dominants

Three new orthogonal sets of reruns of three of the most dominant parameters found in the previous analysis are now simulated. The members of these sets have been mentioned. The resulting data is presented in Tables 13, 14 and 15. It should be mentioned that the ranges of parameter adjustment for each of these three sets has been reduced from ± 10% to ± 5% to try to avoid the second peak phenomenon and possibly

Table 13. Results from First Set of Dominant Comparisons

Dominant Comparisons Set #1

Parameters				Response Variables					
Run	AADA	DABA	AABT$_r$	A_{50-30B}	A_{20B}	A_p	A_{10A}	B_p	
Standard	.20	320	155,5	4.20M	2.43M	229.9M	-21.29M	26.25	
1	.19	304	147.25,4.75	3.57M	2.21M	233.2M	-21.25M	25.56	
2	.21	304	147.25,4.75	3.26M	2.13M	239.9M	-19.33M	11.63	
3	.19	336	147.25,4.75	4.71M	2.70M	226.3M	-21.23M	26.62	
4	.21	336	147.25,4.75	4.57M	2.58M	233.4M	-20.13M	11.60	
5	.19	304	162.75,5.25	4.40M	2.41M	224.6M	-22.32M	913	*
6	.21	304	162.75,5.25	3.54M	2.21M	233.2M	-21.25M	25.56	
7	.19	336	162.75,5.25	4.62M	3.04M	217.0M	-21.56M	418	*
8	.21	336	162.75,5.25	4.71M	2.70M	226.3M	-21.23M	26.62	

* Second peak phenomenon occurred.

Table 14. Results from Second Set of Dominant Comparisons.

Dominant Comparisons Set #2

Parameters				Response Variables				
Run	AADB	DABA	$AABT_r$	A_{50-30B}	A_{20B}	A_p	A_{10A}	B_p
Standard	2.3E-8	320	155,5	4.20M	2.43M	229.9M	-21.29M	26.25
1	2.185E-8	304	147.25,4.75	3.61M	2.29M	249.0M	-21.18M	17.35
2	2.415E-8	304	147.25,4.75	3.20M	2.06M	225.5M	-19.14M	16.93
3	2.185E-8	336	147.25,4.75	4.94M	2.79M	241.9M	-21.83M	17.15
4	2.415E-8	336	147.25,4.75	4.40M	2.50M	219.1M	-19.73M	16.78
5	2.185E-8	304	162.75,5.25	4.01M	2.39M	241.6M	-23.93M	34.01
6	2.415E-8	304	162.75,5.25	3.55M	2.15M	218.8M	-21.67M	32.85
7	2.185E-8	336	162.75,5.25	5.02M	2.97M	233.9M	-23.19M	39.39
8	2.415E-8	336	162.75,5.25	4.52M	2.66M	211.9M	-21.01M	37.95

Table 15. Results from Third Set of Dominant Comparisons.

Dominant Comparisons Set #3

Parameters				Response Variables				
Run	AADB	DABA	AAHT	A_{50-30B}	A_{20B}	A_p	A_{10A}	B_p
Standard	2.3E-8	320	.001343, .04291	4.20M	2.43M	229.9M	-21.29M	26.25
1	2.185E-8	304	.0012759, .0407645	3.46M	2.23M	249.7M	-21.67M	22.21
2	2.415E-8	304	.0012759, .0407645	3.07M	2.01M	226.1M	-19.58M	21.57
3	2.185E-8	336	.0012759, .0407645	4.86M	2.74M	240.9M	-21.29M	22.42
4	2.415E-8	336	.0012759, .0407645	4.33M	2.46M	218.2M	-19.24M	21.85
5	2.185E-8	304	.0014114, .0450555	4.06M	2.42M	242.9M	-23.70M	26.55
6	2.415E-8	304	.0014114, .0450555	3.59M	2.17M	220.0M	-21.47M	25.47
7	2.185E-8	336	.0014114, .0450555	5.02M	3.00M	234.9M	-23.03M	29.22
8	2.415E-8	336	.0014114, .0450555	4.51M	2.69M	212.8M	-20.87M	28.04

unusual interaction effects. As can be seen by the occasionally large brine shrimp peak heights in Table 13, the first of these desires was not met.

The data in Table 13 shows the strong nonlinear nature of some of the algal growth rate data. The brine shrimp peak height, for which this set was run, seems to be most affected by the combination of AADA (maximum clear water light penetration) and $AABT_r$ (the response range for the light factor). Significant interaction terms for this run are anticipated.

The data in Table 14 tests the top dominants for algal peak height and rate of decline. It appears that AADB (the light penetration rate factor) is the dominant parameter affecting algal peak height while AADB and $AABT_r$ seem to affect the rate of decline about equally.

The results in Table 15 show that, as far as the algal growth rate is concerned, DABA (the solar wave amplitude) appears dominant. However the data is not easy to discern due to the nonlinearity involved.

It will be noticed that all of the output characteristics of interest are analyzed with each set of eight reruns, even though the primary reason for each set was for specific characteristics. This merely serves as a double check for the dominant forces identification by providing additional data points. This is useful because of the overall intuitive and nonlinear nature of such simulation models, and the interpretation of the dominant forces results.

The results of the regression analysis for each of the three sets given by Tables 13, 14 and 15 are presented in Tables 16, 17 and 18

Table 16. Regression Analysis Results Determining the Dominant Forces for Each Output Characteristic: Dominant Comparisons Set #1

Output Characteristic	Independent Variable	Sign	% Explained	F-ratio	Reliability % Significance Level	Overall Statistics
Algal peak height	AADA	+	35.7	682.3	>99.9	Total % explained : 99.8%
	AABT$_r$	-	35.7	682.3	>99.9	Overall F-ratio : 381.6
	DABA	-	27.7	530.1	>99.9	Level of significance: >99.9%
	$^{\nabla}$AADAxAABT$_r$	+	0.7	12.4	96.1	Degrees of freedom : 5/3
	$^{\dagger\nabla}$AADAxDABA	+	0.0	0.8	56.1	
Middle algal growth rate	DABA	+	71.3	273.6	99.6	Total % explained : 99.5%
	AADA	-	7.2	27.6	96.6	Overall F-ratio : 63.6
	AABT$_r$	+	6.5	25.0	96.2	Level of significance: 98.4%
	$^{\nabla}$AADAxDABA	+	6.1	23.3	96.0	Degrees of freedom : 6/2
	$^{\nabla}$DABAxAABT$_r$	-	5.4	20.9	95.5	
	$^{\dagger\nabla}$AADAxDABAxAABT$_r$	+	2.9	11.3	92.2	
Late algal growth rate	DABA	+	76.3	158.3	>99.9	Total % explained : 98.1%
	AABT$_r$	+	9.8	20.4	98.9	Overall F-ratio : 50.9
	AADA	-	9.8	20.4	98.9	Level of significance: 99.9%
	†AADAxAABT$_r$	-	2.1	4.3	89.4	Degrees of freedom : 4/4
Algal decline rate	AADA	-	41.5	127.5	99.9	Total % explained : 99.0%
	AABT$_r$	+	41.5	127.5	99.9	Overall F-ratio : 60.8
	AADAxAABT$_r$	-	5.6	17.1	97.4	Level of significance: 99.7%
	DABAxAABT$_r$	+	5.2	15.9	97.2	Degrees of freedom : 5/3
	AADAxDABA	-	5.2	15.9	97.2	
Shrimp peak height	AABT$_r$	+	27.9	7.4	95.8	Total % explained : 31.2%
	AADA	-	27.9	7.4	95.8	Overall F-ratio : 7.2
	^{o}AADAxAABT$_r$	-	25.5	6.8	95.2	Level of significance: 97.1%
						Degrees of freedom : 3/5

† Unreliable statistics (F-ratio below 95% significance level).

$^{\nabla}$ Incongruent sign for interaction: needs further explanation.

^{o} Important interactions.

Table 17. Regression Analysis Results Determining the Dominant Forces for Each Output Characteristic: Dominant Comparisons Set #2

Output Characteristic	Independent Variable	Sign	% Explained	Reliability F-ratio	Reliability % Significance Level	Overall Statistics
Algal peak height	AADB	-	83.4	20803.3	>99.9	Total % explained : 100.0%
	AABT$_r$	-	8.6	2152.8	>99.9	Overall F-ratio : 4156.6
	DABA	-	7.9	1968.8	99.9	Level of significance: >99.9%
	†AADBxDABA	+	0.0	5.7	86.1	Degrees of freedom : 6/2
	†AADBxAABT$_r$	+	0.0	5.7	86.1	
	†∇DABAxAABT$_r$	-	0.0	3.0	77.4	
Middle algal growth rate	DABA	+	80.6	2797.7	>99.9	Total % explained: : 99.9%
	AADB	-	14.5	501.8	>99.9	Overall F-ratio : 693.8
	AABT$_r$	+	3.6	124.1	99.8	Level of significance: >99.9%
	∇DABAxAABT$_r$	-	1.2	41.6	99.2	Degrees of freedom : 5/3
	†AADBxDABA	-	0.1	4.0	86.0	
Late algal growth rate	DABA	+	73.6	497.8	>99.9	Total % explained : 99.4%
	AADB	-	20.4	138.3	>99.9	Overall F-ratio : 168.2
	AABT$_r$	+	5.0	33.9	99.6	Level of significance: >99.9%
	†DABAxAABT$_r$	+	0.4	2.7	82.5	Degrees of freedom : 4/4
Algal decline rate	AADB	-	51.2	979.3	>99.9	Total % explained : 99.8%
	AABT$_r$	+	43.7	834.5	>99.9	Overall F-ratio : 381.6
	∇DABAxAABT$_r$	+	4.9	92.7	99.8	Level of Significance: >99.9%
	†∇AADBxAABT$_r$	+	0.1	1.2	64.6	Degrees of freedom : 5/3
	†DABA	-	0.0	0.3	40.0	
Shrimp peak height	AABT$_r$	+	96.1	16540.0	>99.9	Total % explained : 100.0%
	DABAxAABT$_r$	+	2.0	336.0	99.7	Overall F-ratio : 2868.7
	DABA	+	1.7	293.9	99.7	Level of significance: >99.9%
	AADB	-	0.2	32.9	97.1	Degrees of freedom : 6/2
	†AADBxAABT$_r$	-	0.1	9.4	90.8	
	†AADBxDABAxAABT$_r$	-	0.0	0.3	36.7	

† Unreliable statistics (F-ratio below 95% significance level).

∇ Incongruent sign for interaction: needs further explanation.

o Important interactions.

Table 18. Regression Analysis Results Determining the Dominant Forces for Each Output Characteristic: Dominant Comparisons Set #3

Output Characteristic	Independent Variable	Sign	% Explained	Reliability F-ratio	% Significance Level	Overall Statistics
Algal peak height	AADB	-	83.8	4200.1	>99.9	Total % explained : 99.9%
	DABA	-	10.2	512.4	>99.9	Overall F-ratio : 1002.3
	AAHT	-	5.9	296.6	>99.9	Level of significance: >99.9%
	†AADBxDABA	+	0.0	1.5	68.6	Degrees of freedom : 5/3
	†DABAxAAHT	+	0.0	1.2	65.1	
Middle algal growth rate	DABA	+	76.2	908.7	>99.9	Total % explained : 99.7%
	AADB	-	13.3	159.2	99.9	Overall F-ratio : 238.0
	AAHT	+	7.9	94.0	99.8	Level of significance: >99.9%
	∇DABAxAAHT	-	2.2	26.8	98.6	Degrees of freedom : 5/3
	†AADBxDABA	-	0.1	1.4	68.2	
Late algal growth rate	DABA	+	69.4	1034.1	>99.9	Total % explained : 99.8%
	AADB	-	18.4	273.8	>99.9	Overall F-ratio : 297.6
	AAHT	+	11.5	171.9	99.9	Level of significance: >99.9%
	†DABAxAAHT	+	0.3	4.8	88.3	Degrees of freedom : 5/3
	†AADBxDABA	-	0.2	3.5	84.2	
Algal decline rate	AADB	-	55.9	4937.3	>99.9	Total % explained : 100.0%
	AAHT	+	40.8	3606.2	>99.9	Overall F-ratio : 1767.4
	DABA	-	3.0	268.7	>99.9	Level of significance: >99.9%
	DABAxAAHT	+	0.2	20.5	98.0	Degrees of freedom : 5/3
	†∇AADBxAAHT	+	0.0	4.2	86.8	
Shrimp peak height	AAHT	+	83.9	50.5	>99.9	Total % explained : 90.0%
	†DABA	+	6.1	3.7	89.6	Overall F-ratio : 27.1
						Level of significance: 99.9%
						Degrees of freedom : 2/6

† Unreliable statistics (F-ratio below 95% significance level).

∇ Incongruent sign for interaction: needs further explanation.

° Important interactions.

respectively. Nothing unusual has occurred in these results. The only significant interaction is seen for the brine shrimp peak characteristic in Table 16. This AADA x $AABT_r$ interaction was predicted by the raw data and is not surprising since both parameters deal with the amount of light available to the algae. The other interactions either have low reliability or low percent explained values. The lack of unusual data is encouraging and lends strength to the conclusions already drawn in the previous regression analysis. Such is the value of the extra data points.

The dominant parameters are now clear for each output characteristic measured except the brine shrimp peak height. In this case it appears that $AABT_r$ shares equal dominance with AADA. In view of the second peak phenomenon this result is not surprising. These parameters might best be interpreted as those most responsible for the second peak phenomenon around the algal productivity loop structure. The influence of $AABT_r$ (the response range for the light factor table) is positive while that of AADA (maximum light penetration) is negative.

Algal peak height and rate of decline are each influenced most by the same parameter: AADB (the light penetration rate factor). This factor has a negative influence on algae peak height and also a negative influence on algal rate of decline. Any change in this factor from the standard run will affect both peak height and rate of decline. This is believed true because of the strong positive influence of algal peak height on rate of decline explained previously. Increases in AADB raises the algal height by allowing more light penetration at all levels of algal density. Thus, the algae are not limited by self shading as soon as for the standard run. It is not surprising that this parameter was found to be dominant.

Both of the growth rates measured for the algae population indicate the same dominant parameter: DABA (solar wave amplitude). The influence is positive for both output measurements. The reason larger fluctuations in the annual solar intensity increase growth rate is that productivity is a direct function of solar intensity. While less solar intensity causes the winter algal growth to be slight, the rapid growth in intensity during the spring is reflected by the algae growth. The peak height may not be great, but the algae had to grow from very low levels. Thus the daily average growth is increased by increased solar wave amplitude.

Notice that all of the dominant forces are parameters influencing the amount of photosynthetically active radiation available to the algae. This is in support of the preliminary hypothesis made earlier where it was stated that "those parameters associated with the light factor in the productivity would be most dominant." These parameters were listed as AADA, AADB, DAAA and DABA. The results so far have demonstrated very well the level of understanding of the system being simulated.

Now it is desired to rank order the dominant forces for each of the output characteristics, at least to determine for sure the second place dominant. For the brine shrimp peak height it is fairly clear that $AABT_r$ and AADA are tied for top dominance. It is questionable, however, which parameter is next down the list. It could be either AAHT or AAAA since these two have never been compared with each other.

For the algal rate of decline, the parameter that was second to the dominant AABD in the initial set of reruns, AAAA (see Table 9) has never been tested with the runner up in the second set of reruns, $AABT_r$ (Table 17). However, we do know from Table 16 that AADA is more dominant than $AABT_r$, and from Table 9 we see that AAAA is dominant over $AABT_r$. Thus it may be guessed that AAAA will be more dominant than $AABT_r$.

For the algal peak height AADB is such a strong dominant that it is questionable whether a clear second place can be determined between AAAA and $AABT_r$. In support of this, Table 16 shows that AADA is equivalent in its effect with $AABT_r$ and Table 9 shows AAAA to be only slightly dominant over AADA.

For the growth rates it is not known whether AADB is more dominant than DAAA. These should be tested together.

To accurately determine the second place parameter for each output characteristic two additional runs are needed: AAAA with AAHT and $AABT_r$ in one set (to satisfy the brine shrimp peak height, algal peak height and algal rate of decline), and AADB with DAAA and some other parameters to complete a set of three (to satisfy the algal growth rates). AAHT was chosen to run with the others since it was also being used in the other set. An adjustment range of ± 5% was again used in these two sets, simply for convenience. The data for the two sets is presented in Tables 19 and 20. For these runs only the output characteristic of primary interest was recorded and entered into the regression analysis.

Table 19. Results of Second Place Dominant Comparison.

Set #1

	Parameters		Response Variables		
Run	AADB	DAAA	AAHT	A_{50-30B}	A_{20B}
Standard	2.3E-8	450	.001343, .04291	4.20M	2.43M
1	2.185E-8	427.5	.0012759, .0407645	4.56M	2.55M
2	2.415E-8	427.5	.0012759, .0407645	4.04M	2.29M
3	2.185E-8	472.5	.0012759, .0407645	3.88M	2.38M
4	2.415E-8	472.5	.0012759, .0407645	3.44M	2.14M
5	2.185E-8	427.5	.0014114, .0450555	4.97M	2.83M
6	2.415E-8	427.5	.0014114, .0450555	4.44M	2.54M
7	2.185E-8	472.5	.0014114, .0450555	4.47M	2.56M
8	2.415E-8	472.5	.0014114, .0450555	3.96M	2.30M

Table 20. Results of Second Place Dominant Comparison.

Set #2

	Parameters			Response Variables			
Run	$AABT_r$	AAAA	AAHT	A_p	A_{10A}	B_p	
Standard	155,5	2.1	.001343, .04291	229.9M	-21.29M	26.25	
1	147.25,4.75	1.995	.0012759, .0407645	232.9M	-18.92M	12.06	
2	162.75,5.25	1.995	.0012759, .0407645	225.6M	-20.91M	23.60	
3	147.25,4.75	2.205	.0012759, .0407645	240.4M	-20.97M	18.26	
4	162.75,5.25	2.205	.0012759, .0407645	232.5M	-22.70M	35.38	
5	147.25,4.75	1.995	.0014114, .0450555	226.7M	-20.66M	16.21	
6	162.75,5.25	1.995	.0014114, .0450555	218.8M	-21.77M	47.78	
7	147.25,4.75	2.205	.0014114, .0450555	234.8M	-22.15M	26.46	
8	162.75,5.25	2.205	.0014114, .0450555	226.3M	-22.45M	330	*

* Second peak phenomenon occurred.

The raw data in Table 19 is difficult to interpret. The second place dominance for the algal growth rates is likely to be quite close. The data of Table 20 is also difficult to interpret by eye. It appears that the second place dominant factors will be only slightly dominant over the other major forces affecting each of the output characteristics.

The regression analysis results for the data of Tables 19 and 20 are presented in Table 21, parts A and B, respectively. The second place dominant is not overwhelmingly dominant over its contenders in any of the cases. In Table 21A DAAA (average annual solar intensity factor) is dominant over AADB (the light penetration rate factor) for middle algal growth rate but the reverse is true for late algal growth rate. This is reasonable since late spring algal growth is more likely to be affected by self shading than earlier growth. It is interesting to note that AAHT is more dominant than DAAA as far as late algal growth is concerned. AAHT is the table that converts solar energy to water temperature. Notice too, that the influence of DAAA is negative while that of AAHT is positive. This means that algal growth rate (as measured) is increased with better solar energy to water temperature conversion, but is decreased with simply more solar energy. One point must be remembered, however, before extrapolating any of these interpretations to the real ecosystem. The growth rate measurement is dependent on the population density at the beginning of the measurement period (in this case 20 days prior to peak height) as well as on the end of the period (peak height). The growth rate measurement is not a measure of the final population size attainable before consumption begins after brine shrimp

Table 21A. Regression Results for Second Place Dominant Comparison.

Set #1

Output Characteristic	Independent Variable	Sign	% Explained	F-ratio	Reliability % Significance Level	Overall Statistics
Middle algal growth rate	DAAA	-	39.6	1193.0	>99.9	Total % explained : 99.9%
	AADB	-	31.0	934.3	>99.9	Overall F-ratio : 602.3
	AAHT	+	28.6	861.0	>99.9	Level of significance: >99.9%
	∇DAAAxAAHT	+	0.7	21.0	98.1	Degrees of freedom : 5/3
	†AADBxDAAA	+	0.1	2.3	77.6	
Late algal growth rate	AADB	-	42.5	648.5	>99.9	Total % explained : 99.8%
	AAHT	+	29.2	445.2	>99.9	Overall F-ratio : 304.3
	DAAA	-	26.6	405.2	>99.9	Level of significance: >99.9%
	DAAAxAAHT	-	1.4	21.2	98.1	Degrees of freedom : 5/3
	†AADBxDAAA	+	0.1	1.5	63.8	

† Unreliable statistics (F-ratio below 95% significance level).

∇ Incongruent sign for interaction: needs further explanation.

o Important interactions.

Table 21B. Regression Results for Second Place Dominant Comparison.

Set #2

Output Characteristic	Independent Variable	Sign	% Explained	Reliability F-ratio	Reliability % Significance Level	Overall Statistics
Algal peak height	AABT$_r$	-	39.5	13127.4	>99.9	Total % explained : 100.0%
	AAAA	+	35.7	11862.1	>99.9	Overall F-ratio : 5538.9
	AAHT	-	24.6	8186.1	>99.9	Level of significance: >99.9%
	∇AABT$_r$xAAAA	-	0.1	21.9	95.7	Degrees of freedom : 6/2
	∇AABT$_r$xAAHT	-	0.1	18.7	95.0	
	†∇AAAAxAAHT	+	0.1	17.4	94.7	
Algal decline rate	AAAA	+	42.8	34.1	99.6	Total % explained : 95.0%
	AABT$_r$	+	31.2	24.8	99.2	Overall F-ratio : 18.9
	AAHT	+	14.8	11.8	97.3	Level of significance: 99.3%
	†AABT$_r$xAAHT	+	6.3	5.0	91.2	Degrees of freedom : 4/4
Shrimp peak height	†AABT$_r$	+	19.9	13.3	82.9	Total % explained : 98.5%
	†AAHT	+	16.5	11.0	81.3	Overall F-ratio : 9.4
	†AAAA	+	14.5	9.7	80.2	Level of significance: 75.4%
	†AABT$_r$xAAHT	+	14.1	9.4	79.9	Degrees of freedom : 7/1
	†AABT$_r$xAAAA	+	11.6	7.7	78.0	
	†AAAAxAAHT	+	11.3	7.5	77.8	
	†AABT$_r$xAAAAxAAHT	+	10.7	7.1	77.2	

† Unreliable statistics (F-ratio below 95% significance level).

∇ Incongruent sign for interaction: needs further explanation.

o Important interactions.

hatching. Thus, the algal peak height dominant forces should also be examined together with the growth rate factors. Possibly a more extrapolatable measure of growth rate in the algae would be their actual division rate, or the change in division rate during some period prior to peak height. Perhaps the most useful measure overall would be the annual productivity measured as the integral of the plankton curves over the year.

For algal peak height (Table 21B) $AABT_r$ (the response range of the light factor table) is the second place dominant over AAAA (theoretical maximum algal productivity). However, the difference is not too great. Since their interaction is not too significant, these factors may be adjusted independently to control algal peak height, should some future experiment require this. The negative influence of $AABT_r$ on algal peak height means that as the response range to light intensity is shortened, smaller changes in light intensity produce both larger changes in the light factor (as may be seen from the light factor table illustrated in Figure 49) and a correspondingly rapid increase in algal growth potential. This ultimately leads to a larger algae population as long as the adjustments do not allow the light intensity to exceed the optimum seen in Figure 49. The adjustments of only plus or minus one percent avoided this problem in this case.

For the algal rate of decline it is evident that the deductions made by comparing regression results between data sets were correct in this case. AAAA is in fact dominant over $AABT_r$ and is given the second place for dominance. The reason for the positive influence of maximum

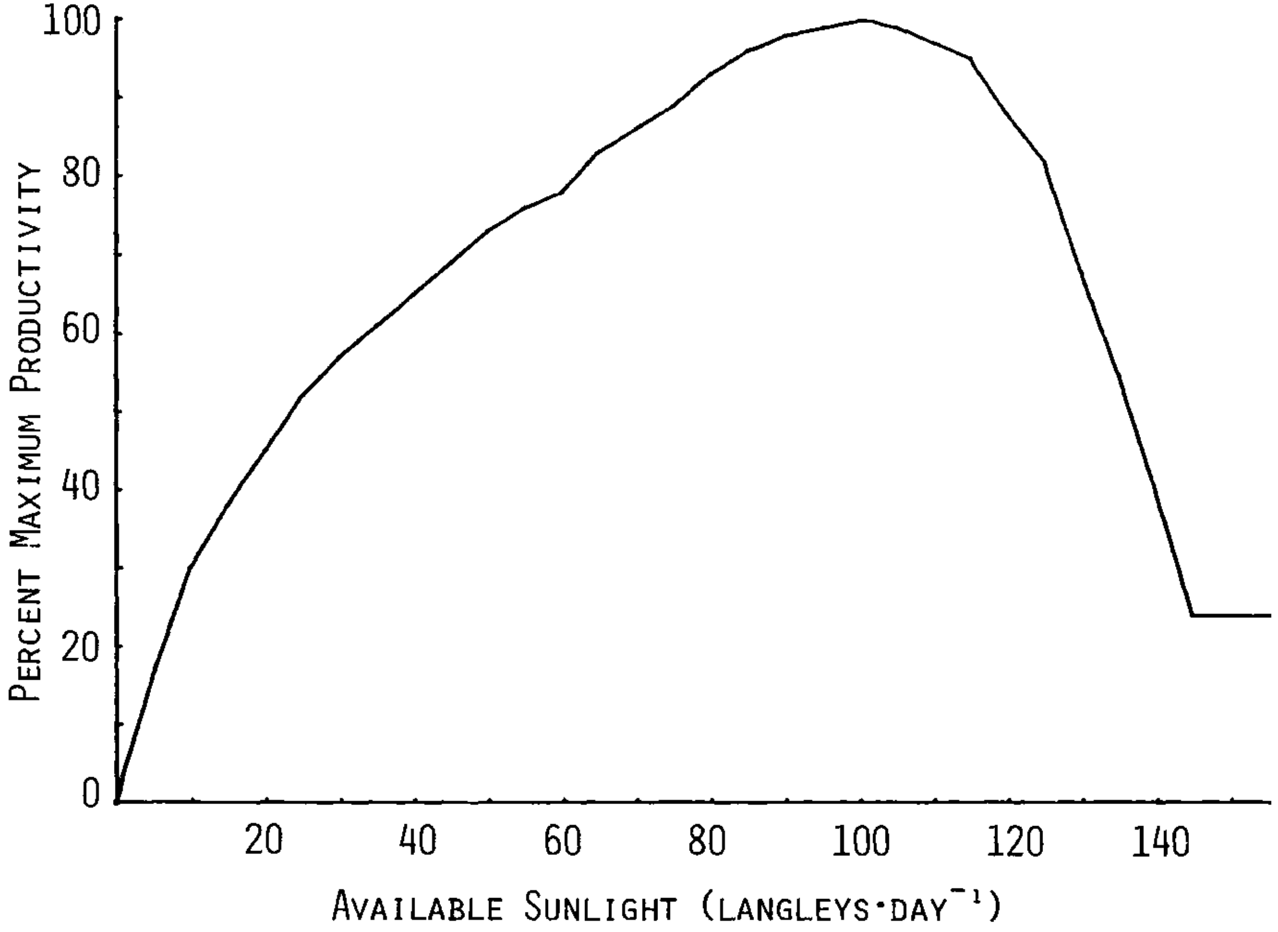

Figure 49. Standard Run Version of the Productivity vs Light Intensity Curve ($AABT_r$ = 155,5).

algal productivity (AAAA) on rate of decline is the great voraciousness of the brine shrimp, expressed in their filtration rate (see Mason, 1963; Reeve, 1963a, 1963b). The decline rate will usually be faster in those runs exhibiting a large algal peak height since a very few brine shrimp will clear very high densities of algae in a short time.

The shrimp peak height test is seen to be of very poor reliability. It is known prior to the test that $AABT_r$ was tied with AADA for top dominance from Table 16. The test is so poor that the only conclusion is that AAHT and AAAA have about the same influence and that this influence is somewhere below that of $AABT_r$ and AADA. These results are not surprising due to the nature of the output characteristic (described earlier).

Conclusions

The final results of the dominant forces identification are presented in Table 22. None of the parameters listed as being dominant are surprising in this respect. As a general conclusion it may be said that light factors are more important than temperature factors around the algal productivity loop structure. This is not surprising since temperature is a delayed function of light, as represented in this model.

In particular, the fact that AADB (the light penetration rate factor) is a strong dominant factor in determining algae peak height is quite reasonable. The negative influence is due to the structure of the exponential function in which this parameter is the rate factor. Decreases in AADB cause the negative exponent function to drop less drastically (see Figure 50). This results in proportionally more light

Table 22. Final Results of the Dominant Forces Identification.

Output Characteristics	Rank Order of Dominants	Sign of Influence
Algal peak height	1. AADB (strong)	-
	2. AABT_r	-
	Others: AAAA (close)	+
	AAHT	-
Middle algal growth rate	1. DABA (strong)	+
	2. DAAA (strong)	-
	Others: AADB (close)	-
	AAHT	+
Late algal growth rate	1. DABA (strong)	+
	2. AADB (strong)	-
	Others: AAHT (close)	+
	DAAA	-
Algal decline rate	1. AADB (weak)	-
	2. AAAA	+
	Others: AABT_r (close)	+
	AADA	-
Shrimp peak height	1. AABT_r (weak)	+
	AADA (close)	-
	2. AAHT	+
	AAAA	+

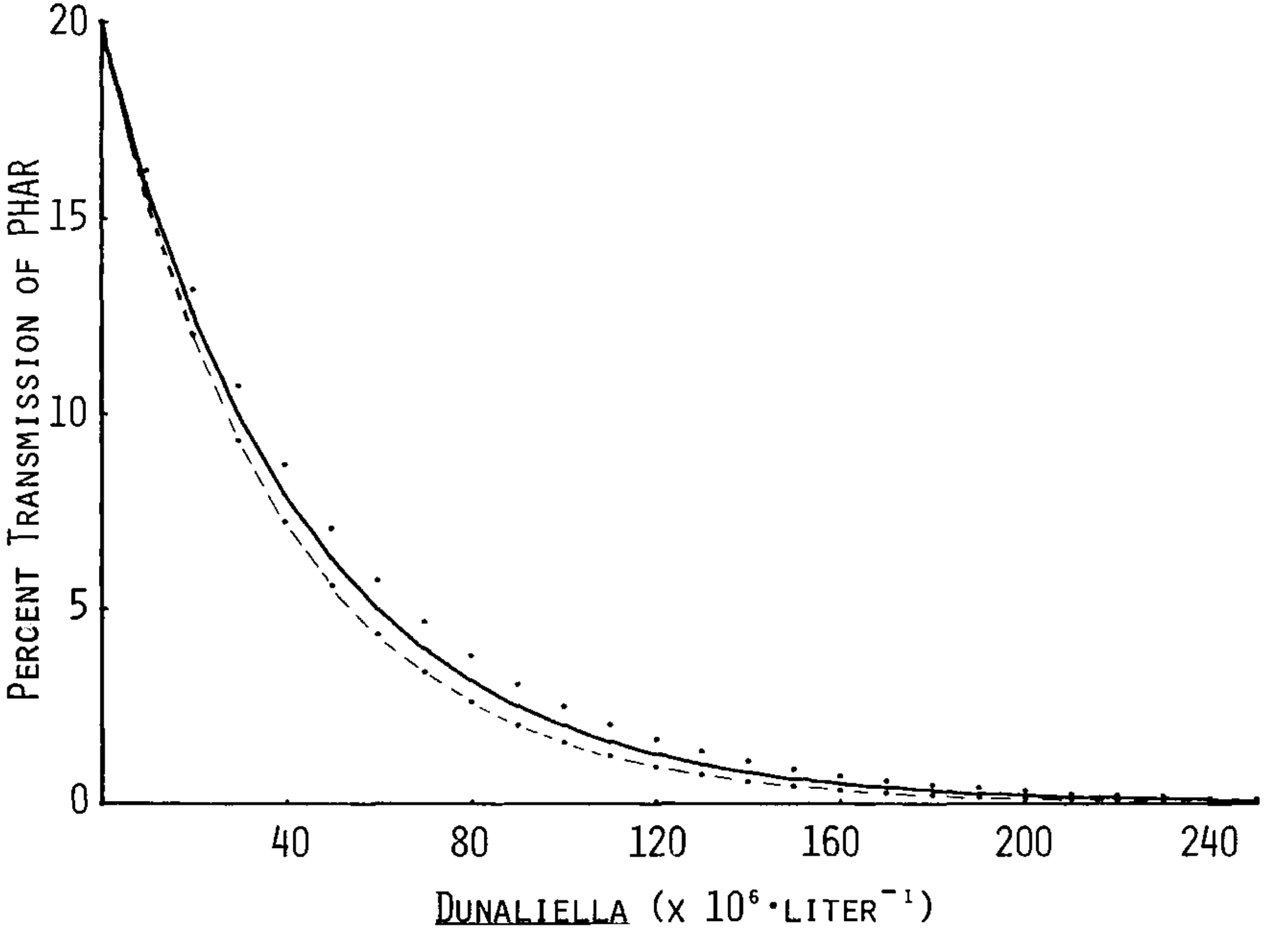

Figure 50. Water Transparency as a Function of Algal Density Illustrating Changes Made for the Dominant Forces Identification: AADB = 2.07×10^{-8} (Dots); AADB = 2.53×10^{-8} (Dashes); Standard Run where AADB = 2.30×10^{-8} (Line).

available to the algae with increasing algal density, yielding increased algal growth.

The second place dominant, $AABT_r$, is much less dominant than AADB and is only slightly more dominant than the other parameters listed: AAAA and AAHT. Its negative influence on algal peak height has been previously discussed. The positive influence of AAAA (theoretical maximum algal productivity) is obvious. The more potential for growth, the greater the peak height. The negative influence of AAHT (the solar energy to water temperature conversion table) is easily explained by observing the temperature factor table $AAET_r$(see Figure 51). When more heat comes from the same amount of light, the algae growth might possibly be slowed by too much heat, passing the optimal heat point for more of the year than when AAHT is at its standard value. This averages out to less algae in the system as a whole.

For the algal growth rate the strong positive influence of DABA (solar wave amplitude) has been previously explained: since solar intensity grows faster in the spring, so does the algae population. The influences of DAAA (average annual solar intensity factor), AADB (light penetration rate factor) and AAHT (solar intensity to water temperature table) on the algal growth rates as well as their order of dominance for the respective growth rate measurements have been discussed.

The factors most important in controlling algal rate of decline are also seen as important in controlling algal peak height, and with the same influence. This is not surprising in view of the dependence

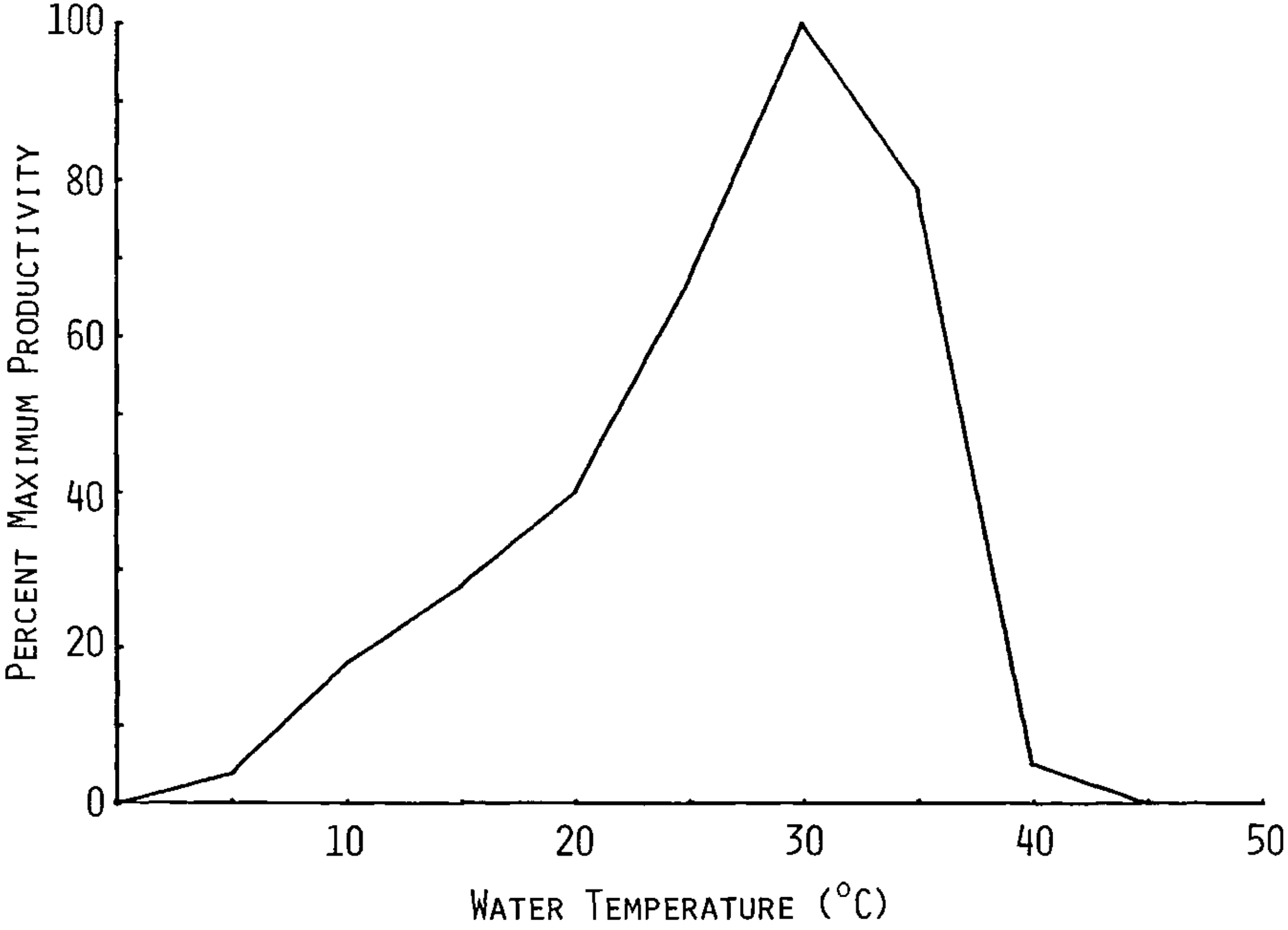

Figure 51. Algal Productivity vs Water Temperature (Adapted from Van Aukin and McNulty, 1973).

of algal rate of decline on algal peak height, previously discussed.

It is hoped that the unreliability and lack of a single dominant in the brine shrimp peak height results have been dealt with thoroughly enough. The nature of the results seen were suspected. Noise in the output due to the model's structure is believed to be the cause of the lack of both reliability and strong dominance.

In analyzing the overall results of this procedure it must be remembered that the data has been collected around only small ranges of parameter values. Larger deviations in parameter values might show different influences or rank ordering due to the passing of optimal points or curves such as those pictured in Figures 48 and 51. However, it is believed that, in general, the stronger dominants will remain strong dominants.

If the model contains optimal values in some of its functions (i.e. Figures 48 and 51) then seemingly strange results may occur. This kind of nonlinearity might produce significant interactions with the "wrong" sign of influence, as was the case for the middle algal growth rate of Table 9 (AAAA x AADA interaction). In cases such as these, structure of the simulation model may be perfectly reasonable. While for some unusual results it is true that the model may be at fault, often a reasonable explanation is possible. Looking for this explanation will increase the modeler's understanding of his model and in many cases that of the system being simulated.

All of the other interaction effects with the "wrong" sign were either unreliable or accounted for so little of the output variation as to be considered inconsequential. The other significantly important interactions are easily explained by the close proximity of the parameters involved with one another in the simulation model structure.

In conclusion, the dominant forces identification succeeded in identifying the dominant parameters around the algal productivity loop structure, with respect to output characteristics associated with the algae. The analysis results were consistent with the preliminary hypotheses and supported the structure and function of the simulation model. The analysis procedure made a large contribution to the ultimate primary goal of understanding the model and the real system. This is the perceived primary goal of all nonlinear simulation and analysis. Achieving a certain level of understanding, predictions about the system will be forthcoming.

In closing, the dominant forces identification represents the beginning development of a set of analytical procedures for nonlinear simulation models. While it is in no way a rote procedure giving detailed analysis of values at particular points in time, it is a pragmatic methodology which can give much information pertaining to the understanding of complex model structures and broad output behavioral features when performed in an intuitive spirit. For this reason care must be taken to document all logical steps used when interpreting results from such a methodology.

Summary

(1) The methodology of dominant forces identification is presented (a method for analyzing complex, nonlinear simulation models).

(2) An actual simulation model (the dynamics of a plankton community in the Great Salt Lake, Utah) is analyzed using this methodology.

(3) The results are presented and discussed. It is concluded that the methodology successfully predicts dominant parameters, and contributes to system understanding.

CHAPTER VI

CONCLUSIONS

The immediate objectives of this research were: 1) to extend the existing simple models and better account for the recurring annual plankton dynamics in the southern basin of the Great Salt Lake via a hypothesis based on feedback loops acting within and between the two plankton species; 2) to bring together the present knowledge and theory concerning the two plankton populations and incorporate these into the dynamic hypothesis; 3) to test this hypothesis using a simulation model and sensitivity analysis; and 4) to use the results to suggest areas of needed research and model improvement. These objectives have been achieved. Some major weaknesses of the present model[8], suggested future research of primary importance, and some speculation stimulated by the model will be discussed here.

Model Weaknesses

The most important weakness of the present model is its failure to incorporate nutrient dynamics as a process affecting phytoplankton productivity. As indicated in the sensitivity analysis and dominant forces identification (where light was shown to control the occurrence of a summer peak of algae in the model), it seems likely that nutrient

---

[8] For additional model weaknesses see Appendix II.

dynamics have a large impact on the plankton community by controlling the algae population during the summer months instead of sunlight. This same conclusion has been reached by Porcella and Holman (1972) and by Stephens and Gillespie (1976).

Nutrients become available to algae from two possible sources: pollution input form the rivers entering the southern basin (Coburn and Eckhoff, 1972; Stephens and Gillespie, 1972, 1976) and by diffusion from a brine sump which exists on the bottom of the Great Salt Lake (Stephens, 1974; Stephens and Gillespie, 1976). This heavy brine sump is resistant to mixing and contains significant amounts of ammonia nitrogen and organic nitrogen, possibly from the degradation of dead plankton and fecal pellets, according to Stephens (1974) and Stephens and Gillespie (1976). The nutrients seem to be plentiful in the Great Salt Lake prior to the springtime algal bloom, but are depleted to limiting levels during this period of rapid growth (Stephens and Gillespie, 1976). Incorporation of this information into the present model should allow a greater understanding of the ecosystem and provide more realistic model behavior during sensitivity analysis.

A second major weakness of the present model is its failure to include the effects of changing lake salinity on plankton production. Enough literature is available to include some of the basic effects of salinity changes on each of these plankton species. The revised model may be helpful in predicting the outcome of decreasing salinity, should this information be incorporated. Because of the construction of a railroad causeway, the southern basin of the Great Salt Lake is presently experiencing decreasing salinity (Adams, 1964; Stephens and Gillespie, 1976; Stephens, 1974; Wirick, 1972).

A third major weakness of the present model was identified recently by K. I. Dahl-Madsen and E. Garges of the Water Quality Institute, Danish Academy of Technical Science (personal communication). Garges (1976) reports that the growth response of phytoplankton to light during a 24 hour period varies with the length of light in the light-dark cycle. Dahl-Madsen and Garges suggested that at different times of year the algal productivity response to light will be different from that given by the function found in Van Aukin and McNulty (1973). This is the function used in the present model. It was developed using a 20-4 hour light-dark cycle according to Van Aukin and McNulty (1973). In view of the great model sensitivity to slight changes in this function (reported earlier) perhaps this detail should be taken into account.

Suggested Research

The research of immediate importance, as indicated by the model, is that pertaining to the most sensitive parameters. Primarily, this involves the parameters associated most closely with algal productivity. In particular, nutrient cycling dynamics in the Great Salt Lake should be identified. The work of Stephens (1974) and of Stephens and Gillespie (1976) is important in answering the question of nutrient limitation. Given that nutrients are important limiting factors, their input and recycling pathways, accumulations, and delay times need to be identified. For example, the importance of the brine sump as a nutrient accumulation should be assessed together with determining how long (on the average) nutrients remain in the sump before becoming available again to algae.

The precise response of algal productivity to various 24 hour light-dark cycles may greatly aid in the accuracy of the present model. Also, the nature of light attenuation on the Great Salt Lake at various algal densities should be more accurately assessed. This, together with determining the growth response of algae at various initial algal concentrations, may help to determine more precisely the nature of algal self shading in this system.

The accuracy of parameters associated with the brine shrimp dynamics are less critical to the overall conception of the model. It would, however, be interesting to more fully understand the contributions made by food stress and by day length to overwintering egg production. This phase of the brine shrimp's life cycle seems to be least understood.

By accomplishing the above research and correcting the weaknesses of the model, a very useful level of understanding will have been achieved for the Great Salt Lake plankton community. This understanding may allow better management of the Great Salt Lake ecosystem and may contribute to the development of theories concerning interactions in simple stressed ecosystems.

Some Speculations

Two interesting thoughts were stimulated by the sensitivity analysis of the present model which have relevance to current belief regarding simple ecosystems. First, even though the model represents a simple ecosystem, there seem to be many checks and balances involved which allow the model to be controlled. None of the parameter changes caused the model to "blow up" or be destroyed. Large amounts of noise in the input function did not disturb the trends of the basic model output. All of the parameter changes allowed the model to approach a repeating pattern of one, two, or three years which was not too far from the real system time history, in most cases. The anomalous behavior patterns that were observed have explanations found in the weaknesses of the model rather than in the biological simplicity of the real system. Perhaps simple ecosystems are not easily destroyed by perturbation as is often assumed. In fact, this ecosystem seems to survive because it is so violently perturbed with nutrient, temperature and light extremes, and unusually high salinity. The two species of plankton seem well able to live in a changing environment, each forming cysts in hard times; and, in fact exist there because the environment is harsh. Indeed, they most certainly would be outcompeted should the salinity drop and remain low long enough for other less tolerant organisms to invade.

Perhaps the level of species diversity does not determine ecosystem stability as is also often assumed. In this system, only two species of plankton survive. However, the system consists of nutrient cycles, temperature, light, and salinity response mechanisms, predator-prey interactions and behavioral adaptations, in addition to the life cycles of two species of plankton. When considering this complex and nonlinear set of interacting feedback mechanisms, the system no longer seems so simple. Models which do not take into account such checks and balances within ecosystems may lead to misleading ecological theory.

The second thought involves the location of the sensitive parameters in the model. There seems to be a rough gradient of increasing sensitivity as parameters closer to the input function are changed. Those parameters associated with the brine shrimp life cycle are furthest from the driving solar energy function and are least sensitive. Those parameters associated with algal productivity are quite sensitive and are quite close to the solar energy input function. Perhaps the delays involved in the pathway from solar energy to brine shrimp reproduction create a smoothing effect on the model output. The implication is that possibly in other systems the details of the producers must be understood more precisely than the details of the consumers. Some simple models employing driving functions and cascaded feedback loops could perhaps help to satisfy this speculation. In any event, understanding the details of the producers in the Great Salt Lake is most important to the whole system dynamics observed.

In final conclusion, the research presented here has assembled the results of many investigations concerning plankton in the Great Salt Lake into a holistic model which emphasizes the importance of feedback loops in determining system behavior. The results of this model have indicated some future directions and provided some speculation for consideration. Future studies similarly directed should continue to add to the understanding of the Great Salt Lake, and of simple ecosystems. A high level of such understanding may eventually lead to the development of new unifying theories in ecology.

APPENDIX I

THE MODEL EQUATIONS

The influence diagrams developed in the Dynamic Hypothesis (Chapter III) are the foundation causal relationships on which the mathematical model is developed. From these relationships a flow diagram has been drawn which aids in equation formation (Figure 52). Each symbol in the flow diagram corresponds to a mathematical relationship: blocks depict accumulations and are represented by first order integral equations. Solid lines entering and leaving blocks represent material flows which are controlled by flow rates represented by valves (⧖). Circles represent auxillary variables which in general help to determine flow rates. Dotted lines represent information flows. Circles and valves are mathematically represented by algebraic equations in general. For a more complex description of the development and use of this symbology refer to Forrester 1961, 1968; Pugh, 1973, and Gutierrez 1974.

The equations which constitute the model presented in this study are algebraic and discretized first order integral equations written in the DYNAMO (Pugh, 1973) simulation language (Table 23). Simulations were performed on a CDC CYBER 74 computer at the Georgia Institute of Technology. The rationale for each equation and the origin of parameter values follow .

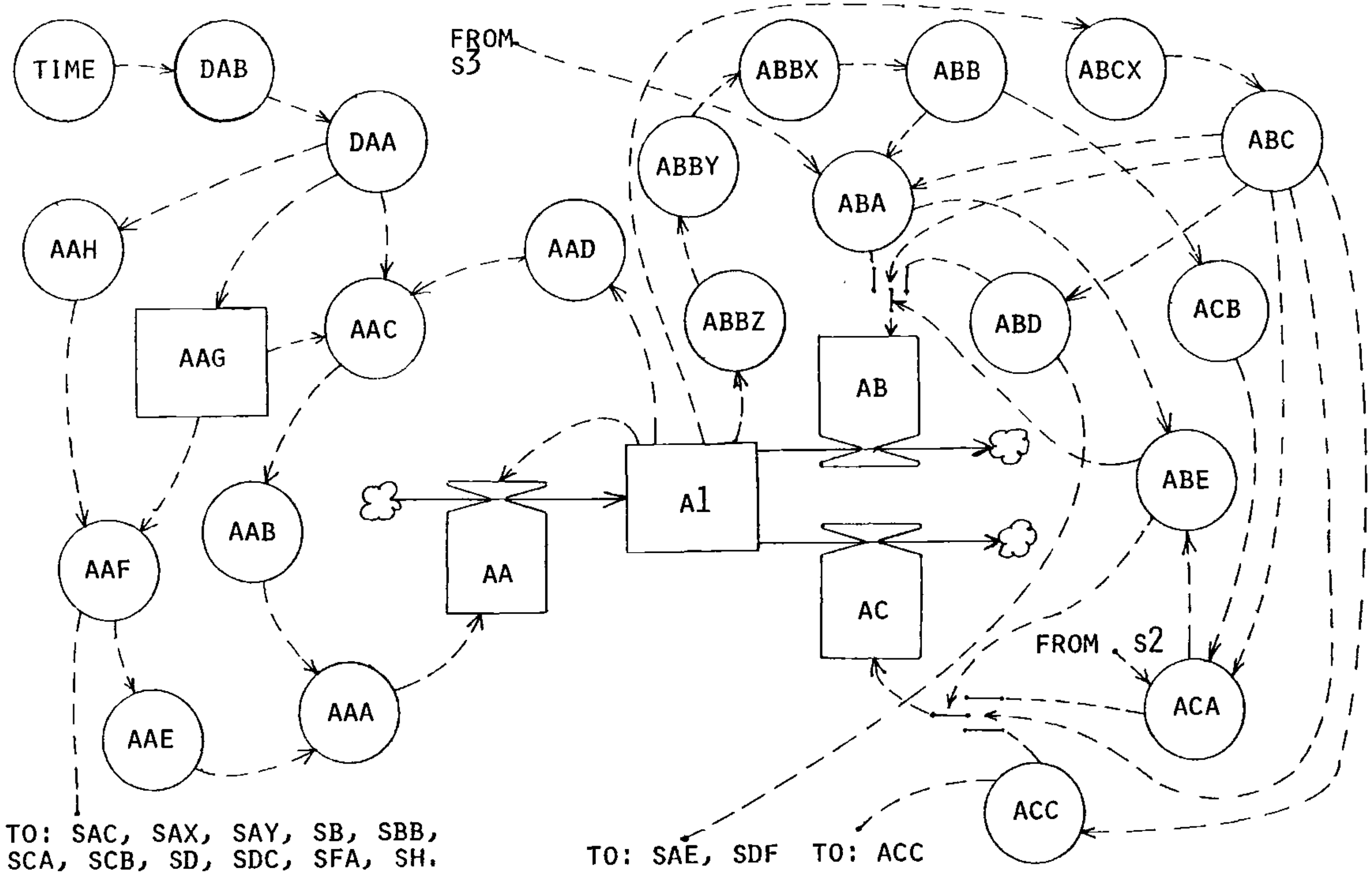

Figure 52. Flow Diagram Allowing Equation Formation for the Dynamics of the Great Salt Lake Plankton Community.

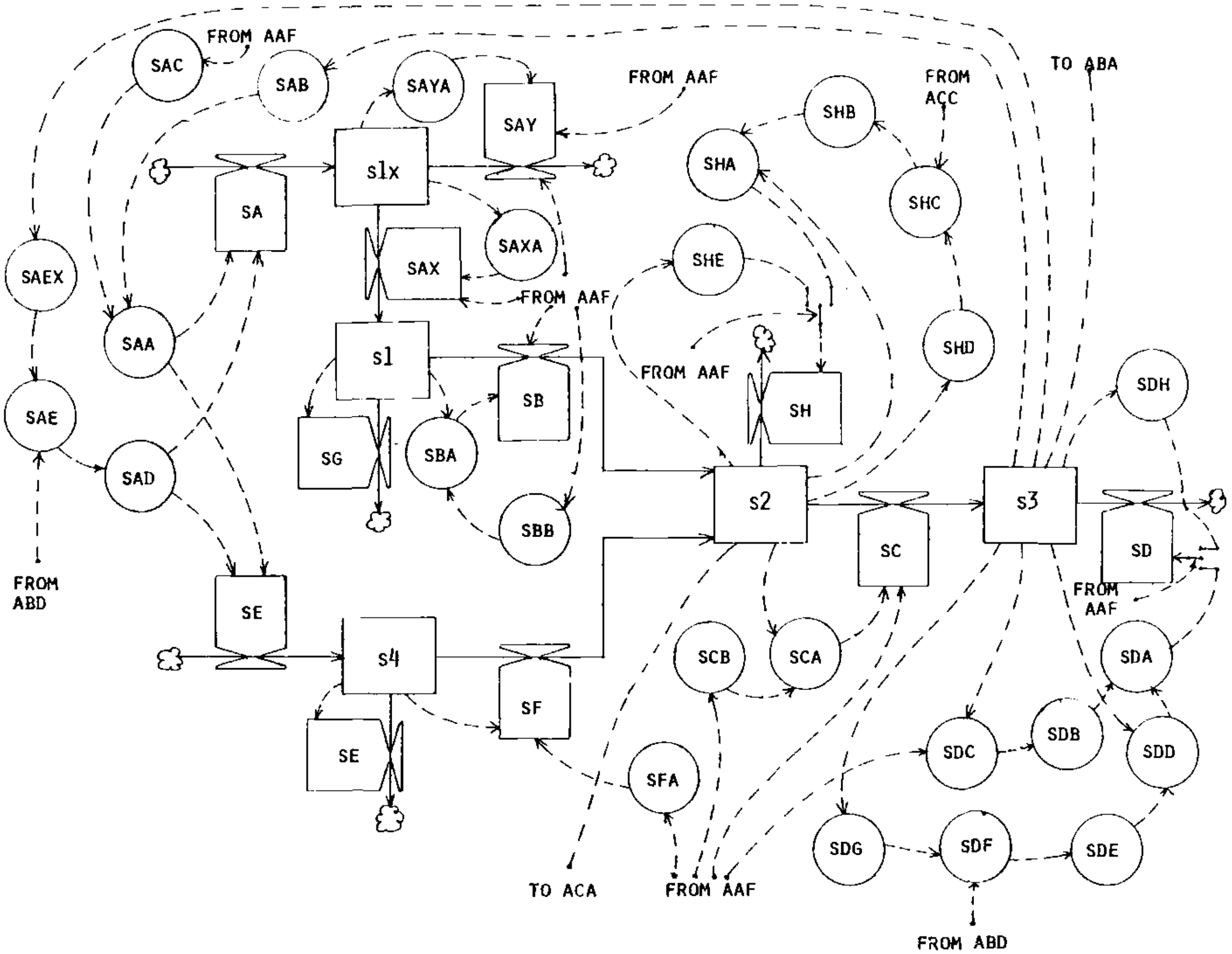

Figure 52. Continued.

Table 23. The Model Equations Written in DYNAMO.

```
*   DYNAMICS OF A PLANKTON COMMUNITY                    P001
NOTE
NOTE       DUNALIELLA (ALGAE) SECTOR
NOTE
DMNIN AABT(32)
DMNIN AAET(10)
DMNIN IACT(9)
DMNIN IADT(11)
DMNIN IBBT(9)
DMNIN ICBT(7)
DMNIN IFAT(9)
NOTE
L   A1.K=A1.J+DT*(AA.JK-AB.JK-AC.JK)                  (1) ALGAE/LITER
NOTE
R   AA.KL=A1.K*AAA.K                                   (2) DIVISION RATE
A   AAA.K=AAAA*AAB.K*AAE.K                             (3) PRODUCTIVITY
A   AAB.K=TABHL(AABT,AAC.K,0,AABT1,AABT2)              (4) LIGHT FACTOR
A   AAC.K=DAA.K*AAD.K                                  (5) AVAIL. LIGHT
A   AAD.K=AADA*EXP(-AADB*A1.K)                         (6) TRANSPARENCY
A   AAE.K=TABHL(AAET,AAF.K,0,45,5)                     (7) TEMP. FACTOR
A   AAF.K=AAG.K*AAH.K                                  (8) WATER TEMP.
L   AAG.K=AAG.J+DT*(1/AAGD)*(DAA.J-AAG.J)              (9) HEAT & COOL DELAY
A   AAH.K=TABLE(AAHT,DAA.K,0,550,550)                 (10) WATER TEMP. FROM SUN
NOTE
A   DAA.K=DAB.K+DAAA+(DAAB*NOISE())                   (11) SUNLIGHT IN LY/DY
A   DAB.K=COS(6.28318*TIME.K/365)*(-DABA)             (12) SOLAR WAVE INPUT
NOTE
R   AB.KL=CLIP(ABD.K,ABA.K,ABE.K,ABC.K)               (13) ALG DEATH DUE TO ADULTS
A   ABA.K=ABB.K*ABC.K*I3.K                            (14) NATURAL ADULT CONSUMP
A   ABB.K=MAX(ABBX.K,ABBC)                            (15) ADULT FILTRATION RT
A   ABBX.K=ABBA*EXP(ABBY.K)                           (16) FILTERING FCN
A   ABBY.K=MAX(ABBZ.K,-675)                           (17) LIMIT IMPOSED BY EXP
A   ABBZ.K=-ABBB*A1.K                                 (18) EXP ARGUMENT
A   ABC.K=MAX(0,ABCX.K)                               (19) ALGAE AVAIL FOR CONS
A   ABCX.K=A1.K-ABCA                                  (20) AVAILABILITY FCN
A   ABD.K=ABC.K*(1-ACCA)                              (21) MAX ALG CONS BY ADULT
A   ABE.K=ABA.K+ACA.K                                 (22) TOTAL NATUR ALG CONS
NOTE
R   AC.KL=CLIP(ACC.K,ACA.K,ABE.K,ABC.K)               (23) ALG DEATH DUE TO NAUP
A   ACA.K=ACB.K*ABC.K*I2.K                            (24) NATUR ALG CONS BY NAU
A   ACB.K=ABB.K/ACBA                                  (25) LITERS FILTERED (NAU)
A   ACC.K=ABD.K*ACCA                                  (26) MAX ALG CONS BY NAU
NOTE        TABLES
T   AABT=0,.16,.30,.38,.45,.52,.57,.61,.65,.69,.73,.76,.78,.83,.86,.89,
X          .93,.96,.98,.99,1.00,.99,.97,.95,.88,.82,.68,.55,.40,.24,.24,.24
C   AABT1=155
C   AABT2=5
T   AAET=0,.04,.18,.28,.4,.67,1,.79,.05,0
T   AAHT=.001343,.04291
NOTE        CONSTANTS
C   DAAA=450                                             LIGHT LEVEL FACTOR
C   DAAB=0                                               INPUT NOISE FACTOR
C   DABA=320                                             SOLAR WAVE AMPLITUDE
C   AAAA=3.1          NEW ALG/OLD ALG/DAY                THEOR MAX PRODUCTIVITY
C   AADA=.20                                             MAX LIGHT TRANSMIS
C   AADB=2.3E-5                                          LIGHT FCN ARGUMENT
C   AAGD=15           DAYS                               HEAT & COOL DEL TIME
C   ABBA=220          L/ARTEMIA/DY                       MAX ADULT FILTR RT
C   ABBB=8.95E-5                                         FILTR FCN ARGUMENT
C   ABBC=1            L/ARTEMIA/DY                       FILTR RT LOWER LIMIT
C   ABCA=3000         ALGAE/LITER                        ALGAL REFUGES
C   ACBA=10                                              FILTR RT FACTOR (NAU)
N   ACCA=1/ACBA                                          FILTR RT FACTOR (AD)
NOTE
```

```
NOTE
NOTE      ARTEMIA (BRINE SHRIMP) SECTOR
NOTE
L   I1X.K=I1X.J+DT*(IA.JK-IAX.JK-IAY.JK)          (27) UNREADY WINT EGGS L
L   I1.K=I1.J+DT*(IAX.JK-IB.JK-IG.JK)             (28) WINTER EGGS/LITER
L   I2.K=I2.J+DT*(IB.JK+IF.JK-IC.JK-IH.JK)        (29) NAUPLII/LITER
L   I3.K=I3.J+DT*(IC.JK-ID.JK)                    (30) ADULTS/LITER
L   I4.K=I4.J+DT*(IE.JK-IF.JK-II.JK)              (31) NONDURABLE EGGS/LITER
NOTE
R   IA.KL=IAA.K*IAD.K                             (32) WINT EGG LAYING RATE
A   IAA.K=IAB.K*IAAA/IAC.K                        (33) TOTAL EGG PROD. RATE
A   IAB.K=I3.K*IABA                               (34) % OF FEMALE ADULTS
A   IAC.K=TABLE(IACT,AAF.K,-5,35,5)               (35) EGG PRODUCTION DELAY
A   IAD.K=TABHL(IADT,IAE.K,.5,1.5,.1)             (36) WINTER EGGS PRODUCED
A   IAE.K=AED.K/(IAEX.K+1E-9)                     (37) FOOD STRESS
A   IAEX.K=I3.K*IAEA                              (38) 50% WINT EGG PROD FCN
NOTE
R    IAX.KL=CLIP(0,IAXA.K,AAF.K,5)                (39) RIPENING RATE
A    IAXA.K=I1X.K/1                               (40) RIPENING FLOW FCN
NOTE
R    IAY.KL=CLIP(IAYA.K,0,AAF.K,5)                (41) UNREADY EGG LOSS RATE
A    IAYA.K=I1X.K*IGXA                            (42) LOSS FLOW FCN
NOTE
R   IB.KL=CLIP(IBA.K,0,AAF.K,IBXA)                (43) WINT EGG HATCH RATE
A   IBA.K=I1.K/IBB.K                              (44) WINT EGG HATCH FCN
A   IBB.K=TABLE(IBBT,AAF.K,-5,35,5)               (45) WINT EGG HATCH TIME
NOTE
R   IC.KL=CLIP(ICA.K,0,AAF.K,ICXA)                (46) NAUPLIUS MATUR RT
A   ICA.K=I2.K/ICB.K                              (47) MATURATION FCN
A   ICB.K=TABHL(ICBT,AAF.K,0,30,5)                (48) MATURATION TIME
NOTE
R   ID.KL=CLIP(IDA.K,IDH.K,AAF.K,IDXA)            (49) ADULT DEATH RATE
A   IDA.K=IDB.K+IDD.K                             (50) SUMMER ADULT DTH RT
A   IDB.K=I3.K/IDC.K                              (51) OLD AGE DTH RT
A   IDC.K=TABHL(IDCT,AAF.K,5,45,5)                (52) ADULT LIFETIME
A   IDD.K=I3.K*IDE.K/IDDD                         (53) STARVATION DTH RT
A   IDE.K=1-MIN(IDF.K,1)                          (54) % ADULTS THAT STARVE
A   IDF.K=ABD.K/(IDG.K+1E-9)                      (55) AVAIL/DESIR ALGAE
A   IDG.K=I3.K*IDGA                               (56) DES ALGAE (ADULTS)
A   IDH.K=I3.K/1                                  (57) THERMAL DTH RT (AD)
NOTE
R   IE.KL=IAA.K*(1-IAD.K)                         (58) NONDUR EGG LAYING RT
NOTE
R   IF.KL=I4.K/IFA.K                              (59) NONDUR EGG HATCH RATE
A   IFA.K=TABLE(IFAT,AAF.K,-5,35,5)               (60) NONDUR EGG HATCH TIME
NOTE
R   IG.KL=I1.K*IGXA                               (61) WINT EGG LOSS RATE
NOTE
R   IH.KL=CLIP(IHA.K,IHE.K,AAF.K,IHXA)            (62) NAUPLIUS DEATH RATE
A   IHA.K=I2.K*IHB.K/IHAD                         (63) STARV DTH RT (NAU)
A   IHB.K=1-MIN(IHC.K,1)                          (64) % NAUPLII STARVING
A   IHC.K=ACC.K/(IHD.K+1E-9)                      (65) AVAIL/DES ALGAE (NAU)
A   IHD.K=I2.K*IHDA                               (66) DAILY ALG REQU (NAUP)
A   IHE.K=I2.K/1                                  (67) THERMAL DTH RT (NAUP)
NOTE
R   II.KL=I4.K*IIXA                               (68) NONDUR EGG LOSS RT
NOTE      TABLES
T   IACT=48,34,24,17,12,8.5,6,4.25,3
T   IADT=1,.969,.938,.875,.75,.5,.25,.125,.062,.031,0
T   IBBT=16,11.2,8,5.6,4,2.8,2,1.4,1
T   ICBT=80,56,40,28,20,14,10
T   IDCT=655,327.5,218.3,163.75,131,109.17,93.57,81.88,72.77
T   IFAT=16,11.2,8,5.6,4,2.8,2,1.4,1
```

```
NOTE       CONSTANTS
C   SAAA=50             EGGS                                 # OF EGGS/FEMALE
C   SABA=.5                                                  ADULTS THAT ARE FEMAL
C   SAEA=30000          ALGAE/SHRIMP                         50% WINT EGG RATION
C   TBWA=12             ◆C                                   HATCHING TEMP
C   SDWA=5              ◆C                                   THERM DTH POINT (AD)
C   SSDA=10             DAYS                                 STARVATION DELAY
C   SLGA=500            ALG/ADULT/DY                         MIN REQU DAILY RATION
C   SWLA=.025                                                WINT EGGS LOST/DAY
C   SHWA=6              ◆C                                   THERM DTH POINT (NAU)
C   SHAD=5              DAYS                                 STARV DELAY (NAUP)
C   SHDA=500            ALG/NAU/DY                           MIN REQ DLY RTN (NAU)
C   SLMA=.08                                                 NONDUR EGGS LOST/DAY
NOTE
NOTE                    SUPPLEMENTARIES
NOTE
S     S1.K=S1W.K+S1.K                                   (63) TOTAL WINTER EGGS/L
NOTE
NOTE
NOTE       INITIAL VALUES
NOTE
N   A1=A1N
N   AAG=AAGN
N   S1W=S1WN
N   S1=S1N
N   S2=S2N
N   S3=S3N
N   S4=S4N
NOTE
C   A1N=.0146
C   AAGN=149.86
C   S1WN=0
C   S1N=44.8
C   S2N=0
C   S3N=0
C   S4N=0
NOTE
PLOT S1=W/S3=* A1=D/S2=N/AAF=T/DAA=L
PRINT  A1(6,3),S1/S3
SPEC   DT=.25/LENGTH=365/PRTPER=0/PLTPER=7
OPT SHPRRN
RUN PD01
 EOI ENCOUNTERED.            1 FILES.
```

Algae Sector

Equation 1 represents the accumulation of algae per liter. It states that the algal concentration of time K equals that at time J plus any new algae during the interval from J to K (AA.JK) and minus the algae that were consumed during that time interval (AB.JK and AC.JK). The interval length in days equals DT. Equation 2 represents the division rate of algae (AA.KL). The number of new algae during interval KL equals the number of algae in the accumulation at time K (A1.K) times the number of new algal cells per old algal cell per day (AAA.K). Equation 3 calculates AAA.K from a maximum productivity (AAAA = 2.1 per day) found at optimal conditions (see Van Aukin and McNulty, 1973). This is multiplied by factors representing actual conditions of sunlight (AAB.K) and temperature (AAE.K). These factors each vary between 0 and 1 and were adapted from empirical relationships established for the Great Salt Lake algal species by Van Aukin and McNulty (1973). These adapted empirical relationships are reconstructed using the DYNAMO table function in Equation 4 and 7. Equation 4 states that the light factor is a function of available sunlight (AAC.K). This function is approximated by the table AABT (adapted from Van Aukin and McNulty, 1973). Available light is a negative exponential function of water transparency (AAD.K) and incident radiation (DAA.K). Water transparency (AAD.K; Equation 6) is approximated from actual secchi disk data, some simulated disk data of Wirick (1972) and from Stephens and Strickland's (1962) curves for attenuation of sunlight in sea water.

As mentioned, algal productivity is attenuated from its maximum value at optimal conditions not only by non-optimal sunlight but also by non-optimal temperatures. The temperature factor (Equation 7) is a function of water temperature at time K (AAF.K). The empirical relationship adapted from Van Aukin and McNulty (1973) is given by table AAET. Actual water temperature (AAF.K; Equation 8) is represented in this model as simply a delayed value of solar energy input at time K (AAG.K) that has been converted to temperature through a conversion factor (AAH.K). The equation for delayed solar energy input (Equation 9) is a first order exponential delay with a delay time (AAGD) determined empirically from the annual incident radiation and water temperature data given in Figure 9 (Chapter III). The sunlight equations (Equations 11 and 12) simply describe a cosine wave of amplitude DABA and period of 365 days and a mean value of DAAA. The values used for amplitude and period were estimated by eye from the data given in Figure 9. In Equation 11 noise may be introduced into the solar energy input function via the DYNAMO "NOISE" function if DAAB > 0.

Outflow from the algae accumulation is described by the equations for algal consumption rate. Algal consumption by adult brine shrimp during the time interval from K to L (AB.KL; Equation 13) is given by a DYNAMO "CLIP" function. That is, the value for consumption by adult brine shrimp at time K (ABA.K) as dictated by their water filtering capability is employed unless the total consumption by both adults and nauplii at time K (ABE.K) exceeds the algae available for consumption at time K (ABC.K). In this case the value for consumption by adult brine shrimp is calculated as a percentage of available algae (ABD.K). Thus, when algae are not limiting to brine shrimp adults, Equation 14 describes algal consumption as the multiple of the number of liters of water filtered per day by adult brine shrimp at time K (ABB.K), the number of algae per liter available for consumption at time K (ABC.K), and the number of adult brine shrimp per liter at time K (S3.K). The filtration rate of brine shrimp is a negative exponential function of algal concentration (A1.K) adapted from the work of Reeve[9] (1963a). Equations 15 through 18 are needed to describe the function. The value for filtration rate at time K (ABB.K; Equation 15) is chosen as the maximum of the value given by the negative exponential or by a constant ABBC where ABBC is the lowest filtration rate believed possible for brine shrimp (where filtration is a function of algal density). The value chosen for ABBC was estimated from the data of Reeve (1963a). The negative exponential function (ABBX.K; Equation 16) has a maximum value of ABBA [estimated from Reeve (1963a)] when algal concentration equals zero. The exponential argument determined by ABBY.K (Equation 17) is either some fraction of algal concentration (ABBZ.K) or is -675 whichever is larger. This is because DYNAMO has a lower limit for exponential arguments of -675. When greater than this value the argument calculated by Equation 18 is used. The fraction -ABBB which is multiplied by the algal concentration at time K (A1.K) is a negative

---

[9] The adaptation made and all associated parameter estimates were erroneous. Please see the section of Appendix II entitled "Corrected Brine Shrimp Filtration Rate".

exponential argument which purports to approximate Reeve's (1963a) data for adult brine shrimp filtration as a function of algal concentration[10].

The algae available for consumption at time K (ABC.K; Equations 19 and 20) are determined by assuming that there is a fixed number of algal refuges (ABCA). Should the number of algal cells per liter fall below the number of refuges per liter then zero available algae occur at time K. This is described by the MAX function in Equation 19.

If the brine shrimp water filtration is algae limited (i.e. brine shrimp are capable of filtering more algae than are available to them) than the consumption rate by adults is determined as a percentage of available algae (Equation 21). The percentage is 1-ACCA where ACCA is the percentage allocated to nauplii. The value for this percentage was estimated from Reeve's (1963a) data which show that adults filter approximately ten times more algae than do nauplii.

The value used to determine whether there will be enough algae to allow the natural consumption rate to occur [as determined through water filtration (ABA.K)] is the addition of the natural rates for both adults and nauplii (ABE.K; Equation 22). Perhaps in future model revisions this method of determining algal consumption will be modified with additional real system information. It is admittedly rather cumbersome at this stage.

---

[10] But see previous footnote.

The rate of consumption of algae by brine shrimp nauplii (Equation 23) is also a CLIP function similar to that for brine shrimp adults (Equation 13). Again the natural consumption rate (ACA.K) is allowed unless the total consumption of both brine shrimp age classes (ABE.K) is calculated to be greater than the algae available for consumption (ABC.K). The natural consumption rate for nauplii (ACA.K; Equation 24) is the number of liters filtered by each nauplius during each day (ACB.K) times the number of available algae per liter (ABC.K) all multiplied by the number of brine shrimp per liter (S2.K). The liters filtered by each brine shrimp (ACB.K; Equation 25) is calculated simply as a fraction (1/ACBA) of the adult filtration rate. The value for ACBA is estimated again from Reeve's (1963a) indication that nauplii filtered a volume of water which was an order of magnitude less than adults at all algal concentrations. Should natural consumption exceed available algae than nauplii are allowed to consume a fraction of what is available (ACC.K; Equation 26) using the same reasoning as above for ACBA (i.e. ACCA = .10).

Brine Shrimp Sector

Equations 27 through 31 are discretized first order integral equations each representing a stage in the life cycle of *Artemia salina*. Equation 27 represents the newly deposited overwintering egg accumulation (S1X.K) with a laying rate, SA.JK, a ripening rate, SAX.JK (which occurs after water temperatures reach a certain low temperature in this model), and an attrition rate, SAY.JK. The accumulation of overwintering eggs that have met their cold requirement (S1.K) is represented by Equation 28 which contains a rate of inflow from the unready (to hatch) egg accumulation (SAX.JK), an outflow to nauplii upon hatching (SB.JK), and an attrition rate (SC.JK). Nauplii concentration (S2.K; Equation 29) changes according to inflows from the hatching of both overwintering eggs (SB.JK) and nondurable eggs (SF.JK); and outflows of maturation into adults (SC.JK) and death (SH.JK). Adult brine shrimp (S3.K; Equation 30) accumulate according to maturation of nauplii (SC.JK) and adult death rate (SD.JK). Finally, nondurable eggs per liter (S4.K) change according to a laying rate (SE.JK), a hatching rate (SF.JK) and an attrition rate (SI.JK).

The overwintering egg laying rate for the time interval K to L (SA.KL; Equation 32) is a variable fraction (SAD.K) of the total egg production rate at time K (SAA.K). Total egg production (Equation 33) is calculated as the number of female adult brine shrimp at time K (SAB.K), and the average number of eggs per clutch. This value (SAAA) was chosen as a middle value estimate from data given by Wirick (1972), Jensen (1918), and Khmeleva (1967). In Equation 33 the above multiple is divided by a variable delay time (SAC.K; Equation 35) which is a temperature dependent ($Q_{10} = 2$) function estimated from data of Khmeleva (1967) (one brood produced every five to seven days at 25°C). The number of female adults (SAB.K; Equation 34) is simply a fraction (SABA = .5) of the total brine shrimp population at time K. A value of 50% females was chosen with the advice of Gillespie (personal communication). Wirick (1972) reports that 57% of the adult population were female in his samples.

The number of overwintering eggs produced (SAD.K; Equation 36) is a function of food stress (SAE.K) in the present model (Wirick, 1972). The function is a sigmoid curve (SADT) representing a guess based on the assumption that a range of food levels will be critical. That is, because populations often exhibit patchiness (see Emlen, 1973; Greig-Smith, 1964) it is assumed that within some critical range of average food accumulation per brine shrimp (food stress; Equation 37) some brine shrimp will produce overwintering eggs while others are producing nondurable eggs. As the average food level per shrimp declines more will produce overwintering eggs. A likely representation of this production percentage (SAD.K) was judged to be a sigmoid curve which allows increasing winter egg production with increasing food stress.

An index of food stress at time K (SAE.K; Equation 37) was calculated as the algae available for consumption at time K (ABD.K) divided by the average number of algal cells needed per adult to produce 50% overwintering eggs and 50% nondurable eggs from the brine shrimp population as a whole (SAEX.K). The small number added to this value (1×10^{-9}) prevents a programming error should the denominator fall to zero.

The number of algal cells needed to produce 50% overwintering eggs (SAEX.K; Equation 38) is calculated as an arbitrarily chosen constant number of cells per adult brine shrimp (SAEA = 30000) times the number of adult brine shrimp (S3.K).

The above method of determining overwintering egg production is largely conjectural. When new information is made available the model may be reconstructed appropriately.

Overwintering eggs hatch as the water warms in the spring. However these eggs must meet some presumed cold requirement prior to hatching. Unready overwintering eggs become ready to hatch through the rate SAX.KL (Equations 39 and 40). These equations simply allow all unready eggs to suddenly become ready to hatch when the water temperature falls to 5°C. The ready eggs will hatch when water temperatures rise again in the spring.

Some unready eggs may never hatch due to loss, or inviability (SAY.KL; Equations 41 and 42). The percentage lost each day in this manner is SGXA = .025 and was chosen in conjunction with some scanty data on overwintering egg dynamics given by Wirick (1972). This estimate is subject to great error. The CLIP function of Equation 41 merely assures that, once 5°C is reached, no more unready winter eggs are lost since they should have all flowed into the ready egg accumulation.

Winter eggs hatch into nauplii at a temperature dependent rate (SB.KL; Equation 43) when water temperature reaches the value represented by SBXA. The value of 12°C for SBXA was chosen from data given by Wirick (1972) who reports a range of hatching temperatures from 9 to 14°C. The outflow of overwintering eggs (SBA.K; Equation 44) is assumed to be the number of eggs at time K (S1.K) divided by a delay time (SBB.K). This delay time is temperature dependent ($Q_{10} = 2$) through the table function SBBT (Equation 45).

Nauplii mature into adult brine shrimp (SC.KL; Equation 46) unless the temperature falls below SHXA = 6°C (when they suffer thermal death according to Wirick, 1972; Jensen, 1918). Maturation rate (SCA.K; Equation 47) is calculated as the number of nauplii at time K (S2.K). divided by a temperature dependent maturation delay time (SCB.K). This delay time is a function of water temperature through a table, SCBT, the values of which were determined with respect to the data of Jensen (1918) (SCB.K; Equation 48).

Adult death rate is represented by a CLIP function (Equation 49) which chooses between thermal death (SDH.K) and non-thermal death (SDA.K). All adult brine shrimp die when water temperatures reach SDXA = 6°C (Wirick, 1972). Otherwise adults may die via old age or starvation (SDA.K; Equation 50). The number of adults dying of old age (SDB.K; Equation 51) is given by the number in the accumulation at time K (S3.K) divided by a variable lifetime (SDC.K). This lifetime is a function of temperature (Equation 52) on a degree-day basis. The values for the table function (SDCT) are estimated from data given by Khmeleva (1967), who found the average lifetime of Artemia to the 130 to 132 days at 25°C.

Adults may also die due to starvation (SDD.K; Equation 53). The number of starvation deaths is given by a fraction of adults which are starving (SDE.K) times the concentration of adults (S3.K) all divided by a starvation delay time(SDDD). The value for this delay time is unknown. A value of 10 days was used with the assumption that it would possibly take an adult 10 days to die after the initial onset of starvation. This is perhaps an overestimate. The percentage of starving adults (SDE.K; Equation 54) is calculated from an index (SDF.K). The MIN function assures that the percentage starving doesn't become less than zero. The index of starvation used (SDF.K; Equation 55) is the ratio of algae consumed by adults to the algae needed by adults to prevent the onset of starvation (SDG.K). The small number added to SDG.K (1×10^{-9}) is used to prevent dividing by zero when SDG.K = 0. The algae needed to prevent starvation (Equation 56) is calculated as the number of adult brine shrimp at time K (S3.K) times the average number of algal cells needed per adult brine shrimp each day to prevent an individual from starving (SDGA = 500). The value chosen of 500 $\text{cells} \cdot \text{shrimp}^{-1} \cdot \text{dy}^{-1}$ is taken from the data of Porcella and Holman (1972).

Equation 57 represents the death rate of adults when temperatures go below SDXA = 6°C. All of the adult brine shrimp leave the adult accumulation within a day, after these temperature conditions occur.

The nondurable egg laying rate (SE.KL; Equation 58) is simply that fraction of total egg production rate (SAA.K) that is not overwintering egg production (i.e. 1-SAD.K). The nondurable egg hatching rate (SF.KL; Equation 59) is the number of nondurable eggs present at time K (S4.K) divided by the average residence time for an egg (SFA.K). This residence time (Equation 60) is a function of temperature ($Q_{10} = 2$) given by SFAT. The values for this table are estimated from data of Jensen (1918), Relyea (1937), Wirick (1972) and Khmeleva (1967).

Equation 61 represents the attrition rate of ready to hatch overwintering eggs (SG.KL). The constant fraction SGXA = .025 of winter eggs (S1.K) is lost each day. This was estimated from a small amount of data collected by Wirick (1972) on overwintering egg dynamics.

Brine shrimp nauplii death rate (SH.KL; Equation 62) is dictated by starvation (SHA.K) at temperatures above SHXA = 6°C (from Wirick, 1972) and by thermal death (SHE.K) otherwise. Death via starvation (Equation 63) is calculated exactly as that for adults. A percentage of total nauplii (SHB.K) times the total nauplii (S2.K) die over a period SHAD = 5 days (the parameter value is simply a guess). The percentage that are starving (Equation 64) is either one minus the ratio of available to needed algae (SHC.K) or one (i.e. if this ratio exceeds one no algae are starving so SHB.K = 0). The calculation of this ratio is given by Equation 65. The small number (1×10^{-9}) again is to prevent a computer error when SHD.K = 0. The needed algae (SHD.K; Equation 66) are the number of algae needed to prevent nauplius starvation (SHDA = 500 from Porcella and Holman, 1972) times the number of nauplii at time K (S2.K).

The thermal death rate (SHE.K; Equation 67) allows all brine shrimp nauplii to die upon the onset of water temperatures low enough to cause thermal death (6°C according to Wirick, 1972).

Equation 68 is the attrition rate of nondurable eggs (SI.KL) calculated as some fraction which is lost daily (SIXA = 0.08) times the number of nondurable eggs present at time K (S4.K). The value for SIXA is merely a guess based on the assumption that perhaps nondurable eggs are subject to more daily attrition than durable eggs. However, no published information was found concerning this parameter.

The final equation simply adds the values for unready and ready to hatch overwintering eggs so that a total overwintering egg value (X1.K; Equation 69) can be plotted.

Initial Values

The model output exhibited a repeating pattern after several years of simulation. The initial values used in all model runs reported were those found for each accumulation at day 365 of the tenth year of simulation. Estimated initial values were used at the beginning to obtain these values. Within the ranges tested different estimates of initial values did not affect the long term repeating pattern which occurred after several years of simulation.

Input and Output Specifications

Specifications include the integration interval (DT), the run length (LENGTH), the period after which a value is printed (PRTPER) and the same for plotting (PLTPER). Lengths, print periods and plot periods varied with the purpose of the simulation output. The integration interval (DT) was established by a series of initial simulation runs. The results of these runs are plotted in Figure 53. If the integration interval is changed a most noticeable change occurred in the plotted peak height of adult brine shrimp (S3.K). As DT was made smaller, the shrimp peak height increased. However, as DT approaches zero the peak height approaches something less than 31 but greater than 30 shrimp$\cdot$liter^{-1}. To compromise between computer turn-around time, expense, and output accuracy a value of 0.25 day was chosen as the

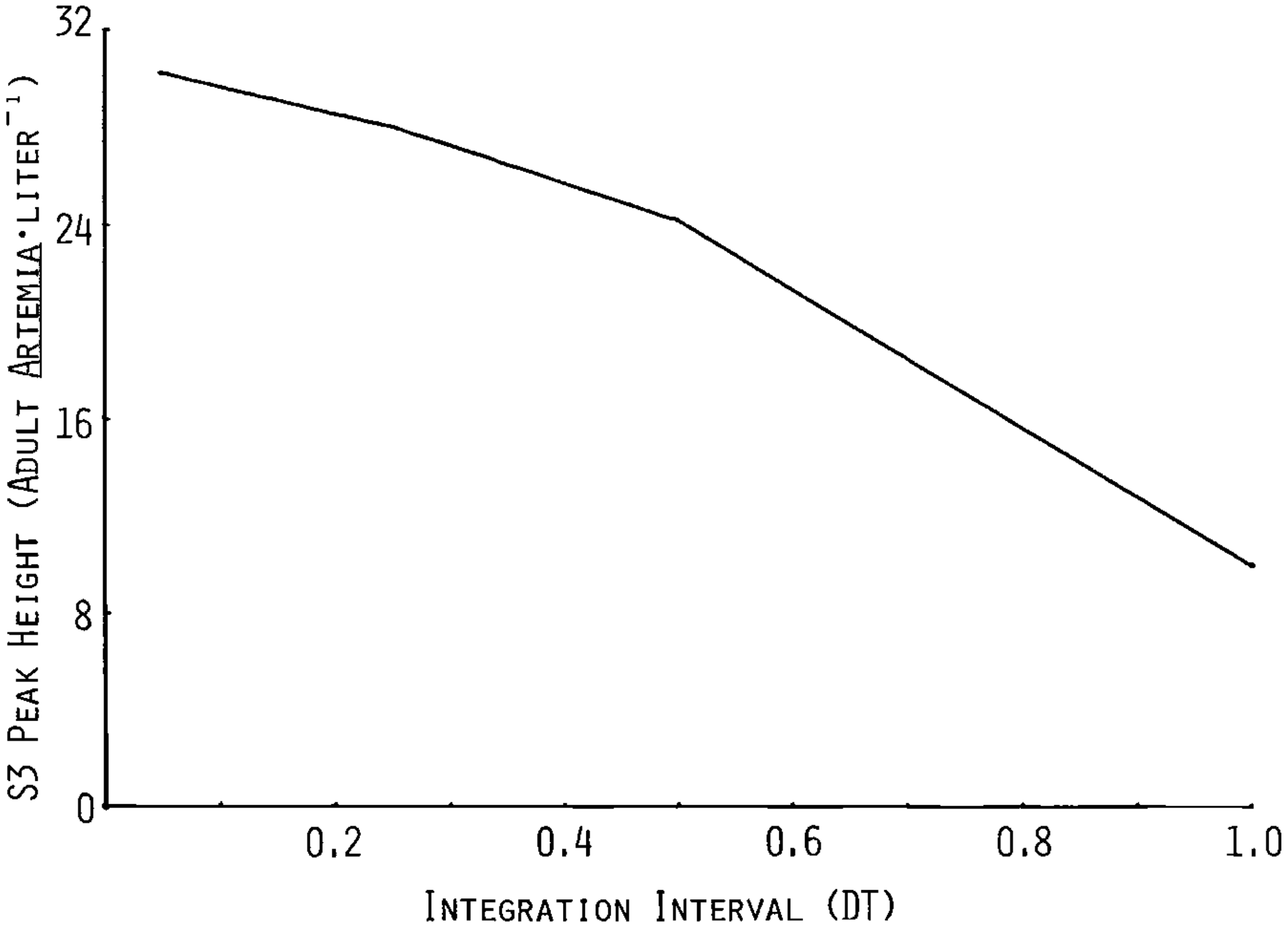

Figure 53. The Effect of Different Integration Intervals on Brine Shrimp Peak Height.

integration interval (giving a brine shrimp peak height of 28 shrimp$\cdot$ liter^{-1}).

Other specifications include the values to be printed and those to be plotted. These are given in DYNAMO by the PRINT and PLOT statements. The values chosen to print or plot varied with the purpose of each computer run.

APPENDIX II

SOME MODEL ERRORS AND THEIR CORRECTION

Since the completion of this work several model errors have been found thanks to discussions with R. G. Wiegert and additional work on the part of the author. These will be presented here along with output from the corrected model's standard run presented for comparison.

Corrected Maximum Algal Productivity: AAAA

In the original model the maximum algal productivity was estimated using the following rationale. The maximum doubling time found by Van Aukin and McNulty (1973) for *Dunaliella viridis* cultures under optimal conditions was ten hours. It was assumed that this meant an algal cell would reproduce once in ten hours or 2.4 times in 24 hours. Since the salinity of the Great Salt Lake is 11% greater than the optimal NaCl concentration for algal growth (Van Aukin and McNulty, 1973), the maximum productivity was reduced to 2.1 new cells·old $\text{cell}^{-1}\cdot\text{dy}^{-1}$.

The above reasoning is erroneous for two reasons: 1) NaCl is not the only chemical species contributing to salinity, and 2) a doubling time of ten hours means, since populations grow exponentially, that $2 = e^{rt}$, where $t = 10$. Thus,

$$r_{max} = \frac{\ln 2}{.42 \text{ day}} = 1.66 \text{ new cells·old cell}^{-1}\text{.dy}^{-1}$$

Figure 54 shows the output when the new AAAA = r_{max} value is used. The new annual repeating pattern is one in which both algal and brine shrimp

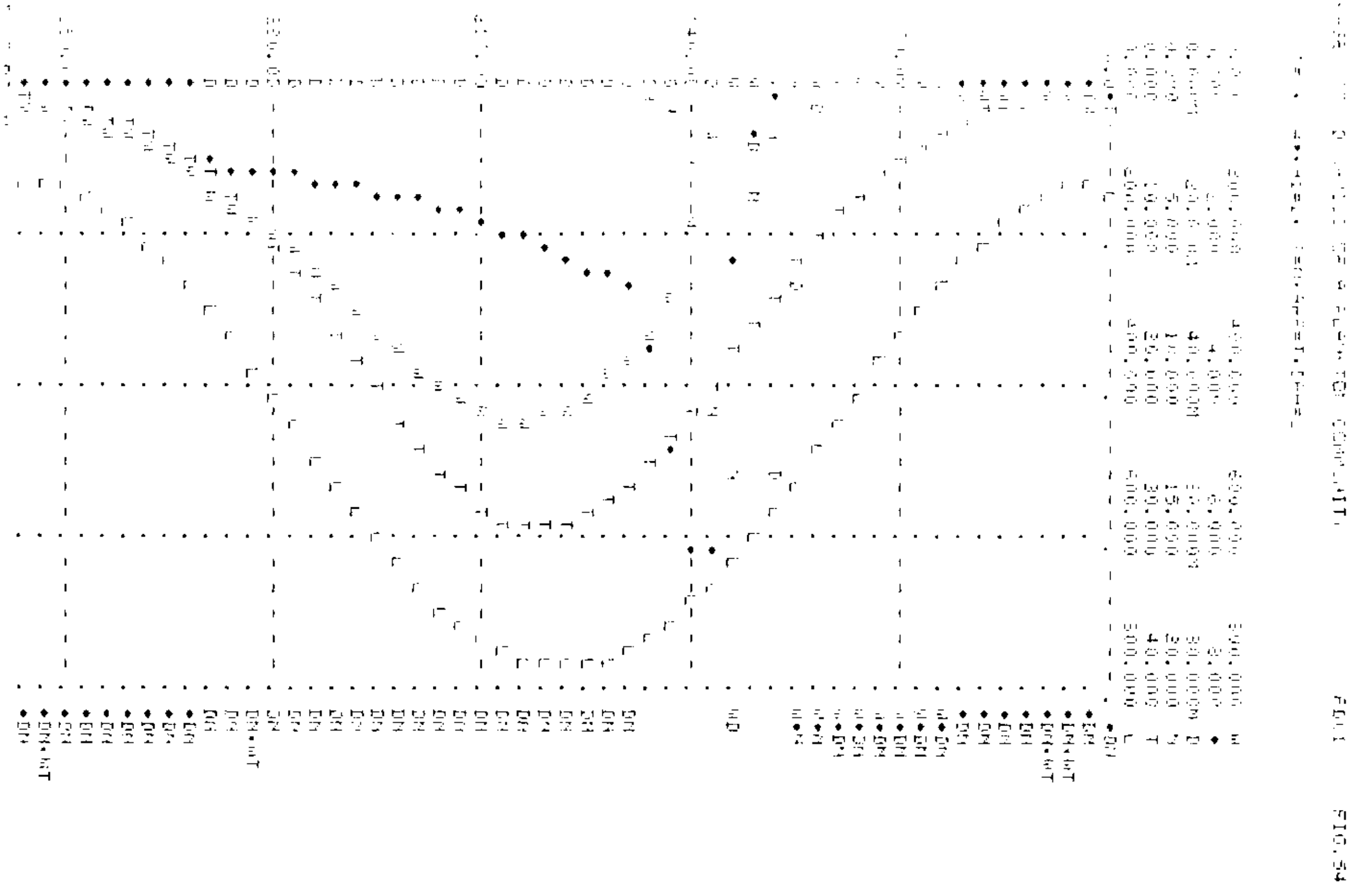

Figure 54. Output after Correcting the Maximum Algal Productivity from 2.1 to 1.66 new cells•old cell^{-1}•dy^{-1}.

production are reduced, however the overall pattern of production in the Great Salt Lake is unchanged. Peaks occur at the same time and the curve shapes are quite similar.

Corrected P vs T Curve: Table AAET

On rechecking the algal production vs water temperature and algal production vs sunlight curves it was noticed that the real data of Van Aukin and McNulty (1973) deviated slightly with respect to the productivity vs water temperature curve (see Figure 55). Because the model testing procedures indicate that the model output is relatively sensitive to small changes in these productivity curves the temperature curve was altered to more closely approximate the data given. The results are given in Figure 56.

The annual production of the repeating pattern is greatly enhanced by this alteration again without changing the location of peaks or the general output shape.

When the above two changes are applied together the output does not represent a linear combination (Figure 57). The algae peak is more similar to that of the first change (AAAA above) as is the brine shrimp peak. The peaks again occur at the same time and the overall output pattern is similar. The dominance of AAAA in this case is consistent with the sensitivity analysis results.

Corrected Brine Shrimp Filtration Rate

The most serious error that has been discovered involved a misunderstanding of Reeve's (1963a) paper concerning brine shrimp filtration

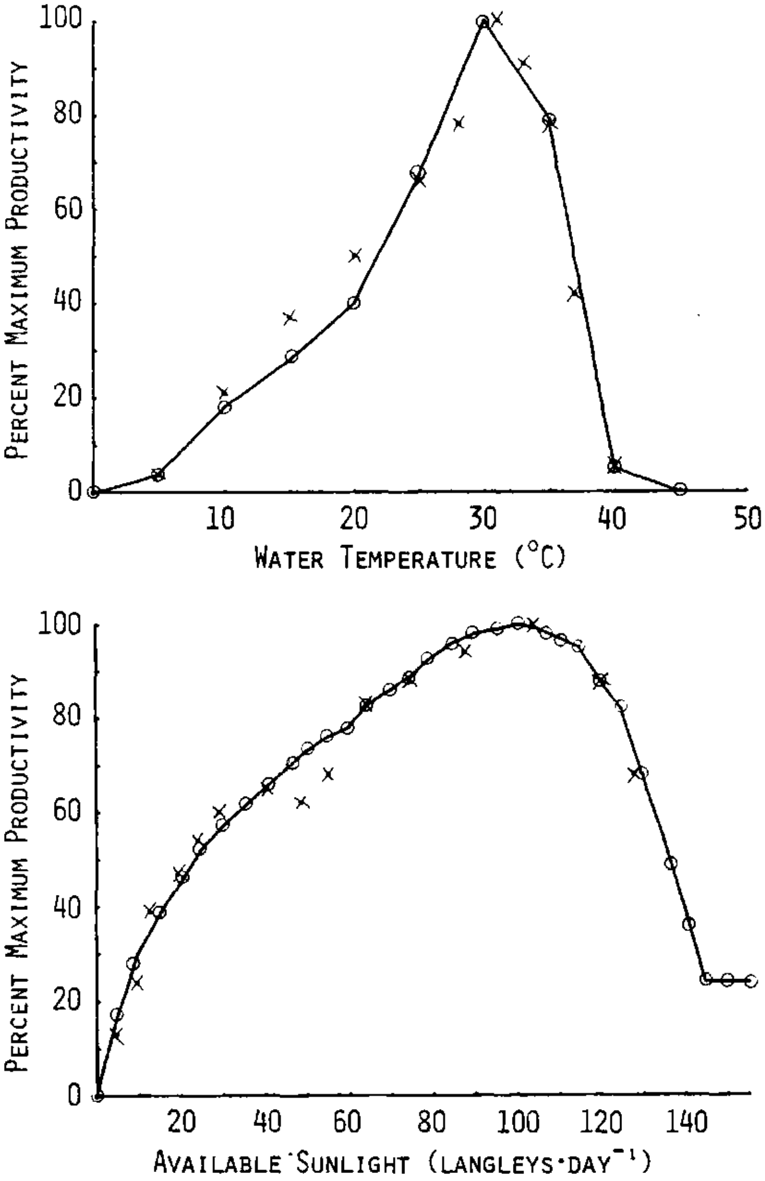

Figure 55. Van Aukin and McNulty's (1973) Productivity vs Sunlight and Productivity vs Water Temperature Curves (x's) Compared with the Data Used in the Model (o's).

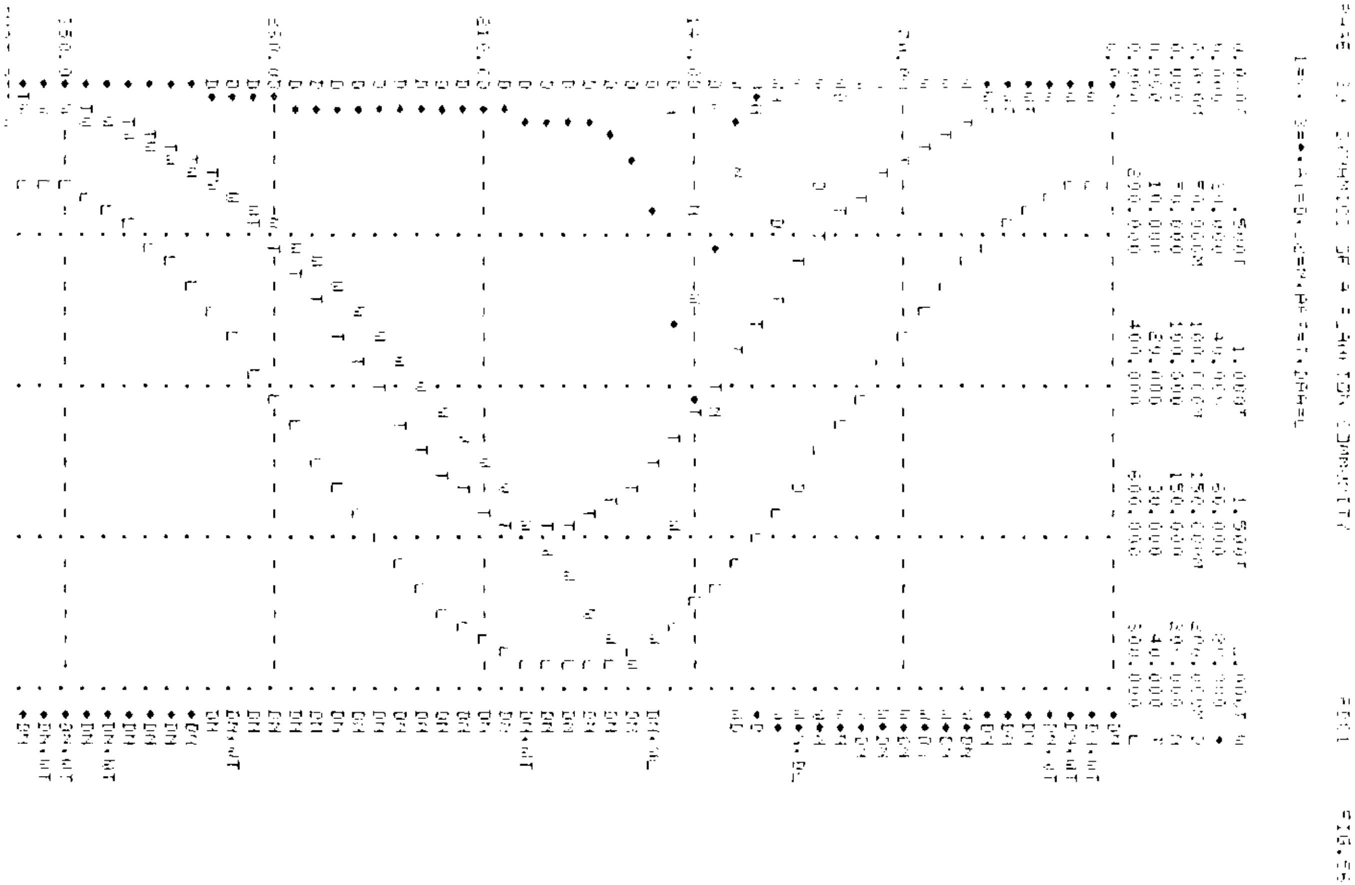

Figure 56. Output after Correcting the Algal Productivity vs Water Temperature Curve.

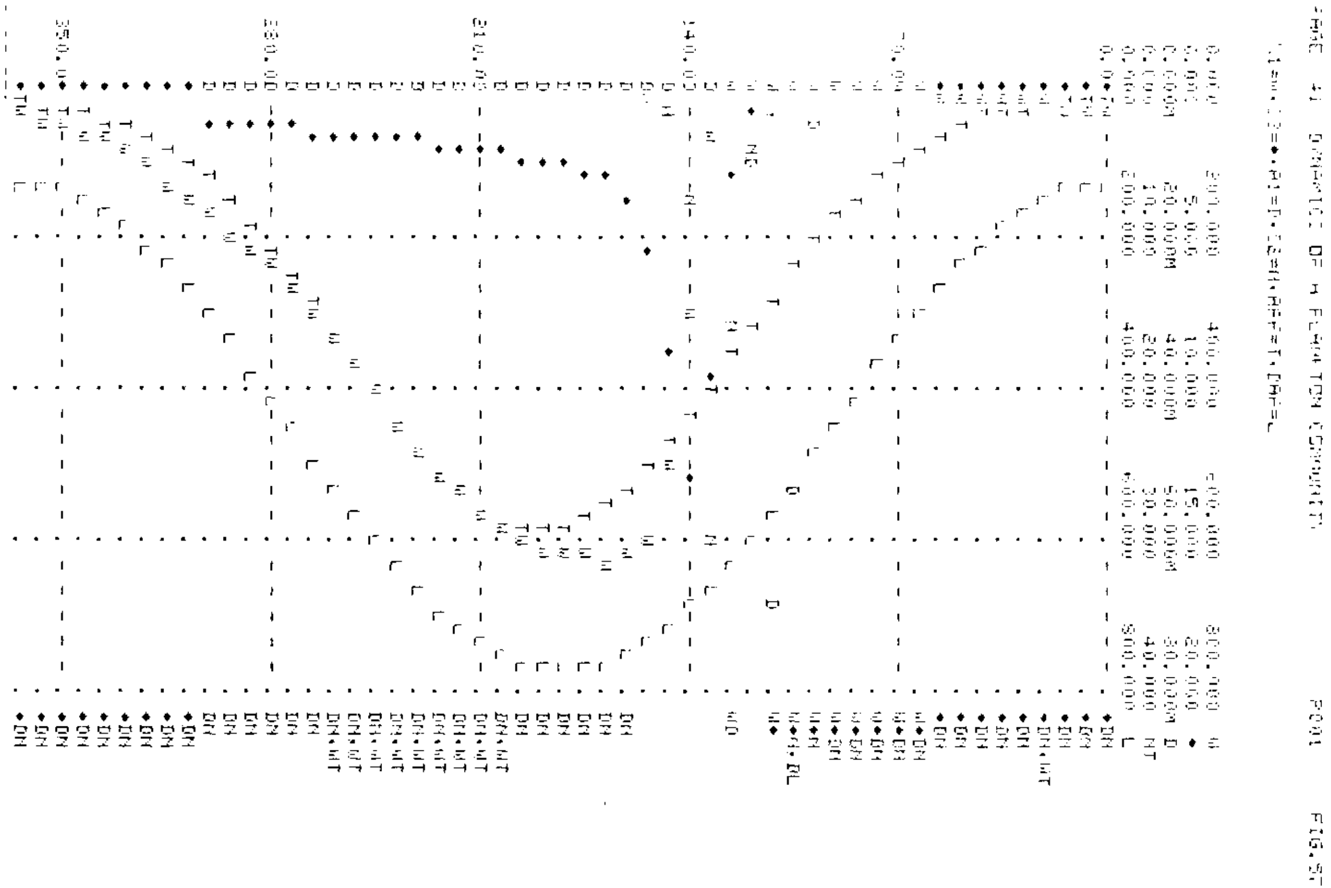

Figure 57. Output after Correcting Both the Maximum Productivity and the Productivity vs Temperature Curve.

rate as a function of algal concentration. The present model assumes that brine shrimp filtration is reduced with increasing algal concentration according to a negative exponential function (Equation 15 through 18, Table 23) with a maximum filtration rate of 220 liters per day, when the water contains no algae (ABBA in Equation 16), and a minimum filtration rate of one liter per day (ABBC in Equation 15) at algal concentrations exceeding about 6×10^5 per liter. This is a gross misinterpretation of Reeve's (1963a) data.

Reeve actually found that below algal concentration of about 7×10^6 per liter (for Artemia feeding on Dunaliella) that the adult filtration rate was at a constant maximum of approximately 0.345 liters per day. Above 7×10^6 algal cells per liter filtration rate (ABBX.K) decreased with increases in algal concentration (A1.K) according to the following power function:

$$\mathrm{ABBX.K} \simeq 4.139 \times 10^5 \, (\mathrm{A1.K})^{-0.8877}.$$

When the above filtration rate replaces the model used in the text the output (Figure 58) is not significantly altered in shape but is altered considerably when considering total system biomass production. This is not surprising since the effect of this alteration was to reduce the filtering ability of the brine shrimp population by about four orders of magnitude. Because of this the algae are not grazed as rapidly; thus more algae can be produced in the spring and more brine shrimp can be supported.

The fact that the overall pattern is relatively unchanged with respect to the points where peaks and declines occur indicate again

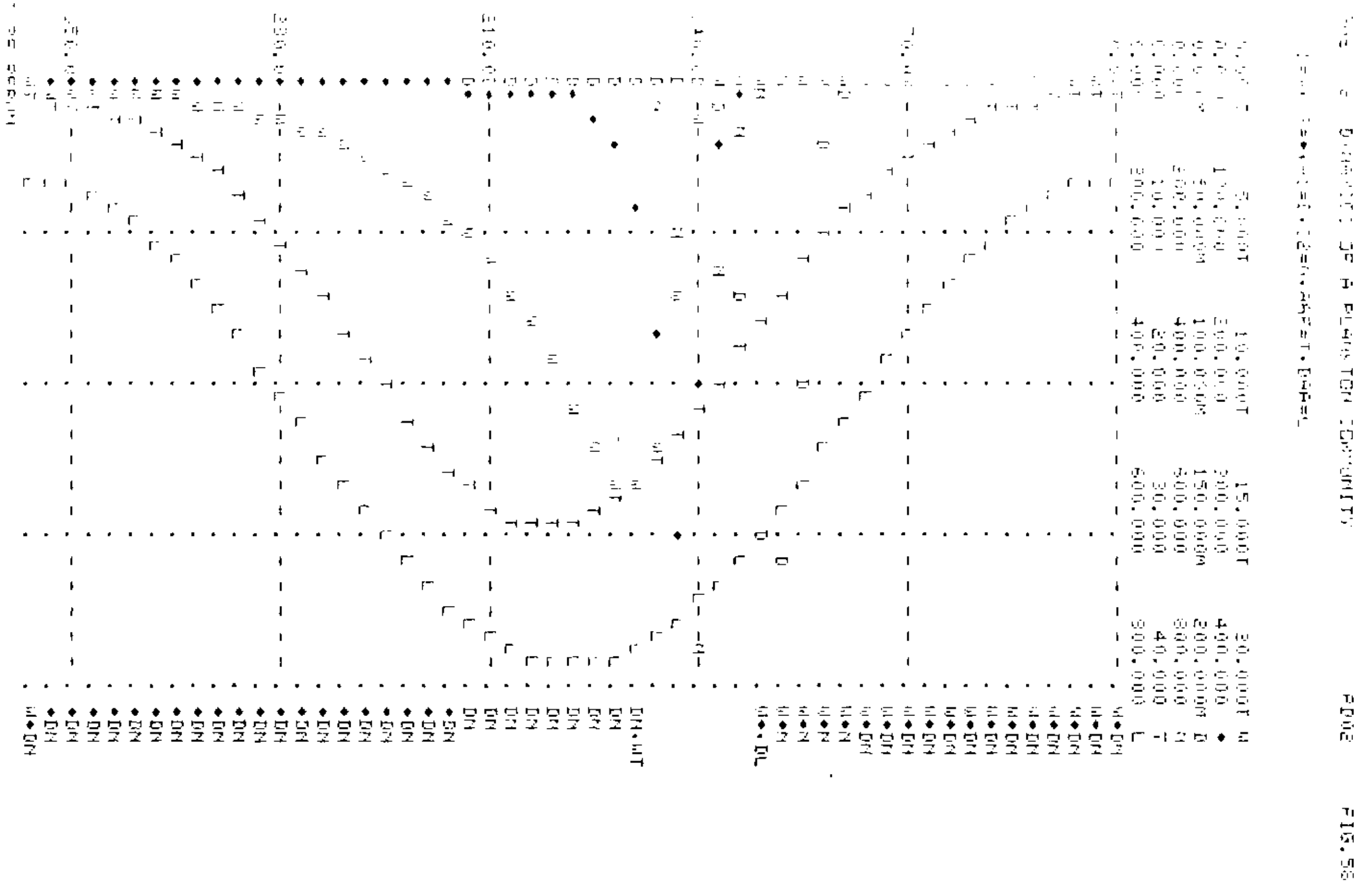

Figure 58. Output after Correcting the Brine Shrimp Filtration Rate.

that the model structure has perhaps found the primary influences governing the annual dynamics in this community. Actual parameter values of relatively insensitive parameters do not alter this observation even over wide ranges. However, future research with this model should perhaps begin with a new analysis of the full ramifications of the above change in filtration rate.

The Output of all Modifications Taken Together

Figure 59 presents the output of all three of the errors found. Obviously, the dominant alteration with respect to annual system biomass production is the filtration rate change. Again the peaks occur at the same time and the general dynamic behavior is the same. Biomass production has been only slightly decreased from the filtration rate adjustment above.

Conclusion

The above represent a continued effort to improve the ability of this model to represent reality. As new information is made available other equations and parameters may be changed. However, confidence may be placed in the major feedback loops and these interactions as identified for this stressed ecosystem in the Dynamic Hypothesis. By way of continued updating this model may provide a useful interactive procedure for directing research in the Great Salt Lake and ultimately provide a predictive model from which to make management decisions.

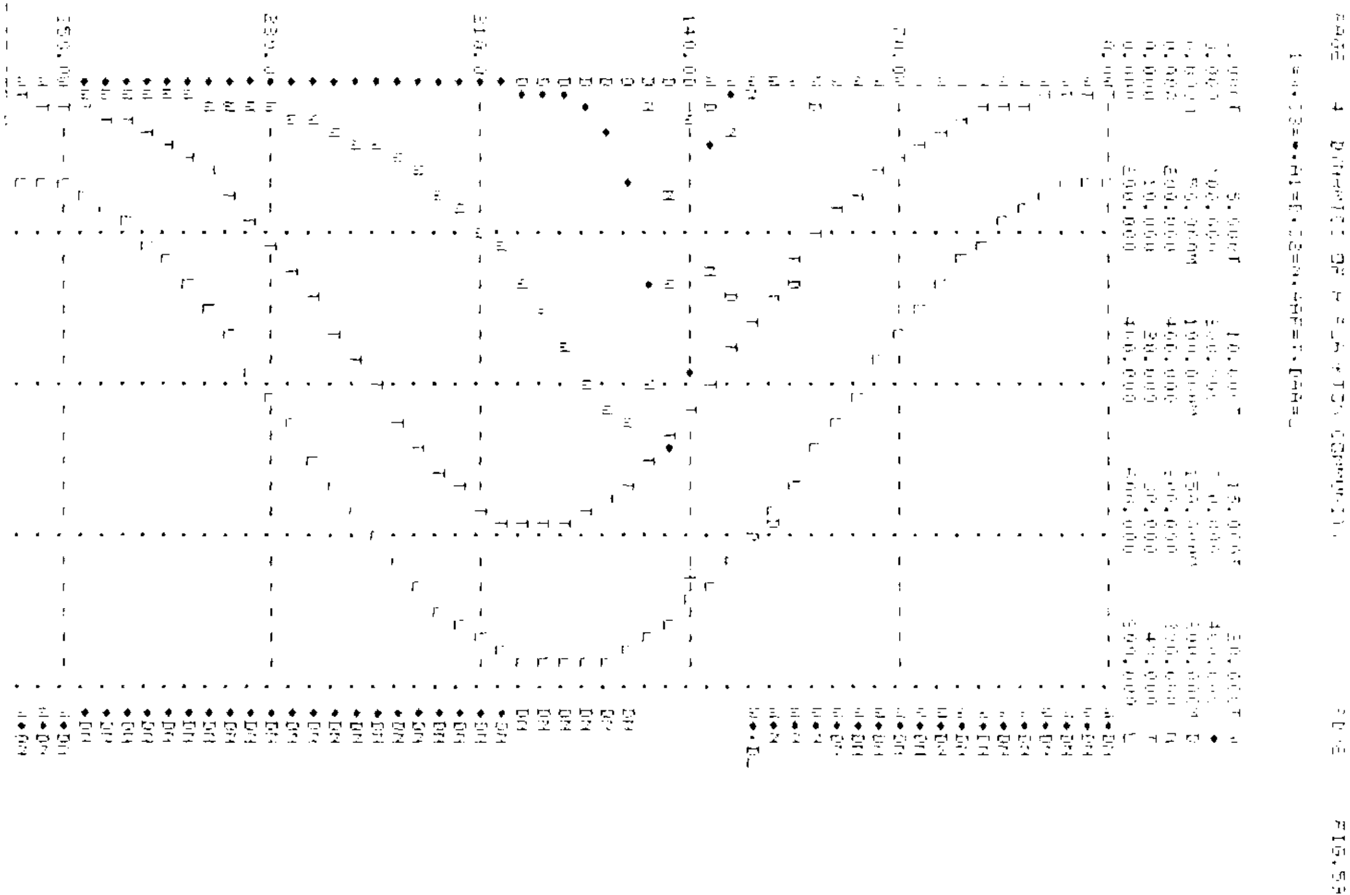

Figure 59. Output after all Corrections have been made.

BIBLIOGRAPHY

Adams, T. C. 1964. "Salt Migration to the Northwest Body of the Great Salt Lake, Utah," Science 143, 1027-1029.

Chapman, V. J. 1968. The Algae. London: MacMillan.

Coburn, A. A., and D. W. Eckhoff. 1972. "Pollution Input from the Lower Jordan Basin to Antelope Island Estuary," in The Great Salt Lake and Utah's Water Resources (J. P. Riley, ed.), pp. 104-120.

Emlen, J. M. 1973. Ecology: An Evolutionary Approach. Addison-Wesley Publ. Co., Menlo Park, Calif. pp. 493.

Engel, D. W., and J. W. Angelovic. 1968. "The Influence of Salinity and Temperature upon the Respiration of Brine Shrimp Nauplii," Comp. Biochem. and Physiol. 26, 749-752.

Forrester, J. W. 1961. Industrial Dynamics. MIT Press, Cambridge, Mass.

Forrester, J. W. 1968. Principles of Systems. Wright-Allen Press, Cambridge, Mass.

Forrester, N. B. 1969. "A Computer Approach to Environmental System Design: Dynamics of a Predator-prey Relationship," N. B. Forrester, Concord, Mass.

Gargas, E. 1976. A Three Box Eutrophication Model of a Mesotrophic Danish Lake. Contributions from the Water Quality Institute, No. 1. Danish Academy of Technical Science.

Greig-Smith, P. 1964. Quantitative Plant Ecology. London: Butterworth.

Gutierrez, L. T. 1974. "Dynamics of Secondary Succession in a Grassland Ecosystem," Ph.D. Dissertation. Georgia Institute of Technology, Atlanta, Ga.

Gutierrez, L. T., and W. R. Fey. 1975a. "Feedback Dynamics Analysis of Secondary Successional Transients in Ecosystems," Proc. Nat. Acad. Sci. USA 72, 2733-2737.

Gutierrez, L. T., and W. R. Fey. 1975b. "Simulation of Secondary Autogenic Succession in the Shortgrass Prairie Ecosystem," Simulation 24, 113-125.

Hahl, D. C., and A. H. Handy. 1969. "Great Salt Lake, Utah: Chemical and Physical Variation of the Brine, 1963-1966," Water Resources Bull. 12. Utah Geol. Min. Soc.

Handy, A. H. 1967. "Distinctive Brines in Great Salt Lake, Utah," U. S. Geol. Survey Prof. Paper 575B, B225-B227.

Handy, A. H., and D. C. Hahl. 1966. "Great Salt Lake: Chemistry of the Water," in The Great Salt Lake. Guidebook to the Geology of Utah (William L. Stokes, ed.), No. 20, pp. 135-151.

Holman, J. A. 1975. "Photoperiod Effects on Reproduction in Artemia salina from the Great Salt Lake," Bull. Ecol. Soc. Amer. 56, 56.

Hutchinson, G. E. 1957. Treatise on Limnology. John Wiley and Sons, Inc., New York. Vol. I.

Jensen, A. C. 1918. "Some Observations on Artemia gracilis, the Brine Shrimp of Great Salt Lake," Biol. Bull. 34, 18-25.

Keunen, D. J. 1939. "Systematical and Physiological Notes on the Brine Shrimp Artemia," Arch. néer. Zool. 3, 365.

Khmeleva, N. N. 1967. "Conversion of Energy in Artemia salina (L.)," Doklady Biological Sciences 175, 435-438.

Knight, J. E. 1971. "Complex Systems Analysis of Water Quality Dynamics: The Feedback Systems Structure," Ph.D. Dissertation. Georgia Institute of Technology, Atlanta, Ga.

Knight, J. E., and W. W. Hines. 1970. "Complex Systems Analysis of Water Quality Dynamics," Completion report OWRR #A-023-GA, School of Indust. Sys. Eng. and Envir. Resources Center, Georgia Institute of Technology, Atlanta, Ga.

Low, W. C., and W. W. Cowles. 1975. "Validation and Evolution of Models," Proc. 1975 Summer Simulation Conference.

Mason, D. T. 1963. "The Growth Response of Artemia salina (L.) to Various Feeding Regimes," Crustaceana 5, 138-150.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS: Statistical Package for the Social Sciences, McGraw-Hall, New York. 2nd. ed.

Odum, E. P. 1971. *Fundamentals of Ecology*. W. B. Saunders Co. Philadelphia.

Odum, H. T. 1971. *Environment, Power and Society*. Wiley-Interscience.

Porcella, D. B., and J. A. Holman. 1972. "Nutrients, Algal Growth, and Culture of Brine Shrimp in the Southern Great Salt Lake," in *The Great Salt Lake and Utah's Water Resources* (J. P, Riley, ed.). pp. 142-155.

Provasoli, L., and K. Shiraishi. 1959. "Axenic Cultivation of the Brine Shrimp *Artemia salina*," *Biol. Bull.* *117*, 347-355.

Pugh, A. L., III. 1973. *Dynamo II User's Manual*. MIT Press, Cambridge, Mass.

Reeve, M. R. 1963a. "The Filter-Feeding of *Artemia*: I. In Pure Cultures of Plant Cells," *J. Exp. Biol.* *40*, 195-205.

Reeve, M. R. 1963b. "The Filter-Feeding of *Artemia*: II. In Suspensions of Various Particles," *J. Exp. Biol.* *40*, 207-214.

Reeve, M. R. 1963c. "The Filter-Feeding of *Artemia*: III. Faecal Pellets and Their Associated Membranes," *J. Exp. Biol.* *40*, 215-221.

Reeve, M. R. 1963d. "Growth Efficiency in *Artemia* under Laboratory Conditions," *Biol. Bull.* *125*, 133-145.

Relyea, G. M. 1937. "The Brine Shrimp of the Great Salt Lake," *Amer. Natur.* *71*, 612-616.

Slobodkin, L. B. 1968. "How To Be a Predator," *Amer. Zoologist* *80*, 43-51.

Stephens, D. W. 1974. "Limnological Considerations of the Great Salt Lake, Utah," Ph.D. Dissertation, University of Utah.

Stephens, D. W., and D. M. Gillespie. 1972. "Community Structure and Ecosystem Analysis of the Great Salt Lake," in *The Great Salt Lake and Utah's Water Resources* (J. P. Riley, ed.). pp. 66-72.

Stephens, D. W., and D. M. Gillespie. 1976. "Phytoplankton Production in the Great Salt Lake, Utah, and a Laboratory Study of Algal Response to Enrichment," *Limnol. Oceanogr.* *21*, 74-87.

Stephens, K., and J. D. H. Strickland. 1962. "Use of a Thermopile Radiometer for Measuring the Attenuation of Photosynthetically Active Radiation in the Sea," *Limnol. Oceanogr.* *7*, 485-487.

Stokes, W. L. (ed.). 1966. *The Great Salt Lake.* Guidebook to the Geology of Utah, No. *20. Utah Geol. Soc.*, Salt Lake City.

Sushchenya, L. M. 1962. "Quantitative Data on Nutrition and Energy Balance in *Artemia salina* (L.)," *Dokl. (Proc.) Acad. Sci. USSR* *143*, 329-330.

Van Aukin, O. W., and I. B. McNulty. 1973. "The Effect of Environment Factors on the Growth of a Halophylic Species of Algae," *Biol. Bull.* *145*, 210-222.

Vorhies, C. T. 1917. "Notes on the Fauna of the Great Salt Lake," *Am. Natur.* *51*, 494-499.

Wetmore, A. 1917. "On the Fauna of Great Salt Lake," *Am. Nat.* *51*, 753-755.

Wiegert, R. G. 1976. *Ecological Energetics*. Dowden, Hutchinson and Ross, Inc., Stroudsberg, Pa.

Wirick, C. D. 1972. "*Dunaliella-Artemia* Plankton Community of the Great Salt Lake, Utah," M.S. Thesis. University of Utah.

Woodbury, A. M. 1936. "Animal Relationships of Great Salt Lake," *Ecology* *17*, 1-8.

Woolley, R. R., and R. E. Marsell. 1946. "Great Salt Lake: A Selected Bibliography with Annotations," *Transactions, Amer. Geophys. Union 27*, 103-107.

Wright, R. D. In Progress. "Some Aspects of Dynamic Model Validation," Ph.D. Dissertation. Massachusetts Institute of Technology. Cambridge, Mass.