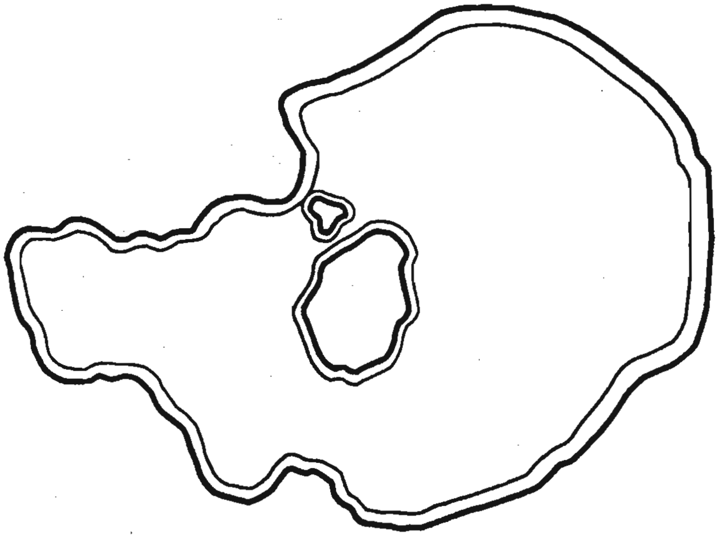
An Auxiliary Report
Prepared for the

MONO BASIN WATER RIGHTS EIR

A Modeling Analysis of *Artemia* Dynamics in Mono Lake



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Mono Basin EIR Auxiliary Report No. 13

An Auxiliary Report
Prepared for the
Mono Basin Water Rights EIR Project

This auxiliary report was prepared to support the environmental impact report (EIR) on the amendment of appropriative water rights for water diversions by the City of Los Angeles Department of Water and Power (LADWP) in the Mono Lake Basin. Jones & Stokes Associates is preparing the EIR under the technical direction of the California State Water Resources Control Board (SWRCB). EIR preparation is funded by LADWP.

SWRCB is considering revisions to LADWP's appropriative water rights on four streams tributary to Mono Lake, Lee Vining Creek, Rush Creek, Parker Creek, and Walker Creek. LADWP has diverted water from these creeks since 1941 for power generation and municipal water supply. Since the diversions began, the water level in Mono Lake has fallen by 40 feet.

The Mono Basin water rights EIR examines the environmental effects of maintaining Mono Lake at various elevations and the effects of possible reduced diversions of water from Mono Basin to Owens Valley and the City of Los Angeles. Flows in the four tributary creeks to Mono Lake and water levels in Mono Lake are interrelated. SWRCB's decision on amendments to LADWP's water rights will consider both minimum streamflows to maintain fish populations in good condition and minimum lake levels to protect public trust values.

This report is one of a series of auxiliary reports for the EIR prepared by subcontractors to Jones & Stokes Associates, the EIR consultant, and contractors to LADWP. Information and data presented in these auxiliary reports are used by Jones & Stokes Associates and SWRCB, the EIR lead agency, in describing environmental conditions and conducting the impact analyses for the EIR. Information from these reports used in the EIR is subject to interpretation and integration with other information by Jones & Stokes Associates and SWRCB in preparing the EIR.

The information and conclusions presented in this auxiliary report are solely the responsibility of the author.

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Draft

A Modeling Analysis of *Artemia* Dynamics in Mono Lake

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`Note revisions of 24 July 1992 attached to back of this report`

Summary

A cohort model of the *Artemia* dynamics was coupled with a description of the major nitrogen fluxes in Mono Lake and used to assess the effects of changing lake levels on the *Artemia* population. The model described many of the general characteristics of the plankton dynamics observed in Mono Lake including the seasonal pattern of the partitioning of nitrogen among ammonium, algal, and *Artemia* pools; reasonable estimates of annual primary, secondary, naupliar, and cyst production; and decreases in production during the recent period of meromixis. However, subadult instar-specific abundances were not well simulated. Further refinement will be limited until a better understanding of the temporal pattern and determinants of cyst hatching are understood and a more detailed description of vertical mixing and the temperature structure of the water column is included in the model. This latter refinement is also necessary to model the vertical fluxes of nitrogen during meromixis, which cannot be accurately simulated with the present two-layer model.

The model was generally insensitive to variation in most of its parameters as measured by annual means in biomass and production except for those affecting nitrogen availability. Reductions in the vertical flux of nitrogen simulated by using the mixed-layer depth from a meromictic year resulted in reduced primary and secondary production compared to a monomictic year. Conversely, increased nitrogen availability simulated by increasing the sediment release of ammonium enhanced production. Other analyses with the model also suggest the availability of nitrogen dominates the plankton dynamics.

The model predicts changes in life history parameters of the *Artemia* derived from salinity bioassays have little effect on mean annual biomass and secondary production estimates of the *Artemia* population on an areal basis. Thus, the model predicts the population level response of the *Artemia* due to salinity is less than that expected from salinity bioassay experiments. The responses to changing lake levels predicted by the

model are little different from those based solely on area or volume changes. Only cyst production is predicted to be more severely effected. Cyst production was estimated to decrease nearly six-fold over the range of salinity from 51 to 120 g l^{-1}. However, decreases in cyst production, as illustrated by the low sensitivity to 20-fold changes in hatching success, are expected to have neglible effects on a subsequent year's dynamics.

The results are largely due to the dominant role of nitrogen in limiting primary production and the simple trophic structure of the plankton community. Because the algae are capable of much higher growth rates than those realized under the nutrient limiting conditions found during much of the season, and *Artemia* growth and fecundity is limited by algal biomass during most of the time they are abundant, the model is insensitive to changes which do not alter the nitrogen availability. This conclusion is based on consideration of the effects of salinity on *Artemia* life history characteristics and maximum algal growth rates. If changes in salinity affect the availability of nitrogen through processes not modeled here then different responses may occur.

Introduction

The impacts of changing lake level on the plankton community in Mono Lake depend not only on the effects of changing salinity on individual species' physiological rates, but also on the interactions among various components of the plankton (cf. Dana *et al.* 1992). Seasonal plankton dynamics in Mono Lake are dominated by annual variation in climate and strong interactions among nutrients, algae, and the macrozooplanktor, *Artemia monica.* Nitrogen limitation of algal growth has been observed both in ammonium bioassay experiments (Jellison *unpubl. data*) and in the field under conditions of varying climate as seen during the recent period of meromixis in which the vertical flux of ammonium was reduced resulting in lower primary production (Jellison and Melack *In press*). However, during the summer, abundant *Artemia* graze the algal population to low levels and ambient ammonium concentrations often increase. Thus, nitrogen limitation of primary production during the summer is likely to be less pronounced or absent. Summer increases of ambient ammonium are due to the combined effects of *Artemia* ammonium excretion, deepening of the mixed layer, and reduced algal demand accompanying low standing biomass. While *Artemia* limit algal biomass, algal biomass to a large extent determines *Artemia* fecundity. In predicting the effects of salinity changes on the overall plankton community, these salient characteristics must be recognized.

The negative impact of increased salinities on physiological characteristics of *Artemia* is well documented (e.g. Dana and Lenz 1986, Herbst and Dana 1980, Drinkwater and Crowe 1991). A recent review of salinity bioassays conducted on *Artemia monica* indicate that most life history characteristics are negatively influenced as salinities increase over the range 76 to 168 g l^{-1} (see Dana *et al.* 1992). Decreases in hatching success, survival, weight, ovigery, brood size, and development rates occur. Delays in maturation and day of hatch, and a lengthening of the inter-brood duration also occur. The extrapolation of these physiological effects on individuals to the population level is difficult due to the strong coupling between trophic levels in Mono Lake.

Over the past two decades, Mono Lake has been the subject of extensive research making it one of the best studied saline lake in the world. A major component of this research has been done by

University of California (Santa Barbara) researchers and consists of an extensive monitoring program conducted 1982 to 1992. During this time both lake level and salinity changed. Despite this extended data record, the direct observation of effects of salinity on the *Artemia* population is difficult and unlikely to be detected even if present. The past decade included a period of unusual climatological conditions at Mono Lake. Changes in the physical mixing regime of Mono Lake associated with the onset, persistence, and breakdown of meromixis dramatically altered the plankton dynamics and most likely obscured effects due to changes in salinity.

In this study, population level responses of the *Artemia* to changes in salinity are predicted utilizing a simulation model of the plankton dynamics which, in addition to including the effects of salinity on individual *Artemia*, also includes interactions among nutrients, algae, and *Artemia*. Effects of salinity changes on *Artemia* are simulated by changing model parameters which describe the growth, reproduction, and mortality of *Artemia*. We have tried to formulate the simplest representation of the plankton dynamics capable of simulating the feedbacks among the various plankton components and predicting *Artemia* responses to changes in salinity. Because salinity affects many different aspects of *Artemia* life history and because *Artemia* are fairly long-lived including a long period of maturation in the spring, this description necessarily includes an *Artemia* population model. Our description of the *Artemia* demographics and nitrogen recycling requires the estimation or measurement of many unknown parameters. While many of these were approximated from field and laboratory data, others were estimated using parameter estimation techniques. Our approach was to estimate the functional dependencies of development rates and mortality on temperature and algal biomass using data from laboratory experiments and then estimate the more uncertain remaining parameters from comparison of model simulations to field data.

Given our current understanding of the plankton processes in Mono Lake and the necessary simplifying assumptions we were forced to make, only modest goals of this modeling exercise are reasonable. Our primary goal is to assess to what extent salinity caused changes in *Artemia* physiological rates are manifest at the population level. A direct extrapolation of reduced fecundity observed in salinity bioassays to the field predicts large declines in the the *Artemia* population (Dana and Lenz 1986). However, the negative feedbacks and control processes entailed by the tight coupling of nutrients, algae, and *Artemia* imply individual physiological rates may be much less important in determining overall production and seasonal patterns. The model is utilized to address the relative importance of these processes. Secondary goals are mainly heuristic: checking the logical consistency of our current understanding and determining further research needs. While gaps in our current understanding have precluded a simple simulation of the EIR 50-year alternative scenarios, we have endeavored to increase the utility of this research for the EIR assessment by conducting a number of simulations under both meromictic and monomictic conditions at various lake levels. These results represent our best scientific judgement of the expected effects of changing lake level on the *Artemia* population and provide general insight into the interactions among ammonium, algae, and *Artemia*.

Description of models

Overview

The model focuses on *Artemia* life history processes and includes only simple descriptions of other processes. The basic design of the moded is to simulate the fluxes of nitrogen between epilimnetic and hypolimnetic dissolved ammonium pools and algal and *Artemia* particulate pools (Fig. 1). Limnological characteristics of the Mono Lake make this representation a reasonable departure for modeling. The dissolved phosphorus concentrations are always high (600 - 1000 μM) and other forms of nitrogen (nitrite and nitrate) are always very low. There are no planktonic forms of heterocystic bluegreens and inputs of nitrogen from inflowing streams are very low. Explicitly formulated processes include algal growth and settling, vertical flux and sediment release of ammonium, and *Artemia* ammonium excretion, grazing, and fecal pellet production. The bacterial dynamics in the lake are virtually unknown, and no description is included in our present modeling efforts. Their exclusion does not imply they are not a major component of the plankton, only that an explicit description of their dynamics is not necessary in describing the major feedbacks and control processes affecting the *Artemia* population.

Process Descriptions

Development -- *Artemia* growth and development are modeled as the movement of individuals through age classes. The rate of development depends on individual grazing rates which are instar-specific and is explicitly dependent on temperature and algal biomass. Originally, *Artemia* were divided into 12 age classes representing distinct instars: seven naupliar (1-7), four juvenile (8-11), and one adult (12+). However, this representation combined with the first order differential equation algorithm results in significant broadening of the age class distributions over time. In some systems this "numerical diffusion" can be prevented by matching the model time step to the development rate. In the present case, this is not possible because the development rates vary widely over the season and are not a simple function of temperature alone. A solution was found by dividing each age class into subclasses. This provided a closer match between the time step and development rates during the early part of the year and prevented the otherwise pronounced "numerical diffusion". However, during the summer period of warm water temperatures, development rates of individuals are such that movement through several subclasses must be allowed. We designed a modification of the ordinary differential equation algorithm which allows individuals to move ahead more than one age subclass during a single time step. This algorithm worked well in describing the development of *Artemia* in the laboratory under different temperatures and algal biomasses (Jellison *et al.* 1988).

The determination of a suitable representation of development has been problematic in the current model development. Previous research (Jellison *et al.* 1989) determined empirical relationships between development rates and temperature and algal biomass. Our current effort differs from these in that development is formulated as explicitly dependent on grazing rates. This is necessary if questions regarding compensatory effects due to tight coupling between the algal and *Artemia* population are to be addressed.

Zooplankton feeding is most often approximated as a simple age-specific filtration process bounded by some upper limit. This characterization is appropriate for *Artemia monica.* However, even this simple model requires specification of instar-specific maximum grazing rates, clearance (i.e. filtering rates), temperature effects, and growth efficiencies. None of these are accurately known for *A monica.* However, experiments conducted at Mono Lake (Lenz 1982, Jellison *unpubl. obs.*) and comparisons to other studies conducted with different but closely related species of *Artemia* allow estimates to be made for some of these parameters. In our initial formulation of grazing, both maximum grazing and filtering rates were assumed to be proportional to weight. However, this explicit formulation of grazing could not reproduce data from laboratory development experiments (Jellison *et al.* 1988). For this reason, we analyzed alternative grazing formulations which specify different relative rates of instar-specific grazing.

A formulation for instar-specific maximum grazing rates was derived by Abreu-Grobois *et al.* (1991) based on feeding experiments conducted with *A. franciscana.* It assumes instar-specific maximum grazing rates are described by a negative exponential equation:

$$grzmax_i = grz_1 \times \left(1 - e^{grz_2 \times wt_i}\right)$$

where $grzmax_i$ is the maximum grazing rate of algae in mg dry weight d^{-1} of the *i*th instar, grz_1 a constant equal to the maximum grazing rate of adults, grz_2 a constant describing the shape of the curve, wt_i the age class specific weight in mg dry weight d^{-1}. This relation predicts higher grazing rates in earlier instars relative to older ones than a rate based on weight (Fig. 2). The formulation agrees with experiments conducted by Reeve (1963) which show a rapid increase in maximum grazing at low weights and early instars followed by saturation at weights equivalent to juvenile instars. The weight-length relationship is similar for *A. monica* under summer conditions (Jellison *et al.* 1988) and that derived for *A. franciscana* by Abreu-Grobois *et al.* (1991). Although we observed differences in the weight-length relationships of *A. monica* raised at different temperatures, we use the summer weight-length relationship throughout. The majority of the *Artemia* seasonal abundance is closer to the conditions observed in our summer treatment. In Abreu-Grobois *et al.* (1991), adult *Artemia* were capable of a maximum daily grazing rate of 70 to 80% of their body weight while earlier instars ingested much higher amounts relative to their weight. Assuming constant N:dry weight conversion of 7% for both *Artemia* and algae, and our summer weight-length relationship, results in grazing coefficients of 0.03 mg N d^{-1} for grz_1 and -239 for grz_2. Oppenheimer & Moreira (1980) found that *Artemia* N:dry weight content ranged from 5.23 to 9.21% among instars.

The above negative exponential only describes maximum grazing rates at near optimal temperatures. A description of grazing at suboptimal temperature and food conditions requires specification of instar-specific filtering rates. We tested formulations in which filtering rates were proportional to weight, length, and maximum grazing rate. The formulation which assumes filtering rates are proportional to weight performed much better than the other two. A level of algal biomass at which grazing is zero, *grzalgmin,* was also added, primarily to help insure numerical stability. This has the not unreasonable effect of adding an algal "refuge". A value near 15, corresponding to 0.75 µg chl *a* l^{-1} was used. In practice, the numerical integration of grazing often overshoots this chlorophyll concentration during periods of high *Artemia* abundance resulting in oscillations about this low value.

The above assumptions result in the following grazing rate:

$$grate_i = \min\left[grz_1 \times \left(1 - e^{grz_2 \times wt_i}\right) \times tmpfac,\ \frac{wt_i}{wt_{\max}} \times tmpfac \times \frac{\max\left[0,\ alg - grzalgmin\right]}{grzalg}\right]$$

where $grate_i$ is the realized grazing rate, wt_{max} is the maximum adult weight, *grzalg* is a constant describing filtering rates below saturating levels of algal biomass, *tmpfac* is a temperature correction factor for below optimum temperatures and other variables are as defined above.

After grazing rates are calculated, they are multiplied by a fixed growth efficiency factor to determine weight gain. The fraction of individuals which move into the next age subclass is the total weight gain of an age subclass divided by the difference of the weight of the next age subclass and the current one. If this exceeds one, then all the individuals move into the next age subclass and a certain portion dictated by the weight of the next age class move ahead another age subclass. The efficiency of all subadult classes (eff_1) was assumed to be 0.44. This is the average efficiency for *A. salina* found by Reeve (1963) under a number of different conditions. Growth beyond the adult stage is not modeled and assimilated energy is assumed to go toward producing eggs at a fixed but possibly different efficiency (*eff2*).

Initially the grazing temperature factor was formulated as a simple exponential dependence. While simulation using this formulation provided a close fit to observed laboratory data, the equivalent "Q_{10}" implied by the exponential temperature coefficient was unreasonbly high and results in a more pronounced temperature effect than likely at the high end of the range of observed temperatures (15 to 20°C). For this reason we used a normal curve to represent the response of grazing to temperature over the observed range.

$$tmpfac = e^{-2.3\left(\frac{t-topt}{grztmp-topt}\right)^2}$$

where *topt* is the temperature of optimal growth, *t* the ambient temperature, and *grztmp,* a constant which defines the width of the curve. The optimal temperature was assumed to be 30°C; Hernandorena (1976) found higher growth rates at 30°C than at 25°C for *A. salina.* The normal curve results in a less pronounced temperature effect over the upper range of temperatures and a more severe decline over the lower range of temperatures. This simulated the laboratory data well (Figs. 4 - 6) and is consistent with the dramatic reduction in growth and increases in mortality observed in treatments beginning near 5 °C

(Jellison *et al.* 1988). Most importantly the timing of instar development was accurately described.

Mortality -- Estimates of zooplankton mortality rates are difficult to extract from field data due to the interplay of recruitment, development, and mortality in generating the observed temporal abundance curves. Direct estimates from the laboratory development experiments were also difficult because individuals were not followed through time. Instead, parameter estimation procedures were used in conjunction with data from the development experiments to determine mortality rates. Instar-specific mortality was formulated as a separate base rate for naupliar, juvenile, and adult age classes with an additional multiplicative mortality factor experienced by naupliar instars at suboptimal temperature and food conditions. Laboratory experiments indicated a large increase in mortality at temperatures below 5°C and an increase in early instar mortality at low food levels. There is no information on the functional form of this dependence so we chose a multiplicative factor in the form of an inverse rectangular hyperbola. This has the desirable properties of being defined by a single constant: going to infinity at zero, and approaching one at several times the "half-saturation" constant.

It was not possible to determine adult mortality rates from the laboratory experiments because they were terminated shortly after individuals reached the adult stage. Adult mortality was estimated by comparison of model output to field data collected from two years representative of meromictic (1984) and monomictic (1990) conditions. Originally a constant adult mortality rate was assumed. However, model comparisons with field data indicated this was insufficient to simulate the autumn decline. Any mortality rate large enough to cause the autumn decline yielded too few adults earlier in the year. Increased mortality in the autumn is likely due to senescence and to simulate this the age-class vector of abundance was lengthened by adding six additional adult age classes. The movement of individuals among the adult age classes (total of nine) is determined by the brood interval (*brdint*). Individuals from the last juvenile age class mature into the first adult class. Thereafter, an individual moves ahead an age class each time it produces a brood. Laboratory experiments yield a natural adult longevity under optimal conditions of seven to ten broods (Browne 1982). The nine adult age classes included here allow increasing mortality with each brood to be modeled. Mortality was assumed to increase linearly through the adult age classes. On reaching the last age class an individual may have further broods but the mortality remains constant. A thirty percent increase in the base mortality after each brood due to senescence (*sen* = *0.3*), yielded an autumn decline similar to that observed in the field data. The above assumptions result in the following equations:

$$mor_{i=1...7} = morn \times \frac{alg + moralg}{alg} \times \frac{tmp + mortmp}{tmp}$$

$$mor_{i=8...11} = morj$$

$$mor_{i=12+} = mora \times \left(1 + sen \times \left(i - 12\right)\right)$$

where mor_i is the instar-specific mortality, *tmp* the mixed-layer temperature; *alg* the algal biomass; *morn, morj,* and *mora* the base mortality rates for nauplii, juveniles and adults; and *mortmp* and *moralg* constants determining the effect of low temperatures and algal biomass.

Cyst hatching -- Cyst hatching was assumed to be normally distributed about a given day of peak hatch (*hday*). Analysis of *in situ* hatching and first instar abundance curves yielded a standard deviation of ca. 15 days (*hsd*). Initially the peak day of hatch was estimated from first instar abundances and previous cohort analysis (Jellison *et al.* 1989). This cohort analysis and estimates of total annual cyst production for the period 1983 to 1988 (*hcyst* = 1.6×10^6) indicate only 0.33 to 2.8% of cysts produced in the previous year hatch (Jellison *et al.* 1989). In using the model to estimate the percent hatch, no distinction can be made between overwintering degradation or mortality occurring immediately after hatching. This may partially explain why these hatching rates are so low compared to those achieved in laboratory studies (cf. Dana and Lenz 1986).

Reproduction -- After individuals reach the adult stage, assimilated energy is assumed to go into reproduction. Reproduction is either oviparous (cyst producing) or ovoviviparous (naupliar producing) depending on antecedent temperature and algal conditions, the day of year, and which adult subclass an individual is in. The determinants of reproductive mode are poorly understood (Jellison *et al.* 1987). An analysis of ovoviviparity determined that 67% of the variance in early summer (late May - June) ovoviviparity could be explained by a multiple regression on temperature and algal biomass at thirty days previous (*ovo1, ovo2, ovo3*). This formulation is used in the current analysis to derive ovoviviparity during most of the year. This regression does not predict the mode of reproduction late in the year when only a small fraction of the females (usually less than 2%) are producing oviparously. Therefore, in the model a single low constant ($ovoi = 0.02$) is specified for all days after a designated day late in the summer ($ovof = 240$). In laboratory experiments, ovoviviparity is observed to markedly decrease in subsequent broods (Dana and Lenz 1986). The model assumes ovoviviparity is limited to the first two broods with the fraction of females whose second brood is ovoviviparous half that of calculated for the first brood ($ovo4 = 0.5$).

Egg production is calculated by dividing the assimilated energy ($grate_j \times eff_2$) by the weight of individual eggs (wt_{egg}) and multiplying by the female fraction (*repff*) and proportion ovigerous females (*repovig*), both of which are assumed constant. A maximum individual egg production rate (*repmax*) is also assumed. This results in egg production per adult, *eggfac*:

$$eggfac = repff \times repovig \times \min\left[repmax,\ \frac{grate_{34...42} \times eff_2}{wt_{egg}} \right]$$

where *grate* is the grazing rate and eff_2 the egg production efficiency. This factor is multiplied by the abundance in each age class and then the ovoviviparity factor to determine naupliar production or (1 - ovoviviparity) to determine cyst production.

Nitrogen fluxes among dissolved, algal, and Artemia nitrogen pools

The model includes a simple description of fluxes between dissolved, algal and *Artemia* nitrogen pools and inputs from the sediments. This description includes algal growth and settling, the vertical flux and sediment release of ammonium, and *Artemia* ammonium excretion, grazing, and fecal pellet production. While nitrogen fluxes among epilimnetic, hypolimnetic, algal and *Artemia* fractions are not our present focus, their inclusion is necessary to simulate properly the effects of changing salinity on *Artemia*. Ammonium concentrations in the water column are divided into mixed-layer (or epilimnion) and hypolimnion (monimolimnion during periods of meromixis) compartments. The surface elevation, depth and temperature of the mixed layer, and daily irradiance are required inputs. *Artemia* are assumed to be uniformly distributed in the mixed layer. To allow for comparison of different lake levels and the changing differences in eplimnetic and hypolimnetic volumes, the surface elevation and mixed layer depth are used to incorporate volume-weighted estimates of various fluxes.

Grazing, ammonium excretion and fecal pellet production -- Total grazing is assumed to be limited to the mixed layer and calculated based on individual grazing rates and *Artemia* abundance. Ammonium excretion and fecal pellet production are assumed equal to the total amount of grazing minus the total weight gain by the population including cyst and naupliar production (1 - *eff*). The partitioning between excretion and pellet production is assumed to be constant and was approximated from comparisons of model output to 1984 and 1990 field data (*grzpar* = 0.75). Ammonium excretion is added to the epilimnetic ammonium pool while fecal pellet production is lost to the sediments. Individual *Artemia* mortality is also modeled as a loss of nitrogen from the mixed-layer particulate pool going either to the sediments or blown ashore.

Sediment release and vertical flux of ammonium -- A constant rate of ammonium release from the sediments is assumed. This is added to the hypolimnetic and epilimnetic dissolved pools based on the area of sediments within each layer. The vertical flux of ammonium during the stratified period is modeled as an entrainment process in which the deepening mixed layer entrains slabs of water with higher ammonium concentrations. The relative volumes of the two layers are included in the calculation of these flux rates. During the period when the mixed layer becomes thinner (thermocline rises) a reverse entrainment process occurs in which more dilute epilimnetic water is mixed with the hypolimnetic water. An estimate of the sediment release rate of ammonium (*nhsed* = 56 mg N m^{-2} d^{-1}) was derived from an analysis of *in situ* ammonium profiles of sediment cores (L. Miller *pers. commun.*).

Algal growth -- Algal growth (nitrogen assimilation) is modeled as a maximum rate modified by temperature and multiplied by the currently more limiting factor, *in situ* light conditions or ambient ammonium concentrations. Both the effect of suboptimal light and ammonium are modeled by a Monod type rectangular hyperbola. Average light within the mixed layer is calculated based on *in situ* attenuation and surface insolation. Attenuation was derived from field measurements assuming a constant coefficient for Mono Lake water (att_1) and an algal specific attenuation factor (att_2). The average mixed-layer light climate (*lit*) is given by:

$$att = att_1 + (att_2 \times alg)$$

$$lit = insol \times \frac{\left(1 - e^{-att \times mix}\right)}{att \times mix}$$

where *insol* is the surface insolation, *mix*, the depth of the mixed-layer, *alg*, the algal biomass. In calculating average irradiance no correction was applied for shallower depths associated with nearshore regions. Given the above assumptions algal growth (*grow*) is determined to be:

$$grow = alg \times algmax \times algtmp^{tmp-20} \times \min\left(\frac{lit}{lit + alglit}, \frac{\max(0, nhe - algnitmin)}{algnit}\right)$$

where *alglit* and *algnit* are half-saturation constants for light and ammonium, *algtmp* is an exponential temperature effect, *algmax* the maximum growth rate, *nhe* the mixed-layer ammonium, and *algnitmin* the minimum ammonium level at which algal growth occurs. This latter constant was included as was done for grazing in case a larger time step than would otherwise be possible is desired.

All of the parameters associated with algal growth are unknown and initial estimates were based on the small size of the dominant phytoplankton and the typical light saturation level observed in incubator measurments of carbon uptake from 1983 to 1992. While trial and error parameter estimation against data from the two different years resulted in some changes to these initial estimates, the results of the model are largely insensitive to these rate constants as will be discussed later.

Algal settling, *sed*, is modeled as a sedimentation process dependent on algal concentration.

$$sed = algsnk \times alg \times \frac{area_e}{vol_e}$$

where *algsnk* is a constant settling velocity and *area* and *vol* are the area and volume of the mixed layer, respectively. Sinking rates of the dominant phytplankton in Mono Lake are low and this parameter was assigned 0.1 m d^{-1}.

Computer implementation

Due to the large computational requirements of parameter estimation most of this model was written and compiled in the C programming language. The program was compiled with a 32-bit compiler (Metaware High C Ver. 1.71) running under the Pharlap 386|Dos Extender Ver. 4.0. and optimized to run on a Intel 80486-based computer running at 33 MHz. While the bulk of the computer code is written in C, input/output, graphical analysis, and data file manipulations are all performed in APL due to its ease of use, interactive facilities, and previously developed auxillary programs.

Even given this relatively fast machine, the computational requirements of simultaneously estimating more than a few parameters at a time remains a formidable task requiring many hours of simulation. A Levenburg-Marquardt algorithm was written and employed for parameter estimation of development and mortality rates from the laboratory development experiments. Estimation of several other parameters against field data was accomplished through trial and error simulations over reasonable ranges of values for unknown parameters.

Initially a fourth order Runga-Kutta algorithm was used to integrate the equations at daily time steps. The fourth order Runga-Kutta algorithm involves a weighted-mean of four partial derivative estimates at conditions estimated from the beginning to end of the time step. The high algal biomass during periods of low ammonium and high zooplankton biomass during low algal biomass present difficulties in numerically integrating these equations. Unless extremely small time steps are used, these periods result in overestimating algal ammonium uptake and zooplankton grazing, respectively, and yield negative ammonium or algal biomass levels. Most of the problem was eliminated by employing quarter day time steps, however under some parameter combinations there were still brief periods in which uptake and grazing were overestimated. Because implicit methods of integration would be too numerically demanding, we modified uptake and grazing to not exceed the current ambient amount ammonium or algal biomass over any six hour time step. This approximation introduces only a small error during the brief periods when it applies while ensuring stability and conservation of nitrogen.

Results

Final parameter estimates and model validation -- Parameter estimation using the full model was necessarily limited to only a subset of the parameters due to the computational requirements of the model. These included two associated with algal growth (*algmax, algnit*), and six associated with *Artemia;* adult mortality (*mora, sen*), hatching (*hfac, hday*), and grazing (*grztmp, grzalg*). The Levenburg-Marquardt which was sucessfully employed in analyzing the laboratory experiments was too computationally demanding to be practical within the constraints of the current analysis. For this reason, estimation was accomplished through trial and error modifications of the six parameters using comparisons between simulated and observed data for meromictic (1984) and monomictic conditions (1990). The final parameter estimates are all within expected ranges for the various processes (Table 1). A complete characterization of the six-dimensional parameter space was not possible. While more extensive parameter estimation could be conducted, it is probably not warranted because the general conclusions of this analysis are robust over a wide range of parameters and analysis indicates a better model description of the vertical structure of the water column is necessary to simulate observed seasonal patterns.

The calibrated model described the timing and abundance of adults under meromictic (1984) and monomictic (1990) conditions reasonably well (Fig. 7). While naupliar abundance in 1990 was also well-described, there was a major discrepancy between observed and predicted naupliar instars in 1984. Also, juvenile abundance was overestimated, particularly in 1990. A series of simulations indicate the timing and distribution of the spring hatch have pronounced effects on predicted distributions of early instars. This particular aspect of the *Artemia* dynamics is not well understood and is likely to be highly variable depending on the details of spring mixing and its effect on temperature and oxygen conditions at the sediment-water interface. Further progress may depend on a better description of the hatching process. However, instar distributions have little impact on overall secondary and cyst production.

The partitioning of nitrogen between dissolved and particulate pools was suitably described under monomictic conditions (1990) but less well under meromictic ones (1984)(Fig. 8). Monitoring data collected from 1982 to 1992 indicate a spring algal bloom in which the ammonium is reduced to near zero in all years except following the breakdown of meromixis. The model correctly simulates the development of an algal bloom in the spring and autumn. However, in 1984 under meromictic conditions, the spring bloom and epilimnetic ammonium during the summer are overestimated. Both of these arise from overestimating the upward vertical flux of ammonium under meromictic conditions. This results from the two layer characterization of the vertical structure. In this approximation, any deepening of the seasonal thermocline results in upward fluxes of ammonium whose magnitude is dictated by the "hypolimnetic" (in this case monimolimnetic) concentration. The actual flux is much less, because mixed-layer deepening only entrains water above the persistent chemocline which has much lower concentrations of dissolved nitrogen. An illustration of this is given by a simulation in which the spring mixing depth was assumed to be constant at 10 m during the spring (Fig. 9). This effectively curtails the upward flux of nitrogen during the spring causing reductions in predicted algal and *Artemia* pools from ca. 600 to 220 mg N m^{-3} and 150 to 100 mg N m^{-3}, respectively. Also, during the summer, a mid-depth maximum of algal biomass is often observed to act as a nutrient trap for upward fluxes of ammonium. This cannot be simulated with the current two-layer model. This highlights the importance of a more detailed characterization of vertical mixing. Because the current formulation only considers two vertical compartments, it cannot simulate the complex vertical temperature stratification observed in the lake. We plan to incorporate a more detailed description of vertical mixing (DYRESM) during this next year.

An eight-year simulation was performed with the single final parameter set, using the surface elevation, thermal stratification, and insolation observed from 1983 to 1990 and the 1983 initial shrimp abundance (Fig. 9, Table 2). Available cysts were assumed to be 1.6 x 10^6 in 1983 and depends on the production during the previous year for 1984 through 1990. Several of the general features of the observed data during this period are simulated by the model. These include the reduced spring algal biomass during meromixis, 1984 to 1988; an increase in summer ambient ammonium, algal and *Artemia* biomass during meromixis as the mixed layer deepened in subsequent years; slightly reduced values in 1986 when a secondary chemocline was formed high in the water column; the large algal bloom immediately following the breakdown of meromixis in late 1988; and subsequent decline in 1990 as epilimnetic ammonium concentrations decreased.

Annual production estimates from the model were reasonable compared to other independent estimates. Annual primary production in the upper mixed-layer was estimated to range from 17 to 43 g N m^{-2} y^{-1}, which, assuming a C:N ratio of 10, yields values for annual carbon production of 170 to 430 g C m^{-2} y^{-1}. Total annual production in the upper 18 m of the water column based on measurements of carbon uptake was estimated to range from 269 to 1064 g C m^{-2} y^{-1} (Jellison and Melack *In press*). The model estimates are expected to be lower because they only include the mixed layer which is often significantly less than the 18 meter depth over which production was integrated in Jellison and Melack (*In press*). Secondary production estimates are also reasonable, although somewhat lower than independent estimates. Model estimates range from 2.6 to 7.5 g N m^{-2} from 1983 to 1990. Assuming a carbon content in *Artemia* of 42% (Oppenheimer & Moreira 1980), this yields, 7 to 18 g C m^{-2} y^{-1}. Independent methods estimate secondary production ranged from 16 to 23 g C m^{-2} y^{-1} during this same time period (Dana *unpubl. obs.*).

A major discrepancy between model and observed estimates is the limited buildup of ammonium in the hypolimnion during meromixis. While there is significant uncertainty in the estimate of the sediment flux of ammonium (*nhsed*), the formulation of vertical mixing in the model causes much of the discrepency. Deep mixing in the autumn followed by stratification high in the water column during the following spring has the effect of diluting the monimolimnetic ammonium concentrations under meromictic conditions using the current algorithm. This arises because when the mixed layer becomes shallower, the algorithm mixes the water beneath to a uniform concentration. This does not occur during meromictic conditions because the water beneath the persistent chemocline does not mix with that beneath the spring thermocline. Accurate simulation of this will require a more detailed model of the veritcal structure of the water column and is part of our proposed research for this coming year. An improved representation of this process will result in a more pronounced buildup of ammonium in the monimolimnion, less upward flux of ammoium during meromictic conditions, and a larger pulse of ammonium following the breakdown of meromixis. This could potentially resolve most of the discrepancies between observed and simulated data.

Analysis of the algal growth rates and *Artemia* grazing rates predicted by the model is informative. The model calculates a potential algal growth rate based on the the maximum growth rate and temperature (Fig. 11A&B). This is then modified by prevailing light and ammonium conditions to calculate the realized growth rate. Realized rates were much lower than potential rates throughout 1990. During the spring and autumn algal-specific growth rates are reduced to near zero due to low light and nutrient conditions. During the summer realized rates are much closer to potential rates as nutrient and light conditions improve. The converse is roughly true for *Artemia* growth as indicated by potential and realized grazing rates. During spring and autumn, *Artemia* grazing is maximal for the prevailing ambient temperatures, while during the summer realized grazing is much lower than potential due to low algal biomass (Fig. 11C&D). These model properties are consistent with findings of our other research conducted at Mono Lake. Also, naupliar production is predicted to be limited to a relatively short period during early summer (Fig. 12) and is in general accordance with observed data (Jellison *et al.* 1988, 1989, 1990).

Sensitivity analysis and model properties -- The sensitivity of the model to variation in key parameters over their possible ranges was evaluated (Table 3). The model is largely insensitive to large variation (0.5 to 2.5) in the maximum algal growth rate (*algmax*). Primary, secondary and naupliar production changed little. Mean annual epilimnetic ammonium was the only variable highly sensitive to maximum algal growth rate decreasing from 139 to 16 mg N m^{-3} over the parameter range. Cyst production increased 125% over the same range. Increasing *Artemia* growth efficiency (eff_1) led to a small increase in mean annual *Artemia* biomass with consequent increases in secondary production and small decreases in algal biomass and primary production. Cyst production decreased slightly as *Artemia* growth efficiency increased. Wide variation in the "half-saturation" constant for the effect of light on algal growth (*alglit*) resulted in almost no response except a modest increase in epilimnetic ammonium. This insensitivity arises because algal growth is seldom limited by light due to low ambient ammonium during periods of high algal biomass. Increased maximum grazing rates (grz_1) resulted in higher *Artemia* biomass, a large increase in secondary production and a slight icnrease in naupliar production. There was almost no response to a twenty-fold variation in hatching success (*hfac*) or a 60 day change in day of peak hatch (*hday*). Changes in the reproductive assimilation efficiency (eff_2) resulted in a roughly proportionate response in cyst production.

The reason the model is so insensitive to variation in its parameters stems from the dominant role of nitrogen limitation. The realized algal growth rate depends on the ambient temperature as modified by low light or nutrient levels. In simulations of 1984 and 1990 the seasonal pattern of the model's temperature, light, and nitrogen factor for algal growth predict nitrogen to limit algal growth during much of the year. Only during brief periods do the predicted algal growth rates approach their temperature-dependent maximum, and light limitation is stronger than nitrogen limitation only during restricted periods in the summer and early in the year in 1990 due to initial elevated ammonium levels. *Artemia* growth is also suboptimal during much of the summer due to low ambient algal biomass levels resulting from grazing. Because *Artemia* are so strongly limited by available food, changes in their maximum grazing rates have little overall effect. One might assume that increases in *Artemia* growth efficiency might translate into proportionate increases in secondary production since this is a direct multiplicative factor in the model. However, smaller than proportionate increases in secondary production accompany increases in growth efficiency. This also stems from nitrogen limitation. Only the fraction of unassimilated ingested nitrogen which goes into fecal pellets is lost to the system. The rest is recycled back into the epilimnetic pool due to ammonium excretion and thus available for algal growth and subsequent grazing by *Artemia*.

The results of the model sensitivity analysis, which identifies nitrogen as the major controlling factor in the model, and the decline in primary production which occurred as a result of reduced ammonium flux during meromixis (Jellison & Melack *In press*) are consistent with the assumption of strong nitrogen limitation of plankton dynamics in Mono Lake. Because the algae are capable of much higher growth rates than those realized under the nutrient limiting conditions found during much of the season, and the *Artemia* have "excess capacity" for growth and fecundity, the model is insensitive to parameter changes which do not alter the nitrogen availability.

This is illustrated most strongly by an analysis of the model's response to changes in the sediment ammonium release rate. Changes from the estimated rate (56 mg N m^{-2} d^{-1}) resulted in near linear responses in all of the measured response variables (Fig. 13).

Effects of salinity due to changes in individual model parameters

The effects of changes in salinity on the *Artemia* population were assessed by altering model parameters associated with the life history characteristics of *Artemia*. The specific parameters altered and the amounts were based on an extensive analysis of all existing salinity bioassays on *Artemia monica* (Dana *et al.* 1992). The altered parameters included assimilation efficiency (*eff1* and *eff2*), juvenile and adult mortality (*morj* and *mora*), ovigerity (*repovig*), ovoviviparity, and peak day (*hday*) and success (*hfac*) of cyst hatching. The effect on naupliar mortality was not included because there was no significant effect observed in the salinity bioassays over the range of salinities observed here. It should also be noted that the calculated mortalities due to suboptimal temperature and food levels in the lake are much higher than seen in the salinity bioassays under food sufficient and warmer conditions. Regressions of the effect of salinity on each of these parameters except assimilation efficiency were derived in a separate analysis (Dana *et al.*

1992). Effects on assimilation efficiency were assumed equal to those as measured by changes in development rates. Because experimental conditions of the various bioassays varied and were often different than those observed in the field, the relative effect of salinity on each parameter was calculated and used to modify the derived model parameters. Life history characteristics were estimated from the regressions for five salinities corresponding to 6360, 6372, 6380, 6385, and 6392 ft. Then value for each characteristic was then divided by the value at 6372 ft. (approximate current elevation, June 1992) to derive the relative effect (Table 4). Associated model parameters were then multiplied by these factors to simulate salinity effects. Because ovoviviparity is not a model parameter but a calculated value based on other parameters, it is treated slightly differently. On each day of a given simulation, the calculated ovoviviparity is multiplied lake level factor in Table 4. The changes in the day of hatch are also treated slightly differently. In the laboratory bioassays, *Artemia* cysts are moved directly from anoxic conditions to those optimal for hatching. Under this procedure hatching occurs in a relatively short period of 5 to 10 days. The model does not calculate a day when optimum conditions occur and thus cannot directly utilize this information. Multiplying the day of hatch by the factor derived in the salinity bioassays would greatly exagerate the probable effect. The absolute number of days by which the hatch was delayed or advanced, as determined by the salinity bioassays, was simply added to the day of peak hatch (*hday)*. This may underestimate the true effect, however, as discussed below, hatching has little effect on the predicted results. The effect of changes in algal growth rates were also assessed based on an approximate 10% change in photosynthesis for each 10% change in salinity (J. Melack 1985). Because of the larger uncertainty associated with the effects of salinity on algal growth rates and the interpretation of changes in ovoviviparity, these are treated separately in the following analysis.

The response of eight annual measures of the plankton dynamics were assessed for changes in individual parameters due the effects of changes in salinity associated with lake level changes to 6380 ft (85 g l^{-1}) and 6360 ft (120 g l^{-1}) from an elevation of 6372 ft (97 g l^{-1}). These include mean annual epilimnetic and hypolimnetic ammonium, algal and *Artemia* nitrogen, and annual primary, secondary, naupliar and cyst production. The analysis was conducted using monomictic conditions of mixed-layer depth and temperature as represented by the 1990 field data.

At increased salinity associated with a drop in lake level to 6360, decreases in mean annual *Artemia* biomass, and secondary, naupliar and cyst production occured (Fig. 14A). The largest relative drop was 12% in naupliar production. At lower salinities these measures increased slightly. Both mixed-layer ammonium and algal biomass increased slightly at the higher salinity, 6 and 2%, respectively. Other responses were smaller. The responses are explainable in terms of strong nutrient limitation and the role of *Artemia* in exporting nitrogen to the sediments via fecal pellets. Within the epilimnion, the ammonium and algal pools turnover on a daily basis due to high algal growth and *Artemia* grazing. Each cycle through the *Artemia* pool exports a certain fraction to the sediments ((1-*eff*) x (1 - *grzpar*)). As efficiency decreases a larger portion of the total epilimnetic ammonium pool (dissolved, algal, and *Artemia*) is exported with each cycle. If export via fecal pellets was absent, recycling would be more complete and we would expect a smaller effect on these variables.

Changes in juvenile and adult mortality rates, had virtually no effect on primary, secondary and naupliar production (Fig. 14B). At the higher salinity, mean annual *Artemia* nitrogen (abundance) was 15% lower leading to slightly higher algal abundance and lower mixed-layer ammonium. Higher *Artemia* nitrogen at the lower salinity had the reverse effect on algae and ammoniun. This indicates the strong top-down influence of *Artemia* on the plankton. Cyst production decreased 5% at the higher salinity.

Changes in ovigerity were directly translated into differences in naupliar and cyst production with virtually no effects on other variables (Fig. 14C). Cyst production decreased 9 % at the higher salinity and increased 5 % at the lower salinity.

The assumed 23 % decrease in maximum algal growth rate at 6360 ft resulted in a 49% increase in mean annual epilimnetic ammonium and a 5 and 13% decline in primary and secondary production, respectively (Fig. 15A). A lower algal growth rate results in accumulation of nitrogen in the epilimnetic pool and fewer cycles of nitrogen through the ammonium-algae-*Artemia* loop. Thus, primary production and cyst production are reduced.

The predicted change in ovoviviparity is quite large over the range of salinities from 85 to 120 g l^{-1} (6360 to 6380 ft). Subsequently a large change in naupliar production is predicted. At the higher salinity, naupliar production increased 18% while decreasing 16 % at the lower salinity (Fig. 15B). The cyst production varied in the opposite direction; higher naupliar production led to lower cyst production. However, these small changes in cyst production are expected to have almost no effect on the next year's plankton dynamics (see later analysis).

Responses to changes in hatching success or day of hatch associated with these two salinities were less than 3 %.(Fig. 15C)

Predicted effects of changing lake levels on the Artemia *population*

Several combinations of altered parameter sets were analyzed to aid in the interpretation of the predicted effects of different lake levels on the *Artemia* population. First, the response to the combined effect of salininty-induced changes in *Artemia* growth efficiency, mortality, ovigerity, hatching success and day of hatch were modeled assuming monomictic conditions represented by 1990 field data. This does not include any effects due to different areas and volumes at the different lake levels. Next, the combined effects of these and the area-volume relationships associated with different surface elevations were added and responses in lakewide totals of primary, secondary, naupliar and cyst production calculated. Next, simulations in which the predicted salinity effect on algal growth were included, followed by adding salinity-induced changes predicted to occur in ovoviviparity.

Two additional analyses were done to illustrate the relative insensitivity of the above predictions.

The predicted response over the range from low to high salinities (high to low lake levels) accompanying salinity induced changes in *Artemia* life-history parameters is decreasing epilimnetic ammonium, *Artemia* biomass, and secondary, naupliar, and cyst production and increasing algal biomass and primary production (Fig. 16, Table 6A). The increase in primary production is a result of increased algal biomass associated with decreased grazing due to fewer *Artemia*. The total response in mean annual *Artemia* ranges from -24% at 6360 ft. to +33% at 6392 ft and the response in cyst production is nearly the same. No changes in ovoviviparity were included in this first analysis since the relevance to the field population of effects determined in salinity bioassays is uncertain.

When the effect of changing lake volume and area are added to the above trials, the decreases in secondary, naupliar, and cyst production are proportionately greater due to the smaller volumes associated with lower lake levels (Fig. 17, Table 6A). Also, the slight increase in areal primary production observed with salinity increases in the previous trial is now more than offset by the decreased lake volume, and as a consequence total lakewide primary production declines.

In the third trial, where the estimated salinity effect on algal growth is added, the declines in the four measures of lakewide production are increased slightly further (Fig. 18, Table 6B). Despite the slightly higher algal biomass at higher salinities observed in both the earliar trials, the net effect on the areal primary production rate is now neglible due to the reduced maximum algal growth rate used by the model. Reduced algal growth in this trial also has the effect of increasing mixed-layer ammonium from -23 to +40 % going from low to high salinities.

The response to adding the more uncertain salinity effect on *Artemia* ovoviviparity was to reduce the total response of naupliar production but increase that of cyst production

(Fig. 19, Table 6B). Other responses were similar to those without considering the effects of changes in ovoviviparity.

The two additional analyses suggest the above responses are robust over a wide range of conditions. The ten variables responded in a similar fashion to changes in salinity under conditions representative of meromixis (1984) except that the response was somewhat smaller in most cases (Fig. 20). In the trial in which both maximum grazing and algal growth rates were doubled (Fig. 21), the responses were also similar.

Conclusion

Different lake levels associated with various EIR alternatives determine the total surface area, volume and salinity of Mono Lake. If no changes in the plankton community resulted from changing salinity associated with the various alternatives, lakewide production would change according to area and volume. While the model predicts various responses to different combinations of salinity-induced changes in parameters, the net affect on primary and secondary production is not markedly different than that which would be predicted from changes in area and volume (Table 8). Cyst production shows a much larger decline at increasing salinities. In an entirely different type of analysis of salinity bioassays, Dana and Lenz (1986) predicted ca. a 5-fold decrease in individual egg production over the same salinity range. However, our analysis indicates large differences in cyst production have little effect on the next year's dynamics. On an areal basis, the model predicts that salinity-induced changes in life history parameters of the *Artemia* and algal maximum growth rate have little effect on mean annual biomass and secondary production. This result is almost entirely due to the dominant role of nitrogen in limiting primary production and the simple trophic structure of the plankton community. Because the algae are capable of much higher growth rates than those realized under the nutrient limiting conditions found during much of the season, and *Artemia* growth and fecundity is limited by algal biomass during most of the time they are abundant, the model is insensitive to changes which do not alter the nitrogen availability. This conclusion is based only on consideration of the effects of salinity on *Artemia* life history characteristics and maximum algal growth rates. If changes in salinity affect the availability of nitrogen through processes not modeled here then different responses may occur.

At present, too little is known to accurately describe a nitrogen budget for Mono Lake or estimate changes which may accompany lake level changes. Measurements of nitrogen fixation (Oremland 1990) in nearshore regions suggest fixation in the water column to be small relative to phytoplankton demands. However, recent measurements by Herbst (*pers. commun.*) indicate significantly higher rates in benthic algal mats. Much more research will be necessary not only to quantify this nitrogen input and determine its fate, but also to predict changes in it accompanying lake level changes. Recently estimated ammonium volatization rates associated with the high mixed layer concentrations immediately following meromixis suggest a significant amount of nitrogen was lost from the lake during this period. An assessment of the significance of these type of events to the long-term productivity of the lake cannot be made without a more accurate nitrogen budget.

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Table 1. Final model parameters

Grazing and Development Parameters			
eff1	growth efficiency	0.44	Reeve (1963)
eff2	reproductive efficiency	0.30	Estimated based on 1984 cyst production
grz1	maximum ingestion	0.03	proportion of maximum weight
grz2	ingestion shape coefficient	-239	Similar to Adreu-Grobois results
grztmp	temperature grazing coefficient	12	Based on model and 1984 amd 1990 data
grzalg	algal grazing coefficient	200	Based on model and 1984 amd 1990 data
grzalgmin	algal level below which grazing rate is zero	15	Set to achieve model stability
grzpar	fraction of egestion going to excretion	0.75	Based on model and 1984 amd 1990 data
brdint20	brood interval at 20 degrees	8.5	Previous analysis of field data
brdtmp	temperature brood interval effect	1.187	Previous analysis of field data
sen	senility factor	0.3	Based on model and 1984 amd 1990 data
tmpopt	optimum temperature	30	Based on laboratory data of related species
Mortality Parameters			
morn	daily naupliar base mortality	0.02	Estimated w/ development experiments
morj	daily juvenile base mortality	0.03	Estimated with model and 1984 data
mora	daily adult base mortality	0.01	Estimated with model and 1984 data
mortmp	temperature mortality factor	2.5	Estimated w/ development experiments
moralg	algal mortality factor	50.7	Estimated w/ development experiments
sen	senility factor (same as above)	0.3	Estimated with model and 1984 data
Reproductive Parameters			
repff	fraction of adults which are female	0.41	Observed field data 1983 - 1990
repovig	fraction of females which are ovigerous	0.84	Observed field data 1983 - 1990
repmax	maximum daily egg production per female	15	Baed on maximum observed fecundity
ovoi	initial and final ovoviviparity	0.02	Field observations
ovo1	constant in ovoviviparity regression	1.432	Regression on field data, 83 - 90
ovo2	temperature regression coefficient	-0.0936	Regression on field data, 83 - 90
ovo3	chla regression coefficient	0.00054	Regression on field data, 83 - 90
ovo4	ovoviviparity factor for second adult age class	0.5	Set during 1984 parameter estimation
ovof	day at which ovovivipary reverts to initial level	240	Set during 1984 parameter estimation
Cyst Hatching Parameters			
hfac	proportion of cysts which hatch	0.005	Based on model and 1984 and 1990 data
hday	day of peak cyst hatch	75	Based on model and 1984 and 1990 data
hsd	standard deviation of cyst hatching distribution	15	Based on 1st instar distributions, 83 - 90
hcyst	number of cysts from previous year	1.6 x 10^6	Based on fecundity from 1984 field data
Algal Growth Parameters			
algsnk	sedimentation rate for algae	0.1	Based on model and 1984 amd 1990 data
att1	attenuation of Mono Lake water	0.3873	Regression from field data 1983 - 1990
att2	algal specific attenuation coefficient	0.000632	Regression from field data 1983 - 1990
algmax	maximum algal growth rate	1	Estimated with model and 1984 and 1990 data
algtmp	exponential temperature coefficient	1.08	Based on laboratory experiments
algnit	nitrogen half saturation coefficient	14	Estimated with model and 1984 and 1990 data
algnitmin	minimum nitrogen at which uptake occurs	7	Set to achieve model stability
alglit	light half saturation coefficient for algal growth	6	Estimated from field research, 1983-1990
Hypolimnetic Ammonium Parameters			
nhsed	constant sediment release rate of ammonium	56	Estimated with 1984 field data

Table 2. Summary of eight-year simulation from 1983 to 1990, using the final parameter set and observed depth and temperature of mixed layer (salinity effects not included).

	Volumetric				Areal				Lakewide Total			
Year	NHH	NHE	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
	mg N m^{-3}				g N m^{-2}		10^6 m^{-2}		10^9 g N		10^{14}	
1983	25	469	401	44	18.58	2.57	0.22	1.73	3.13	0.44	0.38	2.88
1984	43	1126	250	61	25.01	5.24	0.49	2.29	4.43	0.92	0.87	4.07
1985	57	1245	419	81	33.45	7.2	0.73	2.52	5.84	1.25	1.25	4.43
1986	36	1411	322	78	26.46	5.22	0.48	1.83	4.69	0.92	0.85	3.22
1987	106	1743	381	82	33.41	6.88	0.64	2.75	5.85	1.2	1.11	4.84
1988	92	1430	476	86	46.82	7.51	0.64	2.64	7.94	1.27	1.09	4.52
1989	27	202	763	79	29.13	5.12	0.44	2.09	4.84	0.84	0.72	3.51
1990	18	263	515	67	30.35	5.79	0.53	2.17	4.95	0.94	0.85	3.55

Table 3. Sensitivity analysis

Parameter changed	Parameter Value	NHE	NHH	ALG	ART	1°	2°	Naup	Cyst
		mg N m^{-3}				g N m^{-2}		10^6 m^{-2}	
Algmax	0.5	139	342	603	76	36.16	6.35	0.64	1.42
	1	50	301	623	85	38.72	7.25	0.73	2.3
	1.5	26	284	623	88	39.95	7.65	0.79	2.75
	2	20	279	617	89	40.66	7.82	0.79	3.06
	2.5	16	277	615	89	40.95	7.88	0.79	3.21
Eff1	0.36	54	301	639	75	40.29	6.62	0.67	2.4
	0.4	52	301	630	81	39.53	7	0.71	2.35
	0.44	50	301	623	85	38.72	7.25	0.73	2.3
	0.48	49	301	617	88	37.85	7.34	0.73	2.26
	0.52	49	300	612	89	37.03	7.35	0.72	2.21
Alglit	3	28	282	634	86	39.3	7.43	0.76	2.51
	4	33	286	633	86	39.09	7.38	0.75	2.42
	5	42	294	628	86	38.9	7.32	0.74	2.36
	6	50	301	623	85	38.72	7.26	0.73	2.3
	7	58	307	618	85	38.56	7.2	0.72	2.25
Grz1	0.22	132	317	506	98	42.03	6.6	0.77	3.19
	0.26	152	329	500	119	43.91	7.92	0.9	3.32
	0.3	186	371	506	148	46.31	9.69	1.1	3.48
	0.34	223	419	513	171	48.41	11.09	1.26	3.66
	0.38	254	460	517	188	50.32	12.26	1.41	3.85
Hfac	0.005	50	301	623	85	38.72	7.26	0.73	2.3
	0.01	49	301	608	84	38	6.96	0.6	2.16
	0.025	51	302	585	78	37.19	6.2	0.66	2.07
	0.05	56	305	586	77	36.67	5.18	0.6	2.22
	0.1	55	303	554	87	36.01	5.94	0.08	1.98
Hday	45	54	301	639	84	38.76	7.39	0.7	2.37
	60	52	301	629	85	38.83	7.37	0.75	2.34
	75	50	301	623	85	38.72	7.25	0.73	2.3
	90	50	301	619	85	38.49	7.18	0.67	2.24
	105	50	301	622	86	38.49	7.31	0.64	2.23
Eff2	0.22	52	301	631	84	39.2	6.97	0.63	1.78
	0.26	51	301	627	85	38.96	7.12	0.69	2.05
	0.3	50	301	623	85	38.72	7.26	0.73	2.3
	0.34	50	301	619	85	38.48	7.35	0.76	2.56
	0.38	50	301	616	85	38.25	7.43	0.78	2.81

Table 4. Alterations to model parameters affected by salinity changes. Model parameters are multiplied by the shown factors except for *Day of Peak Hatch,* which is simply added.

Lake surface elevation (ft)		6392	6385	6380	6372	6360
Salinity (g/l)		51	77	85	97	120
Growth efficiency	*eff_1*	1.183	1.12	1.075	1	0.87
Egg production efficiency	*eff_2*	1.183	1.12	1.075	1	0.87
Juvenile mortality	*morj*	0.718	0.80	0.879	1	1.21
Adult mortality	*mora*	0.718	0.80	0.879	1	1.21
Ovigerity	*repovig*	1.129	1.102	1.055	1	0.89
Ovoviviparity factor	*ovofac*	0.24	0.538	0.689	1	2.04
Hatching success	*hfac*	1.154	1.12	1.077	1	0.785
Day of peak hatch	*hday*	-3	-2	-1	0	2
Maximum algal growth	*algmax*	1.28	1.2	1.12	1	0.77

Table 5. Model response to changes in individual parameters affected by changes in salinity.

			Volumetric				Areal				Lakewide Total			
	Elev	Salinity	NHH	NHE	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
	ft	$g\ l^{-1}$		mg N m^{-3}			g N m^{-2}		$10^6\ m^{-2}$		10^9 g N		10^{14}	
No change	6372	97	50	301	623	85	38.72	7.25	0.73	2.3	6.32	1.18	1.18	3.77
Growth efficiency	6360	120	54	301	638	78	40.02	6.68	0.65	2.12	6.53	1.08	1.04	3.47
	6380	85	49	301	616	87	37.84	7.36	0.74	2.41	6.18	1.19	1.2	3.95
Mortality	6360	120	47	301	634	72	38.31	7.2	0.73	2.18	6.25	1.17	1.19	3.56
	6380	85	53	301	616	94	38.93	7.29	0.72	2.36	6.36	1.18	1.16	3.86
Ovigerity	6360	120	51	301	626	85	38.92	7.16	0.7	2.09	6.35	1.16	1.13	3.42
	6380	85	50	301	621	85	38.62	7.3	0.75	2.41	6.31	1.18	1.21	3.95
Algal growth	6360	120	75	314	620	82	37.85	6.95	0.69	2.01	6.18	1.13	1.12	3.29
	6380	85	42	296	624	86	39.04	7.37	0.75	2.4	6.37	1.2	1.21	3.93
Ovoviviparity	6360	120	51	301	617	86	38.91	7.51	0.86	2.17	6.35	1.22	1.4	3.55
	6380	85	51	301	627	84	38.9	7.1	0.61	2.63	6.35	1.15	0.99	4.29
Hatching success	6360	120	52	301	626	85	38.8	7.31	0.74	2.33	6.33	1.19	1.2	3.81
	6380	85	50	301	622	85	38.68	7.22	0.72	2.3	6.31	1.17	1.17	3.76
Day of Hatch	6360	120	50	301	622	85	38.7	7.23	0.73	2.3	6.32	1.17	1.17	3.76
	6380	85	50	301	623	85	38.73	7.27	0.73	2.3	6.32	1.18	1.19	3.77

Table 6A. Predicted responses to changes in salinity at different lake levels.

		Volumetric				Areal				Lakewide Total			
Elev	Salinity	NHH	NHE	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
ft	$g\ l^{-1}$	$mg\ N\ m^{-3}$				$g\ N\ m^{-2}$		$10^4\ m^{-2}$	$10^6\ m^{-2}$	$10^9\ g\ N$		10^{14}	
This section assesses the effects of salinity caused changes in efficiency, mortality, ovigerity, hatching success, and day of hatch. The lake level is held constant at the 1990 conditions.													
6392	51	51	300	656	65	39.53	6.39	0.58	1.82	6.45	1.03	0.93	2.98
6385	77	50	301	623	85	38.72	7.25	0.73	2.3	6.32	1.18	1.18	3.77
6380	85	52	301	606	96	37.84	7.38	0.72	2.58	6.18	1.2	1.16	4.22
6372	97	54	301	595	104	37.37	7.48	0.72	2.81	6.1	1.22	1.16	4.6
6360	120	56	301	582	113	36.8	7.58	0.72	3.06	6.01	1.23	1.16	5.01
In addition to those listed immediately above, this section incorporates the effects of areal and volumetric changes associated with the difference lake levels.													
6392	51	47	341	660	63	39.67	6.62	0.6	1.85	5.16	0.86	0.77	2.41
6385	77	47	307	615	82	39.01	7.32	0.73	2.3	5.83	1.08	1.07	3.45
6380	85	54	293	607	97	38.04	7.39	0.72	2.6	6.75	1.3	1.27	4.62
6372	97	56	283	591	106	37.71	7.48	0.72	2.83	7.06	1.4	1.34	5.31
6360	120	56	274	565	111	37.62	7.55	0.72	3.12	7.45	1.49	1.41	6.19

Table 6B. Predicted responses to changes in salinity at different lake levels.

		Volumetric				Areal				Lakewide Total			
Elev	Salinity	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
ft	g l^{-1}	mg N m^{-3}				g N m^{-2}		10^4 m^{-2}	10^6 m^{-2}	10^9 g N		10^{14}	
In addition to those listed in Table 6A, this section incorporates the effects of salinity on ovoviviparity.													
6360	120	70	353	658	61	38.8	6.33	0.57	1.63	5.05	0.82	0.74	2.13
6372	97	47	307	615	82	39.01	7.32	0.73	2.3	5.83	1.08	1.07	3.45
6380	85	45	287	608	99	38.38	7.51	0.74	2.72	6.8	1.32	1.31	4.84
6385	77	42	275	592	108	38.27	7.68	0.75	3.07	7.17	1.43	1.41	5.76
6392	51	39	264	566	113	38.46	7.85	0.76	3.56	7.62	1.55	1.5	7.06
In addition to those listed immediately above, this section incorporates the effects of salinity on algal growth rates.													
6360	120	72	354	654	62	38.86	6.52	0.71	1.42	5.05	0.84	0.92	1.85
6372	97	47	307	615	82	39	7.32	0.73	2.3	5.82	1.08	1.07	3.46
6380	85	45	288	613	98	38.63	7.36	0.65	3.03	6.85	1.3	1.15	5.37
6385	77	42	275	602	107	38.76	7.49	0.61	3.61	7.26	1.4	1.14	6.75
6392	51	38	263	595	110	40	7.63	0.42	5.24	7.92	1.51	0.83	10.37

Table 7. Predicted responses to changes in salinity with different algal growth and *Artemia* grazing rates.

		Volumetric				Areal				Lakewide Total			
Elev	Salinity	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
ft	g l^{-1}		mg N m^{-3}			g N m^{-2}		10^4 m^{-2}	10^6 m^{-2}	10^9 g N		10^{14}	
6392	51	9	313	723	55	38.72	5.95	0.38	2.12	5.04	0.77	0.49	2.77
6385	77	8	276	691	70	38.5	6.54	0.41	2.99	5.75	0.97	0.6	4.49
6380	85	8	260	695	86	38.3	6.95	0.4	3.64	6.79	1.23	0.71	6.47
6372	97	8	249	689	93	38.19	7.08	0.38	4.16	7.15	1.32	0.71	7.8
6360	120	7	240	694	79	38.84	6.17	0.19	5.87	7.69	1.22	0.38	11.64

Table 8. Changes in area, volume and those predicted in four measures of the plankton by the model.

Elevation	Surface Area		Lake volume		Primary	Secondary	Naupliar	Cyst
(ft)	(acres)	% change	(acre-ft)	% change	% change			
6392	48893	22	3037250	34	25.3	28.3	-29.9	175.2
6385	46310	16	2703617	19	14.8	18.9	-3.6	79.3
6380	43670	9	2478494	9	8.37	10.3	-2.4	42.6
6375	39915	-	2269109	-	-	-	-	-
6372	37688	-6	2152772	-5	-7.8	-8.1	-9.6	-8.2
6360	32283	-19	1739027	-23	-20.0	-28.2	-21.9	-50.0

Figure Captions

Figure 1. Schematic of Mono Lake *Artemia* model depicting processes modeled and the partitioning of nitrogen among epilimnetic ammonium (NHE), hypolimnetic ammonium (NHH), the algal and *Artemia* particulate components.

Figure 2. Maximum ingestion rates in which the relative rates of specific instars are proportional to their weight (dotted) or a negative exponential formulation similar to that determined by Abreu-Grobois (1991) for *A. franciscana* .

Figure 3. Weight versus length relationships from experimental development experiments with *Artemia monica* under different conditions of food and temperature and *A. franciscana* raised under optimal conditions. The different conditions for the *A. monica* correspond to spring temperatures and algal biomass during monomictic conditions (Spr-high), spring temperature and alga biomass during meromictic conditions (Spr-low), and summer (Summer) conditions of warm temperature and low algal biomass.

Figure 4. Observed (···) versus predicted (—) instar-specific abundance for *Artemia* reared under conditions representative of spring monomictic conditions (cold temperatures and high food treatment).

Figure 5. Observed (···) versus predicted (—) instar-specific abundance for *Artemia* reared under conditions representative of spring meromictic conditions (cold temperatures and low food treatment).

Figure 6. Observed (···) versus predicted (—) instar-specific abundance for *Artemia* reared under conditions representative of summer conditions during either monomictic or meromictic conditions (warm temperatures and low food treatment).

Figure 7. Observed (···) versus predicted (—) instar-specific *Artemia* abundance under meromictic (1984) and monomictic (1984) conditions. Model parameters are listed in Table 1.

Figure 8. Observed (···) versus predicted (—) partitioning of mixed-layer nitrogen among epilimnetic ammonium, algae, and *Artemia* under meromictic (1984) and monomictic (1984) conditions. Model parameters as listed in Table 1.

Figure 9. Predicted partitioning of mixed-layer nitrogen among epilimnetic ammonium, algae, and *Artemia* under meromictic (1984) assuming a uniform mixing depth (10 m) during the spring.

Figure 10. Eight-year simulation of the partitioning of nitrogen among mixed-layer pools of ammonium, algae, and *Artemia* and hypolimnetic ammoniun using mixed-layer depths, temperature, and insolation observed from 1983 to 1990.

Figure 11. Relative effects of suboptimal temperature (—), light (···), and nitrogen (---) during A) 1984 and B) 1990 simulations. Potential (—) versus realized (---) grazing rates during C) 1984 and D) 1990 simulations.

Figure 12. Naupliar and cyst production rates predicted by the model during 1984 and 1990 simulations.

Figure 13. Model response to changes on sediment ammonium release rate. Response variables are given in percent change relative to the values simulated assuming *nhsed* = 56 mg N m^{-2} d^{-1} and include mean annual values of mixed-layer ammonium (NHE), hypolimnetic (or monimolimnetic) ammonium (NHH); mixed-layer algal nitrogen (ALG) and *Artemia* nitrogen (ART); areal annaul rates of primary (PP) and secondary (SP) production, naupliar, and cyst production.

Figure 14. Model response to salinity-induced changes *Artemia* growth efficiency, mortality and ovigery (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 15. Model response to salinity-induced changes maximum algal growth rate, *Artemia* ovoviviparity, and hatching succes (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 16. Model response to combined effects of salinity-induced changes in *Artemia* growth efficiency, mortality, ovigery, hatching success, and day of peak hatch (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 17. Model response to combined effects of salinity-induced changes in *Artemia* growth efficiency, mortality, ovigery, hatching success, day of peak hatch and lake level (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 18. Model response to combined effects of salinity-induced changes in *Artemia* growth efficiency, mortality, ovigery, hatching success, day of peak hatch, lake level, and algal maximum growth rate (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 19. Model response to combined effects of salinity-induced changes in *Artemia* growth efficiency, mortality, ovigery, ovovivipairy, hatching success, day of peak hatch, lake level, and algal maximum growth rate (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 20. Model response to combined effects of salinity-induced changes in *Artemia* life history parameters, algal growth, and lake level under meromcitic conditions (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6380 ft.

Figure 21. Model response to combined effects of salinity-induced changes in *Artemia* life history parameters, algal growth, and lake level assuming doubled maximum algal growth rate and *Artemia* grazing (Changes listed in Table 4). Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6372 ft.

Schematic of Mono Lake Plankton Model

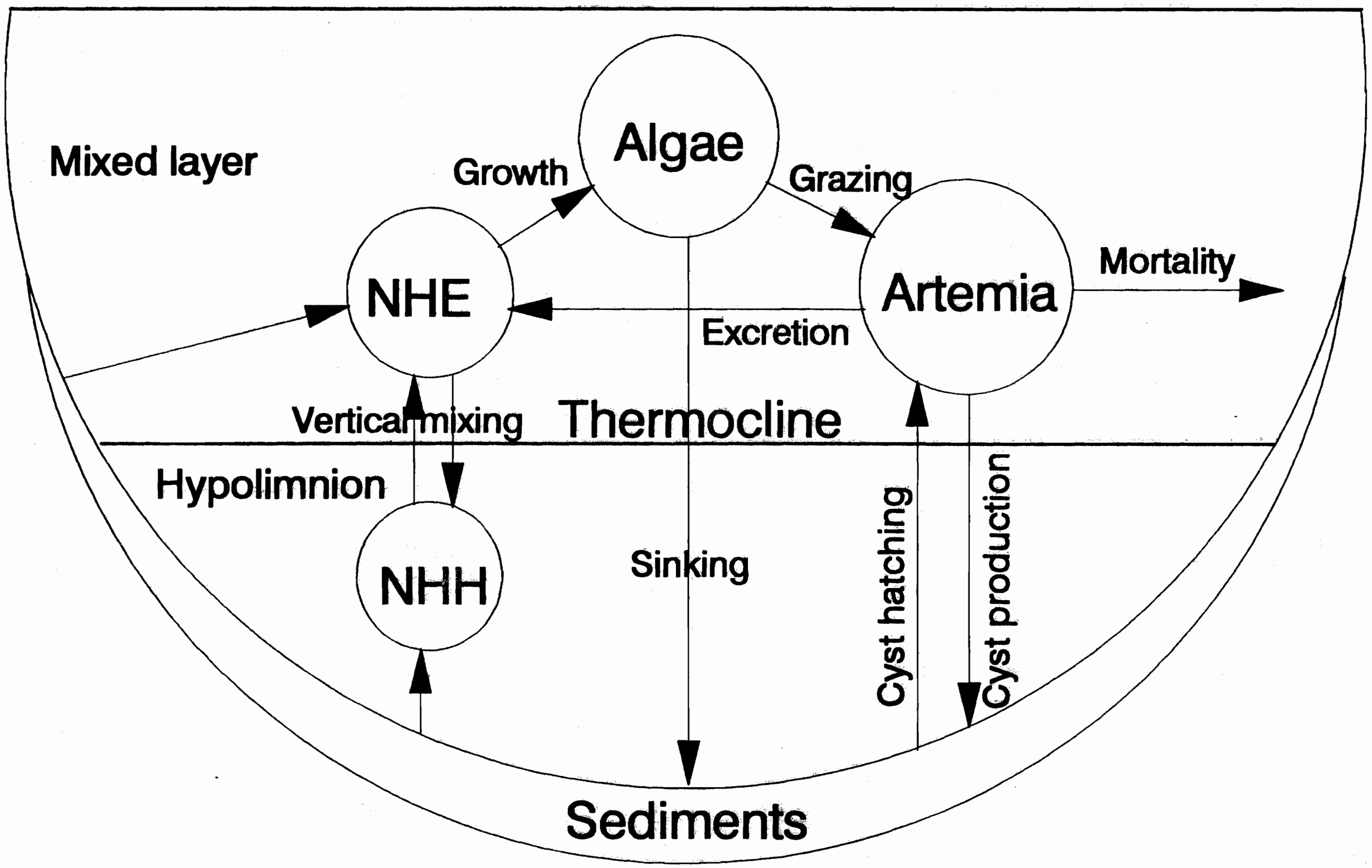


Figure 1

Figure 2

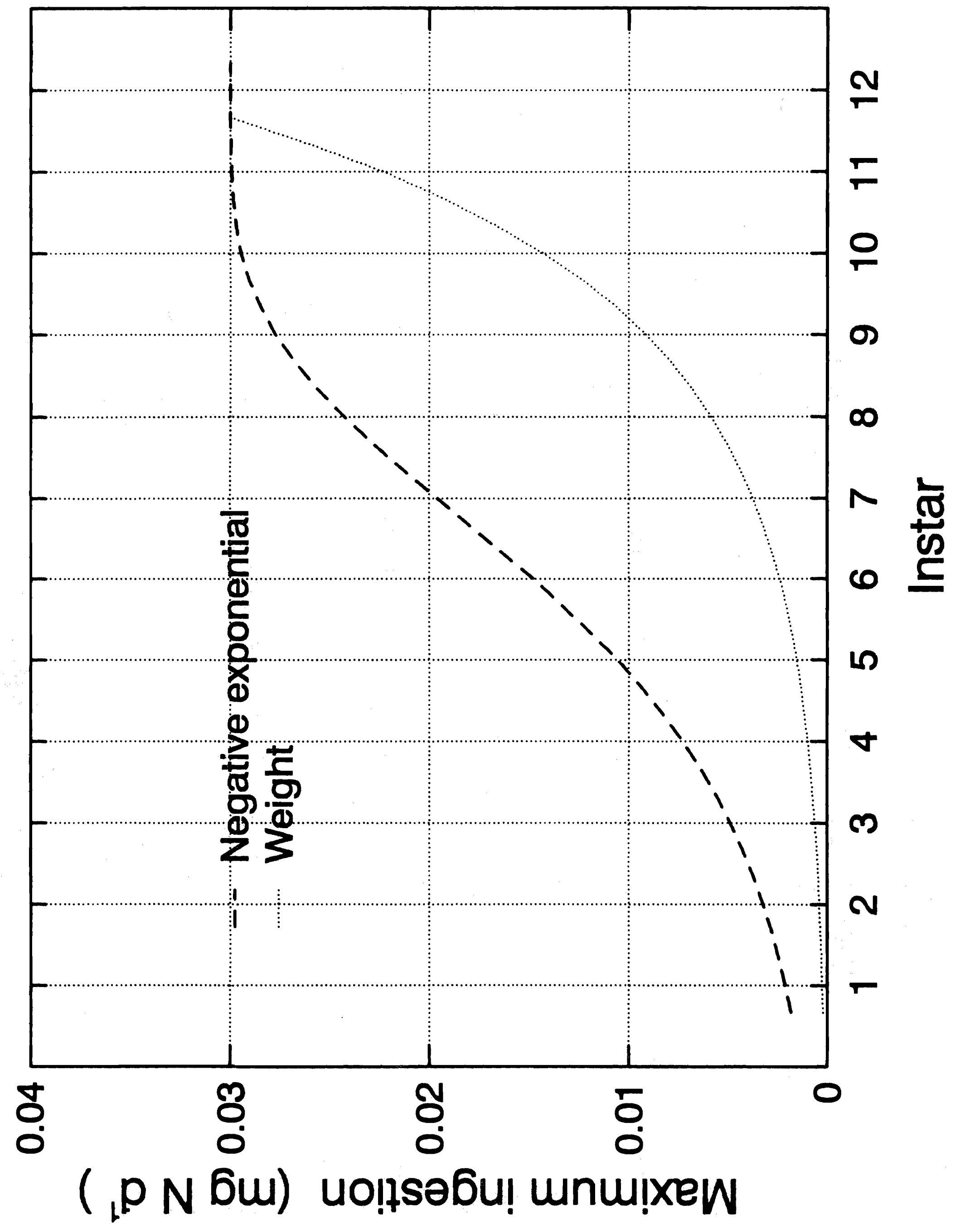
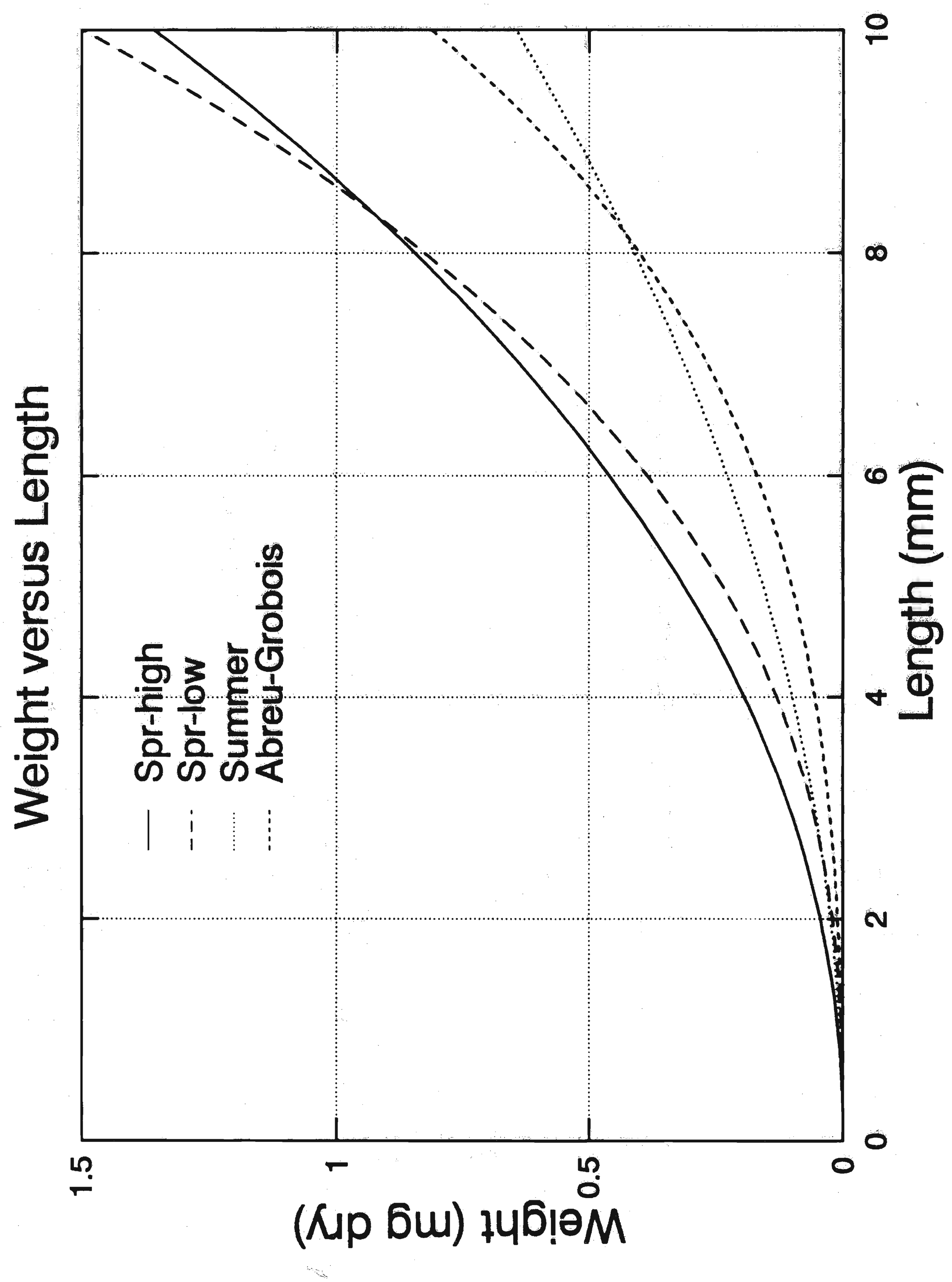

Negative exponential
Weight
Maximum ingestion (mg N d^{-1})
0.04
0.03
0.02
0.01
0
1
2
3
4
5
6
7
8
9
10
11
12
Instar

Figure 3


Weight versus Length
Spr-high
Spr-low
Summer
Abreu-Grobois
Weight (mg dry)
0
0.5
1
1.5
Length (mm)
0
2
4
6
8
10

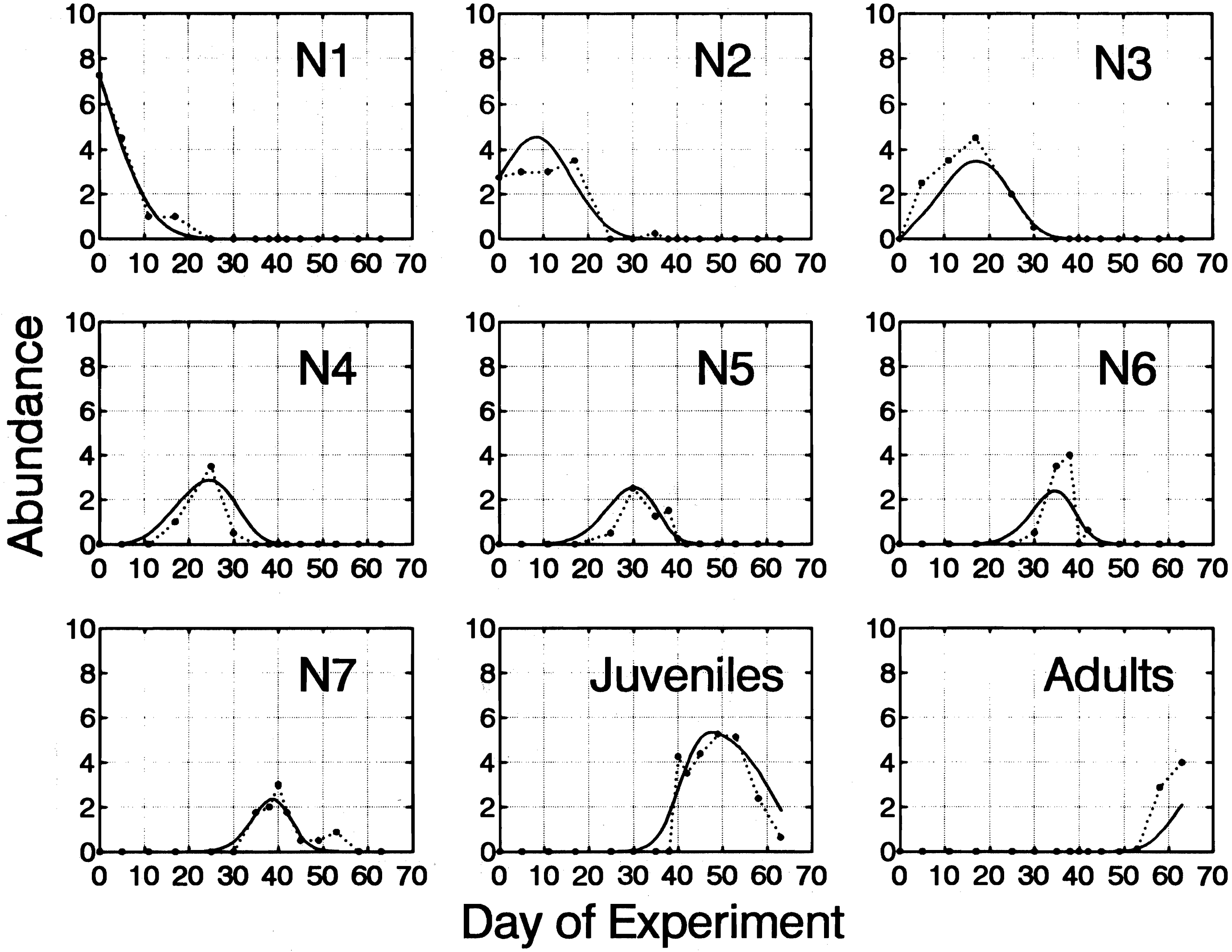
N1
N2
N3
N4
N5
N6
N7
Juveniles
Adults
Abundance
Day of Experiment
0
2
4
6
8
10
0 10 20 30 40 50 60 70

Figure 4

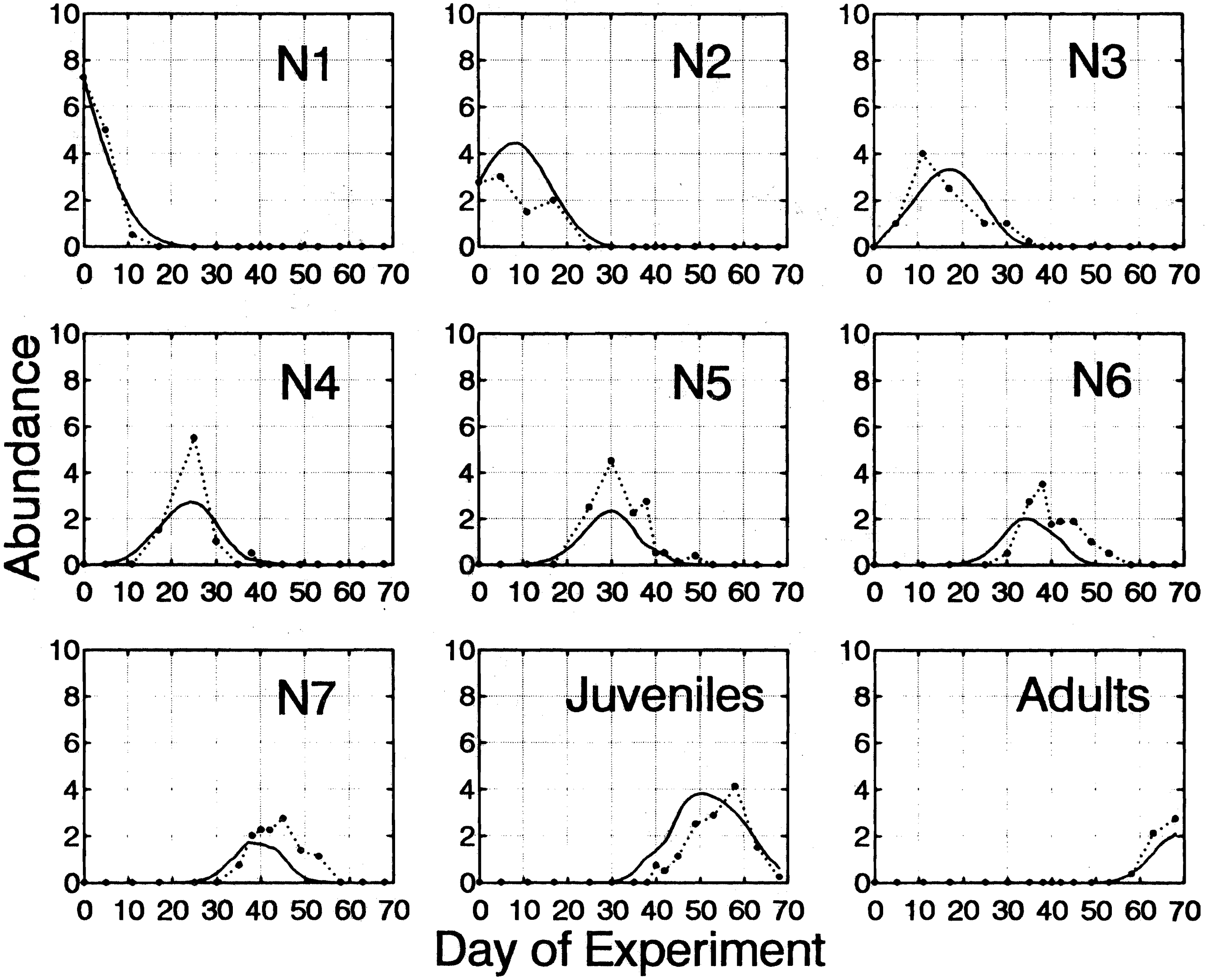

N1
N2
N3
N4
N5
N6
N7
Juveniles
Adults
Abundance
Day of Experiment
0
2
4
6
8
10
0 10 20 30 40 50 60 70

Figure 5

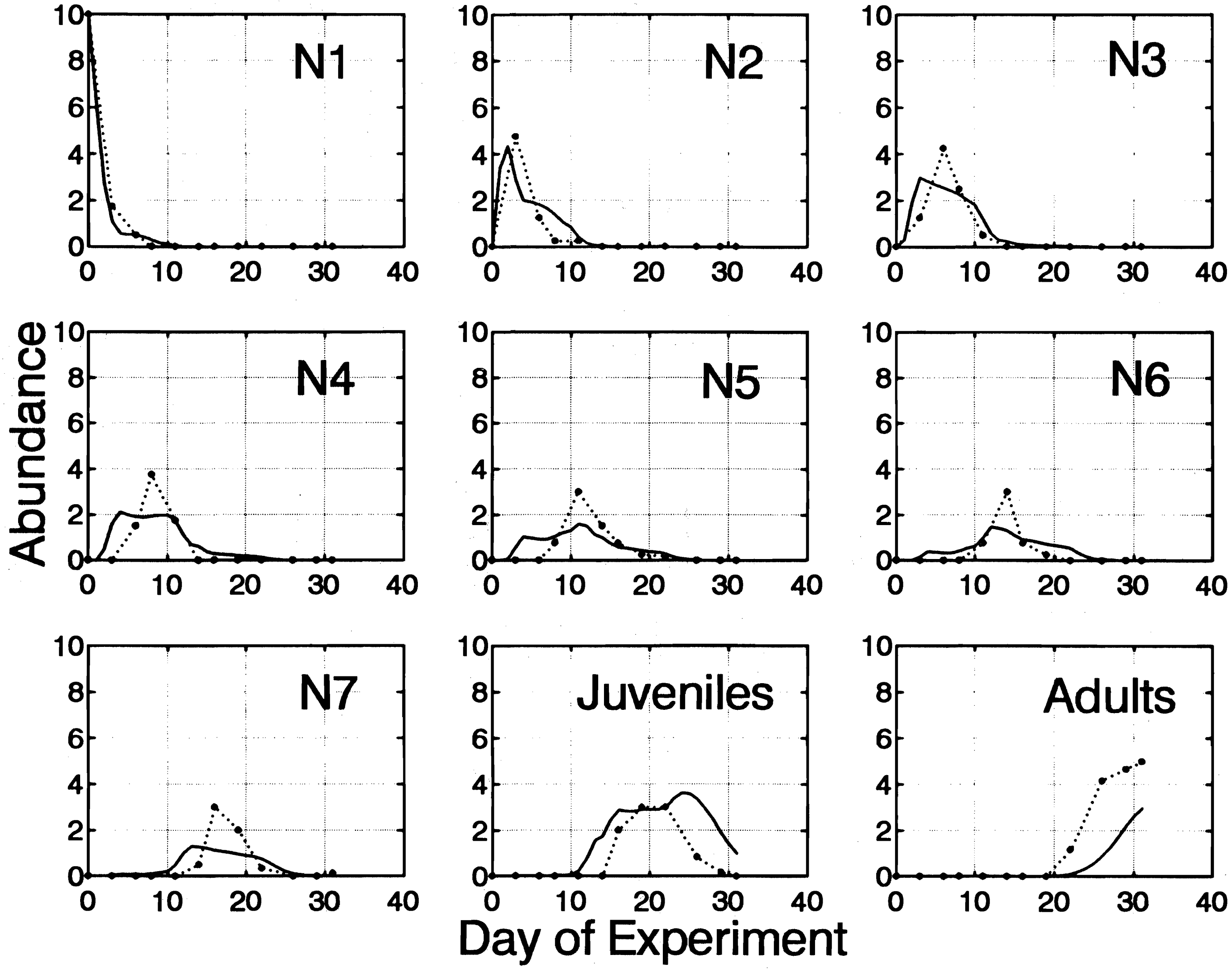
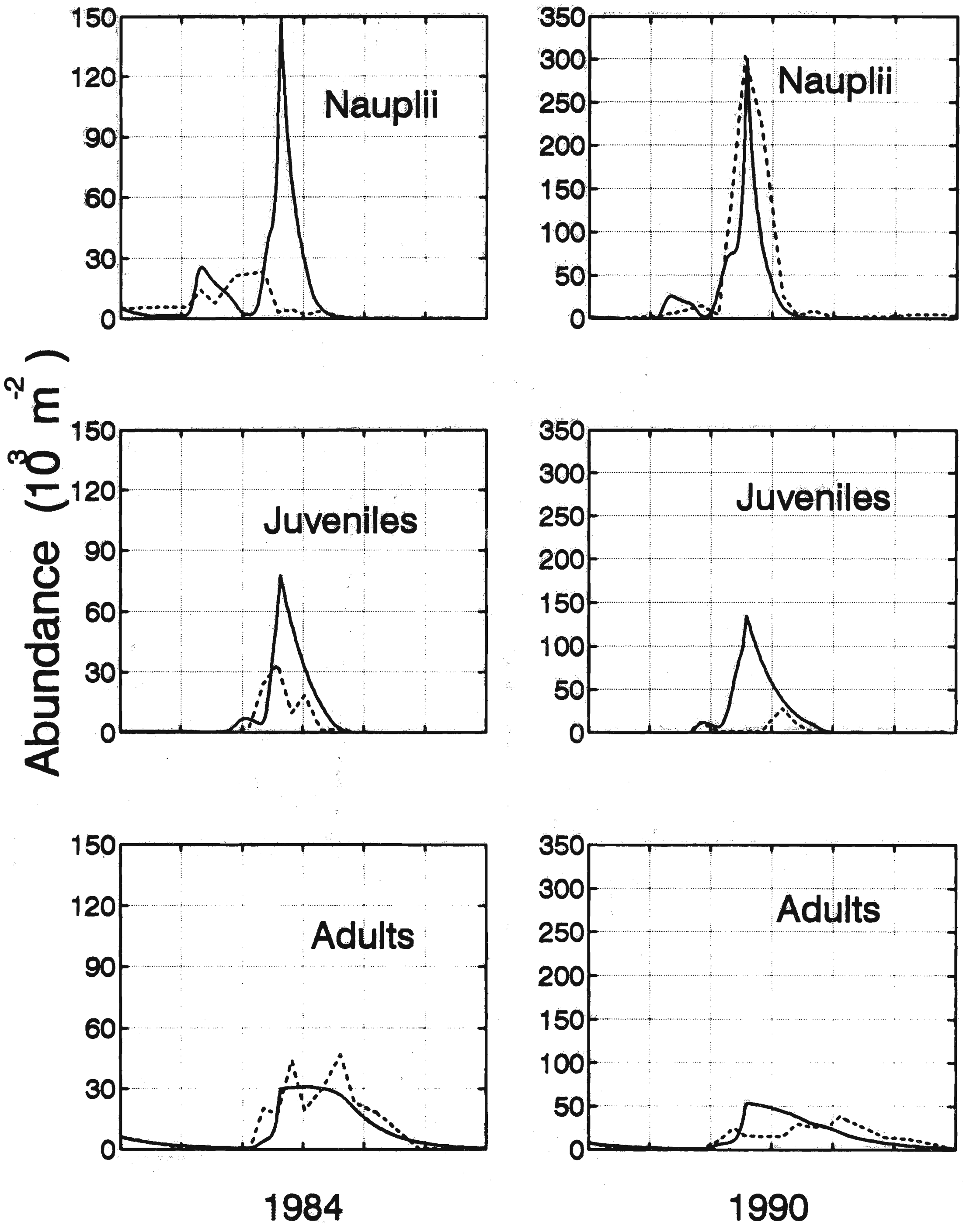

N1
N2
N3
N4
N5
N6
N7
Juveniles
Adults
Abundance
Day of Experiment
0
2
4
6
8
10
0
10
20
30
40

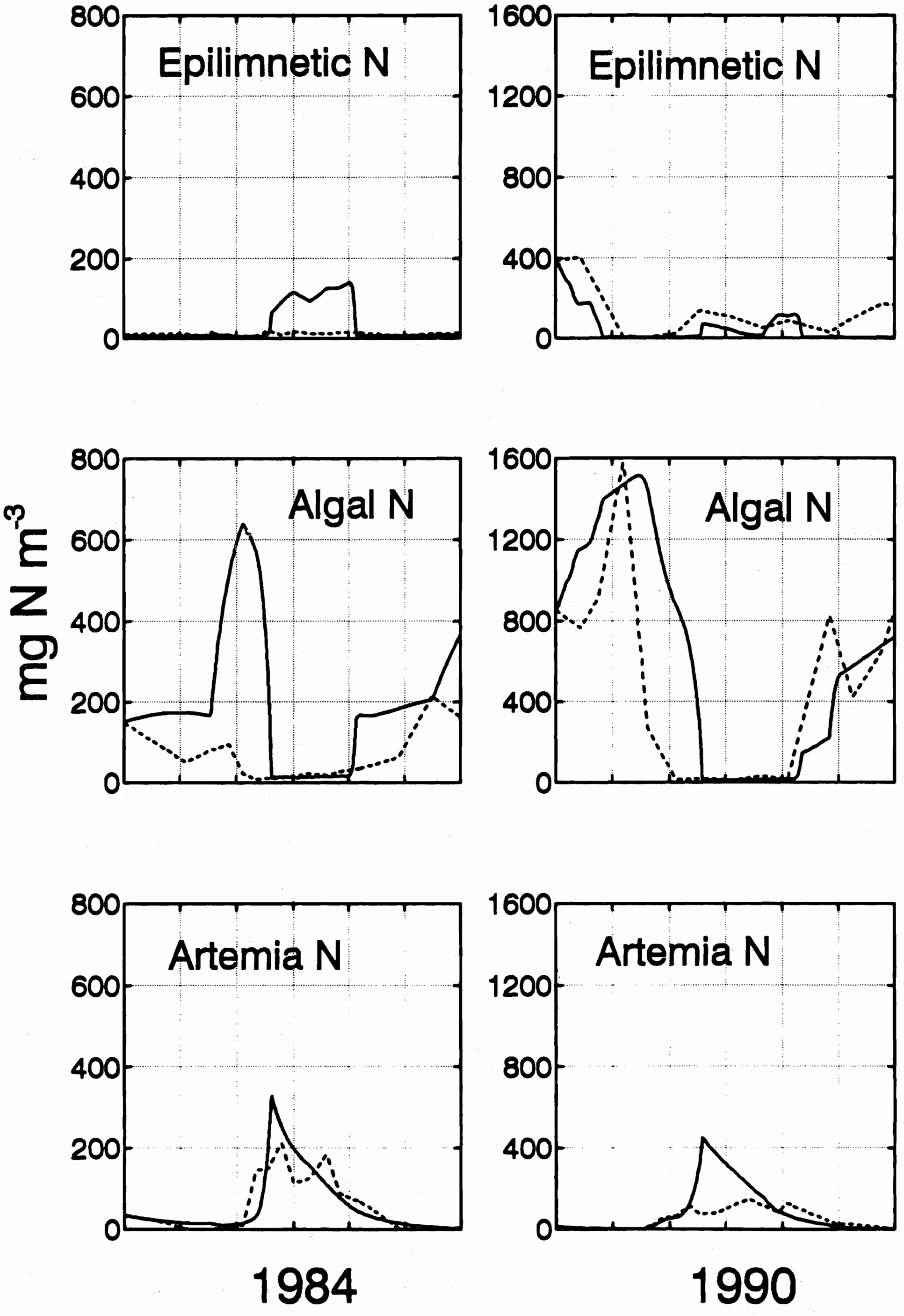
Figure 6

Figure 7



Abundance (10^3 m^{-2})
Nauplii
Juveniles
Adults
150
120
90
60
30
0
350
300
250
200
150
100
50
0
1984
1990

Figure 8


Epilimnetic N
Epilimnetic N
Algal N
Algal N
Artemia N
Artemia N
mg N m-3
800
600
400
200
0
1600
1200
800
400
0
1984
1990

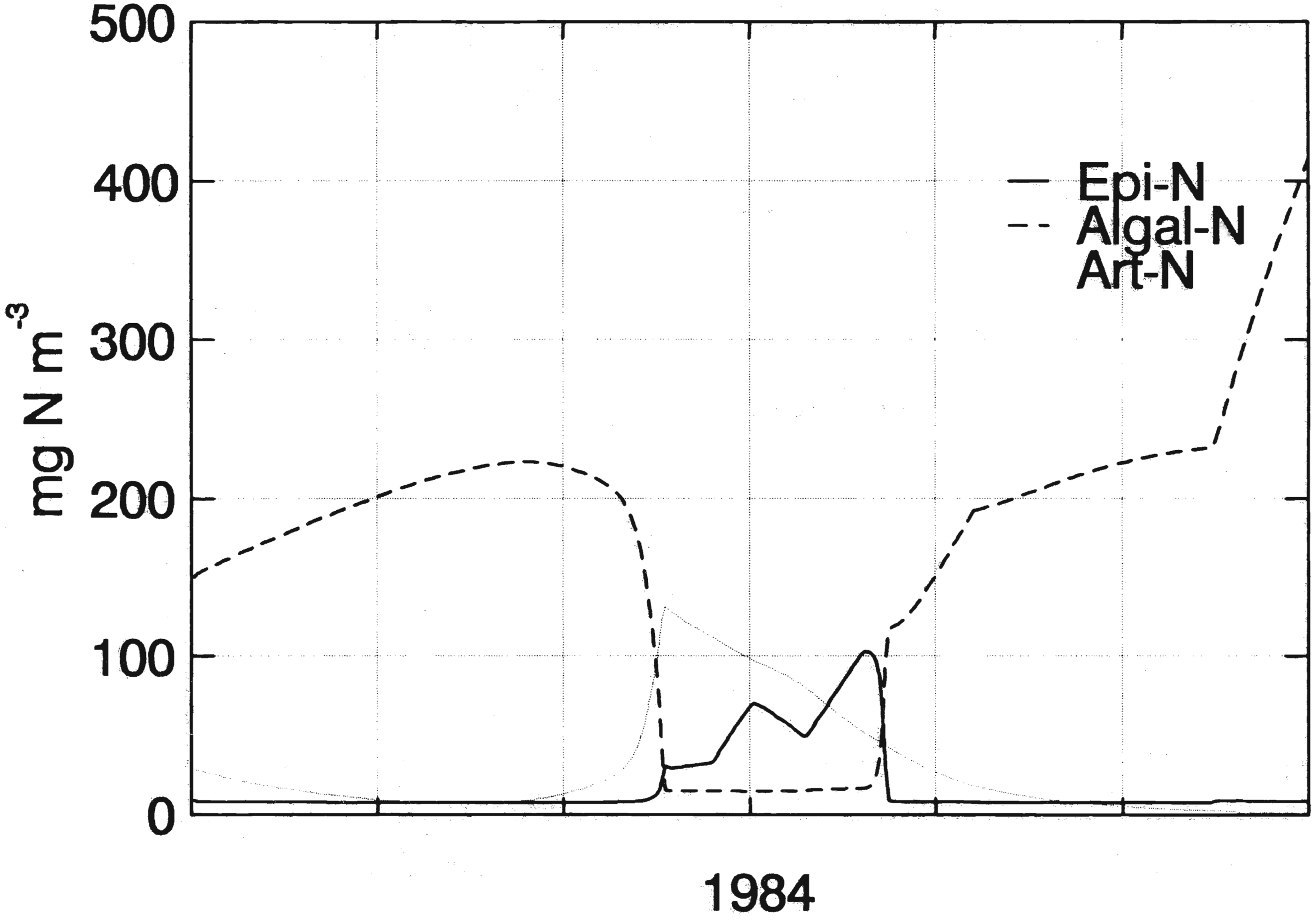


Figure 9

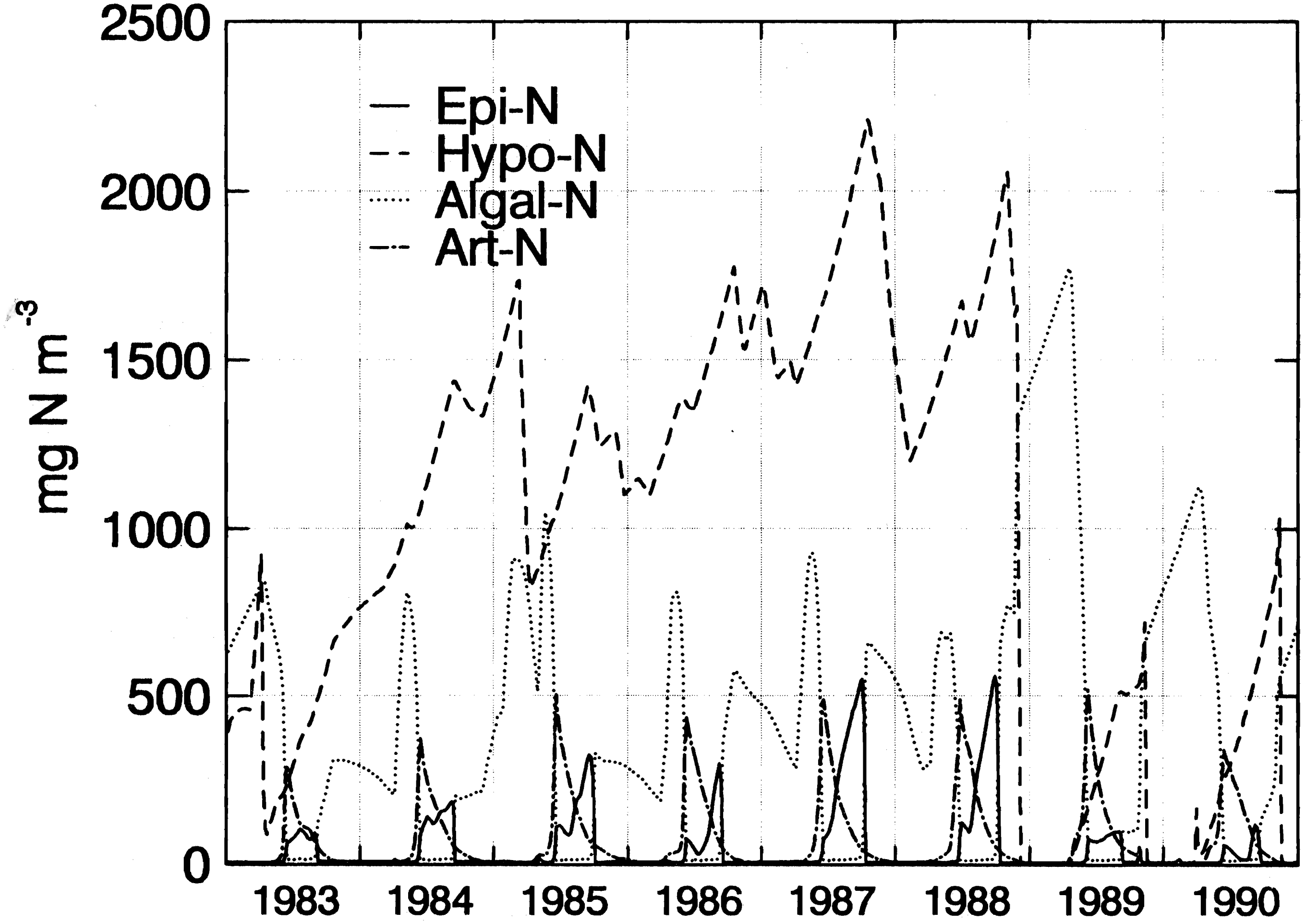

Epi-N
Hypo-N
Algal-N
Art-N
mg N m^{-3}
2500
2000
1500
1000
500
0
1983
1984
1985
1986
1987
1988
1989
1990

Figure 16

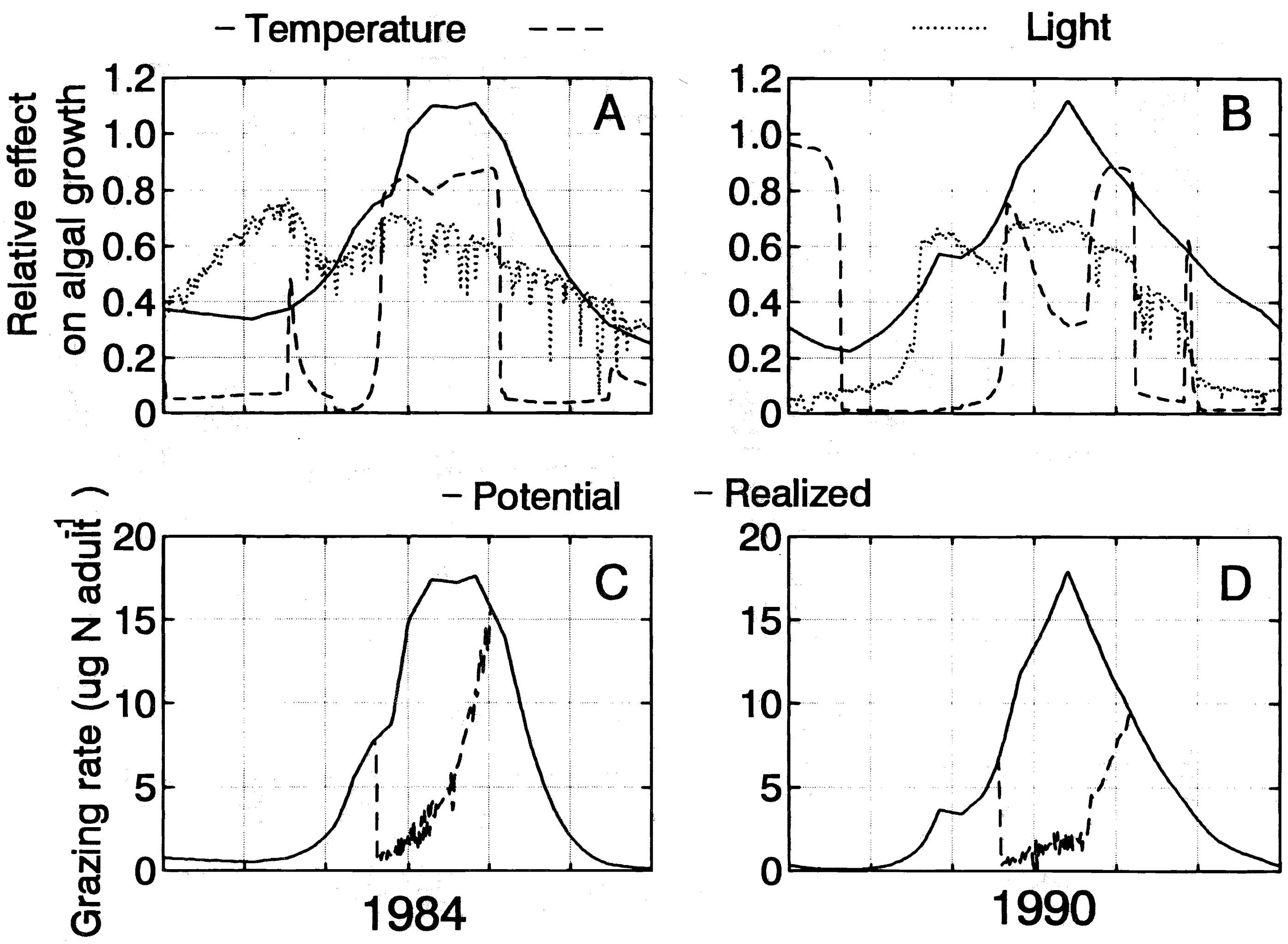

– Temperature - - -
.... Light
Relative effect on algal growth
1.2
1.0
0.8
0.6
0.4
0.2
0
A
B
– Potential
– Realized
Grazing rate (ug N adult^{-1})
20
15
10
5
0
C
D
1984
1990

Figure [illegible]

Figure 12

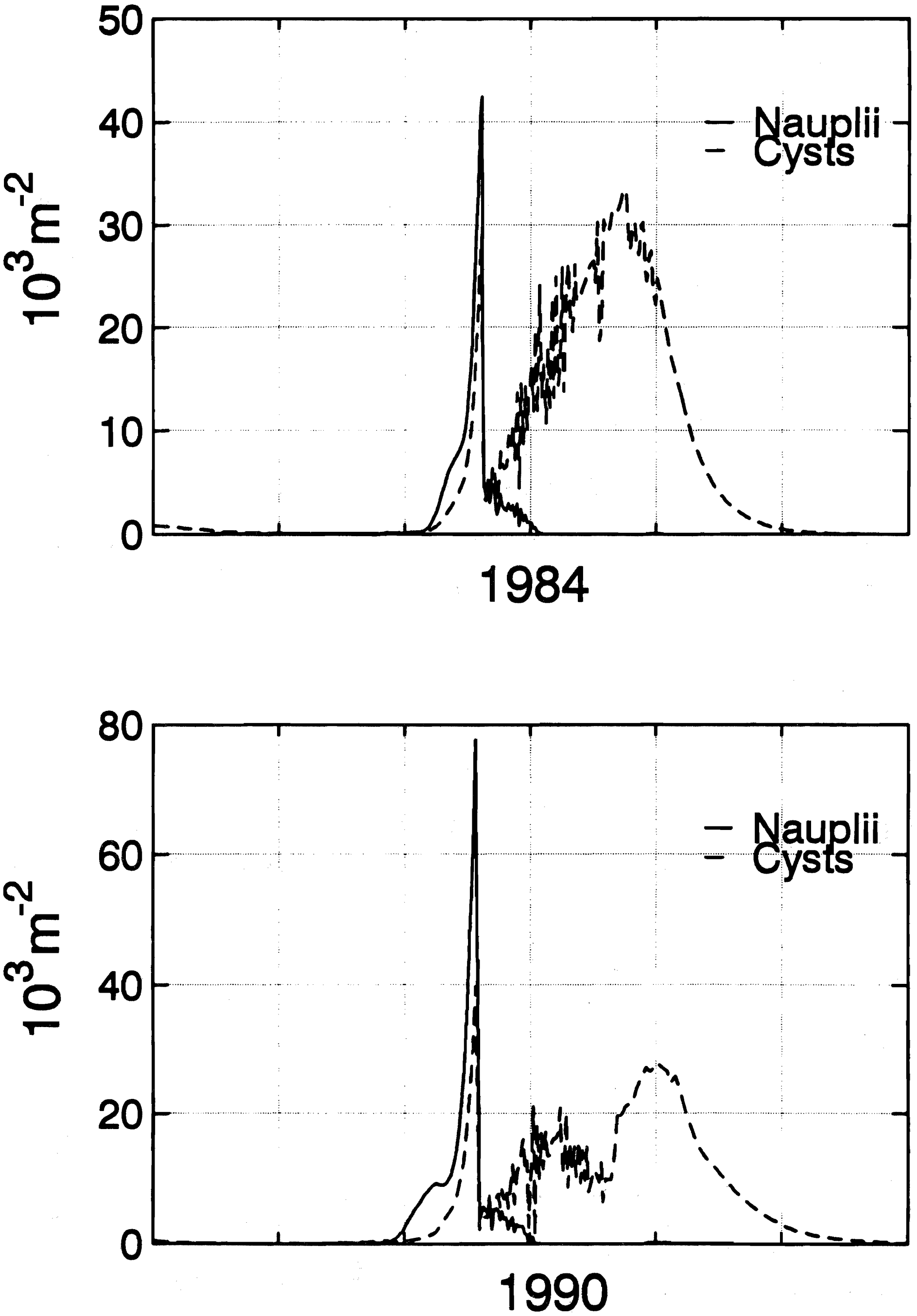

50
40
30
20
10
0
$10^3 m^{-2}$
Nauplii
Cysts
1984
80
60
40
20
0
$10^3 m^{-2}$
Nauplii
Cysts
1990

Figure 13

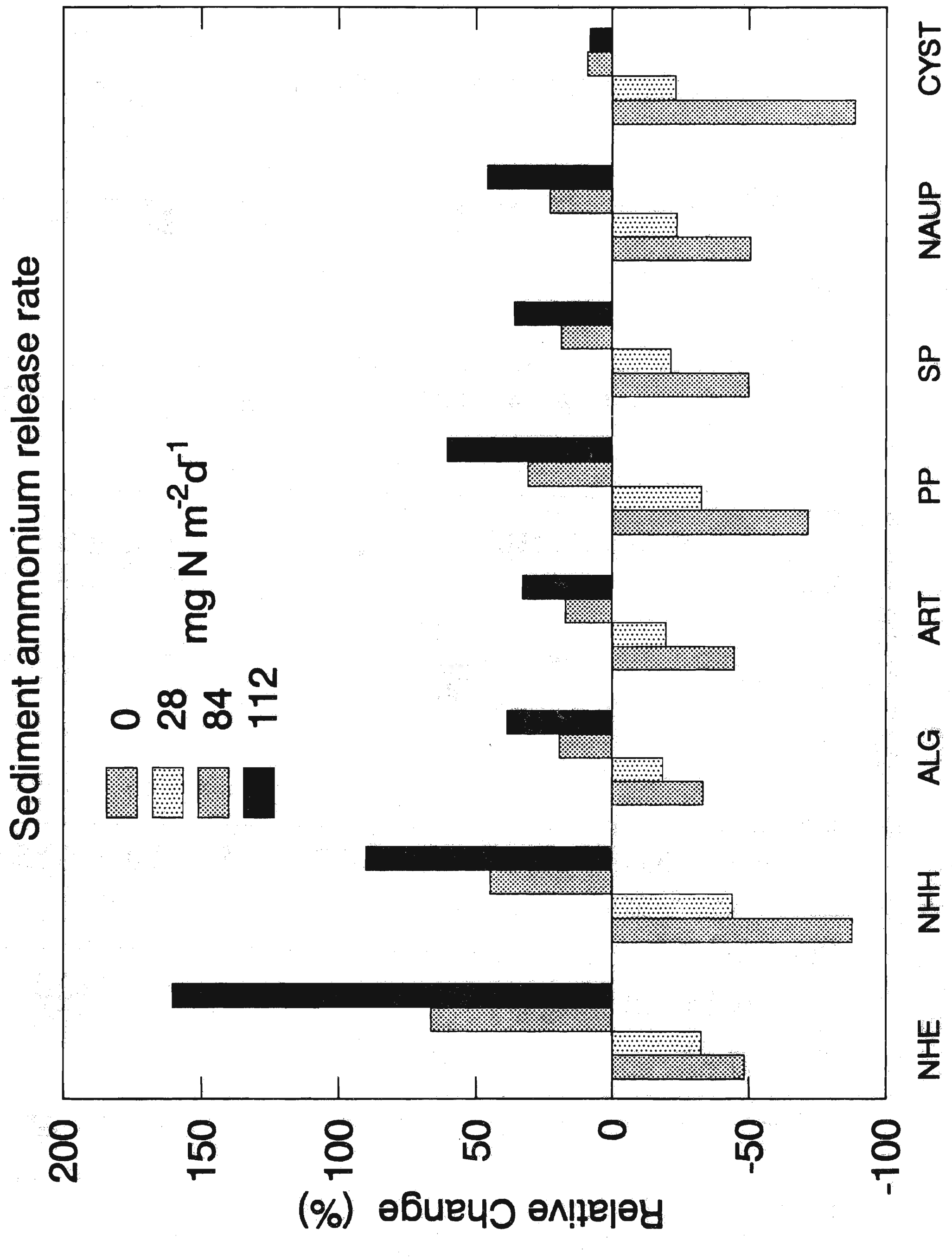

Sediment ammonium release rate
▨ 0
░ 28
▨ 84
■ 112
mg N m-2d-1
Relative Change (%)
200
150
100
50
0
-50
-100
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST

Figure 14

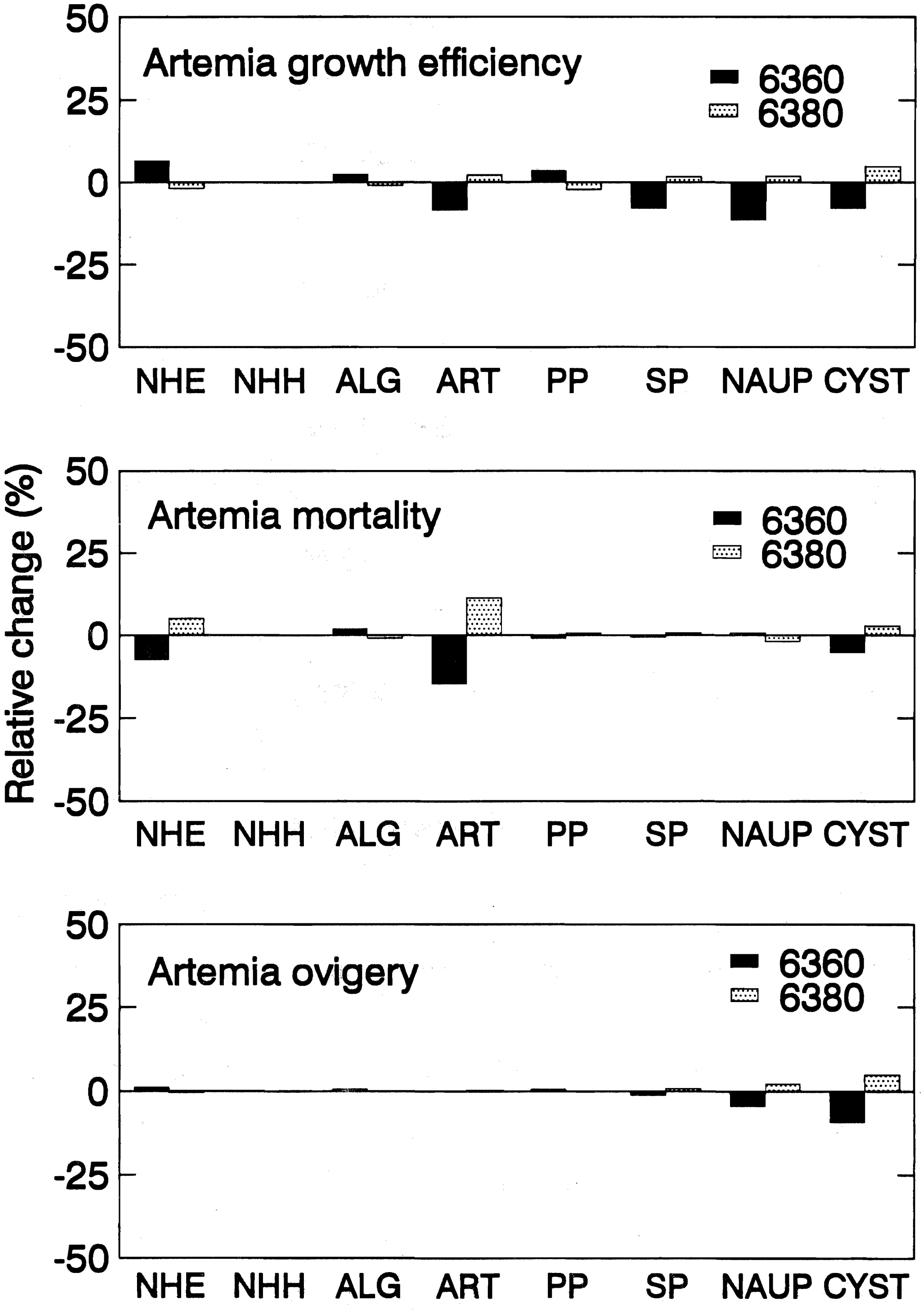
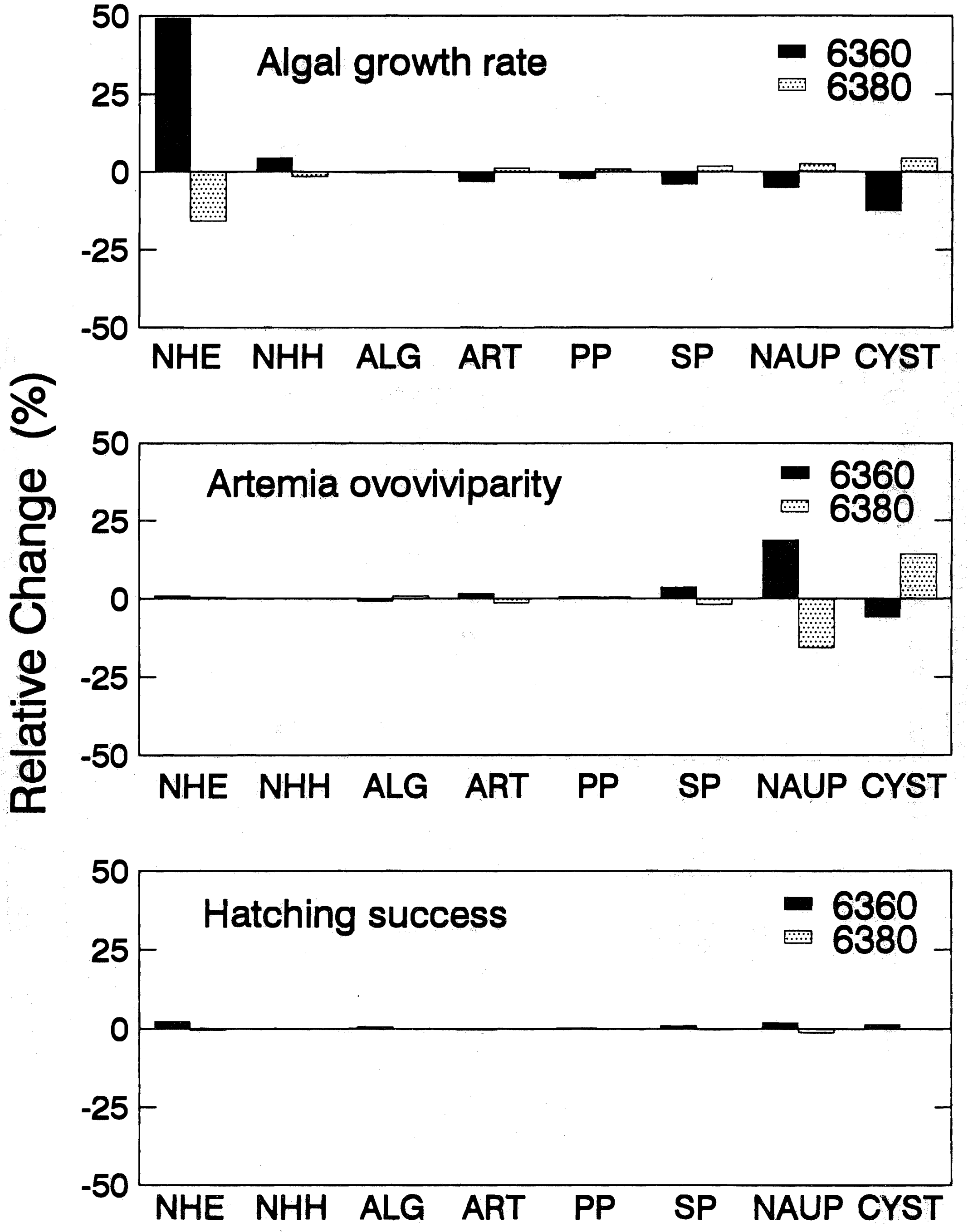

Artemia growth efficiency
6360
6380
Artemia mortality
6360
6380
Artemia ovigery
6360
6380
Relative change (%)
50
25
0
-25
-50
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST

Figure 15



Relative Change (%)
Algal growth rate
Artemia ovoviviparity
Hatching success
6360
6380
50
25
0
-25
-50
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST

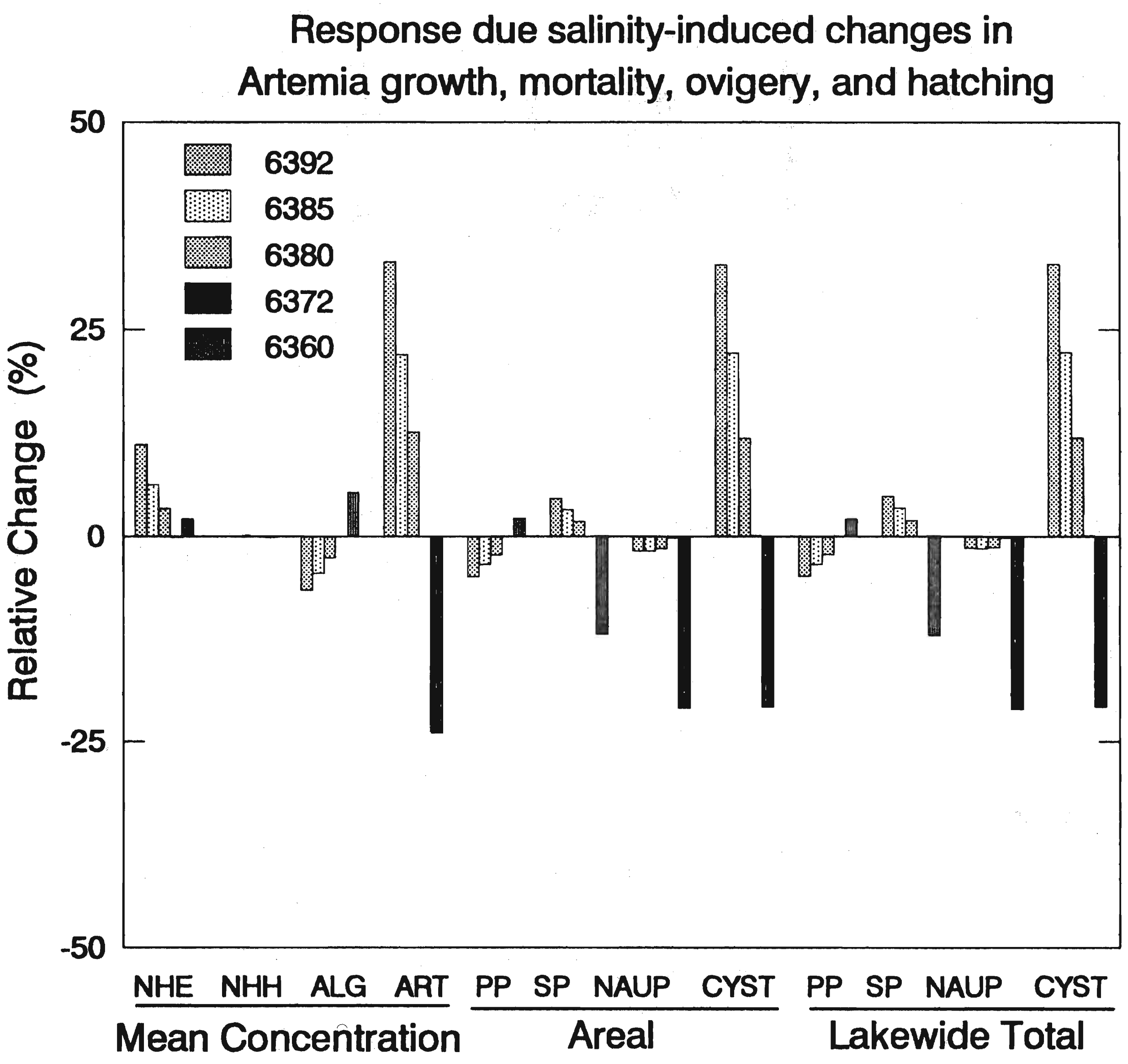

Response due salinity-induced changes in
Artemia growth, mortality, ovigery, and hatching
50
25
0
-25
-50
Relative Change (%)
6392
6385
6380
6372
6360
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
PP
SP
NAUP
CYST
Mean Concentration
Areal
Lakewide Total

Figure 16

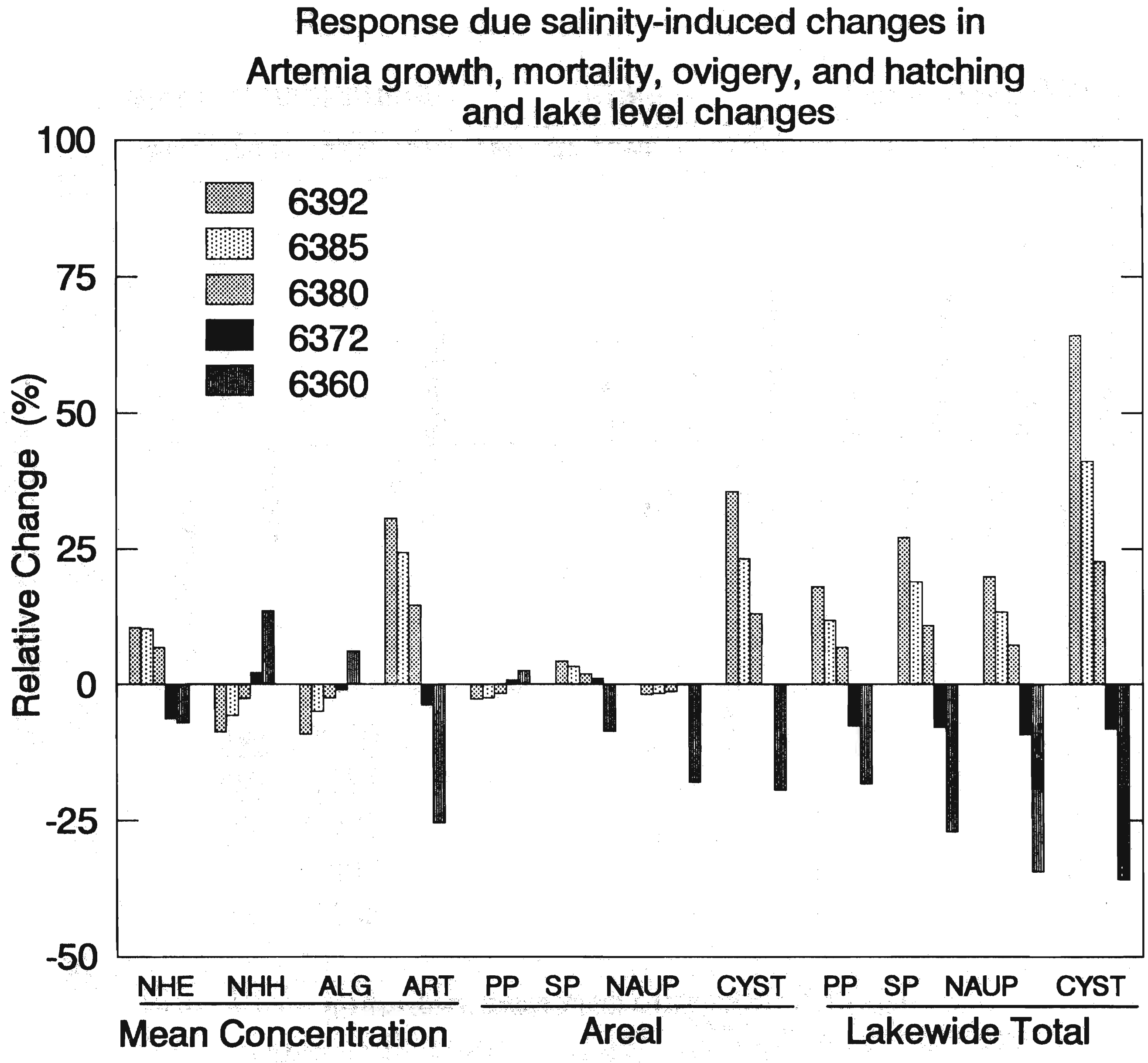

Response due salinity-induced changes in
Artemia growth, mortality, ovigery, and hatching
and lake level changes
100
75
50
25
0
-25
-50
Relative Change (%)
6392
6385
6380
6372
6360
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
PP
SP
NAUP
CYST
Mean Concentration
Areal
Lakewide Total

Figure 17

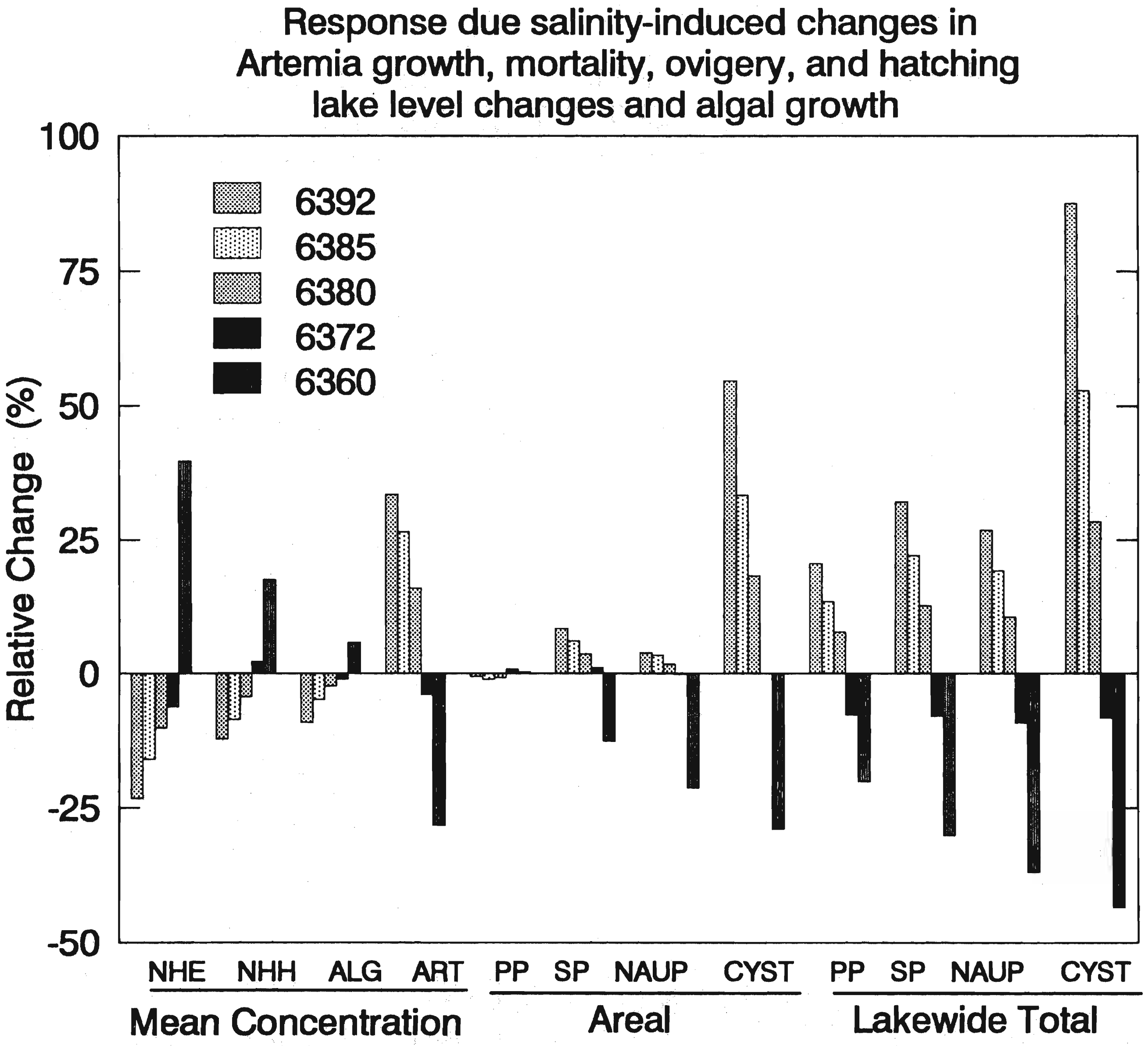

Response due salinity-induced changes in
Artemia growth, mortality, ovigery, and hatching
lake level changes and algal growth
100
75
50
25
0
-25
-50
Relative Change (%)
6392
6385
6380
6372
6360
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
PP
SP
NAUP
CYST
Mean Concentration
Areal
Lakewide Total

Figure 18

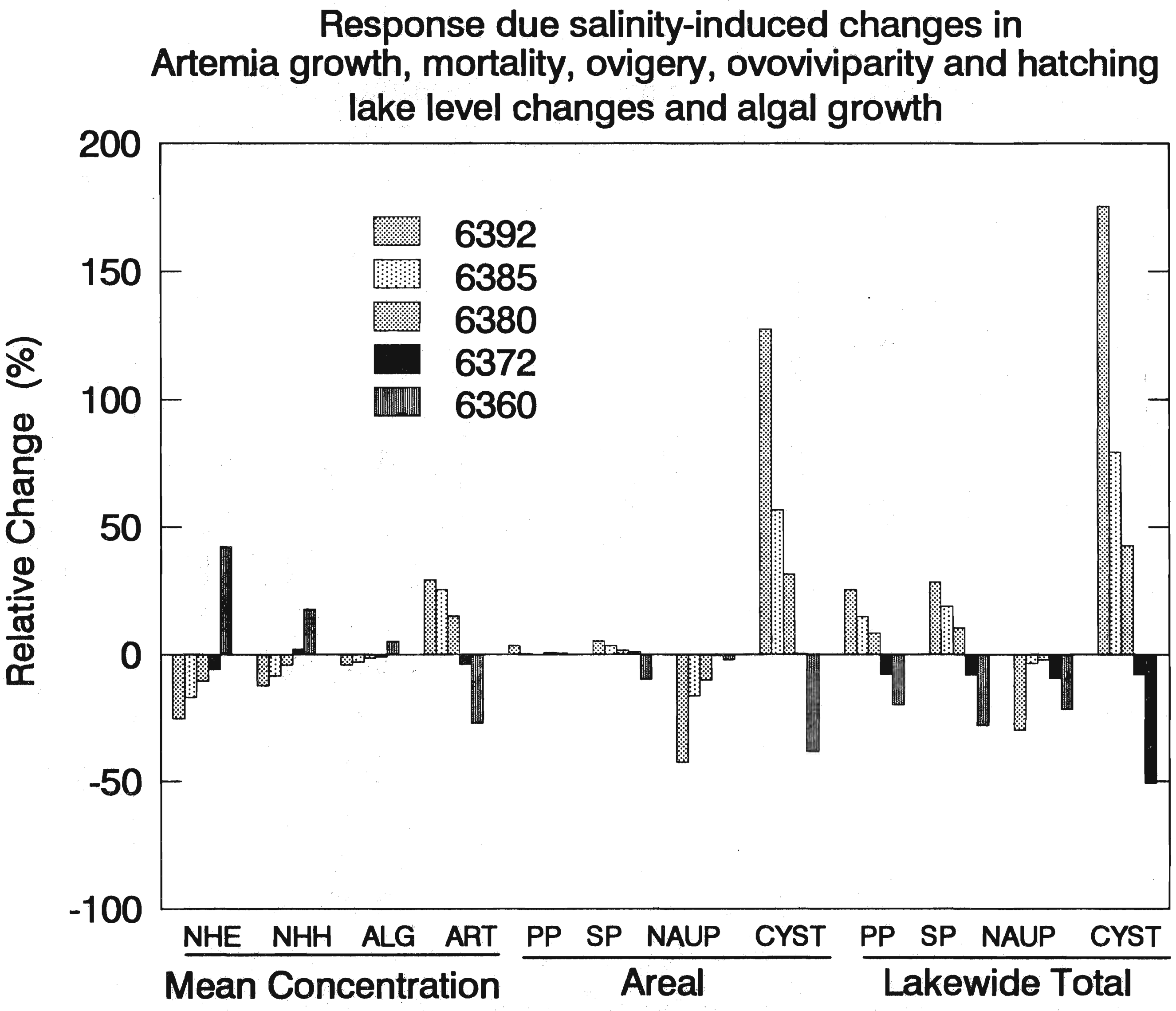

Response due salinity-induced changes in
Artemia growth, mortality, ovigery, ovoviviparity and hatching
lake level changes and algal growth

Figure 19

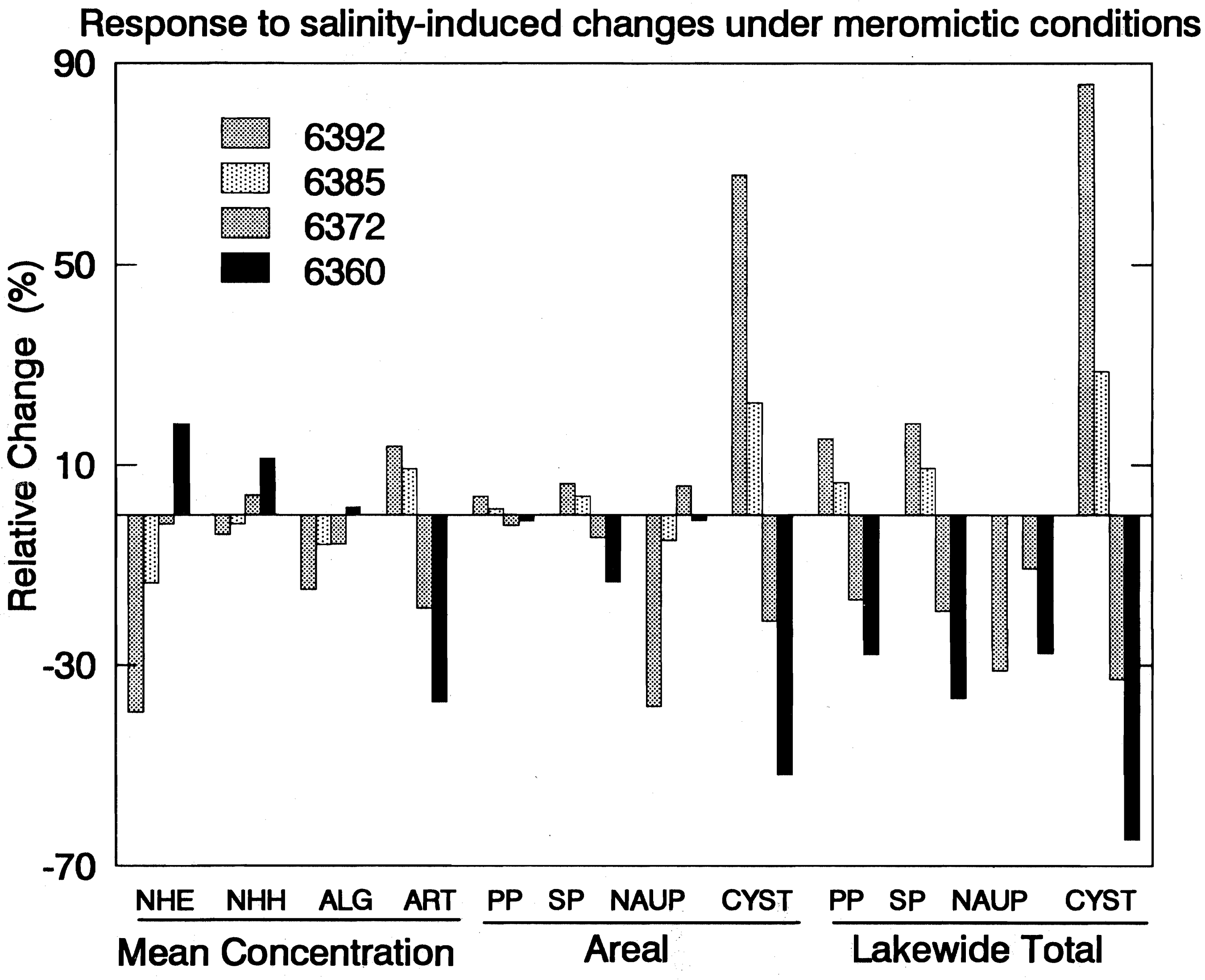

Response to salinity-induced changes under meromictic conditions
90
50
10
-30
-70
Relative Change (%)
6392
6385
6372
6360
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
PP
SP
NAUP
CYST
Mean Concentration
Areal
Lakewide Total

Figure 20

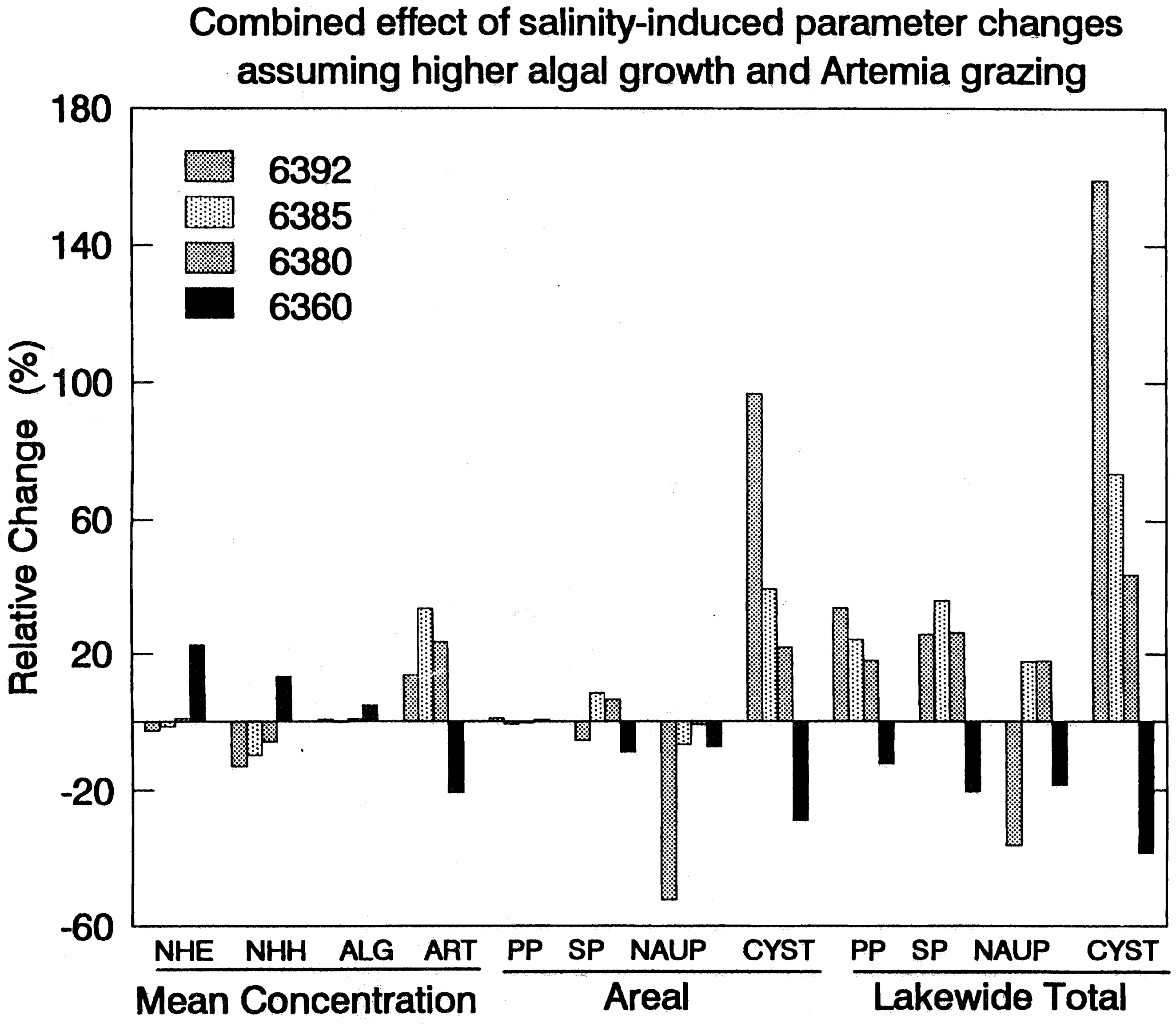

Combined effect of salinity-induced parameter changes assuming higher algal growth and Artemia grazing

Figure 21

Robert Jellison
Sierra Nevada Aquatic Res. Lab
Star Rt. 1, Box 198
Mammoth Lakes, CA

July 24, 1992

Mr. Russ Brown
Jones and Stokes
2600 V Street
Sacramento, CA 95818

Dear Russ:

Enclosed is a diskette of the data we discussed at our July 17th meeting and revised figures and tables for the draft modeling report. During recent analysis, I determined the need to make further revisions to the model, and simulations with the revised model require modification of our earlier results. Because these newer results affect some of our previous conclusions, I have enclosed a new set of tables and figures and will be forwarding a new version of our report as soon as possible.

The revision which affected our previous conclusions, dealt with our derivation of the effects of salinity on assimilation efficiency. In our earlier version, we assumed the relative effect of salinity on assimilation efficiency was approximated by changes in the length of time to maturity of individuals. Because the model assumes a constant weight-instar relationship for *Artemia* under all conditions, we did not consider the effect of salinity on weight. In further review of the model results following our workshop, I noted the large effect *Artemia* growth efficiency has on secondary production. Recognizing the importance of growth efficiency on the overall conclusions, we reconsidered the interpretation of the salinity bioassays and noted the salinity bioassays also indicate significant declines in adult weight at higher salinities. Therefore, a better approximation of the effect of salinity on assimilation efficiency would be the weight of adults divided by the length of time to maturity. This yields a much larger effect of salinity on assimilation efficiency and model results are different under this new assumption.

Sincerely,

Robert Jellison

Robert S. Jellison
Res. Asst.

cc. Melack

Figure Captions

Figure 1. Schematic of Mono Lake *Artemia* model depicting processes modeled and the partitioning of nitrogen among epilimnetic ammonium (NHE), hypolimnetic ammonium (NHH), and the algal and *Artemia* particulate components.

Figure 2. Maximum ingestion rates in which the relative rates of specific instars are proportional to their weight (dotted) or a negative exponential formulation similar to that determined by Abreu-Grobois (1991) for *A. franciscana* .

Figure 3. Weight versus length relationships from experimental development experiments with *Artemia monica* under different conditions of food and temperature and *A. franciscana* raised under optimal conditions. The different conditions for the *A. monica* correspond to spring temperatures and algal biomass during monomictic conditions (Spr-high), spring temperature and alga biomass during meromictic conditions (Spr-low), and summer (Summer) conditions of warm temperature and low algal biomass.

Figure 4. Observed (···) versus predicted (—) instar-specific abundance for *Artemia* reared under conditions representative of spring monomictic conditions (cold temperatures and high food treatment).

Figure 5. Observed (···) versus predicted (—) instar-specific abundance for *Artemia* reared under conditions representative of spring meromictic conditions (cold temperatures and low food treatment).

Figure 6. Observed (···) versus predicted (—) instar-specific abundance for *Artemia* reared under conditions representative of summer conditions during either monomictic or meromictic conditions (warm temperatures and low food treatment).

Figure 7. Observed (---) versus predicted (—) instar-specific *Artemia* abundance under meromictic (1984) and monomictic (1984) conditions. Observed data are from three different pelagic stations. Model parameters are listed in Table 1.

Figure 8. Observed (---) versus predicted (—) partitioning of mixed-layer nitrogen among epilimnetic ammonium, algae, and *Artemia* under meromictic (1984) and monomictic (1984) conditions. Predicted (···) partitioning (1984 only) when mixing depth is held constant during the spring. Model parameters as listed in Table 1.

Figure 9. Eight-year simulation of the partitioning of nitrogen among mixed-layer pools of ammonium, algae, and *Artemia* and hypolimnetic ammoniun using mixed-layer depths, temperature, and insolation observed from 1983 to 1990.

Figure 10. Relative effects of suboptimal temperature (—), light (···), and nitrogen (---) during A) 1984 and B) 1990 simulations. Potential (—) versus realized (---) grazing rates during C) 1984 and D) 1990 simulations.

Figure 11. Naupliar and cyst production rates predicted by the model during 1984 and 1990 simulations.

Figure 12. Model response to changes on sediment ammonium release rate. Response variables are given in percent change relative to the values simulated assuming *nhsed* = 56 mg N m^{-2} d^{-1} and include mean annual values of mixed-layer ammonium (NHE), hypolimnetic (or monimolimnetic) ammonium (NHH); mixed-layer algal nitrogen (ALG) and *Artemia* nitrogen (ART); areal annaul rates of primary (PP) and secondary (SP) production, naupliar (NAUP), and cyst (CYST) production.

Figure 13. Model response to salinity-induced changes A) *Artemia* growth efficiency (eff_1), B) reproductive efficiency (eff_2), and C) juvenile and naupliar mortality (*morj* and *mora)*. Parameter modifications listed in Table 4. Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 14. Model response to salinity-induced changes in *Artemia* A) ovigery (*repovig;* % females bearing eggs), B) ovoviviparity factor (*ovofac;* factor modifying the proportion of life young versus cyst production), and C) maximum algal growth rate. Parameter modifications listed in Table 4. Response variables are given in percent change relative to the values simulated using final parameters in Table 1 and an elevation of 6375.

Figure 15. Model response to the combined effects of salinity-induced changes in *Artemia* A) growth efficiency, mortality, ovigery, hatching success, and day of peak hatch compared to B) salinity-induced changes in ovoviviparity Parameter modifications listed in Table 4. Elevation was held constant at 6375 so areal and lakewide estimates show identical responses.

Figure 16. Model response to the effect of salinity-induced changes in A) maximum algal growth rate compared to those B) due strictly to area and volume changes associated with different lake levels. Parameter modifications listed in Table 4. Elevation was held constant at 6375 assessing effects due to changes in algal growth rate.

Figure 17. Model response to combined effects of salinity-induced changes in *Artemia* life history parameters and area and volume changes associated with different lake levels under A) monomictic (1990) and B) meromictic (1984) conditions. Parameter modifications listed in Table 4.

Figure 18. Model response to combined effects of salinity-induced changes in *Artemia* life history parameters and area and volume changes associated with different lake levels for different model values of A) maximum grazing rates (grz_1) and B) relative instar grazing rates (grz_2). Parameter modifications listed in Tables 4 and 7.

Figure 19. Model response to combined effects of salinity-induced changes in *Artemia* life history parameters and area and volume changes associated with different lake levels for different model values of B) algal dependence of grazing (*grzalg*) and B) proportion of unassimilated ingested material going to ammonium (*grzpar*). Parameter modifications listed in Tables 4 and 7.

Figure 20. Model response to combined effects of salinity-induced changes in *Artemia* life history parameters and area and volume changes associated with different lake levels for different model values of A) light dependence of algal growth (*alglit*) and B) ammoniium supply rate (*nhsed*). Parameter modifications listed in Tables 4 and 7.

Table 1. Final model parameters

	Grazing and Development Parameters		
eff1	growth efficiency	0.44	Reeve (1963)
eff2	reproductive efficiency	0.30	Estimated based on 1984 cyst production
grz1	maximum ingestion	0.03	proportion of maximum weight
grz2	ingestion shape coefficient	-239	Similar to Adreu-Grobois results
grztmp	temperature grazing coefficient	13.3	Based on model and 1984 amd 1990 data
grzalg	algal grazing coefficient	124	Based on model and 1984 amd 1990 data
grzalgmin	algal level below which grazing rate is zero	7.5	Set to achieve model stability
grzpar	fraction of egestion going to excretion	0.5	Based on model and 1984 amd 1990 data
brdint20	brood interval at 20 degrees	8.5	Previous analysis of field data
brdtmp	temperature brood interval effect	1.187	Previous analysis of field data
sen	senility factor	0.3	Based on model and 1984 amd 1990 data
tmpopt	optimum temperature	30	Based on laboratory data of related species
	Mortality Parameters		
morn	daily naupliar base mortality	0.007	Estimated w/ development experiments
morj	daily juvenile base mortality	0.025	Estimated with model and 1984 data
mora	daily adult base mortality	0.01	Estimated with model and 1984 data
mortmp	temperature mortality factor	2.2	Estimated w/ development experiments
moralg	algal mortality factor	45.5	Estimated w/ development experiments
sen	senility factor (same as above)	0.3	Estimated with model and 1984 data
	Reproductive Parameters		
repff	fraction of adults which are female	0.41	Observed field data 1983 - 1990
repovig	fraction of females which are ovigerous	0.84	Observed field data 1983 - 1990
repmax	maximum daily egg production per female	15	Baed on maximum observed fecundity
ovoi	initial and final ovoviviparity	0.02	Field observations
ovo1	constant in ovoviviparity regression	1.432	Regression on field data, 83 - 90
ovo2	temperature regression coefficient	-0.0936	Regression on field data, 83 - 90
ovo3	chla regression coefficient	0.00054	Regression on field data, 83 - 90
ovo4	ovoviviparity factor for second adult age class	0.5	Set during 1984 parameter estimation
ovof	day at which ovovivipary reverts to initial level	240	Set during 1984 parameter estimation
	Cyst Hatching Parameters		
hfac	proportion of cysts which hatch	0.01	Based on model and 1984 and 1990 data
hday	day of peak cyst hatch	75	Based on model and 1984 and 1990 data
hsd	standard deviation of cyst hatching distribution	15	Based on 1st instar distributions, 83 - 90
hcyst	number of cysts from previous year	1.6×10^6	Based on fecundity from 1984 field data
	Algal Growth Parameters		
algsnk	sedimentation rate for algae	0.1	Based on model and 1984 amd 1990 data
att1	attenuation of Mono Lake water	0.3873	Regression from field data 1983 - 1990
att2	algal specific attenuation coefficient	0.000632	Regression from field data 1983 - 1990
algmax	maximum algal growth rate	1.25	Estimated with model and 1984 and 1990 data
algtmp	exponential temperature coefficient	1.08	Based on laboratory experiments
algnit	nitrogen half saturation coefficient	14	Estimated with model and 1984 and 1990 data
algnitmin	minimum nitrogen at which uptake occurs	7	Set to achieve model stability
alglit	light half saturation coefficient for algal growth	6	Estimated from field research, 1983-1990
	Hypolimnetic Ammonium Parameters		
nhsed	constant sediment release rate of ammonium	56	Estimated with 1984 field data

Table 2. Summary of eight-year simulation from 1983 to 1990, using the final parameter set and observed depth and temperature of mixed layer (salinity effects not included).

	Volumetric				Areal				Lakewide Total			
Year	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
	mg N m^{-3}				g N m^{-2}		10^{6} m^{-2}		10^{9} g N		10^{14}	
1983	23	468	296	29	15.18	1.64	0.10	1.11	2.56	0.28	0.17	1.85
1984	33	1129	199	46	19.20	3.59	0.25	1.48	3.40	0.63	0.43	2.63
1985	70	1257	344	52	25.49	4.30	0.35	1.31	4.45	0.74	0.60	2.29
1986	48	1438	283	51	20.96	3.21	0.25	1.05	3.72	0.57	0.44	1.85
1987	123	1753	313	50	26.09	4.19	0.32	1.67	4.57	0.73	0.55	2.94
1988	119	1419	395	58	39.79	4.84	0.34	1.72	6.74	0.82	0.56	2.93
1989	20	202	453	33	23.08	2.15	0.11	1.40	3.84	0.35	0.19	2.35
1990	17	259	323	33	23.69	2.76	0.17	1.40	3.87	0.45	0.27	2.29

Table 3. Sensitivity analysis

Parameter changed	Parameter Value	NHE	NHH	ALG	ART	1°	2°	Naup	Cyst
		mg N m^{-3}				g N m^{-2}		10^6 m^{-2}	
Eff1	0.36	41	278	484	40	31.03	3.12	0.2	1.36
	0.40	42	278	480	44	30.9	3.38	0.22	1.37
	0.44	42	278	477	47	30.79	3.62	0.24	1.41
	0.48	42	278	474	50	30.66	3.85	0.26	1.42
	0.52	42	278	470	54	30.53	4.08	0.28	1.43
Eff2	0.22	39	278	482	44	30.88	3.33	0.21	1.09
	0.26	42	278	479	46	30.83	3.49	0.23	1.24
	0.30	42	278	477	47	30.79	3.62	0.24	1.41
	0.34	42	278	475	48	30.75	3.74	0.26	1.55
	0.38	42	278	473	49	30.72	3.88	0.27	1.7
Grz1	0.022	37	278	496	42	30.4	3.25	0.2	1.33
	0.026	38	278	487	44	30.62	3.46	0.22	1.38
	0.030	42	278	477	47	30.79	3.62	0.24	1.41
	0.034	42	279	469	49	30.91	3.74	0.26	1.42
	0.038	43	279	461	50	30.96	3.77	0.26	1.43
Algmax	0.75	87	295	455	46	30.3	3.45	0.24	1.05
	1.00	54	284	477	46	30.53	3.53	0.24	1.24
	1.25	42	278	477	47	30.79	3.62	0.24	1.41
	1.50	31	275	475	48	31.05	3.74	0.25	1.58
	1.75	26	272	471	48	31.26	3.83	0.25	1.72
Alglit	4	29	272	478	47	30.98	3.69	0.24	1.55
	5	35	275	478	47	30.9	3.67	0.24	1.48
	6	42	278	477	47	30.79	3.62	0.24	1.4
	7	47	282	476	47	30.71	3.6	0.24	1.34
	8	52	285	475	47	30.65	3.59	0.24	1.3
Nhsed	0	22	21	300	20	7.63	1.33	0.1	0.16
	28	27	150	377	36	19.71	2.7	0.17	1.12
	56	42	278	477	47	30.79	3.62	0.24	1.41
	84	66	407	575	58	41.71	4.51	0.33	1.58
	112	106	537	675	68	52.38	5.3	0.42	1.57
Hfac	0.001	43	278	490	42	30.59	3.38	0.24	1.4
	0.005	42	278	483	45	30.72	3.52	0.25	1.41
	0.010	42	278	477	47	30.78	3.62	0.24	1.4
	0.015	42	278	471	49	30.81	3.72	0.23	1.38
	0.020	42	278	465	50	30.81	3.78	0.23	1.36
Hday	45	42	278	480	46	30.76	3.58	0.25	1.41
	60	42	278	478	46	30.78	3.58	0.25	1.41
	75	42	254	477	47	31.45	3.68	0.25	1.42
	90	42	278	476	47	30.77	3.64	0.24	1.39
	105	42	320	479	46	30.69	3.81	0.25	1.42

Table 4. Alterations to model parameters affected by salinity changes. Model parameters are multiplied by the shown factors except for *Day of Peak Hatch,* which is simply added.

Lake surface elevation (ft)		6390	6383	6377	6375	6372	6360
Salinity (g/l)		71	80	89	92	97	120
Growth efficiency	*eff_1*	1.297	1.163	1.039	1	0.937	0.684
Egg production efficiency	*eff_2*	1.237	1.132	1.032	1	0.948	0.727
Mortality	*morj&a*	0.778	0.873	0.968	1	1.053	1.297
Ovigerity	*repovig*	1.094	1.054	1.013	1	0.978	0.874
Ovoviviparity factor	*ovofac*	0.522	0.689	0.911	1	1.168	2.382
Hatching success	*hfac*	1.107	1.067	1.018	1	0.967	0.759
Day of peak hatch	*hday*	-2	-1	0	0	0	+3
Maximum algal growth	*algmax*	1.256	1.139	1.033	1	0.947	0.738

Factors are determined by the ratio of the values derived with the following equations at the specified salinity divided by the value at 92 g l^{-1} corresponding to elevation of 6375.

Growth efficiency factor based on adult weight divided by time to maturity:

$$Eff_1 = \frac{1.743 - (0.0073 \times TDS)}{e^{3.21 + (0.006 \times TDS)}}$$

Egg production efficiency is based on the brood size divided by brood interval:

$$Eff_2 = \frac{65.8 - (0.28 \times TDS)}{e^{1.809 + (0.0036 \times TDS)}}$$

Juvenile and adult mortality: $Mor(\%) = 1 + (0.411 \times TDS)$

Ovigerity: $Ovig(\%) = 135 - (0.429 \times TDS)$

Ovoviviparity: $Ovo(\%) = e^{(0.031 \times TDS) - 1.32}$

Hatching success: $Hfac = 100 - e^{1.21 + (0.021 \times TDS)}$

Day of hatch: $Hday = e^{(0.0116 \times TDS) + 0.865}$

Maximum algal growth rate: $Algmax = 105 \times e^{-0.01 \times \text{percent increase}}$

Table 5. Model response to changes in individual parameters affected by different salinities.

			Volumetric				Areal				Lakewide Total			
	Elev	Salinity	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
	ft	g l^{-1}	mg N m^{-3}				g N m^{-2}		10^{6} m^{-2}		10^{9} g N		10^{14}	
No change	6375	92	42	278	477	47	30.79	3.62	0.24	1.41	5.03	0.59	0.39	2.30
Growth efficiency	6390	71	42	279	467	57	30.38	4.30	0.30	1.45	4.96	0.70	0.49	2.37
	6360	120	42	278	488	34	31.16	2.72	.017	1.27	5.09	0.44	0.27	2.07
Reproduction efficiency	6390	71	42	278	473	49	30.73	3.86	.027	1.67	5.02	0.63	0.44	2.73
	6360	120	40	278	482	45	30.89	3.33	0.21	1.08	5.04	0.54	0.33	1.77
Mortality	6390	71	46	279	470	58	30.91	3.74	0.24	1.42	5.05	0.61	0.39	2.32
	6360	120	34	278	486	37	30.64	3.54	0.24	1.36	5.00	0.57	0.39	2.23
Ovigerity	6390	71	42	278	475	48	30.76	3.72	0.25	1.5	5.02	0.60	0.41	2.45
	6360	120	42	278	478	46	30.82	3.49	0.23	1.25	5.03	0.57	0.37	2.04
Algal growth	6390	71	30	274	474	48	31.11	3.77	0.25	1.62	5.08	0.61	0.40	2.65
	6360	120	60	286	476	46	30.45	3.50	0.24	1.19	4.97	0.57	0.38	1.94
Ovoviviparity	6390	71	37	278	486	42	30.78	3.24	0.17	1.69	5.03	0.53	0.27	2.76
	6360	120	44	279	470	51	30.83	3.99	0.34	1.16	5.03	0.65	0.55	1.89
Hatching success	6390	71	42	278	475	48	30.79	3.65	0.24	1.39	5.03	0.59	0.39	2.27
	6360	120	42	278	480	46	30.76	3.58	0.25	1.4	5.02	0.58	0.40	2.29
Day of Hatch	6390	71	42	278	477	47	30.79	3.63	0.25	1.39	5.03	0.59	0.40	2.28
	6360	120	42	278	477	47	30.78	3.62	0.24	1.4	5.03	0.59	0.39	2.29

Table 6. Predicted responses to changes in salinity at different lake levels.

		Volumetric				Areal				Lakewide Total			
Elev	Salinity	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
ft	$g\ l^{-1}$		$mg\ N\ m^{-3}$			$g\ N\ m^{-2}$		$10^6\ m^{-2}$		$10^9\ g\ N$		10^{14}	
Effects of salinity-caused changes in efficiency, mortality, ovigerity, hatching success, and day of hatch with the lake level held constant at the 1990 conditions.													
6390	71	47	279	453	72	30.25	4.66	0.32	1.87	4.94	0.76	0.52	3.06
6375	92	42	278	477	47	30.79	3.62	0.24	1.41	5.03	0.59	0.39	2.30
6360	120	34	278	507	25	30.90	2.29	0.13	0.86	5.05	0.37	0.21	1.40
Effects of salinity-caused changes in ovoviviparity with the lake level held constant at the 1990 conditions.													
6390	71	37	278	486	42	30.78	3.25	0.17	1.69	5.03	0.53	0.27	2.76
6375	92	42	278	477	47	30.79	3.62	0.24	1.41	5.03	0.59	0.39	2.30
6360	120	44	279	470	51	30.83	3.99	0.34	1.16	5.03	0.65	0.55	1.90
Effects of salinity-caused changes maximum algal growth rates with the lake level held constant at the 1990 conditions.													
6390	71	30	274	474	48	31.12	3.77	0.25	1.62	5.08	0.61	0.40	2.65
6375	92	42	278	477	47	30.79	3.62	0.24	1.41	5.03	0.59	0.39	2.30
6360	120	60	286	476	46	30.46	3.51	0.24	1.19	4.98	0.57	0.38	1.94
Effects of changes in area and volume at different lake levels using 1990 conditions and model parameters held constant.													
6390	71	42	254	477	47	31.45	3.67	0.25	1.42	6.16	0.72	0.49	2.79
6375	92	42	278	477	47	30.79	3.62	0.24	1.41	5.03	0.59	0.39	2.30
6360	120	42	320	477	47	30.73	3.82	0.27	1.43	4.00	0.50	0.34	1.87

Table 7. Predicted responses to changes in salinity and different areas and volumes at various lake levels.

		Volumetric				Areal				Lakewide Total			
Elev	Salinity	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
ft	g l^{-1}		mg N m^{-3}			g N m^{-2}		10^6 m^{-2}			10^9 g N		10^{14}
Input conditions (1990) characteristic of monomictic conditions													
6390	71	34	249	460	68	31.38	4.5	0.25	2.57	6.14	0.88	0.5	5.03
6383	80	38	260	467	59	30.9	4.04	0.25	1.98	5.69	0.74	0.45	3.64
6377	89	41	273	475	50	30.96	3.84	0.25	1.55	5.23	0.64	0.43	2.63
6375	92	42	278	477	47	30.8	3.62	0.24	1.41	5.03	0.59	0.39	2.31
6372	97	43	286	480	42	31.12	3.53	0.25	1.21	4.67	0.52	0.36	1.82
6360	120	50	327	500	26	30.73	2.56	0.22	0.57	4	0.33	0.28	0.75
Input conditions (1984) characteristic of meromictic conditions													
6390	71	15	891	127	61	17.22	3.93	0.21	2.75	3.47	0.79	0.41	5.55
6383	80	22	906	146	55	17.37	3.59	0.2	2.12	3.35	0.69	0.39	4.08
6377	89	28	926	160	49	17.38	3.28	0.2	1.58	3.17	0.6	0.36	2.89
6375	92	30	932	161	46	17.41	3.22	0.2	1.46	3.08	0.57	0.35	2.61
6372	97	28	948	160	43	17.42	3.13	0.2	1.29	2.93	0.53	0.33	2.18
6360	120	28	1008	169	28	17.43	2.45	0.16	0.68	2.37	0.33	0.22	0.92

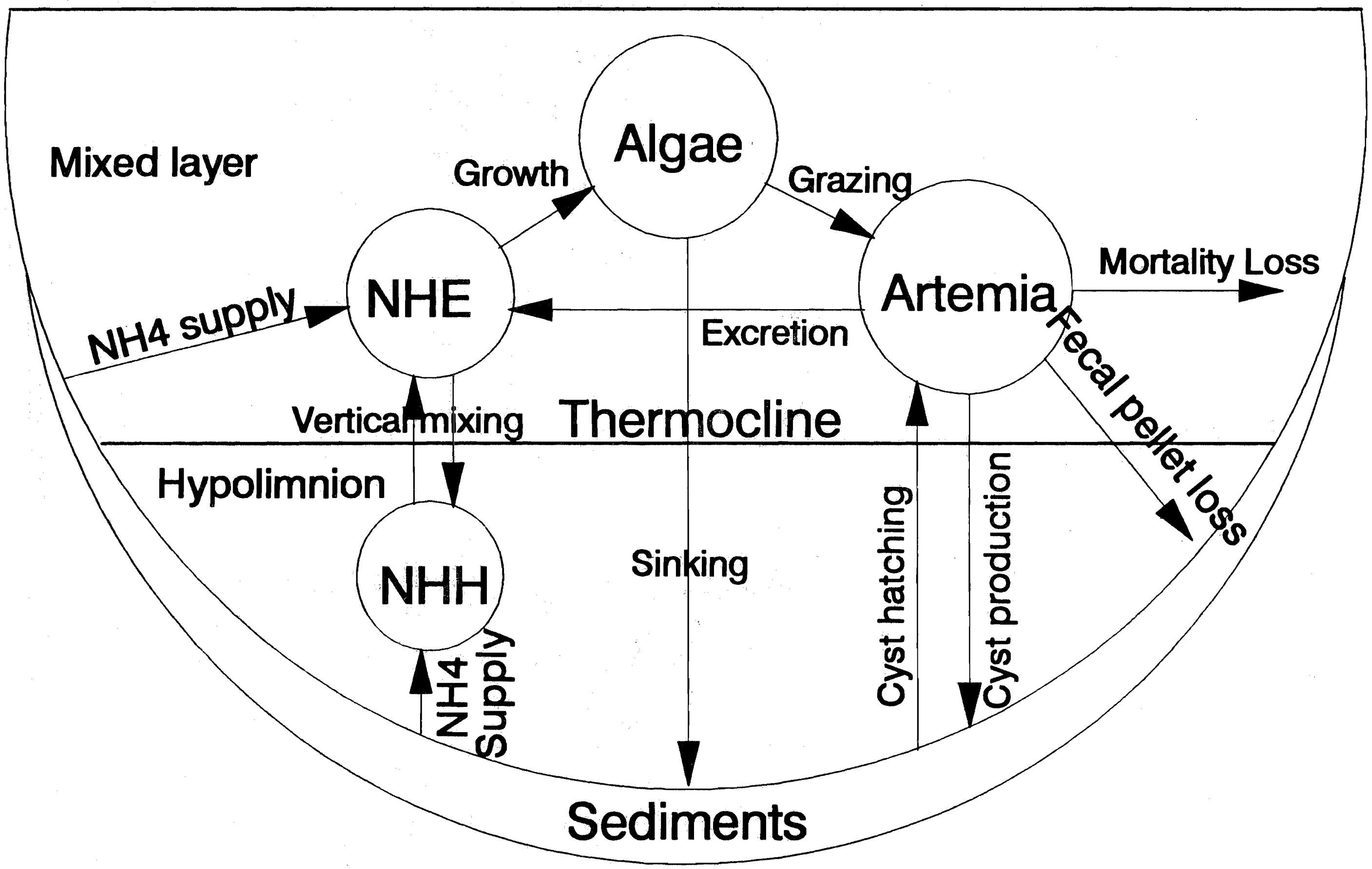
Table 8. Predicted responses (in percentage) to changes in salinity and different areas and volumes at various lake levels.

		Volumetric				Areal				Lakewide Total			
Elev	Salinity	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
ft	g l^{-1}		mg N m^{-3}				g N m^{-2}	10^6 m^{-2}			10^9 g N		10^{14}
Input conditions (1990) characteristic of monomictic conditions													
6390	71	-19	-10	-4	45	2	24	5	82	22	50	26	118
6383	80	-9	-6	-2	26	0	12	1	40	13	26	15	58
6377	89	-2	-2	0	7	1	6	5	10	4	10	9	14
6372	97	3	3	1	-10	1	-3	2	-14	-7	-11	-7	-21
6360	120	21	17	5	-44	0	-29	-11	-59	-20	-43	-28	-68
Input conditions (1984) characteristic of meromictic conditions													
6390	71	-48	-4	-21	32	-1	22	5	88	12	39	20	113
6383	80	-26	-3	-9	19	0	12	3	45	9	21	13	57
6377	89	-4	-1	0	6	0	2	1	8	3	5	4	11
6372	97	-5	2	-1	-8	0	-3	0	-12	-5	-8	-5	-16
6360	120	-4	8	5	-40	0	-24	-16	-54	-23	-41	-35	-65

Table 9. Predicted responses to changes in salinity with different model parameters.

			Volumetric				Areal				Lakewide Total			
		Elev	NHE	NHH	ALG	ZOO	1°	2°	Naup	Cyst	1°	2°	Naup	Cyst
		ft		mg N m^{-3}			g N m^{-2}		10^{6} m^{-2}			10^{9} g N		10^{14}
Std. Set		6375	42	278	477	47	30.78	3.62	0.24	1.4	5.03	0.59	0.39	2.29
Grz1	0.04	6390	35	250	440	68	31.35	4.34	0.25	2.5	6.14	0.85	0.49	4.9
	0.04	6375	43	279	457	49	30.96	3.74	0.26	1.44	5.06	0.61	0.42	2.36
	0.04	6360	52	328	484	29	31.2	2.88	0.26	0.65	4.07	0.37	0.33	0.85
	0.02	6390	30	249	486	58	30.98	4.02	0.19	2.47	6.06	0.79	0.38	4.84
	0.02	6375	36	278	501	40	30.29	3.15	0.18	1.31	4.95	0.51	0.29	2.14
	0.02	6360	47	326	523	23	30.07	2.22	0.13	0.57	3.92	0.29	0.17	0.74
Grz2	-300	6390	33	249	456	69	31.35	4.51	0.25	2.51	6.14	0.88	0.48	4.92
	-300	6375	41	279	472	48	30.85	3.72	0.24	1.4	5.04	0.6	0.39	2.28
	-300	6360	49	327	498	27	30.77	2.67	0.22	0.58	4.01	0.35	0.28	0.75
	-150	6390	34	249	472	62	31.34	4.28	0.25	2.66	6.13	0.84	0.5	5.21
	-150	6375	42	278	487	43	30.64	3.4	0.24	1.42	5	0.55	0.39	2.31
	-150	6360	55	326	506	25	30.47	2.43	0.21	0.57	3.97	0.32	0.27	0.75
Grzalg	200	6390	33	249	459	68	31.46	4.52	0.26	2.64	6.16	0.88	0.5	5.18
	200	6375	40	278	475	47	30.89	3.68	0.25	1.46	5.04	0.6	0.4	2.39
	200	6360	50	327	498	27	30.79	2.66	0.23	0.59	4.01	0.35	0.3	0.76
	60	6390	35	249	462	67	31.3	4.44	0.25	2.48	6.13	0.87	0.49	4.85
	60	6375	42	279	479	46	30.73	3.58	0.24	1.37	5.02	0.58	0.38	2.25
	60	6360	56	327	498	27	30.63	2.59	0.23	0.54	3.99	0.34	0.29	0.71
Grzpar	0.75	6390	42	250	475	79	34.45	5.32	0.31	2.98	6.74	1.04	0.61	5.83
	0.75	6375	56	280	494	54	33.88	4.28	0.29	1.61	5.53	0.69	0.47	2.64
	0.75	6360	73	328	513	33	34.05	3.2	0.29	0.6	4.44	0.42	0.38	0.78
	0.25	6390	28	249	444	59	29.12	3.92	0.21	2.35	5.7	0.77	0.41	4.6
	0.25	6375	34	278	464	41	28.48	3.13	0.2	1.28	4.65	0.51	0.32	2.09
	0.25	6360	43	326	490	23	28.24	2.19	0.17	0.5	3.68	0.28	0.23	0.66
Algnit	21	6390	35	249	460	67	31.35	4.47	0.25	2.56	6.14	0.87	0.49	5.01
	21	6375	43	279	477	46	30.77	3.6	0.24	1.41	5.02	0.58	0.39	2.3
	21	6360	54	327	499	27	30.68	2.61	0.22	0.57	4	0.34	0.29	0.74
	7	6390	32	248	460	68	31.42	4.51	0.26	2.58	6.15	0.88	0.5	5.05
	7	6375	40	278	476	47	30.81	3.66	0.25	1.4	5.03	0.59	0.4	2.28
	7	6360	47	326	500	27	30.73	2.62	0.23	0.58	4.01	0.34	0.29	0.76
Nhsed	76	6390	47	331	526	79	39.2	5.27	0.31	2.88	7.67	1.03	0.61	5.64
	76	6375	58	370	547	55	38.61	4.27	0.31	1.54	6.31	0.69	0.49	2.51
	76	6360	75	435	570	31	38.51	3.03	0.28	0.59	5.02	0.39	0.36	0.77
	36	6390	25	167	395	56	23.41	3.65	0.19	2.12	4.58	0.71	0.38	4.16
	36	6375	29	187	405	39	22.94	3	0.19	1.24	3.75	0.49	0.3	2.04
	36	6360	36	219	425	23	22.83	2.19	0.17	0.51	2.97	0.28	0.22	0.66

Schematic of Mono Lake Plankton Model



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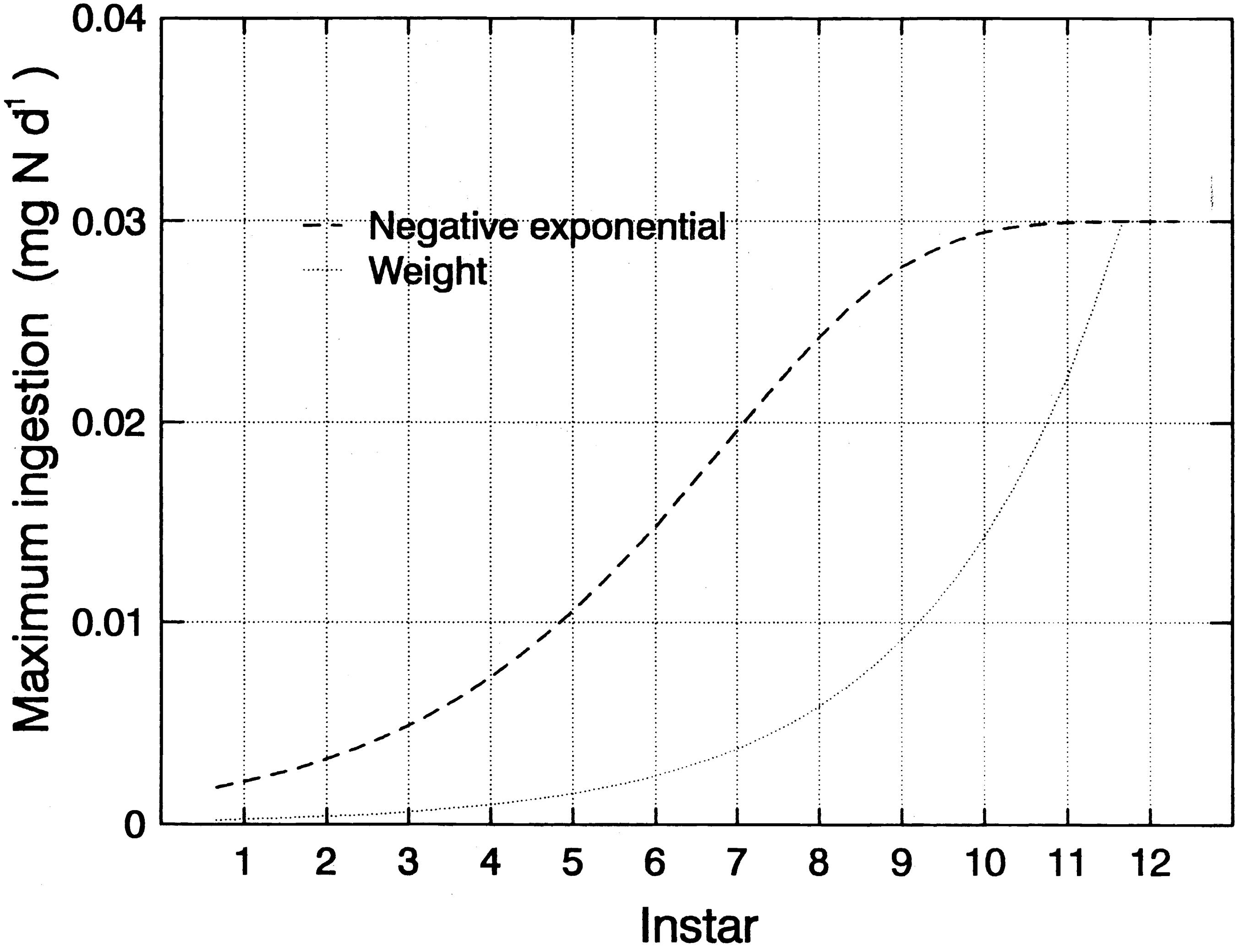
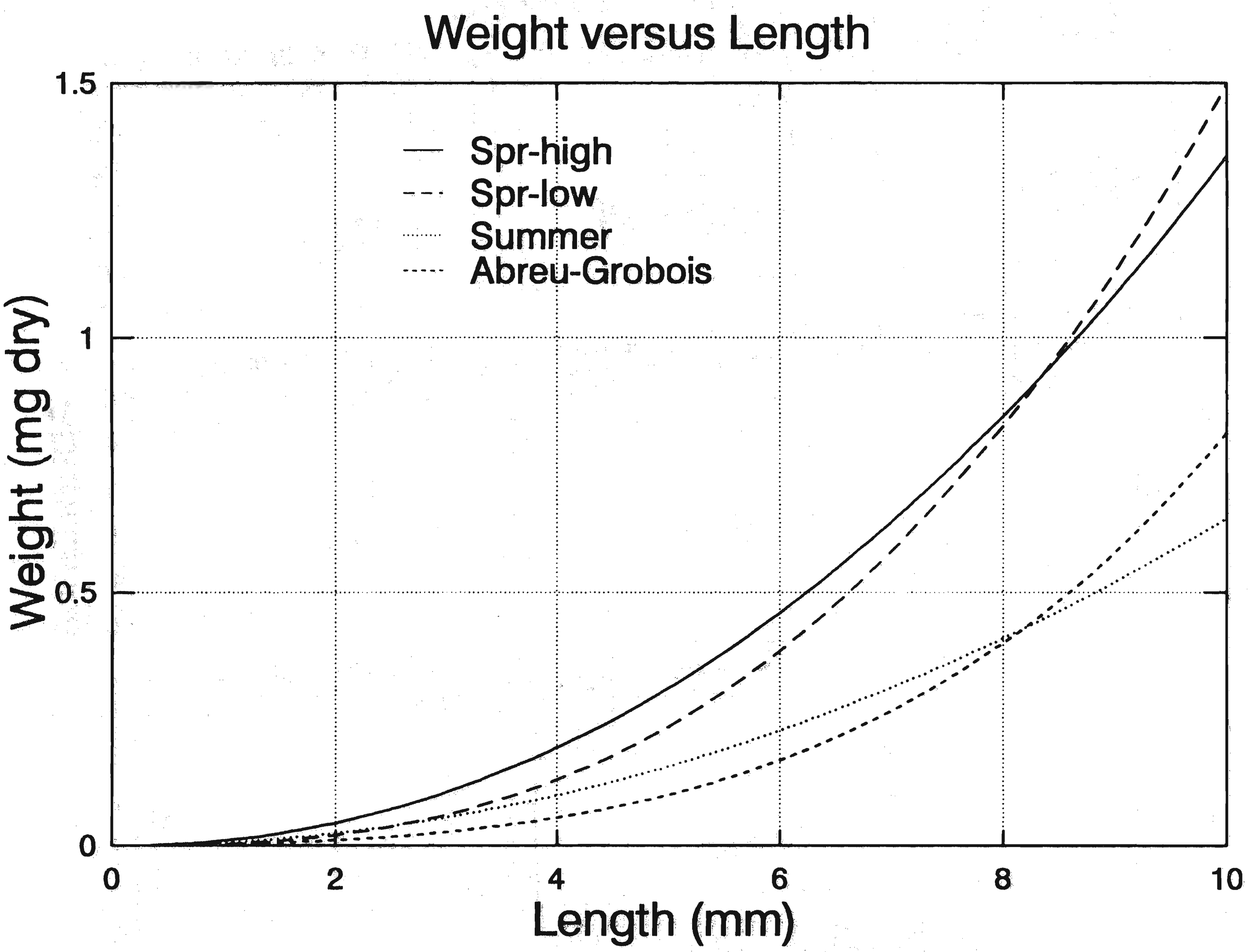
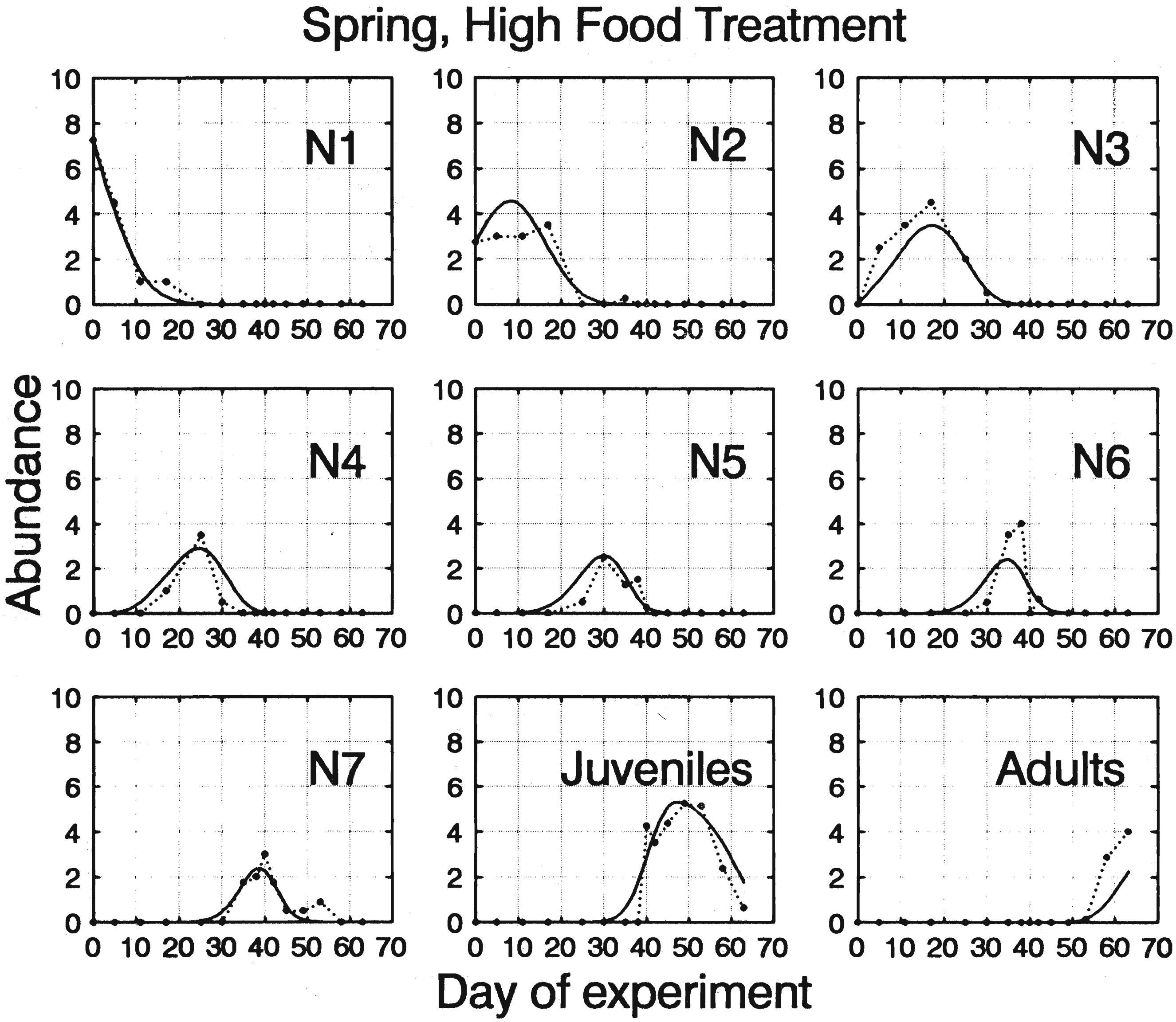
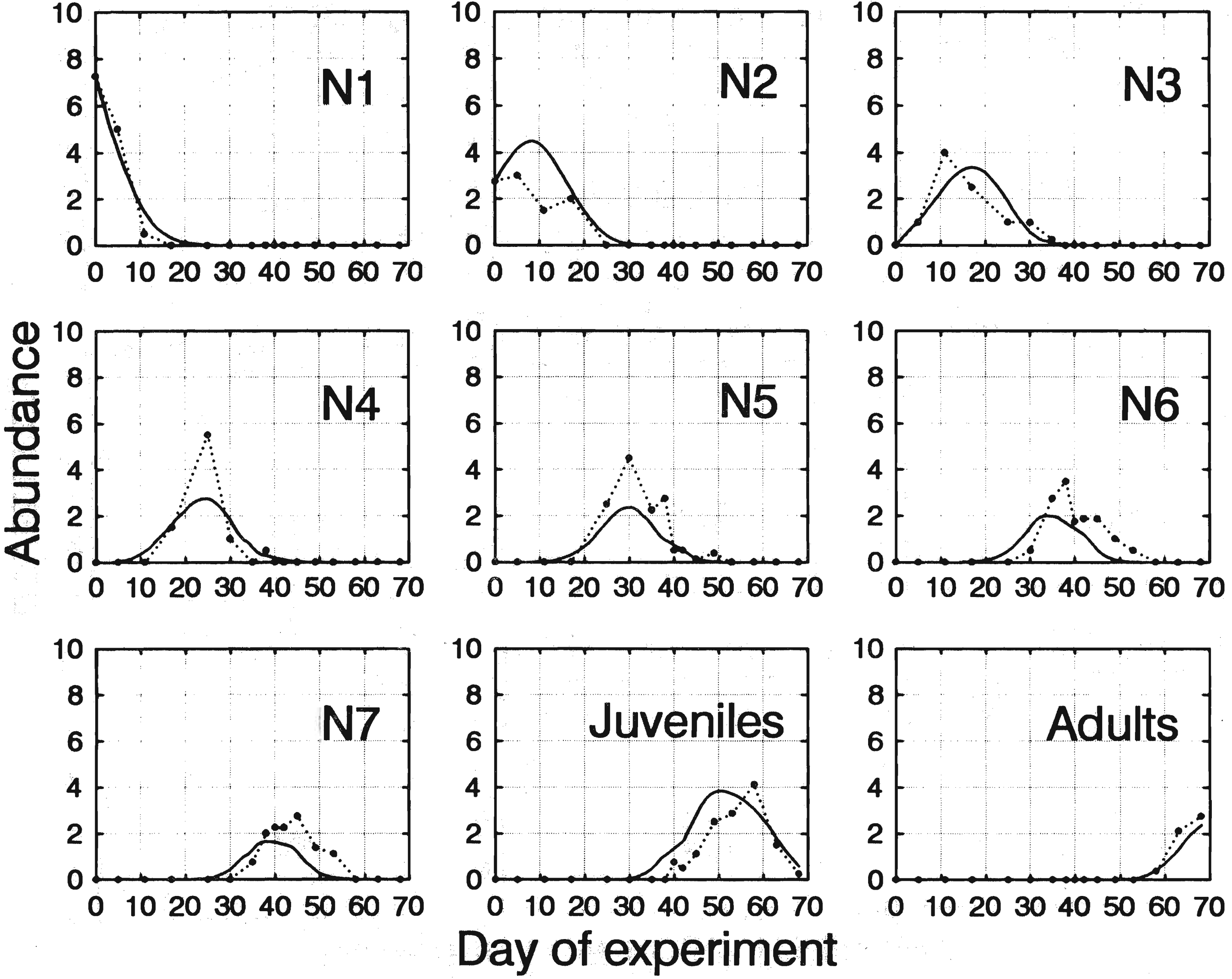
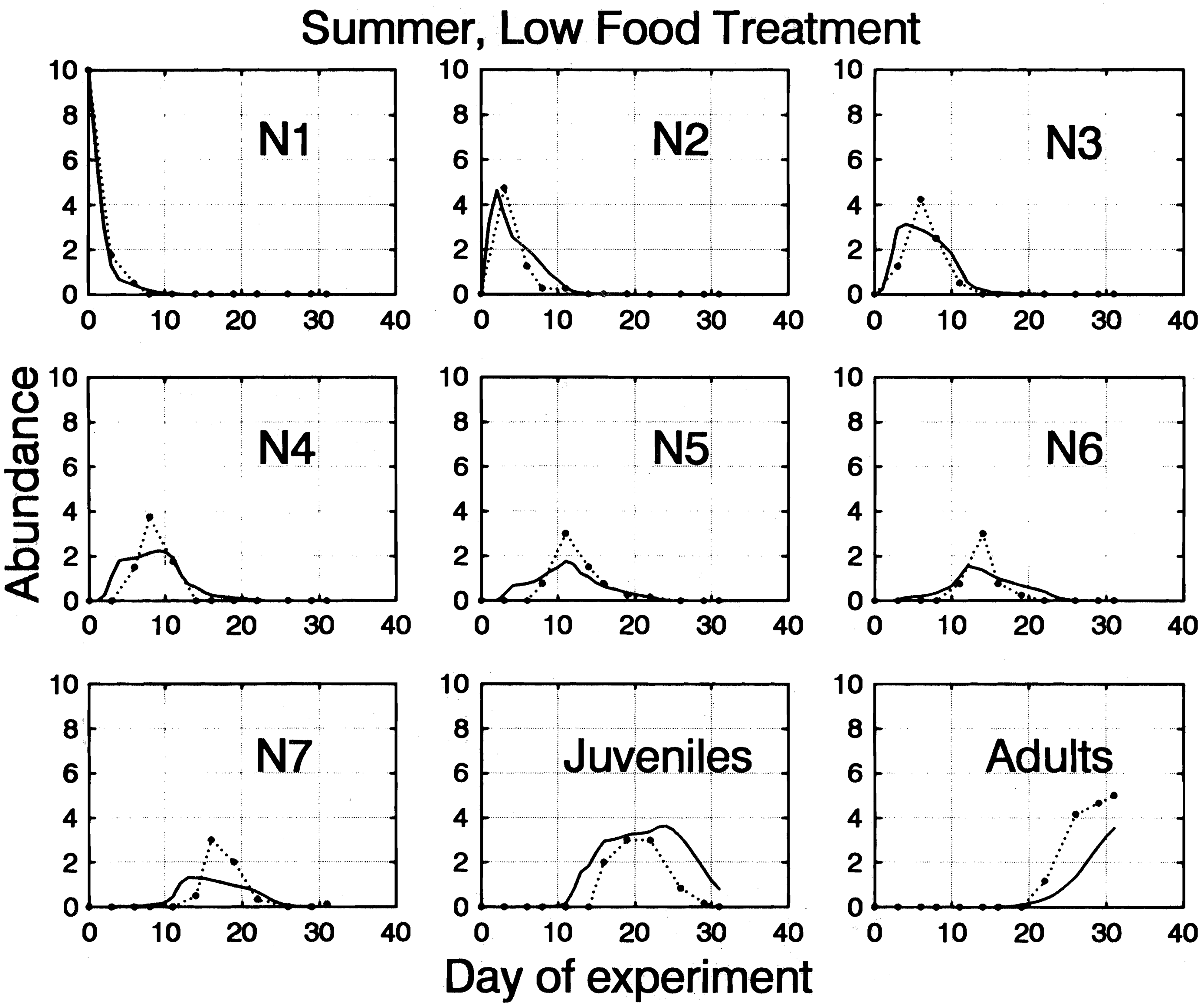

Maximum ingestion (mg N d-1)
0.04
0.03
0.02
0.01
0
1
2
3
4
5
6
7
8
9
10
11
12
Instar
Negative exponential
Weight


Weight versus Length
Spr-high
Spr-low
Summer
Abreu-Grobois
Weight (mg dry)
Length (mm)
1.5
1
0.5
0
0
2
4
6
8
10


Spring, High Food Treatment
N1
N2
N3
N4
N5
N6
N7
Juveniles
Adults
Abundance
Day of experiment
0
2
4
6
8
10
0 10 20 30 40 50 60 70

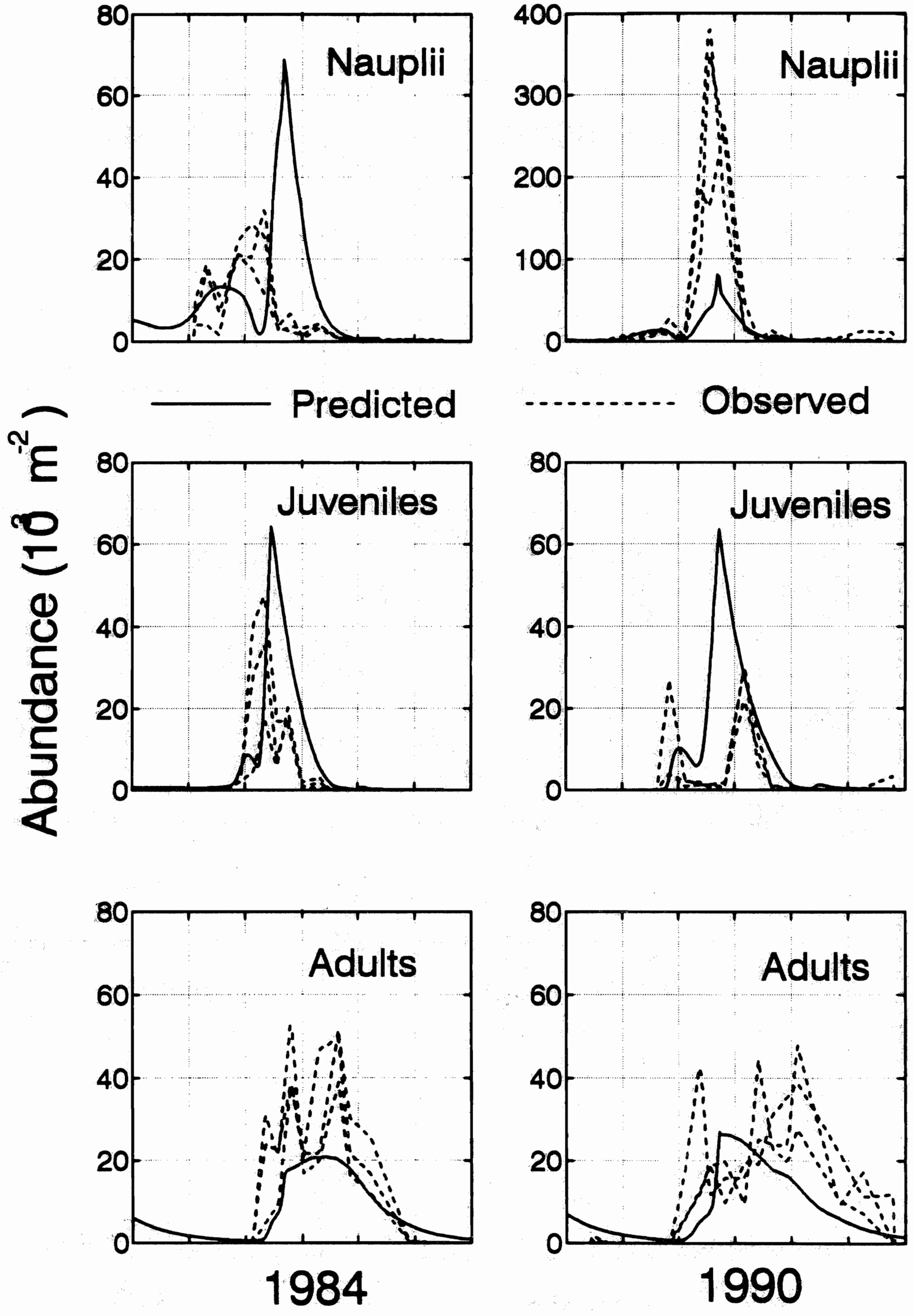


Spring, Low Food Treatment

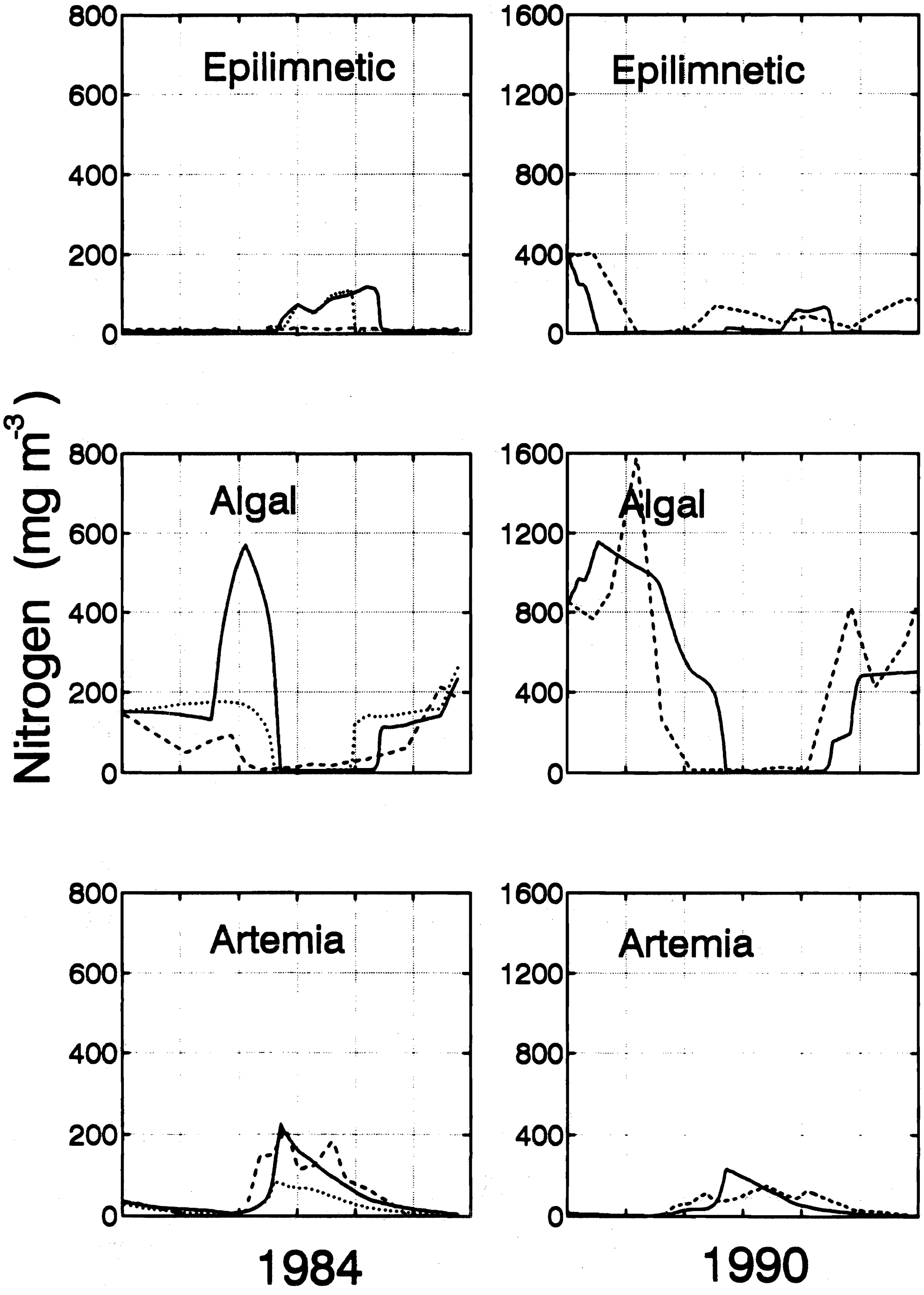


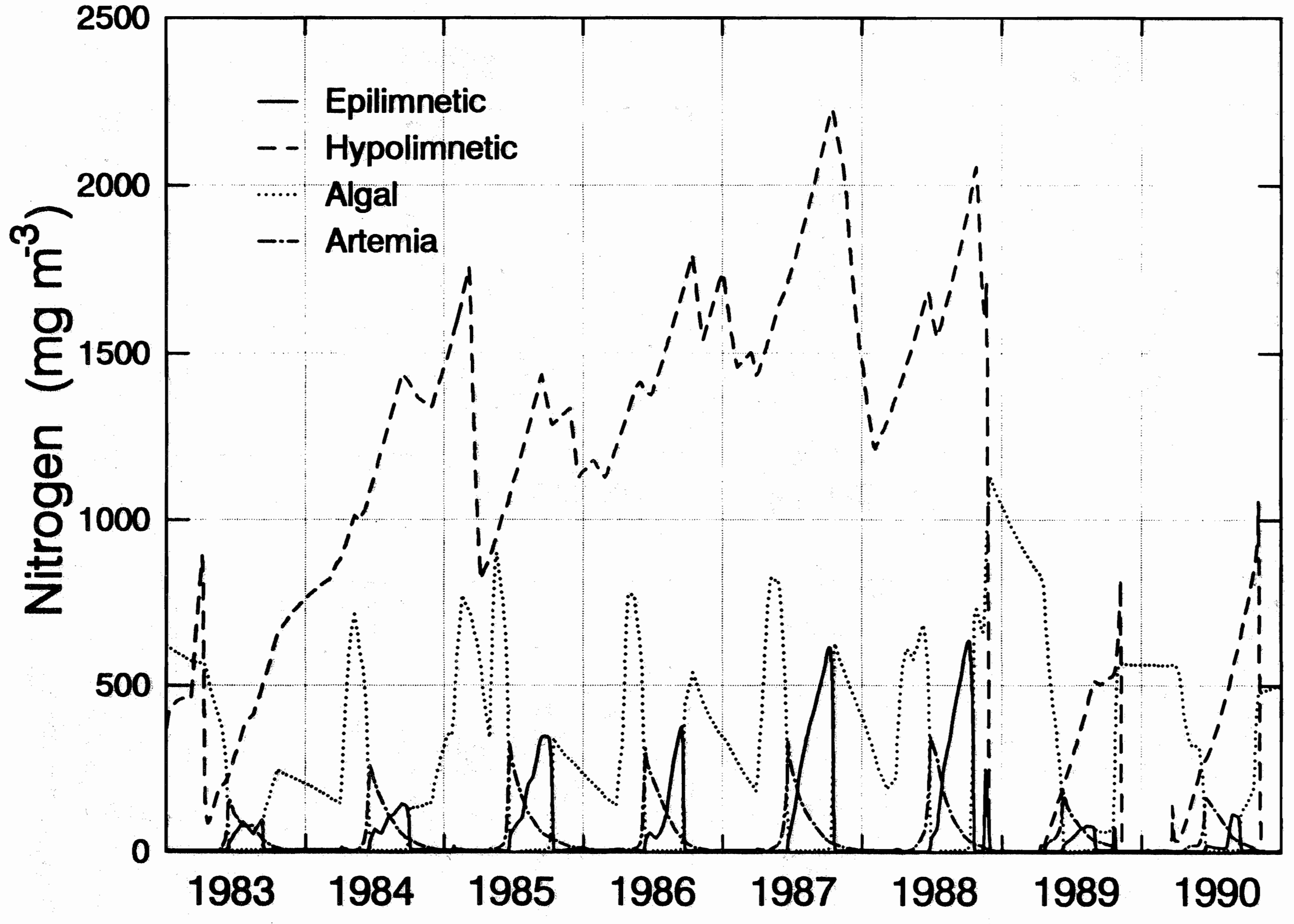
Summer, Low Food Treatment
N1
N2
N3
N4
N5
N6
N7
Juveniles
Adults
Abundance
0
2
4
6
8
10
0
10
20
30
40
Day of experiment

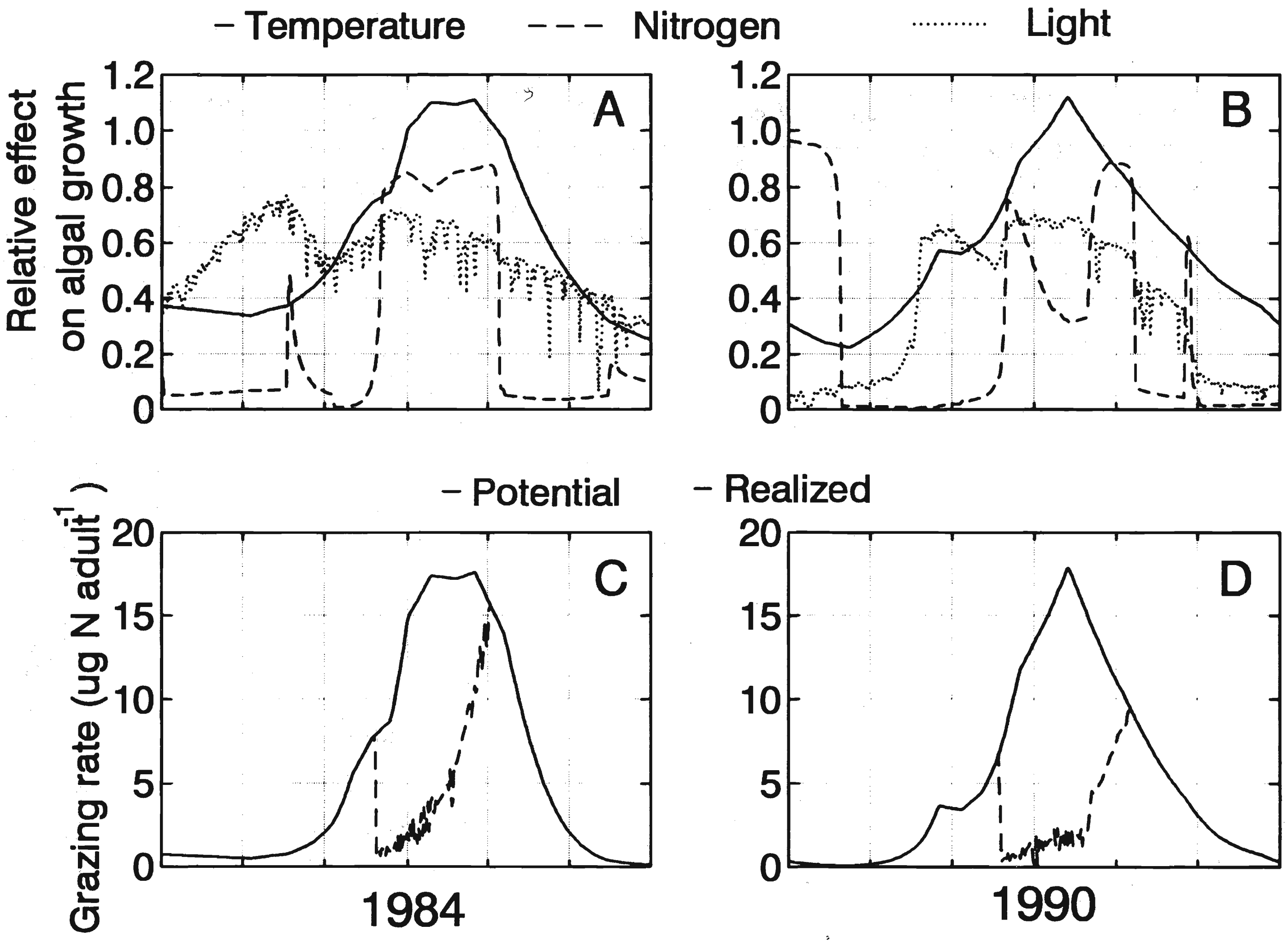
7

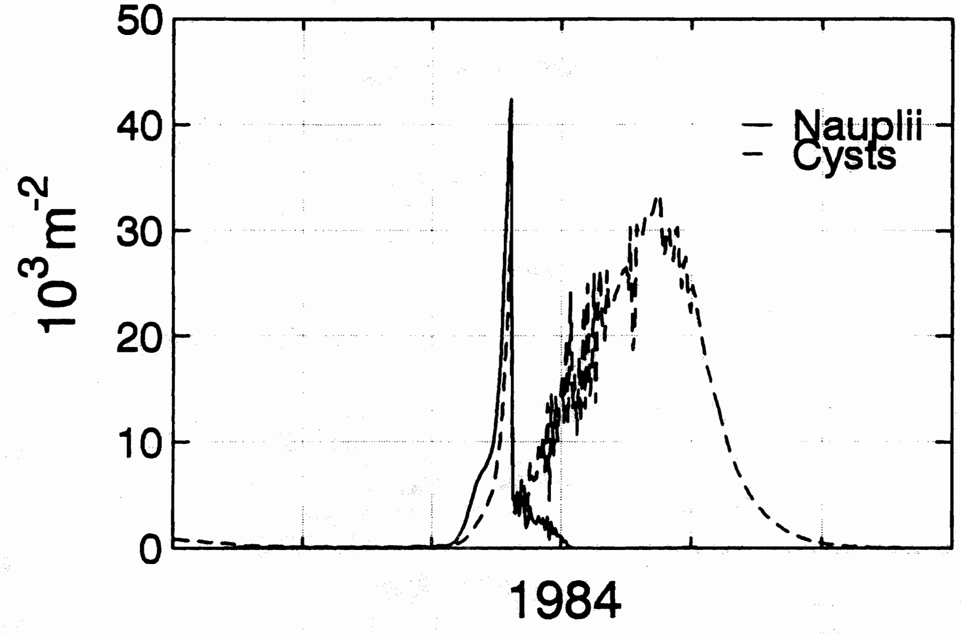

Nauplii
Nauplii
Predicted
Observed
Juveniles
Juveniles
Adults
Adults
Abundance (10^3 m^{-2})
0
20
40
60
80
0
100
200
300
400
1984
1990

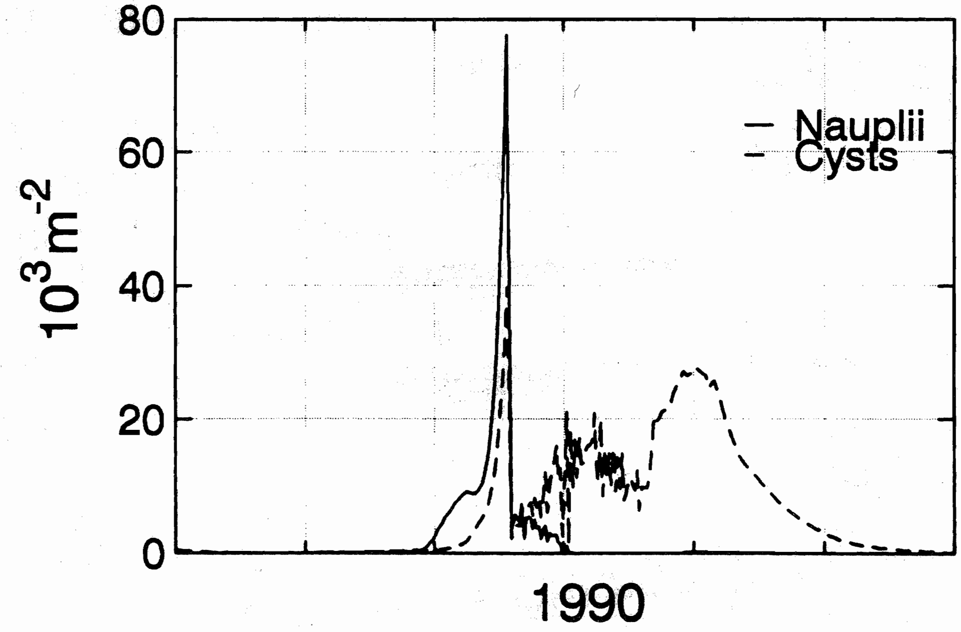
8

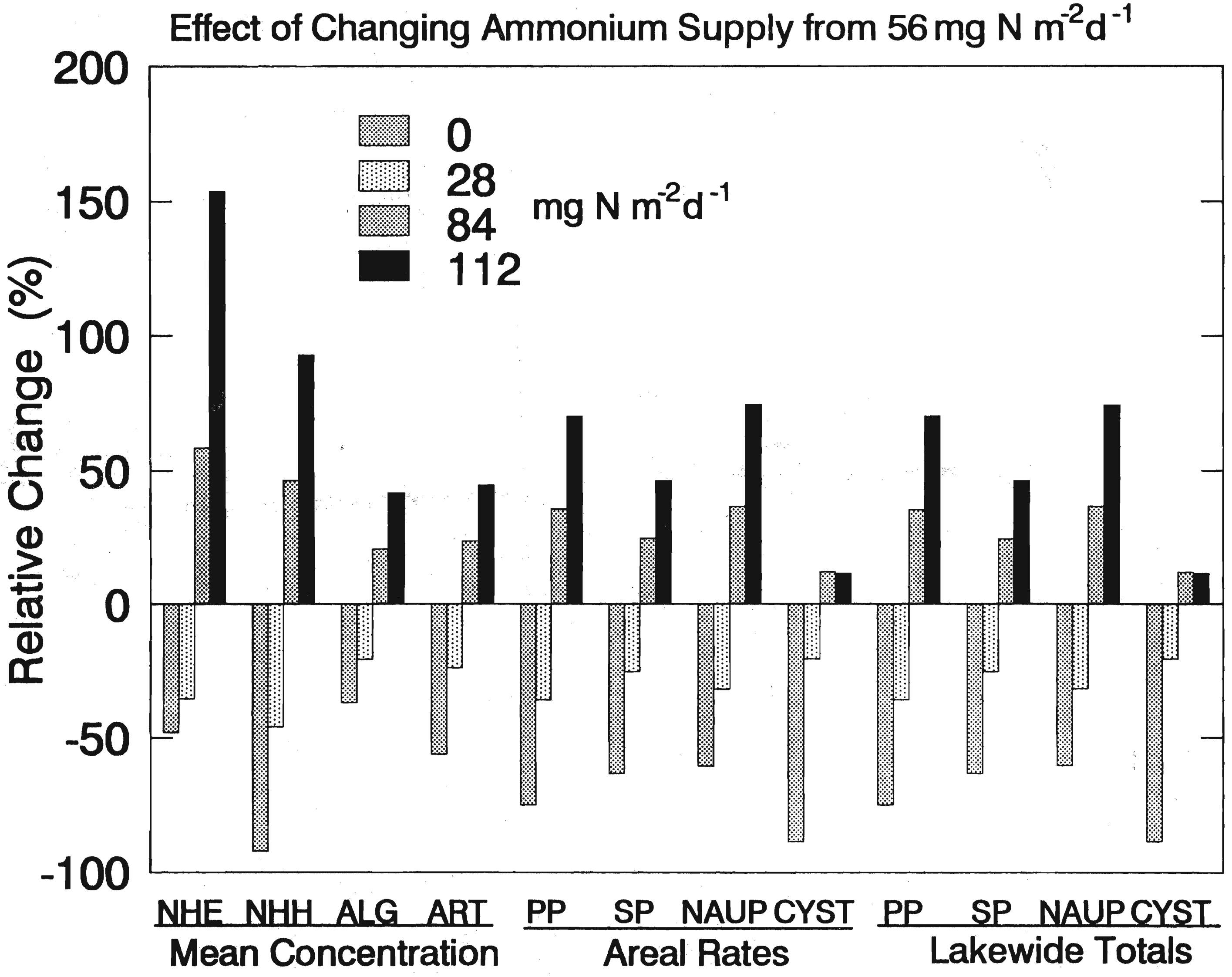

Epilimnetic
Epilimnetic
Algal
Algal
Artemia
Artemia
Nitrogen (mg m^{-3})
800
600
400
200
0
1600
1200
800
400
0
1984
1990

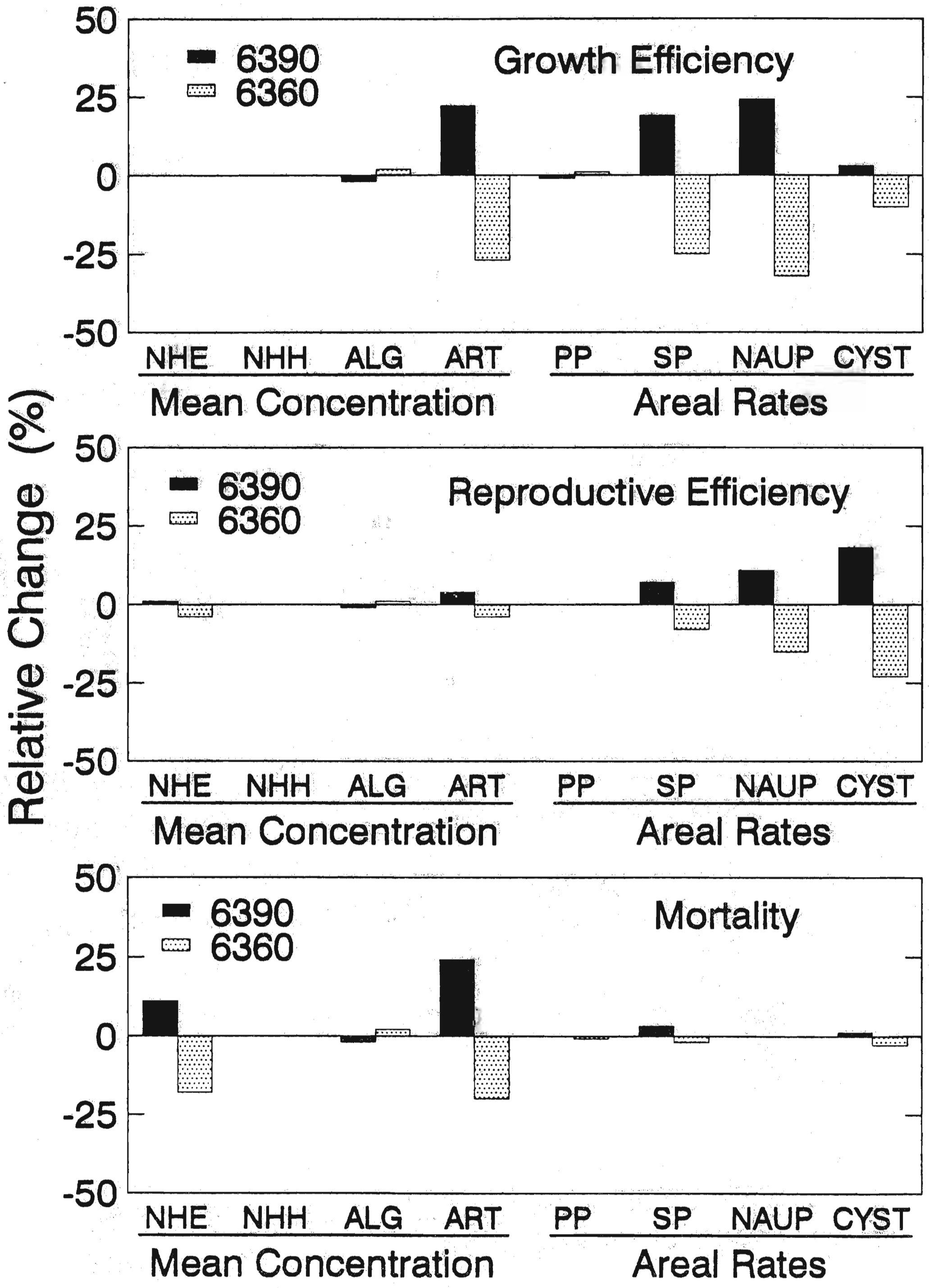

Epilimnetic
Hypolimnetic
Algal
Artemia
Nitrogen (mg m-3)
2500
2000
1500
1000
500
0
1983
1984
1985
1986
1987
1988
1989
1990


- Temperature
- - - Nitrogen
.... Light
Relative effect on algal growth
1.2
1.0
0.8
0.6
0.4
0.2
0
A
B
- Potential
- Realized
Grazing rate (ug N adult^{-1})
20
15
10
5
0
C
D
1984
1990

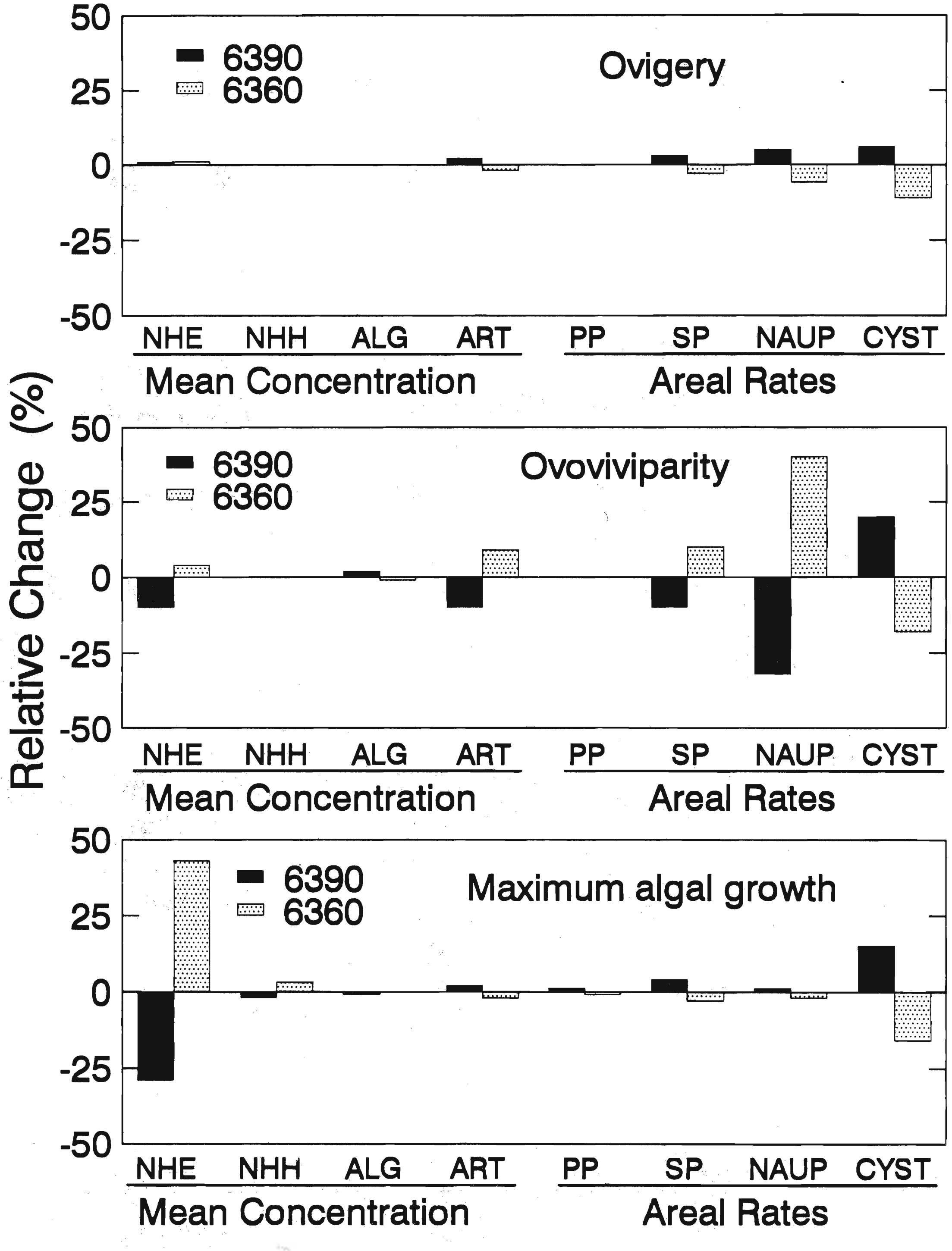

50
40
30
20
10
0
$10^3 m^{-2}$
Nauplii
Cysts
1984

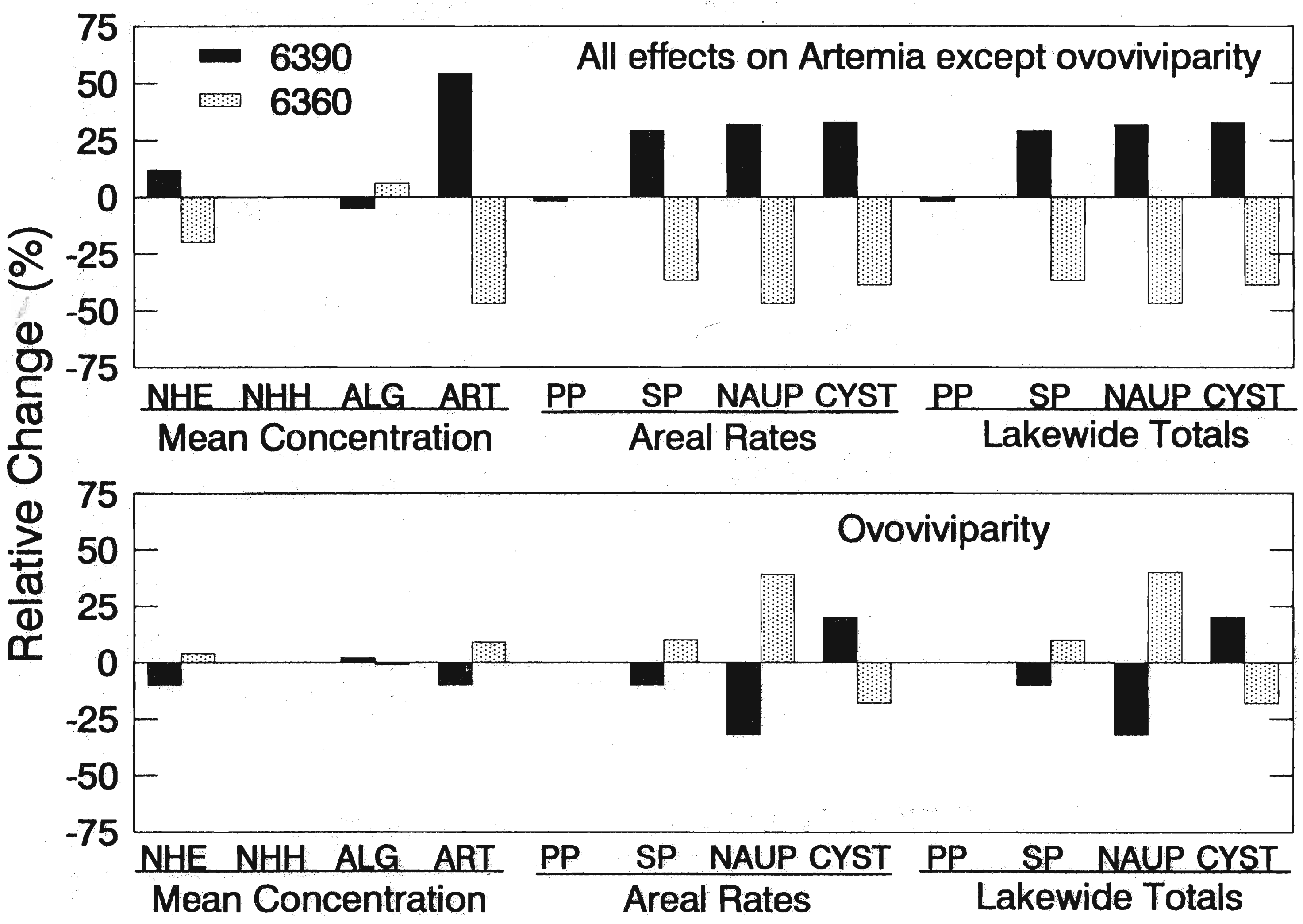

80
60
40
20
0
$10^3 m^{-2}$
Nauplii
Cysts
1990

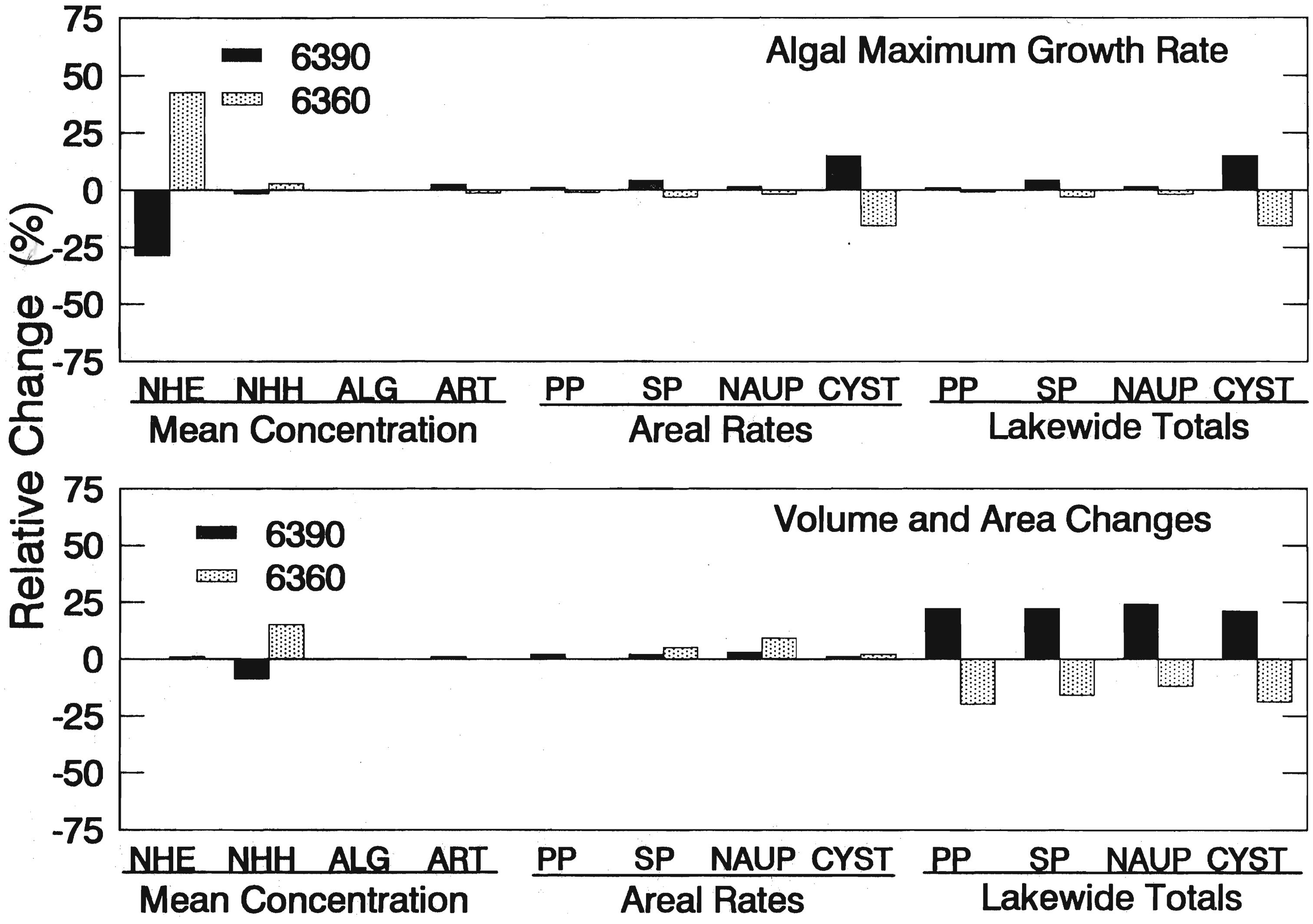

Effect of Changing Ammonium Supply from 56 mg N m-2 d-1
200
150
100
50
0
-50
-100
Relative Change (%)
0
28
84
112
mg N m-2 d-1
NHE
NHH
ALG
ART
Mean Concentration
PP
SP
NAUP
CYST
Areal Rates
PP
SP
NAUP
CYST
Lakewide Totals

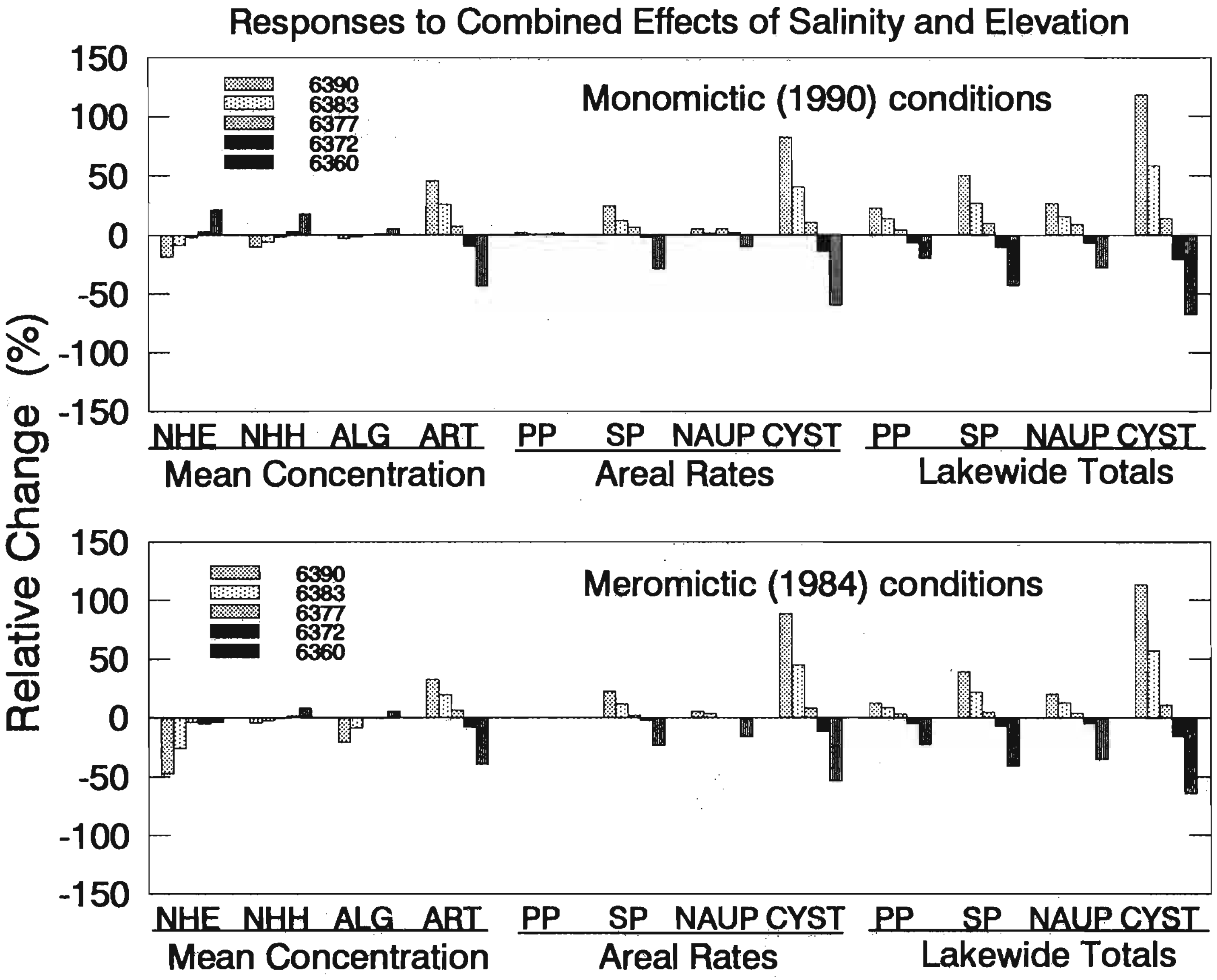

Relative Change (%)
50
25
0
-25
-50
■ 6390
▨ 6360
Growth Efficiency
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
Mean Concentration
Areal Rates
Reproductive Efficiency
Mortality

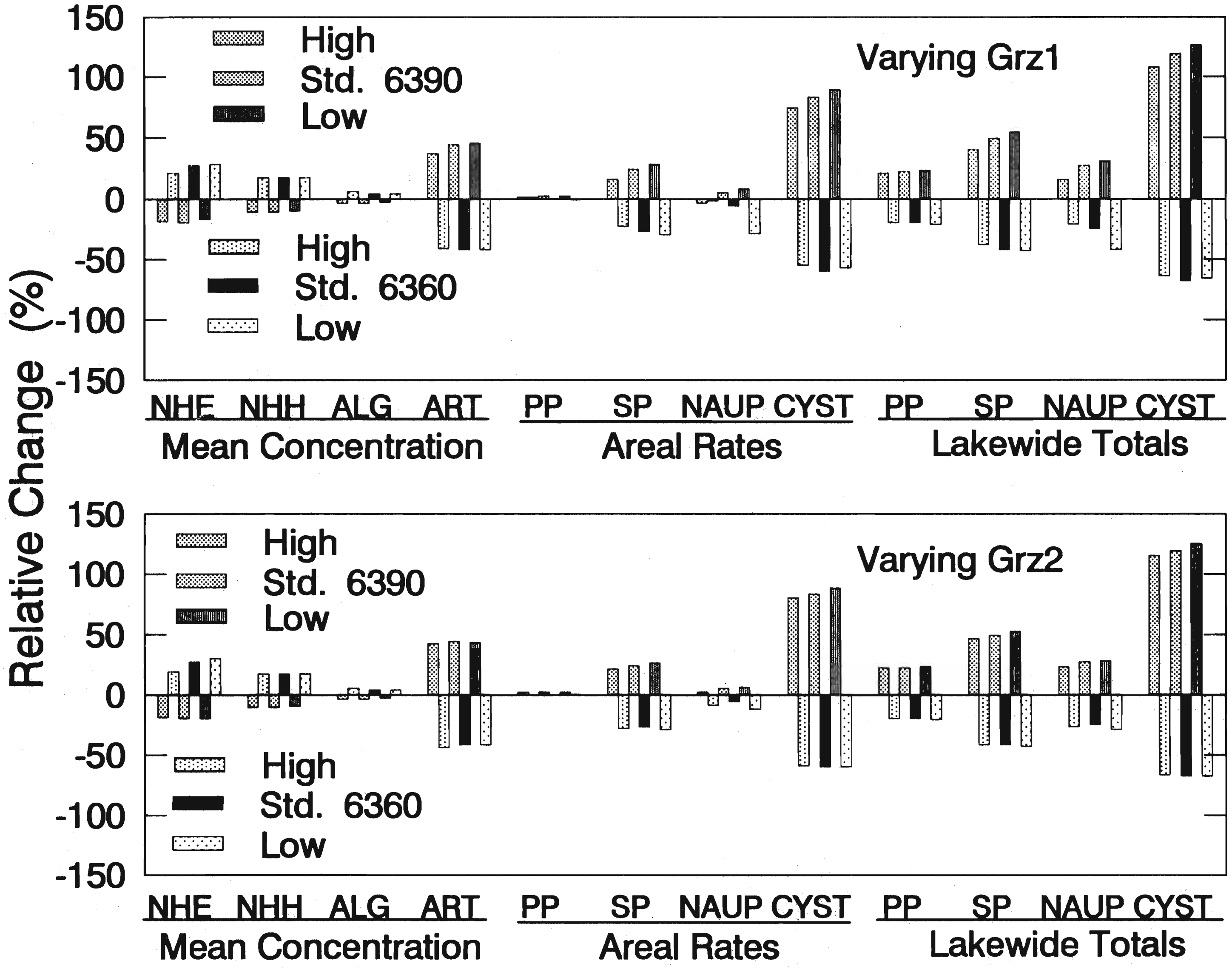
14

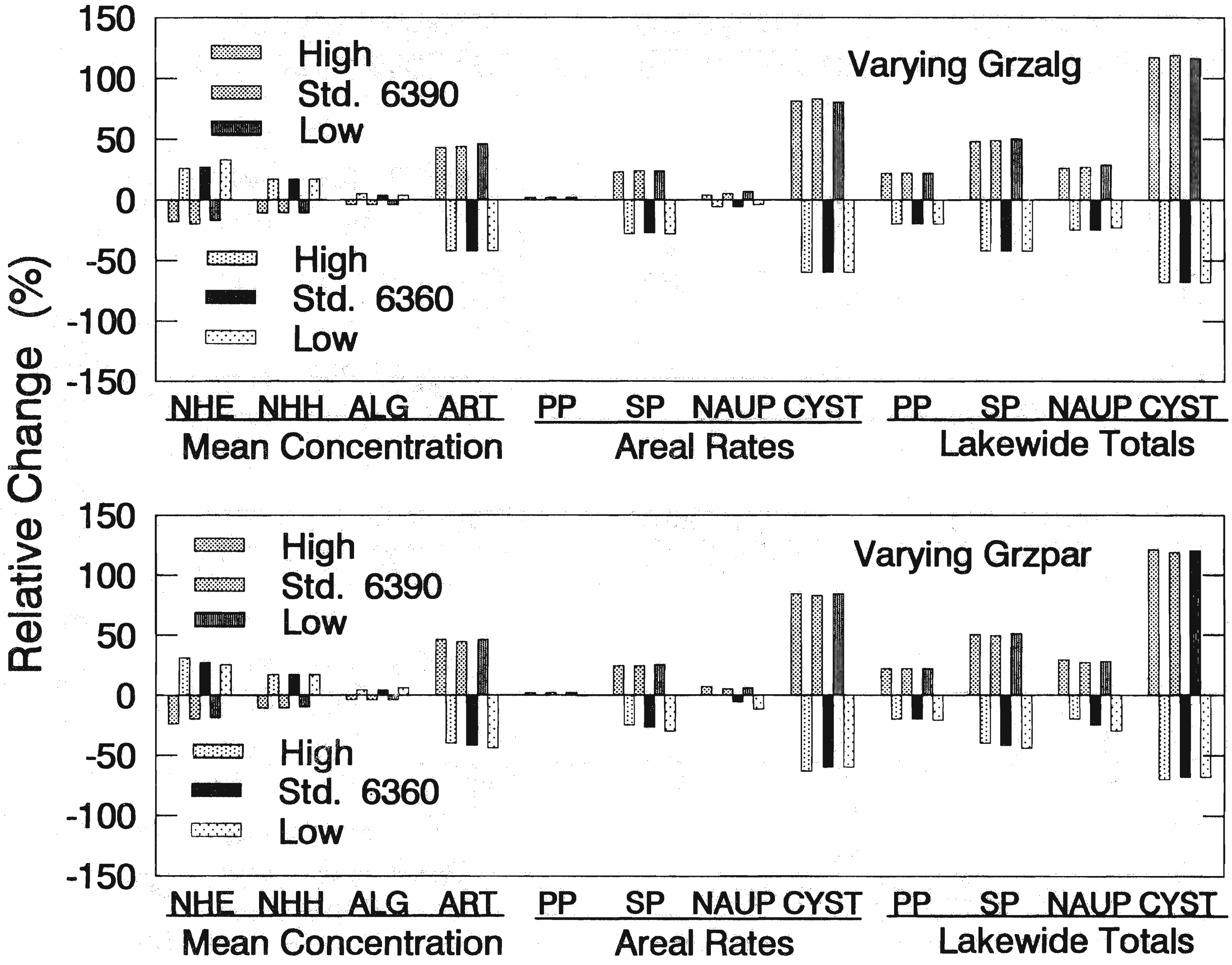

Relative Change (%)
50
25
0
-25
-50
6390
6360
Ovigery
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
Mean Concentration
Areal Rates
Ovoviviparity
Maximum algal growth

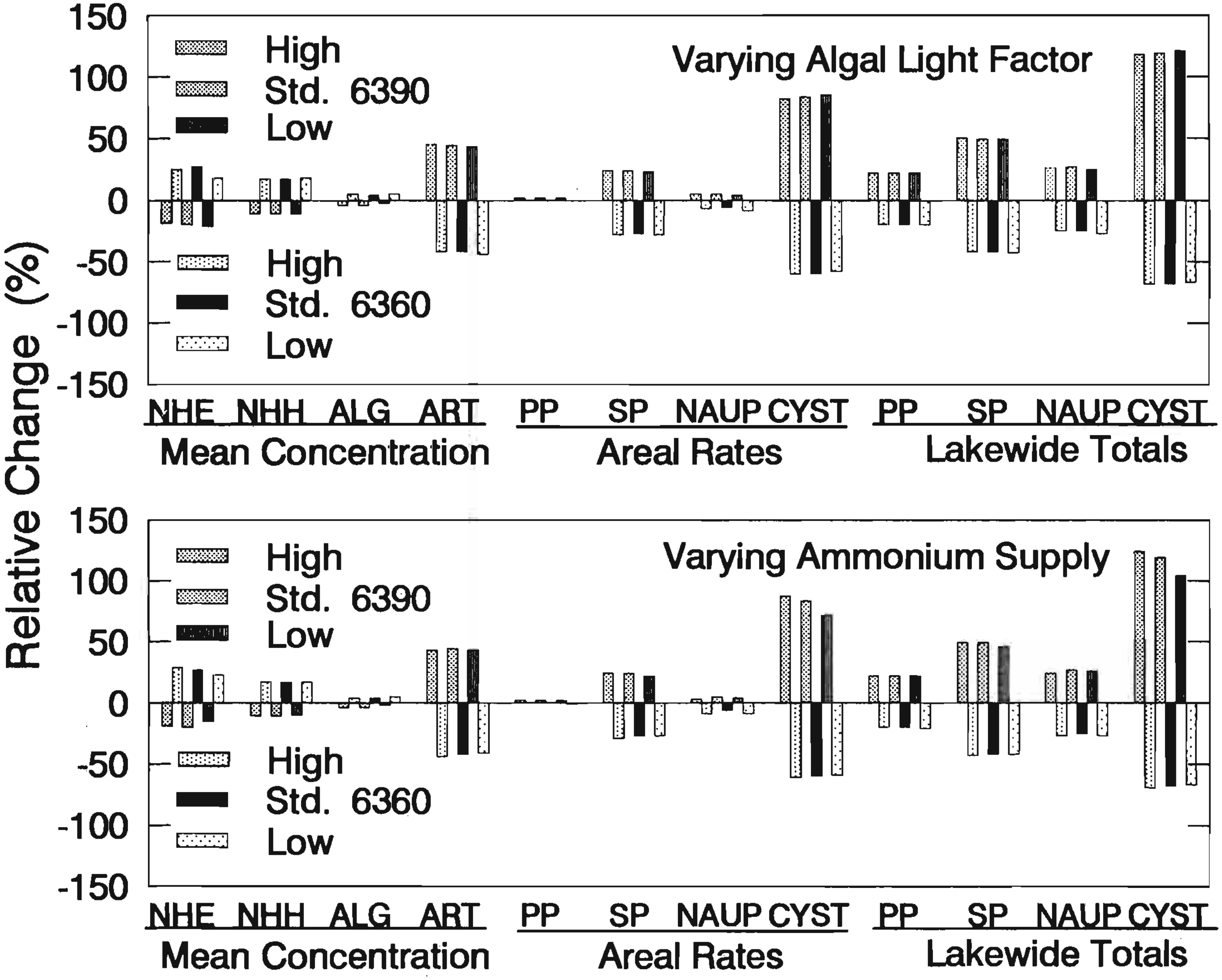

Relative Change (%)
75
50
25
0
-25
-50
-75
■ 6390
▨ 6360
All effects on Artemia except ovoviviparity
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals
Ovoviviparity
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals


Relative Change (%)
75
50
25
0
-25
-50
-75
6390
6360
Algal Maximum Growth Rate
NHE
NHH
ALG
ART
Mean Concentration
PP
SP
NAUP
CYST
Areal Rates
PP
SP
NAUP
CYST
Lakewide Totals
75
50
25
0
-25
-50
-75
6390
6360
Volume and Area Changes
NHE
NHH
ALG
ART
Mean Concentration
PP
SP
NAUP
CYST
Areal Rates
PP
SP
NAUP
CYST
Lakewide Totals


Responses to Combined Effects of Salinity and Elevation
Relative Change (%)
150
100
50
0
-50
-100
-150
6390
6383
6377
6372
6360
Monomictic (1990) conditions
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals
150
100
50
0
-50
-100
-150
6390
6383
6377
6372
6360
Meromictic (1984) conditions
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals


Relative Change (%)
150
100
50
0
-50
-100
-150
High
Std. 6390
Low
Varying Grz1
High
Std. 6360
Low
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals
150
100
50
0
-50
-100
-150
High
Std. 6390
Low
Varying Grz2
High
Std. 6360
Low
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals


Relative Change (%)
150
100
50
0
-50
-100
-150
Varying Grzalg
High
Std. 6390
Low
High
Std. 6360
Low
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals
Varying Grzpar
High
Std. 6390
Low
High
Std. 6360
Low
NHE NHH ALG ART
Mean Concentration
PP SP NAUP CYST
Areal Rates
PP SP NAUP CYST
Lakewide Totals


Relative Change (%)
150
100
50
0
-50
-100
-150
High
Std. 6390
Low
High
Std. 6360
Low
Varying Algal Light Factor
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
PP
SP
NAUP
CYST
Mean Concentration
Areal Rates
Lakewide Totals
150
100
50
0
-50
-100
-150
High
Std. 6390
Low
High
Std. 6360
Low
Varying Ammonium Supply
NHE
NHH
ALG
ART
PP
SP
NAUP
CYST
PP
SP
NAUP
CYST
Mean Concentration
Areal Rates
Lakewide Totals