PART V: RESPIRATION OF ZOOPLANKTON AND BENTHOS

Introduction

245. Respiration is the sum of all physical and chemical processes by which organisms oxidize organic matter to produce energy. During aerobic respiration, oxygen and organic matter are consumed and carbon dioxide and water produced (Pennak 1964). Components of respiration include specific-dynamic action (SDA), basal-respiratory rate (BRR), standard-respiratory rate (SRR), and a respiratory component for activity. Specific-dynamic action refers to the energetics of digestion and is the smallest component of respiration--e.g., 15.4 percent of the total in the plecopteran Acroneuria californica (Heiman and Knight 1975). Basal-respiratory rate is the minimum energy expenditure required to sustain life. Standard-respiratory rate (SRR) is equal to the sum SDA + BRR. The activity component is highly variable and accounts for most of the variation in total respiration (Calow 1975).

246. Respiration is a very important parameter in energy budgets. Maintenance energy constitutes a major portion of energy expenditures by populations of aquatic invertebrates (80 to 90 percent) and therefore can be used as a first approximation of total assimilation (Moshiri et al. 1969). Respiration was 92.7 percent of assimilation in the cladoceran Leptodora kindtii (Moshiri et al. 1969) and 81.8 percent in the isopod Asellus aquaticus (Klekowski 1970). Since maintenance costs must be met for survival, respiration may exceed assimilation under unfavorable environmental conditions. Under such conditions, biomass may be catabolized to meet the increased demand for energy.

Methodology

247. Respiration rates of aquatic invertebrates usually are estimated directly by monitoring oxygen consumption, since the estimation of heat loss from ectotherms is impractical by direct calorimetry (Hughes 1970). By multiplying O_2 consumed by an oxycaloric coefficient,

e.g., 4.83 cal/ml O_2 (Winberg et al. 1934), respiratory rate can be estimated. Some degree of error is inherent to the application of an oxycaloric coefficient because the coefficient varies with the type of body component oxidized. Winberg et al. (1934) found different oxycaloric coefficients for oxidation of carbohydrate (4.686 cal/ml O_2), protein (4.721 cal/ml O_2), and fat (5.043 cal/ml O_2). Without measuring nitrogen excretion and CO_2 production during experiments, one has no way of determining what type of material is being oxidized and therefore is unable to appropriately adjust the oxycaloric coefficient. As a result, the oxycaloric coefficients for the three body components usually are averaged (i.e., it is assumed that specimens burn protein, fat, and carbohydrates equally). Hughes (1970) stated that the error involved in applying a mean coefficient was small--certainly smaller than the error inherent to an extrapolation of lab results to a field situation.

248. Manometric methods (e.g., the use of Warburg, Gilson, and Cartesian diver respirometers) require a manometer to measure decreases in gas pressure within a closed chamber. In the respiratory chamber, specimens consume O_2 and produce CO_2. Because the experimental medium is alkaline and absorbs CO_2, the gas pressure in the chamber decreases in proportion to the rate of O_2 consumption (Umbreit et al. 1964). There are two disadvantages to manometric techniques: (a) alkaline solutions may affect respiration in some species (Sushchenya 1969) and (b) shaking (often employed to ensure absorption of CO_2) may excite specimens and elucidate artificially high rates of respiration (Rueger et al. 1969). In contrast to Warburg and Gilson respirometers, Cartesian divers have extremely small chambers for specimens and, consequently, are the only respirometers suited to measure respiration rates of individual zooplankters. Differences in the respiratory rates of individuals of the same species often become apparent in Cartesian divers (Ivanova and Klekowski 1972). Such differences are usually masked in other methods where many specimens are enclosed concomitantly in one chamber.

249. Chemical methods, usually Winkler titration (American Public Health Association 1971), Modified-Winkler titration, or Micro-Winkler titration, measure O_2 concentrations in a closed system before and after

a suitable experimental period. The period must be long enough for a detectable difference in O_2 concentration to develop but short enough to preclude significant development of bacterial populations or starvation of experimental specimens (Marshall 1973). The difference between the initial and final O_2 concentration is taken to represent oxygen consumption by the cnclosed specimens. The combined use of a closed bottle and Winkler titration has been the most popular means of determining respiration in aquatic invertebrates (Appendix D, Parts I and II). Part of the popularity is due to the fact that the system is simple and can be used in the field or laboratory.

250. Polarographic methods require the measurement of current flowing in the external circuit of a polarographic cell (Lingane 1961). These methods are advantageous in that they provide continuous monitoring of O_2 tensions (Rueger et al. 1969). Electrodes are most often employed in a flow-through chamber (e.g., Jonasson 1964, Berg and Jonasson 1965, Rueger et al. 1969, Calow 1975), but they may be used in a closed bottle (e.g., Brinkhurst et al. 1972, Roff 1973, Foulds and Roff 1976, Swiss and Johnston 1976, Welch 1976) when a stirring mechanism is present. Flow-through systems remove animal wastes which may affect results in long-term experiments (Rueger et al. 1969).

251. No previous investigations found significant differences among respiration methods. Lawton and Richards (1970) found no significant difference between results produced by Cartesian diver and Winkler methods, nor between Cartesian diver and Gilson methods. Richman (1958) obtained similar results when he compared rates for Daphnia pulex determined from Winkler and Warburg methods. Polarographic and manometric methods were deemed suitable for measuring the O_2 consumption of aquatic invertebrates (Rueger et al. 1969). Results produced by a Scholander respirometer (manometric) and Micro-Winkler for Leptodora kindtii were not significantly different. Calow (1972) demonstrated that chemical, manometric, and polarographic techniques all measured similar rates of respiration in the mollusc Planorbis contortus and Ancylus fluviatilis.

Variation Due to Experimental Conditions

252. Laboratory conditions under which measurements of O_2 consumption are taken seldom approximate conditions in the field. Nonetheless, over 95 percent of the respiration studies have been conducted in laboratories (Appendix D). This fact results from the technical difficulties of isolating and determining the respiration of an individual or population in a natural community.

253. Laboratory specimens often are starved 24 to 96 hr prior to experiments, e.g., 24 hr for the mollusc Helisoma trivolvis (Sheanon and Trama 1972), 96 hr for the plecopteran Tarniopteryx nebulosa (Nagell 1973), 24 hr for the cladoceran Daphnia pulex (Richman 1958). When fed during experiments, Diaptomus siciloides (Comita 1968) and Calanus hyperboreus (Conover 1962) exhibited higher rates of respiration than when starved. According to Satomi and Pomeroy (1965), small benthos and most zooplankton are subjected to starvation if held without food for a few hours, and after 24 hr of starvation, small specimens apparently exhibit a significant depression in respiratory rate. In contrast, Ikeda (1971) found that Calanus cristatus exhibited increased rates of respiration during the first few days of starvation. In general, most researchers probably would approve of the recommendation by Cummins (1975) that specimens be fed during or immediately before experiments.

254. Research of Conover (1962), Marshall (1973), and Sushchenya (1969) indicated that increased food concentrations increased rates of respiration in Crustacea. Pilarska (1977c), however, observed increased respiration in the rotifer Brachionus rubens when food concentrations were below or above an optimum. When exposed to changes in food concentration, aquatic invertebrates exhibit respiratory rates that may depend on their present level of feeding and on the degree of previous starvation (Marshall 1973). Obviously, more research is needed. Estimates should be made over a broad range of food concentrations and taxa.

255. Another major cause of variation in respiration rates is inadequate acclimation to test temperature. Unacclimated specimens may be exposed to temperature changes that exceed any in their native

habitat. In many studies, collected specimens were acclimated to test temperatures for 24 to 28 hr (Appendix D, Parts I and II). These specimens may have been acclimated in the sense that they overcame the initial shock of capture and handling (Marshall et al. 1935, Bishop 1968, Roff 1973), but they were far from acclimated to temperature in terms of respiratory rate. According to Geller (1975), the rate of temperature acclimation in Daphnia pulex was proportional to its growth rate, and acclimation required 6 weeks at temperatures of 7° to 10°C and 4 weeks at temperatures above 15°C. Blazka (1966) observed that Daphnia hyalina, acclimated to 20°C in the laboratory, exhibited higher respiratory rates than did field populations at various ambient temperatures. This difference probably resulted from sufficient acclimation to temperature by field populations. To avoid acclimation problems, Cummins (1975) suggested that specimens be studied at the ambient temperature of their native habitat. Some rates in Appendix D, Part I, are for specimens studied at 5° to 10°C above or below their acclimation temperature in the field. These data undoubtedly increase the variance of our data base, but since we have no way to consistently correct aberrant rates, we must consider the error as part of the random variability affecting all estimates.

256. Many of the existing data are conflicting. For example, Roff (1973) and Siefken and Armitage (1968) found no effect of light on the metabolic rates of the copepods Limnocalanus macrurus and Diaptomus sp., respectively. In contrast, Marshall (1973) found that bright light stimulated respiration rates in the copepod Calanus finmarchicus, and Buikema (1972) found that light inhibited respiration in the cladoceran Daphnia pulex. Bishop (1968) observed depressed respiration rates in zooplankton as pressure increased, but Roff (1973) observed no significant effect of pressure on the respiration of Limnocalanus macrurus. Crustaceans exhibited three potential responses to increased salinity: (a) no effect, (b) increased respiratory rates at hypertonia and decreased rates at hypotonia, and (c) increased rates at both hypertonia and hypotonia (Sushchenya 1969). When pH was shifted beyond the compensation limits for a crustacean species, metabolism was either

depressed or disrupted completely (Sushchenya 1969). The problem is that compensation limits vary significantly among freshwater animals. In contrast to the results of Satomi and Pomeroy (1965) for estuarine zooplankton, research on oligochaetes (Brinkhurst et al. 1972) and copepods (Marshall and Orr 1958, Conover and Corner 1968, Siefken and Armitage 1968, Roff 1973) failed to demonstrate any effect of crowding on rates of respiration. Although it is known that a significant correlation exists between respiratory rates and activity, few investigators have effectively quantified activity and certainly not in a manner comparable for a wide variety of aquatic animals.

257. Seasonal trends in metabolic rates are difficult to explain in terms of any one environmental characteristic. Sweeney (1978) pointed out that diel and seasonal shifts in metabolism, as a result of temperature changes, may increase efficiency of resource allocations and energy partitioning. Siefken and Armitage (1968) suggested that seasonal trends were the result of seasonal changes in weight and previous thermal history. Some authors have noted seasonal trends in metabolism and correlated these trends with food concentration (e.g., Conover 1962, Blazka 1966, Marshall 1973, Larow et al. 1975). By contrast, Roff (1973) failed to observe any seasonal trends in the metabolism of Limnocalanus macrurus. Seasonal trends probably emerge as a cumulative effect of several variables on respiration (e.g., temperature, body weight, and oxygen concentration).

258. Experimental conditions that affect respiration rates often differ in laboratory and field experiments--for example, temperature (Moshiri et al. 1969, Hughes 1970, Pourriot 1973), pressure (Bishop 1968, Roff 1973), light (Buikema 1972, Marshall 1973, Sigmon et al. 1978), oxygen concentration (Jonasson 1964, Palmer 1968, Nagell 1973), salinity (Lance 1965, Sushchenya 1969), pH (Sushchenya 1969), size composition (Appendix D, Part II), crowding (Satomi and Pomeroy 1965), interspecific interactions (Brinkhurst et al. 1972), and reproductive condition (Berg and Jonasson 1965, Moshiri et al. 1969, Burky 1971). These variables also may affect activity, an extremely important factor directly influencing respiration rate (Moshiri et al. 1969, Sushchenya

1969, Ulanoski and McDiffett 1972, Trama 1972, Foulds and Roff 1976, Wycliffe and Job 1977). Absence of substrate in laboratory experiments increased the respiration rates of the ephemeropterans Hexagenia limbata and Ephemera simulans (Eriksen 1964). The respiratory rate of the chironomid Lauterbornia sp. decreased 31 percent when a substrate was provided (Welch 1976).

259. The above list of factors that influence rates of respiration is not exhaustive, nor are the effects of all of the factors similar for different species. Of the factors listed, only the effects of temperature, body size, and oxygen concentration are sufficiently documented to allow us to develop constructs. Fortunately, these factors probably are the most important, and model constructs for these factors should greatly reduce the variance of predicted rates.

Variation Due to Conversion of Units

260. Since respiratory rates of aquatic invertebrates have been expressed in a multitude of incomparable units (see "Original Units" in Appendix D, Part II), we converted all literature rates to a standard, weight-specific unit (mg carbon·mg carbon^{-1}·day^{-1}).

261. Factors for the conversion of wet weight to dry weight and for dry weight to carbon are given in a table at the front of Appendix D. Most of the conversions used were obtained from the percent - H_2O Column in Table 2 of Cummins and Wuycheck (1971). Conversion factors for dry weight to carbon were obtained from various sources (Appendix A). When percent - H_2O data were lacking for a taxon, we used data for a closely allied group or that of the next higher taxon for which percentages were available. Since water content undoubtedly varies significantly among species, we introduced an error by using mean factors to convert wet to dry weight for broad taxonomic categories. Fortunately, authors who listed O_2 consumption per unit wet weight were in the minority. A disturbing number of papers from international journals gave no indication of whether their data were in terms of wet, dry, or ash-free weight. Had researchers who used wet weights included data on percent -

H_2O for each species, the magnitude of errors associated with wet to dry weight conversions could have been greatly reduced. Though some error exists in the conversion of dry weight to carbon (Part II), it is insignificant compared to that involved in conversions of wet to dry weight.

262. To convert oxygen consumed to carbon metabolized, we applied an oxy-carbon coefficient derived by combining the mean oxycaloric coefficient of Winberg et al. (1934) (4.83 cal/ml O_2) with the energy to carbon relation for aquatic invertebrates (10.98 cal/mg carbon) derived by Salonen et al. (1976). The result is $\frac{4.83 \text{ cal}}{\text{ml O2}} \cdot \frac{\text{mg carbon}}{10.98 \text{ cal}} = 0.44$ mg carbon/ml O_2. Sources of error due to the use of oxycaloric coefficients are discussed in the section "Methodology," page 127. The variation of energy per unit organic carbon is insignificant (i.e., ca one third less variable than energy per unit ash-free dry weight (Salonen et al. 1976)). The conversion of oxygen consumed to carbon respired probably represents an insignificant error, in proportion to the total error present in laboratory experimentation and extrapolation to real aquatic systems.

263. The worst potential error in our conversions was the extrapolation of respiration per hour to respiration per day. To make this extrapolation we assumed that aquatic invertebrates respire at a constant rate throughout a 24-hr period. Some aquatic invertebrates may behave in this fashion. For example, no diel cycles of metabolism have been observed in the plecopteran Acroneuria californica (Heiman and Knight 1975), the ephemeropteran Stenonema fuscus (Ulansoki and McDiffett 1972), the odonate Anax junius (Petitpren and Knight 1970), the mysid Mysis relicta (Foulds and Roff 1976), the dipteran Chaoborus punctipennis (Sigmon et al. 1978), or the cladoceran Leptodora kindtii (Moshiri et al. 1969). On the other hand, diel cycles in metabolism have been observed in the ephemeropterans Isonychia bicolor (Sweeney 1978) and Isonychia sp. (Ulanoski and McDiffett 1972). There is no way to quantify the error involved, but when we extrapolated from an hourly to a daily rate for species exhibiting a diel cycle of metabolism, we may have significantly underestimated or overestimated daily respiration.

Overestimates would result when experiments were conducted during periods of maximum diel respiration and underestimates when experiments were conducted during periods of low respiration.

Model Constructs

Literature synopsis

264. Previous respiration constructs range from unmodified constants to constants modified by several factors. In all models, respiration terms represent energy loss and either are linear functions of compartment biomass or a percentage of compartment consumption. Ross and Nival (1976) included respiration in a term for death rate (a_2 = 0.42 mg carbon·mg carbon^{-1}·day^{-1}) that was determined from batch experiments on the respiratory rates of starved zooplankton. In the zooplankton models by Scavia et al. (1976) and Chen and Orlob (1975) and in the zooplankton and benthos models by MacCormick et al. (1974), respiration rates were modified exclusively by temperature. Respiration rates were modified solely by the body size of zooplankton in a model by Menshutkin and Umnov (1970). Constructs of respiration rates as functions of temperature and body size have been developed (DiToro et al. 1971, Umnov 1972, Baca et al. 1974, Kremer 1975, Patten et al. 1975). Waters and Efford (1972) developed constructs with respiration rates as functions of temperature, body size, and food intake. Steele (1974) considered body size and food intake effects but omitted a function for temperature effects, since temperature was essentially constant in the North Sea. The most elaborate respiration constructs were those for zooplankton and benthos in a model by Park et al. (1974) and those for benthos by Zahorcak (1974). Park et al. (1974) modeled the effects of temperature, body size, and behavior on rates of respiration. Zahorcak (1974) considered the same factors as Park et al. (1974) but, in addition, developed constructs for the effects of crowding and oxygen concentration.

265. The importance of food consumption as a factor affecting rates of respiration is controversial. Waters and Efford (1972) and

Steele (1974) considered consumption effects important enough to warrant model constructs. We do not believe that sufficient data are yet available to permit us to accurately model the effects of consumption on respiration. Steele (1974) made respiration of copepods a linear function of consumption. However, other data for copepods (Ikeda 1971) and for rotifers (Pilarska 1977c) indicated that the relationship may not be linear. In fact, Swartzman and Bentley (1978) noted that rates predicted by Steele (1974), for copepods at high concentrations of food, were 2.7 times higher than those observed in laboratory populations of Mullin and Brooks (1970). Mayfly and stonefly nymphs (Nagell 1973) did not exhibit significant decreases in metabolism during brief periods of starvation.

266. Our first approach to modeling respiration was to consider it as a proportion of consumption (R/G, Table 14). Figure 38 shows the frequency histogram of R/G ratios for a wide range of taxa. Unfortunately, only a limited number of studies have determined both respiration and consumption, and, therefore, little is known about how the ratio R/G responds to changes in the environment. Because respiration and consumption generally are affected similarly by temperature, oxygen concentration, and body size, the ratio R/G should be less variable than other expressions of respiration. More research is required before the potential of R/G ratios in ecosystem models can be fully realized. Figure 38 provides some insight into the range of potential values for aquatic invertebrates. The product of consumption (mg C·mg C^{-1}·day^{-1}, Part III) and R/G (Figure 38) yields weight-specific respiration for a community. As more data are collated, frequency distributions for major taxa such as Cladocera, Copepoda, Rotatoria, and Diptera could be formed.

267. Our second approach to respiration involved the conversion of literature data on oxygen consumption to rates of weight-specific respiration (mg carbon·mg $carbon^{-1}$·day^{-1}). Respiration rates were tabulated for taxa (Appendix D, Part I), and frequency distributions of rates were constructed for various taxonomic categories and weight classes. Respiration losses are proportional to the biomass of the

Table 14

Respiration as a Percentage of Consumption for Aquatic Invertebrates

Taxon	Trophic Condition	$\frac{\text{Respiration}}{\text{Consumption}} \times 100$	Reference
Mollusca			
Scrobicularia plana	Fed	47.9	Hughes (1970)
Plecoptera			
Acroneuria californica	Starved	51.0	Heiman and Knight (1975)
Pteronarcys scotti	?	6.9	McDiffett (1970)
Ephemeroptera			
Stenonema pulchellum	Fed	37.6, 37.0, 41.2, 38.6	Trama (1972)
Odonata			
Pyrrhosoma nymphula	?	43.5, 41.6, 42.9	Lawton (1971)
Megaloptera			
Corydalus cornutus	Starved	25.7	Brown (1978)
Isopoda			
Asellus aquaticus	?	25.0	Prus (1972)
Mysidacea			
Mysis relicata	Fed	69.3, 63.7, 70.6, 70.5, 70.6, 73.7, 70.2	Lasenby and Langford (1972)
Copepoda			
Macrocyclops albidus	?	ca 20	Klekowski and Shushkina (1966a)
Diaptomus siciloides	?	53.7, 76.3, 53.0, 38.8	Comita (1964)

(Continued)

Table 14 (Concluded)

Taxon	Trophic Condition	$\frac{\text{Respiration}}{\text{Consumption}} \times 100$	Reference
Rotatoria			
Brachionus rubens	Starved	45	Pilarska (1977c)
Brachionus calyciflorus	Fed	7-13	Galkovskaya (1963)
Brachionus plicatilis	Fed	8	Doohan (1973)
Cladocera			
Daphnia pulex	Starved	4-14	Richman (1958)
Simocephalus vetulus	?	11.5-19.5	Klekowski (1970)

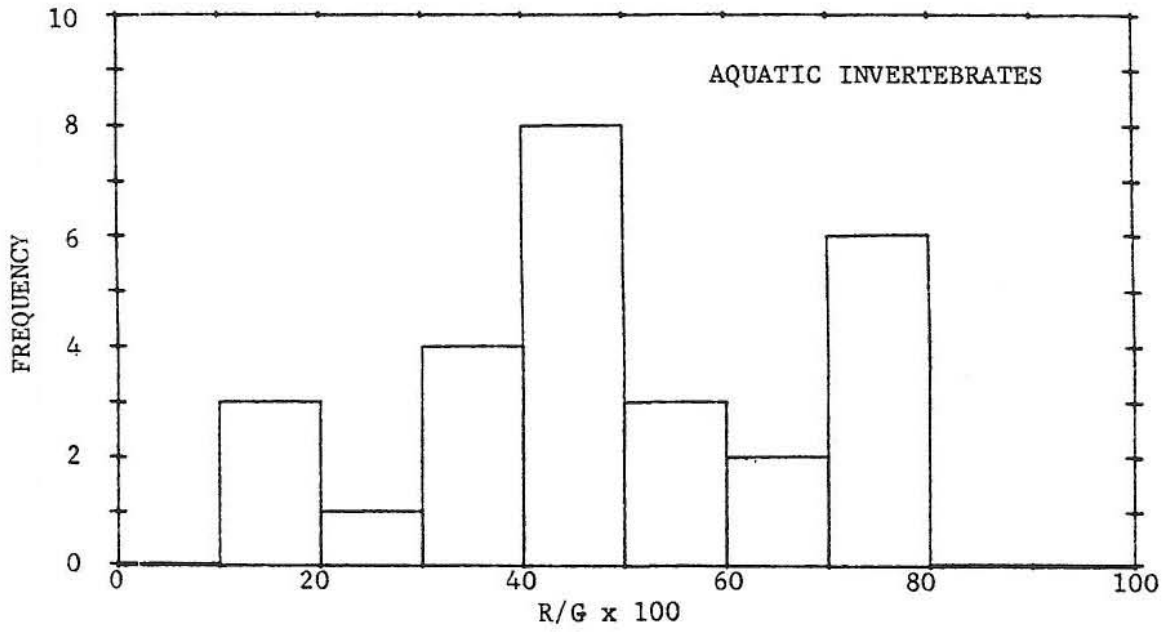

Figure 38. Frequency histogram of respiration (R), as a percentage of consumption (G), for aquatic invertebrates. Based on the data in Table 14

donor compartment. In other words, the product of compartment biomass (mg carbon) and respiration (mg carbon·mg carbon^{-1}·day^{-1}) is the weight of carbon respired daily by that compartment.

268. Frequency histograms were constructed from respiration rates in Appendix D (Part I) for major taxa of zooplankton, i.e., Cladocera (Figure 39), Copepoda (Figure 40), and Rotatoria (Figure 41). All rates in the frequency histograms were corrected to 20°C. Rotifers generally exhibit higher rates ($\bar{x}$ = 0.430; range = 0.20 - 1.10 mg carbon·mg carbon^{-1}·day^{-1}) than entomostracans (Figures 39 and 40; $\bar{x}$ = 0.240; range = 0.050 - 0.800 units). Cladocera exhibit slightly higher rates ($\bar{x}$ = 0.250; range = 0.050 - 0.800 units) than Copepoda ($\bar{x}$ = 0.232; range = 0.050 - 0.800 units). These data are generally within the range of weight-specific rates used in other phytoplankton and zooplankton models (e.g., 0.096 - MacCormick et al. 1972; 0.16 - Bierman et al. 1973; 0.20 - Thomann et al. 1975; 0.23 - Kremer 1975; 0.50 - Steele 1974).

269. Frequency histograms of respiration rates also were constructed for the major taxa of benthos. Rates of benthic Crustacea,

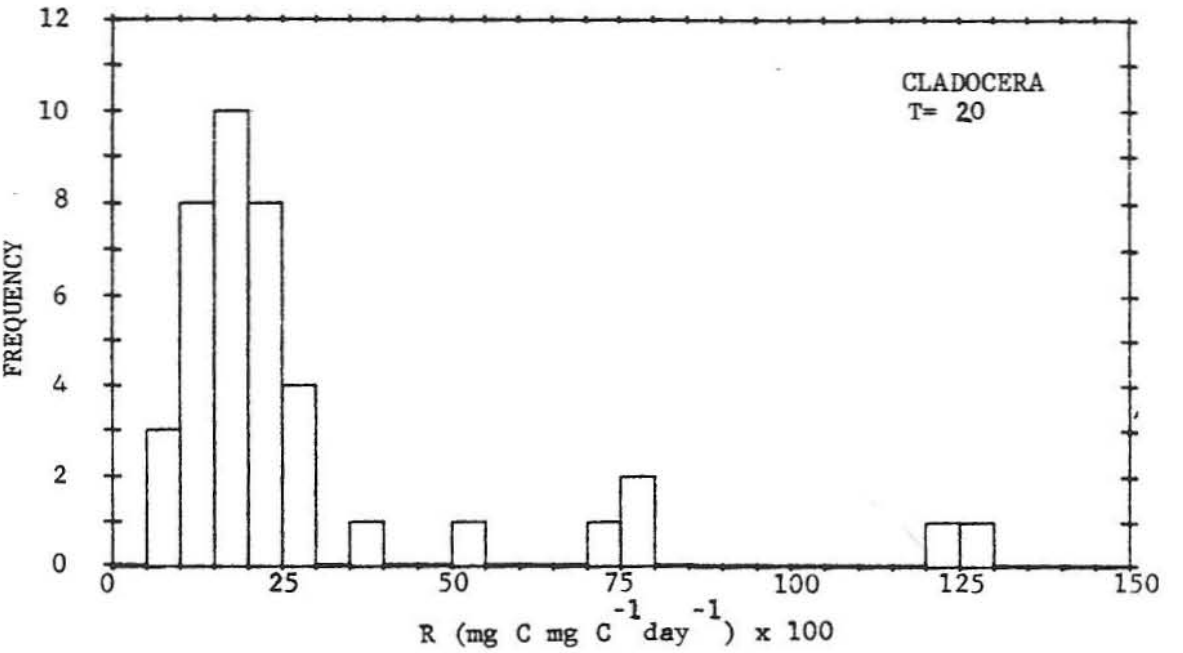

Figure 39. Frequency histogram of respiration rates for Cladocera. Based on data in Appendix D, Part I. T = temperature (°C)

Insecta, Oligochaeta, and Mollusca (Figures 42-45, respectively) are all of equal magnitude but considerably lower than those of zooplankton (Figures 39-41). We anticipated these results, however, based on the relation of weight-specific respiration to body weight.

Effects of Body Weight

270. The fact that rotifers exhibit higher metabolic rates than entomostracans exemplifies the well-documented observation that weight-specific respiration is a negative exponential function of body weight (Appendix D, Part II). For example, Figure 46 illustrates the relationship of respiration to body weight for aquatic invertebrates. The fitted line is log R = log 1.472 - 0.285 log W, where W = weight (carbon units) and R = respiration rate (mg carbon·mg carbon^{-1}·day^{-1}) × 100. This equation has an R^2 of 0.96 and was fitted to data collected at 20°C (Appendix D, Part I).

271. Respiration as a function of body weight is described by the general equation:

$$Y = aW^b \qquad (23)$$

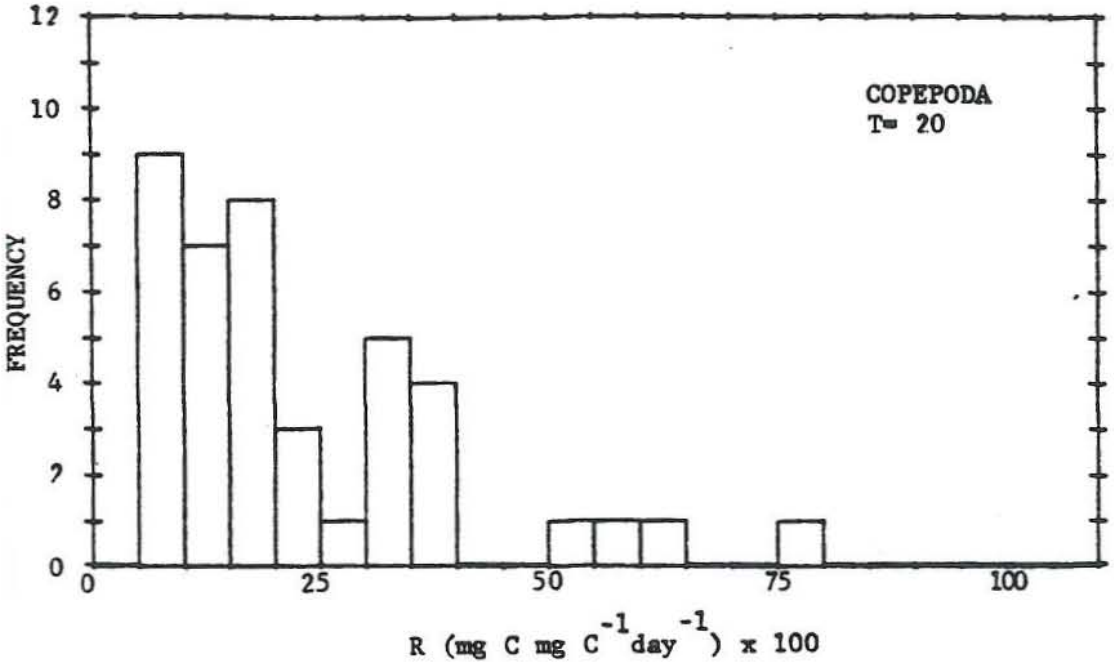

Figure 40. Frequency histogram of respiration rates for Copepoda. Based on data in Appendix D, Part I. T = tempertature (°C)

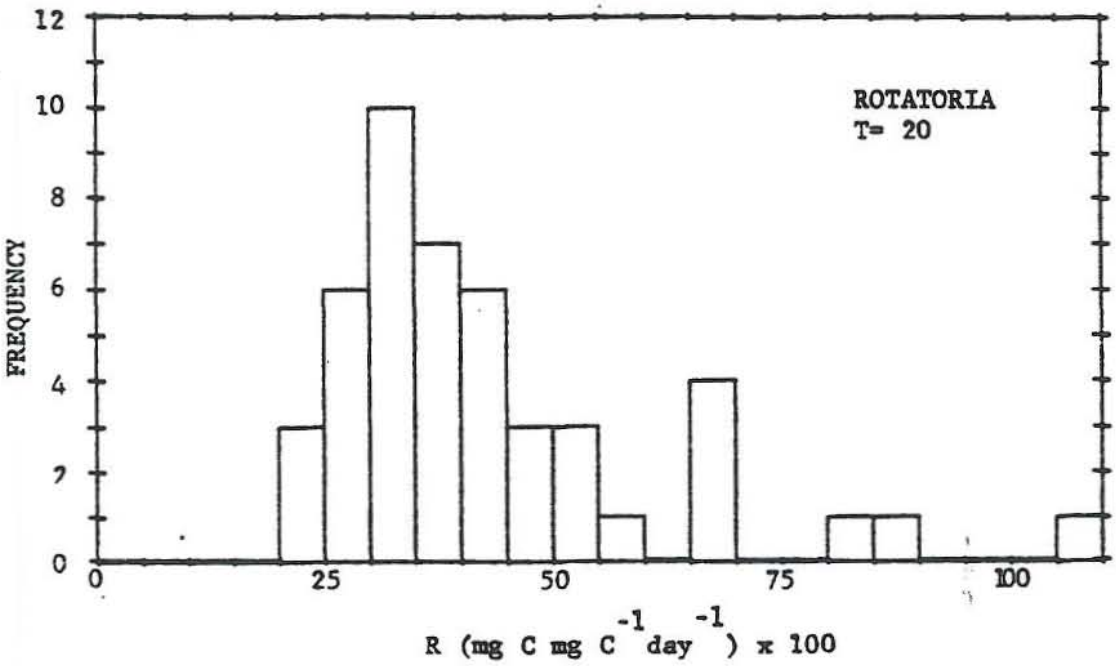

Figure 41. Frequency histogram of respiration rates for Rotatoria. Based on data in Appendix D, Part I. T = temperture (°C)

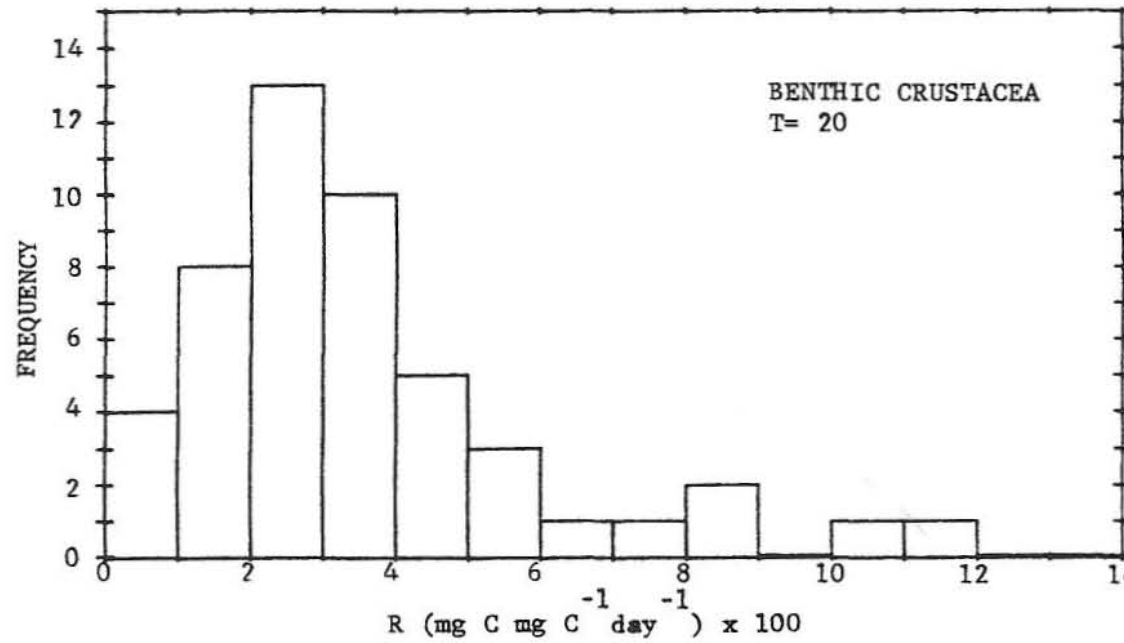

Figure 42. Frequency histogram of respiration rates for benthic Crustacea. Based on data in Appendix D, Part I. T = temperature (°C)

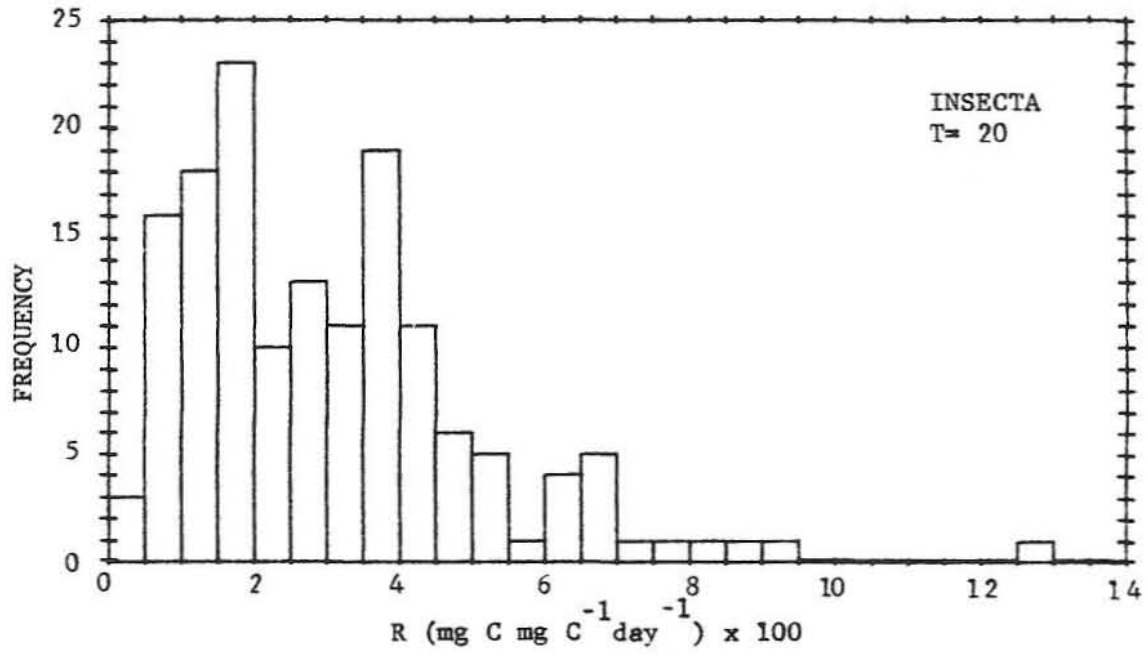

Figure 43. Frequency histogram of respiration rates for aquatic Insecta. Based on data in Appendix D, Part I. T = temperature (°C)

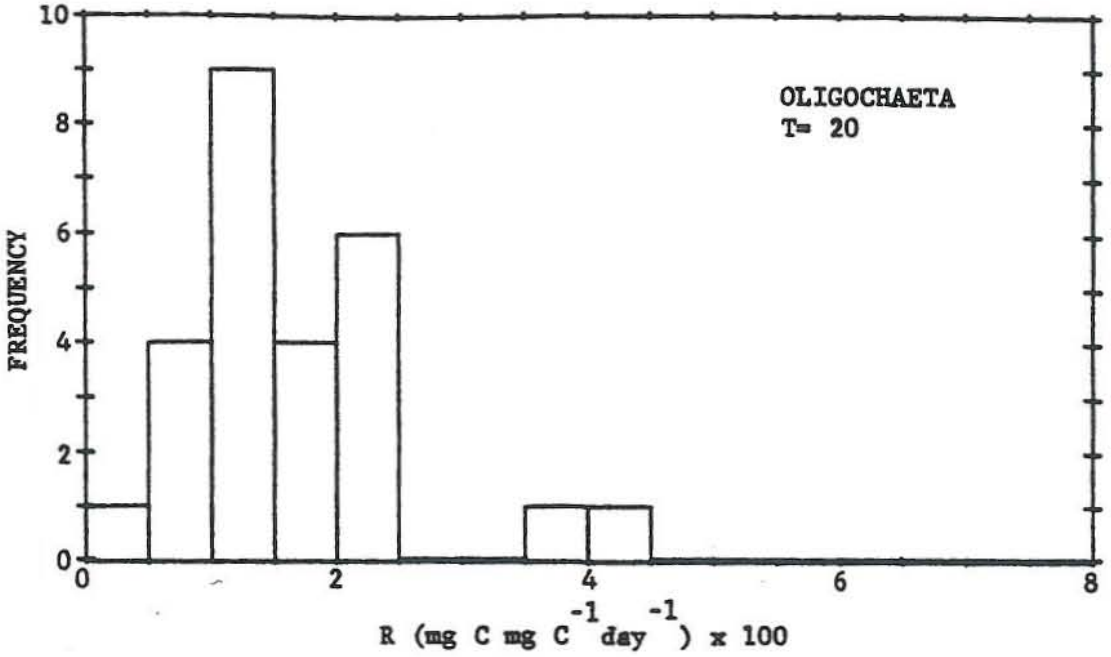

Figure 44. Frequency histogram of respiration rates for Oligochaeta. Based on data in Appendix D, Part I. T = temperature (°C)

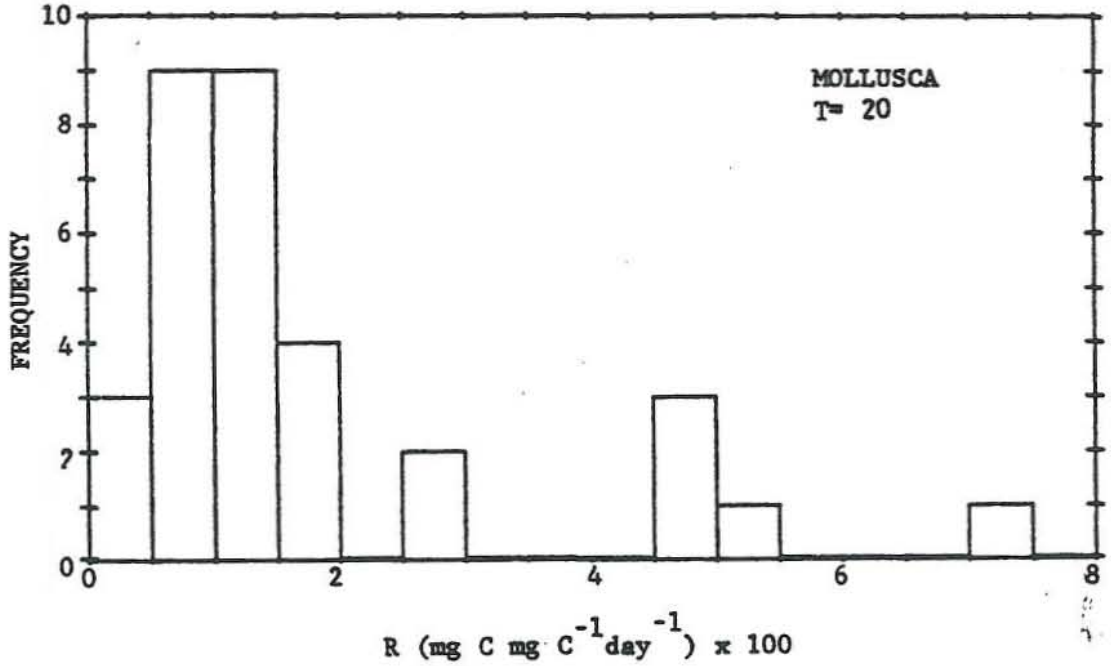

Figure 45. Frequency histogram of respiration rates for Mollusca. Based on data in Appendix D, Part I. T = temperature (°C)

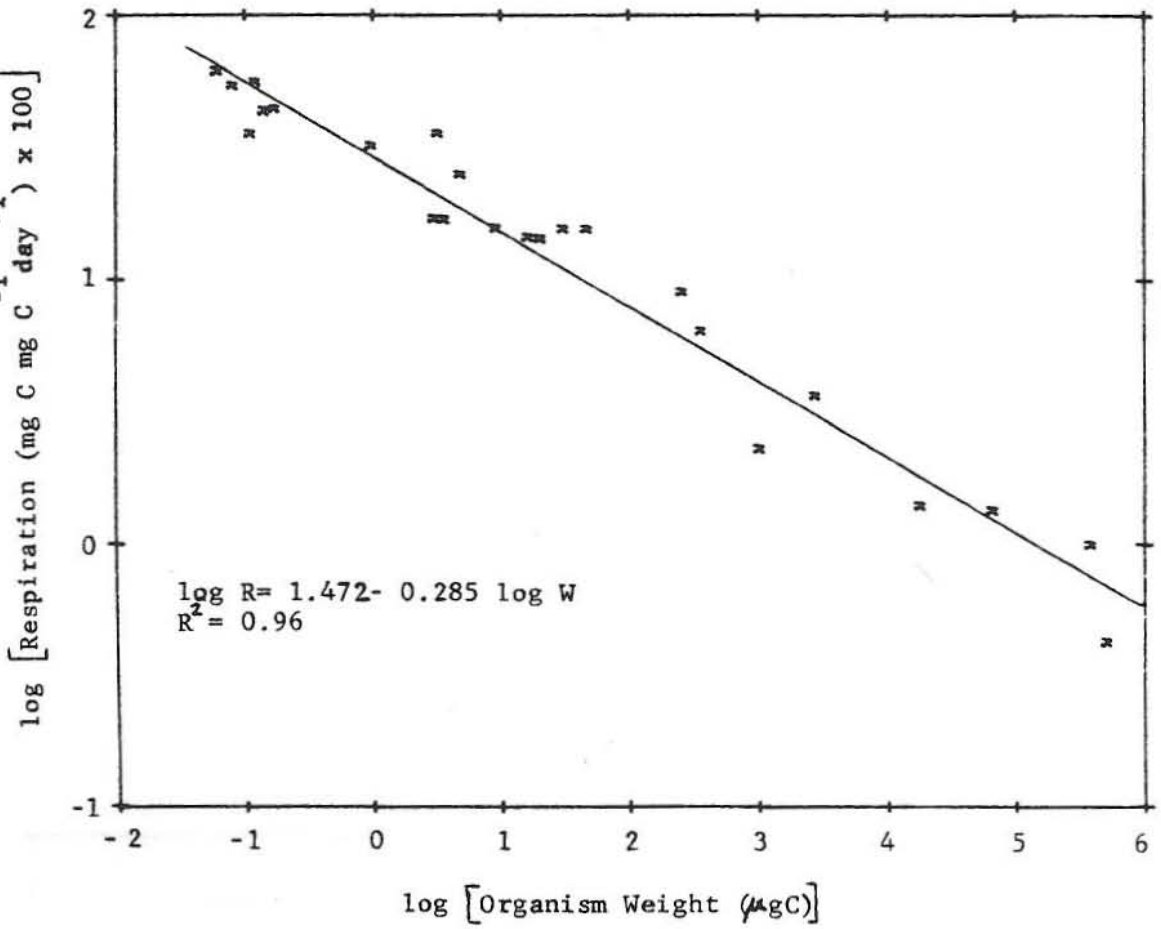

Figure 46. Respiration (R) as a function of organism weight (W) for aquatic invertebrates at 20°C. Based on data in Appendix D, Part I

where Y = respiration rate (mg C/day), W = weight (mg C), and a and b are constants. To obtain weight-specific respiration (R), both sides of Equation 23 must be divided by the specimen's weight:

$$Y/W = aW^b/W \text{ to yield:}$$

$$Y/W = R = aW^{b-1} \qquad (24)$$

where R = weight-specific respiration (mg carbon·mg carbon^{-1}·day^{-1}). Appendix D, Part II, is a tabulation of equations relating weight-specific respiration to body weight for various taxa of aquatic

invertebrates. Weight distributions for various aquatic taxa could be used in these respiration equations to stochastically describe the effects of body size on respiration. Unfortunately, weight distributions for aquatic invertebrates are virtually nonexistent, owing to the dynamic nature of such distributions and to technical difficulties associated with measuring the dry weights of small individuals.

272. Since young animals of large species overlap in size with adults of smaller species, the use of taxonomic categories may be unjustified to separate animals into groups according to their rates of respiration. To justify using taxonomic categories, one must perceive each taxon as a group of a static mean weight, rather than as a continuum of weights. Perhaps a more realistic approach is to classify all species according to weight, without regard to their phylogenetic affinities. We originally formed six weight classes of aquatic invertebrates but later reduced the number to three, since the mean rates of the three heaviest groups were essentially identical. The weight range of each class is: $0 <$ Class I < 0.1 mg dry wt (Figure 47); $0.1 \leq$ Class II < 1.0 mg dry wt (Figure 48); $1.0 \leq$ Class III (Figure 49). Class I consisted exclusively of zooplankton and Classes II and III exclusively of benthos.

273. Bertalanffy (1951) classified aquatic invertebrates into three categories based on the value of b exponents (Equation 23). Accordingly, Type 1 animals have metabolic rates proportional to the 2/3 power of their body weight ($b = 0.67$; $b-1 = 0.33$). Since surface area generally is related to the 2/3 power of body weight, Type 1 specimens supposedly have metabolic rates that are directly porportional to surface area. Bertalanffy cited isopod crustaceans as an example of Type 1 organisms. Type 2 animals (mostly insects) have metabolic rates proportional to their body weight (i.e., $b = 1$; $b-1 = 0$). Type 3 organisms, pond snails for example, have b values between 0.67 and 1 (b-1 values between -0.33 and 0). The b-1 exponents in Appendix D (Part II) illustrate the arbitrary nature of Bertalanffy's classification. Many specimens have b-1 exponents between -0.33 and 0 (Figure 50), but there is no significant correlation between taxa and the magnitude of the b-1 exponent in Equation 24.

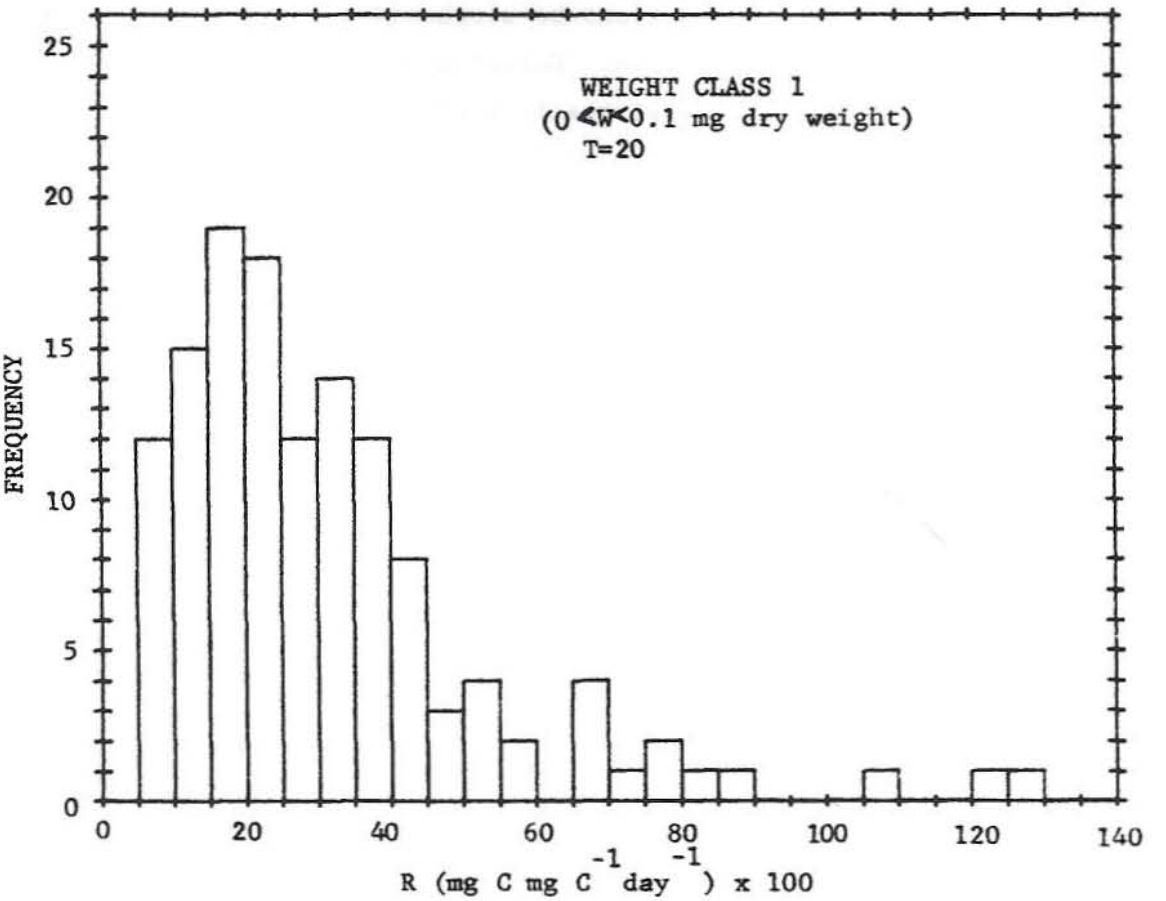

Figure 47. Frequency histogram of respiration rates for aquatic invertebrates of weight class I. Based on data in Appendix D, Part I. T = temperature (°C)

274. The exponent b or b-1 illustrates the effects of body size on oxygen consumption (Bishop 1968) and probably is unrelated to phylogenetic position. Zeuthen (1970) stated that he had always observed invertebrate respiration to be a function of body size, regardless of whether the variation of rates was due to phylogenetic or ontogenetic increases in size. Alimov (Winberg et al. 1973) found similar rates of respiration among molluscs of the same size, although they were of different taxa.

275. Values of b or b-1 (Equations 23 and 24, respectively) are influenced by several factors besides surface area. Knight and Gaufin (1966) found that body shape affected b even when respiration was

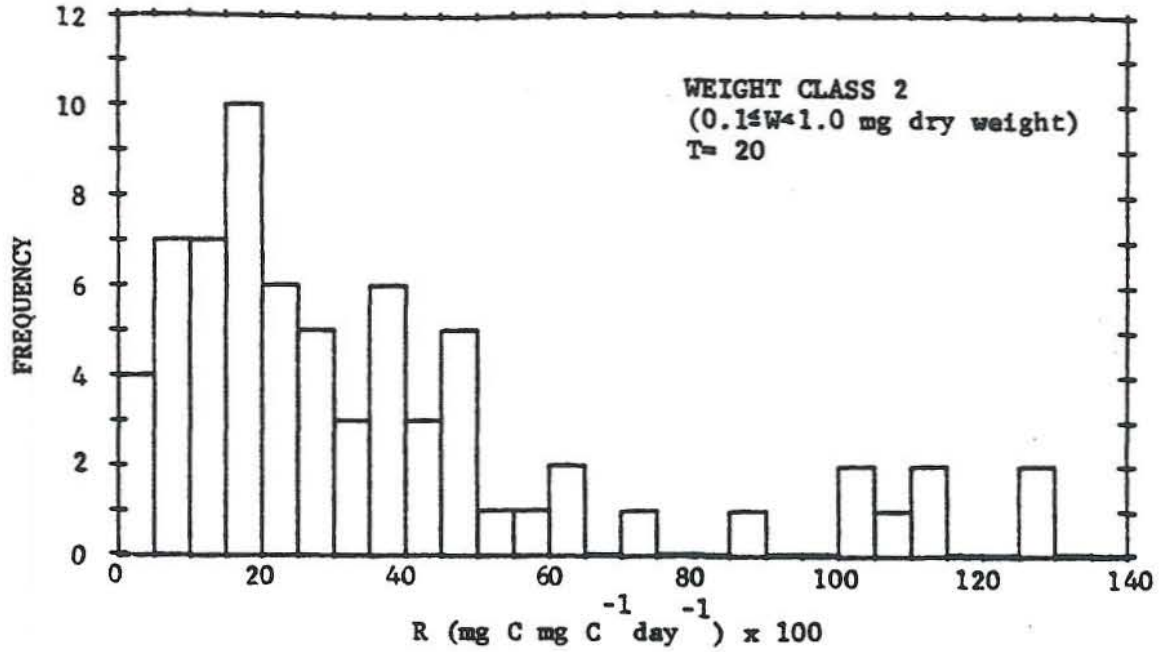

Figure 48. Frequency histogram of respiration rates for aquatic invertebrates of weight class II. Based on data in Appendix D, Part I. T = temperature (^{o}C)

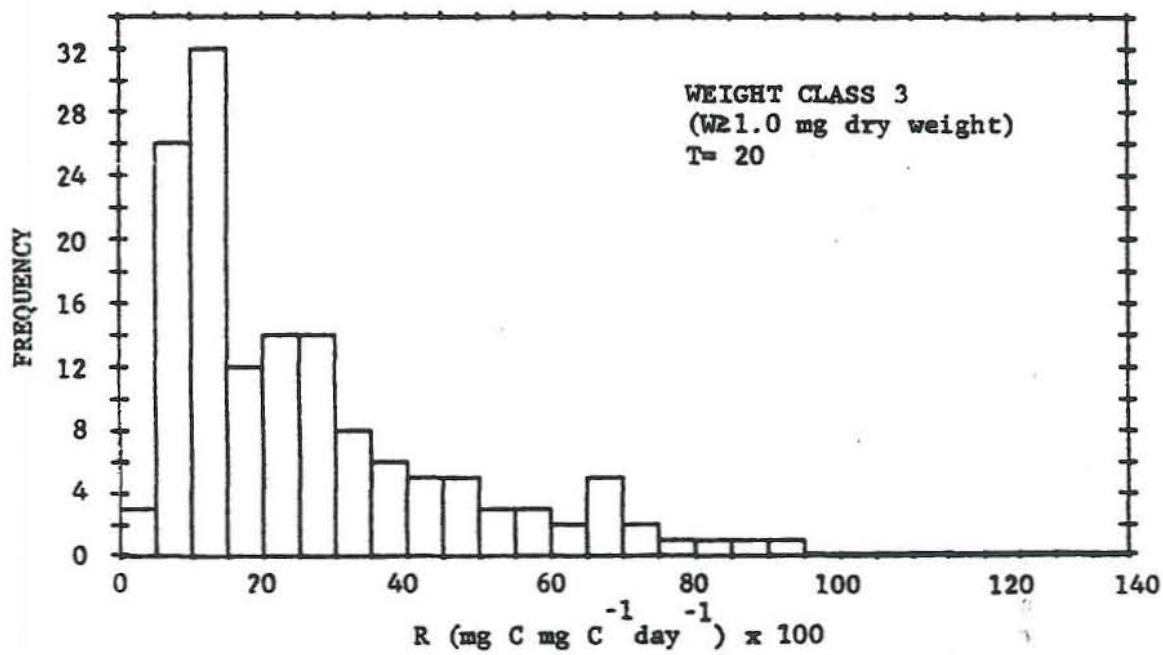

Figure 49. Frequency histogram of respiration rates for aquatic invertebrates of weight class III. Based on data in Appendix D, Part I. T = temperature (^{o}C)

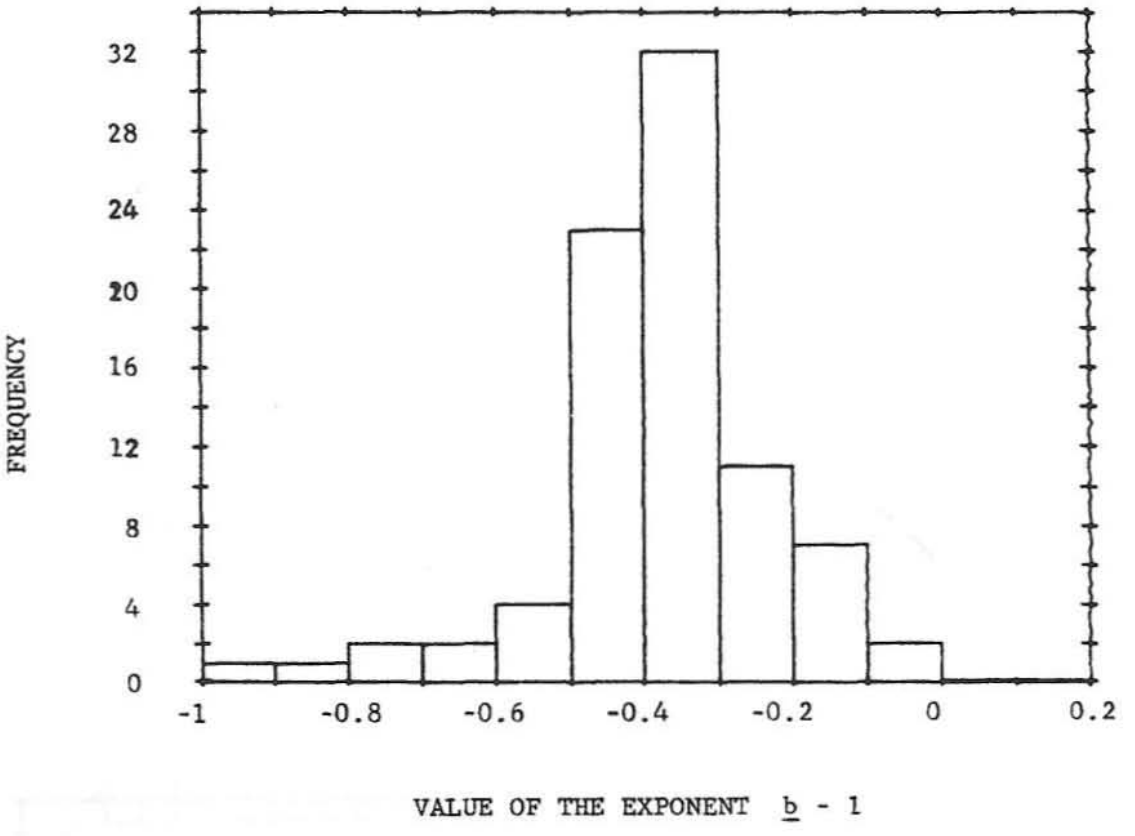

Figure 50. Frequency histogram of the exponent b-1 from the equation: $R = aw^{b-1}$, where R = respiration (mg C·mg C^{-1}·day^{-1}) × 100 and w = weight (mg C)

proportional to surface area. This finding suggested that surface area/volume ratios influence the value of b. The ratio of living to inert protoplasm may affect b exponents (Knight and Gaufin 1966). Calow (1975) found that the b exponents of pond snails were influenced by the type of weight measured (i.e., wet, dry, or ash-free dry weight). Edwards (1957) observed that b had no constant value when wet weight was used as a measure of body size for Chironomus riparius. On the other hand, he found that log transformations of dry weight data suggested that b values were constant. His results further suggested that O_2 consumption was not proportional to surface area, although it varied with dry weight to the 0.7 power. Buikema (1972) determined that b

exponents were higher in unacclimated than in acclimated zooplankton.

276. The relative rates of respiration by animals of equal size is given by the coefficient a in Equations 23 and 24 (Bishop 1968). Several authors (e.g., Comita 1968, Hughes 1970, Calow 1975, Green 1975, Sweeney and Schnack 1977) have correlated a coefficients with temperature. Figure 51 is a frequency histogram of a values for various aquatic invertebrates as tabulated in Appendix D (Part II). Our regression of a coefficients on temperature (Figure 52) was significant ($r^2 = 0.45$; $t_{(0.01,\ 38)} = 5.48$).

277. Frequency distributions of "b-1" and "a" values are of limited utility unless the mean weight of each model compartment is known (e.g., Steele 1974). Nevertheless, we have provided this information with the hope that it will be more useful in the future. Hopefully, when biomass and separation techniques improve for subcategories of zooplankton and benthos, mean biomass will be easier to quantify. Once a mean weight is quantified for a model compartment, the weight can be substituted for W in Equation 24. Randomly selected b-1 and a values, from their respective frequency distributions (Figures 50 and 51), modify W to yield a weight-specific rate of respiration (R). This respiration rate is that of an average individual within the compartment. The product of R and total biomass yields daily respiration for the entire model compartment.

Effects of Dissolved Oxygen Concentration

278. Dissolved oxygen concentrations may significantly affect the rate of respiration of aquatic invertebrates. Two types of animals have been recognized, according to their response to changes in oxygen concentrations (Prosser and Brown 1961). Regulators are able to maintain their metabolic rates at fixed levels, relatively independent of oxygen concentrations. The range over which an animal can regulate varies among species and within species, depending on their physical condition and history of acclimation. Conformers are animals that faithfully track concentrations of dissolved oxygen (i.e., metabolic rates are directly proportional to oxygen concentration).

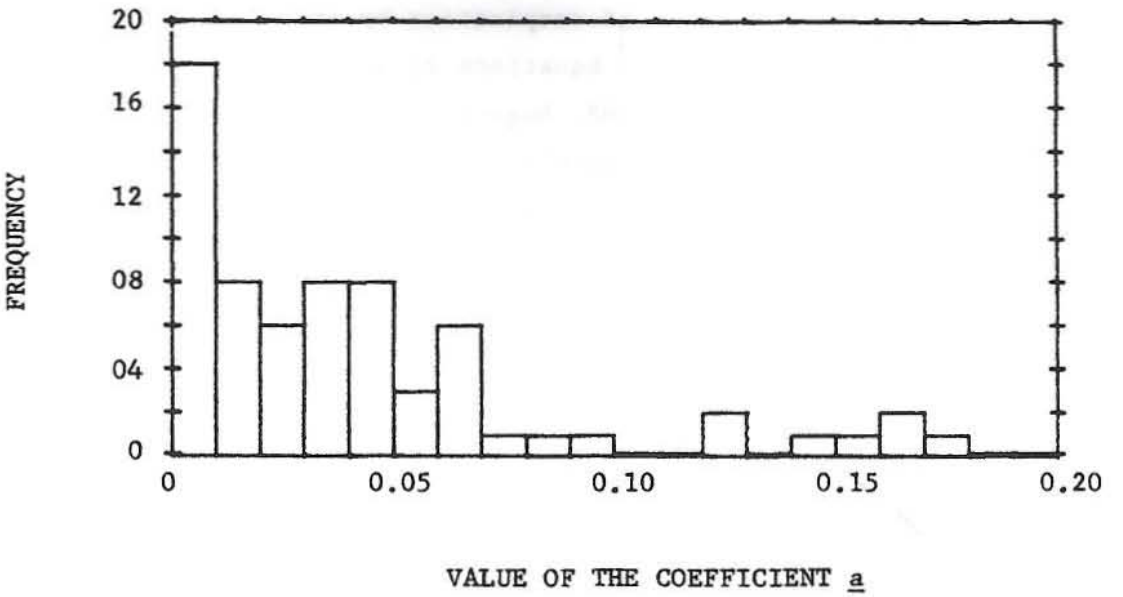

Figure 51. Frequency histogram of the coefficient a from the equation: $R = aw^{b-1}$, where R = respiration (mg C mg $C^{-1}day^{-1}$) × 100 and w = weight (mg C)

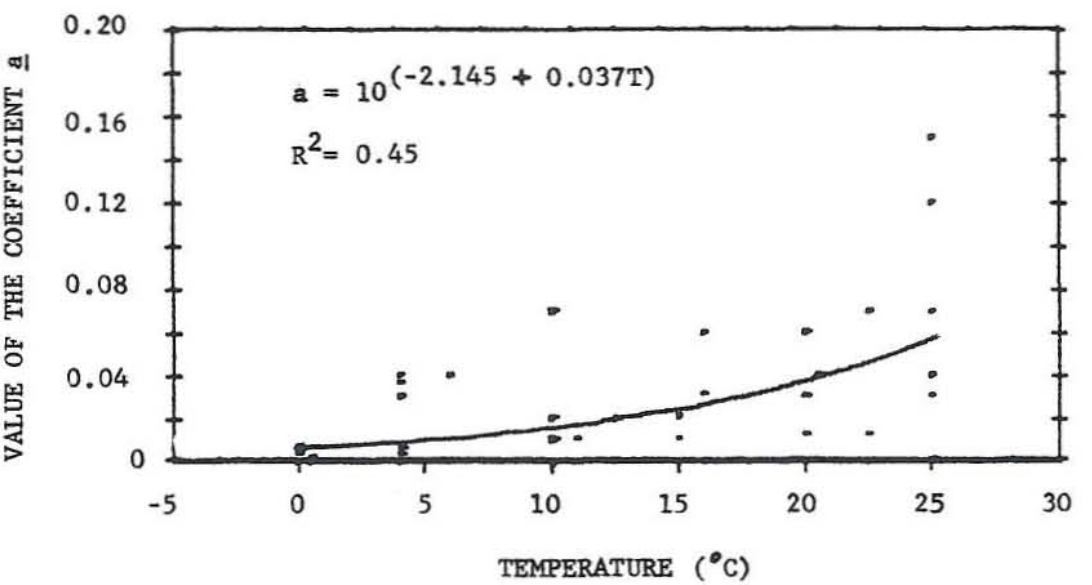

Figure 52. Values of the coefficient *a* as a function of temperature (T) for aquatic invertebrates. Based on data in Appendix D, Part II

279. Whether a species is a conformer or regulator may depend on its history of acclimation to dissolved O_2. In contrast to most conformers that exhibit some degree of regulation at high or low O_2 tensions, the decapod Pacifastacus leniusculus was a conformer over all concentrations of O_2 (Moshiri et al. 1971). Apparently the metabolic response of this species was characteristic of animals living in waters with continually high levels of oxygen. Such organisms would gain little selective advantage by having respiratory systems capable of regulation (Moshiri et al. 1971).

280. Generally, all poikilotherms must conform when concentrations of oxygen fall below a critical level for that species (i.e., the incipient-limiting level of Calow (1975). The gastropods Ancylus fluviatilis and Planorbis contortus were able to regulate down to O_2 concentrations of 4.7 mg/ℓ and 2.7 mg/ℓ, respectively (Calow 1975). Palmer (1968) found that the oligochaete Tubifex tubifex was a regulator down to ca 1.5 percent of saturation. Below this concentration metabolic rates declined sharply. Even diffusion of O_2 into worms at this concentration was insufficient to meet oxygen demands for respiration. Critical concentrations also have been recognized in the ephemeropterans Hexagenia limbata and Ephemera simulans, i.e., 1.2 and 0.80 ml O_2/ℓ (Eriksen 1964). Interestingly, these species regulate when a substrate is provided but conform when none is present. The decapod Caridina fernandoi maintained rates of respiration independent of O_2 concentrations down to approximately 1.4 mg/ℓ (Wycliffe and Job 1977). The oxygen content of water affected the metabolic rate of the copepod Calanus finmarchicus only when it was low (Marshall 1973). Below 3 mg O_2/ℓ, respiration decreased very rapidly (Marshall et al. 1935). Sushchenya (1969) found that the respiration of most Crustacea decreased linearly at O_2 tensions below 20 to 60 percent of saturation.

281. Some aquatic invertebrates are extremely tolerant of low O_2 tensions and exhibit little change in metabolism as O_2 tensions decrease. Chaston (1969) found that Cyclops varicans could withstand deoxygenated water for up to 36 hr by building a lactic acid debt. Respiration rate doubled, however, after specimens were returned to water of normal O_2

tensions. The O_2 consumption of Glyptotendipes polytomus larvae (Chironomidae) was several hundred times lower at low than at high concentrations of oxygen. Tissues of specimens collected from anoxic mud contained traces of lactic acid which indicated that the chironomids had met their metabolic requirements by anaerobic pathways (Kamler and Srokosz 1973).

282. Few models have constructs for the effects of oxygen concentration on respiration, although oxygen often may be limiting to organisms in aquatic ecosystems. Zahorcak (1974) developed the stepwise construct "BEHAVE" which reduced respiration as O_2 concentrations decreased. The function finally reduced respiration to zero when the field concentrations of O_2 fell below the critical level for the compartment.

283. Our oxygen construct decreases the respiration of all invertebrates logarithmically as O_2 tensions decrease. We assumed that most aquatic invertebrates in reservoirs are capable of some degree of regulation over O_2 concentrations in the range of 4 to 14 mg/ℓ. At low concentrations (< ca 4 mg/ℓ), we assumed that most aquatic animals must conform, i.e., exhibit decreased metabolism which is proportional to concomitant decreases in O_2 concentration. When R = 0, the term $\frac{db}{dt}$ in Equation 1: $\frac{db}{dt} = [G(A/G) - R - NPM - PM]$, should not increase significantly because another oxygen construct increases nonpredatory mortality (NPM) when O_2 tensions decrease (see "Oxygen Concentration," page 170, Part VI). Table 15 lists logarithmic equations which describe the relation of respiration to O_2 concentration for several benthic macroinvertebrates. Unfortunately, similar data for zooplankton were few. Data from Appendix D (Part I) for each of the species in Table 15 were corrected to 20°C before regression analysis.

284. Based on the equations in Table 15, we calculated an oxygen-correction factor (F_o) for respiration as a function of ambient concentrations of O_2. We let respiration (R) equal one at 14.6 mg O_2/ℓ (saturation at 0°C and 760 mm Hg) and calculated F_o, according to the last equation in Table 15, for O_2 tensions ranging from 0 to 14.6 mg/ℓ. A curve fitted to these points is described by the equation:

$$F_o = 0.426 + 0.482 \log O_2 \quad (25)$$

where O_2 = O_2 tension (mg/ℓ) and F_o = oxygen correction. Equation 25 is graphically depicted in Figure 53. We assume that R = 0 when O_2 tensions are less than 0.13 mg/ℓ for 24 hr. The product of F_o and weight-specific respiration (from frequency histograms) yields a rate corrected for oxygen effects.

Table 15

Respiration Rates (R) (mg carbon·mg carbon^{-1}·day^{-1}), as a Function of O_2 Concentration (mg/ℓ), for Several Aquatic Invertebrates

Taxon	Equation*	N	R^2
Oligochaeta			
Tubifex tubifex	$R = 0.124 + 0.0062 \log O_2$	5	0.78
Plecoptera			
Tarniopteryx nubulosa	$R = 0.010 + 0.0400 \log O_2$	5	0.98
Nemoura cinerea	$R = 0.023 + 0.0380 \log O_2$	5	0.93
Dirua nanseni	$R = 0.002 + 0.0410 \log O_2$	5	0.83
Ephemeroptera			
Cloeon dipterum	$R = 0.025 + 0.0230 \log O_2$	4	0.95
Crustacea			
Pacifastacus leniusculus	$R = -0.002 + 0.023 \log O_2$	8	0.83
Mean of constants	$R = 0.030 + 0.0370 \log O2$	6	
SE of means	±0.092; ±0.016		

* Equations were calculated from data of Palmer (1968), Nagell (1973), and Moshiri et al. (1970).

285. Due to insufficient data for zooplankton, we were unable to calculate another O_2 correction. Inasmuch as the data of Marshall et al. (1935) and Sushchenya (1969) show that the relation of zooplankton respiration to O_2 concentration is similar to that for benthos (Table 15), we decided to use Equation 25 for all aquatic invertebrates.

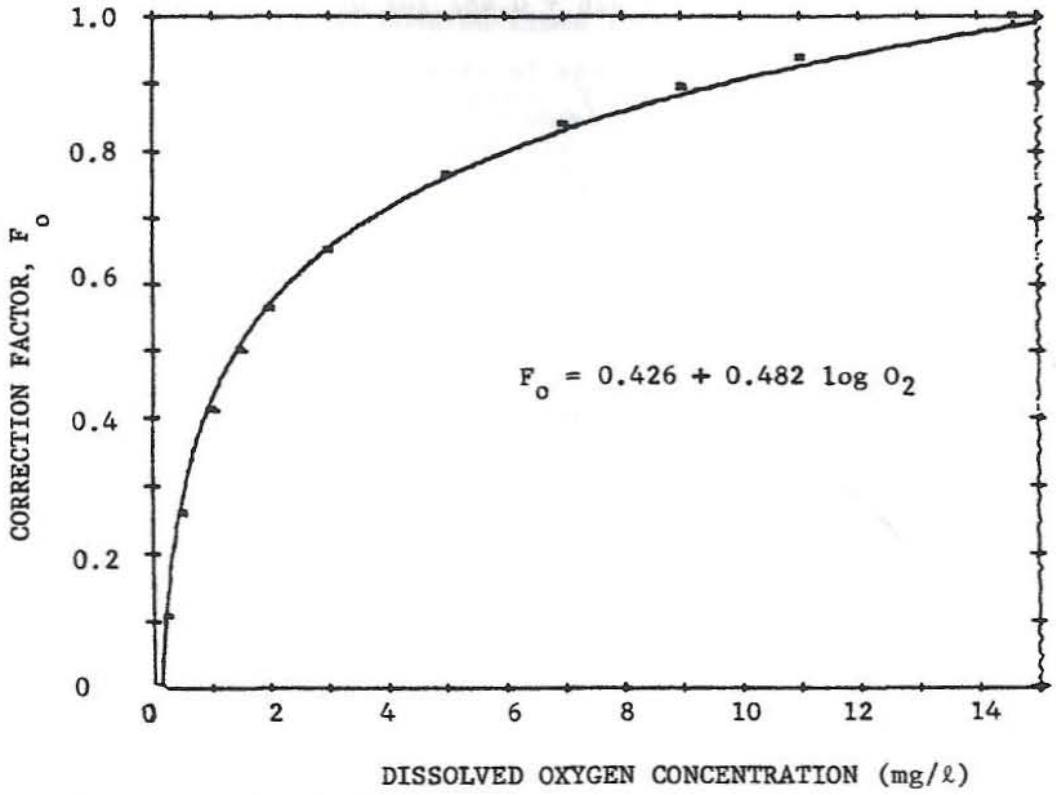

Figure 53. Respiration correction factor (F_o) as a function of dissolved oxygen concentration. Based on equations in Table 15

286. The oxygen correction (F_o) was derived from very limited information and should be treated with caution. Until further research is conducted, especially on the effects of O_2 tensions on zooplankton respiration, constructs like ours and that of Zahorcak (1974) are state of the art. Although such constructs greatly simplify known effects, we believed that some effort should be made to approximate this important relation.

Effects of Temperature

287. Temperature probably affects the respiration of aquatic ectotherms more than any other single factor. Temperature explained 56 percent of the variation in the respiration of the mayfly Isonychia

bicolor (Sweeney 1978). The amounts of variation in respiration explained by temperature ranged from 49 to 79 percent for the copepod Diaptomus sp. (Comita 1968) and from 46.2 to 98.8 percent for the stonefly Acroneuria californica (Heiman and Knight 1975). Larow et al. (1975) found that roughly 34 percent of the variance in zooplankton rates was explained by temperature.

288. Respiration rates usually increase exponentially with increases in temperature until upper lethal temperatures are reached. For example, the metabolism of the coleopteran Dineutes indicus was slow at low temperatures, increased rapidly with increasing temperature, and then suddenly decreased as upper lethal temperatures were approached (Tonapi and Rao 1977). Ivanova (1972) noted similar temperature effects on all instars of the amphipod Gammaracanthus lacustris. Ivanova also noted a sharp decline in rates at upper lethal temperatures (15° to 18°C). Blazka (1966), Comita (1968), Moshiri et al. (1971), Gophen (1976), and others (Appendix D, Part II) noted similar relationships of metabolism to temperature.

289. Equations that predict rates of respiration at different temperatures, e. g., Q_{10} functions (Prosser and Brown 1961) and Krogh's normal curve (Krogh 1914), are reasonably accurate for many aquatic ectotherms. Better still are the predictive equations derived specifically for one species (See Appendix D, Part II). Nevertheless, deviations from predicted rates do occur (Conover 1962, Sushchenya 1969, Hughes 1970, Marshall 1973, Roff 1973). Most often, deviations result from acclimation or compensation.

290. Acclimation was defined by Prosser and Brown (1961) as the ability of ectotherms to maintain respiration rates independent of temperature within narrow ranges. Buffington (1969) defined acclimation as a shift in metabolic rate from that which would be predicted on the basis of purely physical and chemical processes. Acclimation has been observed in many aquatic invertebrates, for example, Mollusca (Calow 1975, Burkey 1971), Decapoda (Moshiri et al. 1971), Diptera (Buffington 1969), Copepoda (Conover 1962, Suschenya 1969, Ostapenya et al. 1969, Marshall 1973), and Cladocera (Blazka 1966, Moshiri et al. 1969).

Although the capability of temperature acclimation apparently is common among aquatic invertebrates, it is not universal and varies with sex (Moshiri et al. 1969) and among species based on genetic differences.

291. Because temperature greatly influences respiration, constructs are imperative for models of aquatic systems where temperature fluctuates seasonally. Respiration was considered to be a linear function of temperature in models by DiToro et al. (1971) and Baca et al. (1974). More often, an exponential function is used to describe the relation of respiration to temperature (Umnov 1972, Patten et al. 1975, Chen and Orlob 1975, Scavia et al. 1976). An exponential form that is widely used for ecological work is the Q_{10} function (Prosser and Brown 1961). This function is the ratio of two rate constants for respiration at temperatures 10°C apart. A typical equation is $k_2 = k_1 Q_{10}^{(T_2 - T_1)/10}$, where k_2 is a rate constant at T_2 (2nd temperature) and k_1 is a rate constant at T_1 (1st temperature). By knowing T_1, k_1, and the Q_{10} for the temperature range T_1 to T_2, k_2 may be calculated for the second temperature (Lassiter 1975). Krogh's normal curve (Krogh 1914) has been used to describe respiration-temperature relations for many aquatic ectotherms and may be approximated by a set of Q_{10} coefficients (Winberg 1956). MacCormick et al. (1974), Park et al. (1974), and Zahorcak (1974) in the Eastern Deciduous Forest Biome models (International Biological Program) used a respiration-temperature function in which respiration increased exponentially with temperature to an optimum and then decreased as temperatures approached upper tolerance limits. They also used Q_{10} values.

292. Our construct for the relation of respiration to temperature is bascially exponential, with the added assumption that respiration rate drops to zero when the upper lethal temperature (34°C) is reached. The construct is essentially a Krogh curve (Krogh 1914, Winberg 1956), but was calculated from the data tabulated in Appendix D (Part I). Rates of respiration for aquatic invertebrates, regardless of taxon or size, were selected from Appendix D, Part I. The criterion for selection was the availability of estimates of metabolic rates at a minimum of three experimental temperatures. Rates of these specimens were averaged for each temperature and plotted (Figure 54). The curve fitted to these points

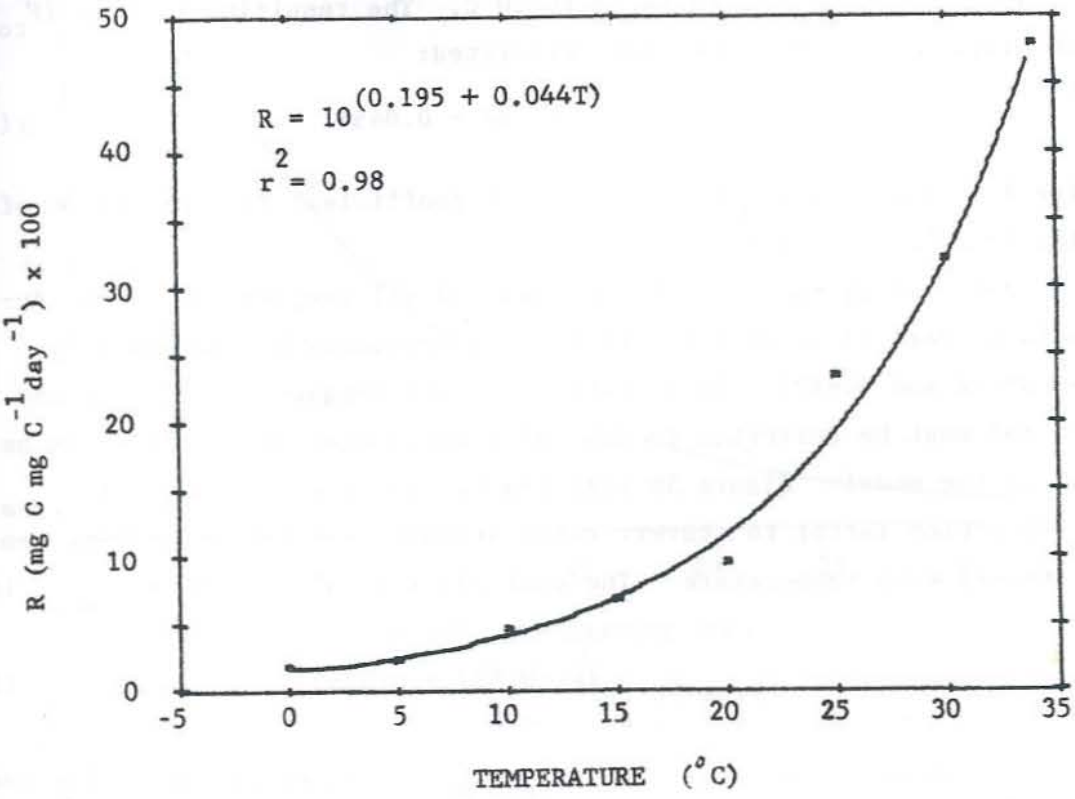

Figure 54. Mean rates of respiration (R) as a function of temperature (T) for aquatic invertebrates. Based on data in Appendix D, Part I

has the form $R = 10^{(0.195 + 0.044T)}$ ($r^2 = 0.98$), where T is temperature (°C) and R is respiration rate [(mg carbon·mg carbon^{-1}·day^{-1}) × 100].

293. The variance of mean rates of respiration at different temperatures (Figure 54) was high. Most of the variation resulted from size differences among selected taxa. For example, Brachionus rubens Rotatoria ($\bar{x}$ - dry weight = 7.6×10^{-5} - 1.4×10^{-4} mg, Pilarska (1977c)) had weight-specific rates that were ca 60 times those of Ferrissia rivularis Mollusca ($\bar{x}$ - dry weight = 1.38 - 1.62 mg, Burky (1971)). For this reason, we were interested in the shape of the curve and not the predicted rates themselves.

294. To obtain coefficients that would permit the conversion of rates in Appendix D (Part I) to rates at 20°C, we assigned the value of one to the respiration rate at 20° (Figure 54) and calculated the appropriate temperature correction ($F_{\text{to } 20}$), to convert rates at 0°, 5°,

10°, 15°, 30°, and 34°C to rates to 20°C. The resulting factors ($F_{to\ 20}$) were plotted, and the curve was calculated:

$$F_{to\ 20} = 0.887 - 0.045T \quad (26)$$

where T = temperature (°C) and $F_{to\ 20}$ = coefficient for correction of rates to 20°C (Figure 55).

295. Using Equation 26, we adjusted all respiration rates (Appendix D, Part I) to 20°C before forming frequency histograms (Figures 39-41 and 43-49). Thus, rates from any frequency histogram are at 20°C and must be corrected to ambient temperatures before they can be used in the model. Figure 56 illustrates the rate of change of $F_{from\ 20}$ (a correction factor to convert rates at 20°C to rates at ambient temperatures) with temperature. The equation for calculating $F_{from\ 20}$ is:

$$F_{from\ 20} = 10(-0.887 + 0.045T) \quad (27)$$

where T = ambient temperature and $F_{from\ 20}$ = correction factor for temperatures at 20°C. At the same temperature, the factor $F_{from\ 20}$ is the reciprocal of $F_{to\ 20}$. The product of weight-specific rates of respiration (from frequency histograms) and $F_{from\ 20}$ yields a weight-specific rate which is corrected for temperature effects.

Summary of Constructs

296. Weight-specific rates of respiration (R) at 20°C may be obtained from frequency distributions of rates for major taxa of zooplankton and benthos (Figures 39-41 and 42-45, respectively) or from similar distributions for three weight classes of aquatic invertebrates (Figures 47-49). Selected rates must be modified to rates at ambient temperatures and oxygen concentrations. Modification is accomplished by multiplying R by $F_{from\ 20}$ (temperature correction from Equation 27) and by F_o (oxygen correction from Equation 25). Respiration is set to zero when temperatures are below zero or above 34°C for 24 hr. Similarly, R = 0 when oxygen concentrations fall below 0.13 mg/ℓ for 24 hr. When R

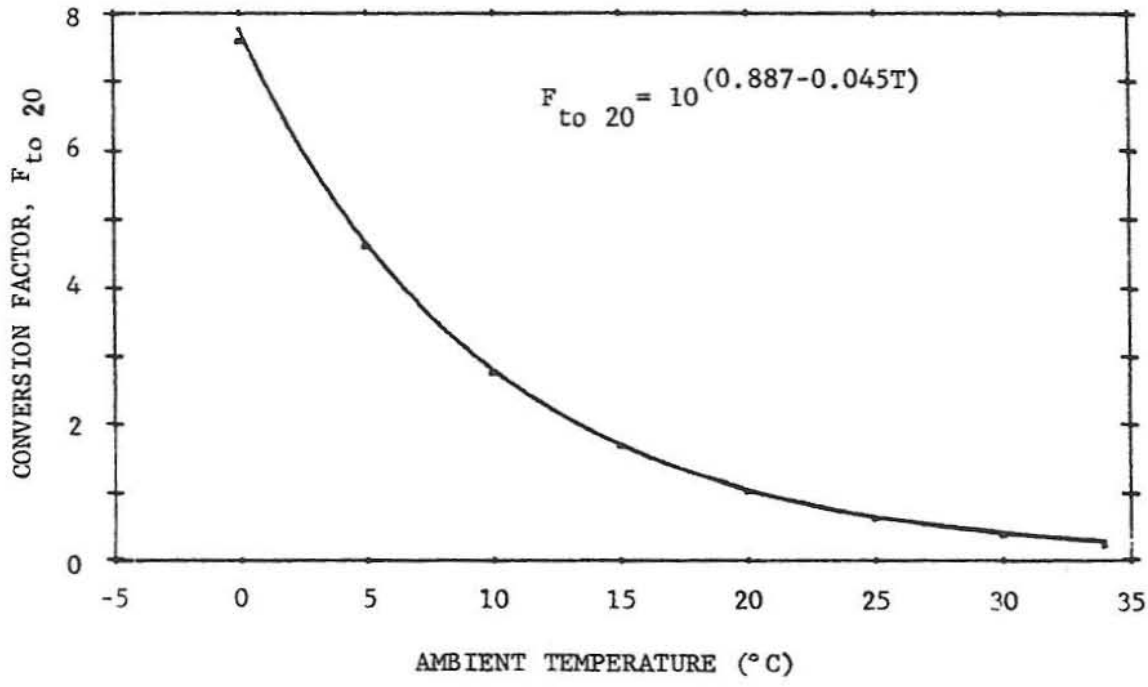

Figure 55. The conversion function, $F_{to\ 20}$, for adjusting respiration rates (R) at ambient temperatures to rates at 20°C

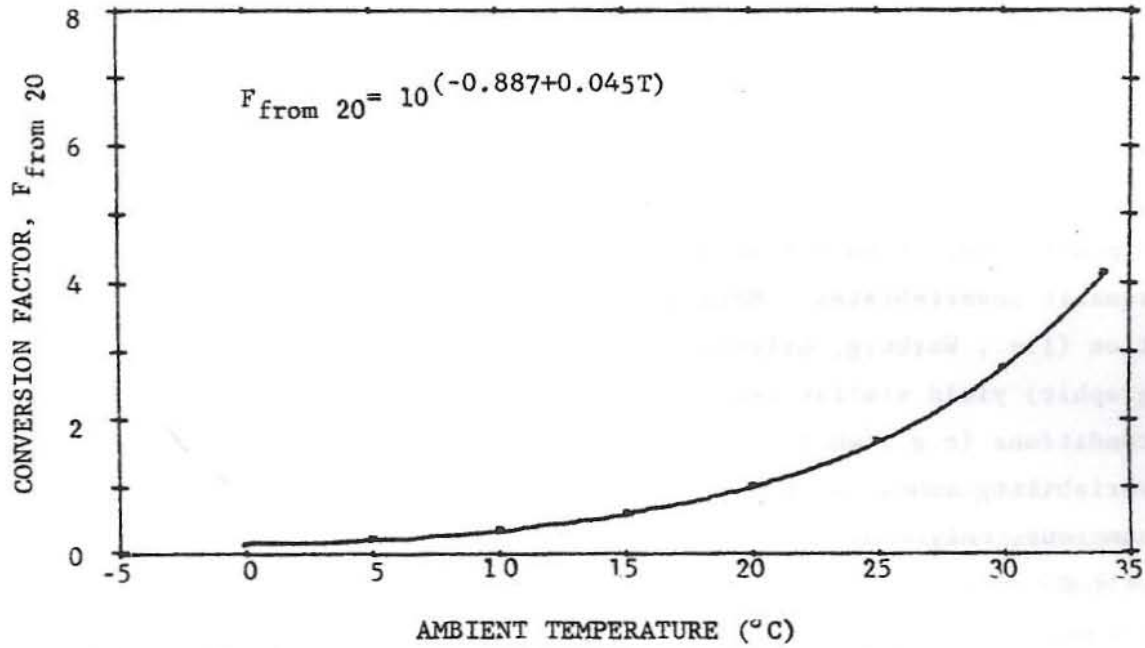

Figure 56. The conversion function, $F_{from\ 20}$, for adjusting respiration rates (R) at 20°C (i.e., respiration histograms) to rates at ambient temperature

(mg carbon·mg carbon^{-1}·day^{-1}), corrected for the effects of temperature and oxygen concentration, is multiplied by the initial biomass of the model compartment, the result is the total carbon respired by the compartment daily. According to Equation 1, respiration rates should be subtracted from assimilated carbon: $\frac{db}{dt} = b\ [G(A/G) - R - NPM - PM]$.

297. Because we had no realistic way to apportion total benthic biomass among smaller taxonomic compartments, respiration rates should be selected from a probability distribution formed from Figures 48 and 49. Rates for zooplankton may be obtained from Figure 47, which was formed exclusively from zooplankton data, or from Figures 39-41 if the users wish to divide the zooplankton compartment. When the compartment is divided, zooplankton biomass should be assigned as follows: Cladocera = 60 percent, Copepoda = 35 percent, Rotatoria = 5 percent (when no better data are available). Copepod respiration rates at 20°C, for example, may be calculated as 0.35b(R), where b = total zooplankton biomass (mg carbon) and R = weight-specific respiration at 20°C (Figure 40). The sum of this result and similar results for Cladocera and Rotatoria represents total zooplankton respiration at 20°C.

Conclusions

298. Because respiration constitutes a major portion of energy expenditures, it is a very important parameter in the energy budgets of aquatic invertebrates. Methods employed to determine rates of respiration (i.e., Warburg, Gilson, Cartesian diver, chemical, and polarographic) yield similar results, but differences in experimental conditions (e.g., whether specimens are fed or acclimated) increase variability among rates. Though factors potentially affecting rates are numerous, only body size, O_2 concentration, and temperature effects were well documented by published data. Apparently, these effects account for most of the variability among respiration rates in field populations.