

Appendix M. Brine Shrimp Productivity Model

The brine shrimp productivity model was used to predict effects on brine shrimp productivity of various Mono Lake elevations resulting from alternative management scenarios. The model includes separate physical and biological limnology models to simulate temperature, light level, vertical mixing, and salinity changes and their effects on algae and brine shrimp production.

PHYSICAL LIMNOLOGY MODEL

Mono Lake brine shrimp are generally restricted to the upper mixed layer of Mono Lake because low dissolved oxygen concentrations and cold temperatures limit growth in deeper layers. Algal production and salinity in the upper mixed layer are both strongly affected by vertical mixing between the surface and bottom layers. Vertical mixing is controlled by the temperature and salinity gradient between layers. Therefore, effects of alternative lake levels on the vertical mixing regime must be understood to estimate brine shrimp production patterns.

Vertical temperature, salinity, and mixing patterns in Mono Lake were simulated with a computer model, Dynamic Reservoir Simulation Model (DYRESM) (Jellison et al. 1991). DYRESM models the lake as a vertical stack of horizontal layers of uniform temperature and salinity (as conductivity). Conductivity is the measure of salinity used in University of California, Santa Barbara (UC Santa Barbara) monitoring of Mono Lake limnology. The surface mixed layer, in which temperature and conductivity are relatively uniform, is modeled as thick slabs, whereas the thermocline and chemocline, in which temperature and conductivity change rapidly with depth, are modeled as a number of thin sections. These layers fluctuate vertically with changes in volume caused by inflows, rainfall, and evaporation.

DYRESM simulations for each lake level alternative were run for a 50-year period beginning with the point-of-reference elevation of 6,376.3 feet. Inflows and lake level fluctuations simulated with the Los Angeles Aqueduct Model (LAAMP) (Appendix B) were used as input for the DYRESM model. Daily meteorological data for 1990 were used for all 50 years of simulation.

The inputs that are required to run the DYRESM model, a brief account of how the model operates, and a description of the model outputs are given below.

DYRESM Model Description

The DYRESM model simulates the vertical patterns of temperature, salinity, and mixing within Mono Lake. The model uses mass balance equations to calculate a water budget, a salt budget, and a heat budget for each of the vertical water layers. Each water layer has a storage term (i.e., volume, heat, or salt mass) and may have inflow, outflow, and vertical mixing exchange terms.

All the modeled inflows and outflows occur near the surface of Mono Lake, so these surface exchange processes are quite important for accurate model results. Water inflows from runoff and rainfall enter the surface mixed layer. Groundwater inflows rise rapidly to the surface because of the large density difference between fresh water and Mono Lake water.

Wind and thermal energy inputs produce a surface mixed layer that is usually several meters deep in Mono Lake. Surface heat exchange governs the heating and cooling of Mono Lake. Evaporation removes water and heat from the surface mixed layer. Because of the effects of salinity on density, ice usually does not form on Mono Lake, and the lake surface is exposed to wind energy throughout the year.

No inflow or outflow of salt from Mono Lake is assumed to exist, but salt is moved between modeled layers by vertical mixing exchange processes. Surface evaporation increases the salinity concentration in the surface mixed layer, while freshwater inflow dilutes the salinity concentration in the surface mixed layer.

The water budget, heat budget, and salt budget are directly linked in several important ways. The density of Mono Lake water is directly dependent on the temperature and salinity, so the volume of a modeled layer changes slightly as the temperature or salinity changes. These relationships are described by the "equations of state" for Mono Lake water (Jellison et al. 1991).

Vertical mixing is strongly dependent on the density differences between layers, so that heating or reduced salinity from freshwater inflows greatly restrict vertical mixing. Cooling and evaporation will increase the density of the surface mixed layer and allow greater mixing with underlying layers. Mixing exchanges of water, heat, and salinity are directly related.

The DYRESM model algorithms are more fully described in the model documentation (Imberger and Patterson 1981) and the UC Santa Barbara application to Mono Lake (Jellison et al. 1991, Dana, Jellison, Romero, and Melak 1992).

DYRESM Water Budget

The bathymetry of Mono Lake describes the surface area and volume at any elevation. DYRESM uses the metric equivalent of the Pelagos Corporation bathymetry described in Appendix L. The deepest portion of Mono Lake is at elevation 6,230 feet (1,899 meters), so the total depth of Mono Lake is 44.5 meters at the August 1989 point-of-reference elevation of 6,376.3 ft (1,943.5 meters). The model layer volumes and exchange areas between layers are estimated from the bathymetric tables.

The DYRESM model uses variable layer depths, but the resulting temperature and salinity patterns are output at 1-meter increments, using linear interpolation of the modeled layer values. The surface mixed layer is modeled with several layers that are completely mixed with each other and so have the same temperature, salinity, and density.

The model calculations are made several times within each day, although the boundary conditions of inflow and meteorology are daily average values. Rainfall and surface runoff were simulated to enter the surface layer because of the large density difference between fresh water and Mono Lake water, regardless of the temperature of these inflows. Groundwater inflows were modeled to enter the lake with an assumed vertical distribution that provided some inflow to all layers (Dana, Jellison, Romero, and Melak 1992). Daily evaporation from the surface was calculated using daily average meteorology and daily mixed layer temperatures. The annual total evaporation for the 1990 meteorology was estimated to be about 48 inches.

Mono Lake volume changes directly with the addition and removal of water. Slight volumetric changes are caused by thermal expansion and salinity effects. The water budget for Mono Lake was internally adjusted to match the historical or LAAMP model simulated lake elevation fluctuations. Because evaporation is internally calculated, the daily modeled inflows are reduced or increased to provide this matching surface elevation. The LAAMP model assumes an unmeasured inflow of about 34,000 acre-feet per year (af/yr) plus 5% of the diverted tributary runoff (Appendix A). Because DYRESM uses the measured or simulated tributary streamflows, DYRESM assumes all the "adjusted" inflow is groundwater.

DYRESM Salt Budget

Salinity is defined as the mass of total dissolved solids per unit of water volume, usually reported as grams per liter (g/l) for Mono Lake. Based on available field measurements, the total mass of dissolved solids in Mono Lake is estimated to be 285 million tons (258.5 metric tons). For the August 1989 point-of-reference elevation, the volume of Mono Lake was approximately 2.33 million af, and the salinity was about 90 g/l.

UC Santa Barbara field data for salinity are vertical profiles of electrical conductivity (EC) measurements, adjusted to a standard temperature of 25°C. Because EC exhibits a linear relationship with salinity in the 65-95 g/l range tested, EC was modeled as salinity in DYRESM. Because EC is a strong

function of temperature, the EC values are all adjusted to 25°C, regardless of the modeled layer temperature. The assumed relationship (Jellison 1992) between EC and salinity is:

$$\text{Salinity (g/l)} = 1.4205 \times \text{EC (microsiemens/centimeter [mS/cm])} - 35.64$$

Salinity will increase as evaporation removes water from the surface layer and will be reduced as inflows add water to the surface layer. All other changes in salinity within Mono Lake will be caused by mixing from the surface layer. During periods of complete mixing, the entire lake will have the same average salinity. Salt is redistributed by mixing processes, but none is added or removed from Mono Lake.

As salinity increases, part of the salt will increase the water density without changing the volume, while the remainder will expand the volume of water, much as heat will cause the water volume to expand and the density to decrease. Figure M-1 shows the experimental determination of the density of Mono Lake water that was diluted and concentrated to a wide range of salinities (LADWP 1987). The experiment indicates a linear response of density to salinity increases, with approximately 80% of the dissolved solids increasing the density and 20% increasing the volume. For example, the density of 125 g/l salinity (12.5% by weight) has increased 10% to a density of 1,100 g/l (specific gravity of 1.10). If the salt is removed from a liter of water, the remaining water will weigh 975 grams and occupy 0.975 liter, indicating that the volume increased 2.5% as the salt was dissolved. The DYRESM model properly simulates these effects of salinity on density and volume.

DYRESM Heat Budget

The heat content of each modeled layer is calculated from the temperature multiplied by the density multiplied by the heat capacity. Because of Mono Lake's high salt content, the density and heat capacity of its waters are higher than that of fresh water. The relative effects of temperature on thermal expansion (density) are similar to fresh water, except that the maximum density does not occur at 4°C, as it does for fresh water (Mason 1967).

Heat is exchanged at the surface only, except for photosynthetically available radiation (PAR) attenuation that is generally confined to the surface mixed layer. DYRESM considers turbulent bulk aerodynamic exchange of sensible (dry) and latent (moisture) heat that depend directly on wind speed and the difference between air and water temperature or vapor pressure. The unmeasured bulk transfer coefficient is often adjusted during calibration to include the effects of the differences between average wind speed for the entire lake and wind speed at the measurement location.

The largest heat exchange terms are long-wave radiation between the water surface and the atmosphere. The long-wave radiation processes are proportional to the emissivity multiplied by absolute temperature raised to the fourth power. While the temperature can be measured, the emissivity of the

water and the atmosphere must be estimated. Water emissivity is estimated at 0.97, while the atmospheric emissivity is estimated as a function of temperature and cloud cover.

The overall accuracy of the heat budget is determined by calibration with the available temperature profiles. Temperature profiles are governed by both surface exchange and mixing processes, however, and the absolute accuracy of these approximate heat exchange formulations cannot be certain. Nevertheless, the ability of the DYRESM model to simulate the surface temperatures of Mono Lake during 1990 is indicated in Figure M-2. Observed surface temperatures were best matched with a 20% reduction in the bulk exchange evaporation coefficient, approximating 48 inches of evaporation.

DYRESM Vertical Mixing

Vertical mixing is simulated as mass exchanges (entrainment) caused by energy inputs and momentum transfers. For Mono Lake, the dominant energy inputs are kinetic energy from wind and convective overturn energy caused by surface cooling. The wind energy input is assumed to be proportional to the wind speed squared, while the convective overturn energy is simulated by the heat budget. Both of these processes cause a slight deepening of the surface mixed layer and a small transfer of turbulent energy into underlying layers. Turbulent mixing is simulated with an effective diffusivity coefficient that depends on the overall energy input. Density gradients at the thermocline or chemocline greatly reduce the transfer of mixing energy to deeper layers.

DYRESM Model Inputs

Daily flows and temperatures of streams and other inflows to Mono Lake are required inputs of DYRESM (Dana, Jellison, Romero, and Melack 1992). Fifty-year projections of monthly inflows associated with each lake level alternative were obtained from the LAAMP model (Appendix B). LAAMP provided estimates of tributary inflow and unmeasured inflow (ungaged runoff and groundwater) into Mono Lake. Average daily stream temperatures of Convict Creek in 1990 were used as estimates of Mono Lake tributary temperatures. The Convict Creek temperatures were measured at the Sierra Nevada Aquatic Research Laboratory (SNARL), 25 miles southwest of Mono Lake at an elevation of 7,087 feet, which is about 700 feet higher than Mono Lake (Jellison et al. 1991). The 1990 stream temperature data were used for all years of simulation. Because of the large difference in density, tributary inflows enter the surface layer regardless of temperature. Daily rainfall was obtained from monthly Cain Ranch values used in LAAMP.

DYRESM also requires inputs of daily average air temperature, vapor pressure, wind speed, short wave (solar) radiation, and cloud cover. These meteorological inputs were computed with data collected from November 17, 1989, to November 16, 1990, at weather stations at SNARL (relative humidity), Cain Ranch (solar insolation), and Paoha Island (wind speed and air temperature). Cain Ranch is 4 miles southwest of Mono Lake and about 500 feet higher in elevation. Paoha Island is in the middle of Mono

Lake. Further details about meteorological data used in the DYRESM simulations are given in Dana, Jellison, Romero et al. (1992).

The vertical attenuation with depth of incident PAR (400-700 nanometers of wavelength light) affects near-surface temperatures. PAR profiles were measured monthly and attenuation coefficients were calculated. Attenuation of PAR in Mono Lake is controlled primarily by the algal biomass. Daily attenuation coefficients were estimated by linearly interpolating between measured dates. The daily attenuation coefficients for 1990 were input to the model for each of the 50 years. This implies that similar algal biomass patterns would develop each year. Because the surface mixed layer is usually between 5-15 meters deep, the majority of PAR is absorbed within the surface mixed layer for any reasonable algal biomass.

DYRESM Model Outputs

The DYRESM model outputs 1-meter-increment depth profiles of temperature, conductivity, and water density of Mono Lake on a daily basis. Daily outputs include surface elevation, evaporation estimate, depth of the surface mixed layer (determined by a specified temperature gradient) and average surface mixed layer temperature, salinity (as conductivity), and density. Temperature, salinity, and density at the 35-meter depth also were output for determining meromictic conditions. For comparing alternatives, however, monthly average values for the 50-year simulations were used to characterize the simulations.

DYRESM Calibration and Validation

The accuracy of the overall simulation of heat exchange and vertical mixing is indicated by Figure M-3 showing the measured and simulated temperature profiles in Mono Lake for 1990. Simulated surface mixed layer depths and temperatures are well matched with field measurements. The only major discrepancy is the bottom temperatures; field data indicate that bottom temperatures increased during 1990 from about 2.5°C on day 99 (April 9) to about 4°C on day 250 (September 7), while the simulated temperatures remained nearly constant at 2°C without warming. The simulated temperature gradient in the thermocline also may be too strong compared to the field data. This gradient may indicate slightly too little mixing in the hypolimnion but does not significantly affect the seasonal development of the surface mixed layer nor the chemocline that is caused by large freshwater inflows.

The 1982-1990 period of UC Santa Barbara monitoring of Mono Lake temperature and salinity profiles was used to validate the DYRESM model results. The simulated and measured surface mixed layer depth is shown in Figure M-4. The seasonal deepening from about 5 meters in spring to 15-20 meters in fall was well simulated. In addition, the development of the strong chemocline in 1983, its reinforcement in 1986, and its erosion and overturn in subsequent years was generally well simulated. The simulated

overturn was not quite complete in fall 1988, when it was observed to occur, but the simulated surface mixed layer depth had increased to about 25 meters. A slightly greater mixing during the meromictic period might have given an even better match with the observed conditions. Nevertheless, this multiple-year DYRESM simulation provides a strong test of the model and indicates that DYRESM is certainly sufficiently accurate for comparative simulations of the alternative lake levels.

BIOLOGICAL LIMNOLOGY MODEL

The dynamics of the brine shrimp population in Mono Lake are governed by strong interactions between trophic levels; nitrogen, light, and brine shrimp grazing may limit algae production, but excretion by brine shrimp is an important source of nitrogen for algae, and brine shrimp grazing clears the water and increases light penetration. Vertical mixing affects nitrogen availability, and the surface mixed layer depth affects average mixed-layer light levels.

A computer model was developed to simulate the major limnological features that determine algal and brine shrimp production (Figure M-5). The model contains two linked submodels: a nitrogen submodel that simulates the nitrogen balance in Mono Lake and a brine shrimp submodel that simulates brine shrimp population dynamics. Although the submodels are described separately, they operate in tandem during simulations.

The biological effects of alternative lake levels were assessed by simulating the nitrogen balance and brine shrimp population dynamics at a daily time scale for a period of 1 year at each of the alternative lake levels. Different model parameter values were used to reflect salinity effects on the nitrogen balance and brine shrimp dynamics.

Nitrogen Balance Submodel

Submodel Description

Nitrogen is the limiting nutrient in the pelagic food chain of Mono Lake (Jellison, Dana, Romero, and Melack 1991). The nitrogen balance submodel simulates nitrogen movement among pools representing the sediments, the hypolimnion, the epilimnion, the planktonic algae, and the brine shrimp population (Figure M-5). Nitrogen in the hypolimnetic and epilimnetic pools is present almost entirely as ammonium (NH_4^+), while that in the algae and brine shrimp is bound up in tissues, feces, or other particulate forms. Only the ammonium nitrogen, which is dissolved, is immediately available to algae. Both dissolved and particulate nitrogen are present in the sediments. Dissolved ammonium is released from the sediments into the epilimnion and hypolimnion.

Hypolimnetic and Epilimnetic Ammonia. The nitrogen submodel assumes a constant rate of ammonium release from the sediments (56 milligrams of ammonium nitrogen per square meter per day) (Jellison, Dana, Romero, and Melack 1992). When Mono Lake is holomictic (not stratified), the released ammonium moves directly into the combined epilimnetic and hypolimnetic pool. When the lake is stratified, the ammonium is added to the hypolimnetic and epilimnetic pools separately, based on the area of sediments within each layer. Vertical movement of ammonium between the hypolimnion and epilimnion is modeled by moving slabs of water with the ammonium they contain back and forth between the water layers as the epilimnetic depth changes. When the lake is stratified and the epilimnion is deepening, the slabs are moved from the hypolimnion to the epilimnion, whereas when the epilimnion is thinning (i.e., when the thermocline is rising), the water slabs are moved in the reverse direction. The model calculates daily average areal concentrations of hypolimnetic and epilimnetic ammonia as the products of the daily mean volumetric concentrations and the daily hypolimnetic and epilimnetic depths.

Excretion by brine shrimp also adds ammonium to the epilimnion, while ammonium uptake by algae decreases ammonium. Modeling of these biological processes is described in the following section and the section on the brine shrimp pool. The model assumes that no ammonium is lost by volatilization (Dana et al. 1992).

Algal Nitrogen Pool. Movement of nitrogen from ammonium to the algae (nitrogen assimilation) is modeled as a photosynthetic growth process. The model assumes algal growth rate is regulated by temperature, light, ammonium concentration, and salinity in the epilimnion. A standard growth rate of 1.25 per day, the maximum (specific) growth rate when temperature is 20°C and salinity is 92 g/l, is input into the model. The maximum growth rate is the growth rate for a given combination of temperature and salinity when light and nutrient conditions are optimal. The equation for the maximum growth rate is as follows (Dana, Jellison, Romero, and Melak 1992):

$$G_m = A \times 1.25 \times 1.08^{T-20} \times e^{-P_s}$$

where

G_m = maximum growth of algae (milligrams of nitrogen/cubic meter/day [mg N/m³/d]),

A = standing crop of algae nitrogen (mgN/m³),

T = average mixing layer temperature (°C), and

P_s = proportional increase (or negative decrease) in salinity from the point of reference (92 g/l).

The maximum growth rate decreases exponentially with decreasing temperature and with increasing salinity. For example, the maximum growth rate at 10°C is about half of that at 20°C and maximum growth rate at 120 g/l (corresponding to lake level of 6,360 feet is about three quarters that at 92 g/l (corresponding to lake level 6,375 ft asl).

When light levels or ammonium concentrations in the epilimnion are below optimal values, algal growth rates are reduced below the maximum rates. The effects of light and ammonium on algal growth are modeled as Monod-type rectangular hyperbolic functions, which describe an asymptotic increase in growth rate as light levels or ammonium concentrations approach their optimal values. If both light and ammonium are below optimal levels, then the growth rate is determined by whichever is more limiting (i.e., predicted growth rate is the lower of the growth rates computed from the equations for light level effects and ammonium concentration effects).

Ambient light conditions of the algae are estimated as the average light level for the epilimnion. The average light level is determined by surface insolation of PAR, the depth of the epilimnion, and an attenuation factor (i.e., rate of light reduction with depth) derived from *in situ* determinations of average attenuation of Mono Lake water. Algal biomass increases attenuation. The depth of the epilimnion affects light level because it determines the depth to which the algae are mixed. The model assumes that no algal growth occurs below the epilimnion. In reality, algal growth does occur below the epilimnion, but this growth is usually insubstantial (Jellison, Dana, Romero, and Melack 1991). When algal growth rate is limited by light level, the realized growth rate (G) is computed with the following equations:

$$G = G_m \times \frac{L}{L + 6}$$

and

$$L = I \times \frac{1 - e^{(K \times D)}}{K \times D}$$

where

L = average light level in the mixing layer (einsteins per meter squared per day [E/m²/d]),

I = insolation at lake surface (E/m²/d),

D = depth of the mixing layer (m),

K = light attenuation = 0.3873+(0.000632 x A), and

A = standing crop of algae nitrogen (mgN/m³).

When the growth rate is limited by nitrogen concentration, the realized growth rate is computed as follows:

$$G = G^m \times \frac{(E - 7)}{14}$$

where

E = ammonium concentration in the mixed layer (mgN/m³).

If E is less than 7, then G is set to 0 to avoid negative values for growth.

Nitrogen leaves the algal pool by two paths: sedimentation and brine shrimp grazing. Sedimentation is the rate of settling of algae out of the epilimnion. The model uses a constant sinking rate of 0.1 meter per day, so the settling loss rate (mg N/m²/d) is computed as 0.1 multiplied by the algal standing crop (mg N/m³) divided by the mean epilimnetic depth. Grazing is discussed below.

Brine Shrimp Pool. Although the brine shrimp population is an integral and important constituent in the nitrogen cycle of Mono Lake, population dynamics of the brine shrimp require a separate submodel for their description. In this section, only those processes that directly affect movement of nitrogen in and out of the brine shrimp pool are covered. Other properties of the brine shrimp population are described in the section on the brine shrimp submodel.

Transfer of nitrogen from the algal pool to the brine shrimp pool occurs entirely by brine shrimp grazing on the algae. The grazing is modeled as a filtration process bounded by an upper limit. The upper limit is the maximum grazing rate that occurs when algal biomass is not limiting. The maximum grazing rate is dependent on the individual weight of the brine shrimp and temperature as follows:

$$C_m = 0.03 \times (1 - e^{-239 \times W_i}) \times e^{-0.008 \times (T - 30)^2}$$

where

C_m = maximum grazing rate (mg N/d),

W_i = weight of individuals of the i th brine shrimp weight class (mg N), and

T = temperature (°C).

The weight classes, which are artificial groupings created to improve model performance, were produced by dividing growth of the brine shrimp lifestages (instars) in thirds (Table M-1). The class weights were derived from measured weights of the instars (Jellison et al. 1989b) by linear interpolation.

When the grazing rate is below maximum (because algal biomass is below the upper limit), grazing rate (C) is computed by the following equation:

$$C = (W_i/.5) \times e^{-.008x(T-30)^2} \times (A-7.5)/124$$

where

A = algal biomass (mg N/m³).

The temperature factor produces a normal distribution in the response of grazing to temperature with a peak grazing rate of 30°C, well above Mono Lake temperatures. The temperature optimum was adopted from experiments with another brine shrimp species (Jellison, Dana, Romero, and Melack 1992).

Total daily transfer of nitrogen from the algal pool to the brine shrimp pool is the sum over all subclasses of the subclass grazing rate multiplied by the number of brine shrimp in the subclass.

Nitrogen leaves the brine shrimp pool by several pathways. Most importantly, brine shrimp excrete nitrogen as ammonium into the epilimnion where it is immediately available for reuse by the algae. The other exports of nitrogen occur via defecation, cyst production, and mortality. These processes result in particulate nitrogen that settles to the lake bottom. The model assumes no direct release of nitrogen to the epilimnion or hypolimnion during settling of the particulates.

Nitrogen excretion and defecation rates are assumed equal to that portion of nitrogen from ingested algae not used for growth or production of cysts or nauplii (i.e., grazing minus production). The assumed model parameters allocate 56% of ingested nitrogen to the waste products, 75% of which is assumed to be excretion and 25% of which is assumed to be feces.

Cyst production and mortality are discussed in the section on brine shrimp submodel.

Submodel Inputs

Daily surface insolation, initial nitrogen pool concentrations, and epilimnetic estimates of depth, surface and bottom areas, volume, and temperature are required inputs of the nitrogen submodel. Values for these variables were obtained from field data; 1984 field data were used to simulate meromictic conditions, and 1990 field data were used to simulate monomictic conditions. Other model parameters are derived from these inputs or are input as constants. The constants were approximated from field and laboratory data or were adopted from other studies (Jellison, Dana, Romero, and Melack 1992).

Submodel Outputs

The nitrogen submodel outputs daily nitrogen concentrations of the hypolimnetic, epilimnetic and algal pools. The submodel also provides estimates of algal production of nitrogen. All model outputs are given in volumetric or areal units of nitrogen; Table M-2 gives the formulas used for converting the model outputs to the measurement units of the field data.

Submodel Validation

The nitrogen balance submodel was validated by comparing simulation results with field data. A meromictic year, 1984, and a monomictic year, 1990, were used for most validations. Values of the input variables were derived from the field data for these years.

The model predicted the partitioning of nitrogen among the epilimnetic, algal, and brine shrimp pools fairly accurately for 1990, but results for 1984 were less satisfactory (Figure M-6). The simulation for meromictic conditions was only partially successful because, as noted earlier, the model simulates two layers, whereas the actual vertical structure of Mono Lake, after the thermocline forms in the spring, is three-layered (epilimnion, hypolimnion, and monimolimnion). The model successfully simulates meromictic conditions during the spring and fall mixing periods when the lake has only two layers, the mixed layer and the monimolimnion. During the summer stratification period, however, the model treats the hypolimnion and monimolimnion as a single combined layer. Deepening of the thermocline during summer transfers water to the epilimnion from this combined layer. Under actual meromictic conditions during summer, mixing transfers water from the hypolimnion only. The monimolimnion has much higher ammonium concentrations than the hypolimnion, so the model overestimates the amount of ammonium transferred to the epilimnion. A three-layer model might be able to isolate monimolimnetic ammonium properly, but such a model has not yet been developed.

In the 1984 simulation, epilimnetic ammonium that was overestimated by the model in spring was converted to algal biomass, producing an algal bloom that was much greater than the observed bloom (Figure M-6). The model also overestimated epilimnetic ammonium concentration for summer 1984 (Figure M-6). In this case, the lower observed values may have been caused by the presence of a subthermocline layer of algae that absorbed ammonium before it could reach the epilimnion (Jellison, Dana, Romero, and Melack 1992). The two-layer model is unable to simulate any such complex layering.

A second validation of the nitrogen submodel was carried out by simulating nitrogen partitioning from 1983 through 1990, a period that included both meromictic (1983-1988) and monomictic (1989-1990) years (Figure M-7). Surface elevations, temperatures, epilimnetic depth, and insolation were input using observed values. Observed initial 1983 shrimp abundances and available cysts also were input. The model successfully duplicated several general features of the observed data. These include reduced algal biomass in late winter and early spring during meromixis, increased epilimnetic ammonium and brine shrimp biomass during summer in the latter part of the meromictic period (because of mixed layer

deepening), and a large algal bloom following the breakdown of meromixis in late 1988. Because the model simulates two layers only and thus combines the hypolimnion and monimolimnion, it overestimates ammonium concentration in the hypolimnion during meromixis and underestimates ammonium concentration in the monimolimnion.

The model estimates of annual primary production for 1983-1990 ranged from 15 to 40 g N/m², which is equivalent to 90-240 grams of carbon per meter squared per year (g C/m²/yr) (Jellison, Dana, Romero, and Melack 1992). These estimates are well below measured rates reported by Jellison and Melack (in press). However, the measured rates are for the upper 18 meters of the water column, while the model estimates are for the mixed layer only, which was often substantially less than 18 meters. Brine shrimp production estimates for same period ranged from 1.6 to 4.8 g N/m²/yr or, equivalently, 9.6 to 28.8 g C/m²/yr (Jellison, Dana, Romero, and Melack 1992). These values agree well with independent estimates of 16-23 g C/m²/yr for the period.

Brine Shrimp Submodel

Model Description

The brine shrimp submodel simulates hatching of cysts, grazing, growth, development, naupliar production, cyst production, excretion, defecation, and mortality of a population of brine shrimp (Jellison, Dana, Romero, and Melack 1992). As noted earlier, the brine shrimp and nitrogen submodels are linked in the assessment model to reflect the strong feedbacks between algal biomass, brine shrimp grazing, and brine shrimp excretion.

Brine Shrimp Growth and Development. Brine shrimp growth is modeled by incrementing their weight by a fixed proportion (44%) of the weight of the grazed algae. Grazing and growth are computed in terms of nitrogen content (i.e., weight of nitrogen consumed and nitrogen weight added to body tissue). Linking growth directly to grazing was necessary to capture the tight coupling of the algae and the brine shrimp population. Because grazing rate is influenced by algal biomass and temperature, growth rate also is linked to these variables.

Development of the brine shrimp is modeled as movement of individuals through lifestages. As noted earlier, each of the 12 stages (instars) of the brine shrimp is divided into three weight classes (Table M-1). Movement of the brine shrimp from one weight class to the next depends on their growth. The fraction of the brine shrimp that move to the next weight class each day is computed as the weight gain per individual in the weight class divided by the difference in weights of the two weight classes. If, for example, the weight gain in the first weight class is 0.0211 µg N per individual, the difference between the weights of the first and second weight classes is 0.0422 µg N (Table M-1), so $0.0211 / 0.0422 = 1/2$ of the shrimp in the first weight class move to the second weight class.

Brine Shrimp Reproduction. The model assumes no growth takes place during the adult stage. For ovigerous females, all retained nitrogen (i.e., that grazed but not lost to feces and excretion) is devoted to production of nauplii (ovoviviparity) or cysts (oviparity). The reproductive efficiency, or proportion of grazed algae used by ovigerous females for production of nauplii and cysts, is 0.3. The model assumes that adult males and nonovigerous females retain no nitrogen (i.e., they immediately recycle all ingested nitrogen through excretion, defecation, or mortality). To compute naupliar and cyst production, the model first computes total grazing by ovigerous females as the product of total weight (as nitrogen) of algae grazed by the adults multiplied by the proportion of adults that are female and the proportion of females that are ovigerous. Both proportions are assumed constant (proportion female = 0.41; proportion ovigerous = 0.84). The product is multiplied by 0.3, the reproductive efficiency. The total number of nauplii and cysts produced is determined by dividing the total naupliar and cyst production by the individual weight of a nauplius or cyst (0.2636 µg N).

Division of the total number of nauplii and cysts produced depends on the time of year, water temperature, algal biomass, and the number of broods previously produced. However, the relative importance of these factors is not well understood. For most of the year, a regression equation is used to determine the proportion of nauplii (P_n) on the basis of algal biomass (A) and temperature (T) (Jellison, Dana, Romero, and Melack 1992):

$$P_n = 1.432 - 0.936xT + 0.00054xA$$

This equation poorly predicts the proportion of nauplii during September-December when only a small fraction of the females (usually less than 2%) are producing nauplii. Therefore, the model assumes a constant 2% naupliar production for this period. The model also assumes that naupliar production is limited to the first two broods of a female and that the proportion of second broods consisting of nauplii is half that of first broods.

The initial size of the brine shrimp population each year depends on the number of cysts produced in the previous year and their hatching success. However, for simulations comparing alternative lake levels, number of cysts produced was held constant at 1.6 million cysts per square meter (the estimated number produced in 1984) to simplify comparisons. The percentage of cysts that hatch was set at 1%. The mean day of cyst hatching in the model is March 15. A normal distribution with a standard deviation of 15 days was used to model the variability in the day of hatching. Thus, 95% of the cysts are assumed to hatch between mid-February and mid-April.

Brine Shrimp Mortality. Mortality of brine shrimp was modeled by removing from the population each day a proportion (mortality rate) of the individuals in each age class. Separate mortality rates were estimated for nauplii, juveniles, and adults. The model uses a constant mortality rate (0.025 per day) for juveniles, but the mortality rate for nauplii (M_n) increases as algal biomass (A) and temperature (T) decrease, in accordance with the following equation:

$$M_n = 0.007 \times (A+45.5)/A \times (T+2.2)/T$$

The mortality rate for adults is set at 0.01 per day initially and is increased 30% for each brood produced. The constant increase in mortality rate of adults was required to simulate the observed population decline in fall.

Salinity Effects. The effects of salinity on brine shrimp population dynamics were estimated from results of the salinity bioassays (Jellison, Dana, Romero, and Melack 1992). Effects on algal growth were taken from Melack (1985). The model probably underestimates the effects of salinity on the brine shrimp because food was abundant in all the salinity bioassays. Jellison, Dana, Romero, and Melack (1992b) argue that salinity effects are probably greater under low food conditions than under high food conditions because the requirement to maintain osmotic balance takes precedence over other energy needs.

The effect of salinity on brine shrimp growth is incorporated into the model by computing growth efficiency (GE) with the following equation:

$$GE = 17.67 \times \frac{1.743 - (0.0073 \times TDS)}{e^{3.21 + (0.006 \times TDS)}}$$

where TDS is salinity as g/l TDS. Growth efficiency is increased by about 30%, from 0.44 to 0.57, as salinity is reduced from 92 g/l to 71 g/l (corresponding to an increase in lake surface elevation from 6,375 feet to 6,390 feet) (Jellison, Dana, Romero, and Melack 1992). Conversely, growth efficiency is reduced by about 32%, from 0.44 to 0.30, if salinity is raised to 120 g/l (corresponding to a lake level of 6,360 feet).

Reproductive efficiency (RE), percent ovigerity (i.e., percent ovigerous females) (PO), cyst hatching success (HS), and maximum rate of algal growth (AG) also increase in the model as salinity declines, whereas base mortality rates of juveniles (MJ) and adults (MA), the peak day of cysts hatching (HD), and percent ovoviviparity (i.e., percent of broods containing nauplii rather than cysts) (PV) decrease. The equations used to calculate all these effects are as follows:

$$RE = 0.064 \times \frac{65.8 - (0.28 \times TDS)}{e^{1.809 + (0.0036 \times TDS)}}$$

$$PO = 0.0088 \times 135 - (0.429 \times TDS)$$

$$HS = 0.00013 \times 100 - e^{1.21 + (0.021 \times TDS)}$$

$$AG = 1.25 \times e^{((TDS - 92) / 92)}$$

$$MA = 0.00026 \times 1 + (0.411 \times TDS)$$

$$MJ = 0.00064 \times 1 + (0.411 \times TDS)$$

$$HD = 75 - (6.90 \cdot e^{(0.0116 \times TDS) + 0.865})$$

$$PV = P_n / 64.85 \times e^{(0.031 \times TDS) + 1.32}$$

where P_n is computed using the regression equation given earlier. All changes in model parameters cause higher brine shrimp production at lower salinities (i.e., higher lake levels) except for the change in percent ovoviviparity, which has the opposite effect. However, the ovoviviparity results are suspect because percent ovoviviparity in the bioassays was consistently much lower than that observed in the first generation of brine shrimp in the field (Jellison, Dana, Romero, and Melack 1992).

Because of trophic interactions, productivity of the brine shrimp population would probably be much less affected by increases in salinity than are suggested by the direct effects of salinity on the brine shrimp. For instance, because brine shrimp food is limited much of the year, reductions in brine shrimp growth efficiency because of higher salinity would result in more ammonium excretion and algal growth, thereby allowing higher brine shrimp grazing and growth rates. The effects of salinity cannot be properly understood in isolation from the other factors that affect brine shrimp production.

Submodel Inputs

Daily mean epilimnetic depth, temperature, and algal biomass are required inputs for the brine shrimp submodel. Algal biomass is estimated in the nitrogen submodel, while values for the other variables are estimated from 1984 (for meromictic conditions) or 1990 (for monomictic conditions) field data. Adjustment factors are input for several model parameters to account for effects of the different salinities at the alternative lake levels.

Submodel Outputs

The brine shrimp submodel outputs daily biomass (as nitrogen) and numerical density estimates for each brine shrimp instar. These estimates can be used to plot trajectories of instar abundance over time. The submodel also provides daily and annual estimates of secondary production and cyst production. Daily rates of excretion and grazing are output and used as inputs to the nitrogen submodel.

Submodel Validation

The brine shrimp submodel was validated by comparing simulation results of brine shrimp abundance in 1984 and 1990 with field data. The model fairly accurately described the timing and abundance of adults, but naupliar and juvenile abundances were less well simulated (Figure M-8). Naupliar and juvenile abundances in the model are strongly affected by the timing and distribution of the spring hatch (Jellison, Dana, Romero, and Melack 1992). In reality, the spring hatch is likely to be highly variable, but the factors affecting it are poorly understood. In any case, naupliar and juvenile abundance patterns seem

to have little effect on overall brine shrimp and cyst production (Jellison, Dana, Romero, and Melack 1992). Annual brine shrimp production for 1983-1990, as noted earlier, was simulated quite accurately.

CITATIONS

- Dana, G. L., R. Jellison, and J. M. Melack. 1992. Functional relationships of *Artemia* life history characteristics with salinity. 1991 draft manuscript submitted to *Hydrobiologia*. Marine Science Institute, University of California, Santa Barbara, CA.
- Dana, G. L., R. Jellison, J. Romero, and J. M. Melack. 1992. Mixing and plankton dynamics in Mono Lake, California. (1991 Annual Report to the Los Angeles Department of Water and Power.) Marine Science Institute, University of California, Santa Barbara, CA.
- Imberger, J., and J. C. Patterson. 1981. A dynamic reservoir simulation model - DYRESM:5 in H. B. Fischer (ed.), *Transport Models for Inland and Coastal Waters*. Academic Press, New York, NY.
- Jellison, R., G. L. Dana, and J. M. Melack. 1989b. Phytoplankton and brine shrimp dynamics in Mono Lake, California. (1988 Annual Report to the Los Angeles Department of Water and Power.) Final revision December 15, 1989. Marine Science Institute, University of California, Santa Barbara, CA.
- Jellison, R., G. L. Dana, J. Romero, and J. M. Melack. 1991. Phytoplankton and brine shrimp dynamics in Mono Lake, California. Draft annual report 1990. Marine Science Institute, University of California, Santa Barbara, CA.
- Jellison, R., and J. M. Melack. 1992. Algal photosynthetic activity and its response to meromixis in hypersaline Mono Lake. Draft manuscript. Department of Biological Sciences and Marine Science Institute, University of California, Santa Barbara, CA.
- Jellison, R., J. M. Melack, and G. L. Dana. 1992b. A preliminary modeling analysis of *Artemia* dynamics in Mono Lake. Draft manuscript. Marine Science Institute, University of California, Santa Barbara, CA.
- Los Angeles Department of Water and Power. 1987. Mono Basin geology and hydrology. Aqueduct Division, Hydrology Section. Los Angeles, CA.
- Mason, D. T. 1967. Limnology of Mono Lake, California. *University of California Publications in Zoology* 83:1-110.
- _____. 1985. The ecology of Mono Lake. *National Geographic Society Research Reports*. 1979 projects.