To the Graduate Council:

I am submitting herewith a thesis written by Cynthia M. Lovelock entitled "The Effect of Temperature and Dissolved Oxygen on a Model Fish Population." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Mathematics.

Thomas Hallam, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

THE EFFECTS OF TEMPERATURE AND DISSOLVED OXYGEN ON A MODEL FISH POPULATION

A Thesis

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Degree

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Abstract

Environmental and chemical stressors affect the physiological processes of aquatic organisms in many ways. The effects of changes in temperature and dissolved oxygen concentration on the dynamics of a model fish population are the primary focus of this research. Also discussed is the effect of a nonpolar, lipophilic narcotic administered at a level slightly below the lethal concentration (LC_{50}) for two-year simulation periods. Temperature and dissolved oxygen concentration ranges for persistence of the population are given for a number of different scenarios, including simulations with the presence of a toxicant.

The result of the study of the individual dynamics was that optimal growth for an individual occurred at a temperature of $18°C$ and for dissolved oxygen concentrations greater than 7.84 $\frac{mg}{l}$. The initial simulations for use in studying the population dynamics demonstrated the differences in optimal temperatures and dissolved oxygen concentrations for the population as opposed to the individual as well as the importance of allowing the temperature to fluctuate with the time of year. The population was able to persist in a fluctuating temperature environment for dissolved oxygen concentrations above 4.3 $\frac{mg}{l}$. With the addition of a toxicant for a two-year simulation, the population persisted in the same range of dissolved oxygen concentrations, with the exception of some of the ecotypes in the first age class, who went to extinction.

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1 Introduction

A model that is individually-based is essential to study effects at the population level because, for the most part, environmental variables, such as temperature and dissolved oxygen concentration, affect the physiological processes of individuals, not the behavior of the population as a whole. It is only after the effects on the physiological processes at the individual level have been assessed and the individuals combined to form a population that a study of the dynamics of the population is viable.

In this paper, the individually-based model for a female fish developed by Hallam et. al [24] is modified to include the effects of changes in temperature and concentration of dissolved oxygen on three physiological processes at the individual level and one parameter at the population level. After these modifications have been implemented, the model will serve as part of the ecological portion of a set of models that will be used to assess the state of Fort Loudoun Lake in Knoxville, Tennessee.

Temperature Effects. The importance of the adaptation of fish to temperature changes is well documented. Temperature is considered one of the most critical environmental factors affecting the success of fish [1], [7], [12], [28]. It has a direct effect on spawning, egg and larval development, activity, feeding, and, in general, on the growth of fry and older life stages [1]. Experimental studies have shown that increasing the temperature of the environment increases the respiratory metabolism and

maintenance requirements of fish. The increase in activity also leads to an increase in feeding [7], [34]. Gray's study of brown trout states that adult mortality is high for temperatures above $20°C$ and complete for temperatures above $25°C$ [22]. The upper lethal temperature for one- and two-year lake trout was estimated at $23.5°C$ [21]. The literature demonstrates the importance of adding temperature effects to the fish model.

Dissolved Oxygen Effects. In addition to the effects that excessively low and high temperatures can have on fish, the level of dissolved oxygen also plays an important role. "Of the many pollutional changes of water quality that can affect freshwater fisheries adversely, none is generally believed to be more common and important than is the reduction of dissolved oxygen" [13]. Davis and Doudoroff et al. present information and sources for a number of different species of fish which indicate how reduced levels of dissolved oxygen can have undesirable effects on physiological processes, including feeding, swimming ability, repiration, activity, fecundity and spawning activity [11], [13]. In Garside's studies of the effect of oxygen on the embryos of brook, rainbow, and lake trout, the data demonstrate that reduced levels of dissolved oxygen inhibit the developmental rate of the embryos and the time to hatching increases as well as the appearance of the various developmental stages [16], [17]. Other experimental studies on the embryos and larvae of various species also indicate that the size

at hatching, the initial feeding, the percentage of larvae that survive to the juvenile period, and, in general, the growth of embryos, are affected by the level of dissolved oxygen [9], [13], [38], [46]. Symptoms of oxygen distress are exhibited by salmonids at a dissolved oxygen concentration of approximately 6.00 $\frac{mg}{l}$ at a temperature of $15°C$; for salmonid larvae, oxygen distress is observed beginning at a level of 8.09 $\frac{mg}{l}$ at a temperature of $9°C$ [11]. The importance of the effect of dissolved oxygen on the physiological processes of fish is apparent.

1.1 Review of an Individual Fish Model

In this section, an overview of an individual fish model, employed as the reference model, is presented. For a more detailed look at the life history of a fish and the associated model, see the manuscript by Hallam et. al [24]. With the exception of the changes to the different parameter values of the processes discussed in Section 2, the model described in this paper is identical to the reference model [24]. Previously, the nominal parameter values were constants chosen from rainbow trout data with a temperature range of 11 to $15°C$ in mind; the relevant parameter values are now replaced with functions of the physical variables temperature and dissolved oxygen.

The mathematical model employed in [24] is based on the energetics of an individ-

ual female fish (see Figure 1) [1]. Each organism is composed of two major components, lipid and structure (protein and carbohydrates), each component consisting of a labile and a nonlabile portion. The dynamics of an individual fish are represented by ordinary differential equations which give the rates of change of the mass of lipid and the mass of structure, denoted respectively by m_L and m_S (g). These rates are determined by the difference in the inputs and the outputs. The inputs are represented by the growth of the lipid and structure compartments whereas the outputs are the losses from these compartments. Growth of lipid and structure of a fish is obtained from feeding on a constant level of resource which also has lipid and structure components, the densities of which are denoted by x_L and x_S $(\frac{g}{cm^3})$. The amount of resource that can be converted to viable energy is based on the assimilation efficiencies of the lipid and structure, represented by A_{0L} and A_{0S} (nondim) in the model. The losses consist of lipid and structure allocation for egg production and energy allocation for maintenance, work (activity), and reproduction. Maintenance and activity losses occur on a continuous time scale; reproductive losses are discrete and occur periodically.

The life history of a female fish is followed from the deposition and fertilization of the eggs to when the fish eventually dies. There are two sets of differential equations describing two stages in the life of a fish. The first set is for the growth during the

[1] All Figures and Tables appear in the appendix.

embryonic stage. At age 0, an egg which has the initial component weights

$$m_S(0) = m_{S_0},\ m_L(0) = m_{L_0} \tag{1}$$

is deposited and fertilized. During the first 51 days, the eggs will hatch and survive on the nutrients of the yolk sac [36], [39]; however, since the fry are not feeding during this period, they actually decrease in size. The change in mass of lipid and structure is therefore represented by

$$\frac{dm_L}{dt} = -B_1 m_L \tag{2}$$

$$\frac{dm_S}{dt} = -B_2 m_S \tag{3}$$

where B_1 and B_2 are the compartmental rate coefficients in units of $(\frac{1}{d})$.

The fry begin to feed after the 51 days have passed. This is the next stage in the life of the organism and there are a new set of differential equations to describe the growth process:

$$\frac{dm_L}{dt} = \frac{A_{0L}x_L}{[a_d]^{-1} + [\frac{s_d}{M_p \delta v} + [kM_g]^{-1}]x} - \begin{cases} A_3(m_L - \epsilon m_{PS}) & \text{for } D > E \\ A_3(m_L - \epsilon m_{PS})\frac{D}{E} & \text{for } D \leq E \end{cases} \tag{4}$$

$$\frac{dm_S}{dt} = \frac{A_{0S}x_S}{[a_d]^{-1} + [\frac{s_d}{M_p \delta v} + [kM_g]^{-1}]x} - \begin{cases} A_4(m_L - m_{PS}) & \text{for } D > E \\ A_4(m_L - m_{PS})\frac{D}{E} & \text{for } D \leq E \end{cases} \tag{5}$$

where the initial conditions are given by the terminal conditions from the embryonic stage equations (1), (2), (3). In the above equations, m_L, m_S, A_{0L}, A_{0S}, x_L, x_S are

defined as previously; $x = x_L + x_S$ $(\frac{g}{cm^3})$; M_p is the mass of the prey (g); s_d is the reactive distance of the fish (cm) given by $s_d = [aL_p+b]L_f^{0.5}$ where L_f and L_p represent the lengths of the fish and prey (cm) and a $(cm^{-0.5})$ and b $(cm^{0.5})$ are constants; a_d is the encounter rate coefficient $(\frac{cm^3}{d})$ given by $a_d = 8.64 \cdot 10^4 \pi s_d^2 (v_p^2 + 3v_h^2)/3v_h$; v_p is the prey velocity $(\frac{cm}{s})$ given by $v_p = s_p \cdot L_p$ where s_p denotes the body lengths per second of the prey; v_h is the fish velocity $(\frac{cm}{s})$ while hunting for prey given by $v_h = s_h \cdot L_f$ where s_h denotes body lengths per second of the fish while hunting; δv $(\frac{cm}{d})$ is the difference in the pursuit velocity of the fish and the escape velocity of its prey given by $\delta v = 8.64 \cdot 10^4 (v_c - v_p)$ where $v_c = s_c \cdot L_f$ $(\frac{cm}{s})$; k is the gut clearance rate coefficient $(\frac{1}{d})$; M_g is the mass capacity of the fish's gut (g) which is given by $M_g = \rho_p \cdot V_g$ where ρ_p is the body density of the prey (dry weight) and V_g (cm^3) is the volume of the fish's gut given by $V_g = c \cdot m_{PS}$; c is a constant with units of $(\frac{cm^3}{g})$. A_3 is the labile lipid mobilization rate $(\frac{1}{d})$; A_4 is the labile structure mobilization rate $(\frac{1}{d})$; m_{PS} is the mass of the protected structure (nonlabile) (g) given by $m_{PS} = \alpha m_S$ where α is a constant fraction; ϵm_{PS} is the nonlabile lipid (g) where ϵ is a dimensionless parameter which gives the ratio of nonlabile lipid to nonlabile structure; D is the total energy demand (J); and E is the available energy (J). Available energy is determined by

$$E = 3.768 \cdot 10^4 A_3 (m_L - \epsilon m_{PS}) + 1.675 \cdot 10^4 A_4 (m_S - m_{PS}).$$

The growth of each organism is described by equations (4) and (5) until reproduc-

tion occurs after maturation size is reached. At the time when reproduction occurs, discrete losses of labile lipid and structure associated with reproduction are subtracted from m_L and m_S. The organism then begins to grow again according to (4) and (5) with the initial conditions on m_L and m_S reset to the values after the reproductive losses have occurred. This process is repeated periodically, with reproduction occurring every year as long as the organism has sufficient lipid and structure to produce eggs, until death occurs.

In order to explain where the temperature and dissolved oxygen effects will be incorporated later, it is necessary to go into more detail about the different components of the differential equations (4) and (5).

The expression for a single predator feeding upon a single prey is given by

$$F = \frac{x}{[a_d]^{-1} + [\frac{s_d}{M_p \delta v} + [kM_g]^{-1}]x}, \tag{6}$$

where all of the parameters are defined as in equations (4) and (5). Notice that

$$\frac{A_{0L}x_L}{x}F, \frac{A_{0S}x_S}{x}F$$

are the growth rate inputs to the lipid and structure compartments as in (4) and (5). Dividing the numerator and denominator of (6) by x yields

$$F = \frac{1}{[a_d x]^{-1} + \frac{s_d}{M_p \delta v} + [kM_g]^{-1}}$$

which can also be written as

$$F = \frac{1}{T_e + T_p + T_d} \tag{7}$$

where T_e is the characteristic time to encounter ($\frac{d}{g\ encountered}$), T_p is the characteristic time for pursuit ($\frac{d}{g\ captured}$), and T_d is the characteristic time for digestion ($\frac{d}{g\ cleared}$).

The equation for the energy allocated for maintenance is

$$E_M = A_7 m_L + A_8 m_S. \tag{8}$$

A_7 and A_8 are constants in ($\frac{J}{g \cdot d}$) which represent the energy to maintain 1 g of lipid and structure, respectively.

1.2 Population Dynamics

To study the dynamics of the population, the individual growth model is incorporated into a system of hyperbolic partial differential equations of McKendrick-von Foerster type:

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \frac{\partial(\rho \cdot g_L)}{\partial m_L} + \frac{\partial(\rho \cdot g_S)}{\partial m_S} = -\mu\rho \tag{9}$$

where $\rho = \rho(t, a, m_L, m_S)$ in numbers per age, per mass of lipid, per mass of structure, per volume of environment, is the population density function, a represents age, g_L and g_S are the growth rates ($\frac{g}{d}$) of the individual lipid and structure compartments, respectively, μ, which is a function of ρ, is the mortality rate ($\frac{1}{d}$) and the remaining

parameters are as defined previously. While the mortality rate is given explicitly in the differential equation, the birth process is specified by a boundary condition

$$\rho(t, 0, m_{L_0}, m_{S_0}) = \int\int\int \beta(t, a, m_{L_0}, m_{S_0}, m_L, m_S)\rho(t, a, m_L, m_S)da\ dm_L\ dm_S$$

where β is the birth function representing the number of eggs with lipid content m_{L_0} and structure content m_{S_0} born to an individual of age a with lipid content m_L and structure content m_S at time t. Using the method of characteristics, (9) reduces to the following system of ordinary differential equations

$$\frac{da}{d\tau} = 1$$

$$\frac{dt}{d\tau} = 1$$

$$\frac{dm_L}{d\tau} = g_L$$

$$\frac{dm_S}{d\tau} = g_S$$

$$\frac{d\rho}{d\tau} = -(\mu + \frac{\partial g_L}{\partial m_L} + \frac{\partial g_S}{\partial m_S})\rho$$

where τ is the characteristic parameter. The reference model numerically solves this set of differential equations and the dynamics of the population can then be studied.

2 Methodology and Model Implementation

The reference fish model developed by Hallam et al. [24] is modified to include the effects of temperature and dissolved oxygen on the relevant response functions for which experimental studies were available. Effects of both temperature and dissolved oxygen are introduced into the feeding rate, length of the embryonic stage, respiration rate, and egg mortality. Temperature is denoted by T and values are in units of $(^{\circ}C)$; C_{DO} represents the concentration of dissolved oxygen in units of $(\frac{mg}{l})$.

2.1 Incorporation of Temperature Effects

2.1.1 Feeding Rate

As in the model for the effects of temperature on *Daphnia magna* [29], the function describing the effects of temperature on the biological response of an individual organism developed by Lassiter [33] is used here to represent the effect of temperature on the feeding rate and the length of the embryonic stage. This generic temperature response has the form

$$\kappa = \kappa_{opt} e^{\gamma(T-T_{opt})} \left(\frac{T_{max}-T}{T_{max}-T_{opt}}\right)^{\gamma(T_{max}-T_{opt})} \tag{10}$$

where κ_{opt} is the optimal value for κ evaluated at the optimal temperature, T_{opt}, and γ is a rate constant. In the case of feeding, T_{max} is the minimum temperature above

T_{opt} at which feeding ceases to occur. The feeding rate modifier initially increases with temperature until it reaches its maximum at T_{opt}; it then decreases to 0 as T_{max} is approached and remains at 0 for all temperatures higher than T_{max}. For brown trout, the optimal and maximal temperatures for feeding are $18°C$ and $22°C$, respectively [10], [14], [15]. The parameter values $\kappa_{opt} = 0.0259$ and $\gamma = 0.25$ were found using a least squares fit to the feeding rate function for a 50 g brown trout feeding on excess resource [10]. Following [41], it was assumed that 21.65% of the 50 g wet weight was dry weight and 20% of the dry weight mass was lipid in order to make these calculations. In the model, the feeding rate modifier function (see Figure 2) is normalized to 1 at $18°C$ and multiplies equation (7); the feeding rate is given in units of $(\frac{J}{d})$.

2.1.2 Length of the Embryonic Stage

The length of the embryonic stage is the time from fertilization to the first time that the fry feed; this time defines the start of the juvenile period. As discussed above, the length of this stage is assumed to have the generic response of the form (10). In this case, the length of time to the onset of feeding is initially decreasing with temperature up to T_{opt} and then increasing for temperatures higher than T_{opt}. Assuming that the optimal and maximal temperatures are respectively 13 and $28°C$ [1] for the length of the embryonic stage and using the data for brown trout from [28], κ_{opt} and γ were

found to be 27.68 and -0.78, respectively. Note that as the temperature approaches T_{max}, the length of the embryonic stage approaches ∞; this mathematical constraint, however, does not come into play since the lethal temperature for trout eggs, when not only the effect of temperature on the length of the embryonic stage is taken into consideration, ranges between 11 and 15°C [7], [14], [36]. Following Smith's study of rainbow trout [39] and [36] as in the reference model, the length of time to the first feeding was scaled to give a value of 51 days at 10°C. This new function for the duration of embryonic development as a function of temperature (see Figure 3) replaces the 51 days that was used throughout the reference model. The time to the onset of the juvenile period is given in days.

2.1.3 Respiration Rate

Using equations developed by [10] and data for brown trout, a function, R_1, that modifies the respiration rate, yielding the resultant fraction of respiration was employed in the model. R_1 is defined by

$$R_1 = \frac{e^{0.17T}}{e^{3.4}}.$$

The scaling factor, $e^{3.4}$, is equivalent to the numerator, $e^{0.17T}$, evaluated at $T = 20°C$; for coding purposes, R_1 takes on a nominal value of one at 20°C. R_1 scales the rate constants, A_7 and A_8 in equation (8). Note that the modification function for the

respiration rate (see Figure 4) is increasing exponentially with temperature and the respiration rate is given in units of $(\frac{J}{d})$.

It should be noted that the formulation for the respiration rate, mentioned above and given by equation (8), is actually the equation for maintenance as discussed in Section 1.1. It is acceptable to assume that respiration and maintenance are equivalent processes when no growth occurs during the time period under consideration [31]. In the equations developed by Cuenco [10], he uses experiments in which it is assumed that a constant level of weight is maintained, i.e., no growth takes place during the experiments. Hence, respiration and maintenance can be used interchangeably here.

2.1.4 Egg Mortality

Using data from Jungwirth and Winkler [28] and assuming a parabolic shape, the following function representing the percentage of eggs that die at a given temperature was found using a least squares fit:

$$M = 1.58T^2 - 21.89T + 92.42.$$

In the model, the fraction of eggs that survive, not the fraction that die, is important. In order to find this function, divide M by 100 and subtract the result from 1, which yields

$$S_1 = -0.0158T^2 + 0.219T + 0.0758. \tag{11}$$

(See Figure 5.) In the model, this function is only valid between temperatures of -0.34 and 14.2°C due to the nature of the function; S_1 is a parabola which has a negative second derivative for all values of T and when evaluated at $T = -0.34$ or $T = 14.2$, $S_1 = 0$. To make biological sense, S_1 must be equal to 0 for all temperatures smaller than -0.34°C and all temperatures greater than 14.2°C so that the function does not result in a negative number of eggs surviving. The high temperature for which the survival fraction becomes 0 is reasonable since [22] states that the mortality of larvae is high for temperatures above 15°C. The fraction of eggs that survive is assessed immediately after the eggs have been deposited; this means that the mother still allocates lipid and structure to the eggs and then, due to the physical environment, a fraction of these eggs will not survive. Notice that the temperature at which the most number of eggs survive is $T = 6.9°C$ and that S_1 gives a value of 0.83 at this temperature. The fraction of eggs surviving is never greater than 0.83 because there are always some nonviable eggs in nature; therefore, the fraction of eggs that survive is never 1. The effects of adding this change to the model will not be noticed when looking at the growth of an individual because the fraction of eggs that survive is a population-level parameter and, thus, affects the dynamics of the population and not the individual.

2.2 Incorporation of Dissolved Oxygen Effects

2.2.1 Feeding Rate

Following [10] and [37], the effect of dissolved oxygen on the feeding rate is incorporated by introducing the following factor:

$$f = \begin{cases} 1.0 & \text{if } C_{DO} > 7.84 \ \frac{mg}{l} \\ \frac{C_{DO}-4.16}{3.68} & \text{if } 4.16 \leq C_{DO} \leq 7.84 \ \frac{mg}{l} \\ 0.0 & \text{if } C_{DO} < 4.16 \ \frac{mg}{l} \end{cases}$$

(see Figure 6) which multiplies the feeding rate as a function of temperature discussed previously. $DO_{crit} = 7.84 \ \frac{mg}{l}$ is the minimum concentration of dissolved oxygen at which feeding is a maximum. Similarly, $DO_0 = 4.16 \ \frac{mg}{l}$ is the maximum level of dissolved oxygen at which no feeding occurs. These threshold dissolved oxygen levels were found in [11].

2.2.2 Length of the Embryonic Stage

Using data for lake trout from [9] and data for brook trout from [38], a new multiplying factor, d, for the number of days until the juvenile period begins was developed:

$$d = \frac{0.278}{C_{DO} - DO_{thr}} + 1.22.$$

Here, $DO_{thr} = 1.7 \ \frac{mg}{l}$ is the threshold dissolved oxygen level, the concentration for which the number of days in the length of the embryonic stage is infinite. d (see Figure

7) multiplies the previous multiplying factor as a function of temperature discussed in Section 2.1.2, which in turn replaces the 51 days used throughout the reference model.

2.2.3 Respiration Rate

A multiplying factor similar to the one used for the feeding rate is utilized here. R_2 is the factor that accounts for the effect of dissolved oxygen on the respiration rate and multiplies the respiration rate as a function of temperature developed in Section 2.1.3:

$$R_2 = \begin{cases} 1.0 & \text{if } C_{DO} > 9.06 \ \frac{mg}{l} \\ 0.37 + 0.63(\frac{C_{DO}-4.59}{4.47}) & \text{if } 4.59 \leq C_{DO} \leq 9.06 \ \frac{mg}{l} \\ 0.37 & \text{if } C_{DO} < 4.59 \ \frac{mg}{l} \end{cases}.$$

(See Figure 8.) The threshold dissolved oxygen values, 4.59 and 9.06 $\frac{mg}{l}$ for respiration, were extracted from [11]. The value for the routine metabolic rate, 0.37, comes from [37].

Note that maintenance and respiration are assumed to be equivalent processes in this section for the same reason as was discussed in Section 2.1.3.

2.2.4 Egg Mortality

Data for lake and brook trout from [9] and [38] were used here in determining a new fraction for the number of eggs which survive in various levels of dissolved oxygen and temperature. The survival function is now

$$S_2 = \begin{cases} 0.0 & \text{if } C_{DO} \leq DO_{low}(T) \\ \frac{C_{DO} - DO_{low}(T)}{DO_{mid} - DO_{low}(T)} \cdot f_{mid}(T) & \text{if } DO_{low}(T) < C_{DO} < DO_{mid} \\ \frac{f_{high}(T)(C_{DO} - DO_{mid}) + f_{mid}(T)(DO_{high} - C_{DO})}{DO_{high} - C_{DO}} & \text{if } DO_{mid} \leq C_{DO} < DO_{high} \\ f_{high}(T) & \text{if } C_{DO} \geq DO_{high} \end{cases} \tag{12}$$

where $DO_{mid} = 5.25\ \frac{mg}{l}$ and $DO_{high} = 10.5\ \frac{mg}{l}$ following [9] and [38]; DO_{low}, $f_{mid}(T)$ and $f_{high}(T)$ are given as functions of temperature:

$$DO_{low}(T) = \begin{cases} 0.608T^2 - 9.925T + 42.067 & \text{if } 0.608T^2 - 9.925T + 42.067 \leq DO_{mid} \\ DO_{mid} & \text{if } 0.608T^2 - 9.925T + 42.067 > DO_{mid} \end{cases},$$

$$f_{mid}(T) = \begin{cases} 0.0 & \text{if } T \leq 5.80 \\ \frac{-16.66T^2 + 268.78T - 998.81}{100} & \text{if } 5.80 < T < 10.33 \\ 0.0 & \text{if } T \geq 10.33 \end{cases},$$

$$f_{high}(T) = \begin{cases} 0.0 & \text{if } T \leq 5.23 \\ \frac{-10.17T^2 + 167.20T - 596.43}{100} & \text{if } 5.23 < T < 11.21 \\ 0.0 & \text{if } T \geq 11.21 \end{cases}.$$

(See Figures 9 and 10.) Note in the equation for $DO_{low}(T)$ that $0.608T^2 - 9.925T + 42.067 \leq DO_{mid}$ with $DO_{mid} = 5.25\ \frac{mg}{l}$ is equivalent to $5.70 \leq T \leq 10.62$, and, similarly, $0.608T^2 - 9.925T + 42.067 > DO_{mid}$ is equivalent to $T < 5.70$ or $T > 10.62$.

There is a special case for which S_2 will take on a different form than the one shown in (12). The following equation is used when $DO_{low}(T) = DO_{mid}$:

$$S_2 = \frac{f_{mid}(T)}{100}.$$

The new factor, S_2, (see Figure 11) is a function of both dissolved oxygen and temperature; therefore, it does not multiply equation (11) in Section 2.1.4, but replaces it.

3 Results

Three of the modifications made due to the effects of temperature and dissolved oxygen, the modification to the feeding rate, to the respiration rate and to the egg mortality, were factors that had a multiplicative effect on the corresponding parameter in the reference model. The fourth alteration, which was a modification to the number of days until the first feeding took place, was a replacement for the fifty-one days until the end of the embryonic stage in the original model. For each modification, with the exception of the egg mortality function, the effect due to dissolved oxygen multiplied the effect due to temperature, which in turn either modified, or, in the case of the length of the embryonic stage, replaced the original parameter; for the egg mortality function, there were two different functions which modified the number of eggs that survived in the reference model: one which was a function of temperature only, and the other which was a function of both temperature and dissolved oxygen.

Due to the abundance of information available on the effect of temperature on individual growth processes, the functions of temperature added to the model were unique to the processes being modified. On the other hand, the functions of dissolved oxygen were primarily linear because of the lack of experimental data on how varying levels of dissolved oxygen affect the different physiological processes of an individual.

3.1 Individual Dynamics

3.1.1 Temperature in a Reference DO Environment

The reference model with the changes for temperature effects incorporated was simulated for a period of 2920 days, the maximum age of an individual fish. The runs were for one ecotype (see Table 1 for parameter values) with a fixed level of resource; temperature varied between 4 and 21°C. Based on total biomass for the last year of the run, the optimal temperature for the growth of an individual in a reference dissolved oxygen environment is 18°C (see Figure 12). There are articles which concur with this result ([7], [15], [36]), as well as ones that disagree ([27], [34], [42]). Brown's study of the effect of temperature on the growth of two-year-old brown trout found the growth to be optimal at 18°C, but it must be noted that only a small number of fish (twelve) were used in this experiment [7]; it was reported in [15] that maximum growth occurred between 16 and 19°C; and in [36], the optimal temperature range for the growth of brown trout was between 18.3 and 23.9°C. Jensen's experiments showed that the optimal temperature for the growth of brown trout occurred at approximately 14.9°C [27]; however, these experiments were correlated with water temperatures in Norweigan rivers which did not exceed 15°C, and, therefore, note that the optimal temperature for growth occurred essentially at the highest possible water temperature which does not rule out the possibility of optimal growth at

temperatures above $15°C$. Swift's experiments found an optimal growth temperature of $12°C$ in the spring and $14°C$ in the fall [42]; the experiments dealt with yearling trout where growth was measured as a function of the length, not the mass, and, once again, the maximal growth temperatures corresponded to the highest possible water temperature. Pentelow found that optimal growth for brown trout occurred between 10 and $15.6°C$; however, only twelve fish were used in the experiments and, as stated in the article, "The experiments were not designed to study the effect of temperature" [34]. Although Pentelow's optimal temperature for growth does not agree with the $18°C$ found by our model, it is interesting to note that in Pentelow's experiments, the optimal temperature for the growth of an individual fish occurred at the same temperature for which feeding was optimal. In our implementation of the model, the feeding rate and the growth rate were both optimal at $18°C$.

3.1.2 Temperature and Dissolved Oxygen Combined

The reference model with the changes due to temperature and dissolved oxygen included was simulated for a period of 2920 days for one ecotype with constant resource density. The optimal dissolved oxygen level for the individual was determined from dissolved oxygen levels which varied between 2 and 12 $\frac{mg}{l}$; since the dissolved oxygen effects require the inclusion of temperature, the optimal temperature, $18°C$, as discussed in Section 3.1.1, was used. A range of dissolved oxygen levels which op-

timize the total biomass of an individual for the last year of the run were found: $C_{DO} \geq 7.84\ \frac{mg}{l}$. Only one of the sources discusses the ideal dissolved oxygen levels. Davis indicates that a dissolved oxygen level of at least 7.84 $\frac{mg}{l}$ was ideal for freshwater salmonids [11]. Notice that 7.84 $\frac{mg}{l}$ was also the critical dissolved oxygen level used in the feeding modifications discussed in Section 2.2.1. It is interesting to note that, for the growth of an individual, both the optimal temperature and the optimal concentration of dissolved oxygen correspond to the critical levels of temperature and dissolved oxygen associated with the feeding rate.

3.2 Population Dynamics

In the following discussion, a population is considered *persistent* if the population density function is positive ($\rho > 0$) throughout the simulation. Conversely, a population goes to *extinction* if the population density function goes to zero ($\rho = 0$) at any time during the simulation. Clearly, the definitions for persistence and extinction depend on the length of the run time of the simulation; however, if the run time is sufficiently long, greater than eight years for these simultations, extinction is independent of the run time.

In the following simulations, twenty-seven different ecotypes were initially generated for use as a starting population. Combinations of three different variables were

used to produce the population: fraction of lipid in the food (15%, 20%, 25%), food density in the environment (4.0×10^{-11}, 1.0×10^{-8}, 5.0×10^{-7} $\frac{g}{cm^3}$), and k_3, which is a constant used to vary the gut clearance time (16.0, 16.5, 17.0 $\frac{g^{k_1}}{d}$ where k_1 is a nondimensional constant).

3.2.1 Temperature Without Seasonality

The model was simulated in a reference dissolved oxygen environment for a period of 3000 days for twenty-seven different ecotypes feeding on a fixed level of resource. The result of these simulations was extinction of the population for temperatures less than $6.5°C$ and for temperatures greater than $14.2°C$.

Since the result of the study of the individual dynamics was that an individual grows optimally at a temperature of $18°C$, it is odd that the population went to extinction for temperatures greater than or equal to $14.2°C$. The output from the simulations indicates that individuals in the population are reproducing, but the eggs are not surviving, and hence, the population density function eventually goes to zero. Recall from Section 2.1.4 that the high temperature at which egg mortality started to occur was $14.2°C$. The egg mortality that is assessed due to temperature obviously has a strong impact on the range of temperatures for persistence at the population level.

The result of the population level simulations in a reference dissolved oxygen envi-

ronment indicates the importance of including a temperature that fluctuates with the seasons. Therefore, temperature is no longer a constant throughout the simulations to follow, but is modified to be a function of the time of year, fluctuating between $0°C$ and $22°C$, the temperatures for which it is possible for an individual fish to grow based on the results of the simulations of the individual dynamics. (See Figure 13.)

Since reproduction is a process that occurs periodically with a year between reproductions, the effect of adding a temperature which fluctuates with the seasons in the same way from year to year is that reproduction will occur at the same temperature every year. The way the temperature as a function of time is administered yields a temperature of $7.9°C$ for the time when reproduction takes place. The temperature at which eggs are produced and egg mortality is assessed is also used to set the number of days to the onset of feeding. Both the number of eggs that survive and the number of days to the beginning of the juvenile period are subject to modification because dissolved oxygen concentration still has an effect on these parameters.

A more realistic way to handle the temperature at which reproduction occurs, so as to avoid using the same temperature every year, might be to have the period between successive reproductions depend on the temperature. This would allow for variation in the length of time between reproductions, and as a consequence, the temperature for reproduction would vary from year to year. This method was not

used because there are few experimental studies on the effect of temperature on the period between successive reproductions available in the literature.

3.2.2 Temperature With Seasonality

For a simulation with twenty-seven different ecotypes in a reference dissolved oxygen environment, the population persists when the temperature is modified to fluctuate with the time of year. (See Figure 14.) The next simulation introduced a toxicant with a concentration of 1.5 $\frac{mg}{l}$ in the water and an octanol-water partition coefficient of $K_{ow} = 10^5$ to the reference dissolved oxygen environment. A two-year simulation, in which the toxicant was present for the entire period, resulted in persistence for the population, but not for all of the individuals in the population. Some of the ecotypes that were slightly over a year old, having just reproduced, died due to a combination of the toxicant and the rapid mobilization of lipid for the production of eggs.

When the model was simulated with twenty-seven different ecotypes with both the effects of temperature and dissolved oxygen included, a range of dissolved oxygen concentration values in which the population persists was found. The values for persistence in a fluctuating temperature environment were $C_{DO} \geq 4.3$ $\frac{mg}{l}$. Adding a toxicant with a concentration of 1.5 $\frac{mg}{l}$ and $K_{ow} = 10^5$ to an environment where both temperature fluctuations and dissolved oxygen concentration are included also results in extinction for some of the ecotypes who have just deposited eggs and are

slightly greater than one year old.

4 Conclusion

The result of the simulations at the individual level were that optimal growth for a certain ecotype of individual occurs at a temperature of $18°C$ with a dissolved oxygen concentration which is greater than 7.84 $\frac{mg}{l}$. The individual cannot survive in temperatures below $0°C$ or above $22°C$, nor can it persist in dissolved oxygen concentrations which are less than 2 $\frac{mg}{l}$ when the temperature is set at the optimal, $18°C$.

At the population level, the results of the initial simulations indicated the importance of not keeping the temperature constant throughout each year, but allowing it to fluctuate with the seasons. Without these fluctuations in temperature, the egg mortality function, being a population level parameter, has a strong effect on the number of eggs that survive and causes the population to go to extinction for temperatures greater than $14.2°C$. The result of these simulations was the incorporation of a fluctuating temperature for all of the future simulations.

After the fluctuating temperature was added, the population was able to persist in a reference dissolved oxygen environment as well as in an environment where the dissolved oxygen concentration was greater than 4.3 $\frac{mg}{l}$. The addition of a nonpolar,

lipophilic chemical to the environment allowed persistence for the population in the same range of dissolved oxygen concentrations, but caused extinction for some of the ecotypes in the first age class, who died just after reproduction due to a combination of the toxicant and the rapid mobilization of lipid for producing eggs.

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Appendix

Figure 1: Individual Model for an Adult Fish

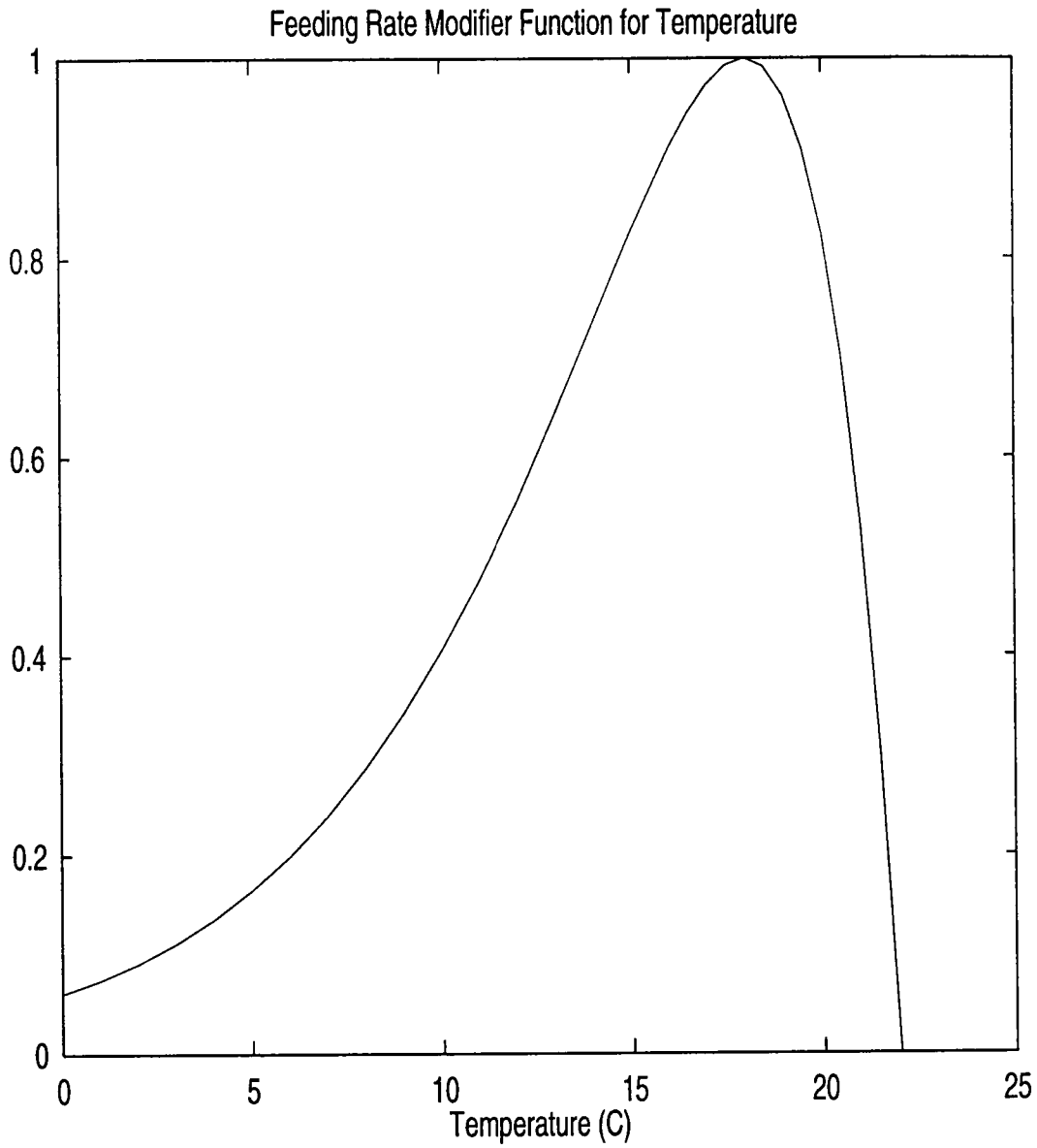


Figure 2: Feeding Rate Modifier Function for Temperature

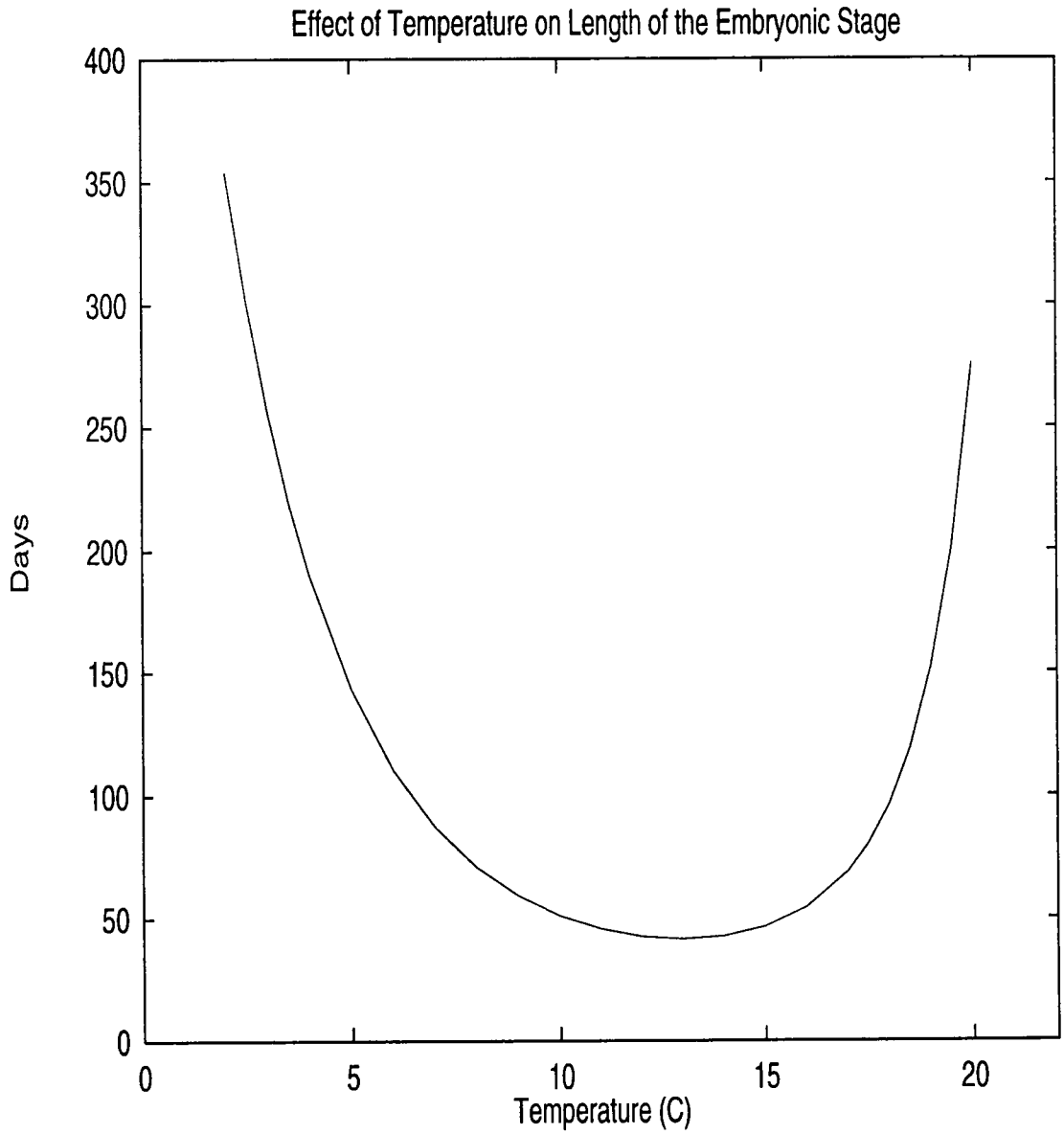


Figure 3: Effect of Temperature on Length of the Embryonic Stage

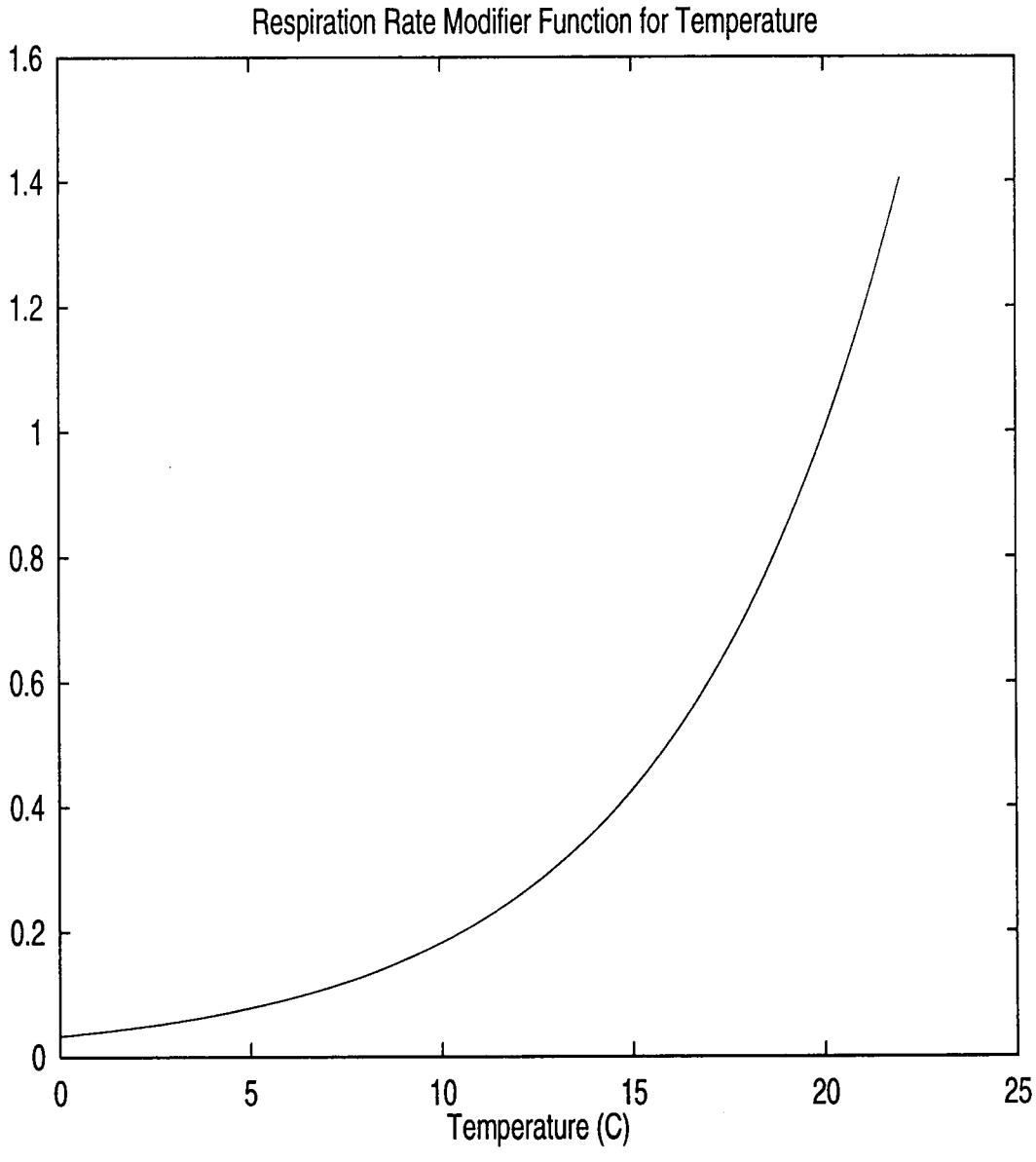


Figure 4: Respiration Rate Modifier Function for Temperature

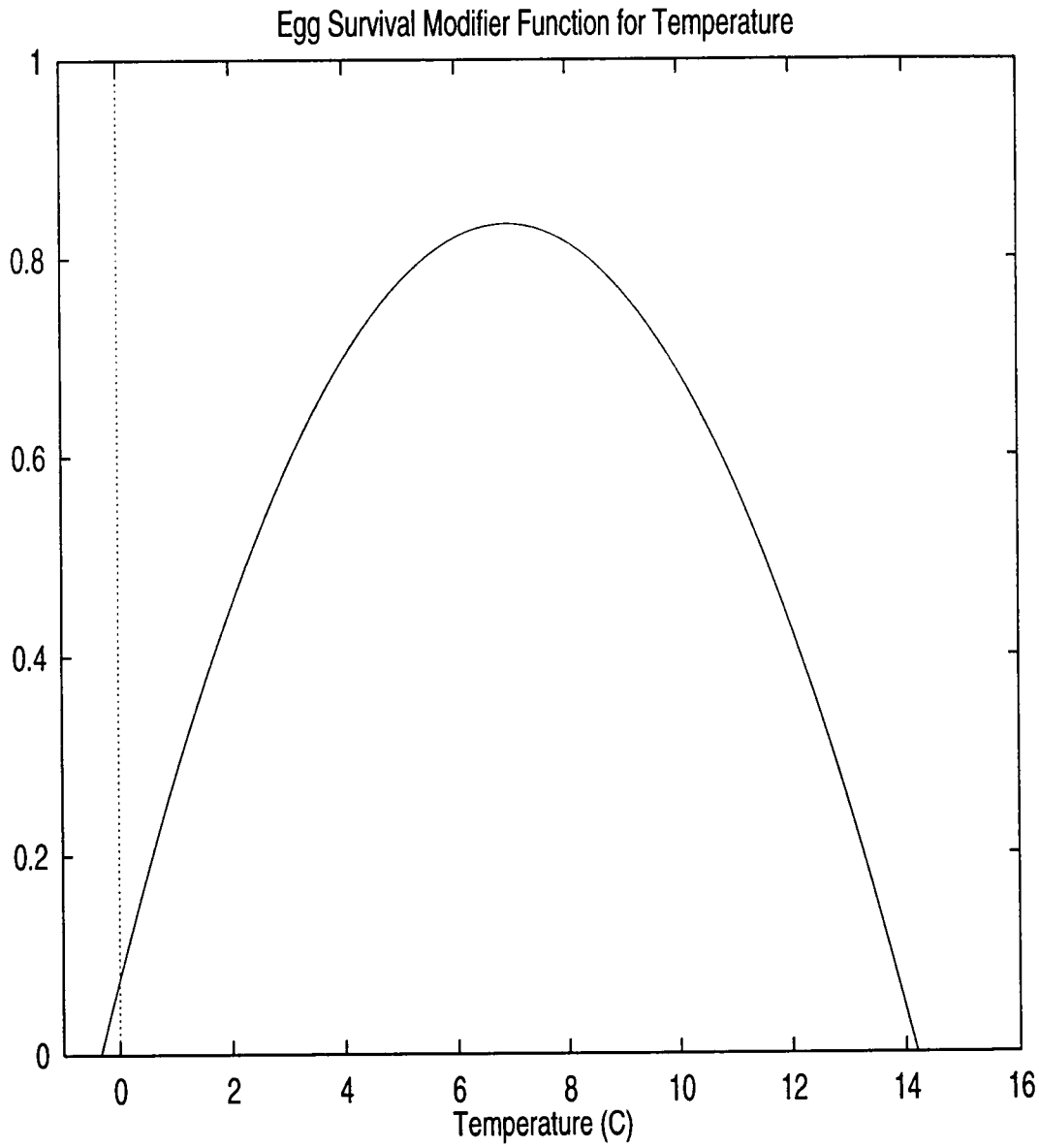


Figure 5: Egg Survival Modifier Function for Temperature

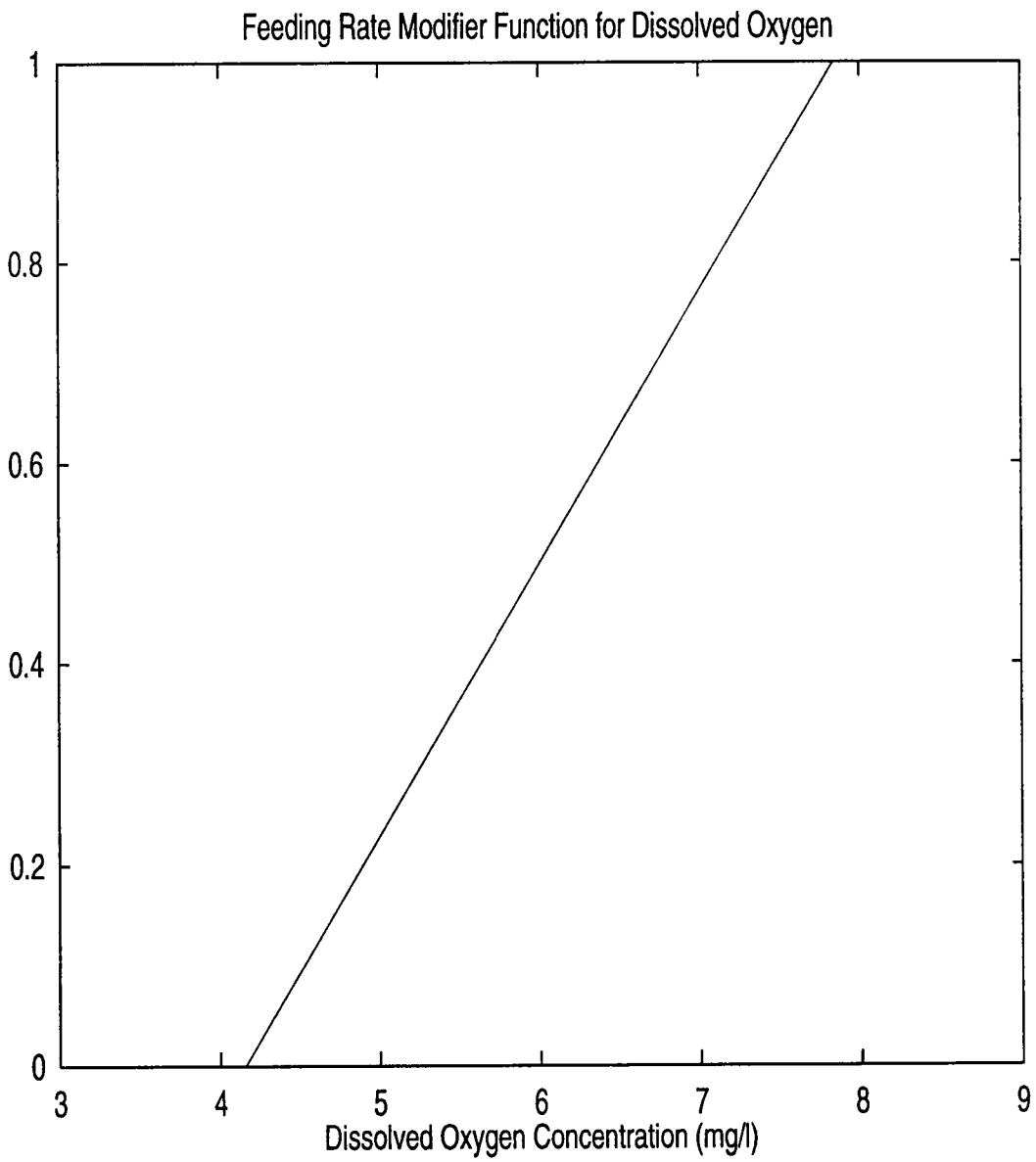


Figure 6: Feeding Rate Modifier Function for Dissolved Oxygen

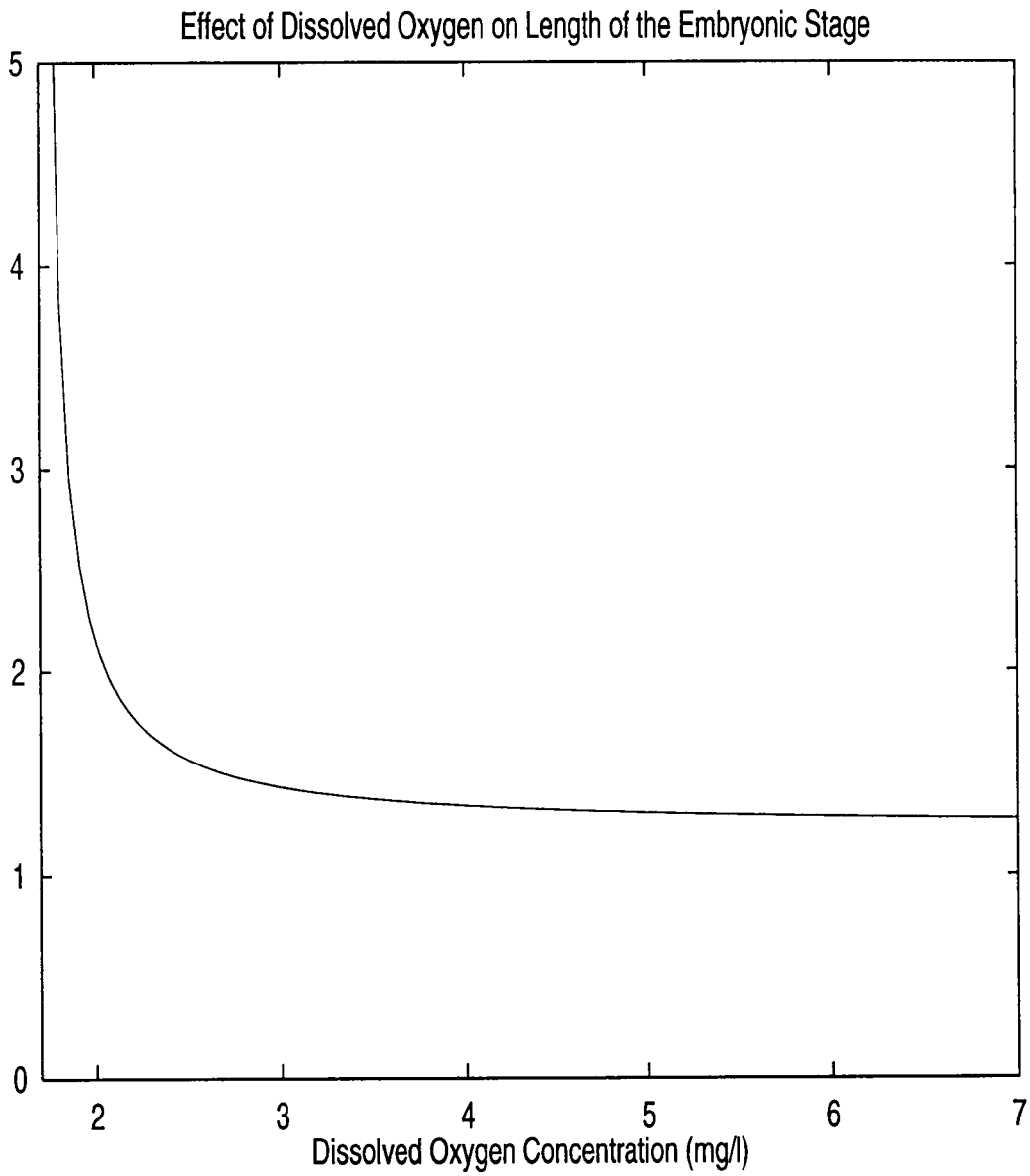


Figure 7: Effect of Dissolved Oxygen on Length of the Embryonic Stage

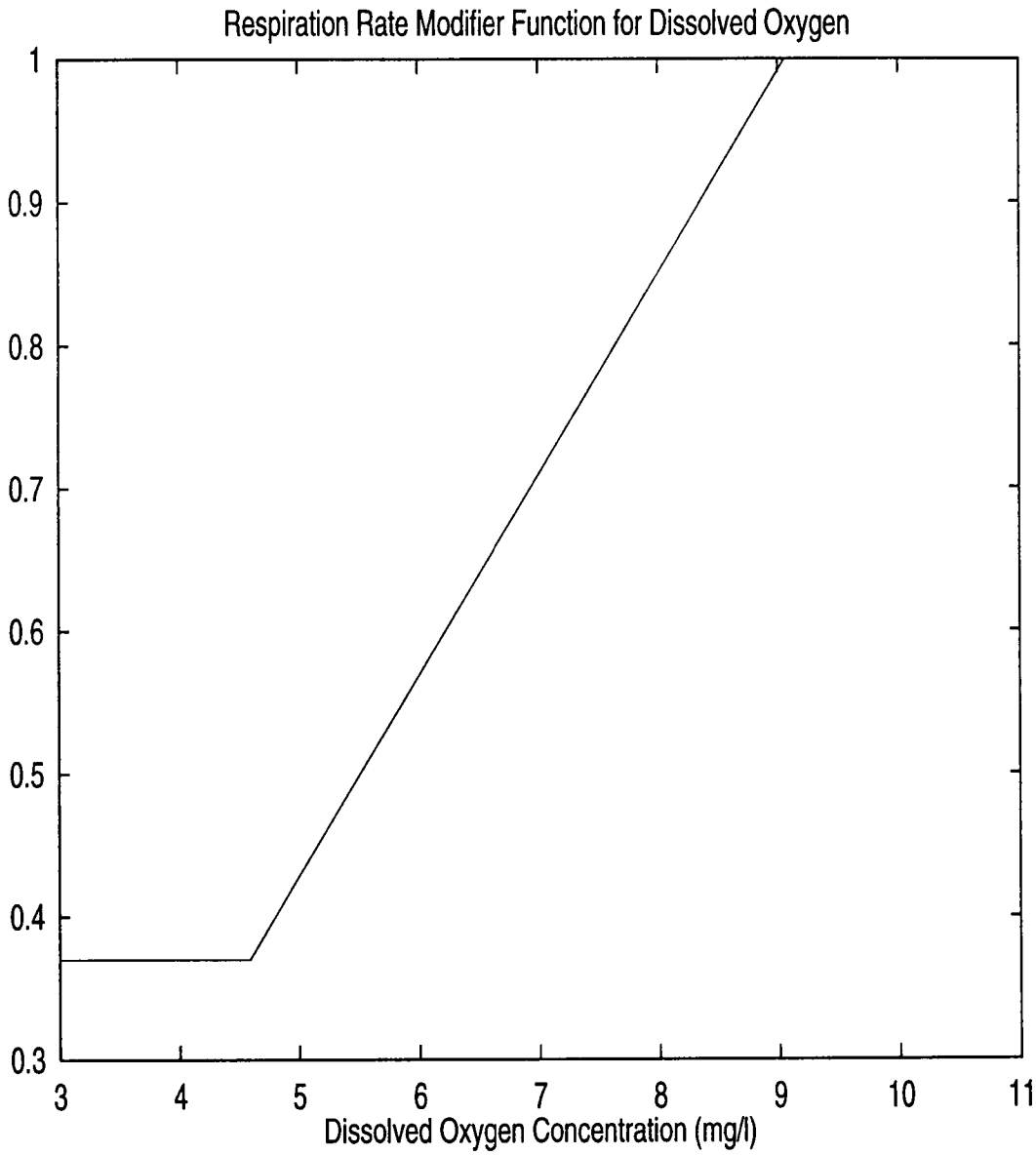


Figure 8: Respiration Rate Modifier Function for Dissolved Oxygen

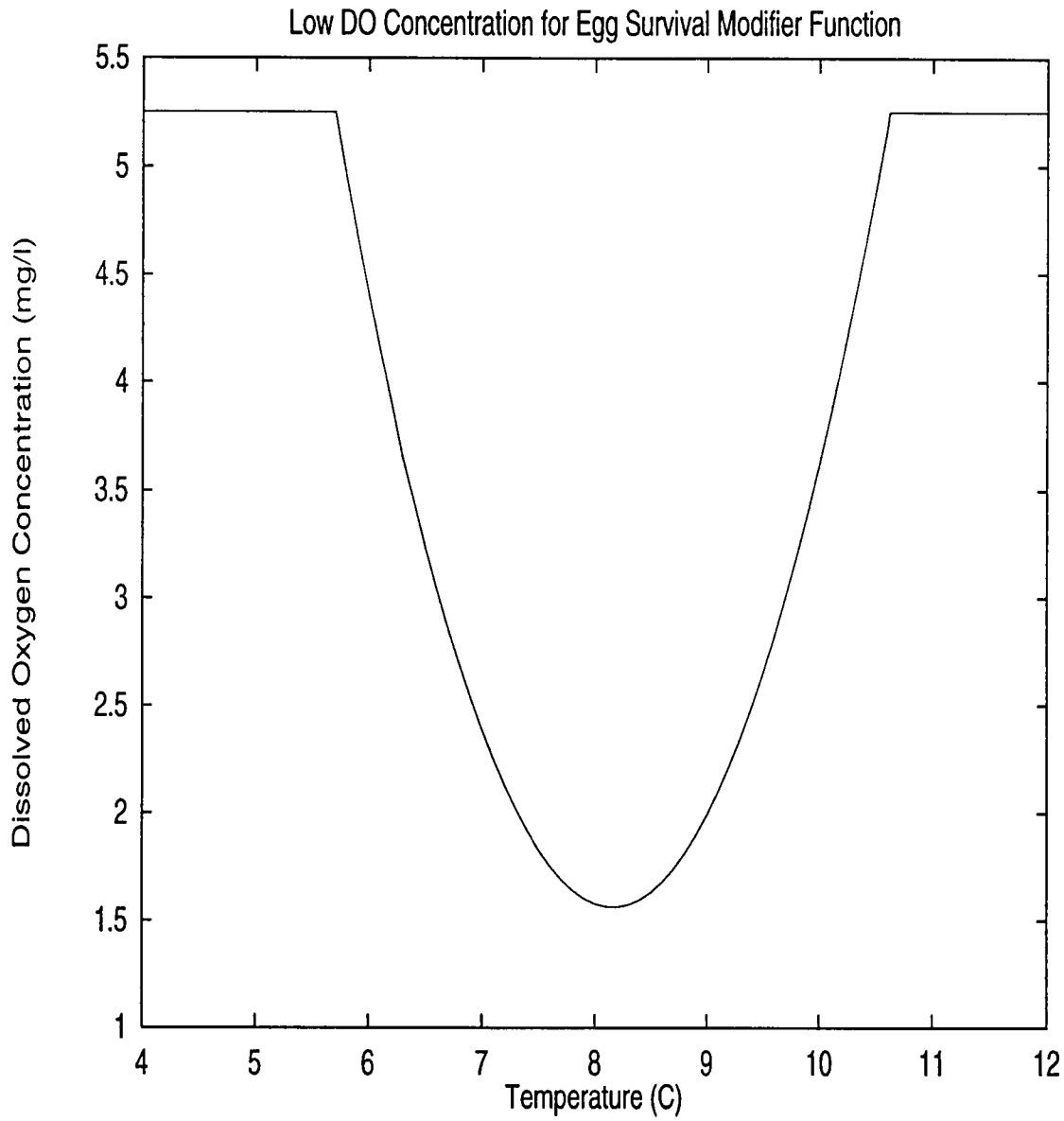


Figure 9: Low DO Concentration for Egg Survival Modifier Function

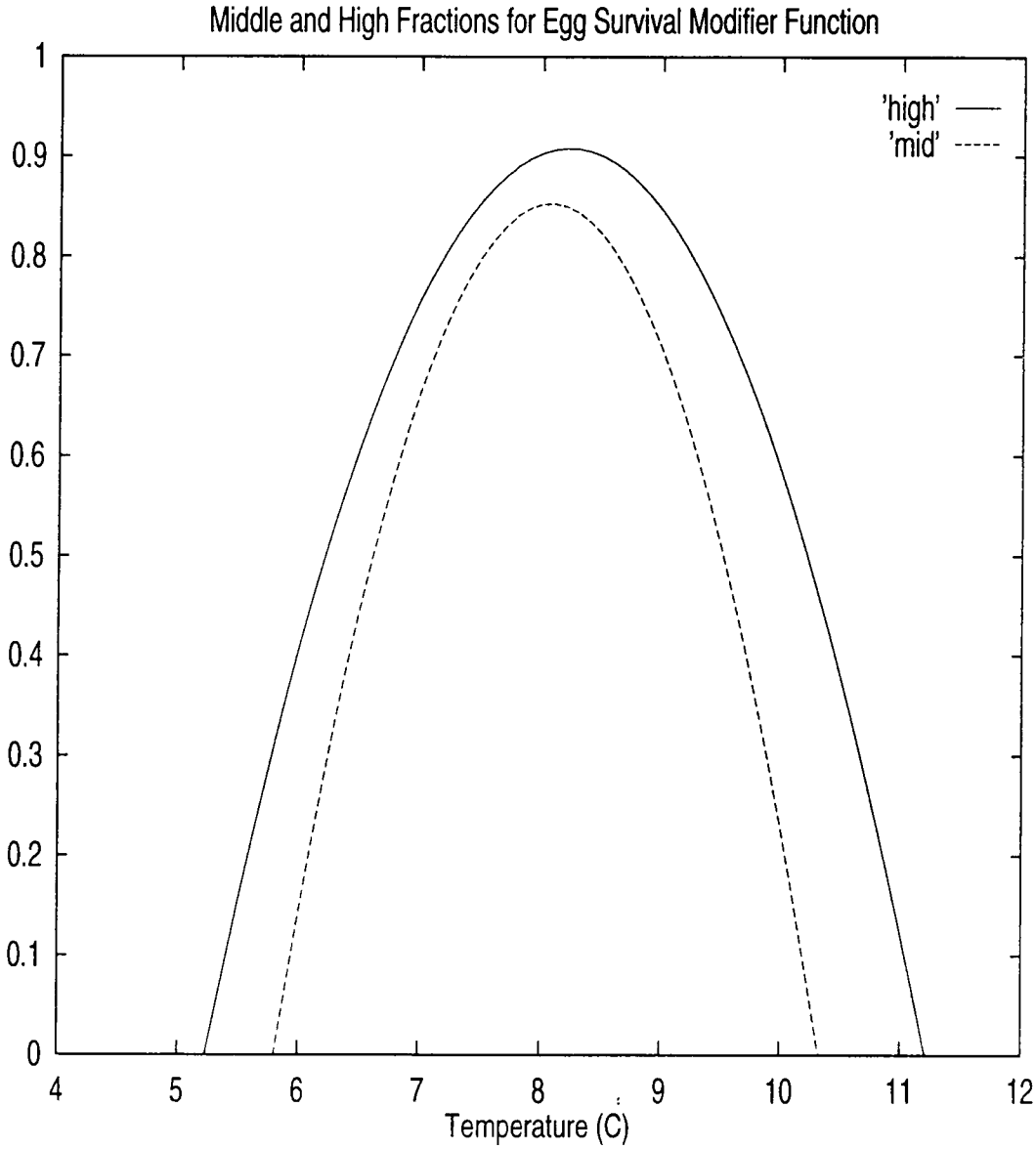


Figure 10: Middle and High Fractions for Egg Survival Modifier Function

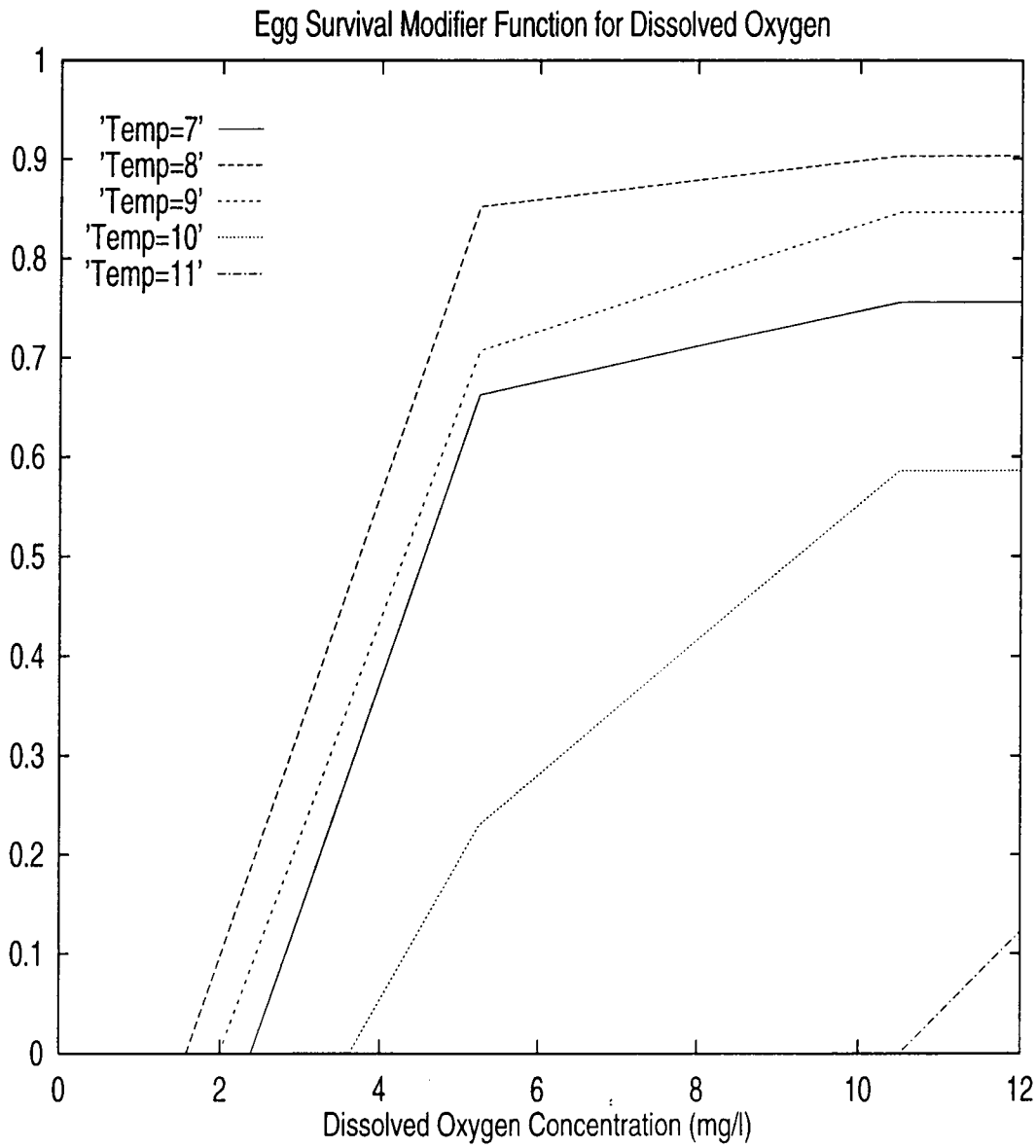


Figure 11: Egg Survival Modifier Function for Dissolved Oxygen

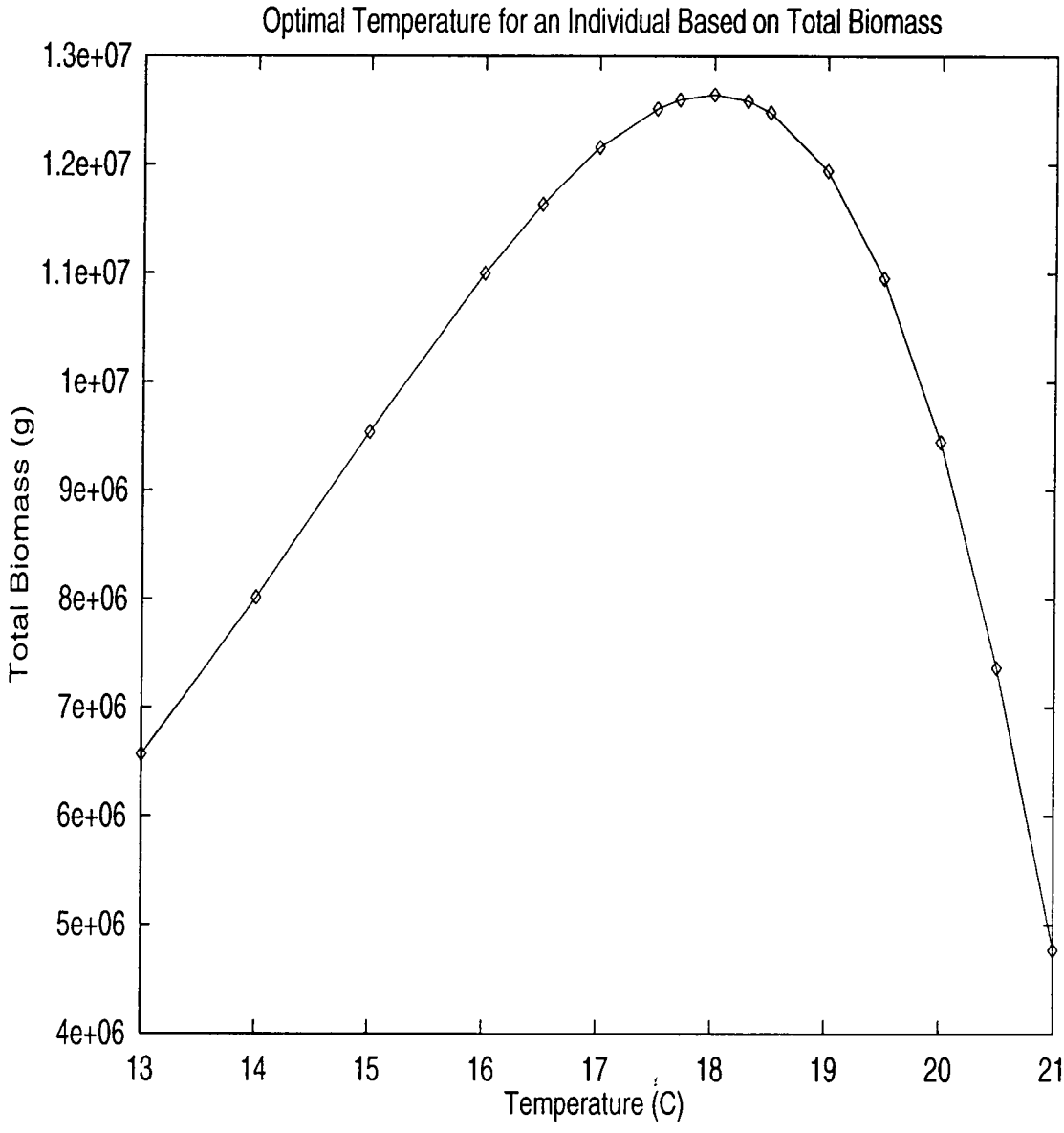


Figure 12: Optimal Temperature for an Individual Based on Total Biomass

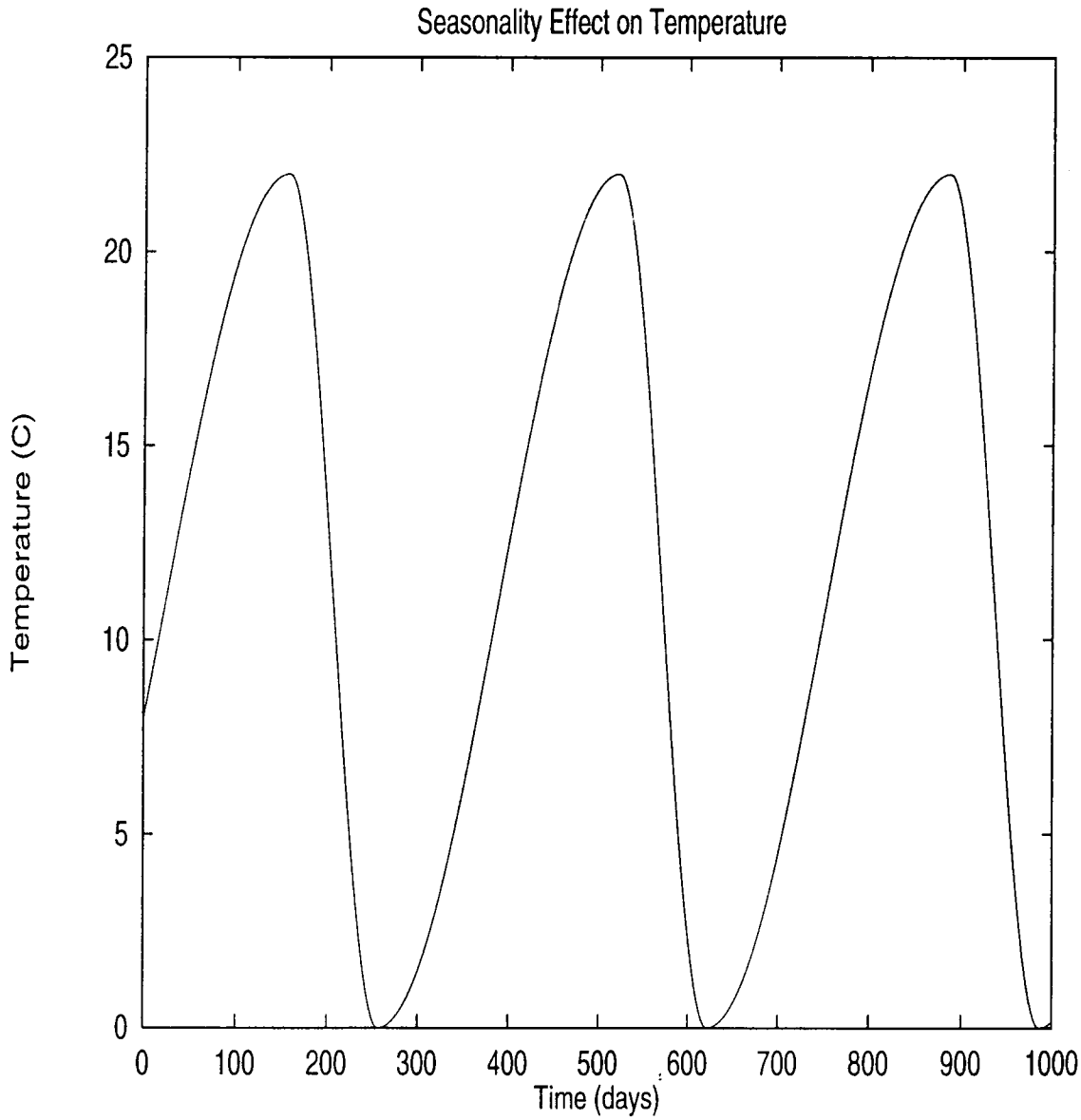


Figure 13: Seasonality Effect on Temperature

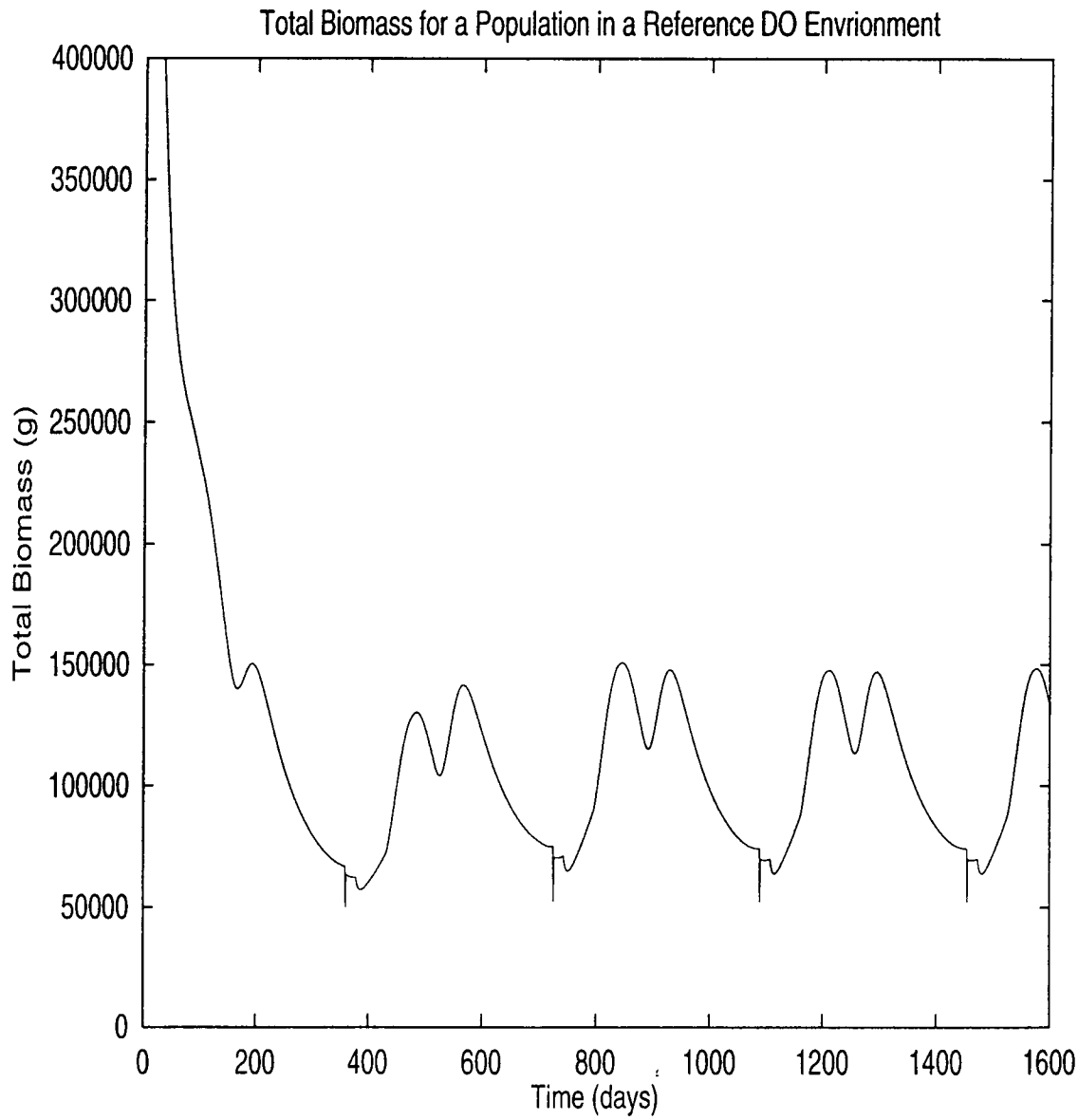


Figure 14: Total Biomass for a Population in a Reference DO Environment

Table 1. Parameter values and units used in the individual model

Symbol	*Interpretation*	*Value (unit)*	*Source*
x	density of resource	$5.0 \cdot 10^{-7}$ $(\frac{g}{cm^3})$	created
M_p	mass of prey	$2.7 \cdot 10^{-4}$ (g)	[32]
ϵ	fraction lipid associated with nonlabile structure	0.12 (nondim)	[41]
B_1	decay constant for lipid	$3.12 \cdot 10^{-3}$ $(\frac{1}{d})$	[25],[40]
B_2	decay constant for structure	$1.38 \cdot 10^{-3}$ $(\frac{1}{d})$	[25],[40]
s_p	body lengths/sec of prey	0.3 $(\frac{length}{s})$	[20],[35]
s_h	body lengths/sec of hunting fish	0.36 $(\frac{length}{s})$	[2],[45]
s_c	body lengths/sec of fish in pursuit	5.0 $(\frac{length}{s})$	[2]
α	as in $m_{PS} = \alpha m_S$	0.71 (nondim)	[41]
ρ_p	density of prey, as in $M_g = \rho_p \cdot V_g$	0.052 $(\frac{g}{cm^3})$	[30]

Table 1. (continued)

Symbol	*Interpretation*	*Value (unit)*	*Source*
a	as in $s_d = [aL_p + b]L_f^{0.5}$ for reaction distance	7.5 $(cm^{-0.5})$	[4],[43],[44]
b	as in $s_d = [aL_p + b]L_f^{0.5}$ for reaction distance	5.2 $(cm^{0.5})$	[4],[43],[44]
c	as in $V_g = c \cdot m_{PS}$ for gut volume	0.864 $(\frac{cm^3}{g})$	[23],[41]
P	reproductive period	365 (d)	[36]
A_{0L}	lipid assimilation efficiency	0.85 (nondim)	[3],[18],[19],[41]
A_{0S}	structure assimilation efficiency	0.684 (nondim)	[3],[18],[19],[41]
A_3	labile lipid mobilization rate	0.006 $(\frac{1}{d})$	created
A_4	labile structure mobilization rate	0.012 $(\frac{1}{d})$	created

Table 1. (continued)

Symbol	*Interpretation*	*Value (unit)*	*Source*
A_7	energy to maintain lipid	32.5 $(\frac{J}{g \cdot d})$	[5]
A_8	energy to maintain structure	32.5 $(\frac{J}{g \cdot d})$	[5]
A_9	half saturation constant modulated by E_s	$3.0 \cdot 10^{-4}$ $(\frac{g}{egg})$	created
A_{10}	energy to mobilize labile structure for eggs	$2.0 \cdot 10^2$ $(\frac{J}{g})$	created
A_{11}	energy to mobilize labile lipid for eggs	$2.0 \cdot 10^2$ $(\frac{J}{g})$	created

Vita

Cynthia M. Lovelock was born in Kitchener, Waterloo, Ontario, Canada on September 12, 1972. She grew up in Tucson, Arizona and graduated from Sabino High School in May, 1990. The following August, she entered the University of Arizona Engineering Mathematics program. She received a Bachelor of Science degree in Engineering Mathematics from the Department of Engineering and Mines in May, 1994. In August, 1994 she entered the University of Tennessee, Knoxville and in August, 1996 received a Master of Science degree in Mathematics.

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