PART VI: NONPREDATORY MORTALITY OF ZOOPLANKTON AND BENTHOS

Introduction

299. The mortality rate of a population may be expressed as a ratio of total deaths to total population per unit of time (Pennak 1964). In aquatic models, mortality is often subdivided into predatory and nonpredatory categories. This approach separates two processes which differ significantly in their effects on aquatic ecosystems. Predation primarily results in a flow of energy to higher trophic levels and may act to control population size. Nonpredatory mortality (NPM) may also act to control a population but primarily results in the addition of organic matter and nutrients to the detrital pool. The two categories are indirectly related. Environmental conditions that increase NPM also weaken organisms and may increase their susceptibility to predation. Natural mortality is a term occasionally used to refer to NPM (e.g., Otto 1975). We prefer the usage NPM because predatory mortality (PM) may also be considered natural.

300. When acquiring NPM data, we limited our review to literature data that were obtained under typical environmental conditions, i.e., conditions which would normally prevail in temperate reservoirs. Similarly, we discuss those factors most likely to influence NPM in temperate reservoirs, although many factors (physical, chemical, and biological) potentially affect NPM.

Previous Models

301. The differential equations for biomass in most aquatic models treat NPM as a loss from zooplankton or benthos compartments. Nonpredatory mortality may be treated as a single negative term (Chen and Orlob 1975, DiToro et al. 1971, Scavia et al. 1976), as a constant proportion of the biomass in the donor group (MacCormick et al. 1974, Zahorcak 1974, Waters and Efford 1972, Menshutkin and Umnov 1970, Umnov 1972), or in combination with other losses. Ross and Nival (1976)

combined NPM with metabolic losses. Nonpredatory mortality was included with egestion and molting losses by Patten et al. (1975) and with respiration and sinking by Parker (1973). Baca et al. (1974) and Steele (1974) discussed the inadequacy of this approach for most environmental situations. Steele also proposed the alternative assumption that mortality tends primarily to occur during certain critical periods, i.e., NPM is a function of age.

302. Although the magnitude of NPM is variable and a function of a multitude of chemical, physical, and biological factors, NPM often is an empirical constant in aquatic models (e.g., 1.5 percent/day, DiToro et al. 1971; 0.5 percent/day, MacCormick et al. 1974; 0.14 to 0.34 percent/day, Ross and Nival 1976; 0.1 percent/day, Umnov 1972). Attempts have been made to make NPM a function of season (Umnov 1972), temperature (Scavia et al. 1974, Zahorcak 1974, Park et al. 1974), dissolved oxygen concentration (Zahorcak 1974, Menshutkin and Umnov 1970), and density (Scavia et al. 1974, Zahorcak 1974, Park et al. 1974).

Experimental Estimates

303. The constant NPM values cited above are within the range of values we tabulated in Appendix E, Part I. Though values potentially range from 0 to 100 percent of biomass per day, given ideal and catastrophic conditions, respectively, NPM normally is less than 1 percent/day in both zooplankton and benthos (Figures 57 and 58, Appendix E: Part I). Welch (1976) could not demonstrate chironomid mortality until their last year of larval life, when fish predation began. However, Thornton and Wilhm (1975) observed two critical periods of increased NPM in larval *Chironomus attenuatus*. *Daphnia* exhibited an estimated 0.12 and 0.17 percent/day NPM during April-June and July-August, respectively, in Canyon Ferry Reservoir, Montana (Wright 1965). Nonpredatory mortality was probably underestimated in most field studies because of initial assumptions. For example, Wright (1965) assumed that *Leptodora kindtii* was the sole predator and that predation was negligible when *Leptodora* populations were low. Hall (1964) suggested that the

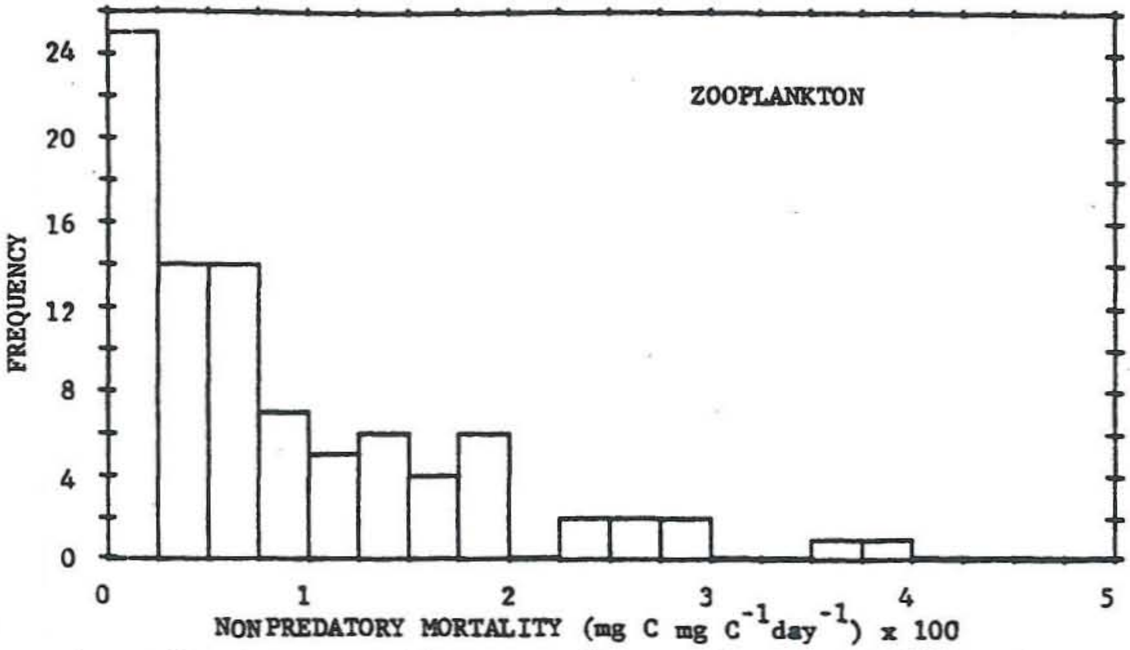

Figure 57. Frequency histogram of nonpredatory mortality rates (NPM) for zooplankton. Based on data in Appendix E, Part I

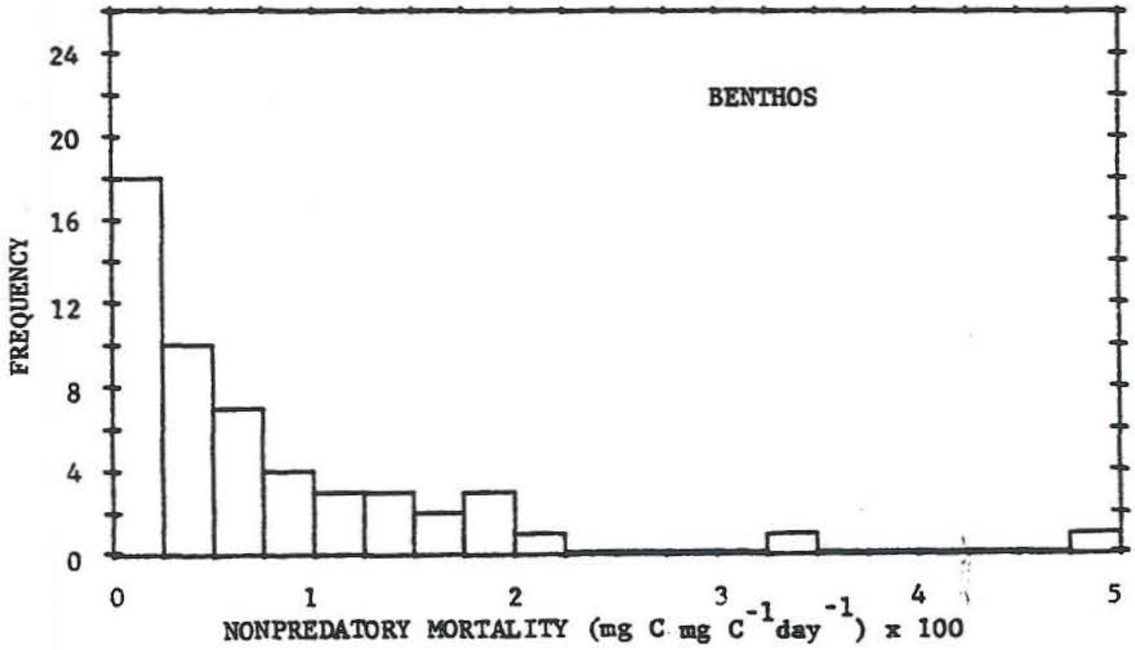

Figure 58. Frequency histogram of nonpredatory mortality rates (NPM) for benthos. Based on data in Appendix E, Part I

physiological mortality rate of Daphnia galeata was probably less than 3 percent per day throughout the year. His suggestion was based on observations of the laboratory survival of this species.

304. Estimates of NPM are difficult to obtain in the field and when obtained usually involve questionable assumptions or uncertain correlations of population phenomena (Hall 1964). For example, Dodson (1972) assumed that Chaoborus spp. and salamanders were the only predators of Daphnia rosea. After estimating PM he obtained NPM by difference, i.e., NPM = total mortality - PM. Clark and Carter (1974) considered predation on cladocerans in Sunfish Lake, Ontario, to be insignificant because the lake lacked planktonic predators, and fish supposedly were restricted to the littoral zone. A direct approach is to cage animals and eliminate predators altogether (e.g., Otto 1974). Still, researchers must assume that conditions within field cages closely approximate the conditions outside the cages with respect to factors such as food, density, light. Given the problems inherent in accurately sampling zooplankton (Bottrell et al. 1977) and benthos (Brinkhurst 1974), and the broad assumptions required in most field estimates of NPM, one must consider field data to be crude approximations at best. By contrast, laboratory studies produce analyses that often yield accurate knowledge of fundamental population growth. Unfortunately, laboratory work is often limited to conditions that are not found in nature (Hall 1964). Furthermore, study specimens are seldom given sufficient time to acclimate to experimental conditions (e.g., temperature, food concentration, and density). In short, investigators often are torn between potentially inaccurate estimates of NPM from field studies and accurate estimates of NPM from unnatural laboratory experiments. Nevertheless, some NPM data from laboratory and field experiments are surprisingly close (Appendix E, Part I). Hall et al. (1970), who constructed life tables for Ceriodaphnia reticulata and Simocephalus serrlatus from both laboratory and field data, found that although temperatures fluctuated from 20° to 26°C in the field and were constant at 23°C in the lab, rate functions produced by laboratory and field experiments were similar.

Factors Affecting Nonpredatory Mortality

Chemicals

305. The concentrations of many chemicals in natural waters influence the NPM of aquatic invertebrates, and, though in most cases we lack sufficient published data to accurately model these effects, some are worth mentioning. Toxicity models must be highly specific (as to animal and chemical species considered) and therefore are beyond the scope of this general ecosystem model. For example, the fairy shrimp *Parartemia zietziana* exhibited tremendous NPM as a result of mild increases in salinity (Marchant and Williams 1977). By contrast, Thornton and Sauer (1972) found a high optimum salinity near 68.4 millimoles per litre in *Chironomus attenuatus*. Willoughby and Sutcliffe (1976) found that a combination of low pH, low cation concentration (especially K^+), and unsuitable food supply prohibited *Gammarus pulex* from colonizing a stream. Apparently, osmoregulatory mechanisms were insufficient to maintain homeostasis at extreme ion concentrations. High concentrations of organic chemicals may indirectly affect NPM by way of low dissolved oxygen concentrations that result from increased biological oxygen demand (Lieberman 1970). High concentrations of some chemical may be directly toxic to biota (e.g., copper sulfate, pesticides, herbicides). Heavy sedimentation of tripton (Willoughby and Sutcliffe 1976) may result in increased mortality, especially in the headwaters of some reservoirs.

Diet

306. Seasonal fluctuations in the quantity and quality of foods may produce seasonal variations in the NPM of *Gammarus pulex* (Willoughby and Sutcliffe 1976). Paffenhofer (1971, 1976) found that the quality or digestibility of foods, as well as its concentration, influence the NPM of *Calanus helgolandicus*. Similar observations were made for *Rhincalanus nasutus* (Mullin and Brooks 1970). The diversity of food types in natural waters and the diversity in invertebrate diets combine to make impossible any realistic attempt at modeling the effects of diet.

Age and density

307. Nonpredatory mortality depends on the age structure of a population but does not affect all species in the same manner. For example, 85.9 percent of total NPM occurred in the naupliar stages of *Calanus helgolandicus* (Paffenhofer 1976) and *Diaptomus clavipes* (Gehrs and Robertson 1975). By contrast, young *Daphnia pulex* survived the effects of high temperature better than did mature specimens (Craddock 1976), and, in the bivalve mollusc *Sphaerium striatinum*, the oldest generation exhibited the highest NPM (Avolizi 1976). Similar results were obtained for the trichopteran *Potamophylax cingulatus* (Otto 1975), the mollusc *Anodonta anatina* (Negus 1966), and the cladoceran *Daphnia pulex* (Frank et al. 1957). Because the effect of age on NPM varies among species, we made no attempt to model this parameter.

308. Denisty is another population parameter which may influence the magnitude of NPM. Though data are limited, Frank et al. (1957) found that increased density of *Daphnia pulex* increased its survival. Because population density modifies such important variables as metabolic rates, intraspecific competition, and food availability, density may eventually (i.e., after further research) be acknowledged as a principal factor affecting NPM. Presently, however, scientific data to substantiate hypotheses of density dependent or independent mortality for zooplankton and benthos are lacking.

Temperature

309. *Mechanisms*. There are several mechanisms by which temperature can affect the survival of aquatic ectotherms (Goss and Bunting 1976). First, animals have upper and lower temperature tolerances, above and below which mortality occurs. Second, within tolerance limits, high rates of temperature change can produce shock and increase NPM. Third, the first two mechanisms can function together, producing an emergent effect.

310. Upper limits of thermal tolerance have been examined to a greater extent than other aspects of temperature response, probably due to a general concern for the effects of thermal pollution on aquatic biota. Upper lethal temperatures (ULT's) and lower lethal temperatures

(LLT's) are tabulated in Appendix E, Part II. Unfortunately, we found few data on the LLT's of aquatic invertebrates.

311. The ULT's and LLT's both depend on the acclimation temperature of study specimens. For example, the LLT of Corbicula manilensis was 12°C when the clams were acclimated to 30°C, and only 2°C when they were acclimated to 15°C. Clams acclimated to 5°C and 30°C exhibited ULT's of 24° and 34°C, respectively (Mattice and Dye 1976). Figure 59 is a graphical representation of these results. Comparable results were obtained by Becker et al. (1977), Sprague (1963), and Goss and Bunting (1976), as shown in Appendix E, Part II. Surprisingly, the range of ULT's, even for such a diverse group of animals as aquatic invertebrates in various

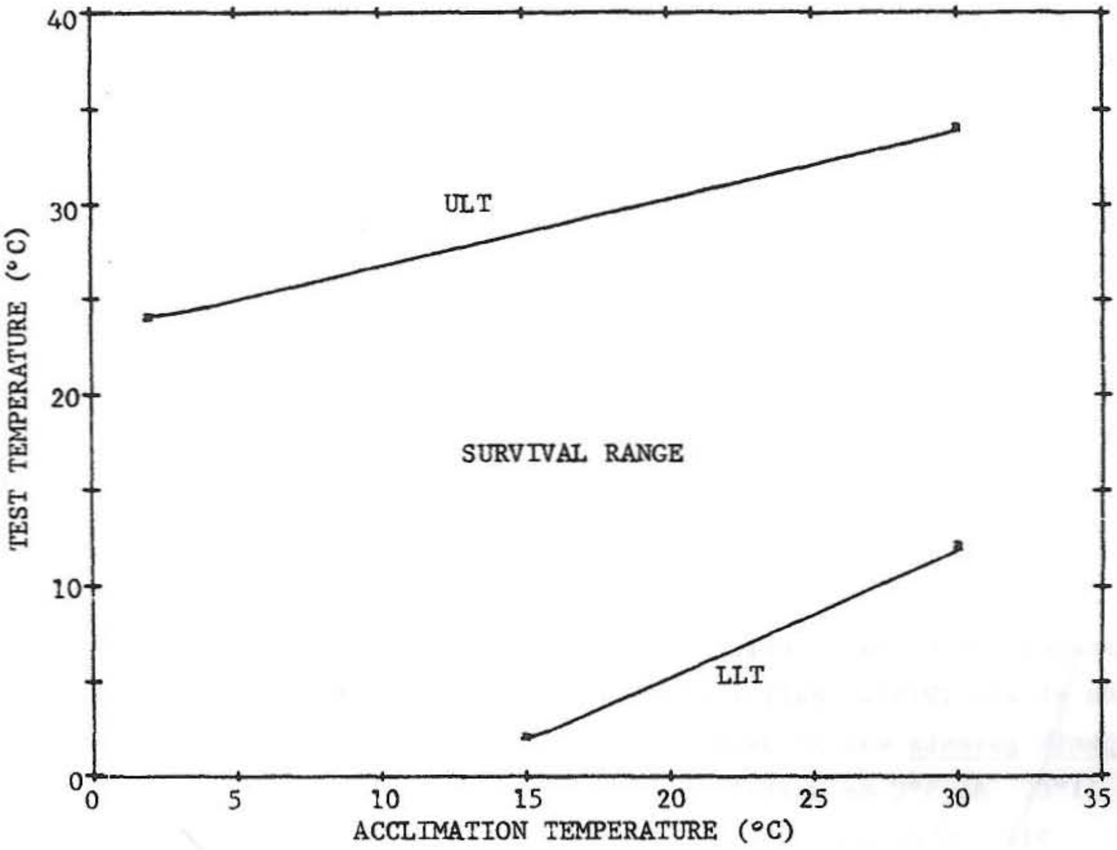

Figure 59. Upper lethal temperatures (ULT) and lower lethal temperatures (LLT) for the clam Corbicula manilensis acclimated to different temperatures. After Mattice and Dye (1976)

states of acclimation, is fairly narrow (Figure 60).

312. In a reservoir, animals normally have enough time to acclimate to slowly changing temperatures. Rapid changes in temperature such as those produced by entrainment in the effluent of a power plant, however, may exceed the rate at which a species can acclimate and therefore result in high NPM. Goss and Bunting (1976) found that the NPM of Daphnia pulex increased significantly with an increasing rate of change in temperature between 20° and 35°C. Unfortunately, their experiment did not demonstrate the exact cause of the high NPM. The increased rates of temperature change (ΔT) may have been the cause, but a better hypothesis is that increased NPM resulted from longer exposure to lethal temperatures after water reached the ULT. There was not sufficient information available to accurately model NPM as a function of ΔT. Because rapid temperature changes on the order of 3°C per hour are rare in nature, the lack of such a construct probably will not affect the performance of the model, unless it is applied to a thermally polluted reservoir.

313. Model construct. We formed a construct for temperature effects (Figure 61) by using data that related NPM to temperature (Appendix E, Part I) and data for upper and lower lethal temperatures (Appendix E, Part II). According to Figure 61, NPM increases exponentially toward asymptotes located at about 0° and 35°C. However, between 5° and 25°C inclusive, NPM is very low (≤2 percent/day). Previous research corroborates this relationship (see Cooper 1965, Mattice 1976, Ginn et al. 1976). Hall (1964) found that the median life span of Daphnia galeata was 30 days at 25°C, 60 to 80 days at 20°C, and 150 days at 11°C. At 5°C no mortality was observed in 2 months.

314. When ambient temperatures are less than 5°C or greater than 25°C, ambient temperature should be substituted for T in,

$$\mathrm{NPM} = \left[10^{(1.121 - 0.261T)} + 10^{(0.145T - 2.978)}\right] \div 100 \qquad (28)$$

where NPM = nonpredatory mortality ($\mathrm{mg\ C \cdot mg\ C^{-1} \cdot day^{-1}}$) and T = temperature (°C). The equation should be solved for NPM.

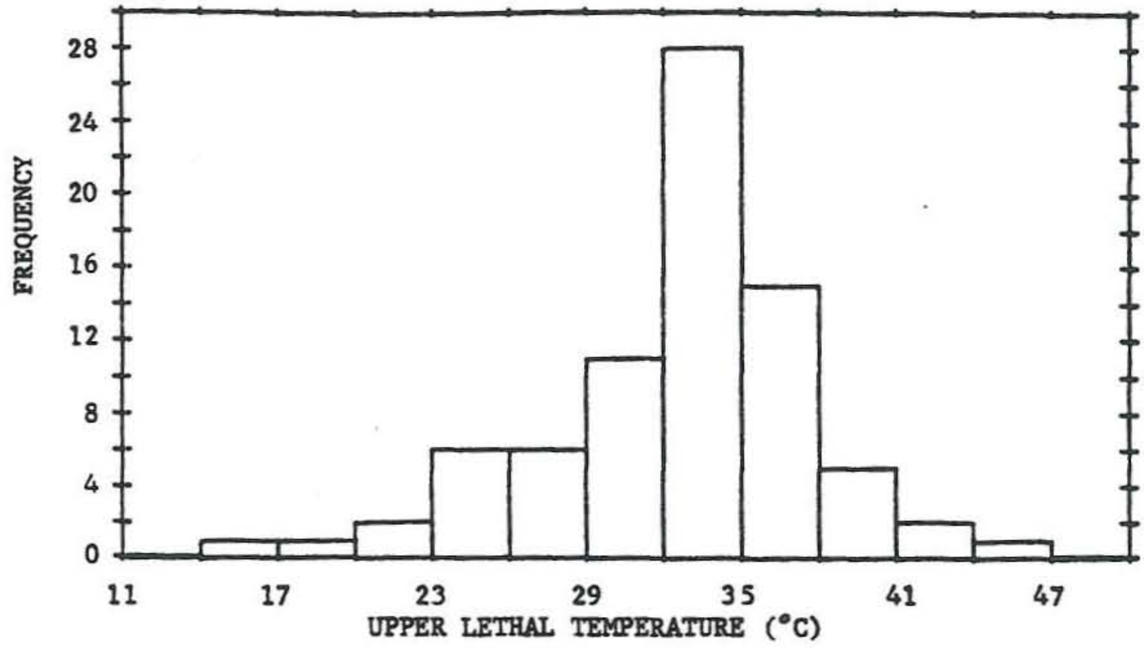

Figure 60. Frequency histogram of upper lethal temperature (ULT) for aquatic organisms. Based on data in Appendix E, Part II

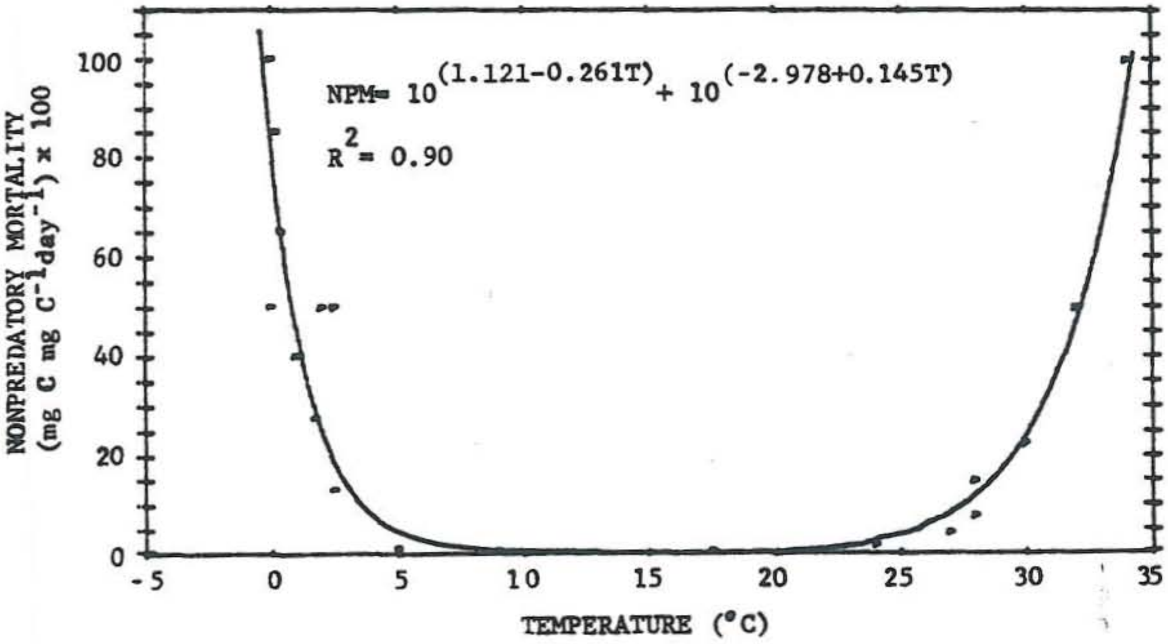

Figure 61. Nonpredatory mortality (NPM) as a function of temperature (T) for aquatic organisms. Based on data in Appendix E, Parts I and II

Oxygen concentration

315. Effects. Low dissolved oxygen (DO) concentrations have a profound effect on the survival of aquatic invertebrates. Above a critical concentration, however, NPM is unaffected (Berg and Jonasson 1965). The effects of low DO concentrations have been modeled in two ways. Menshutkin and Umnov (1970) increased NPM when DO concentrations were less than those needed to meet the respiration of the total community. NPM was increased to a point where the remaining animals could meet their respiratory demand. In the Lake George model (Zahorcak 1974), a construct "BEHAVE" stepped mortality above a base level, when DO fell below some critical concentration for several days. With the data currently available, these constructs probably are the most sophisticated yet applied.

316. Critical concentrations of DO may vary among individuals of the same species. This is especially true when the duration of exposure is varied (Berg and Jonasson 1965). Table 16 shows the concentrations of DO at which 50 percent mortality of insects occurred in 96-hr and 30-day experiments. All species listed, with the exception of Tanytarsus dissimilis, which exhibited no detectable mortality in either case, show more tolerance for short-term than for long-term exposure to critically low levels of DO.

317. Animals may be able to acclimate or behaviorally adjust to low DO tensions. Evidence presented in the section on "Respiration of Zooplankton and Benthos," page 127, showed that animals limit their metabolic rates during periods of low O_2 concentration. These types of adjustments alter the rate of NPM when oxygen becomes limiting. To date, there is no method of accurately modeling these phenomena.

318. Model constructs. Using data for various insects (Nebeker 1972), especially for the burrowing mayfly Ephemera simulans and for the limnetic copepod Limnocalanus macrurus (Roff 1973), we developed a model construct (Figure 62) that exponentially increases NPM above a normal rate, as O_2 falls below a critical concentration. A base rate of NPM (4 percent per day) was chosen from Appendix E, Part I, because it represents maximum NPM under optimal environmental conditions. We let NPM_{DO} equal

Table 16

Comparison of Critical Concentrations (mg/ℓ) of DO (i.e., Those Producing 50 Percent Mortality) for Insects Exposed to These Conditions for 96 hr and 30 days

(Berg and Jonasson 1965)

	Concentrations	
	Exposure Time	
Insect	96 hr	30 days
Pteronarcys dorsata	2.2	4.6
Baetisca laurentina	3.5	5.0
Tanytarsus dissimilis	<0.6	<0.6
Ephemerella spp.	3.9	4.5

four and solved the following exponential equation for O_2:

$$NPM_{DO} = 10^{(1.04 - 0.15O_2)} \qquad (29)$$

$$r^2 = 0.80$$

where NPM_{DO} = oxygen correction and O_2 = ambient O_2 concentration. The result, 2.9 mg/ℓ, is the critical concentration. When DO concentrations fall below 2.9 mg/ℓ, NPM should be increased above the selected rate (i.e., the rate obtained from frequency histograms; Figures 57 or 58) by $(NPM_{DO} - 4) \div 100$ mg $C \cdot mg\ C^{-1} \cdot day^{-1}$. Rates of NPM may be obtained by substituting the ambient oxygen concentration for O_2 in Equation 29. After tensions drop to zero for 24 hr, we assumed that NPM = $1 \cdot mg\ C \cdot mg\ C^{-1} \cdot day^{-1}$.

319. Data in Figure 62 are from aquatic organisms that are fairly intolerant of low DO concentrations. Therefore, this figure is taken to represent zooplankton and littoral benthos. Though the critical concentration (2.9 mg/ℓ) seems low, evidence suggests that it is reasonable. For example *Hexagenia limbata* had a 96-hr LC50 of 1.4 mg/ℓ (Nebeker 1972). Roff (1973) observed that *Limnocalanus macrurus* began to settle

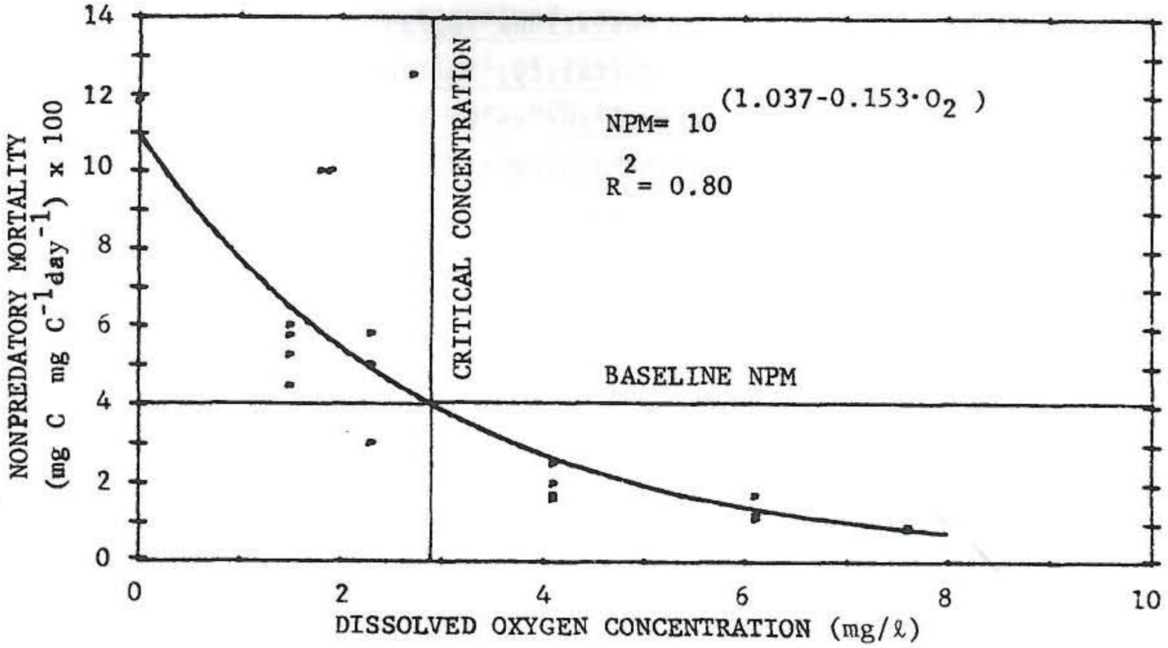

Figure 62. Nonpredatory mortality (NPM) as a function of dissolved oxygen concentration (O_2) for zooplankton and littoral benthos. Based on data from Nebeker (1972) and Roff (1973)

out and die at 2 mg O_2/ℓ. Moina brachiata survived DO concentrations approaching zero for extended periods of time (Lieberman 1970). Some zooplankton undoubtedly will exhibit high NPM at concentrations above our critical O_2 concentration of 2.9 mg/ℓ. On the other hand, some species probably will be more tolerant to low concentrations than our hypothetical average species.

320. Figure 63 depicts the NPM of profundal benthos as a function of DO concentration. Figure 63 is similar to Figure 62 in that it still contains data points for Ephemera simulans. The retention of these data points was essential to provide sufficient data on NPM at nonlethal concentrations. Figure 63 differs from Figure 62 to the extent that we added data points for Chaoborus flavicans (Berg and Jonasson 1965), Tanytarsus dissimilis (Nebeker 1972), and Planorbis contortus (Calow 1975) and deleted data points for the intolerant species in Figure 62. By manipulating the data in this fashion, we obtained:

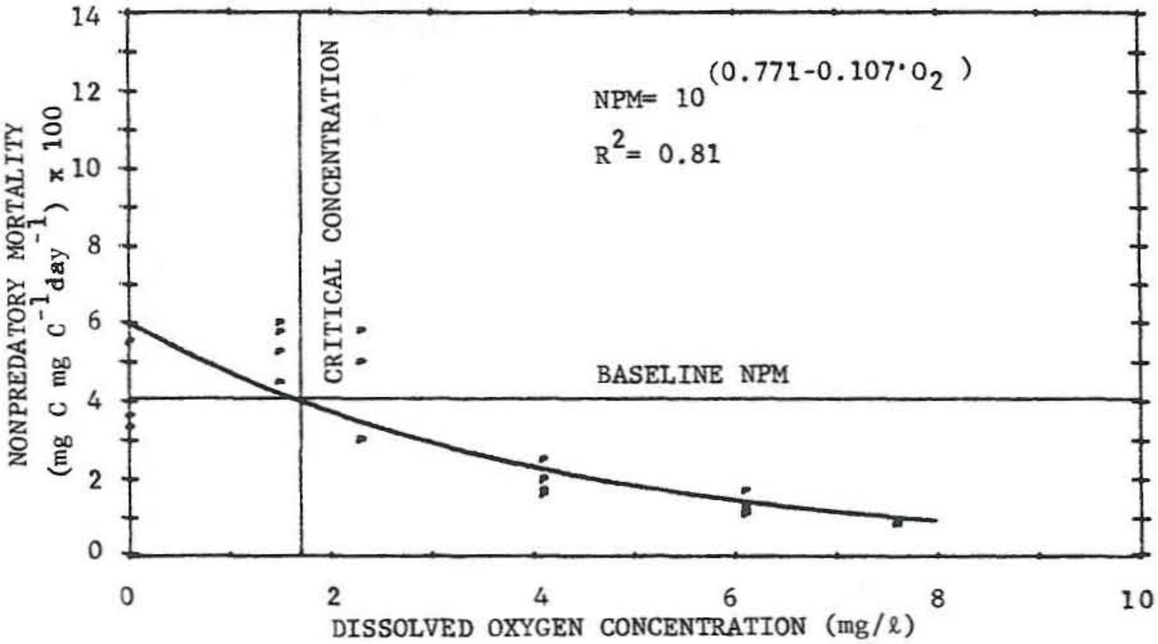

Figure 63. Nonpredatory mortality (NPM) as a function of dissolved oxygen concentration (O_2) for profundal benthos. Based on data from Berg and Jonasson (1965), Calow (1975), and Nebeker (1972)

$$NPM_{DO} = 10^{(0.77 - 0.11 O_2)} \qquad (30)$$

$$r^2 = 0.81$$

We again let NPM_{DO} = 4 percent/day (maximum NPM under optimal environmental conditions) and solved for O_2. We obtained a critical concentration of 1.7 mg O_2/ℓ. When O_2 concentrations drop below 1.7 mg/ℓ, NPM should be increased by $[(NPM_{DO} - 4) \div 100]$.

321. Observations indicate that many species of profundal benthos are extremely tolerant of low DO concentrations. Curry (1965) indicated that some midges (Chironomidae) can tolerate concentrations as low as 1.0 mg/ℓ for indefinite periods. Tanytarsus dissimilis exhibited no NPM in 30 days at concentrations less than 0.6 mg/ℓ (Nebeker 1972). Tubifex tubifex and Ilyodrilus hammoniensis were able to live in anoxic water for 1 month, and Chironomus anthracinus and Procladius pectinatus lived for 3 weeks at zero mg/ℓ (Berg and Jonasson 1965). Chaoborus flavicans

survived for a few days without oxygen but then exhibited 50 percent NPM in 2 weeks (Berg and Jonasson 1965). Similar observations were made for chironomids by Cole (1921). Calow (1975) found that *Planorbis contortus* and *Ancylus fluviatilis* exhibited 50 percent NPM only after 9 and 4.5 days, respectively, in anoxic water. To make our construct consistent with these data, we assumed that NPM = $1 \cdot \mathrm{mg\ C} \cdot \mathrm{mg\ C}^{-1} \cdot \mathrm{day}^{-1}$, after 24 days of anoxia.

Summary of Constructs

322. Nonpredatory mortality represents loss of biomass from a model compartment. Zooplankton and benthos NPM, corrected for the effects of temperature and oxygen concentration, are readily obtained from the following steps.

Step 1

323. Convert frequency histograms of zooplankton and benthos NPM (Figures 57 and 58, respectively) to probability distributions.

Step 2

324. Select a series of rates from the appropriate probability distribution (zooplankton or benthos). Users may set confidence limits on the distribution to restrict the selection range to the more probable rates.

Step 3

325. Based on ambient temperatures in the reservoir, determine whether a temperature correction is required.

- *a*. Not required - Ambient temperatures are between 5° and 25°C, inclusive. Proceed to Step 4.
- *b*. Required - Ambient temperatures are below 5° or above 25°C. Substitute ambient temperature for T in:

$$NPM = \left[10^{(1.121 - 0.261T)} + 10^{(0.145T - 2.978)}\right] \div 100 \qquad (28)$$

where T = temperature (°C) and NPM = nonpredatory mortality (mg $\mathrm{C} \cdot \mathrm{mg\ C}^{-1} \cdot \mathrm{day}^{-1}$, and solve for NPM. Proceed to Step 4.

Step 4

326. Based on the concentration of O_2 in the pelagic or profundal zone of the reservoir, determine whether an O_2 correction is required for zooplankton or benthos, respectively.

a. Not required.

(1) Zooplankton - O_2 tensions in the pelagic zone exceed 2.9 mg/ℓ.

(2) Benthos - O_2 tensions in the profundal zone exceed 1.7 mg/ℓ.

Use rates obtained from Step 3a or 3b above and proceed to Step 7.

b. Required.

(1) Zooplankton - O_2 tensions in the pelagic zone are less than or equal to 2.9 mg/ℓ. Proceed to Step 5.

(2) Benthos - O_2 tensions in the profundal zone are less than or equal to 1.7 mg/ℓ. Proceed to Step 6.

Step 5

327. Substitute O_2 in the pelagic zone for O_2 in:

$$NPM_{DO} = 10^{(1.04 - 0.15\ O_2)} \tag{29}$$

where $NPM_{DO} = O_2$ correction and O_2 = ambient concentration and solve for NPM_{DO}. Add $[(NPM_{DO} - 4)] \div 100$ to NPM rates obtained from Step 3a or 3b above. If O_2 tensions = 0 mg/ℓ for 24 hr, NPM = 1 mg C·mg C^{-1}·day^{-1}. Proceed to Step 7.

Step 6

328. Substitute O_2 concentration in the profundal zone for O_2 in:

$$NPM_{DO} = 10^{(0.77 - 0.11\ O_2)} \tag{30}$$

where $NPM_{DO} = O_2$ correction and O_2 = ambient oxygen concentration. Solve for NPM_{DO}. Add $[(NPM_{DO} - 4) \div 100]$ to NPM rates obtained from Step 3a or 3b above. If O_2 tensions = 0 mg/ℓ for 24 days, NPM = 1 mg C ·mg C^{-1}·day^{-1}. Proceed to Step 7.

Step 7

329. Multiply compartment biomass (mg C) and NPM (mg C·mg

$C^{-1} \cdot day^{-1}$) to obtain the biomass of carbon lost to nonpredatory mortality daily. According to Equation 1, the NPM rate (mg $C \cdot mg\ C^{-1} \cdot day^{-1}$) should be subtracted from assimilated carbon: $\frac{db}{dt} = b[G(A/G) - NPM - R - PM]$.

Conclusions

330. Nonpredatory mortality is important because it represents the loss of biomass from model compartments to a detrital pool. In previous models NPM often has been designated as an empirical constant, although it may vary significantly in response to environmental factors such as oxygen concentration, temperature, and chemicals or to biological factors such as diet, age, and density. Attempts have been made to express NPM as a function of season, temperature, oxygen concentration, and density. Investigators are often torn between accurate estimates of NPM under potentially unrealistic conditions in the laboratory and potentially inaccurate estimates from field experiments.

331. Though many factors influence NPM, we only found sufficient data to model the effects of dissolved oxygen concentration and temperature. Oxygen corrections must be made when O_2 is less than or equal to 2.9 mg/ℓ in the pelagic or 1.7 mg/ℓ in the profundal zone of a reservoir. Temperature corrections must be made when ambient temperatures are less than 5° or greater than 25°C.

PART VII: RECOMMENDATIONS

General

332. The present model represents a framework that should be tested, refined, and calibrated prior to use as a predictive tool. New data should be added when appropriate, and old constructs should be modified or new ones developed. Modelers should use new data from research to improve the model, and the improved model should in turn be used to direct research - thereby completing a cycle that efficiently advances the science.

333. We strongly recommend that published literature on zooplankton and benthos production be reviewed to provide a check for this model.

334. Literature and data on the skewed-horizontal distribution of aquatic animals in reservoirs should be examined in detail. Greater numbers, biomass, and diversity of animals in headwater areas may be related to significantly greater energy flow through detrital pathways.

Chemical Composition

335. Carbon, nitrogen, and phosphorus data, as determined for broad taxonomic categories of aquatic invertebrates (e.g., zooplankton) or for preserved specimens, should not be used in the data base.

336. Carbon, nitrogen, and phosphorus data as determined for marine plankton (except for medusoid forms) should be used in the data base.

337. Frequency histograms of C:N and C:P ratios for macrobenthos (Figures 1 and 5, respectively) and similar ratios for zooplankton (Figures 2 and 6, respectively) should be used to estimate N and P movements through model compartments. When greater resolution is desired, zooplankton biomass should be divided as follows: 60 percent Cladocera and 40 percent Copepoda, with Figures 7 and 8 used to determine appropriate ratios.

Consumption by Zooplankton and Benthos

338. We recommend the use of the Ivlev function (Equation 3 for acclimated specimens or Equation 9 for unacclimated specimens) to describe the relation between zooplankton and benthos grazing rates and food concentration.

339. We suggest that a threshold food concentration not be included in the grazing construct.

340. Equation 7 should be tested as an estimate of the grazing rate for any ambient food concentration. Results should be compared to simulations based on Equations 3 and 9.

341. The grazing construct should only allow the zooplankton community to feed on particles of 100 μm or less.

342. We recommend that food preference be considered equal among all potential foods except filamentous blue-green algae. A preference factor (Equation 11) should be introduced to modify the grazing equation when zooplankton are feeding on these species.

343. We believe that a linear model should be used to describe the relation between grazing rate and temperature for fully acclimated animals (Figure 19). We recommend that the reaction rate function of Thornton and Lessem (1978) be used to define the relation between grazing rate and temperature for incompletely acclimated animals.

344. We recommend that a correction factor for diel variations in grazing be tested in initial simulations to see whether such a term improves model performance. We suggest using Method No. 3.

345. The same model constructs used to describe grazing by filter-feeding zooplankton should be used to describe grazing by predatory zooplankton and benthos. When zooplankton are to be split into herbivores and predators, we recommend that predators be assigned 20 percent of total zooplankton biomass, based on the ecological growth efficiencies cited by Welch (1968).

346. We need accurate methods for determining the percent composition and turnover of detritus, bacteria, and phytoplankton in seston. In addition, more studies are needed of assimilation and survival when

zooplankton are fed protozoa, detritus or bacteria, or various combinations, for several generations.

347. More research is necessary to determine what types of animals in reservoirs, if any, can directly (by uptake) or indirectly (through a bacterial trophic link) utilize the energy available in dissolved organic matter (DOM).

348. Further research is needed to describe synergistic effects among variables influencing grazing rates.

349. Considerably more research needs to be done to describe the feeding relationships of zooplankton and benthos in a quantitative manner (i.e., as carbon or energy consumed). Special attention must be directed toward studying the responses of acclimated animals to fluctuations in food concentration and temperature.

Assimilation Efficiency (A/G), Egestion (F), and Excretion (E)

350. Although physiologically incorrect, F and E should be considered as a single loss in the model and calculated as 1 - A/G. Research that accurately quantifies excretion by aquatic invertebrates is needed to fill a tremendous void in published data.

351. Methods used to determine A/G have not produced similar results and therefore should be experimentally compared so that results can be standardized. When accurate methods are perfected, researchers should investigate how A/G is affected by factors such as temperature, food concentration, food type, development, consumption, and reproductive condition.

352. Because the distribution of A/G values for cladocerans (Figure 32) was essentially uniform, we recommend that zooplankton be considered as a single compartment (Figure 26). When greater resolution is required, the frequency histograms of rotifer and copepod A/G (Figures 30 and 31, respectively) should be used, but cladoceran A/G values should be randomly selected from a range of 5 to 55 percent. Biomass of zooplankton should be arbitrarily assigned as follows: 60 percent

Cladocera, 35 percent Copepoda, and 5 percent Rotatoria, unless more accurate data are available.

353. Benthos should be compartmentalized into carnivores and herbivores-detritivores on the basis of their respective assimilation efficiencies (Figures 28 and 29). Based on the ecological growth efficiencies of a nematode (Duncan et al. 1974), a chironomid (Kajak and Dusoge 1970), and an oligochaete (Ivlev 1939), we believe carnivores should constitute 20 ± 10 percent of total benthic biomass when the compartment is divided.

Respiration

354. Oxygen consumption should only be considered as an index to respiration and should be converted to carbon or energy equivalents by the original investigators. Because these investigators can measure CO_2 evolution and N excretion from respiring specimens, they can accurately adjust oxycaloric and oxy-carbon coefficients to account for the proportions of fat, carbohydrate, and protein oxidized.

355. Experimental specimens (especially small individuals) should be adequately fed and acclimated prior to respiration experiments.

356. Effects of environmental and biological factors (e.g., temperature, salinity, pH, O_2 concentration, density, consumption, and reproductive state) on rates of respiration should be examined for more species of benthos and zooplankton.

357. The ratio of respiration to consumption (R/G) should be experimentally explored to determine its variability due to biological and environmental perturbations and thereby evaluate its potential as a modifier of consumption.

358. During calibration of the model, special attention should be directed at achieving a balance between decreased respiration (R) and increased nonpredatory mortality (NPM) at critically low concentrations of dissolved oxygen.

359. Because data that relate zooplankton respiration to oxygen

concentrations are few, research specifically designed to describe these effects should be conducted.

360. Although many equations that relate R to individual body weight have been developed, they cannot be used to correct for body weight effects in models unless the mean weight of the individuals in a compartment is known. Seasonal changes in length frequency and the regressions of body weight on length for zooplankton should be explored as a method of estimating mean weight.

361. Because we found no realistic way to apportion total benthic biomass among smaller taxonomic compartments, respiration rates should presently be selected from a probability distribution formed from Figures 48 and 49. Weight-specific rates of respiration for zooplankton can be obtained from Figure 47, or from Figures 39-41 provided that zooplankton biomass is apportioned among groups. We suggested 60 percent Cladocera, 35 percent Copepoda, and 5 percent Rotatoria (unless better data are available).

362. Rates of respiration for selected zooplankton and benthos should be corrected for the effects of temperature and oxygen concentration, as described in "Summary of Constructs" (Part IV, page 120).

Nonpredatory Mortality (NPM)

363. Published data that relate NPM to concentrations of natural chemicals are few. Future bioassay research should examine the effects of single chemicals over a full range of O_2 concentrations, temperatures, specimen ages, or any other factors that have potential synergistic effects.

364. More research is needed to determine the effects of age and density on the NPM of a wide variety of zooplankton and benthos species.

365. Information on the NPM of zooplankton as a result of decreased O_2 concentrations and lower lethal temperatures is minimal and represents another area for additional research.

366. Rates of NPM for zooplankton and benthos should be selected from Figures 57 and 58, respectively, and selected rates should be corrected for the effects of temperature and oxygen concentration, as described in "Summary of Constructs" (Part V, page 158).