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> A computer simulation model of the growth and life history of the aquatic predator Nephelopsis obscura

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## FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled, "A computer simulation model of the growth and life history of the aquatic predator Nephelopsis obscura" submitted by Larry Ralph Linton in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

R.E Ower

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 1985



#### Abstract

A computer model was written to simulate a simple conceptual bioenergetics model of the growth and life history of the aquatic predator Nephelopsis obscura Verrill. The data required to simulate each of the major variables in the conceptual model were discussed, the available data reviewed.

Experiments were performed to estimate rates of capture of Chironomidae and Cladocera prey at different temperatures and prey densities, by different sized N. obscura. Preliminary experiments showed a marked effect of experimental arena size on capture rates. Simulations of 1 yr of growth using field temperature and prey abundance data resulted in weight losses over winter equivalent to growth during summer, demonstrating that the respiration and prey capture rate data can not be successfully extrapolated to winter conditions.


Simulations suggested that N. obscura growth is more sensitive to natural variation in prey availability within and among years, than to natural variation in temperature. Simulated body sizes appeared consistent with observed body sizes in the prairie pond from which the simulation input data were obtained. Simulations also suggested that in summer, large N. obscura may either experience periods of weight loss when small instars of Chironomidae prey are present.

Experiments were performed to measure embryo production and energy invested in reproduction as functions of temperature, food ingestion
and body size. No data were available on the intensity of specific martality factors except post-reproductive mortality, which was considered to be complete, making $N_{\text {. }}$ obscura a strictly semelparous species. However, the experiments performed to measure reproductive output provided evidence that post-reproductive mortality is related to temperature, body size and prey availability. Furthermore, all of the specimens in a sample of the individuals who survived 90 d after breeding had ceased, were found to have entered breeding condition for a second time.

Simulations investigating life-history optima suggested that iteroparous N. obscura have a distinct reproductive advantage over semelparous N. obscura and that the degree of advantage is closely related to food availability. Reduced food availability was predicted to reduce both maximum body size and post-reproductive survivorship, resulting in populations of small, apparently semelparous individuals. Habitats with high food availability are predicted to produce larger individuals, and have a much greater proportion of them surviving to breed more than once. It is thus suggested that contrary to previous thought, N. obscura has the genetic capacity for iteroparity, but due to the characteristics of the particular habitats (prairie ponds) in which its life history has been carefully described, it has been observed to be only semelparous.

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The simulation model required much more data than could be generated by one person. I must commend Drs. Wrona, Baird and Davies and Mr. Tom Gates for generously supplying their raw data for analysis.

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## Chapter 1

Introduction

### 1.0 General Introduction

A model is a statement about the way in which a system functions, and as such it is an hypothesis about the system. The model predictions can be compared with the actual behaviour of the system being modelled, and if sufficient correspondence is found, the model is considered to have been corroborated. However the correctness of the hypothesis can never be proven. For the purposes of this thesis a model that describes in abstract terms the relationships among the variables of the system will be referred to as a conceptual model. A conceptual model can be formally represented with a set of mathematical and logical operations, which will be referred to as a simulation model. In this context, a simulation model is not intended to be a representation of a real world process, but rather a representation of a conceptual model.

Conceptual models and simulation models differ in the use they make of data and in the predictions they make. Conceptual models tend to consider available data in a less rigorous manner than do simulation models. Based on observations of the system, a conceptual model is usually considered adequate if the predicted directional trends of the dependent variables are considered reasonable.

Although the trends predicted by a conceptual model may be acceptable, no statements are made as to their magnitude, hence the conceptual model may appear qualitatively adequate, but cannot provide quantitative predictions. If a system is reasonably complex, there may be a large number of variables which drive the system (independent
variables), some of which may be antagonistic in the way that they influence variables of the system (dependent variables). Thus it may be difficult, or logically impossible, to predict trends in the dependent variables without parameterizing the relationships among the variables. For instance, the growth rate of an individual may be modelled as the difference between assimilation rate and respiration rate. Depending upon the relative magnitudes of these two variables, the individual could grow, remain the same size, or lose weight. Hence, without knowing the magnitudes of these variables it is not possible to predict the growth rate (positive or negative).

The criteria upon which simulation models are judged are similar to those for conceptual models with the exception that the magnitudes of the variables may also be considered, since the simulation model is quantitative. For instance, if the above simulation of growth resulted in a projected individual many orders of magnitude larger than real individuals of that species, then the simulation model would not be acceptable since its predictions are too far from reality. Deviation of the prediction from the observed behaviour of the system could be due to an incorrect conceptual model or, incorrect empirical estimates of the model's parameters. The simulation process does not distinguish between these potential errors. However if the conceptual model was erroneous but had not been used as the basis for a simulation model, its prediction (growth) may have led to its acceptance. Including the simulation process allows for closer scrutiny of the hypothesis.

Explaining the data from which an hypothesis has been designed is only one of the criteria by which scientific models can be evaluated. The ability of an hypothesis to accurately predict the behaviour of the
system under novel circumstances is generally considered to be a more powerful test. This may be approached through experiments designed to place the model in jeopardy. Successful prediction of the experimental outcome by the model increases faith in the model. Simulations are particularly useful in this process because their numerical predictions are less ambiguous than the predictions of conceptual models and thus they can be more rigorously compared with experimental results.

A model that is poorly predictive may be as informative as one that is perfectly predictive. This apparent paradox is based upon differences in the objectives of the modelling process. Some models are built primarily for the purpose of providing accurate predictions of the state of a system under particular sets of circumstances. A simple example of such a model could be a growth equation fitted by multiple regression. In this instance, terms would be included in the equation, and their parameters set to minimize the deviation between observed system behaviour and the predictions made by the model. There would be little concern as to whether the form of the equation bore any resemblance to mechanisms that may be operating in the growth process. For the purposes of this thesis, models of this type will be referred to as predictive models. Alternatively, a simulation model is built to explore the logical consequence of theory, and in this sense, the objective should be to find those circumstances in which the model is poorly predictive since it is the disparity between prediction and reality that can be used to suggest areas in which theory is weak and to which research effort should be directed. As understanding of the system grows, the continuous formalization of this understanding in a simulation model helps to suggest new directions for research. When this research
is complete its results can be incorporated into the model. The model can also be used by future researchers, as an overview of the most current state of knowledge, and can also help to formulate new hypotheses and investigate the relative plausibility of alternative hypotheses.

An important benefit arising out of the modelling process is integration and critical evaluation of the available data. Large research endeavours involving numerous researchers and extending over a considerable time period may tend to inadvertently fail to investigate important aspects of the system or the research objectives may become diffuse. The inadequacies of the data become evident when the data are scrutinized to develop the mathematical and logical relationships necessary to build the simulation model. Thus, the simulation model acts as a unifying force which synthesizes efforts by different researchers working at different times. Modelling should not be a one time simulation exercise, but rather part of an ongoing interaction between research and synthesis.

### 1.1 Objectives

The objectives of this study were to develop a computerized bioenergetics simulation model to investigate the growth, life history and population dynamics of the leech Nephelopsis obscura Verrill, 1872. Dr. R. W. Davies and his colleagues have conducted approximately 15 man yr of research on various aspects of the biology of N. obscura including, but not restricted to, feeding rates, respirometry, reproductive output, growth and a number of field population studies. Much of the data available were obtained from Stephenson's Pond ( $114^{\circ} 16^{\prime} \mathrm{W}, 51^{\circ}$ $9^{\prime} N$ ) near Calgary, Alberta, or from similar ponds in the vicinity. The intent of the simulation study was to integrate the available data using the structure of a simple conceptual model of population dynamics and individual growth (Calow 1981). During the modelling process the existing data were critically evaluated for completeness and in cases where the data were found to be insufficient for the model to be completed, experiments were performed to obtain the necessary data. The model was then used to formulate hypotheses about aspects of the biology of N. obscura.

Nephelopsis obscura is a predatory leech belonging to the family Erpobdellidae. - It is widely distributed in freshwater habitats of North America (Davies 1973; Davies, Reynoldson and Everett 1977) and is one of the most abundant species of Erpobdellidae in Alberta (Davies, Wrona and Everett 1978). It occurs in both lotic and lentic habitats, although it is more common in lentic habitats, with densities of adult individuals as high as $300 \mathrm{~m}^{-2}$ (Wrona 1982).

The eggs of $N$. obscura are deposited in cocoons attached to a firm substrate, such as aquatic macrophytes or the undersides of rocks.

In southern Alberta animals only larger than about 150 mg breed (Davies and Everett 1977), and are believed to die shortly after depositing their cocoons (Davies and Everett 1977). In Alberta prairie ponds cocoon production often occurs in two distinct periods of the year (May-June and August-September) with two cohorts produced each year. Depending upon the age at which breeding size is attained, the spring cohort breeds after either 12 or 15 mo , while the fall cohort breeds after either 12 or 19 mo (Davies and Everett 1977). If all individuals of a cohort were to breed at one of these ages, normal life expectancy would not exceed 20 to 21 mo . In Minnesota, N. obscura has been reported to have a lifespan of 2 yr and iteroparity is suspected to occur (Peterson 1983).

### 1.2 Modelling criteria and literature review

There were a number of criteria considered for the basic design of the simulation model. Firstly, the model should be reductionist (Paloheimo, Crabtree and Taylor 1982) in its design so that its structure represents a mechanistic representation of how growth is believed to occur (Kerr 1971), as opposed to simply being a statistical fit to observed growth data (eg. Iwama and Tautz 1981). Second, the parameters of the model should be easily measured under either field or laboratory conditions so that the validity of aspects of the model can be determined experimentally, or if necessary, so that experiments upon which model parameters are based can be replicated. Third, the model should be as simple as possible (Roff 1983). Complexity in models increases the difficulty of obtaining accurate measures, but, realism must not be sacrificed for the sake of simplicity. Fourth, the model must be open ended, in the sense that if greater complexity is required, it can be incorporated without resorting to an entirely different model. Fifth, the model must be easily modified to facilitate its use in the investigation of alternative scenarios of life history or habitat variables. For these reasons, the model is based upon the basic energy balance equation (Ricker 1971): .

$$
\begin{equation*}
\Delta B=C-F-U-R \tag{1.1}
\end{equation*}
$$

where $\Delta \mathrm{B}$ is the total change in the energy value of body materials (growth or loss in energy content - termed production below) and includes any reproductive products released, $C$ is the total energy content of the food consumed, $F$ is the energy value of the feces, $U$ is the energy value of the excretory products and $R$ is the total
metabolism. This equation has formed the basis, to a greater or lesser degree, for growth models for fish (Makorova and Zaika 1971; Kerr 1971a, 1971b; Solomon and Bradfield 1972; Ware 1975; Elliott 1976; Kitchell, Stewart and Weininger 1977; Ware 1978; Kitchell. and Breck 1980; Stewart, Weininger and Rottiers 1983) and invertebrates (Bayne, Widdows and Thompson 1976; and Paloheimo et al. 1982), and its components have been thoroughly reviewed by Calow (1981). This formulation of growth has a number of important features. It integrates (Bayne et al. 1976) the major physiological processes (Calow 1981) which are considered to be the important components of growth; and it permits inclusion of feedbacks (Hubbell 1971) among the different components of growth, and feedbacks between environmental variables (eg. temperature and food abundance) and the growth components.

Hubbell (1971) has extensively reviewed the importance of feedbacks in simulation models. He points out that organisms control their growth homeostatically through built-in mechanisms for evaluating their growth performance, and through mechanisms for modifying energy intake and expenditure to compensate for deviations from the desired rate due to environmental or physiological disturbances. This concept of active regulation of growth has been incorporated into the optimization models of Calow (1976 and 1981) who argues that rather than being maximized, growth might be regulated to some value less that the maximum possibly atainable, in order to maximize fitness (classical fitness - sensu Dawkins 1982) Two examples of how growth could be regulated would be to decrease feeding rate when growth exceeds the desired maximum; or to reduce metabolic demands and route a greater proportion of available energy to growth when food is limiting. The mechanisms that control
metabolism. This equation has formed the basis, to a greater or lesser degree, for growth models for fish (Makorova and Zaika 1971; Kerr 1971a, 1971b; Solomon and Bradfield 1972; Ware .1975; Elliott 1976; Kitchell, Stewart and Weininger 1977; Ware 1978; Kitchell and Breck 1980; Stewart, Weininger and Rottiers 1983) and invertebrates (Bayne, Widdows and Thompson 1976; and Paloheimo et al. 1982), and its components have been thoroughly reviewed by Calow (1981). This formulation of growth has a number of important features. It integrates (Bayne et al. 1976) the major physiological processes (Calow 1981) which are considered to be the important components of growth; and it. permits inclusion of feedbacks (Hubbell 1971) among the different components of growth, and feedbacks between environmental variables (eg. temperature and food abundance) and the growth components.

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biological processes are almost bewildering in their variety, some involving actual reference values, others not (Hubbell 1971). For the purposes of models of interest to the ecologist, it need not matter if the mechanism of control embodied in the simulation model has an actual physical analogue in the animal being simulated, provided that the model has similar properties to the real world. Thus at some level in its construction, the simulation must trade off real mechanisms of control for simpler representations of them which mimic the result of the mechanism. For example, if feeding in the real animal ceases after a certain amount of food has been ingested, it may not be necessary to limit feeding based upon submodels which simulate gut stretching or the concentration of nutrients in the blood (or whatever the mechanism might be). Rather, experimentally measured values of the ingestion rates at which feeding ceases might be sufficient. In the simulation, comparisons can be made between these empirical values and simulated feeding rates, and when simulated ingestion equals the empirical values, feeding in the model is stopped. The level of detail built into the model depends to a large extent upon the desired application of the model.

Few models of invertebrate growth which integrate numerous components of growth as well as empirical values for feedbacks among physiological components and environmental variables are reported in the literature (Calow 1981). Bayne et al. (1976) describe a model of the growth of the mussel Mytilus edulis L. that integrates empirical studies of metabolic rates, ingestion rates, assimilation efficiencies and reproductive rates, and includes feedbacks between these growth components and temperature, season and food abundance. The model of the growth
of Daphnia by Paloheimo et al. is substantially less complete and suffers from omission of temperature dependence in the components of growth as well as questionable procedures for estimation of parameters for some equations.

The most extensive bioenergetics modelling literature applies to fish. Some of the reported models are not mechanistic (eg. Iwama and Tauty 1981; Roff 1983) and predict growth based simply upon regression of observed growth rates, so will not be discussed here. Other models succeed in incorporating various degrees of biological detail, and a few of these will be reviewed here to provide a brief overview of the state of the science.

Kerr (1971a, 1971b) developed a model of lake trout growth which allowed inclusion of information on the size and abundance of prey organisms in order to estimate ingestion rates. Empirically obtained estimates of the proportions of four prey types in the diet are used as input for the model. Total prey density is then altered and the proportional feeding rates used to estimate ingestion. Metabolism was moḍelled as power functions of swimming speed and body weight. A fixed temperature of $10^{\circ} \mathrm{C}$ was used. The metabolic level is estimated as that value which maximizes the ratio of growth efficiency to ration, hence metabolic demands are not estimated mechanistically. The model was tested (Kerr 1971b) using observed prey densities and lake trout sizes.

Elliott (1976) developed a model for growth of brown trout (Salmo truta L.) based upon 21 man-years of research. Functions estimating food consumption were not included in the model. Rather, trout were allowed to feed upon alternative prey types in the laboratory, and
these observed feeding rates were used as model inputs, and simulated growth was compared to the observed growth of the laboratory specimens.

Kitchell et al. (1977) and Kitchell and Breck (1980) developed models for the growth of yellow perch, walleye and sea lamprey. These models were similar, the major differences being in equation parameters. Maximal food consumption and metabolic demands were modelled as allometric functions of body size. Proportionality constants in the equations were then adjusted to cause model output to mimic observed growth rates in the field. Thus, these models represent a combination of the mechanistic and regression approaches. Model output was checked by comparing its output with observed data sets from which many of the parameters of the model were estimated. It is pointed out (Kitchell et al. 1977) that functional feeding response estimates of ingestion rates are not generally included in simulation models because they are too difficult to obtain.

Stewart et al. (1983) developed a model for growth of lake trout which also simulated changes in tissue energy content per unit weight, enabling prediction of weight from energy content. Variability in the energy-weight relationship is due to varying proportions of high energy storage products (fats) in the tissues. Energy conversion efficiency (energy routed to production / energy ingested) was found to be higher than biomass conversion efficiency and was found to be highest in fast growing individuals. These authors estimated prey consumption rates from observed trout growth rates in an attempt to estimate the impact of the trout population on its prey resource, and hence provide estimates of optimal stocking rates in a put-and-take fishery.

### 1.3 The conceptual model

A simple conceptual bioenergetics model (Figure l.1) was designed to reflect the data available for N. obscura. In this model the body of N. obscura is considered to be a pool of energy (cal). The size of the body (energy content) is determined by three processes: assimilation which increases body size, and respiration and reproduction which decrease body size. The number of prey items captured (ingested) is a function of N. obscura body size, temperature and prey density (for each prey species), and the amount of energy ingested is the sum of the calorific values of all prey items captured. Depending upon temperature, the amount of energy ingested and the body size, a portion of the ingested energy is assimilated across the gut wall to increase the size of the body, while the remainder of the energy ingested is lost. The rate of energy loss due to respiration is influenced by temperature, the amount of energy assimilated (the nutritional state of the animal), the body size and the reproductive state. The amount of energy removed from the body due to reproduction is a function of temperature and body size. Body size is allowed to vary up or down, depending upon the magnitudes of assimilation, respiration and reproduction. This portion of the model is referred to in this thesis as the growth model.

The population size of N. obscura was modelled as a function of the two opposing processes, mortality and natality (Figure 1.1). The probability of mortality of each individual in the population is a function of the size of the individual and its reproductive state as well as the size (density) of the population (which also influences prey density). The reproductive output of an individual (in calories removed from the

Figure 1.1 Block diagram of the conceptual model upon which the computer simulation was based. Each box represents a variable in the model. Lines represent functional relationships which were parameterized from existing data.

body and the number of embryos added to the population) is a function of temperature, the nutritional state and body size of the individual, and the population size.

A computer model was written to reflect the structure of the conceptual model (Figure 1.1). A separate chapter is dedicated to each of the major variables in the conceptual model (ingestion, respiration, natality etc.) and in each chapter the data required to simulate the variable are described, the available data are reviewed, experiments performed (when necessary) to augment the available data are described, functions are developed to simulate the process and suggestions are made for further research.

Chapter 2 outlines general program structure and the model's data input routines. Chapters 3 through 5 describe the development of the growth, feeding and respiration functions. Chapter 6 discusses validation of the growth model and describes the validation procedures used to test it. Chapters 7 through 9 describe the development of the reproduction and mortality functions. Chapter 10 uses the simulation model to investigate alternative life-history strategies of N. obscura.

## Chapter 2

General design

### 2.0 Introduction

This chapter describes the main driving routine (GROW.FORTRAN) of the bioenergetics growth simulation of an individual Nephelopsis obscura and the general modelling strategy used for the simulation.

### 2.1 General design strategy

The simulation program was written using a top down design strategy (Yourdon 1975). This is a problem solving strategy in which the problem is solved repeatedly, each time in greater detail. In the process of applying this technique the problem is viewed as having a number of hierarchical levels of abstraction, with the upper levels being most abstract and the solution least detailed, and the lower levels being less abstract and the solution being most detailed. At each level of abstraction the problem is broken down into a number of sub-problems, the set of which forms the next lower level of abstraction. At the next lower level each of these sub-problems is further broken down into a set of smaller problems. The process of subdividing the problem into more and more sub-problems is continued until a level of detail is attained from which the main problem can be solved. This procedure was followed to develop a conceptual bioenergetics model describing the growth of an individual (Figure 1.1). A. set of computer routines was written to reflect the layered structure of this solution, with (more abstract) routines higher up in the program structure drawing
information from (less abstract) routines at lower levels in the structure. The routines used in the simulation are diagrammed in Figure 2.1.

The program is intended to be modified by future researchers so a simple structure will make it relatively easy for them to identify the level of complexity of the program to which data obtained in the future apply. Once the level is determined, a minimum number of FORTRAN instructions can be inserted which may then start a new, downward branching tree that incorporates the new data and concepts into the simulation.

Figure 2.1 Network diagram showing the names of the subroutines subsidiary to the driver program GROW.FORTRAN in the simulation of individual growth.


### 2.2 Program GROW.FORTRAN

The upper most abstract level in the bioenergetics simulation of the individual is represented by the program GROW.FORTRAN (Appendix A) (Figure 2.1) in which the instructions fall into two categories. The first fetches the data required to run the simulation through subroutine DATAIN and the second simulates a number of weeks of growth for an individual and prints the reṣults of the simulation for each week. Growth (in calories) was modelled as the simple arithmetic difference between calorific income (assimilation) and calorific losses through respiration and reproduction (Calow 1981, Wrona 1982). This simple energy budget model was implemented at the GROW.FORTRAN level of the program.

Due to insufficient data, excretion and secretion have not been included in the model. Organic compounds in the forms of amino acids, purines, urea and creatinine are known to be components of the urine of some leeches (Mann 1962) and represent potential sources of energy loss which have not been accounted for in the simulation. Mucus secretion rates by $N_{0}$ obscura have not been measured however, when individuals are handled in the laboratory, mucus production can sometimes be copious (personal observation). Whether this occurs in the field is unknown. Excluding excretion and secretion will result in simulated growth rates being over estimated by the amount of those two variables.

For each simulated week calorific values for assimilation, respiration and reproduction are determined for the individual by subroutines ACTASS, RESPIR, and BREED respectively. Production is computed as:

## production = assimilation - respiration <br> [2.1]

and the new body size as:

$$
\begin{aligned}
& \text { new body size }=\text { old body size }+ \text { production } \\
& \text { - energy to reproduction. }
\end{aligned}
$$

### 2.3 Data entry

Data are entered into the simulation from the data file FILEll (Appendix B) through the subroutine DATAIN and its subsidiary routines (Figure 2.1). Subroutine DATAIN reads in control parameters for the simulation and calls subroutines PREYIN and TEMPIN to enter prey and temperature data respectively. Growth parameters are entered through subroutine GRWIN. In subroutine DATAIN, provision is made to enter dissolved oxygen concentrations, through a call to subroutine OXYIN, however, this subroutine was not written due to lack of data on rates of activities such as feeding, respiration and movement as functions of hypoxia.

### 2.4 Summary

The simulation model was designed with a hierarchical structure in which routines higher in the structure are more abstract and general in their function while routines lower in the program structure are more specific and detailed. This structure will simplify future modifications of the simulation when new data and concepts are included.

The upper, most abstract level of the program is the routine GROW.FORTRAN which views the growth of an individual as a simple arithmetic sum of energy income due to feeding, and expenditure of energy due to reproduction and respiration. The values of these three variables are complex functions of the characteristics of the environment as well as characteristics of the individual. The details of their computations are left to routines subordinate to GROW.FORTRAN in the logic hierarchy.

## Chapter 3 <br> Maximal assimilation rates

### 3.0 Introduction

The respiration rate of $N$. obscura is known to be a function of nutritional state, with animals fed ad libitum having higher respiration rates than starved animals (Wrona 1982). Thus, to accurately compute respiration rate, it was necessary to first estimate nutritional state. Furthermore, it was necessary to include in the model a mechanism to cause feeding to cease when the animal becomes satiated. For the purposes of the simulation the nutritional state was computed as the ratio
NSTATE = AASS / MASS
where NSTATE is the nutritional state and AASS is the (simulated) number of calories actually assimilated. MASS is the maximum number of calories assimilated under ad libitum food conditions (fully satiated), and was defined as the sum of growth in calories under ad libitum food conditions plus calories respired under these conditions. Thus

$$
\begin{equation*}
\text { MASS }=\text { GROWTH + RESPIRATION } \tag{3.2}
\end{equation*}
$$

This chapter discusses subroutine MAXASS which computes maximal assimilation (MASS), with particular reference to the calculation of the GROWTH component of MASS.

### 3.1 Published equations

Growth equations for N. obscura at $5^{\circ} \mathrm{C}, 10^{\circ} \mathrm{C}, 15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$ were presented by Wrona (1982). These equations were based upon measured growth of a number of individuals over a 12 wk period, under ad libitum food conditions in rearing containers with no substrate, using Enchytraeus sp. (Oligochaeta) as prey. These equations modelled weight at time $t\left(W_{t}\right)$ as an exponential process:

$$
\begin{equation*}
W_{t}=a \exp (r t) \tag{3.3}
\end{equation*}
$$

with the growth parameter ( $r$ ) being presented for each of the four temperatures. Using field temperatures from Stephenson's Pond (Figure 3.1) and the measured growth parameters, simulation of 1 yr growth under ad libitum food, resulted in an individual that weighed about 11 kg , which is approximately four orders of magnitude larger than any known specimens of N. obscura. Therefore, the only available equations for growth of N. obscura were rejected as appropriate general models for ad libitum growth.

Figure 3.1 Weekly mean temperature $\left({ }^{\circ} \mathrm{C}\right.$ ) at 1 m depth in Stephenson's Pond from 80-11 to 82-04.


### 3.2 Function estimation

It was thus necessary to estimate a different growth function. The raw data used by Wrona (1982) to fit his equations [3.3] were the only data available from extended growth experiments with ad libitum food in which large specimens were used. The data provided weights of each of the individual animals in the experiment at various times over a 55 wk period (Figure 3.2 and Table 3.1). No strong tendency for growth at $10^{\circ} \mathrm{C}$ or $5^{\circ} \mathrm{C}$ is apparent, however growth did occur at $20^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$.

Inspection of Figure 3.2 suggests that growth at $20^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ may be exponential as suggested by Wrona (1982). If exponential growth is being exhibited, a plot of the weight gain per week of an individual versus time should also be exponential. The weights for each weighing time were sorted into ascending order and weight gains between weighing times were computed as the difference between weights of equivalent rank order. These differences were divided by the number of weeks between weighings and plotted versus time (Figure 3.3). No weight gains were calculated for a period if any individuals died between weighing times. The data show marked fluctuations in growth rate, including periods with negative growth rates, thus rejecting an exponential growth model. Food limitations may have occurred periodically due to a technical error (Wrona pers. comm.), causing the periods of negative growth.

For those periods when growth was positive, the proportional weight change per week

$$
\begin{equation*}
\mathrm{pwc}=\mathrm{w}_{\mathrm{t}+1} / \mathrm{w}_{\mathrm{t}} \tag{3.4}
\end{equation*}
$$

Figure 3.2 Wet weights (mg) of Nephelopsis obscura under experimental ad libitum food conditions at $5^{\circ} \mathrm{C}, 10^{\circ} \mathrm{C}, 15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Table 3.1 Weekly mean wet weights (mg) of cohorts of Nephelopsis



Figure 3.3 Weight gain ( $\mathrm{mg} \mathrm{wk}^{-1}$ ) for Nephelopsis obscura with ad libitum food at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.

was plotted versus $W_{t}$, where $W_{t}$ is the weight at time $t$ (wk) (Figure 3.4). A trend for decreasing growth rate with increasing size is present, in a form suggesting an exponential decay process. Figure 3.5 is the $\log -\log$ transform of Figure 3.4, and appears linear which is consistent with the idea of exponential decrease in growth rate with increasing size. The regression equations (Sokal and Rholf 1976) fitted to the $20^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ data were:

$$
\begin{align*}
& \mathrm{pwc}_{20}=2.05 \exp (-0.1106 \mathrm{wt})  \tag{3.5}\\
& \mathrm{pwc}  \tag{3.6}\\
& 15=1.78 \exp (-0.0859 w t)
\end{align*}
$$

where wt is wet weight (mg). These equations are unacceptable as estimates of proportional growth rate since they predict zero growth rate (pwc $=1.0$ ) at 630 mg and 823 mg respectively, results that are inconsistent with the observed data (Figure 3.2).

Since no simple growth function was evident, a table lookup procedure was tried. Weight ranges were defined (Table 3.2) and the mean of the weekly proportional weight change (Figure 3.4) was computed for each weight range. To test the accuracy of these rates simulation runs were performed for 52 wk using constant temperatures of $20^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ representing the original experimental conditions. Growth rate as a function of size was determined by referring to Table 3.2 for the appropriate rate. The growth rates for 1638 mg at $20^{\circ} \mathrm{C}$ and 819 mg at $15^{\circ} \mathrm{C}$ were used when simulated weights exceeded these values (an extrapolation).

The results of the simulation (Figure 3.6) show that at $20^{\circ} \mathrm{C}$, the observed and simulated weights closely agree up to about 14 wk ,

Figure 3.4 Proportional weight change versus wet weight (mg) for Nephelopsis obscura with ad libitum food at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Figure 3.5 Logarithm of proportional weight change versus wet weight (mg) for Nephelopsis obscura with ad libitum food at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Table 3.2 Proportional growth rates of different weight classes of Nephelopsis obscura at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. Details of the method of calculation are given in the text.


Figure 3.6 Simulated and observed mean wet weight (mg) of Nephelopsis obscura versus age (wk) based upon the growth rates in Table 3.2.

while at $15^{\circ} \mathrm{C}$ there is close agreement up to about 22 wk . The lack of agreement between the remainder of the simulation and the observed weights was not due to extrapolation beyond 1638 mg at $20^{\circ} \mathrm{C}$ and 819 mg at $15^{\circ} \mathrm{C}$ since simulated weights were too high before extrapolation took effect. The proportional growth rates in Table 3.2 thus appear acceptable up to weights of about 102 mg at $20^{\circ} \mathrm{C}$ and 204 mg at $15^{\circ} \mathrm{C}$. From Figure 3.3 it would appear that the ages 14 wk at $20^{\circ} \mathrm{C}$ and 22 wk at $15^{\circ} \mathrm{C}$ are associated with the commencement of erratic growth and mortality in the experimental cultures, suggesting that data beyond these ages are inadequate for precise parameter estimation. Further analyses of these data were therefore abandoned.

Until more accurate data are available the following approximation will be used in the simulation. It was estimated from inspection of Figure 3.2, Figure 3.3 and Table 3.1 that had the experiment been executed as designed, the final mean weight after 52 wk would have been approximately 3000 mg at $20^{\circ} \mathrm{C}$ and 1000 mg at $15^{\circ} \mathrm{C}$. The difference between the last satisfactory simulated weight and estimated mean weights after 52 wk were divided by the number of weeks for which simulation was poor ( 38 wk at $20^{\circ} \mathrm{C}$ and 30 wk at $15^{\circ} \mathrm{C}$ ). These weekly weight gains (WWG) 76.3 mg for $20^{\circ} \mathrm{C}$ and 26.5 mg for $15^{\circ} \mathrm{C}$ ) were introduced into the following formula:

$$
\begin{equation*}
\text { pwc }=W_{t}+W W G / W_{t} \tag{3.7}
\end{equation*}
$$

where $W_{t}$ is weight at time $t$ from the generating function

$$
\begin{equation*}
W_{t}=W_{t-1}+W W G \tag{3.8}
\end{equation*}
$$

with $t$ starting from 14 wk or 22 wk for $20^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ respectively
using $W_{14}=102 \mathrm{mg}$ and $W_{22}=204 \mathrm{mg}$. The proportional growth rates generated from this procedure are presented in Table 3.3, and in the input data (Appendix B) were substituted for the growth rates in the bottom of Table 3.2 (from 102 mg at $20^{\circ} \mathrm{C}$ and 204 mg at $15^{\circ} \mathrm{C}$ ). Simulations were performed (Figure 3.7) by referring to this new table for weekly growth rates. Since agreement between simulation and experimental results was close, estimated growth rates from this table will be used until more accurate data become available.

Table 3.3 Proportional growth rates of different weight classes of Nephelopsis obscura at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. Details of the method of calculation are given in the text.

| $20^{\circ} \mathrm{C}$ |  |  | $15^{\circ} \mathrm{C}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| WeTght | CTass | Prop <br> Growth <br> Rate | Weight Class |  | $\begin{aligned} & \text { Prop } \\ & \text { Growth } \\ & \text { Rate } \end{aligned}$ |
| Lower Boundary (mg) | Upper Boundary (mg) |  | Lower <br> Boundary (mg) | Upper Boundary (mg) |  |
| 102.0 | 178.3 | 1.748 | 204.0 | 230.5 | 1.130 |
| 178.3 | 254.6 | 1.428 | 230.5 | 257.0 | 1.115 |
| 254.6 | 330.9 | 1.300 | 257.0 | 283.5 | 1.103 |
| 330.9 | 407.2 | 1.231 | 283.5 | 310.0 | 1.093 |
| 407.2 | 483.5 | 1.187 | 310.0 | 336.5 | 1.085 |
| 483.5 | 559.8 | 1.158 | 336.5 | 363.0 | 1.079 |
| 559.8 | 636.1 | 1.136 | 363.0 | 389.5 | 1.073 |
| 636.1 | . 712.4 | 1.120 | 389.5 | 416.0 | 1.068 |
| 712.4 | 788.7 | 1.107 | 416.0 | 442.5 | 1.064 |
| 788.7 | 865.0 | 1.097 | 442.5 | 469.0 | 1.060 |
| 865.0 | 941.3 | 1.088 | 469.0 | 495.5 | 1.057 |
| 941.3 | 1017.6 | 1.081 | 495.5 | 522.0 | 1.053 |
| 1017.6 | 1093.9 | 1.075 | 522.0 | 548.5 | 1.051 |
| 1093.9 | 1170.2 | 1.070 | 548.5 | 575.0 | 1.048 |
| 1170.2 | 1246.5 | 1.065 | 575.0 | 601.5 | 1.046 |
| 1246.5 | 1322:8 | 1.061 | 601.5 | 628.0 | 1.044 |
| 1322.8 | 1399.1 | 1.058 | 628.0 | 654.5 | 1.042 |
| 1399.1 | 1475.4 | 1.055 | 654.5 | 681.0 | 1.040 |
| 1475.4 | 1551.7 | 1.052 | 681.0 | 707.5 | 1.039 |
| 1551.7 | 1628.0 | 1.049 | 707.5 | 734.0 | 1.037 |
| 1628.0 | 1704.3 | 1.047 | 734.0 | 760.5 | 1.036 |
| 1704.3 | 1780.6 | 1:045 | 760.5 | 787.0 | 1.035 |
| 1780.6 | 1856.9 | 1.043 | 787.0 | 813.5 | 1.034 |
| 1856.9 | 1933.2 | 1.041 | 813.5 | 840.0 | 1.033 |
| 1933.2 | 2009.5 | 1.039 | 840.0 | 866.5 | 1.032 |
| 2009.5 | 2085.8 | 1.038 | 866.5 | 893.0 | 1.031 |
| 2085.8 | 2162.1 | 1.037 | 893.0 | 919.5 | 1.030 |
| 2162.1 | 2238.4 | 1.035 | 919.5 | 946.0 | 1.029 |
| 2238.4 | 2314.7 | 1.034 | 946.0 | 972.5 | 1.028 |
| 2314.7 | 2391.0 | 1.033 | 972.5 | 999.0 | 1.027 |
| 2391.0 | 2467.3 | 1.032 | 999.0 | 1025.5 | 1.027 |
| 2467.3 | 2543.6 | 1.031 |  |  |  |
| 2543.6 | 2619.9 | 1.030 |  |  |  |
| 2619.9 | 2696.2 | 1.029 |  |  |  |
| 2696.2 | 2772.5 | 1.028 |  |  |  |
| 2772.5 | 2848.8 | 1.028 |  |  |  |
| 2848.8 | 2925.1 | 1.027 |  |  |  |
| 2925.1 | 3001.4 | 1.026 |  |  |  |

Figure 3.7 Simulated and observed mean wet weight (mg) of Nephelopsis obscura versus age (wk) based upon the proportional growth rates in Table 3.3.


### 3.3 Summary


#### Abstract

Estimates of the maximum number of calories assimilated by an individual under ad libitum food conditions are necessary to terminate feeding in the simulation when satiation is attained and for the calculation of respiration rate. Maximal assimilation was calculated as the sum of maximal growth plus maximal respiration.

To date, no experiments have been successfully performed to determine the form of the growth trajectory of N. obscura. Continuing these experiments until the specimens die of old age would also provide information about the maximum life span of N. obscura, a value that has been inferred only from field sampling (Davies and Everett 1977). For the purposes of the simulation, a simple approximation of growth was used for weights greater than 204 mg at 150 C and 102 mg at 200 C .


## Chapter 4

## Respiration

### 4.0 Introduction

A large array of environmental and physiological influential factors have been found to influence the oxygen uptake rates of leeches. The associated literature on this topic has been critically reviewed by Wrona (1982). The factors include species differences, temperatures, oxygen availability, salinity, body size, stage of development, nutritional state, activity levels, acclimation and diurnal and seasonal rhythms. There are at least two problems associated with including all these variables in a simulation model. Some variables, such as activity and degree of acclimation change dynamically as the physiological circumstances of the animal change (i. e. as a function of the simulation output itself). Including them in the simulation would require that the model contain a set of sub-models to predict the necessary values, and there may also be a requirement to solve these sub-models iteratively, due to the dynamic feedbacks involved between them and the main simulation. Such an undertaking could be as extensive an endeavor as the present simulation. Secondly, the experiment necessary to investigate all the variables which influence respiration rate would be prohibitively large, especially if, interaction terms are important or if the relationships are not linear. Such an extensive data set is not available for N.obscura but some respiration rate determinations have been done. This chapter deals with the fitting of a response surface to the available data and makes suggestions for areas of further research.

### 4.1 Methods

### 4.1.1 Aerobic versus anaerobic respiration

Metabolism can use either aerobic or anaerobic pathways. Wrona (1982) investigated survivorship of N. obscura under anoxia at various temperatures. At $20^{\circ} \mathrm{C} 100 \%$ mortality occurred within 4 d , however at $5^{\circ} \mathrm{C}$, only $40 \%$ mortality had occurred after 30 d . These results suggest that N. obscura must have utilized anaerobic metabolic pathways in order to have survived. Estimates of respiration rate based upon only oxygen uptake (aerobic pathways) are available, so to the extent that N. obscura uses anaerobic pathways, these will be underestimates of respiration as will also be the case if anaerobic pathways are used under aerobic conditions.

### 4.1.2 Temperature, weight, ration and activity

Unpublished oxygen uptake data were obtained from F. J. Wrona and R. W. Davies. The design and operation of the apparatus used to make the determinations of oxygen uptake rate are presented in Wrona and Davies (1984). The independent variables used and their levels were: weight - l-2 $\mathrm{mg}, 20-30 \mathrm{mg}, 80-120 \mathrm{mg}$ and approximately 350 mg ; ration level - fed to satiation versus starved; and temperature $-5^{\circ} \mathrm{C}, 10^{\circ} \mathrm{C}, 1.5^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. Animals were acclimated for 28 d before readings were taken. Movements of the animals in the respirometry chambers were monitored concurrently to the measurement of oxygen uptake and activity was coded as to type (resting $=0$, random movement $=$ 1 , and ventilating movement $=2$ ).

To test whether oxygen uptake of randomly moving and ventilating animals were significantly different, a one-way analysis of covariance was performed on logarithm of respiration rate, with the main effects being the three levels of activity, and the remaining variables being included as covariates. The test for parallel lines among the covariates was not significant $\left(F_{(6,192)}=0.74, p \gg 0.05\right)$ while treatment effects were highly significant $\left(F_{(2,198)}=58.19, p \ll 0.001\right)$. A posteriori testing using Scheffe comparisons showed ventilating uptake and random movement uptake to be not significantly different (geometric means being 20.87 $\mathrm{ul} \mathrm{hr}{ }^{-1}$ and $20.77 \mathrm{ul} \mathrm{hr} r^{-1}$ respectively) but, the resting uptake rates were significantly smaller (geometric mean $=11.85 \mathrm{ul} \mathrm{hr}^{-1}$ ). Thus, randomly moving and ventilating animals were pooled into a class called active animals, and activity was thus simplified into a binary variable.

To fit a response surface to the data regression analysis was performed using Minitab (Ryan, Joiner and Ryan 1981) on the main effects and all interaction (cross product) terms. Interaction terms were included to account for curvature in the response surface. If the highest order interaction terms were not significant ( $\alpha=0.05$ ) they were removed from the regression model and the data refit to the reduced regression model. This procedure of iteratively reducing the model was repeated until only significant terms remained in the regression. Unless stated otherwise, this same iterative procedure was used for all remaining regressions performed for this thesis.

In some instances some of the independent variables (including interaction terms) were highly correlated with other variables in the regression model. This condition can arise due to real correlations among the data, or due to numerical instability in the regression algorithm
when there are large differences between scales of the independent variables. When this occurred, the means of the main effects independent variables were adjusted toward zero (coded - Sokal and Rholf 1969) by subtracting a value close to the observed mean from each of reading. In all cases this solved the problem of high correlation. Regressions were performed on these coded data and regression statistics reported for them. The regression equation was algebraically transformed back to the original mensural scales and these resulting coefficients reported as uncoded coefficients. The uncoded coefficients were used in the simulation model.

The equation (Table 4.1) resulting when this statistical procedure was applied to the respirometry data was programmed into subroutine RESPIR. This model of respiration is intended strictly as a predictive model, and no mechanistic interpretation is implied. The uncoded equation includes both main effects terms and interaction terms. The coefficients on the main effects terms describe the slope of the respiration rate response surface at the intercept (where all independent variables $=$ 0.0), while the coefficients on the interaction terms (cross products) describe how the slope of the response surface changes with increasing distance from the intercept. Three of the main effects terms have negative slopes at the intercept, which may not appear biologically reasonable, however, this region is outside the range of biological interest (eg. it does not make biological sense to discuss an individual of zero weight). Since all the interaction terms have positive coefficients it is expected that the gradient of this equation will be positive within the region of biological interest. This will be tested when simulations are performed.

Table 4.1 Regression equation of oxygen uptake ( $\mu \mathrm{l} \mathrm{hr}{ }^{-1}$ ) by Nephelopsis obscura. For numerical stability the independent variables were coded: temperature -13.0; ration -0.7; weight -200.0; activity -0.7. The coded coefficients are those generated by the regression algorithm, and the uncoded coefficients are those resulting from rearrangement of the regression equation back to the original mensural scales (see text). $S D=$ standard deviation of regression coefficient, $\mathrm{t}=$ regression coefficient/SD.

| Variable | Coded |  |  | Uncoded |
| :---: | :---: | :---: | :---: | :---: |
|  | Coefficient | SD | t | Coefficient |
| Intercept | 16.9496 | 0.4610 | 36.7 | 5.20593 |
| $\left({ }^{\circ} \mathrm{C}\right)$ | 1.11370 | 0.08159 | 13.6 | -0.58043 |
| Ration (R) | 10.641 | 1.173 | 9.0 | 1.2433 |
| Wet Wt (mg) (W) | 0.044819 | 0.003435 | 13.0 | -0.0105431 |
| Activity (A) | 10.4791 | 0.9298 | 11.2 | -7.0275 |
| $\mathrm{T} \times \mathrm{R}$ | 0.7229 | 0.2111 | 3.4 | 0.7229 |
| $T \times W$ | 0.0037529 | 0.000636 | 5.9 | 0.0037529 |
| $T \times A$ | 1.0938 | 0.1677 | 6.5 | 1.0938 |
| $W \times \mathrm{A}$ | 0.016436 | 0.006524 | 2.5 | 0.016436 |

### 4.1.3 Dissolved oxygen

Dissolved oxygen concentration was not included as an independent variable, although some determinations of oxygen uptake rate have been made under hypoxia. The available data for hypoxia (Wrona 1982) are for individuals that were maintained under hypoxia for 1 wk , and they showed a decreased oxygen uptake rate for the initial few days, and then an increase in oxygen uptake rate toward the end of the 1 wk period suggesting an acclimation response was occurring. This experiment thus measured pre-acclimation uptake rates and the data are therefore inappropriate for the model.

### 4.2 Discussion

The respiration equation (Table.4.1) is based upon only two ration levels (fed and starved) but the actual amount of food ingested by each individual was not measured. It is therefore necessary to assume that the relationship between ration and oxygen uptake rate is linear. If the relationship is concave-up, then this equation will tend to underestimate oxygen uptake rate at intermediate ingestion rates, while if the relationship is concave-down, the equation will overestimate oxygen uptake rate at intermediate ingestion rates.

A simple multiplicative increase in oxygen uptake rate was coded into subroutine RESPIR for reproductive individuals. This factor was determined from data obtained at only one temperature $\left(15^{\circ} \mathrm{C}\right.$ ) (Wrona 1982) and is assumed to apply for all temperatures at which reproduction occurs. Furthermore, it is assumed that there is an instantaneous switch from one respiration level to the next, rather than a gradual change in respiration rate over a number of weeks. It was also assumed that this increased respiration rate applies to only the period of cocoon production. Since reproductive respiration rate was measured independently from the rates used to determine the equation in Table 4.1, it was also necessary to assume no interaction among reproductive condition and the other variables.

The estimates of metabolic rate are based upon oxygen uptake rate. Since the currency of the model is calories, it was necessary to convert the estimates of oxygen uptake into estimates of the number of calories liberated through catabolism. However, the conversion depends
upon the chemical nature of the substrate being catabolized (Guise 1968) as follows:

| Substrate | $0^{2}$ Col $\mu 1^{-1}$ of |
| :--- | :--- |
|  | 0.005007 |
| Glucose | 0.004686 |
| Fat | 0.004500. |

The amount of oxygen consumed to liberate 1 cal of energy from the food assimilated will vary depending upon which of these substrates is being metabolized, which will in turn depend upon their relative proportions in the prey item and the nutritional state of the individual. As no data are available regarding either the chemical composition of the assimilated fraction of a prey item, or the proportions of various substrates being metabolized under different circumstances, the arithmetic mean ( 0.004731 ) of these values was used in subroutine RESPIR. Errors in this estimate will have an inverse relationship with the simulated growth, but will be small due to the small variation among the substrates.

## Chapter 5

## Feeding rates

### 5.0 Introduction

The feeding rate of N. obscura was measured by Anholt (1982) using Chironomidae and Oligochaeta as prey. Since he used only one size of predator, and conducted his experiments at only one temperature $\left(20^{\circ} \mathrm{C}\right.$ ) these data were insufficient for the purposes of the model. Laboratory experiments were therefore performed to measure feeding rates of N. obscura as a function of temperature, prey density, prey type and predator size.

There are a number of factors which could potentially influence the rate of prey ingestion by $\mathrm{N}_{0}$ obscura. In the field, a number of prey. types are likely to be present simultaneously, so it would be expected that N. obscura would consume a mixture of them. The relative proportions of the prey types present at any one time would be expected to alter the proportion of each type taken, based simply on probability of encounter. . Imposed upon this may be some form of prey discrimination by the predator. (search image or preference for example) such as that observed by Anholt (1982) in which the proportion of Oligochaeta prey decreased to zero when N. obscura was offered increasing densities of Chironomidae and Oligochaeta in equal proportions. Prey of the same species but of different sizes may be consumed in different proportions by different sized predators. For instance, large N. obscura may tend to take larger prey of a particular prey species than are taken by smaller individuals, or, alternatively, small N. obscura may prefer a smaller prey species such as Cladocera relative to larger
prey such as Chironomidae. A further factor to be considered is the spatial distribution of prey. Hatchlings of N. obscura emerging from cocoons deposited on the upper portions of macrophytes would be exposed to Cladocera in the water column and Chironomidae which live on plants, but would not be exposed to other Chironomidae species located on the mud substrate below. Unfortunately, it is not known at what size $N_{\text {. obscura }}$ hatchlings move off the macrophytes and down onto the mud. It is also to be expected that temperature may influence the rate of prey capture.

### 5.1 Chironomidae as prey

The main prey types consumed by larger N. obscura in Stephenson's Pond are Oligochaeta and Chironomidae (Anholt 1982), but since the consumption rate of Oligochaeta is very low (Anholt 1982) the experiments for large N. obscura were conducted using only Chironomidae as prey. Driver (1977) found typically 21 chironomid species in permanent ponds of sizes comparable to Stephenson's Pond but in 1981 in Stephenson's Pond there were only two abundant species of Chironomidae (Glyptotendipes paripes (Edwards) and Chironomus riparius Meigen) (Rasmussen, 1983) as was the case when the present experiments were conducted. It would thus appear that Stephenson's Pond is relatively depauperate in Chironomidae species. Since the present experiments were conducted in winter, only large Chironomidae instars were available for collection, so prey size effects upon capture rates could not be investigated.

### 5.1.1 Prey collection and acclimation

Sediments containing Chironomidae prey were collected from Stephenson's Pond through holes cut in the ice. The sediments were either returned to the laboratory (if sediments were required for laboratory experiments) or sieved using a 450 um mesh sieve bucket (if only the Chironomidae were required). Collections were made weekly or more frequently from November through March. Chironomidae were maintained in the laboratory at $5^{\circ} \mathrm{C}$ for no longer than 1 wk prior to the experiments. When experimental temperatures were greater than $5^{\circ} \mathrm{C}$, the Chironomidae were acclimated to the experimental temperatures in steps no greater than $5^{\circ} \mathrm{C}$ per 12 hr . Mean Chironomidae wet weight from each of
three samples each of 100 pooled individuals, collected at various times throughout the experiment were $5.9 \mathrm{mg}, 5.4 \mathrm{mg}$, and 5.7 mg .

### 5.1.2 Nephelopsis obscura collection and acclimation

Nephelopsis obscura collection and acclimation procedures were the same as for Chironomidae, however, individuals of N. obscura were acclimated to the experimental temperature for a minimum of $l$ wk. N. obscura was acclimated to the experimental prey density for a minimum of 3 d (Arholt, 1982) before being placed into the experiments.

### 5.1.3 Preliminary experiments

### 5.1.3.0 Introduction

Before experiments measuring the rate of Chironomidae capture by N. obscura were performed, a series of preliminary experiments were undertaken to investigate possible experimental bias due to: 1) Chironomidae death in the experiments which may be confused with predation; 2) N. obscura egestion of whole prey which may be missed in the count of numbers captured; 3) N. obscura discriminates between genera of Chironomidae as suggested by Anholt (1982), requiring that the proportions-of Chironomidae genera in the experiments be controlled.

### 5.1.3.1 Substrate

The substrate to be used in the experiments was pond mud that passed through a 450 um sieve but was retained on a $250 \mu \mathrm{~m}$ sieve. Chironomidae that passed through the $450 \mu \mathrm{~m}$ sieve and were thus entrained within the experimental substrate were eliminated by heating the sieved mud to $50^{\circ} \mathrm{C}$, cooling it, and then inoculating it with pond
water to introduce a bacterial flora. Examination of this mud at regular intervals after heating showed that after $4 d$ no remains of Chironomidae were visible.

To determine whether Chironomidae would survive in the previously heat treated mud, 56 Chironomidae were placed in a 250 ml plastic container with $28 \mathrm{~cm}^{2}$ of bottom area and 2 cm depth of mud, (approximately the same arena size used by Anholt (1982)). This container was maintained at $20^{\circ} \mathrm{C}$ for 72 hr ( 24 hr longer than the experiments) after which time there had been zero mortality.

### 5.1.3.2 Chironomidae acclimation time

To determine how long the Chironomidae required to construct tubes in the sieved mud, 56 Chironomidae were placed into a container maintained at $5^{\circ} \mathrm{C}$ (the experimental temperature at which it was assumed that tube building rate would be minimum). After $29 \mathrm{hr} 87.5 \%$ of the Chironomidae had built tubes, Extrapolation of this result suggested that after $34 \mathrm{hr} 100 \%$ of the Chironomidae should have built tubes. For a safety margin, Chironomidae were allowed 48 hr in the experimental containers before $N$. obscura were introduced.

### 5.1.3.3 Egesta

N. obscura that consumed a large number of prey might egest prey parts which could potentially be confused with dead Chironomidae present in the experimental chambers at the end of the experimental period. Five replicate experiments were' set up in each of which one N. obscura, initially maintained in substrate containing a high density
of Chironomidae, was placed in a petri dish with 20 Chironomidae and no substrate, thus enabling N. obscura to feed at a rate much higher than that expected in experiments with substrate. This experiment was checked regularly and Chironomidae added as they were consumed. After 48 hr (the length of most subsequent experiments) no egesta which could be confused with live Chironomidae were found. It was thus concluded that egesta would not be a confounding factor in the functional feeding response experiments.

### 5.1.3.4 Prey preference without substrate

To determine if there was a different rate of predation on the two genera of Chironomidae as suggested by Anholt (1982) a sample of Chironomidae collected from the field was identified to genus. There was a 1:4 ratio of Chironomus : Glyptotendipes and very rare occurrences of Cryptochironomus. One N. obscura, 13 Chironomus and 7 Glyptotendipes were placed in a petri dish with no substrate. After 24 hours at $20^{\circ} \mathrm{C}$ one Chironomus and five Glyptotendipes had been consumed, a result significantly different from the rate expected for no discrimination between prey types (probability $=0.022$ based upon exact calculation of the probabilities of the binomial with parameters $p=0.65, q=0.35$ and $n$ $=6$ ).

### 5.1.3.5 Prey preference with substrate

To determine whether this result would also be obtained in experiments with substrate, five replicate experiments were performed at $20^{\circ} \mathrm{C}$, in $28 \mathrm{~cm}^{2}$ arenas each with 2 cm depth of mud, 56 Chironomidae identified to genus, and one N. obscura (mean wt $=366.8 \mathrm{mg}, \mathrm{SD}=41.5 \mathrm{mg}$ )
per arena. Five replicate controls without N. obscura were also established, from which it was later possible to recover all Chironomidae. Thus, Chironomidae missing from the experimental containers were assumed to be eaten. During the experiment, some Chironomidae pupated, so were not identified at the conclusion of the experiments. All other remaining Chironomidae were identified.

The pupae as well as the Chironomidae eaten were classified as "unaccounted for" and $2 \times 2$ contingency tables were constructed for each replicate, as well as for the pooled data. Each replicate and the pooled data were tested for heterogeneity and independence of classification using a chi-square test corrected for continuity (Table 5.1) (Parker, 1979). There was significant heterogeneity, suggesting that replicates were significantly different, so could not be pooled. Replicates 1 and 4 showed chi-square values larger, than the alpha=0.05 critical value of 3.84 ( $\mathrm{df}=1$ ) suggesting discrimination by N. obscura, while the remaining three showed no significant difference.

When the replicates are ranked according to their chi-square value, the ranking of the number of pupae in each replicate followed the same order, suggesting that the significant differences between the species were due to differential pupation rather than differential prey consumption. To test this, pure cultures of each of Chironomus and Glyptotendipes were established and after 1 wk (a period longer than the experiment) Chironomus pupated whereas Glyptotendipes did not. Under the assumption that all the pupae in the original experiment were Chironomus, chi-square statistics were recalculated and no significant differences were found. Therefore it would appear that there was no

Table 5.1 Chi-square ( $X^{2}$ ) analysis of the feeding rates of Nephelopsis obscura on Chironomus riparius (Chir.) and Glyptotendipes paripes (Glyp.) Significant differences indicated by * at $p<0.05, * *$ at $p<0.01$ and $* * *$ at $p<0.001$.

| Arena | Initial counts |  | Final counts ( 72 hr ) |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Chir. Glyp. |  | Chir. Glyp. Pupae Eaten $\overline{X^{2}}$ |  |  |  |  |  |
| 1 | 20 | 36 | 14 | 35 | 3 |  | 4 | 8.355** |
| 2 | 20 | 36 | 18 | 35 | 0 |  | 3 | 1.346 |
| 3 | 13 | 43 | 12 | 38 | 0 |  | 6 | 0.594 |
| 4 | 15 | 41 | 10 | 37 | 2 |  | 7 | 4.142* |
| 5 | 17 | 39 | 13 | 36 | 1 |  | 6 | 2.476 |
| df |  |  |  |  |  |  |  |  |
| Independence of Classification |  |  |  |  | (1) | 11.094*** |  |  |
| Heterogeneity |  |  |  |  | (4) |  | 5.819** |  |
| Total |  |  |  | (5) 16 |  |  | 16.913 |  |

differential predation upon the two prey species when substrate is present and they can thus be classified simply as Chironomidae prey.

### 5.1.3.6 Arena size

The arenas used for the previous experiment (section 5.1.3.5) were approximately the same size as those used by Anholt (1982) and were chosen to determine whether our results are comparable, hence eliminating the need to repeat his experiments. Under comparable conditions of temperature, prey density and leech size there was good agreement between his results (approximately 2.0 Chironomidae leech ${ }^{-1}$ $d^{-1}$ ) and those of the above experiment (1.73 Chironomidae leech ${ }^{-1}$ $\left.d^{-1}\right)$. However, after observing the behaviour of N. obscura in the arenas it was felt that the arenas may have been too small and thus have an effect on the predation rate.

To test for the effect of arena size, the feeding experiment was repeated using two other arena sizes ( $60 \mathrm{~cm}^{2}$ and $227 \mathrm{~cm}^{2}$ ). There were two N. obscura used in the $60 \mathrm{~cm}^{2}$ arenas, and eight in the $227 \mathrm{~cm}^{2}$ (mean N. obscura wet wt $=335 \mathrm{mg}, \mathrm{SD}=46 \mathrm{mg}$ ) arenas, providing a constant predator density of approximately one N. obscura per $29 . \mathrm{cm}^{2}$ of substrate. The prey density used was 2 Chironomidae $\mathrm{cm}^{-2}$. Both predator and prey densities were comparable to field densities (Rasmussen 1983). Experiments were conducted at $20^{\circ} \mathrm{C}$. Due to the increased time requirements for processing these larger arenas, only three replicates of the middle sized and two replicates of the large arenas were used. The result obtained for each arena represents a mean for a number of N. obscura.

Figure 5.1 Capture rate ( $d-1$ ) of Chironomidae prey by Nephelopsis obscura versus experimental arena size (prey density $2 \mathrm{~cm}^{-2}$ ).


There was a highly significant arena size effect (Figure 5.1). with the largest arenas giving predation rates in the order of two fold higher than the smallest arenas. Therefore, it was inappropriate to use the results of Anholt (1982) since they were biased due to the small size of the arenas used. Most of the container effect had disappeared at an arena size between the medium and large arena (Figure 5.1), thus the largest arenas were used to estimate functional feeding response of N. obscura feeding on Chironomidae (section 5.1.4).

### 5.1.3.7 Discussion

These preliminary experiments have shown that the experimental arenas do not stress the Chironomidae prey, hence non-predation mortality cannot be confounded with predation mortality. Further, N. obscura does not egest whole prey which might decrease the estimate of predation rate.

Anholt (1982) reported that N. obscura has different predation rates upon Chironomus and Glyptotendipes, while the present experiments do not support this conclusion. Since Anholt's experiments were conducted at the same time of year, at the same experimental temperatures, with comparable sized arenas and with comparable. sized Chironomidae to those used here, the reason for the disparity between the two studies is not clear.

Arena size effects upon predation rate were very strong, with smaller arenas yielding reduced capture rates. It appears that the arena-size effect becomes negligible when arena diameter is in excess of twice the total body length of N. obscura.

### 5.1.4 Functional feeding response

### 5.1.4.0 Introduction

The relationship between prey capture rate and prey density is referred to as a functional feeding response (Holling 1959a). The three basic forms of the response identified by Holling (1964) are: Type I a linear increase in capture rate with prey density; Type II - a rapid rise in capture rate with initial increase in prey density, followed by a constant rate of prey capture at higher densities; and Type III - an S shaped response with an initial low rate of capture at low prey densities, followed by a rapid increase in prey capture rate at intermediate densities, followed by a plateau in capture rate. The Type II response can be linearized by plotting capture rate versus (capture rate)/(prey density) if Holling's (1959b) disk equation models the feeding process.

### 5.1.4.1 Methods

To provide estimates of Chironomidae capture rates for the simulation model, a three factor experimental design was used with three levels per factor: prey density $-3 \mathrm{~cm}^{-2}, 2 \mathrm{~cm}^{-2}$ and $0.5 \mathrm{~cm}^{-2}$; predator size - small ( 100 mg to 130 mg ), medium ( 300 mg to 400 mg ) and large ( 500 mg to 600 mg ) and temperature $-5^{\circ} \mathrm{C}, 12.5^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. The prey densities of $0.5 \mathrm{~cm}^{-2}$ and $3.0 \mathrm{~cm}^{-2}$ were above and below ambient field prey densities for Chironomidae of the size used in the experiments (Rasmussen 1983). N.`obscura sizes used approximately spanned the range in the field. The minimum N. obscura body size used was based upon a preliminary experiment that showed that individuals $<80 \mathrm{mg}$ wet wt took none of the large Chironomidae used in these experiments.

The arenas used were $227 \mathrm{~cm}^{2}$ (section 5.1.3.6) and contained previously heated pond mud for substrate (section 5.1.3.1). Control arenas with no N. obscura were established for all treatments.

Stephenson's Pond warms quickly in spring and cools quickly in fall (Figure 3.1), so most of the time the temperature is either cold (about $2-3^{\circ} \mathrm{C}$ ) or warm ( $>12.5^{\circ} \mathrm{C}$ ) with intermediate temperatures being transitional and brief in spring and fall. The experiments at $5^{\circ} \mathrm{C}$ approximated field winter temperature, and $12.5^{\circ} \mathrm{C}$ and $20.0^{\circ} \mathrm{C}$, represented the approximate summer minimum and maximum temperatures respectively (Figure 3.1). For a series of experiments using large N. obscura, high prey densities and all three experimental temperatures there was no detectable prey consumption at $5^{\circ} \mathrm{C}$ after 48 hours. Extrapolation of the $20^{\circ} \mathrm{C}$ and $12.5^{\circ} \mathrm{C}$ rates for these initial experiments suggests that feeding stops at about $11^{\circ} \mathrm{C}$. Thus the $5^{\circ} \mathrm{C}$ temperature in the experimental design was changed to $15^{\circ} \mathrm{C}$, intermediate in the range of summer temperatures.

### 5.1.4.2 Results

The rates of capture of prey by, small, medium and large N. obscura are presented in Figures 5.2 through 5.4 as functions of prey density and temperature. A linear model (Holling's (1965) Type I) was used to fit the functional feeding response surface using multiple regression with all independent variables and their interaction terms (Table 5.2). The main effects coefficients in this equation are all positive as would be expected, and the first order interaction terms are negative, suggesting a flattening of the response surface with increasing distance from the origin (see section 4.1.2). This flattening will be ameliorated to some

Figure 5.2 Capture rates ( $\mathrm{d}-1$ ) of Chironomidae prey by small $100-130 \mathrm{mg}$ ) Nephelopsis obscura, versus Chironomidae prey density $\left(\mathrm{cm}^{-2}\right)$ at $12.5^{\circ} \mathrm{C}, 15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Figure 5.3 Capture rates ( $\mathrm{d}^{-1}$ ) of Chironomidae prey by medium (300-400 mg) Nephelopsis obscura, versus Chironomidae prey density $\left(\mathrm{cm}^{-2}\right)$ at $12.5^{\circ} \mathrm{C}, 15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Figure 5.4 Capture rates ( $\mathrm{d}^{-1}$ ) of Chironomidae prey by large ( $500-600 \mathrm{mg}$ ) Nephelopsis obscura, versus Chironomidae prey density $\left(\mathrm{cm}^{-2}\right)$ at $12.5^{\circ} \mathrm{C}, 15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Table 5.2 Regression of the functional feeding response of Nephelopsis obscura feeding on Chironomidae. For numerical stability the temperature and predator weight data were coded ( -15 and -300 respectively) before regression (see Section 4.1.2). The coefficients for the coded and uncoded data are presented, along with statistics for the coded coefficients. $\mathrm{SD}=$ standard deviation of the regression coefficient, $t=$ regression coefficient/SD.

|  | Coded |  |  | Uncoded |
| :---: | :---: | :---: | :---: | :---: |
|  | Coefficient | SD | t | Coefficient |
| Intercept | -0.0270 | 0.1855 | -0.15 | -1.3854 |
| $\begin{array}{r} \text { Prey density }(P) \\ \left(\mathrm{cm}^{-2}\right) \end{array}$ | 0.89518 | 0.09038 | 9.90 | 1.16518 |
| $\underset{\left({ }^{\circ} \mathrm{C}\right)}{\text { Temperature }}$ | -0.0242 | 0.05660 | -0.43 | 0.06706 |
| Wet wt (mg) (B) | 0.001175 | 0.001053 | 1.12 | 0.005738 |
| $\mathrm{P} \times \mathrm{T}$ | 0.05849 | 0.03028 | 5.23 | -0.03729 |
| $\mathrm{P} \times \mathrm{B}$ | 0.0009645 | 0.0005282 | 1.83 | -0.0088245 |
| T $\times$ B | -0.0003042 | 0.0003340 | -0.91 | -0.0003042 |
| $P \times T \times B$ | 0.0006526 | 0.0001900 | 3.43 | 0.0006526 |
| $\mathrm{df}=20 \quad \mathrm{r}^{2}$ | $=0.939$ |  |  |  |

extent by the highest order interaction term. This equation was programmed into subroutine ACTASS to estimate the actual assimilation rate. A wet weight to calories conversion for Chironomidae ( $0.8015 \mathrm{cal} \mathrm{mg}^{-1}$ ) was obtained from D. J. Baird (pers. comm.).

### 5.1.4.3 Discussion

In experiments in which $\mathrm{N}_{\mathrm{o}}$ obscura was offered a mixture of G. paripes and C. riparious prey in arenas with no substrate, N. obscura consumed significantly more G. paripes than expected from random choice; but in experiments in which mud substrate was included in the arenas, there was no significant difference between the capture rates of the two prey types. The reasons for the difference in results between these experiments is not clear. In the experiment without substrate the Chironomidae were not able to build tubes or feed. Anholt (1982) reports that when substrate is present C. riparious spends a greater proportion of its time out of its tube than G. paripes. It is thus possible that G. paripes is more stressed than C. riparious when it is not in a tube. If this leads to $\underline{G}$. paripes more actively searching for tube building materials than C. riparious, there may be an increase in its encounter rate (and hence capture rate) with N. obscura. It is also possible that increased activity of G. paripes while searching for tube building material leads to exhaustion and hence less efficient escape behaviour. Increased metabolic rate due to stress or metabolic differences between species could also result in G. paripes being stressed by starvation more quickly in arenas without food, and thus suffering a reduction in escape efficiency. Escape efficiency could also be reduced
if the physical characteristics of a mud substrate are associated with retreat into tubes embedded in the mud.

This study also demonstrated a marked reduction in the capture rates of Chironomidae prey by N. obscura $^{\text {as arena size decreased. }}$ The greatest reduction in capture rate appeared to occur when the diameter of the arena was less that the the length of N. obscura. Small arenas may restrict the foraging efficiencies of N. obscura, or it may tend to forage less actively if its movements are restricted. In the smallest arenas N. obscura tended to lay along the junction between the surface of the mud substrate and the wall of the arena, but in larger arenas N. obscura tended to forage more actively over the surface of the mud. Since N. obscura uses the solid walls of the arena for attachment of its posterior sucker, it is also possible that increased time spent foraging is associated with the proportional decrease in wall circumference to surface area of mud which occurs in larger arenas. Thus, it is expected that both decreased crowding and a proportional decreased in solid substrate for attachment lead to increased foraging time with an attendant increase in prey capture rate.

Based upon a regression of feeding rate versus temperature from the complete data set, feeding rate was predicted to become zero at $8.8^{\circ} \mathrm{C}$ Field data show that $\mathrm{N}_{0}$ obscura does feed at a low rate under winter ice-covered conditions (Davies, Wrona and Everett 1978). The estimate of $8.8^{\circ} \mathrm{C}$ is based upon a straight line extrapolation from the experimental data to the temperature axis. The fact that feeding occurs in the field at temperatures much lower than $8.8^{\circ} \mathrm{C}$ indicates that the relationship between feeding rate and temperature cannot be linear. Rather, the function must show an increasing slope as temperature
increases up to the experimental temperatures. It should also be noted that the estimate of $8.8^{\circ} \mathrm{C}$ is an approximation that is influenced by the mean prey densities and mean predator sizes used in the experiments. Since both of these variables also influence prey capture rate (Table 5.2), it is not possible to exactly predict at what temperature feeding ceases without specifying values for these covariates. The prey capture rate equation predicts that large N. obscura experiencing high prey densities will continue feeding at colder temperatures than small individuals experiencing low prey densities. Further, it is possible that under winter conditions the feeding rate necessary for maintenance might be sufficiently small that excluding it from the simulation will result in only minor errors in estimated body size (tested in Chapter 6).

Although Anholt (1982) reports a Holling (1965) Type II functional feeding response for $N$. obscura feeding on Chironomidae, the present study does not support this conclusion. Careful examination of the figures presented by Anholt (1982) reveals that his highest prey density treatment ( 3.5 Chironomidae $\mathrm{ml}^{-1}$ ) is most influential in producing the flattening of the curve which defines a Type II response, and that at this density the confidence interval on the mean is so broad that it approaches zero, and exceeds values consistent with a linear relationship. The extreme variability of his data makes it impossible to distinguish between a Type I and a Type II response.

### 5.2 Functional feeding response on Cladocera prey

### 5.2.0 Introduction

In the field, small individuals of N. obscura feed on Chironomidae and Cladocera/Copepoda (Davies, Wrona and Everett 1978). Since small individuals ( $<80 \mathrm{mg}$ ) of N . obscura did not take Chironomidae in the above functional feeding response experiments (Section 5.1.4) it is expected that the results reported by these authors are due to N. obscura feeding on smaller sized Chironomidae than were available for the above experiments. However, Cladocera were available, so these were chosen as the experimental prey for small specimens of N. obscura.

### 5.2.1 Methods

Cladocera were collected from the second sewage lagoon at Bow River Correctional Centre, Calgary, Alberta, maintained in laboratory culture at room temperature and fed on baker's yeast. The specimens of. N. obscura used in the experiments were collected from Stephenson's Pond and acclimated to the experimental temperatures for 1 wk . The experimental temperatures used were $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$. Cladocera densities in the sewage lagoon were estimated to be approximately $1 \mathrm{ml}^{-1}$, so prey density in the experiments were set at $0.25 \times, 1 \times, 4 \times$ and $8 \times$ this field density. N. obscura used in the experiments were $5-10 \mathrm{mg}$, $20-30 \mathrm{mg}$ and $40-70 \mathrm{mg}$. The experimental design thus had 18 cells, with three factors: temperature (two levels); prey density (four levels); and predator size (three levels).

Since the Cladocera prey do not dwell in mud substrate and small individuals of N. obscura appear to forage on Potamogeton plants
in Stephenson's Pond rather than on the mud substrate of, the pond, no substrate was used in the experimental arenas. The size of the experimental arena was changed with each experimental size class of N. obscura so that the diameter of the arena was always at least three times the length of the largest leech. N. obscura was acclimated to the prey density for 3 d before being introduced to the experimental arenas. Each experiment was run for 6 hr . To prevent undue prey depletion, the water was changed every 3 hr and a new set of prey added at the experimental density.

A Phillipson (1964) microbomb calorimeter was used to determine the calorific content of a pooled sample of Cladocera (Table 5.3).

### 5.2.2 Results

Capture rate increased with increasing prey density up to a prey density of four Cladocera $\mathrm{ml}^{-1}$ (Figure 5.5 and 5.6 ) and then remained relatively constant thereafter, indicating a Holling (1965) Type II response. Plots of capture rate versus (capture rate)/(density) gave no indication of a linear relationship so did not support the Holling (1959) disk-equation model. A t-test comparing capture rates at prey density $4 \mathrm{ml}^{-1}$ versus capture rate at prey density $8 \mathrm{ml}^{-1}$ was not significant. Prey capture rate was fit to the variables temperature, prey density (with the $8 \times$ data excluded), predator size and all interaction terms. The resulting equation (Table 5.4) was used in the simulation model (subroutine ACTASS) to estimate Cladocera prey capture rates.

Table 5.3 Conversion from wet weight to dry weight and dry weight to calories for Cladocera.


Figure 5.5 Cladocera prey capture rate ( $\mathrm{hr}^{-1}$ ) by Nephelopsis obscura versus prey density $\left(\mathrm{ml}^{-1}\right)$ at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Figure 5.6 Cladocera prey capture rate ( $\mathrm{hr}^{-1}$ ) by Nephelopsis obscura versus Nephelopsis obscura wet weight (mg) at $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$.


Table 5.4 Regression of the functional feeding response of Nephelopsis obscura on Cladocera. For numerical stability the temperature and predator weight data were coded ( -17 and -30 respectively) before regression (see Section 4.1.2). The coefficients and regression statistics for these coded data are presented along with the coefficients resulting from algebraic rearrangement of the regression equation' back to its original mensural scales. $S D=$ standard deviation of the regression coefficient, $\mathrm{t}=$ regression coefficient/SD.


### 5.2.3 Discussion

No estimates of Cladocera prey density are available from Stephenson's Pond, however they are most abundant in spring and fall when blooms of the blue-green alga Aphanizomenon flos-aquae ( $L$ ) Ralfs are not present. Until data are available, Cladocera prey density data will be simulated using an equation for a downward facing parabola:

$$
\begin{equation*}
P D_{t}=-a t^{2}+b \tag{5.1}
\end{equation*}
$$

where $P D_{t}$ is prey density at time $t$ weeks from the mid-point of the Cladocera bloom, and $a$ and $b$ are parameters that can be used to adjust the shape of the distribution. This equation generates a symmetric distribution of Cladocera densities over time, with its maximum at the centre of the bloom. The parameter $b$ sets the maximum Cladocera density and the parameter a is used to adjust the width of the distribution. The value of the parameter a can be obtained by solving the equation

$$
\begin{equation*}
a=b / t_{0}^{2} \tag{5.2}
\end{equation*}
$$

where $t_{0}$ is the number of weeks from the mean at which it is desired that $P D_{t}$ becomes zero. This equation is intended only as a rough estimate of Cladocera density and is to be removed from the simulation model when field data become available.

### 5.3 Assimilation efficiency

### 5.3.0 Introduction

The equations developed in Section 5.1 and 5.2 can be used to estimate food ingestion rates, however the model requires estimates of the amount of food assimilated, rather than simply the amount ingested. No estimates of assimilation efficiency could be found in the literature for N. obscura so experiments were carried out to estimate it.

### 5.3.1 Methods and Results

Two groups of ten N. obscura ranging in size from approximately 90 mg to 380 mg were acclimated to $10^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ for 1 wk while being fed Tubifex tubifex (Linn.) ad libitum. Each N. obscura was maintained in its own container of dechlorinated tap water so that its food consumption and weight gains could be monitored. After acclimation the animals were fed a preweighed amount of food every 3 d , for a total of 27 d . Food remaining 24 hr after it was supplied was weighed, as was the leech. Food consumed was determined as the difference between food supplied and food remaining.

Using the respirometry equation derived in Chapter 4, the metabolic costs of each individual were estimated over each of the 3 d periods, and converted from calories to mg wet wt of T. tubifex using the relationship

```
calories = 1.066 T. tubifex wet wt - 0.528
```

(Calow and Riley 1980). The caloric equivalent of the growth of each N. obscura over each 3 d period was determined using the conversion
factor $0.6577 \mathrm{cal} \mathrm{mg}^{-1}$ (determined using a Phillipson (1964) microbomb calorimeter), which was then converted into equivalent wet wt of T. tubifex using equation [5.3].

Assimilation efficiency was computed using two different methods. In one, the T. tubifex wet weight equivalents of respiration and growth in each 3 d period were summed and divided by the wet wt of T. tubifex actually consumed during the 3 d period. The mean of the nine estimates for each animal was then taken. In the other method, the total T. tubifex equivalents for respiration and growth over the 27 d period was divided by the total wet wt of T. tubifex consumed over the 27 d period. For each method of calculation the estimates for $10^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ were compared using a t-test and no significant difference was found for either method between temperatures, so the estimates from the two temperatures were pooled and the mean taken for each method (method one: mean $=0.773, \mathrm{SE}=0.0018$; method two: mean $=0.807$, $S E=0.024$ ). Since no justification could be seen for choosing one method over the other, the mean of all 32 estimates ( $0.79, \mathrm{SE}=$ 0.028 ) was used to estimate assimilation efficiency in subroutine ACTASS.

### 5.4 Discussion

The feeding rates of N. obscura on Chironomidae measured by Rasmussen (1983) in field enclosures were much lower than the rates obtained in this study. There are a number of reasons for this discrepancy. His experiments were performed in August through October, when temperatures were declining toward the winter minimum (Figure 3.1). It would be expected that the N. obscura was not feeding or had a greatly reduced feeding rate during this time (Section 5.1.4.3). Furthermore since he was attempting to investigate the influence of N. obscura populations on Chironomidae populations the N. obscura used in his experiment ranged from 20 mg to 250 mg . The present study has shown that N. obscura $<80 \mathrm{mg}$ wet wt are unable to consume the large $4^{\text {th }}$ instar Chironomidae present in Rasmussen's (1983) experiments. Thus, his estimates of prey consumption per predator will be lower than the rates obtained here.

The functional feeding response of N. obscura feeding on Cladocera showed a marked deviation from linearity, but, the response cannot be fit to Holling's (1959b) disk equation. Up to a prey density of $4 \mathrm{ml}^{-1}$ the increase in capture rate appears to be linear, suggesting that in this region capture rate may be related to the frequency of encounter between N. obscura and Cladocera. There was no detectable increase in capture rate between prey densities of $4 \mathrm{ml}^{-1}$ and $8 \mathrm{ml}^{-1}$, possibly suggesting that N. obscura became satiated at a prey density in the region of $4 \mathrm{ml}^{-1}$, so did not increase prey consumption rate at higher prey densities. This is speculation which must be confirmed by further experimentation.

## Chapter 6

## Validation and verification of the growth model

### 6.0 Introduction

Verification is the process of determining the correctness of the model with regard to its intended algorithmic structure (Mihram 1981). Validation is the process of comparing the output from the verified model with the behaviour of the real world system being modelled, and as such investigates the correctness of the conceptual model which the simulation is designed to emulate. These two endeavours are interrelated and on-going throughout the process of model building, rather than being performed upon completion of the simulation model. For instance, in the present case the correctness and validity of a number of relationships describing various aspects of the growth of an individual have been investigated and those which were successful have been discussed in Chapters 3 through 5. Those which have been incorporated into the model appear to be reasonable representations of the underlying conceptual model (Figure l.1), and in this context have been verified. Further, an attempt has been made to identify those variables which, based upon either published literature or basic biological principles, could be expected to have an influence upon various aspects of the growth process. Those for which data were available were incorporated into the model. When data were lacking or insufficient, experiments were conducted to obtain the riecessary information when this was feasible. A number of variables expected to influence growth have been excluded from the model due to lack of data, and by their exclusion, the structure of the simulation is not a faithful representation of its underlying
conceptual model. Research is now being undertaken into some of these neglected aspects of the biology of N. obscura. As these new data become available, they will be incorporated into the simulation by future researchers as the cycle of research and synthesis continues.

In this chapter, the verification and validation of the growth model will be discussed and, the behaviour of the simulation under a variety of environmental circumstances will be investigated.

### 6.1 Sensitivity analysis

The output from a simulation model depends upon the values of the parameters in the model. In the present case; most of the model parameters have been estimated statistically, and thus there is a degree of statistical uncertainty regarding the accuracy of each parameter. Since choosing a slightly different value of a parameter may influence the simulation result it is desirable to determine how sensitive the simulation is to potential errors in the values of each parameter. To perform sensitivity analysis (Miller 1979) a simulation run with all model parameters set at their estimated values (the baseline run) is made, then each parameter in the model is in turn altered by a fixed amount while holding all other parameters at their estimated values, and the output of the altered model is compared to the output of the baseline run. The value of each altered parameter is reset to its estimated value before the next parameter is altered. The model is said to be most sensitive to those parameters which cause the greatest change when altered.

There are three data sets required to run the model: l) weekly temperature readings; 2) weekly estimates of Chironomidae prey density and mean Chironomidae size; and 3) weekly estimates of Cladocera density. The temperature data used for the baseline run were the field temperatures in Stephenson's Pond presented in Figure 3.1. The Chironomidae density and size data (Figure 6.1) used are from Stephenson's Pond (Rasmussen 1983) and cover part of the same time period as the temperature data. The time of coincidence of the temperature and Chironomidae data is a 50 wk period from 80-05-13 to 81-04-22. The

Figure 6.1 Chironomidae density $\left(\mathrm{cm}^{-2}\right)$ (solid line) and mean individual wet weight (mg) (broken line) in Stephenson's Pond in 1980-1981. After Rasmussen (1983).


MONTH

Cladocera densities were simulated using equation 5.1, with parameters $b=3.0, a=0.1875$ and $t_{0}=4$ centered at the $3^{\text {rd }} w k$ in May, and $b=2.5$, $a=0.2778$ and $t_{0}=3$ centered at the $2^{\text {nd }} w k$ of September. These values provide for a 7 wk spring bloom with maximum density of three Cladocera $\mathrm{ml}^{-1}$ and a fall bloom of 5 wk duration with a maximum density of $2.5 \mathrm{ml}^{-1}$.

When the simulation was run with these data it failed because under certain conditions the respiration rate became negative demonstrating that the gradient of the respiration equation was still negative within regions of biological interest (see Section 4.1.2). The feeding equations derived in Chapter 5 also had negative derivatives in this region. These functions were thus rejected as appropriate models of these processes.

New equations were fitted to the respirometry and feeding data by excluding terms whose signs were inappropriate. This constrained the fit of the respiration equation to a simple straight line equation for the temperature, ration and activity variables. Oxygen uptake was distinctly curved with body size, so a simple straight line model was not appropriate for this variable. Fitting oxygen uptake (QO2) by including a second order term for body size, resulted in an equation which became negative at about 200 mg body size, so this functional form was rejected. Using BMDP (Dixon 1981) subroutine PAR the body size variable was successfully fitted with an exponent along with simple linear terms for the other independent variables (Table 6.1).

The feeding equations produced non-significant slopes and poor fits (determined from scattergrams) to the data when the interaction terms were excluded. The data for the three temperatures 12.50 C ,

Table 6.1 Coefficients for the fit of Nephelopsis obscura respiration rate, and functional feeding response to functions that are monotonic. SD = standard deviation of the regression coefficient, $t=$ regression coefficient/SD.

|  | Variable | Coefficient | SD | t |
| :---: | :---: | :---: | :---: | :---: |
| Respiration equation |  |  |  |  |
|  | Intercept | -0.0385 | 0.0113 | 3.41 |
|  | $\begin{array}{r} \text { Temperature } \\ \left({ }^{\circ} \mathrm{C}\right) \end{array}$ | 0.0043 | 0.0007 | 6.31 |
|  | Nutritional |  |  |  |
|  | state | 0.0184 | 0.0097 | 1.90 |
|  | Body size (mg) | ) 0.3427 | 0.0209 | 16.40 |
|  | (exponent). | -0.0147 | 0.0017 | 8.65 |
|  | Activity $r^{2}=76.3 \%$ | 0.0669 | 0.0077 | 8.69 |
| Cladocera capture rate equations |  |  |  |  |
| $15^{\circ} \mathrm{C}$ |  |  |  |  |
|  | Intercept | 0.2470 | 0.1686 | 1.47 |
|  | $\begin{aligned} & \text { Prey density } \\ & \left(\mathrm{cm}^{-2}\right) \\ & \mathrm{r}^{2}=68.7 \% \end{aligned}$ | 0.5290 | 0.0729 | 7.26 |
| $20^{\circ} \mathrm{C}$ |  |  |  |  |
|  | Intercept | 0.3651 | 0.1740 | 1.86 |
|  | $\begin{aligned} & \text { Prey densityy } \\ & \left(\mathrm{cm}^{-2}\right) \end{aligned}$ | 0.6282 | 0.0830 | 8.43 |

Table 6.1 continued
Variable Coefficient

Chironomidae capture rate equations $12.5^{\circ} \mathrm{C}$
$\left.\begin{array}{llll}\text { Intercept } & 0.2438 & 0.3674 & 0.66 \\ \text { Prey density } \\ (\mathrm{cm}-2)\end{array}\right) 0.4016 \quad 0.1748$
$15^{\circ} \mathrm{C}$

| Intercept | -0.1606 | 0.5361 | 0.30 |
| :--- | :--- | :--- | :--- |
| Prey density |  |  |  |
| $r^{2}=69.8 \%$ | 1.0258 | 0.2551 | 4.02 |

$20^{\circ} \mathrm{C}$

| Intercept | -0.1002 | 0.7467 | -0.13 |
| :--- | ---: | :--- | ---: |
| Prey density |  |  |  |
| $r^{2}=72.4 \%$ | 1.8133 | 0.3734 | 4.86 |

150 C and $20^{\circ} \mathrm{C}$ were successfully fit separately (Table 6.1). These equations were substituted into the model. When the data were split into separate temperature groups, the predator body size variable was no longer significant.

Three different methods of sensitivity analysis were used. In the first, each parameter within an equation was varied (up and down) by one standard error determined in the regression analysis. This method set each parameter to either end of its $68 \%$ confidence interval, and produced a $68 \%$ confidence band about the simulation output. The second method varied each parameter by $50 \%$ of its value, resulting in a constant proportional change in each parameter. Finally, the output from each equation was varied up and down by $50 \%$ of its value.

When the model parameters were varied by the standard errors of their estimates, each week's output of the altered model was compared with the corresponding week of the 50 wk baseline run (Figure 6.2). The parameters which caused the largest deviation were the coefficients on temperature and activity in the respiration equation, and the slope and intercept of the Chironomidae prey capture rates at $12.5^{\circ} \mathrm{C}$ (Table 6.2). The differences appear to result from extrapolation of these equations along the temperature axis beyond the lowest temperature at which data were gathered. Other coefficients produced smaller deviations suggesting that the simulation is relatively robust with regard to statistical parameter uncertainty.

Varying each parameter by a fixed proportion is used to investigate the sensitivity of simulation output to each of the independent variables (Miller 1979, Majkowski and Waiwood 1981), and to the extent that the structure of the simulation model reflects the structure of the real

Figure 6.250 wk of simulated Nephelopsis obscura body size (cal), using temperature and Chironomidae prey data from Stephenson's Pond in 1980-1981.


Table 6.2 Sensitivity analysis of the growth simulation model with each coefficient (Coef) in the respiration and feeding rate equations plus or minus one standard deviation (SD). The maximum differences in calories from the baseline over 50 wk simulation are given.

|  | Chirono <br> Temp <br> ( ${ }^{\circ} \mathrm{C}$ ) | omidae cap <br> Coef | apture ra SD | Adj Coef | Maximum Differenc (cal) |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Intercept | 12.5 | 0.2438 | 0.3674 | 0.6112 | 71 |
|  |  |  |  | -0.1236 | -16 |
| Prey density | 12.5 | 0.4016 | 0.1748 | 0.5764 | 61 |
|  |  |  |  | 0.2268 | -33 |
| Intercept | 15 | -0.1606 | 0.5361 | 0.3755 | 16 |
|  |  |  |  | -0.6967 | -24 |
| Prey density | 15 | 1.0258 | 0.2551 | 1.2809 | 29 |
|  |  |  |  | 0.7707 | -30 |
| Intercept | 20. | -0.1002 | 0.7467 | 0.6465 | 8 |
|  |  |  |  | -0.8469 | -8 |
| Prey density | 20 | 1.8133 | 0.3737 | 2.1867 | 15 |
|  |  |  |  | $1.4399$ | -15 |
| Cladocera capture rates |  |  |  |  |  |
| Intercept | 15 | 0.2470 | 0.1686 | 0.4156 | 39 |
|  |  |  |  | 0.0794 | -41 |
| Prey density |  | 0.52898 | 0.07285 | 0.60183 | 36 |
|  |  |  |  | 0.45613 | -38 |
| Intercept | 20 | 0.3651 | 0.1740 | 0.5391 | -3 |
|  |  |  |  | 0.1911 | 15 |
| Prey density | 20 | 0.62821 | 0.08299 | 0.71120 | -2 |
|  |  |  |  | 0.54522 | 15 |

Table 6.2 (continued)

| Respiration rate |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Coef | SD | Ad j Coef | Maximum Difference (cal) |
| Intercept | -0.0385 | . 0.0113 | -0.0272 | -15 |
|  |  |  | -0.0498 | 24 |
| Temperature ( ${ }^{\circ} \mathrm{C}$ ) | 0.0043 | 0.0007 | 0.0050 | 60 |
|  |  |  | 0.0036 | 73 |
| Nutritional state | 0.0184 | 0.0097 | 0.0281 | 0 |
|  |  |  | 0.0087 | 0 |
| Wet wt (mg) | 0.3427 | 0.0209 | 0.3636 | -2 |
|  |  |  | 0.3218 | -2 |
| (exp) | -0.0147 | -0.0017 | -0.0130 | -9 |
|  |  |  | -0.0164 | 5 |
| Activity | 0.0669 | 0.0077 | 0.0745 | -48 |
|  |  |  | 0.0592 | 55 |

world process being modelled, provides evidence about the sensitivity of the system to the independent variables. Each of the parameters of the foraging and respiration equations were increased and decreased by 50\% (Miller 1979, Majkowski and Waiwood 1981), and percentage change in weight on wk 19 of the simulation (corresponding to the peak body size in Figure 6.2) was used to determine percentage change due to each parameter (Table 6.3). The variables which appear to be most influential on growth rate are the rate of use of Chironomidae prey ( $34.7 \%$ ) and the body size parameters ( 0.3427 and -0.0147 ) in the respiration equation ( $16.4 \%$ and $13.4 \%$ respectively).

A number of the differences between the base line run and the output of the altered model reported in Tables 6.2 and 6.3 are asymmetric. There are three reasons for this. First, it usually occurs when slopes in the equations are varied, since varying the slope in an equation up and down by a fixed amount results in an asymmetric change in the values predicted by the modified equation. Second, the interactions within the model (Figure l.1) contain a number of feedbacks so that symmetric model response would not be expected due to these feedbacks. Third, when the slope and intercept of the $12.5^{\circ} \mathrm{C}$ Chironomidae capture rate equation are varied the constraint in the model that feeding cannot be negative is involked. At cooler temperatures, when downward adjustments of the coefficients resulted in negative ingestion rates, the ingestion rates were set to zero, thus limiting the range of variation. Increases in feeding rates due to upward adjustment of the coefficients were not limited.

Table 6.3 Sensitivity analysis of the growth simulation model with each coefficient (Coef) in the respiration and feeding rate equations plus or minus $50 \%$. The percent difference (\% Diff.) from wk 21 of the baseline simulation are given.


Table 6.3 (continued)


### 6.2 Validation

The output of a verified simulation model is always correct in the sense that it logically follows from the assumptions and assertions of its underlying conceptual model, and the data upon which the simulation rests. In order to test the conceptual model, it is desirable to compare the simulation output with the real world process being modelled to assess whether, in some sense, the degree of correspondence between them is satisfactory. The likelihood of a simulation model precisely describing the real world process is small indeed because it makes strong assertions about the nature of the world. Model parameters, once set, result in very precise output values. However, neither the user nor the modeller would expect exact correspondence between model output and the real world. Thus some other, less stringent, criterion must be used.

The process being modelled is not usually deterministic and therefore, has a random error term associated with it (Hurlbert 1984). This fact is readily evident when replicate experiments are performed and each replicate produces slightly different results. Furthermore, the input data to a simulation model, if real world data, themselves contain random sampling errors which will be reflected in the model output. Granger and Newbold (1973) thus assert that it is pointless to compare the distributional and time series properties of the (random) model output with the (random) real world process.

Two random processes could be compared using a statistical approach, which allows for random variability within each process, although there may be problems associated with the statistics applied. Granger and

Newbold (1973) have examined a number of these statistics and demonstrated that some are biased by the variance of the output in such a way that increasing variability (error) in model output increases the value of the goodness-of-fit estimate. Others are logically poor estimators of similarity in the sense that simply random-walk simulations can produce high similarity estimates.

A further problem with comparing model output with the real world process is that data sets describing the real world process being modelled must be available for comparison. In the present case, no such data are available. No researcher has followed a cohort of N. obscura under field conditions to determine their growth patterns, or the size structure of the cohort over time. This is partly due to the fact that individuals from the field cannot be aged. Aside from monitoring the N. obscura population, the experimenter must also take simultaneous measurements of temperature and prey density, which would act as input data to the model. If data from a different time or place were used as model input, it would not be clear whether the relationship between model output and the field cohort was due to model performance or due to the unrelated data set.

Judgments of model performance should not only be based upon the time series of model output, but also upon criteria such as the relationships among various variables and the positions of critical points in the output, and their frequency (Caswell 1979). Furthermore, since the model is a theory, it should be tested as such, by designed experiments which test the validity of aspects of its behaviour which are of interest.

To demonstrate how an experiment might be used to test the model, an experiment was designed to investigate the ability of the
respiration equation in the growth simulation to predict the maintenance ration level for N. obscura of various sizes and at various temperatures when fed on T. tubifex. Specimens of N. obscura with a broad range of body sizes were collected from Stephenson's Pond and from the Alberta foothills pond Lac des Arcs ( $115^{\circ} 10^{\prime} \mathrm{W}, 51^{\circ} 4^{\prime} \mathrm{N}$ ), and were acclimated for $l \mathrm{wk}$ at either $10^{\circ} \mathrm{C}, 15^{\circ} \mathrm{C}$ or $20^{\circ} \mathrm{C}$, while being fed ad libitum on T. tubifex. At the end of the acclimation period, each animal was weighed, and the simulation model was used to predict its maintenance T. tubifex ration. Each N. obscura was then maintained in an individual container and fed weekly a weight of t. tubifex equivalent to the predicted maintenance ration. At the end of each week, any un-eaten T. tubifex were removed from the container and weighed before the next week's ration was added. After 4 wk each animal was again weighed.

Some N. obscura did not consume the entire ration provided, and these individuals lost weight (Table 6.4). Of the specimens that consumed their entire ration, most showed only minor changes in weight over the 4 wk period. Among those individuals that consumed their entire ration the group that changed weight the most consisted of medium sized individuals at $20^{\circ} \mathrm{C}$ that demonstrated weight gains ranging up to $31.6 \%$ with the mean weight change being $16.9 \%$. At the other two temperatures, the mean weight change was small ( $3.6 \%$ and $-0.2 \%$ ). The large deviation of the animals at $20^{\circ} \mathrm{C}$ may be due to a non-linearity in oxygen uptake with temperature which cannot be detected in the present data. Thus, it appears that the growth simulation is acceptable at $10^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$ but deviates at higher temperatures.

Table 6.4 Weight change of Nephelopsis obscura when maintained at $10^{\circ} \mathrm{C}$, $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$ for 4 wk while fed a maintenance ration of Tubifex tubifex estimated from the simulation model. $W W=$ wet weight, $P C=$ percent weight change, $P F=$ percent of food ration consumed. Means and standard deviations (SD) are based on individuals that consumed $100 \%$ of their ration.

| $10^{\circ} \mathrm{C}$ |  |  | $15^{\circ} \mathrm{C}$ |  |  | $20^{\circ} \mathrm{C}$ |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| un | PC | PF | un | PC | PF | UW | PC | PF |
| 358.9 | 7.7 | 100 | 146.8 | 0.0 | 100 | 120.6 | -15.4 | 100 |
| 413.7 | 0.6 | 100 | 178.1 | 17.1 | 100 | 370.3 | 31.6 | 100 |
| 424.3 | -11.8 | 60 | 351.3 | 21.7 | 100 | 411.5 | 22.3 | 100 |
| 432.8 | -15.6 | 75 | 408.2 | -10.9 | 100 | 601.8 | 24.4 | 100 |
| 437.2 | 9.6 | 100 | 411.1 | -1. 5 | 100 | 673.2 | 28.1 | 100 |
| 440.6 | -7.0 | 60 | 417.3 | -6.5 | 100 | 688.9 | 27.1 | 100 |
| 542.0 | -17.2 | 71 | 503.4 | -3.3 | 100 | 1369.3 | 3.5 | 42 |
| 556:9 | -11.8 | 100 | 506.1 | -5.5 | 100 | 1639.6 | 14.0 | 100 |
| 576.8 | -18.7 | 52 | 577.2 | -2.8 | 100 | 1890.0 | -1.0 | 92 |
| 623.2 | -17.1 | 83 | 630.6 | -0.4 | 100 | 2207.0 | 3.4 | 100 |
| 648.4 | -16.5 | 42 | 821.0 | -2.9 | 100 | 2728.6 | -13.2 | 21 |
| 672.5 | 2.8 | 100 | 883.5 | -6.0 | 100 |  |  |  |
| 699.0 | 12.6 | 100 | 920.9 | 0.0 | 100 | Mean | $16.9{ }^{-}$ |  |
| 720.3 | -15.2 | 46 | 1194.7 | -1.1 | 100 | SD | 15.9 |  |
| 984.1 | 1.5 | 100 | 2215.3 | -18.5 | 24 |  |  |  |
| 740.7 | 2.6 | 100 | 2585.2 | -18.0 | 66 |  |  |  |
| 248.6 | -12.6 | 61 | 2960.3 | -19.8 | 38 |  |  |  |
| 343.3 | 8.8 | 100 | 3734.9 | -22.4 | 54 |  |  |  |
| 334.0 | 1.7 | 100 |  |  |  |  |  |  |
| Mean | 3.6 | - |  | - 0.0 |  |  |  |  |
| SD | 6.8 |  |  | 8.9 |  |  |  |  |

Another way to test a model is to develop alternative models or sub-models (for instance, different respiration equations). Comparisons made between alternative models will demonstrate the strong and weak points of each. New models can then be developed which include the strongest aspects of the different models.

Although the veracity of the theory can never be proven (Caswell 1979), if it successfully withstands the tests of experiments, field observation and alternative models, it can be considered to be corroborated through the process of strong inference. Alternatively, if a model fails a test, it should not be thrown away. Rather, that portion of the model which causes the failure should be identified and altered (i. e. a new hypothesis should be generated) and the model tested again. Without recycling this testing procedure nothing is gained by refuting a model. When the model is modified, it should not be changed in some arbitrary manner that forces its output to correspond with the expectations of the modeller. If this is done, then the model degenerates from being a theory and it becomes, simply, a predictive model (Chapter 1). Such alterations would be contrary to the intent of the modelling process, which is to investigate consistency between theories and the real world. Furthermore, since the model is a theory, the objective of the scientist should be to refute it, since by its refutation, the weaknesses of our understanding can be determined. As far as the present model is concerned, much of it will have to be tested by other workers, when data become available. When it fails, or when new data become available, the model should be modified appropriately to reflect the growth in knowledge.

### 6.3 Simulations

In this section, the results of a number of simulation runs are presented, to demonstrate the behaviour of the simulation model under different environmental conditions. The data used to perform these simulations were the 1980-1981 data used in the sensitivity analysis (section 6.1), as well as a set of weekly Chironomidae prey density data (Figure 6.3) and temperature data (Figure 6.4) obtained from Stephenson's Pond between 84-06-13 and 84-10-25, representing an 18 wk time period. Potential areas for further research were determined by investigating alternative scenarios of the N. obscura simulation.

Figure 6.2 presents simulation output for the 1981 data. The simulation was started with a 2.0 cal ( 3 mg ) animal, representing a spring hatchling. Growth occurs steadily up to late September, after which time feeding ceased due to cooler temperatures. From late September to late April, the animal continuously shrank from a maximum of $154.2 \mathrm{cal}(234.5 \mathrm{mg})$ to a minimum of 3.5 cal. Gates (1984) has shown that under laboratory conditions mortality at $10^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$ was high (approximately 50\%) when N. obscura was starved to $50 \%$ of its initial body size. The present simulation would thus suggest very high ( $100 \%$ ) over-wintering mortality due to starvation. This amount of shrinkage and very high mortality are contrary to field observation (Davies and Everett 1977). The excessive shrinkage in the simulation could be due to two, not necessarily mutually exclusive processes. The simulated respiration rate under cold wịnter conditions may be too high, due to extrapolation of the respiration equation. Alternatively, contrary to the speculation in Chapter 5, feeding over the winter

Figure 6.3 Chironomidae prey density (numbers $\mathrm{cm}^{-2}$ ) (solid line) and mean individual Chironomidae wet weight (mg) (broken line) in Stephenson's Pond from 84-06-13 to 84-10-25.


Figure 6.4 Weekly mean temperature $\left({ }^{\circ} \mathrm{C}\right)$ at 1 m depth in Stephenson's Pond from 84-06-13 to 84-10-25.

WEEKLY MEAN TEMPERATURE $\left({ }^{\circ} \mathrm{C}\right)$

may contribute significantly to the energy budget of N. obscura. The feeding rate that would be necessary to offset weight loss due to respiration would be something in the order of one to two Chironomidae wk-l. This very low rate would have been undetectable in the functional feeding experiments previously described (Chapter 5). These results point out the necessity of performing both respiration and feeding experiments at temperatures below the values which are presently used as the minimum experimental temperatures.

Nephelopsis obscura is usually assumed to live no longer than about 21 mo (Davies and Everett 1977). In Stephenson's Pond the mean adult size is about 300 mg ( 200 cal ), but individuals of 600 to 800 mg ( 400 to 525 cal ) are occasionally found. The simulation represented in Figure 6.2 would suggest that because a hatchling grows to only 250 mg over one summer it would take more than one summer's growth (assuming no shrinkage over winter) to attain the larger sizes observed in the field. To determine the expected age of a 600 mg individual, simulations of 5 yr growth were performed in which no shrinkage was allowed over winter. The simulation result for the entire 5 yr period is presented in Figure 6.5, and for ease of detailed comparisons the numerical output for the final year is presented in Table 6.5. There are two related features of the output to note. It appears that growth asymptotes at about $450 \mathrm{cal}(680 \mathrm{mg})$, and the growth rate over summer fluctuates. The periods of shrinkage correspond to different stages of the Chironomidae life cycle. Rasmussen's (1983) data show an emergence of adult Chironomidae in mid-June (Figure 6.1), followed by a large increase in Chironomidae density, and a large decrease in mean Chironomidae size. The periods of shrinkage observed in Figure 6.5

Figure 6.5 A 220 wk simulation of body size (cal) of Nephelopsis obscura, using 1980 Chironomidae data and 1980 temperature data from Stephenson's Pond.


Table 6.5 Simulated Nephelopsis obscura body size (cal), maximal assimilation rate per week (cal) and actual assimilation rate per week (cal) from the fifth year of 5 yr simulations based, upon prey data from either 1980 or 1984, and temperature data from 1980.

Simulation using 1980 prey data with 1980 temperature data:

| Week | Temp Data <br> ( ${ }^{\circ} \mathrm{C}$ ) | Simulated |  |  | Chironomidae Prey Data |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \text { Body } \\ & \text { Size } \\ & \text { (cal) } \end{aligned}$ | Assimilation |  |  |  |
|  |  |  | Maximal (cal) | $\begin{gathered} \text { Actual } \\ (c a l) \end{gathered}$ | $\begin{aligned} & \text { Density } \\ & \left(\mathrm{cm}^{-2}\right) \end{aligned}$ | $\begin{aligned} & \text { Size } \\ & (\mathrm{mg}) \end{aligned}$ |
| 197 |  | 465.8 |  |  |  |  |
| 198 | 11.8 | 467.6 | 85.9 | 29.4 | 1.135 | 4.2 |
| 199 | 13.2 | 471.1 | 75.0 | 36.3 | 0.286 | 4.3 |
| 200 | 11.7 | 483.4 | 87.6 | 41.4 | 0.212 | 4.2 |
| 201 | 10.7 | 500.2 | 98.1 | 43.5 | 0.139 | 4.1 |
| 202 | 12.2 | 508.3 | 88.6 | 40.2 | 0.065 | 4.0 |
| 203 | 16.1 | 502.5 | 76.1 | 38.4 | 5.203 | 0.1 |
| 204 | 18.9 | 487.3 | 103.4 | 34.4 | 4.871 | 0.3 |
| 205 | 16.0 | 458.6 | 72.4 | 9.1 | 4.545 | 0.4 |
| 206 | 17.1 | 433.8 | 81.4 | 14.0 | 4.216 | 0.6 |
| 207 | 17.5 | 415.4 | 81.0 | 20.2 | 4.013 | 0.8 |
| 208 | 16.7 | 408.6 | 73.2 | 29.8 | 3.796 | 1.4 |
| 209 | 16.8 | 411.1 | 73.6 | 40.2 | 3.579 | 2.0 |
| 210 | 16.1 | 415.6 | 67.1 | 41.3 | 3.247 | 2.5 |
| 211 | 13.6 | 413.1 | 65.4 | 26.9 | 2.915 | 3.0 |
| 212 | 14.4 | 414.8 | 59.7 | 34.6 | 2.768 | 3.3 |
| 213 | 13.4 | 429.9 | 66.6 | 46.9 | 2.486 | 3.6 |
| 214 | 12.0 | 444.8 | 78.7 | 42.9 | 2.182 | 3.7 |
| 215 | 12.0 | 461.9 | 81.0 | 46.3 | 2.129 | 3.8 |
| 216 | 11.3 | 472.9 | 89.3 | 37.9 | 2.076 | 3.9 |
| 217 | 9.1 | 469.7 | 88.2 | 15.7 | 2.065 | 4.0 |

Table 6.5 (continued)
Simulation using 1984 prey data with

| Week | Temp Data <br> ( ${ }^{\circ} \mathrm{C}$ ) | Simulated |  |  | Chironomidae Prey Data |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \text { Body } \\ & \text { Size } \\ & \text { (cal) } \end{aligned}$ | Assimilation |  |  |  |
|  |  |  | $\underset{(\mathrm{cal})}{\operatorname{Maximal}}$ | Actual <br> (cal) | $\begin{aligned} & \text { Density } \\ & \left(\mathrm{cm}^{-2}\right) \end{aligned}$ | $\begin{aligned} & \text { Size } \\ & (\mathrm{mg}) \end{aligned}$ |
| 201 |  | 455.2 |  |  |  |  |
| 202 | 12.2 | 494.7 | 81.2 | 73.5 | 4.000 | 5.5 |
| 203 | 16.1 | 520.2 | 74.5 | 74.5 | 2.167 | 3.9 |
| 204 | 18.9 | 563.4 | 102.9 | 102.9 | 4.400 | 5.4 |
| 205 | 16.0 | 588.8 | 80.8 | 80.8 | 5.733 | 5.4 |
| 206 | 17.1 | 589.2 | 93.6 | 56.4 | 12.800 | 2.4 |
| 207 | 17.5 | 584.8 | 97.7 | 51.9 | 11.733 | 2.1 |
| 208 | 16.7 | 583.0 | 89.3 | 52.2 | 7.533 | 2.3 |
| 209 | 16.8 | 602.8 | 90.0 | 77.8 | 6.933 | 3.4 |
| 210 | 16.1 | 596.5 | 85.4 | 46.9 | 10.533 | 2.3 |
| 211 | 13.6 | 581.1 | 88.6 | 25.0 | 5.333 | 2.0 |
| 212 | 14.4 | 578.9 | 78.3 | 43.6 | 12.133 | 2.9 |
| 213 | 13.4 | 572.7 | 88.6 | 33.6 | 9.200 | 2.9 |
| 214 | 12.0 | 559.6 | 102.2 | 19.3 | 5.267 | 3.0 |
| 215 | 12.0 | 544.5 | 100.1 | 16.2 | 9.400 | 2.6 |
| 216 | 11.3 | 529.8 | 104.5 | 13.0 | 9.600 | 3.5 |
| 217 | 9.1 | 510.9 | 98.8 | 0.0 | 5.800 | 2.0 |
| 218 | 9.1 | 492.6 | 95.3 | 0.0 | 5.267 | 2.8 |
| 219 | 10.3 | 471.8 | 103.4 | 0.1 | 5.467 | 2.7 |

correspond with the first 6 wk of the new Chironomidae cohort (Table 6.5). During this period, capture rate is high (in numbers) but energy return is low, due to the small prey size. Once the Chironomidae have grown to about 2 mg they are large enough to provide sufficient energy return to balance respiration, and growth thus resumes. This period of shrinkage is thereafter balanced by an equivalent amount of growth during the remainder of the summer, so that net annual change approaches zero.

These results suggest that large sized N. obscura in Stephenson's Pond require at least two summers growth to attain 600 mg which is consistent with the life-history data presented by Davies and Everett (1977). Comparing Rasmussen's data (Figure 6.1) with the 1984 data (Figure 6.3) reveals that in 1984 the average Chironomidae size in early summer does not drop as drastically as it did in 1980. The larger prey size may not result in the negative growth rates observed in Figure 6.5. To test this, the simulation was run again using the 1980 temperature data and the 1984 Chironomidae data (Figure 6.6, Table 6.5). The two simulations are not exactly comparable since there are only 18 wk of 1984 data, while the previous simulation ran for $20 \mathrm{wk} \mathrm{yr}{ }^{-1}$. The 1984 data also start 4 wk later, at a time comparable to the week of adult Chironomidae emergence in the 1980 data.

In both Figure 6.5 and Figure 6.6 there are periods of shrinkage, but, in the second run, shrinkage in the final year is delayed 6 wk relative to the final year of the first run (Table 6.5). There is a common period of shrinkage from wk 210 to wk 212, after which the run based upon the 1980 Chironomidae data shows an increase in body size, while the one based upon the 1984 Chironomidae data shows the

Figure 6.6 A 220 wk simulation of body size (cal) of Nephelopsis obscura, using 1984 Chironomidae data and 1980 temperature data from Stephenson's Pond.


AGE (wooks)
animal continuously decreasing in size. The difference between environmental conditions during the period from wk 213 to wk 217 is in only the Chironomidae prey. In the first run, prey densities ranged from 2.0 Chironomidae $\mathrm{cm}^{-2}$ to $2.5 \mathrm{~cm}^{-2}$, while in the second, they range from $9.6 \mathrm{~cm}^{-2}$ to $5.3 \mathrm{~cm}^{-2}$.

This result demonstrates a further problem with the available data upon which the simulation model was built. The prey sizes used in these simulations represent mean individual biomass and ignores size variation among Chironomidae. If N. obscura forages selectively upon larger Chironomidae, its ingestion rate (cal) would probably be well above that necessary to maintain growth. Laboratory experiments have been performed (Anholt 1982) which suggest that N. obscura shows prey selectivity between T. tubifex and Chironomidae, but the effect of different prey sizes within prey types has not been investigated. Table 6.5 suggests that selection for even slightly larger prey (say 25\%) could drastically alter the growth pattern of N. obscura.

Figures 6.5 and 6.6 represent the effects of altering prey density while leaving temperature unchanged. A similar pair of simulations was done (Table 6.6) using the 1984 temperature and Chironomidae data (Figure 6.7) and the 1980 temperature and 1984 Chironomidae data (Figure 6.8). Figure 6.6 and 6.7 are based upon the same prey data (1984), but different temperatures. Aside from a minor scale factor, the two growth trajectories are identical. The simulations represented in Figures 6.5 and 6.8 differ in the temperature data used, but the similarity in model output is marked. The major difference between these two figures is the lack of an ascending portion at the beginning of each summer in Figure 6.8. Due to lack of data, this

Figure 6.7 A 220 wk simulation of body size (cal) of Nephelopsis obscura, using 1984 Chironomidae data and 1984 temperature data from Stephenson's Pond.


Table 6.6 Simulated Nephelopsis obscura body size (cal), maximal assimilation rate per week (cal) and actual assimilation rate per week (cal) from the fifth year of 5 yr simulations based upon prey data from either 1980 or 1984, and temperature data from 1984.

| Simulation using 1980 prey data with |  |
| ---: | :--- |
|  | 1984 temperature data: |


| Week | Temp Data <br> ( ${ }^{\circ} \mathrm{C}$ ) | Simulated |  |  | Chironomidae Prey Data |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Body Size (cal) | Assimilation |  |  |  |
|  |  |  | $\begin{gathered} \text { Maximal } \\ (\text { cal }) \end{gathered}$ | Actual <br> (cal) | $\begin{aligned} & \text { Density } \\ & \left(\mathrm{cm}^{-2}\right) \end{aligned}$ | $\begin{aligned} & \text { Size } \\ & (\mathrm{mg}) \end{aligned}$ |
| 203 | 7.2 | 570.5 | 89.4 | 89.4 | 4.000 | 5.5 |
| 204 | 8.7 | 604.3 | 106.5 | 97.4 | 2.167 | 3.9 |
| 205 | 9.4 | 653.3 | 119.9 | 119.9 | 4.400 | 5.4 |
| 206 | 8.5 | 695.6 | 115.8 | 115.8 | 5.733 | 5.4 |
| 207 | 9.8 | 694.6 | 134.1 | 74.9 | 12.800 | 2.4 |
| 208 | 9.1 | 684.2 | 126.5 | 61.5 | 11.733 | 2.1 |
| 209 | 9.5 | 681.7 | 128.8 | 70.9 | 7.533 | 2.3 |
| 210 | 0.0 | 711.5 | 133.5 | 109.2 | 6.933 | 3.4 |
| 211 | 8.9 | 703.3 | 127.4 | 65.0 | 10.533 | 2.3 |
| 212 | 7.5 | 687.5 | 111.0 | 50.0 | 5.333 | 2.0 |
| 213 | 3.1 | 672.7 | 107.2 | 29.8 | 12.133 | 2.9 |
| 214 | 2.2 | 654.8 | 116.5 | 20.7 | 9.200 | 2.9 |
| 215 | 9.6 | 629.6 | 132.5 | 0.0 | 5.267 | 3.0 |
| 216 | 9.7 | 605.0 | 129.4 | 0.0 | 9.400 | 2.6 |
| 217 | 4.5 | 599.0 | 31.5 | 0.0 | 9.600 | 3.5 |
| 218 | 0.8 | 575.2 | 120.0 | 3.7 | 5.800 | 2.0 |
| 219 | 9.9 | 552.1 | 121.9 | 0.0 | 5.267 | 2.8 |
| 220 | 0.1 | 560.2 | 5.3 | 0.0 | 5.467 | 2.7 |

Table 6.6 (continued)

| $\begin{aligned} \text { Simulation using } & 1980 \text { prey data with } \\ & 1980 \text { temperature data: }\end{aligned}$ |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Week | Temp Data <br> ( ${ }^{\circ} \mathrm{C}$ ) | Simulated |  |  | Chironomidae Prey Data |  |
|  |  | $\begin{aligned} & \text { Body } \\ & \text { Size } \\ & \text { (cal) } \end{aligned}$ | Assimilation |  |  |  |
|  |  |  | $\begin{gathered} \text { Maximal } \\ (\mathrm{cal}) \end{gathered}$ | Actual (cal) | $\begin{array}{r} \text { Density } \\ \left(\mathrm{cm}^{-2}\right) \end{array}$ | $\begin{aligned} & \text { Size } \\ & (\mathrm{mg}) \end{aligned}$ |
| 202 |  | 414.0 |  |  |  |  |
| 203 | 17.2 | 418.5 | 78.0 | 43.7 | 0.065 | 4.0 |
| 204 | 18.7 | 419.8 | 89.3 | 43.6 | 5.203 | 0.1 |
| 205 | 19.4 | 412.2 | 95.8 | 35.4 | 4.871 | 0.3 |
| 206 | 18.5 | 386.6 | 91.0 | 12.2 | 4.545 | 0.4 |
| 207 | 19.8 | 366.3 | 97.5 | 18.5 | 4.216 | 0.6 |
| 208 | 19.1 | 354.3 | 93.1 | 23.9 | 4.013 | 0.8 |
| 209 | 19.5 | 357.7 | 94.1 | 40.4 | 3.796 | 1.4 |
| 210 | 20.0 | 374.6 | 99.8 | 56.4 | 3.579 | 2.0 |
| 211 | 18.9 | 392.2 | 86.7 | 57.5 | 3.247 | 2.5 |
| 212 | 17.5 | 406.3 | 77.6 | 53.0 | 2.915 | 3.0 |
| 213 | 13.1 | 403.6 | 67.7 | 24.5 | 2.768 | 3.3 |
| 214 | 12.2 | 414.0 | 72.9 | 36.8 | 2.486 | 3.6 |
| 215 | 9.6 | 419.4 | 83.8 | 24.2 | 2.182 | 3.7 |
| 216 | 9.7 | 427.9 | 86.2 | 28.2 | 2.129 | 3.8 |
| 217 | 4.5 | 423.7 | 22.3 | 0.0 | 2.076 | 3.9 |
| 218 | 10.8 | 427.4 | 85.7 | 26.0 | 2.065 | 4.0 |
| 219 | 9.9 | 412.7 | 90.6 | 2.8 | 2.054 | 4.0 |
| 220 | 0.1 | 418.8 | 4.0 | 0.0 | 2.043 | 4.1 |

Figure 6.8 A 220 wk simulation of body size (cal) of Nephelopsis obscura, using 1980 Chironomidae data and 1984 temperature data from Stephenson's Pond.


AGE (weoks)
period was not simulated in the process of generating Figure 6.8 so it may occur if data were available for the simulation.

In Chapter 3 maximal growth rates of animals greater than 102 mg ( 155 cal) were approximated and in the model these estimates were used, along with respiration rates, to calculate satiation and thus limit feeding. It was stated that this approximation may bias the simulated growth rates downward by limiting ingestion to an artificially low value. Comparison of the maximal and actual assimilation columns of Table 6.5 and 6.6 reveals that for these large animals, actual assimilation was always less than maximal. Therefore, the approximation did not bias growth.

### 6.4 Discussion

The simulation results suggest that prey availability is more influential upon N. obscura growth rates than temperature. From Figure 6.5 through 6.8 , it would appear that N. obscura could grow to the 525 cal maximum size observed in Stephenson's Pond within about two summers. The simulations also suggest that periods of summer shrinkage occur in Stephenson's Pond, otherwise N. obscura would be found to be much larger there.

In Lac des Arcs, a shallow pond in the foothills of Alberta, specimens of N . obscura weighing 3000 mg ( 2000 cal ) are not uncommon. The present simulations would suggest that it is not temperature which primarily contributes to the much larger size of N. obscura in Lac des Arcs. Rather these simulations suggest the hypothesis that the average prey sizes in this pond are consistently large, so that periods of shrinkage are less likely to occur, and growth rate is higher. This could be due to a more diverse Chironomidae community than that which is found in Stephenson's Pond (Section 5.1).

The laboratory experiment designed to test the accuracy of the maintenance ration level predicted by the respiration equation suggests that this equation is accurate at $10^{\circ} \mathrm{C}$ and $15^{\circ} \mathrm{C}$, but may overestimate at $20^{\circ} \mathrm{C}$. Although no attempt has been made to validate the growth simulation model by comparing its projected growth trajectory with the actual growth of a cohort in the field, the model output is not inconsistent with the body sizes of N. obscura observed in Stephenson's Pond and the model has generated a number of hypotheses related to field populations which can be used to test the validity of the model. These are:

1) Shrinkage does not occur over winter in Stephenson's Pond because feeding occurs over winter at a very low rate equivalent in calories to the respiration rate.
2) Differences in prey size distributions between years are more influential upon N. obscura growth patterns than are differences in thermal regimes. 3) Periods of N. obscura shrinkage occur in Stephenson's Pond following the spring Chironomidae emergence.
3) If periods of shrinkage do not occur when mean prey size is small, N. obscura forages size selectively for larger prey types. Field or laboratory testing of these hypotheses will further test the validity of the simulation model, and experiments conducted to test hypotheses one and four should result in new data that can be used to modify the simulation.

The runs described herein have also pointed out the need for conducting respiration and feeding experiments at lower temperatures than have been used to date. Furthermore, more information is needed regarding the details of the feeding of $N_{0}$ obscura, since this variable appears to be more influential upon growth patterns than the effect of temperature on respiration.

## Chapter 7

## Reproduction

### 7.0 Introduction

Natality is one of the two factors in the model (Figure 1.1) which were considered to contribute directly to population size, hence estimates of total numbers of offspring produced per individual are required to address population processes, and estimates of energy investment into reproduction are required to simulate individual growth when reproduction occurs. The main factors which were expected to influence cocoon production and energy investment in cocoons were temperature (Wrona 1982), ingestion rate and size (age) (Calow 1983). The number of studies which have investigated reproduction in N. obscura are limited, and frequently did not provide information about functional relationships. Verrill (1874) reported that field collected N. obscura cocoons contained five to ten eggs per cocoon but gave no information about the total number of cocoons produced by an individual. Davies and Everett (1977) reported that field collected adults produced an average of 15.4 hatchlings (emerging from cocoons) when maintained in the laboratory at $20^{\circ} \mathrm{C}$ with no food supplied. Wrona (1982) showed the mean number of cocoons and embryos produced per individual to range from zero at $5^{\circ} \mathrm{C}$ to 7.29 and. 26.54 respectively at $20^{\circ} \mathrm{C}$. None of these studies simultaneously controlled for all three variables, temperature, ration and size so were insufficient for the purposes of the model. This chapter describes an experiment performed to measure the rates of embryo production and energy investment in cocoons as functions of all three variables.

### 7.1 Methods

### 7.1.1 Experimental design

To ensure an even distribution of sizes in each temperature and ration level treatment three weight ranges were used (small: 80 100 mg , medium: $200-300 \mathrm{mg}$, and large: $300-450 \mathrm{mg}$. Two temperatures ( $15^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$ ) were used which approximately span the range of water temperatures in Stephenson's Pond during the breeding season and were the temperatures at which Wrona' (1982) found successful embryo development. The weekly maintenance ration $(X)$ for each combination of temperature and size range of reproductive N. obscura was estimated using the equations developed in Chapter 6. The ration levels used in the experiment were $0 X$ (starvation), $1 \times$ (the entire weekly maintenance ration at one feeding), $2 \times$ (double the weekly maintenance ration at one feeding). Ten N. obscura were used in each combination of temperature, ration and weight range. Each animal was maintained in a separate 250 ml plastic container and allowed to feed on T. tubifex for 48 h , at the end of which time the T. tubifex remaining and the leech were weighed. Actual food ingestion was determined from the difference between food supplied and food remaining.

All containers were inspected daily and the cocoons deposited during the previous 24 h period were removed, the eggs counted, and the cocoon was weighed as was the N. obscura. If the N. obscura had died the number of days since it deposited its first cocoon was recorded. The experiment was continued for 90 d after cocoon deposition had ceased in all containers.

The calorific values of 50 cocoons were determined using a Phillipson (1964) microbomb calorimeter and a wet weight to calorific value conversion was estimated as:

$$
\begin{equation*}
\text { calories }=0.66 \text { wet } w t+2.72 \tag{7.1}
\end{equation*}
$$

### 7.1.2 Collections

Specimens of N. obscura were collected from Stephenson's Pond in May 1984 shortly after the beginning of the ice free period, when water temperature was $8^{\circ} \mathrm{C}$. Field observations at the time of collection confirmed that these $\mathrm{N}_{\text {. obscura }}$ were all pre-reproductive since no cocoons could be found in the field. The specimens were acclimated for 7 d at one of the experimental temperatures under a 12 h light 12 h dark regime with ad libitum food (T. tubifex), then assigned to one of the cells of the experimental design. Before any N. obscura were assigned to the experiment, 20 specimens were dissected to assess the state of gonad development.

### 7.2 Results

Of the 180 N. obscura originally in the experiment 110 deposited cocoons. All of the individuals dissected at the commencement of the experiment had gonads containing mature sperm and ova, suggesting that not all sexually mature individuals underwent reproduction.

Multiple linear regression was used to determine the functional relationships between each of the dependent variables (total egg production and total energy in cocoons) and the independent. variables temperature, ingestion and weight and all cross product terms (Table 7.1).

Table 7.1 Regression of total egg production and total caloric content of cocoons produced by Nephelopsis obscura on temperature ( ${ }^{\circ} \mathrm{C}$ ), proportional food ingestion rate and body size (mg). Food ingestion rate was not significant in either regression so was removed from the regression models. Temperature and body size were additively coded to increase numerical precision, and both coded and uncoded coefficients are presented (see Section 4.1.2). SD $=$ standard deviation of the coefficient. $t=$ coefficient/SD.

Egg production

|  | Coded |  |  | Uncoded |
| :---: | :---: | :---: | :---: | :---: |
|  | Coefficient | SD | t | Coefficient |
| Intercept | 21.5364 | 0.9578 | 22.49 | 27.49758 |
| Wet wt (mg) | 0.07315 | 0.01433 | 5.11 | 0.07315 |
| Temperature ( ${ }^{\circ} \mathrm{C}$ ) | 1.6998 | 0.3877 | 4.38 | 1.6998 |

## Cocoon calories

|  | Coded |  | t | UncodedCoefficient |
| :---: | :---: | :---: | :---: | :---: |
|  | Coefficient | SD |  |  |
| Intercept | 38.601 | 1.352 | 28.56 | -25.875 |
| Wet wt (mg) | 0.16123 | 0.02022 | 7.97 | 0.16123 |
| Temperature ( ${ }^{\circ} \mathrm{C}$ ) | 1.4672 | 0.5471 | 2.68 | 1.4672 |
| $\mathrm{df}=109$ | $r^{2}=41.2 \%$ |  |  |  |

### 7.3 Discussion


#### Abstract

The regression analysis could not detect a relationship between food ingestion rate and either egg production or the caloric contents of cocoons. While the regression equations (Table 7.2) can be used to predict the cocoon output of a reproductive individual, they will overestimate the population rate of reproductive output if some individuals of reproductive size do not reproduce, as was the case in the present experiment.

While the present data provide information regarding the expected reproductive output of an individual, it is not clear which environmental factors initiate reproduction. Specimens of N. obscura have been reared in the laboratory for well over a year (Chapter 3) without reproducing, despite attaining sizes (Figure 3.2) well in excess of the size that is considered necessary for reproduction (Davies and Everett 1977). At age 1 yr , when they were clitellate, experimentally varying photoperiod and temperature did not induce reproduction. In the field it appears that reproduction occurs in spring and fall (Davies and Everett 1977), with fall breeding occasionally not occurring, as was the case in Stephenson's Pond in 1984. Whether this is due to some combination of a late spring and early fall, or to some other factor is not known. In the simulation model, reproduction can be initiated in spring and fall, or spring only or fall only.


## Chapter 8

## Mortality

### 8.0 Introduction

The size of a population is determined by the action of opposing factors, those which increase population size (natality and immigration), and also those which decrease it (mortality and emigration). For many mortality factors to which N. obscura is exposed, the mortality hazard (risk) may vary through time and with the size (age) of the individual. For instance, after ice cover is established on a pond and hypoxic oxygen concentrations stabilize, conditions under the ice may not vary much until spring thaw. However, with increasing exposure time to these conditions individuals may change their susceptibility to mortality from hypoxia. Likewise, individuals of different ages may experience different probabilities of mortality when exposed to the same mortality factors. Equations describing these variations in age specific mortality risk were needed since one of the objectives of the simulation was to examine population age (size) structure. The equations to estimate mortality risk would ideally have a term for each of the mortality factors considered, such as predation or hypoxia, as well as terms which describe the way in which mortality associated with each varies as a function of time, season and age.

Largely anecdotal evidence suggests several sources of mortality for pond populations of N. obscura. 1) Deformed cocoons that do not hatch are occasionally deposited, and laboratory observations suggest that over the range of $5^{\circ} \mathrm{C}$ to $20^{\circ} \mathrm{C}$ the rate of their production is
inversely related to temperature. 2) Cocoons in the field are frequently found to be damaged, apparently by snails. 3) Predation by Helobdella stagnalis (L. 1758) has been observed in the field and predation by Amphipoda, Odonata and other erpobdellid leech species has been observed in the laboratory. Vertebrates such as fish, ducks or amphibians could also be predators on $N$ obscura. 4) In the laboratory, small individuals appear to be more susceptible to long term anoxia at $5^{\circ} \mathrm{C}$ than larger individuals suggesting potentially increased mortality risk for small individuals during winter when oxygen concentrations under the ice approach zero. These are the mortality factors for which some evidence has been obtained, but, there are undoubtedly many other mortality factors such as disease or parasitism for which no evidence exists. Despite the observations mentioned above, no data were available that allowed estimation of any functional relationships between any of these factors and mortality. Lacking functions relating specific mortality factors to risk, it was decided to estimate mortality rate simply as a function of age. This approach greatly reduces the power of the simulation, since it is no longer possible to attribute differences in simulated population characteristics to differences in specific habitat variables.

### 8.1 Published Mortality Tables

The only set of age specific mortality schedules that has been published for N. obscura (Everett 1974) indicate frequent periods with large negative mortality. This impossible result is likely due to small sample sizes (usually fewer than 50 specimens per sampling time). These data were rejected for estimation of a mortality function.

### 8.2 Estimation of Mortality Schedules from Field Data

Nephelopsis obscura density was sampled monthly in Stevenson's Pond from April 1979 through to October 1980 by Wrona (unpublished data). He divided the pond into three sampling zones: zone 1 - the littoral zone, being the shallow area near the bank; zone 2 - a deeper zone within which samples were taken at a depth of 1.0 m ; and zone 3 - the deepest zone with depth greater than 1.5 m . Along shore leeches were sampled using artificial substrates (baskets of stones) of area approximately $0.1 \mathrm{~m}^{2}$, while Ekman dredge samples ( $0.0225 \mathrm{~m}^{2}$ ) were taken in other zones. A number of samples were taken in each zone at each sampling time and the leeches from each of the samples were counted and weighed. These data were standardize to the equivalent of one Ekman dredge sample per zone.

The data from which the growth rates were estimated (Chapter 3) were used to estimate the relationship between the mean weight of a cohort and its standard deviation. The mean weights and standard deviations of the cohort were computed for the $20^{\circ} \mathrm{C}$ data for each of the first 33 wk (Figure 8.1). The coefficient of variation was roughly constant, indicating that for a single cohort, plots of frequency of occurrence versus logarithm weight will have a constant width, irrespective of the mean weight of the cohort. Thus, in a plot of logarithm weight versus frequency of occurrence for a population containing more than one cohort, each cohort should be distinguishable as a separate symmetric bell shaped curve.

A program was written to standardize the sample counts as described above and tally them into logarithm weight intervals. To

Figure 8.1 Standard deviation ( mg ) of the weight of a cohort of Nephelopsis obscura raised at $20^{\circ} \mathrm{C}$ under ad libitum food versus the mean weight ( mg ) of the cohort over time. The raw data are presented in Figure 3.2. The coefficient of variation (slope) is roughly constant.

determine the number of histogram classes that provided the maximum separation of cohorts the program was run a number of times, with the total number of weight ranges being changed each run. A three dimensional plotting program was written and the most discriminating plot, based upon 16 weight classes, is presented (Figures 8.2 - 8.3).

An extensive effort was made to estimate mortality schedules for the cohorts identifiable from these data. However this undertaking was unsuccessful, and resulted in erratic and large negative mortality rates. Several factors contributed to this failure: 1) the relative sizes of the three sampling zones was not known, so simply pooling standardized samples tends to over-emphasize zones with small areas, and under-emphasize zones with large areas. 2) there is movement among the zones. This problem appeared most prominent after ice cover when zone 1 (at the shore) was no longer sampled. As the ice thickened in fall, the benthic area of zone 1 became progressively smaller, forcing the animals from this zone into the other two. Thus immigration and mortality were happening simultaneously in zones 2 and 3 during this time, and the two processes could not be distinguished using these data. Other authors who attempted to estimate field mortality of erpobdellid leeches found similar problems confounding their studies (Murphy and Learner, 1982; Dall, 1979; Elliott, 1973). 3) the heaviest weight group has lighter cohorts growing into it and concurrent loss as individuals die. Since it is not possible to age individuals these two opposing processes confound estimation of age specific mortality. 4) the two sampling techniques (Ekman dredge and artificial substrate) are not likely comparable in their ability to capture N. obscura and are possibly biased to different size classes. The failure of these data to
provide sound mortality estimates made it necessary to obtain estimates from related species.

Figure 8.2 Nephelopsis obscura frequency of occurrence in Stephenson's Pond versus time (1979-1980) and leech weight.


Figure 8.3 Nephelopsis obscura frequency of occurrence in Stephenson's Pond versus time (1979-1980) and leech weight.


### 8.3 Related species

The results of a literature search for mortality schedules of other erpobdellid leech species (Mann 1962, Elliott 1973, Dall 1979, Murphy and Learner 1982) suggest very high mortality within the first two to three months of life (Figure 8.4A), then low mortality thereafter (a type III mortality curve). To estimate age specific mortality rates, these data were fitted to two alternative functions, one being an hyperbolic function of the form

$$
\begin{equation*}
S(t)=p_{1} e^{P_{2} t}+p_{3} e^{p_{4} t} \tag{8.1}
\end{equation*}
$$

where $S(t)$ is the probability of survival to age $t$ months and the $P_{i}$ are parameters which were estimated using BMDP's non-linear curve fitting program PAR. The estimates (Coef) and their standard deviations (SD) are:

> Coef SD

| $P_{1}$ | 85.62 | 4.22 |
| :--- | :--- | :--- |
| $P_{2}$ | -2.38 | 1.84 |
| $P_{3}$ | 14.38 | 3.72 |
| $P_{4}$ | -0.11 | 0.04 |

with residual mean square of 0.043 (Figure 8.4 A ).
The data were also fitted to a two parameter Weibull function (Kalbfleish and Prentice 1980) which models the instantaneous mortality rate at age $t(h(t))$ as the exponential model

$$
\begin{equation*}
h(t)=h p(h t)^{p-1} \tag{8.2}
\end{equation*}
$$

where $h$ and $p$ are estimated parameters. The survivorship function is

Figure 8.4 (A) Erpobdellidae survivorship obtained from published literature (triangles) with fitted hyperbolic function (equation [8.1]).
(B) Erpobdellidae survivorship data with fitted Weibull function (equation [8.2]).


$$
\begin{equation*}
S(t)=e x p-(h t)^{p} \tag{8.3}
\end{equation*}
$$

The parameters were estimated by least squares regression of $\ln [-\ln$ $S(t)$ ] versus in $t$ (Kalbfleish and Prentice 1980), the slope of which is an estimate of $p$ and the $\ln t$ intercept an estimate of $-\ln h$. The parameter estimates (Coef) and their standard deviations (SD) were:

$$
\begin{array}{rcc}
p= & \text { Coef } & S D \\
\text { intercept }= & 0.187 & 0.0877 \\
h= & 24.598 & 0.1832
\end{array}
$$

The residual mean square was 0.044 (Figure 8.4B). Since the hyperbolic model is less easily interpreted ecologically and there is little difference between the residual mean squares of the two models the Weibull model (equation [8.3]) was used to simulate survivorship as a function of age in subroutine MORT.

### 8.4 Discussion

The mortality function used in the model has the distinct disadvantage that mortality hazard cannot be expressed as a function of season or any particular mortality factor. The general lack of detailed empirical investigations of mortality factors seems to be a fundamental shortcoming of research upon the Erpobdellidae.

## Chapter 9 <br> Post-reproductive mortality

### 9.0 Introduction

Observations of reproductive Nephelopsis obscura (Davies and Everett 1977; Linton, Davies and Wrona 1983) have suggested it to be a strictly semelparous (Cole 1954; and see also Kirkendall and Stenseth 1985, page 190 re: life history models) species since all reproductive animals in the laboratory died 2 wk to 4 wk after cocoon deposition had ceased. Contrary to this observation, some reproductive individuals survived 90 d after cocoon production had ceased in the reproduction experiment described in Chapter 7, and it appeared that both ration and temperature influenced post-reproductive survivorship. It was decided to investigate the relationship between post-reproductive mortality in these specimens and a number of potentially important environmental variables.

### 9.1 Methods

The independent variables used in the analysis (Table 9.1) were fitted to the proportional hazards model of Cox (1972). The model can be derived as follows: Initially assume that under a specified and constant set of environmental conditions each individual in a population has an equal and constant probability of dying. Under these initial restrictive assumptions the hazard (h) associated with this environment for each individual can be represented as

$$
\begin{equation*}
h=e^{r} \tag{9.1}
\end{equation*}
$$

where the parameter $r$ is unique to the specified set of environmental conditions. Relaxing the assumption that the environment is constant, and assuming that some ( p ) of the characteristics of the environment are allowed to vary, implies that the parameter $r$ in equation [9.1] is no longer constant. Assume rather that for each environmental factor $\left(z_{i}\right)$ which is varying, there is a regression parameter $\left(B_{i}\right)$ that can be used to predict r as:

$$
\begin{equation*}
r=m+B_{1} z_{1}+B_{2} z_{2}+\ldots B_{p} z_{p} \tag{9.2}
\end{equation*}
$$

where $m$ is the intercept of the regression equation. Substituting equation [9.2] into equation [9.1] gives the hazard under the environmental conditions specified by the values of the environmental variables:

$$
\begin{align*}
h(\underline{z}) & =e^{\left(m+B_{1} z_{1}+B_{2} z_{2}+\ldots B_{p} z_{p}\right)}  \tag{9.3}\\
& =e^{m^{\prime}} \underline{B}^{\prime} \underline{z}
\end{align*}
$$

where $\underline{B}$ and $\underline{z}$ are vectors of the regression coefficients and environmental variables respectively. Now relax the assumption that under constant environmental conditions there is a constant hazard. Varying hazard could be due, for instance, to senescence of the individuals, thus increasing their probabilities of death even though the environment is unchanged. This underlying hazard function is introduced into equation [9.3] by making the constant intercept term em a function of time ( $h_{0}(t)$ ). Thus equation [9.3] becomes:

$$
\begin{equation*}
h(t ; \underline{z})=h_{0}(t) e e^{\prime} \underline{z} \tag{9.4}
\end{equation*}
$$

This was the proportional hazards model fitted to the experimental data, where the covariate vector $\underline{z}$ was a vector of independent variables (Table 9.1) and the elements of $B$ were estimated using the maximum likelihood method in BMDP program 2L (Hopkins 1981). Plots of residuals after regression were used to confirm the appropriateness of the proportional hazards model for these data. The term $e^{b^{\prime} z}$ z of equation [9.4] (where the vector $\underline{b}$ is the estimate of the vector $\underline{B}$ ) will be referred to as the risk factor, and it is this term which varies with the experimental variables.

### 9.2 Results

Since post-reproductive mortality was being investigated, only those individuals in the experiment which deposited cocoons were used in the analyses. The experiment was terminated before all specimens had died, so the data for the specimens surviving at the end of the experiment must be considered censored. There was considerable variability among individuals with regard to the amount of food consumed at each of the ration levels at which food was provided, so the actual food consumed by each individual was used in the regression analyses rather than the experimentally fixed ration levels. The coefficients from the fit to the proportional hazards model (Table 9.2) are the estimates of the elements of the vector $B$ in equation [9.4]. A negative value of a covariate denotes a negative effect on hazard (and hence a positive effect on survival) and vice versa. The coefficient/standard error values (Table 9.2) were used to test the null hypothesis that the coefficient is equal to zero, and in this case are distributed as $\underline{z}$. Based upon a priori arguments (Calow 1983) all variables except temperature were

Table 9.1 The variables used to fit Nephelopsis obscura mortality to the proportional hazards model. $T=$ temperature; $B_{\Gamma}=$ body size in calories at the start of cocoon deposition; $\mathrm{dB}_{\mathrm{r}}=$ change in body size during cocoon depostion; $C=$ total calorific value of cocoons produced; $n_{r}=$ the number of meals offered during the cocoon depostion period; $\mathrm{I}_{\mathrm{i}}=$ calorific value of the food consumed at each meal; $\mathrm{B}_{\mathrm{i}}=$ body size at the start of each meal; $t_{i}=$ the length of time (d) between means; $n_{p}=$ the number of meals offered after cocoon deposition had ceased.

| Variable | Definition |
| :---: | :---: |
| Temperature | T |
| Initial size | $\mathrm{B}_{\mathrm{r}}$ |
| Proportional energy loss during reproduction | $\arcsin \left(\mathrm{dB}_{\mathrm{r}} / \mathrm{Br}_{\mathrm{r}}\right)$ |
| Proportional reproductive output | $\arcsin \left(C / B_{r}\right)$ |
| Proportional daily feeding rate during reproduction | $\left(1 / n_{r}\right) * \sum_{i=1}^{n_{r}} I_{i} / B_{i} / t_{i}$ |
| Proportional daily feeding rate after reproduction | $\left(1 / n_{p}\right) * \sum_{i=1}^{\Pi_{p}} I_{i} / B_{i} / t_{i}$ |

Table 9.2 Regression equation from the fit of Nephelopsis obscura mortality to the proportional hazards model. $\mathrm{t}=$ regression coefficient/ standard deviation of the coefficient. Variables defined in Table 9.1.

## Complete model

| Variable | Coefficient | t |
| :---: | :---: | :---: |
| Temperateure | 0.3319 | 7.49 ${ }^{\text {F }}$ * |
| Initial size | -0.0034 | -2.34** |
| Proportional energy | 1.5316 | 2.43** |
| loss during reprodu | tion |  |
| Proportional reprod. output | 0.9050 | 0.94 n.s. |
| Feeding rate during reproduction | 4.2692 | 1.53 n.s. |
| Feeding rate after reproduction | -29.6433 | -4.43*** |

Reduced model

tested using a one tailed test. The two non-significant variables (Table 9.2) were removed from the covariate vector $\underline{z}$ and the reduced model fitted to the data (reduced model coefficients are also given in Table 9.2). The underlying hazard function $h_{0}(t)$ from equation [9.4] was approximately normally distributed with a mean of 42.7 d , standard deviation of 10.5 d and $h_{0}(42.7)=0.00037$. Mean weekly underlying hazard was also programmed into the simulation.

Since the risk factors lie on a four dimensional hypersurface which is difficult to represent graphically, loci of the risk factor for certain values of the covariates were computed by varying only one of the covariates from its minimum to its maximum experimentally observed value while holding all other covariates at their respective means (Figure 9.1). The ranking of the covariates in terms of the difference between the highest and lowest risk factor over the range of experimentally observed covariate values was: weight loss (250-30) > temperature (250 - 40) > post-reproductive feeding rate (185 - 15) > size (175 - 40). The abscissa of Figure 9.2 has been arbitrarily labelled from best to worst since movement along it from left to right represents simultaneous movement along all four of the abscissae of Figure 9.1, from the regions of lowest risk to the regions of highest risk. This figure shows that the risk factor of individuals drawn from a single population can vary two to three orders of magnitude over a range of conditions that could reasonably occur in the field.

At the end of the experiment, 18 of the surviving specimens, all of which had reproduced, were dissected to determine the condition of the gonads. All dissected animals possessed mature ova and sperm, indicating that they had come into breeding condition for a second

## time and would presumably enter another breeding cycle if allowed sufficient time.

Figure 9.1 Value of the risk factor in the proportional hazards model of Nephelopsis obscura mortality when temperature ( ${ }^{\circ} \mathrm{C}$ ), body size ( mg ), proportional energy loss to reproduction and proportional feeding rate were varied independently.


Figure 9.2 Value of the risk factor in the proportional hazards model of Nephelopsis obscura mortality when temperature ( ${ }^{\circ} \mathrm{C}$ ), body size (mg), proportional energy loss to reproduction and proportional feeding rate were varied simultaneously.


### 9.3 Discussion

A major problem in interpreting field observations of interpopulation variation in life history is the difficulty in distinguishing between genetic and environmental factors causing post-reproductive mortality. Populations which are genetically iteroparous could appear to be semelparous if post-reproductive mortality is high. In this study, the variability of the post-reproductive mortality response of a single population, was measured in relation to a variety of experimental conditions. The four habitat related variables - initial size, temperature, energy loss during reproduction and post-reproductive feeding rate - were found to have an extremely large influence on post-reproductive mortality risk. Within ecologically reasonably limits the influence of these variables on mortality risk ranged over two to three orders of magnitude (Figure 9.2). Combinations of these variables which produce high mortality risk would virtually guarantee total post-reproductive mortality, whereas a combination producing low mortality risk would favour post-reproductive survival. The fact that the specimens that were dissected at the end of the experiment had not only survived reproduction, but had also re-entered breeding condition suggests that N. obscura is genetically iteroparous, although at the field sites studied so far it displays a semelparous life history. These results strongly support the hypothesis that variation in. the life history of N. obscura observed in the field is easily within the range of phenotypic variation, and genetic differences need not be invoked to explain it.

Proportional reproductive output and feeding rate during reproduction have been strongly implicated on theoretical and empirical grounds as
being important in determining post-reproductive mortality (Calow 1983). In this study they had no significant effect. The results presented here indicate that, for N. obscura, proportional energy loss during reproduction is more appropriate as a measure of mortality risk associated with reproduction, since it integrates energy ingestion, increased metabolic demands associated with reproduction, and direct energy losses due to cocoon output.

The fact that temperature had a strong positive effect on hazard is not surprising, since it has been demonstrated that at $15^{\circ} \mathrm{C}$ the metabolic rate of N. obscura doubles as animals pass into reproductive condition (Wrona 1982). This increase would presumably be compounded by increasing temperature and would have to be met either by increasing ingestion rate or increasing the rate at which body tissues are catabolized, the latter increasing mortality hazard.

This study shows that unfavourable post-reproductive feeding conditions can significantly increase post-reproductive mortality risk, a conclusion which is supported by field observation. In Stephenson's Pond in 1983 there was a major crash in the population of the important prey species Chironomus riparius (Rasmussen 1983). The consequent loss of their brood caused a crash in Chironomidae prey density which was followed by a marked decline in the N. obscura population size, the numbers of which are presently below peak densities recorded before 1983. The fact that N. obscura can survive in the laboratory for a number of months with no food, suggests that the primary mortality factor in this circumstance was post-reproductive mortality due to low food supply.

The broad range of post-reproductive mortality response demonstrated by N. obscura in this study suggests that it has adapted to habitat unpredictability, and thus its reproductive strategy is to adopt a flexible life history rather than being strictly semelparous or strictly iteroparous.

In Stephenson's Pond, reproductive N. obscura first appear in the population at about 150 mg , whereas in Rocky Mountain foothills ponds in western Alberta (such as Lac des Arcs), and in Minnesota (Peterson 1983), reproduction is apparently not initiated until a much larger size ( 1500 mg ) possibly due to delayed reproduction associated with an iteroparous life history. If the temperature in the foothills habitats is cooler than prairie ponds, the attendant decrease in post-reproductive mortality risk (Figure 9.1) may be sufficient to explain the life-history difference between these two habitats. Minnesota ponds are not any cooler than Stephenson's Pond, but differences in food availability in these habitats may account for increased post-reproductive survivorship and hence the potential for iteroparity. The possibility also exists that life-history differences among these populations do have a genetic basis, which may relate to the age at which reproduction starts, rather than to post-reproductive mortality. Alternatively, the age at first reproduction, like post-reproductive mortality, may display phenotypic plasticity controlled by environmental variables. However, based upon the present information, the most parsimonious explanation of differences in life history of N. obscura is phenotypic plasticity as opposed to genetic differences between populations.

## Chapter 10

## Life history

### 10.0 Introduction

Various aspects of the life history of N. obscura have been shown to be variable. Davies and Everett (1977) report age at first reproduction to be 12,15 or 19 months, while Peterson (1983) reported it to be 24 months. These studies also report that N. obscura dies shortly after reproduction and is therefore semelparous. The present study (Chapter 9) has shown that post-reproductive survival is dependent upon habitat variables and those individuals that survive reproduction enter breeding condition again, thus demonstrating the potential for iteroparity under favourable field conditions.

Delaying age at first reproduction from 12 to 24 months would tend to decrease fitness (Cole 1954) all other things being equal. If older individuals are larger, they will produce more offspring (Chapter 7) which may compensate for the fitness loss due to delayed reproduction (Sibly and Calow 1983). Delaying reproduction in favour of growth will also decrease post-reproductive mortality risk (Chapter 9) thus increasing the probability of breeding again. The additional broods so produced could also compensate for the negative effect on fitness of postponing reproduction.

The objective of the work described in this chapter was to evaluate the relative fitness of different life histories and determine under which conditions N. obscura might become iteroparous. The parameters of the growth model were varied, as were the reproductive output equation (Chapter 7), the mortality equation (Chapter 8) and the
ages at which reproduction occurs. Varying these parameters in selective ways allowed all five of the basic life-history variables identified by Sibly and Calow (1983) to be manipulated. They are: brood size; age at first reproduction; time between broods; probability of surviving to the first breeding age; and probability of surviving between reproductive bouts. A method of comparing the fitness associated with different life histories remained to be developed in the model.

### 10.1 Computational methods

Since the model does not contain a complete set of density dependent feedbacks on mortality it was necessary to compensate for different population densities in some other manner. The population densities of N. obscura in Stephenson's Pond are very high ( $>300$ adults mss-2s - Wrona 1982), so the characteristics (density and individual size) of the prey population observed in Stephenson's pond can be considered to be those that result from the interaction between dense populations of N. obscura and its Chironomidae prey. Thus, observed Chironomidae data from Stephenson's Pond were used to simulate N. obscura populations which are very dense. The relationship between sparse populations of N. obscura (when density effects should be minimal) and its prey were then simulated by increasing prey consumption rates in the model from those predicted from simulations based upon observed Stephenson's Pond Chironomidae prey data. The mortality equation (Chapter 8) was not adjusted in the simulations, but it is expected that decreasing density would either reduce mortality generally, in which case the shape of the mortality function would not change, or juvenile mortality may be reduced more quickly than adult mortality, in which case the mortality function (Figure 8.4B) would more closely approximate a straight line. The consequences of these potential changes will be discussed later.

Simulations were performed in sets to allow comparisons of various scenarios of population density (food availability) or life history. The various parameters of the model were set to represent the desired scenario, and the simulation was run for one year, with a starting point of one individual. The expected survivorship of the individual
was plotted each week, until reproduction occurred, at which time the sum of the expected survivorship of the individual plus its expected number of offspring was also plotted. Initial plots of different scenarios overlapped to such an extent that differences between plots were difficult to distinguish. For this reason, the simulation for each scenario was repeated fifteen times, without varying the parameters of the model, except that each repetition of the simulation started with the number of individuals at which the previous one had ended. Thus differences between alternative scenarios were compounded 15 fold, making them more visible on the plots. The final numbers plotted after 15 repetitions (labelled years on the plots) were very high, and are not to be interpreted as real predicted population sizes after 15 yr , but simply the result of compounding a single year's population change 15 times. The ordinates of the plots (labelled population size) used a logarithmic (base 10) scale so the slopes of the plots can be used to estimate the parameter $r$ in the equation:

$$
\begin{equation*}
1=\sum_{x} e^{-r x_{x}} m_{x} \tag{10.1}
\end{equation*}
$$

where $x$ is age in weeks, $I_{x}$ is survivorship from birth until age $x$, and $m_{X}$ is the number of offspring an individual that attains age $x$ is expected to produce at. age $x$. The slopes of the plots in this chapter are approximately equal to $r / 2.303$. If the survivorship $\left(l_{x}\right)$.schedule and natality $\left(m_{x}\right)$ schedule represent those which would be displayed by a particular phenotype in a particular environment, then $r$ measures the fitness of the phenotype in that environment (Sibly and Calow 1983). Thus the slopes of the plots can be used to compare fitnesses associated with the various scenarios being simulated.

### 10.2 Life history traits

### 10.2.1 Introduction

The simulations described in this section were designed to investigate the population growth rates of N. obscura when life-history parameters are varied, or when certain habitat variables are changed. An attempt was made to predict the optimum life history for N. obscura in various habitats, and to determine whether the optimum is different in different habitats.

Sibly and Calow (1983) addressed the problem of predicting life-history optima using a graphical technique. This approach is limited since only two life-history variables can be manipulated at one time. The simulation model does not suffer from this constraint since the variables of the model interact with one another (Figure l.1) so that varying one will produce a change in other variables.

### 10.2.2 Longevity

### 10.2.2.1I Introduction

Increasing longevity increases the number of clutches an individual could potentially produce. The contribution of these offspring to future generations may be small if high adult mortality decreases the probability of the adult surviving to breed repeatedly.

### 10.2.2.1 Methods

Three levels of longevity were used: annual, corresponding to a semelparous life history; maximum life span of 3 yr ; and no upper
bound on longevity. The input data used were the 1984 Chironomidae and temperature data from Stephenson's Pond (Figures 6.3 and 6.4).

### 10.2.2.2 Results

The population growth rates produced by the three simulations were very similar (Figure 10.1) suggesting that under the conditions which existed in Stephenson's Pond in 1984 longevity has little effect upon the population growth rate.

### 10.2.2.3 Discussion

These simulations did not represent a true life-history trade off since reproductive output was not sacrificed in order to increase longevity. Limiting reproductive output in early life in favour of increased output in later life may result in faster population growth rates than those obtained in Figure 10.1, and would represent a true trade off.

### 10.2.3 Age at first reproduction

### 10.2.3.0 Introduction

The most extreme form of limiting reproductive output early in life would be to completely skip reproduction. If decreased post-reproductive mortality risks and increased reproductive output associated with larger size can offset delayed reproduction, delaying age at first reproduction would cause an increase in population growth rate.

Figure 10.1 Simulated sizes of three populations of Nephelopsis obscura with maximum individual life expectancy of 1 yr (dash dotted line), 3 yr (dashed line) and no upper boundary on longevity (solid line) versus time (weeks).


### 10.2.3.1 Methods

Simulations were performed in which the age at first reproduction was set to $12 \mathrm{mo}, 24 \mathrm{mo}$ or 36 mo irrespective of size.

### 10.2.3.2 Results

Delaying age at first reproduction decreased population growth rate (Figure 10.2).

### 10.2.3.3 Discussion

Gains in reproductive output and decreases in post-reproductive mortality due to increased body size were insufficient to compensate for losses due to delaying reproduction. Thus, in habitats such as Stephenson's Pond, age at first reproduction would be expected to be 1 уг.

### 10.2.4 Feeding rates

### 10.2.4.0 Introduction

In the previous two simulations the earlier breeding individuals were smaller than the later breeding individuals, but the growth rate of small individuals was approaching the maximum attainable, while that of larger individuals is less than maximal (Table 10.1). Increasing feeding rate of later breeding individuals may increase their growth rates (and hence their reproductive output) sufficiently for them to attain population growth rates comparable to those that breed early.

Figure 10.2 Simulated sizes of three populations of Nephelopsis obscura in which age at first reproduction was 1 yr (solid line), 2 yr (dash dotted line) or 3 yr (dashed line) versus time (weeks).


Table 10.1 Simulated proportional satiation and body size of Nephelopsis obscura.

| $\begin{aligned} & \overline{A g e} \\ & (y r) \end{aligned}$ | Proportional Satiation | $\begin{gathered} \text { Body Size } \\ (\mathrm{mg}) \end{gathered}$ |
| :---: | :---: | :---: |
| 1 | $0.73 \overline{0} 1$ | 122.7 |
| 2 | 0.4888 | 311.8 |
| 3 | 0.4116 | 354.6 |
| 4 | 0.4045 | 362.1 |
| 5 | 0.4039 | 363.5 |
| 6 | 0.4032 | 363.7 |
| 7 | 0.4030 | 363.8 |

### 10.2.4.1 Methods

Feeding rate was manipulated by either doubling mean individual Chironomidae biomass or by setting the feeding rate to its maximum value. These manipulations represented N. obscura feeding in habitats containing larger Chironomidae or switching from Chironomidae to some larger prey item. Age at first reproduction was set to $1 \mathrm{yr}, 2 \mathrm{yr}$ and 3 уг.

### 10.2.4.2 Results

Doubling average Chironomidae prey size resulted in a slight increase in individual growth rate during the first year, and proportional satiation of the largest individuals increased from 0.4039 (Table 10.1) to 0.4813 . The increased growth rate resulted in a slight increase in population growth rate of the population with age at first reproduction equal to 1 yr (Figure 10.3) and decreased the disparity between the three ages at first reproduction. The late breeding individuals still do not display as large a population growth rate as the earlier breeding ones.

Setting feeding rate at its maximum resulted in body size exceeding the maximum value in Table 3.3 and the exponential term of the respiration equation producing an exponential underflow. To avoid these problems, the maximum body size attainable was constrained to 10,000 mg . Even at these extreme growth values, older breeding populations always had lower population growth rates than younger breeding populations (Figure 10.4). Note however, that the older breeding populations now show marked irregularities in population size between the major breeding

Figure 10.3 Simulated sizes of three populations of Nephelopsis obscura using observed field Chironomidae prey sizes and Nephelopsis obscura age at first reproduction of 1 yr (solid line), double observed field prey sizes with Nephelopsis obscura age at first reproduction at 1 yr (long dashed line), and double observed field prey sizes with Nephelopsis obscura age at first reproduction at 2 yr (short dashed line) versus time (weeks).


Figure 10.4 Simulated population sizes of Nephelopsis obscura with age at first reproduction at 1 yr (solid line), 2 yr (dotted line), 3 yr (dash dotted line), 4 yr (short dashed line) and 5 yr (long dashed line). All simulations had ingestion rate set at ad libitum.

LOGARITHM OF
SIMNLATED Nephelopsis obscuri POPULATION SIZE

times, due to increased post-reproductive survival of the large individuals and their reproduction in subsequent years.

### 10.2.4.3 Discussion

When feeding rates are very high, delaying reproduction until large sizes are attained benefits post-reproductive survivorship sufficiently for clutches other than the first to contribute significantly to population growth. However, these contributions are insufficient to allow populations with delayed age at first reproduction to have higher population growth rates than earlier breeding populations.

### 10.2.5 Number of offspring and juvenile survivorship

### 10.2.5.0 Introduction

Increasing the number of offspring can be accomplished by either trading off energy among offspring, or alternatively by trading off energy between offspring and the adult. If energy invested in reproduction is fixed, then the energy content of each individual offspring could be reduced proportionally to an increase in offspring numbers. Alternatively, the amount of energy per offspring could remain fixed, but the adult could increase its total energy investment (reproductive effort). The former method would tend to increase juvenile mortality risk if risk is size related, but would represent no increase in risk for the adult, and thus represents a trade off between number of offspring and their survival rates. The second method would tend to increase adult post-reproductive mortality risk and represents a trade off between adult and juvenile survivorship.

### 10.2.5.1 Methods

Alternative trade offs were simulated by: 1) doubling the number of offspring and halving their size; 2) doubling the number of offspring and doubling reproductive effort; 3) halving the number of offspring and doubling their size; and 4) doubling offspring size and doubling reproductive effort but not varying number of offspring. Individuals were not allowed to breed until they had attained 80 cal ( 125 mg ) (Davies and Everett 1977).

### 10.2.5.2 Results

Doubling the number of offspring by doubling reproductive effort caused the largest increase in population growth rate (Figure 10.5), followed by doubling offspring size by doubling reproductive effort. Halving the number of offspring but doubling their size resulted in a decrease in population growth rate. Doubling the number of offspring but halving their size, reduced population growth rate and also caused a switch of age at first reproduction from one year to two years.

### 10.2.5.3 Discussion

Life histories which trade off reproductive effort for offspring increase population growth rate, while those that trade off energy among offspring result in decreases in population growth rates.

Figure 10.5 Simulated population sizes of Nephelopsis obscura from the unaltered simulation (solid line), number of offspring doubled and offspring size halved (dotted line), number of offspring doubled and reproductive effort doubled (dashed dotted line), number of offspring halved and their size doubled (short dashed line) and size of offspring doubled and reproductive effort doubled (lang dashed line).

LOGARITHM OF
SIMNLATED Nephelopsis obscure POPULATION SIZE


### 10.2.6 Iteroparity versus semelparity

### 10.2.6.0 Introduction

Some populations of N. obscura have been reported (eg. Peterson 1983) to contain much larger individuals ( $>2000 \mathrm{mg}$ ) than are present in Stephenson's Pond (<600-800 mg). The large individuals must have a higher feeding rate than those from Stephenson's Pond, since the latter appear to be unable to grow much beyond 400 cal ( 600 mg ) with the prey available (Figures 6.6 through 6.8). The larger individuals would be predicted to have lower post-reproductive mortality (Chapter 9), so would possibly benefit more by becoming iteroparous than the smaller individuals in Stephenson's Pond. The simulation model was used to investigate the relative advantage of iteroparity.

### 10.2.6.1 Methods

Simulations were performed to compare the population growth rates arising from semelparous and iteroparous life histories under various feeding rates and ages at first reproduction. Feeding rate was set at three different levels: feeding as modelled for Stephenson's Pond; feeding at a rate half way between maximal and the rates estimated for Stephenson's Pond; and maximal feeding rate. Age at first reproduction was set to either $1 \mathrm{yr}, 2 \mathrm{yr}$ or 3 yr of age. Semelparous individuals were removed from the populations immediately after breeding, while iteroparous individuals had no upper limit on longevity.

### 10.2.6.2 Results

In all cases semelparous populations had a lower rate of population
growth than did iteroparous populations (Figures 10.6 through 10.8), and as feeding rate was increased, population growth rates also increased. Comparison among the B plots and among the C plots in Figures 10.6 through 10.8 reveals steps in population size of the iteroparous populations between the major steps evident for the semelparous populations. The magnitudes of these steps increases along the series of figures, indicating that as feeding rate increases reproductive output in reproductive bouts after the first also increases. Inspection of Figures 10.6 through 10.8 reveals that gains associated with an iteroparous life history decrease with age at first reproduction and increase with feeding rate.

### 10.2.6.3 Discussion

This series of simulations has shown that in all cases, an iteroparous life history results in a faster rate of population growth than a semelparous life history (all other thing being equal), and that the advantage of the iteroparous life history increases with feeding rates. The ratios between population sizes at the end of the 15 yr simulation can be used to measure the proportional advantage of the iteroparous life history over the semelparous life history, which for the A plots yields: 17.8 (Plot 10.6 A), 510.9 (Plot 10.7A) and 5623.4 (Plot 10.8A). This result suggests a marked advantage to being iteroparous in habitats with higher food availability than in Stephenson's Pond. In the simulation in which food consumption was set half way between maximal and that predicted for Stephenson's Pond (Figure 10.7) the equilibrium body size attained was in the order of 1200 cal ( 1825 mg ), which approaches the body sizes reported for Minnesota (Peterson 1983) and those observed in foothills ponds in Alberta. Thus, it is predicted from the present simulations

Figure 10.6 Simulated population sizes of Nephelopsis obscura with ingestion rates simulated using 1984 Chironomidae prey data from Stephenson's Pond. Populations were either semelparous with death occurring directly after reproduction (solid lines) or iteroparous with probability of mortality set by the mortality equations (equation [8.4] and Table 9.2) (dash dotted lines). Age at first reproduction was 1 yr (10.6A), 2 yr (10.6B) or 3 yr (10.6C).


Figure 10.7 Simulated population sizes of Nephelopsis obscura with ingestion rates simulated from 1984 Chironomidae prey density data from Stephenson's Pond and then increased to half way between the simulated value and ad libitum ingestion rate. Populations were either semelparous with death occurring directly after reproduction (solid lines) or iteroparous with probability of mortality set by the mortality equations (equation [8.4] and Table 9.2) (dash dotted lines). Age at first reproduction was 1 yr (10.7A), 2 yr (10.7B) or 3 yr (10.7C).

LOGARITHM OF
SIMNLATED Naphelopsis obscura POPULATION SIZE


Figure 10.8 Simulated population sizes of Nephelopsis obscura with ad libitum ingestion rate. Populations were either semelparous with death occurring directly after reproduction (solid lines) or iteroparous with probability of mortality set by the mortality equations (equation [8.4] and Table 9.2) (dash dotted lines). Age at first reproduction was 1 yr (10.8A), $2 \mathrm{yr}(10.8 B)$ or 3 yr ( 10.8 C ).

that careful examination of the life history of N. obscura in these habitats will reveal the populations to be primarily iteroparous.

The prediction of iteroparity in habitats with abundant food does not necessarily contradict previously published descriptions of the life history of N. obscura (Davies and Everett 1977). These studies were conducted in prairie ponds which tend to be relatively warm, and in which food limitation is suspected to occur (Davies, Wrona, Linton and Wilkialis 1981, Davies, Wrona and Linton 1982). These factors would contribute to post-reproductive mortality, and consequently populations would appear semelparous. Peterson (1983) reported populations of N. obscura with much larger body sizes, suggesting increased prey availability, and although he was not able to provide data to demonstrate iteroparity, he suspected that it may occur in the populations he studied.

### 10.2.7 Reproductive effort versus delayed reproduction

### 10.2.7.0 Introduction

It has already been shown that delaying reproduction decreases population growth rate (Figure 10.2) however; increasing food consumption reduces this disadvantage (Figure 10.4) due to increased growth rates (and the attendant increase in reproductive output associated with larger size) and increased survival probabilities. If a small increase in reproductive effort could offset the disadvantages associated with delayed reproduction, it is possible that there may be only weak selection for early reproduction. Simulations were performed to determine what increase in reproductive effort would be necessary for life histories that breed later in life to have equal population growth rates as those which breed at one year of age.

### 10.2.7.1 Methods

The three feeding rates described in Section 10.2.6 were used, and for each feeding rate, a base line 15 yr simulation was performed in which reproductive effort and embryo production were those estimated when subroutine BREED was unaltered, and breeding occurred at age 1 yr. Maximum body size was constrained to 2300 cal ( 3500 mg ).

For each feeding rate, age at first reproduction was then delayed to 2 yr .and the reproductive effort (both ealories and embryo production) estimated in subroutine BREED were both multiplied by an estimate of the constant amount by which they must be increased to produce population growth rates equal to the populations breeding at age 1 yr . The population size of the base line run at 15 yr was than compared.
with the 15 yr population size produced by the altered model, and a new estimate of the multiplier was obtained. Using this iterative process, a multiplier was determined which produced the same population size (to three places of accuracy) after 15 yr as was obtained in the base line run. The necessary increase in reproductive effort was also determined for populations which bred at age 3 yr . For N. obscura which breed at either 2 yr or 3 yr , the maximum number of annual reproductive bouts per individual was either unconstrained, or set to a maximum of three.

### 10.2.7.2 Results

For populations with age at first reproduction of 2 yr and no limit on the number of reproductive bouts, a 2.55 fold increase in reproductive effort (Table 10.2) was necessary to produce equal population growth rates as a population with age at first reproduction of 1 yr . When the maximum number of reproductive bouts was not constrained, this figure declined very slightly to 2.54 , demonstrating that very high post-reproductive mortality resulted in very few individuals surviving to breed a third time. Increasing feeding rate resulted in a decline in the necessary increase to approximately 1.36 (Table 10.2) when life span was limited to three reproductive bouts. It was not possible to produce equal population growth rates when reproduction was delayed to 3 yr .

### 10.2.7.3 Discussion

Only when N. obscura feeds at its maximal rate did the necessary increase in reproductive effort approach zero. The value of 1.25 times

Table 10.2 Proportional increase in reproductive effort (PI) and embryo production necessary for simulated populations of Nephelopsis obscura with age at first reproduction of 2 yr and 3 yr to have equal population growth rates as populations with age at first reproduction of 1 yr . Simulations were performed with the populations feeding at three different ration levels. AAFR = Age at first reproduction (yr), MNB = maximum number of reproductive bouts per individual.

reproductive effort (Table 10.2) lies near the $95 \%$ confidence boundary of reproductive effort predicted for a 2300 cal individual using the cocoon calorie equation in Table 7.1. All other necessary increases in reproductive effort were well beyond this band. Thus, it is unlikely that a population which delayed reproduction to 2 yr could increase its reproductive effort sufficiently to have population growth rates equal to a population which breeds at 1 yr of age (except when food is readily available).

### 10.3 Discussion

The simulations performed in this chapter, using the unaltered model and data obtained from Stephenson's Pond resulted in a positive slope in the population size trajectory (solid line in Figure 10.2). If it is assumed that: (1) N. obscura in Stephenson's Pond breeds at age 1 yr , (2) it dies directly after reproduction, and (3) the population size in Stephenson's Pond is not changing from year to year (i. e. $r=0$ ); then it can be estimated from the slope of the solid line in Figure 10.2 that the combined overestimation of reproduction and the underestimation of mortality result in $r=2.0$ rather than $r=0.0$. Using the 1980 data, this estimate drops to only $\mathrm{r}=1.2$. If N. obscura breeds at 15 , 19 or 24 months (Davies and Everett 1977) or if some individuals in the field do not breed (section 7.3) then these estimates of $r$ will be even samller. It thus appears that the model's estimates of mortality and natality are not unreasonable, and depending upon environmental variation and potential variation in life history, may be quite accurate.

In the simulations conducted in this chapter, mortality was not decreased when food availability was increased (representing habitats with low densities of N. obscura). Since the estimates of reproductive output (Chapter 7) and post-reproductive mortality (Chater 9) do vary with varying food availability, the model has built into it these density dependent factors. Even if it is assumed that when food availability -increases to ad libitum mortality becomes zero, careful inspection of Figures 10.4 and 10.8 reveals that the order of the lines would not change, and hence, nor would the conclusion drawn from the graphs. The same arguement holds for the intermediate prey availability plots
(Figures 10.3 and 10.7). Thus, although some portions of density dependent feedback on mortality have been excluded from the simulation, the basic form of the results, and hence the conclusions, would not change.

Increasing reproductive effort resulted in increased population growth rates (Figure 10.5). Thus, it is expected that when N. obscura reproduces, it would tend to make a maximal effort. This may explain the observation that there was no measurable difference in reproductive effort between those individuals which survived reproduction (Chapter 7), and those which did not. If environmental conditions after reproduction are good (Figure 9.2) N. obscura can apparently recover from the large investment into reproduction and survives. If conditions after reproduction are poor, it is not able to recover and dies.

The simulations provide estimates of the optimum phenotype under different fixed environmental circumstances. If environmental circumstances vary, due to increases or decreases in population size or changes in prey availability due to non-density dependent factors, then so will the optimum phenotype change. Estimates of changes in the optimum phenotype can be obtained by comparing simulations which represent different environments along the axis of change. For example, comparing Figures 10.1 with 10.4 suggests that increasing food availability strongly increases the advantage associated with surviving reproduction. Habitats intermediate to the two simulated would be expected to display an intermediate benefit. This also suggests an evolutionary mechanism explaining the maintenance in the population of the ability to breed repeatedly (Chapter 9). If food availability varies from year to year, then in those years in which food availability is low (Figure 10.1 and 10.6), there is little advantage to being iteroparous (surviving reproduction),
but, in years when food is abundant (Figure 10.8) the iteroparous phenotypes. can produce many more offspring than the semelparous phenotypes (Section 10.2.6.3). When poor years return, there would be proportionally more of the iteroparous phenotypes than there would have been otherwise. For the semelparous phenotype to compensate for the advantage obtained by the iteroparous phenotype, it would have to increase its reproductive output. Since reproductive output was not related to post-reproductive survivorship (Chapter 9) there is evidence that this does not happen. Thus, the iteroparous phenotype could capitalize upon periods of ecological release that a strictly semelparous phenotype could not use and would thus tend to proliferate in the population.

The proportion of the population which possesses an iteroparous phenotype may depend upon the proportional frequency of occurrence of years with high prey availability. The high rate of survival of N. obscura in. the least stressful experimental cells used to estimate post-reproductive survival (Chapter 9) suggests that a relatively high proportion of the population in Stephenson's Pond possesses the potential for iteroparity.

The simulations were designed to investigate the range of life-history flexibility that N. obscura may demonstrate and the relative fitness consequences of the different life histories. The life-history flexibility is due simply to physiological flexibility. No evolutionary changes are implied. If environmental circumstances, such as food availability, remained relatively constant for an extended period of time, then evolutionary change may occur. The type of change which would occur, would depend upon the characteristics of the habitat. For instance, if the population density of N. obscura was low, and hence food was abundant, evolutionary processes may reshape the iteroparous life history prediced
in Figure 10.8. The direction of change could depend upon the relative mortality of adults and juveniles (Sibly and Calow 1983). If the population densities were low due to extremely low juvenile survivorship, then an evolutionary shift toward an iteroparous life history would be predicted (Sibly and Calow 1983). On the other hand, if the adults had extremely low survivorship, then an evolutionary shift toward semelparity would be predicted. The simulations do not address these evolutionary changes because evolutionary change of N. obscura would imply changing the model parameters from what they are presently set at to new values representing the product of these evolutionary changes. Since the animals used to estimate model parameters were from Stephenson's Pond, the model simulations represent the range of life histories that N. obscura from Stephenson's Pond could be expected to display as a result of their physiological flexibility. The results suggest that much of the variability in life history displayed by N. obscura in different habitats falls within the range of responses of a single population.

Hamilton (1966) and Mertz (1971) predict that in declining populations, late breeding individuals should have a selective advantage over early breeding individuals. It is thus possible that the prediction from Figure 10.3, that early breeding individuals have greater fitness ( $r$ ), might be reversed in declining populations. To test this, the mortality rate in the model was increased so that $r$ was negative, and simulations run with age at first reproduction of 1 yr and 2 yr , using 1984 Stephenson's Pond prey data as well as ad libitum food. Under both conditions of food availability the life history with age at first reproduction of 1 yr had higher fitness. Thus, the predictions of early breeding individuals having higher fitness holds for increasing, stable and declining populations. The difference
between the results of the present study and the predictions of Hamilton (1966) and Mertz (1971) may be due to the fact that their models presume life histories with a large number of reproductive bouts whereas these simulations were performed using semelparous individuals.

## Chapter 11

## Discussion

### 11.0 Sources of error

One of the major objectives of preparing the N. obscura simulation model was to objectively evaluate the data for N. obscura. A number of inadequacies in the data have been pointed out throughout this thesis, and in some cases they were sufficiently large to prevent completion of the simulation without augmentation by additional experiments (Chapters 5, 7 and 9). In terms of predicting the growth of an individual, there is a paucity of information regarding over-wintering populations and data at extreme values of variables such as body size and temperature. It seems that past researchers tended to gather information close to the center of ranges and ignore the extremes. This results in less accurate fitting of regression equations and frequently requires extrapolation of the function well beyond the range of data upon which it is based. The problem of extrapolation is not simply a simulation problem, but relates generally to the problem of external validity of experimental results i. e. their applicability to circumstances other than those in which the experiments were performed. Researchers frequently wish to use data from a set of experiments to explain or predict. However, this process may well represent an unrecognized extrapolation of experimental results. The process of building a simulation model makes extrapolation more obvious than it might be when only conceptual models are used.

Further information is required on the rates of energy use by very large individuals, and by individuals under hypoxic conditions,
particularly long term winter hypoxia. Much more extensive information is also required on feeding. The range of prey types used by N. obscura in the field is much broader than that used in the simulation (Davies, Wrona and Everett 1978, Davies, Wrona, Linton and Wilkialis 1981, Davies, Wrona and Linton 1982). No information exists regarding preference among different prey types (with the exception of Anholt (1982) whose data may be seriously flawed by arena size effects) or among different prey sizes as function of predator size, or whether feeding rate is related to satiation. Lack of satiation data required the upper boundary of prey ingestion rates in the simulation to be arbitrarily set to that which provided maximal growth rate under laboratory conditions, rather than limiting feeding rate by measured functional feeding responses. Simulations using only the average sized Chironomidae from Stephenson's Pond as prey, suggest that the maximum body size attainable by N. obscura is of the order of 600 mg (Chapter 6), despite the fact that very high prey densities were used (Rasmussen 1983). Improving the feeding data and including measured field prey abundance data may aid in explaining the large body sizes attained by N. obscura in Minnesota (Peterson 1983) and in the Alberta foothills.

Further to broadening the prey range, and including selectivity, feeding experiments must also be conducted at lower temperatures than those used in Chapter 5. Feeding is known to occur in the field at winter temperatures (Davies, Wrona and Everett 1978, Davies, Wrona, Linton and Wilkialis 1981, Davies, Wrona and Linton 1982), but extrapolating the laboratory measured relationship between feeding rate and temperature predicts feeding ceases at $8.8^{\circ} \mathrm{C}$ (Chapter 5). Thus, the relationship
between feeding rate and temperature must be markedly curved at cold temperatures.

The reproductive rates (Chapter 7) and post-reproductive mortality rates (Chapter 9) were estimated using N. obscura from only one habitat (Stephenson's Pond) and the largest specimens were of the order of 600 mg . Simulations investigating life-history strategies (Chapter 10) required extrapolation well beyond the upper boundary of body size, which may also occur in future simulations investigating the population dynamics of N. obscura in habitats which produce large specimens. .

The model at its present stage of development is unable to address questions regarding the population dynamics of N. obscura since no data are available regarding density-dependent feedback on population size. Evidence exists for inter-specific competition for food between. N. obscura and Erpobdella punctata (Leidy) (Davies, Wrona and Linton 1982). It is also possible that regulation of $N$. obscura population size is mediated by mechanisms other than prey availability.

Including density-dependent feedback in the model mediated by food availability would require extensive research into the population dynamics of the prey. Non-predatory prey mortality rates would have to be known, and then these rates increased during simulation by the rate of feeding by $N$. obscura. The individual growth rates of the prey would have to be investigated as functions of prey population density since cropping by $N_{0}$ obscura may increase individual prey growth rates if prey growth is itself limited at high prey densities as suggested for Chironomidae by Rasmussen (1983). If individual prey growth rates are increased as a result of N. obscura cropping, the impact of N. obscura upon its food resources may be ameliorated if individual prey grow
faster in response, thus providing fewer, but larger prey items. The simulation would also have to model migratory movements of different size groups of N. obscura (Gates 1984) within the water body being simulated to accurately predict population density of N. obscura.

Density-dependent population regulation can act by either increasing mortality or decreasing natality. The non-reproductive mortality function (Chapter 8) presently in the simulation is a very crude approximation and inappropriate for detailed population simulations. Before den-sity-dependent mortality could be included in the simulation, estimates of density-independent mortality must be obtained as a function of age as well as environmental variables such as temperature, hypoxia and density of predators on N. obscura. Density-dependent mortality (such as starvation) would then be added to the density-independent mortality. Density-dependent decreases in natality may operate by food limitation decreasing individual growth rates, with the result that the smaller individuals produce fewer offspring and suffer higher post-reproductive mortality. Clearly, extending the model to encompass the population dynamics of N. obscura will require an extensive research effort to provide the necessary mechanisms and functional relationships.

### 11.1 Strengths of the model

The model should help to increase the efficiency of the data gathering process of future researchers. As the model is updated, it will summarize the state of understanding and data available on the biology of N. obscura. Examination of the model for weaknesses in terms of incomplete information or questionable assumptions, will help future researchers to formulate concise research questions within the context of the unified body of knowledge. Concise research objectives, clearly defined within the context of a body of knowledge, usually contribute more efficiently to that body of knowledge than research questions whose context is less clearly defined. This is not intended to imply that future researchers should slavishly dedicate their work to expanding the model. To the contrary, like a concise review article, the simulation should be used to inspire imaginative research. As new information becomes available, including it in the simulation model simply keeps the synthesis up to date.

To aid in the updating process, the FORTRAN code has been extensively documented, possibly excessively. The objectives of this documentation were twofold. Those readers of the code who are not acquainted with FORTRAN, should be able to read the documentation and examine the equations and clearly understand all aspects of the simulation. This objective also resulted in the FORTRAN code being written in ways which are not elegant from a programmer's point of view, but which are easily understood. Secondly, some equations which were tried, but found to be unsuccessful have been left in the program as documentation in such a way that they can be easily reintroduced into the simulation if future users wish to explore the model's behaviour
with these equations included. This is recommended for those who update the model.

As the model presently stands, its growth predictions appear to be biologically reasonable and correct to the extent that they have been tested (Chapter 6). Thus, viewing the model as an hypothesis about the growth of N. obscura, it appears that our understanding or this process is not inconsistent with laboratory observation. Whether this will be borne out in the field has yet to be demonstrated.

Model output has generated some hypotheses regarding growth (Chapter 6) and the life-history (Chapter 10) of N. obscura which have already led to experimentation. In this respect, the objective of the modelling endeavor to generate concise research questions has already begun to be fulfilled.

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## Appendix A

The simulation model and its subroutines


| c | meter (3) - temperature | (loaded in actass.fortran) | grow | 31 |
| :---: | :---: | :---: | :---: | :---: |
| $c$ | meter (4) - temperature | (loaded in respir.fortran) | grow | 32 |
| c | meter 5 ) - body size in calories at | the beginning of the week. | grow | 33 |
| c |  | (loaded in maxass.fortran) | grow | 34 |
| c | meter (6) - body | (loaded in actass.fortran) | grow | 35 |
| c | meter (7) - body | (loaded in respir.fortran) | grow | 36 |
| c | meter (8) - body size at the end of | he week | grow | 37 |
| c |  | (loaded in grow.fortran) | grow | 38 |
| c | meter (9) - maximal assimilation | (loaded in maxass.fortran) | grow | 39 |
| c | meter (10)- actual assimilation | (loaded in actass.fortran) | grow | 40 |
| c | meter (ll)- chironomid prey density | (loaded in actass.fortran) | grow | 41 |
| c | meter (12)- chironomid prey wet wt | (loaded in actass.fortran) | -grow | 42 |
| c | meter (13)- Cladocera prey density | (loaded in actass.fortran) | grow | 43 |
| c | meter (14)- respiration | (loaded in respir.fortran) | grow | 44 |
| c | meter (15)- maximal growth rate | (loaded in mgainl.fortran | grow | 45 |
| c |  | or mgain2.fortran) | grow | 46 |
| c | meter(16)-calories invested in | oduction | grow | 47 |
| c |  | (loaded in effort.fortran) | grow | 48 |
| c | meter (17)- embryo production | (loaded in effort.fortran) | grow | 49 |
| c | meter (18)- growth efficiency | (loaded in grow.fortran) | grow | 50 |
|  |  |  | grow | 51 |
|  | array cohort is used to keep track | $k$ of different cohorts | grow | 52 |
| c | which may be present simultaneous | y in the population | grow | 53 |
| c | (up to a maximum of 50 without re | setting the dimension | grow | 54 |
| c | statement above). its contents a | e as follows: | grow | 55 |
| c |  |  | grow | 56 |
| c | the rows each represent a cohor | the index of the last cohort | grow | 57 |
| c | being stored below in "lc", and | the cohort counting | grow | 58 |
| c | index is "ic". |  | grow | 59 |
|  | the columns are: |  | grow | 60 |
|  | column 1 - the age of the coh | ort in weeks | grow | 61 |
| c | column 2-the size of the | ort in numbers. these | grow | 62 |
|  | values may be fra | tional. | grow | 63 |
| $\mathrm{c}$ | column 3-the average size of | an individual of the | grow | 64 |


| cohort | grow | 65 |
| :---: | :---: | :---: |
| c column 4-the body size at the commencement of | grow | 66 |
| c reproduction | grow | 67 |
| c column 5-a switch set to the week of the beginning | grow | 68 |
| c of reproduction and 0.0 at the end. | grow | 69 |
| c the array rep is used to control breeding. | grow | 70 |
| c...the array rep is used to control breeding. its contents are | grow | 71 |
| c zero or unity and are read from the input data. it contains | grow | 72 |
| c $\quad 52$ elements, on for each week of the year. in any week | grow | 73 |
| c in which the correspond element of rep is set to l.0, | grow | 74 |
| c breeding will occur. | grow | 75 |
|  | grow | 76 |
|  | grow | 77 |
|  | grow | 78 |
| c...open data | grow | 79 |
| c...open data | grow | 80 |
| open(ll, mode="in", access="sequential" | grow | 81 |
|  | grow | 83 |
| pen output | grow | 84 |
|  | grow | 85 |
| open(12,mode= "out ${ }^{\text {, acce }}$ | grow | 86 |
| c...open input file for input of base line run results. The results of | grow | 87 |
| simulations under different environmental conditions | grow | 88 |
| c are compared to these bench mark results read in from this | grow | 90 |
| c file to investigate the effects of varying environmental | grow | 91 |
| c conditions or model parameters. | grow | 92 |
|  | grow | 93 |
| open(13,mode= 'in',access='sequential', form='formatted') | grow | 94 |
| c sensitivity analysis output is to filely | grow | 95 |
|  | grow | 97 |
| open(14,mode $=$ out, access $=$ 'sequential', form='formatted') | grow | 98 |

```
```

c...call data initialization routine

```
```

c...call data initialization routine
call datain(prey,temp,o2,growth,wdgr, nweeks,body,iged,nd,rep)
call datain(prey,temp,o2,growth,wdgr, nweeks,body,iged,nd,rep)
cohort(1,3) = body
cohort(1,3) = body
cohort(1,2) = 1.0
cohort(1,2) = 1.0
lc = 1
lc = 1
mindif = 10.**7
mindif = 10.**7
maxdif = -10.**7
maxdif = -10.**7
c******************************************************************
c******************************************************************
c
c
c************ main loops through years, weeks and cohorts **********
c************ main loops through years, weeks and cohorts **********
c
c
c
c
c
c
c...loop through years
c...loop through years
c
c
ny=15
ny=15
do 510 year = 1 , ny
do 510 year = 1 , ny
c
c
c...loop through weeks
c...loop through weeks
do 500 nweeks(3) = nweeks(2) , nweeks(2) + nweeks(1) - 1
do 500 nweeks(3) = nweeks(2) , nweeks(2) + nweeks(1) - 1
c
c
c...loop through cohorts
c...loop through cohorts
c
c
do 490 ic = 1, lc
do 490 ic = 1, lc
c
c
c...age the cohort
c...age the cohort
C
C
cohort(ic,l)= cohort(ic,l)+1.0
cohort(ic,l)= cohort(ic,l)+1.0
c
c
c...if the cohort is dead, skip to next one
c...if the cohort is dead, skip to next one
c

```
```

c

```
```

```
grow }9
grow 100
grow l01
grow l02
grow 102
grow l03
grow l04
grow l05
grow l06
grow 107
grow l08
grow }10
grow ll0
grow lll
grow ll2
grow ll3
grow ll4
grow }11
grow 116
grow 117
grow ll8
grow ll9
grow 120
grow 121
grow l22
grow l23
grow l24
grow l25
grow l26
grow 127
grow l27
grow l29
grow 130
grow 131
grow 132
```

```
    if(cohort(ic,2).It.0.0) go to 490 grow 133
c grow 134
c...if the cohort can breed, set the breeding condition flag grow l35
c
    if((rep(nweeks(3)) .gt. 0.5 . and. rep(nweeks(3)-1). It. 0.5
    1 .and. cohort(ic,3).ge. 80.0).or.
    l (rep(nweeks(3)).gt. 0.5..and. cohort(ic,5).gt.0.0))then
c if(rep(nweeks(3)).gt.0.5.and.cohort(ic,l).ge.52)then
                bfl=.1.0
                bf2=1.0
    else
            bfl=0.0
    end if
c
c
c
    call maxass(nweeks(3),temp,growth,wdgr, cohort(ic,3),mass,
    l igcd,nd,meter,bfl)
    call actass (temp, nweeks(3), prey, cohort(ic, 3), nstate,
    l mass,aass,meter)
        call respir (nweeks(3),temp, nstate, cohort(ic,3),resp,meter,bfl)
    prod = aass - resp
c
c...reproduct ion
c
    if (bfl.gt. 0.5) then
        call breed(nweeks(3), cohort,ic,lc,aass,meter,temp,repeff)
    else
        repeff}=0.
        meter(16)=0.0
        meter(17)=0.0
    end if
    cohort(ic,3)= cohort(ic,3) + prod - repeff
```

c...compute growth efficiency
c
- if (aass .gt. 0.0) then
meter(18) = prod / aass.
else
meter (18)=0.0
end if
meter(l) = nweeks(3)
meter(8) = cohort(ic,3)
c
c...mortality
c
c set maximum longevity
c
if(cohort(ic,l).ge. ll2.)then
cohort(ic,2)=-1.0
else
proportional feeding rate after reproduction
if(cohort(ic,5) .ne. 0.0 .and.
nweeks(3).gt. cohort(ic,5)+3 . and.
nweeks(3).It. cohort(ic,5)+10)then
cohort(ic,6)=cohort(ic,6)+aass/0.79/cohort(ic,3)/7.0
far = cohort(ic,6)/(cohort(ic,5) + 3. - nweeks(3))
else
cohort(ic,6) = 0.
far = 0.
end if
call surviv(nweeks(3),temp, cohort,ic,far,p)
cohort(ic,2) = cohort(ic,2) * p
c
end if

```
grow 167
grow 168
grow 169
grow 170
grow 171
grow 172
grow 173
grow 174
grow 175
grow 176
grow 177
grow 178
grow 179
grow 180
grow 181
grow 182
grow 183
grow 184
grow 185
grow 186
grow 187
grow 188
grow 189
grow 190
grow 191
grow 192
grow 193
grow 194
grow 195
grow 196
grow 197
grow 198
grow 199
grow 200
```

c...call for sensitivity analysis
c
c call sensit(nweeks(3), cohort(ic, 3),mindif,maxdif)
c
4 9 0 ~ c o n t i n u e
c
c******* end cohort loop ********
c
c
c...incriment the index of the last cohort (lc) if
c reproduction is finished and breeding has ocurred.
c
if(rep(nweeks(3)) .gt. 0.5 .and. rep(nweeks(3)+1).lt.0.5
l and.bf2.gt. 0.5)then
1c}=1c+
bf2=0.0
end if
c
c...reset the reproduction marker in column 5 if l0 weeks
c have elapsed since the commencement of reproduction.
c
do 492 i = l, lc - l
if(cohort(i,5) .gt. 0.0 . and. nweeks(3) .eq. cohort(i,5)+9)
l
cohort(i,5)=0.0
4 9 2
continue
c...write out total population at the end of each week
c
total = 0.0
do 495 i = 1, 1c
c write(12,i002)(cohort(i,j),j=l,6)
495 if(cohort(i,2).gt. O.)total = total + cohort(i,2)
4 9 5 ~ c o n t i n u e ~
tweek = (year-1)*52+nweeks(3)

```
grow 201
grow 202
grow 203
grow 204
grow 205
grow 206
grow 207
grow 208
grow 209
grow 210
grow 211
grow 212
grow 213
grow 214
grow 215
grow 216
grow 217
grow 218
grow 219
grow 220
grow 221
grow 222
grow 223
grow 224
grow 225
grow 226
grow 227
grow 228
grow 229
grow 230
grow 231
grow 232
grow 233
grow 234

```

    do 600 i = 11,14 grow 269
    continue
    stop
    1000 format('week', 4x,'body',4x,'max. assim.',4x,'assim',4x,'resp',4x,
1 'prod',4x,'rep. eff.'
1001
1002
1006
1008
l008 format(f6.0,fl0.1/)
l011 format(' mindif = ',fl0.5,' minb=',fl0.5,' minwk=',i4,/
1 ' maxdif =',fl0.5,' maxb=',fl0.5,' maxwk=',i4}
end

```
grow 269
grow 270
grow 271
grow 272
grow 273
grow 274
grow 275
grow 276
grow 277
grow 278
grow 279
grow 280
grow 281
grow 282
grow 283
grow 284
```

    subroutine datain (prey,temp,o2,growth,wdgr, nweeks,body,iged,nd, data l
    l rep
    dimension prey(100,3),temp(100),o2(1),growth(5),rep(52)
    dimension nweeks(5),wdgr(80,10), nd(5)
    c...get the number' of weeks for which the simulation is to run
and the week within which simulation is to commence.
read(11,) nweeks(1)
read(11,) nweeks(2)
c...get the prey density data.
call preyin(prey)
c...get the temperature data
call tempin (temp, nweeks(4))
c...get the oxygen concentration in mg/l
o2(1)=10.
c...get the growth data
call grwin(growth,wdgr,nd,igcd)
c...get initial body size in calories
read(11,)body
c...load array of breeding weeks
data l
data 3
data 4
data }
data 6
data }
data }
data }
data l0
data 11
data }1
data 13
data }1
data 15
data 16
data 17
data 18
data }1
data 20
data 2l
data 22
data 23
data 24
data 25
data }2
data 27
data 28
data 29
data 30
data 31
data 32
data 33
data 34

```
```

read(11,)(rep(i), i=1,52)
return

```
end
data 35
data 36
data 37



```

grwi 103
C
write out the weight dependent growth rates
c write(12,1000)
1000 format(" temperature and weight dependent growth rates - ",/,
l 10x,"0 C"llx,"5 C"llx,"l0 C"llx,"15 C"llx,"20 C")
do 30 i = 1 , 80
c write(12,1001)(wdgr(i,j),j=1,10)
l001 format(2x,5(f8.0,1x,f5.3))
30 continue
else
call err2(igcd)
end if
return
end

```
grwi 104
grwi 105
grwi 106
grwi 107
grwi 108
grwi 109
grwi 110
grwi 111
grwi 112
grwi 113
grwi 114
grwi 115
grwi 116
grwi 117
grwi 118
grwi 119
grwi 120
grwi 121
grwi 122
grwi 123


```

c read the digitized x,y coordinates in cm and transform temp 69
M temp 70
c them to degrees celcius and store in vector temp temp 7l
c if an end of file mark is encountered, an error has ocurred temp 72
c since there are fewer data than specified by JWEEK. temp 73
do 20 i = l', jweek temp 74
read(11,,end-40,err=40)ir,x,y temp 75
read(11,,end=40,err=40)ir,x,y temp 76
temp(ir)=t*y/my
continue
c
c
c write out the computed temperatures
c
c write(12,1000)(temp(i),i=1,jweek)
1000 format(8f9.1)
else if (icode .eq. 2) then
temp 78
temp }7
temp 79
t emp 80
temp 81
temp 82
t emp 83
temp 84
temp 86
temp 87
t emp 88
c...for this section of the progr, temp 89
c...for this section of the program to be executed, the temperature temp 90

```

```

c data being read. temp 93
c First read the number of weeks of data being provided in the file, then read the data. temp 94
in the file, then read the data. temp 95
read(11,,end=40,err=40) jweek temp 96
t emp }9
c
t emp 98
c
c
c write(12,1001)
temp 99
temp 100
temp 101
temp l02

```
```

1001 format(///lx,"week",lx,"temp"/)
temp 103
do 30 i = 1 , jweek
read(ll,)j, temp(j)
write(i2,1002)j,temp(j)
format(i4,f5.1)
1002
30
c
continue
else
call errl
end if
return
4 0 ~ c o n t i n u e
call err9('tempin',jweek,i)
end
temp 104
temp }10
temp }10
temp }10
temp 108
temp }10
temp 110
temp l11
temp 111
temp 112
temp}111
temp 1114
temp 116
temp 116
temp 118
temp ll8
temp l20
temp 120
temp 122

```

```

        prey(j,l)=999.
    10 continue
c...read the number of weeks of data
c
read(11,)iw
c
c...read the data
c
do 20'j = l , iw
read(1l, ,end=30,err=30)ir,(prey(ir,k),k=l,3)
20 continue
c
return
c
30 continue
call err9('preyin',j,iw)
end

```
prey 35
prey 36
prey 37
prey 38
prey 39
prey 40
prey 41
prey 42
prey 43
prey 44
prey 45
prey 46
prey 47
prey 48
prey 49
prey 50
prey 51
prey 52
```

    subroutine maxass (iweek,temp,growth,wdgr,body,mass,igcd,nd,meter,maxa l
    l breed) maxa 2
    c
dimension temp(100),growth(5),wdgr(80,10),nd(5), dummy (2)
maxa 3
maxa 4
c
real máss,mg,meter(35)
c
c...load metering array with temperature and body size*at the
beginning of the week.
meter(2)=temp(iweek)
meter(5)=body
c
c
c...call for maximal respiration requirements, which will occur when
14
c . Nax locer when m
c equals l.0). This is accomplished by transfereing a parameter maxa l6
c dummy array with 1.0 in element 2 to subroutine respir_ maxa l7
c dumny array with l.0 in element 2 to subroutine respir.
maxa 18
dummy (2) = 1.0
maxa
c
c
call respir(iweek,temp,dummy,body,resp,meter,breed).
maxa 20
maxa 21
maxa 22
c
c...compute maximum number of calories gained due to growth under maxa 24
23
c ad libitum food conditions
c if'(igcd .eq. 1) call mgainl(growth,body,iweek,temp(iweek),
l meter,calgan)
if (igcd.eq. 2) call mgain2(wdgr,body,temp,iweek,nd,
l meter,calgan)
c
maxa 25
c if'(igcd .eq. 1) call mgainl(growth,body,iweek,temp(iweek),
maxa 26
maxa 27
maxa 28
maxa 29
maxa 30
maxa 31
maxa 31
c
c...compute maximal assimilation rate as the maximal growth plus
maxa 33
maxa 34

```
```

c maximal respiration maxa 35
mass = resp + calgan
c
c
c
c
meter(9)=mass
return
c
end

```
maxa 35
mass \(=\) resp + calgan
c
c... load metering array
c
meter (9) =mass return
end
maxa 36
\(\operatorname{maxa} 37\)
maxa 38
maxa 39
maxa 40
maxa 41
maxa 42
maxa 43
maxa 44
\(\operatorname{maxa} 45\)
\(\operatorname{maxa} 46\)
```

c
subroutine mgainl(growth, body, iweek,temp,meter, calgan)
mgai
1
dimension growth(5)
c
real mg,meter(35)
c
c...compute maximal weight gain under ad libitum food conditions.
mgai 2
c the equation is obtained by re-arranging those of Dr.F.J. Wrona
c the equation is obtained by re-arranging those of Dr. F. J. Wron
c only small individuals
c
c...check that temperature data are valid.
c
if (temp .eq. 999.) call err5(iweek,"mgainl")
c
c this equation requires body size in mg wet weight
c the conversion to calories from wet weight of 0.6577 cal/mg wet
c weight was determined by D. J. Baird.
weight was de
c...compute the exponential growth rate (interpolate between
c temperatures)
c
if (temp.le. 5.0) then
r = (growth(2)-growth (1))*temp/5.0 + growth(1)
if (r .1t. 0.0) then
calgan = 0.0
return
end if
else if (temp.gt. 5 . and. temp.le. l0.0) then
r=(growth(3)-growth(2))*(temp-5.0)/5.0 + growth(2)
else if (temp .gt. 10 .and. temp .le. 15.0) then
mgai }
c
mgai 4
mgai 5
c
mgai 6
mgai }
mgai 8
mgai 9
mgai lo
mgai ll
mgai l2
mgai 13
mgai ll
mgai l5
mgai 16
mgai 17
mgai
mgai 19
mgai
mgai 21
mgai 22
mgai 23
mgai 24
mgai 25
mgai 26
mgai 27
mgai 28
mgai 29
mgai 30
mgai 30
mgai 31
mgai 32
mgai 33
33
mgai }3

```
```

        r = (growth(4) - growth(3))*(temp-10.0)/5.0 + growth(3) mgai 35
        else if(temp .gt. l5 .and. temp .le. 20) then
        r = (growth(5) - growth(4))*(temp-15.0)/5.0 + growth(4)
        else
            call err7(iweek,temp)
        end if
    c
c...load metering array with maximal growth rate.
c
meter(15)=r
c
c...weight gain is in mg wet weight.
c
calgan = wtgain * 0.6577
c
return
C
end
mgai 36
mgai 37
mgai 38
mgai 39
mgai 40
mgai 4l
mgai 42
mg̣ai 43
mgai 44
mgai 45
mgai 46
mgai 47
mgai 48
mgai 49
mgai 50
mgai 5l
mgai 52
mgai

```
```

    subroutine mgain2(wdgr,body,temp,iweek,nd,meter,calgan) mgai l
    c...this subroutine computes maximal caloric requirements using weight
c and temperature dependent growth rates.
C
integer cl,cu,rl,ru
real mg,meter(35)
dimension wdgr(80,10),nd(5),temp(100)
c
c...the array wdgr contains columns of weight dependent growth rates
and their associated weights. Each pair of columns is for
c and their associated weights. Each pair of columns is for
c a different temperature. The indices of the columns associated
c below the present working temperature (temp) must be computed

```

```

c interpolation.
c Growth rates are in the even numbered columns.
********************************************************
lol
Clol

```

```

lol
lol
*******************************************************
C
c...variables used in this subroutine:
cl - (column lower) - column of wdgr associated with the lower mgai 28
part of the temperature range spanned mgai 29
by the growth data which cover the mgai 30
present temperature being used mgai 31
cu - (column upper) - column of wdgr associated with the upper mgai ma, 32
temp mgai
mgai
mgai
mgai
mgai 4
mgai
mgai 5
mgai 6
mgai }
mgai -
mgai rr
mgai
mgai 12
mgai 13
mgai 13
c
mgai 15

```

```

mgai l6
mgai l7
mgai l8
mgai 19
*******************************************************
mgai 20
*******************************************************
mgai 21
must be appropriately modified. mga, 22
mgai 22
mgai 23
mgai 24
mgai 25
mgai 26
c cl - (column lower) - column of wdgr associated with the lower
mgai27
mgai 3l
mgai 32

```

```

c also fail if temperature exceeds 20 C, unless appropriately mgai 69
c
modified. .
if(temp(iweek) .eq. 20.) cu = l0
c
if(temp(iweek) .lt. 20) cu = cl + 2
compute the temperatures associated with these indices
tl=(float(cl) / 2.0-1.0)*5.0
tu=t1+5.0
c
c. convert body from calories to mg
mg = body / 0.6577
c
c maximum for which data are available.
if(mg.gt. wdgr(nd(cl/2),cl-1) .or.mg.gt. wdgr(nd(cu/2),cu-1))
1 call err4(mg,temp(iweek))
search the array wdgr for the rows associated with this
weight at both temperatures tl \& tu
do 10 i = 1,50
if (wdgr(i,cl-1).gt. mg) then
rl=i
go to l5
end if
l0 continue
l5 continue
c

```
```

    do 20 if = l , 50
                ru = i
            go to 25
        end if
    20
continue
continue
interpolate between these growth rates to find the rate to
be used.
scale = (temp(iweek) - tl) / (tu - tl)
rate = wdgr(rl,cl) + (wdgr(ru,cu) - wdgr(rl,cl)) * scale
c
c...load metering array
c
meter(12) = rate
c
c compute weight gain
c
wtgain = mg * rate - mg
c
c convert to calories
c
calgan = wtgain * 0.6577
c <
c...write out computed theoretical maximal caloric gain
c
c write(12,1003)calgan
l003 format(" maximal theoretical growth in calories = ",flo.5)
return
end

```
mgai 103
mgai 104
\(\begin{array}{ll}\text { mgai } & 105 \\ \mathrm{mgai} & 105\end{array}\)
mgai 106
mgai 107
mgai 108
mgai 109
mgai 110
mgai 111
mgai 112
mgai 113
mgai 114
mgai 115
mgai 116
mgai 117
mgai 118
mgai 119
mgai 120
mgai 121
mgai 122
mgai 123
mgai 124
mgai 125
mgai 126
mgai 127
mgai 128
mgai 129
mgai 130
mgai 131
mgai 132
mgai 133
mgai 134
```

    subroutine actass(temp, iweek,prey,body,nstate,mass,aass,meter) acta l
    c
c
c...function:
c this subroutine computes ACTual ASSimilation rate
as a function of temperature, nutritional state, and
prey density.
c...transfered parameters:
c temp - the temperature - input
iweek - the week of the simulation - input
prey - a two dimensional array of prey density and
mean prey wet biomass. - input
body - the body size of the predator in calories - input
nstate - a.one dimensional array with two elements containing
the nutritional state in the previously simulated
week and the week presently being simulated.
- output.
mass - maximal assimilation rate. - input
aass - actual assimiltion rate. - output
C
c
dimension temp(100), prey(100,3)
real nstate(2)
real meter(35), ingest,mass
c
c...load metering array
c
c
meter(3) = temp(i week)
meter (6)=body
C
c...check for valid prey densities (see subroutine datain
c* for explanation of 999. code)
acta 2
acta 3
acta 4
acta 5
acta 6
acta 7
acta 8
acta 9
acta 10
acta ll
acta l2
acta 13
acta 14
acta 15
acta 16
acta 17
acta 18
acta 18
acta 20
acta 21
acta 22
acta 23
acta 24
acta 25
acta 26
acta 27
acta 28
acta 29
acta 30
acta 31
acta 32
acta 33
acta 34

```
```

c acta 35
if (prey(iweek,l).eq. 999.) call err6 (iweek,"actass") acta 36
c
c...check for valid temperatures
c
if (temp(iweek) .eq. 999.) call err5(iweek,"actass")
c
c
c note l: since feeding is assumed to stop at 8.8 degrees
celcius, aass is assigned zero for temperatures
lower than this.
note 2: the variable body transfered in is in calories,
so must be converted to mg in the consumption
equation by dividing by 0.6577.
note 3: numbers consumed are converted into calories by
multiplying the number of prey consumed by their
mean wet biomass in mg and by calories per mg
wet weight. the conversion factor of 0.80l564
calories per mg wet biomass of chironomids is
compliments of Mr. T. Gates
note 4: the regression equation below estimates number of
prey taken per day, so consumption must be multiplied
by 7.0 to make per week estimates.
if (temp(iweek).le. 8.8) then
aass = 0.0
else
c
c...Chironomi dae prey capture
c
c**************************************************************
c

```
acta
acta 37
acta 38
acta 39
acta 40
acta 41
acta 42
acta 43
acta 44
acta 45
acta 46
acta 47
acta 48
acta 49
acta 50
acta 51
acta 52
acta 53
acta 54
acta 55
acta 56
acta 57
acta 58
acta 59
acta 60
acta 61
acta 62
acta 63
acta 64
acta 65
acta 66
acta 67
acta 68
NOTE: the following equation was found to produce unacceptable acta 69
        results since its first derivitive was negative within acta 70
        some of the region of the independent variable. It acta 71
        sould be stricity positive. The data acta 72
        for each temperature were refit, and it was found that body acta 73
        size had no significant effect, so was eliminated. acta 74
        Only prey density was used as an independent variable, acta 75
        and, slope is estimated for temperatures other than acta 76
        those at which experiments were conducted by interpolation. acta 77
    consum \(-1.3854+1.16518 *\) prey (iweek, 1)
    consum \(=-1.3854+1.16518 * \operatorname{prey}(\) iweek, 1\()\)
    \(1+0.06706 *\) temp (iweek) acta 80
    \(2+0.005738 *\) body / 0.6577 acta 81
    \(3-0.03729\) * prey (iweek,1) * temp (iweek) acta 82
    \(4-0.0088245 *\) prey (iweek, 1 ) * body / 0.6577 acta 83
    \(5-0.0003042 *\) temp (iweek) * body / \(0.6577 \quad\) acta 84
    \(6+0.0006526 * \operatorname{prey}(\) iweek, 1\() *\) body / \(0.6577 *\) temp (iweekacta 85
************************************************************** \(\quad 86\)
c
    at 12.5 C consum \(=0.244+0.402\) prey density
    at 15.0 C consum \(=-0.161+1.03\) prey density acta 91
    at 20.0 C consum \(=-0.100+1.81\) prey density acta 92
    if (temp (iweek).le. 15)then 93
    \(a=0.2438-(0.2438-(-0.1606)) *(t \operatorname{emp}(i\) week \()-12.5) / 2.5 \quad\) acta 95
    \(b=0.4016-(0.4016-(1.0258)) *(t e m p(\) iweek \()-12.5) / 2.5 \quad\) acta 96
else
    \(a=-0.1606-(-0.1606-(-0.1002)) *(\) temp (iweek) -15.0\() / 5.0 \quad\) acta 98
    acta 97
    \(b=1.0258-(1.0258-(1.8133)) *(t e m p(i w e e k)-15.0) / 5.0 \quad\) acta 99
    end if
consum=a \(+b\) * prey (iweek, 1 ).
acta 100
acta 101
acta 102
```

    acta 103
    this is chironomid prey capture per day. convert to calories
        per week
    using simple linear regression of all capture rates
        on temperature suggested feeding ceases as approximately
        8.8 C. However, the above equation for consumption
        can produce negative capture rates at temperatures
        slightly above 8.8 C, depending upon prey density.
        Therefore, if consum is negative, simply set it
        to zero.
    if (consum .gt. 0.0) then
ingest = consum * prey(iweek,2) * 0.801564 * 7.0
else
consum = 0.0
ingest = 0.0
end if
if prey density is large, and mean prey size is large;
the above feeding equation may produce estimates
of ingestion which are greater than the maximal
rate determined in subroutine maxass.
On the assumption that when these conditions prevail
the leech would stop feeding when it bacame satiated,
set the ingestion rate to the maximal ingestion
rate. Since food is 'super-abundant' and
the animal is satiated simply return to
the calling routine, and don't bother
going through the Cladocera section of this
routine.

```
acta 104
acta 105
acta 106
acta 107
acta 108
acta 109
acta 110
acta 111
acta 112
acta 113
acta 114
acta 115
acta 116
acta 117
acta 118
acta 119
acta 120
acta 121
acta 122
acta 123
acta 124
acta 125
acta 126
acta 127
acta 128
acta 129
acta 130
acta 131
acta 132
acta 133
acta 134
acta 135
acta 136
```

c if(ingest *0.79 .gt. mass)then
c if(ingest *0.79.gt. mass)then
aass = mass
c
c
c...compute nutritional state as the proportion actual
c assimilation to maximal assimilation
c
n_ nstate(1)}=\mp@code{nstate(2)
n_ nstate(1)}=\mp@code{nstate(2)
c
c
c...load metering array
c
meter(10)=aass
meter(11)=prey(iweek,l)
meter(12) =prey(iweek,2)
meter(13)=prey(iweek,3)
return
end if
c
c...Cladocera as prey
c
if(prey(iweek,3) .ne. 0.0) then
c
c
c
NOTE: the following equation was generated from the Cladocera
consumption data using all interaction terms. It doesn't
work.
consum = -1.31212 + 0.32205*prey(iweek,3) + 0.09191*temp(iweek) acta 169
acta 137
c
acta 138
acta 139
acta 140
acta 141
acta 142
acta 143
acta 144
acta 145
acta 146
acta 147
acta 148
acta 149
acta 150
acta 151
acta 152
acta l52
acta 154
acta 155
acta 156
acta 157
acta 158
acta 158
acta 160
acta 161
acta 162
*acta 163
acta 164
acta 165
acta 166
acta 167
acta 168
1
+0.000895*body/0.6577 + 0.007459*prey(iweek,3)*body/0.6577 acta l70
acta 169

```
```

C
c
c**********************************************************************
c
c
C
c at 15 C consum = 0.247 + 0.52898 * prey(iweek)
c
c
a=0.2470-(0.2470-0.3651)*(temp (iweek)-15.)/5.0
b}=0.52898-(0.52898-0.62821)*(temp(iweek) - l5.)/5.
if(prey(iweek,3) . le. 4.) then
consum =a + b * prey(iweek,3)
else
consum =a +b*4.0
end if
c
c
c
c
c
c
c
c
c
c
c
C
end if
c
this is consumption per hour, so convert it to
consumption per week (*l68) and multiply by the caloric
value of a single Cladocera (*0.173 cal).
ingest = ingest + consum * 168. * 0.173
end if
now convert total calories ingested to calories assimilated
using an assimilation efficiency of 0.79.
aass = ingest * 0.79

```
acta 171
```

c As explained above, the these equations may result acta 205
c in ingestion rates above satiation (mass). If this acta 206
c occurs, set actual assimilation to the satiation
value.
if(aass .gt. mass) aass = mass
c
c...compute nutritional state as the proportion actual
c assimilation to maximal assimilation
c
nstate(1) = nstate(2)
nstate(2) = aass/mass
c
c write(l0,1000)iweek,aass
cl000 format(" subroutine actass - week =",i3," actual assimilation=",
c l f6.3)
c...load metering array
c
meter(10)=aass
meter(ll)=prey(iweek,l)
meter(12)=prey(iweek,2)
meter(l3)=prey(iweek,3)
return
end

```
```

c
subroutine respir(iweek,temp,nstate,body,resp,meter,breed) resp, l
dimension temp(100) . . resp resp 3
real meter(35) resp 4
real nstate(2),mg,n resp 5
c
c
c...load metering árray
c
meter(4)=temp(iweek)
meter(7)=body
c
c...This subroutine computes the oxygen uptake rate for an
c individual of the size, nutritional state and at the
temperature specified in the transfered parameters
and then converts this oxygen uptake rate to its calorific
equivalent.
the returned parameter resp will be the caloric uptake equivalent
to the computed oxygen uptake.
c...internally used variables are:
a = activity => the proportion of time for which an individual
is active.
This variable has not been measured, so has
been arbitrarily assigned a value of 0.4 for
baseline runs. Its impact upon growth rate
will be assess using sensitivity analysis.
u = oxygen uptake in microlitres per hour
c
c...check for valid temperature data.
c
if (temp(iweek) .eq. 999.) call err5(iweek,"respir")
c

```
```

c resp 35
c...initialize the internal variables
a=0.4
c
c...compute total oxygen uptake per hour (mo2).

```

```

    oxygen uptake = 5. 2059-0.58043(temperature) + l. 24533(ration)
                            + 0.7229(temperature)(ration)
                            + 0.0037529(temperature)(wet weight)
                            + 1.0938(temperature)(activity level)
    + +0.016436(wet weight)(activity level)
            u=5.20593-0.58043*temp(iweek) + 1.2433*nstate(2)
            1 - 0.0105431*body/0.6577 - 7.0275*a
            2 + 0.7229*temp(iweek)*nstate(2)
            3+0.0037529*temp(iweek)*body/0.6577
            + 1.0938*temp(iweek)*a
        4 + 1.0938*temp(iweek)*a
    c...the above equation has first derivitives = 0.0 within the
resp
36
resp
resp }3
resp 39
resp 40
resp 41
resp 42
resp 42
resp 43
resp 44
resp 45
resp 46
resp 47
resp 48
resp 49
resp 50
resp 51
resp 52
resp 53
resp 54
resp 55
resp 56
c region define by ecological constraints, so was discarded
and the following equation derived from the data using
BMDP program PAR
The following equation computes qo2, so uptake must be
multiplied by body size to obtain mo2.
u = -0.0385 + 0.0043*temp (iweek) + 0.0184*nstate(2)
1 + 0.3427*exp(-0.0147*body/0.6577) + 0.0669*a
resp 57
resp 58
resp
resp 59
resp 60
resp 61
resp 62
resp
resp 63
resp 64
resp 65
resp 66
resp 67
c...now convert this oxygen uptake rate to its caloric equivalent
resp 68

```
```

c resp 69
cal=u* 0.004731 resp 70
c...this is the caloric expenditure in respiration per hour.
c compute the caloric uptake per week (24* 7 hours per week)
c
resp = cal * 168
c
c...increase this value if reproduction is occurring
if(breed .gt. 0.5) resp = resp * 2.0
c
c
c
c
c write(12,1000)temp(iweek),mg,n,a,u
resp 85
loov format(/" subroutine respir: temp =",f5.l," wet weight=", resp 86
l f7.l," nutritional state=",f5.2," activity=",f5.2, resp 87
2 / 20x," oxygen uptake=",f5.l," microlitres per hour") resp 88
c
c...load metering array
c
meter(14)=resp
return
end
resp 71
resp 72
resp 73
resp 74
resp 75
resp 76
resp 77
resp 78
resp 79
resp 80
resp 81
resp 82
resp 83
resp 84
8
resp }9
resp 91
meter(14)=resp
resp }9
resp }9
resp }9
resp 95

```
```

    subroutine breed(iweek, cohort,ic,lc,aass,meter,temp,repeff) bree l
    dimension cohort(50,6), temp(100)
    real meter(35)
    c
c
c
c
c
if(cohort(ic,5).1t.0.5)then
cohort(ic,4)= cohort(ic,3)
cohort(ic,5) = iweek
end if
compute reproductive effort and embryo production
The ingestion rate used in the regression equation for
caloric reproductive output is calories ingested per day
per calorie of the body. The transferred parameter AASS
is ASSIMILATION PER WEEK, so must be converted to INGESTION
PER DAY, then taken as a ratio to body size.
consumption = AASS / assimilation efficiency/ 7 days / body size
consum = aass / 0.79/7.0/ cohort(ic,3)
the variable for body size used in the regression is in caloric
so does no have to be converted.
c...compute cocoon calories
c
ccal = - 25.875 + 0.16123* cohort(ic,3) + 1.4672*temp(iweek)
c
c...report an error if ccal is negative

```
```

c bree 35
if(ccal .1t. 0.0) then
write(12,1000)iweek, ccal
ccal=0.0
return
end if
c
c...compute cocoon calories per week. the value calculated above
c is for the entire reproductive period. assume that cocoon
deposition lasts 4 weeks.
repeff=ccal / 4.0
meter(16) = repeff
c
c...compute number of embryos
c
embro = -27.4975 + 0.07315*cohort(ic,3) + 1.6998*temp(iweek)
c
c...compute embryos per week. the value calculated above
c is for the entire reproductive period. assume that cocoon
deposition lasts 4 weeks.
if (embro.gt. 0) then
embro = embro / 4.0
else
embro = 0.0
end if
C
meter(17)= embro
c
cohort(lc+1,2)= cohort(llc+l,2) + embro*cohort(ic,2)
cohort(lc+l,l) = cohort(lc+l,l) + l.0
c
bree 36
bree }3
bree 38
bree }3
bree 40
bree 4l
bree 42
bree 43
bree 44
bree 45
bree 46
bree 47
bree 48
bree 49
bree 50
bree 5l
bree 52
bree 53
bree 54
bree 55
bree 56
bree 57
bree 58
bree 59
bree 60
bree 61
bree 62
bree 63
bree 64
bree 65
bree 66
bree 67
bree 68

```
        cohort \((1 c+1,3)=15.3\)
bree 69
return
bree 70
bree 71
1000 format (i5,f8.4)
1001 format (50x,4f13.6)
bree 72
bree 73
end
bree 74

```

cc write(14,l009)week,bmsize,body,pvar mens 35
c
C
C
C
c
c
c
c
c
c
c
c
c
C
c
c
c
c
C
c
c
c1010
c end if
end if
return
end
format(3f6.0,flo.5)
if(diff..lt. mindif)then sens 37
mindif}=dif
sens 37
minwk = iweek sens 39
minb = bmsize sens 40
end if m
end if .
sens 4l
if(diff'.gt. maxdif)then sens.42
maxdif = diff
sens 43
maxwk = iweek sens 44
maxb = bmsize sens 45
end if sens 46
else
sens 46
sens 47
call errl0 sens 48
end if
sens 49
this section determines the difference at week 47 of the sens 50
run
sens 51
sens 52
if(iweek .eq. 47) then
sens 53
diff=body - bmsize sens 54
diff = body - bmsize, sens 54
pct =100.0 * diff / bmsize
write(l4,1010)pet
sens 56
57
sens 58
sens 59
sens 60

```
```

    subroutine surviv(iweek, temp, cohort,ic,far,p) surv l
    c...this subroutine computes survival probability to next week,
surv
c using one of two functions, depending upon whether
surv 3
c the animal is reproducing (or has recently reproduced)
c...transfered parameters are:
iweek - the number of the current week being simulated surv 7
temp - a vector of weekly temperatures surv 8
cohort - an array of information about the cohorts in the surv 9
population. (see grow.fortran)
ic - an integer identifying which row in array cohort
surv 11
far - feeding rate after reproduction (set to zero if
far - feeding rate after reproduction (set to zero if
reproduction has not ceased).
p - probability of surviving to next week.
dimension temp(100), hot(10), cohort (50,6)
surv
surv 12
surv 13
surv 14
surv 15
surv 16
surv 17
c
surv 18
c...define underlying post-reproductive hazard function
surv 19
c
data (hot(i), i=1,10)/1.1970e-5, 1.970e-5, 1. 1970e-5, 3.0144e-5, surv 2l
surv 20
1 8.0997e-5, 1.5063e-4, 3.5832e-4, 4.1416e-4, 2.1826e-4, surv 22
2 1.5815e-4/
surv 23
c
c...test whether the animal is reproducing or has reproduced within surv 25
surv 24
c...test whether the animal is reproducing or has reproduced within surv 25
c. the last l0 weeks (the period for which values of the Ho(t)
surv 26
function exist).
surv 27
c
c
if(iweek.ge. cohort (ic,5). and. iweek.le. cohort (ic,5)+9)then
surv 28
if(iweek.ge.cohort(ic,5).and.iweek.le.cohort(ic,5)+9)then surv 29
c
c use the proportional hazards model
surv 30
surv 3l
surv 32
c compute proportional energy loss during reproduction surv 33
c

```
        pelrep = (cohort(ic,4)-cohort(ic,3))/cohort(ic,4) surv 35
            surv 36
            compute the risk factor portion of the proportional hazards surv 37
                    model surv
            surv 38
                            surv 39
                            surv 40
    I
        risk=exp(0.3366*temp(iweek)-0.0038*cohort(ic,4)+1.457*pelrep
    surv 4l
    surv 42
    surv 43
    surv 44
    surv 45
    surv 46
    surv 47
    surv 48
    surv 49
    surv 50
    surv 51
    surv 52
    surv 53
    surv 54
    surv }5
    surv 56
    surv 57
    surv 58
    surv }5
    surv 60
    surv 61
    surv 62
    surv 6}
    surv 64
    else
    surv 65
    surv 66
    surv 67
surv 68
```



```
    subroutine errl errl l
    write(12,1000)
    errl
    do ( error in temperature input data")
    do 10 i = 11 , 14
    close(i)
    continue
    stop
    end
    subroutine err2 (icode)
    write(12,1000)icode
    format(" error in growth data type code. code = ",i5)
    do l0 i = 11 ; 14
        close(i)
    continue
    stop
    end
    subroutine err3
    write(l2,1000)
    format(" the assumption of a zero trip do loop in subroutine",/,
    1 " grwin is not supported - fatal error.",/,
    2 " exit via subroutine err3")
    do 10 i = 11, 14
    close(i)
1 0
continue
stop
end
```

```
        subroutine err4(body,temp) err4 l
        write(12,1000) temp,body
    err4 2
1000 format(" error exit from mgain2 via err4 - body has exceeded" err4 3
    l,/, " available data in wdgr - temperature =",f5.1,/, err4 4
    2" " body =",f9.2) err4 5
    do 10 i = 11 14 
    close(i) err4 8
    continue
    stop
    . end
    subroutine err5(iweek, subr)
    character*6 subr
    write(12,1000)subr,iweek
    format(" error exit from " a6," via errs (")
    format(" error exit from ",a6," via errs - temperature at week",
    i4)
        do 10 i = 11, 14
        close(i)
        continue
        stop
        end
        subroutine err6(iweek, subr)
        character*6 subr
        write(12,1000)subr,iweek
        format(" error exit from ",a6," via err6 - prey density at week",
    1 i4)
        do 10 i = 11 , 14
            close(i)
        continue
        s.top
        end
9
err6 10
```

```
        subroutine err7(i,t) err7
        write(12,1000)i,t
1000 format(' error.exit from mgainl, temperature at week',i4,
    1 exceeds 20 C. temperature = ',f4.0)
        do 10 i = 11 , 14
            close(i)
        continue
        stop
    end
        subroutine err8(ccal, c,b,t,w)
        writel2,1000)ccal,c,b,t
err7 l
erry 2
    format(' reproductive effort negative in subroutine EFFORT',/,
    l ' cocoon calories = ',flo.2,/,
    2 ' consumption= ',f10.4,/, err8
    3'body= ',fl0.5,/, err8
    4.' temperature = ',f5.1
    5 ' week = ', i5)
    5' week = ',i5)
        close(i)
        continue
        stop
        end
        subroutine err9(name,j,i)
        character*6 name
        write(12,1000) name,j,i
l000 format(' read error in subroutine ',a,' for week ', i5,
    l ' out of ',i 5,' weeks.'')
        do 10 i = 11, 14
        close(i)
    continue
    stop
    end
erry 3
err74
err7 5
5
10
    - err8
    err8
errg
err8 8
err8 9
erre 10
err8 10
err8 11
err8 12
err8 13
err9 1
err9 2
err9 3
err9 4
4
err9 5
err9 6
1 0
```

```
        subroutine errl0
    write(12,1000)
l000 format(' bench mark week and simulation week do not match in
l program grow.fortran.')
do*l0 i = 11 , 14
    close(i)
l0 continue
stop
end
errlo 1
errio 2
errio
errelo 4
errio 5
errlo 6
errlo 7
errlo 8
errl0 9
```


## Appendix B

## A sample data set

The data file which includes the 1980-1981 Chironomidae data and the 1984 temperature data from Stephenson's Pond and the weight dependent growth rates for Nephelopsis obscura is presented. Columns of dots represent data which have been excTuded from the file for the purposes of presentation in this appendix. When these data are included, the file, complete with its internal documentation, can be used as input to the growth simulation model.

```
18 => this is the number of weeks that the simulation is to run
32 => this is the week where simulation is to start
55 => this is the number or weeks of prey density data.
27 1.273 3.990 0.0 05/06/80 The order of fields in the prey
28 1.135 4.234 l.3 05/13/80 density data is:
29 0.286 4.253 2.3 05/20/80 1) week
30 0.212 4.173 2.8 05/27/80
    2) chironomid density
31 0.139 4.093 3.0 06/03/80
```




```
    4) Cladocera density (numbers per ml)
33 5.203 0.148 2.3 06/17/80 5) date (not read)
. . . . . .
80}00.\dot{897 4.\dot{299 1.3 05/i3/81}
81 0.046 4.336 2.3 05/20/81
```

```
2 => code for measured, not digitized, temperature data
l8 }=>\mathrm{ this is the number of weeks of data which are to be read from this file
    32 17.2 13/06/84 The order of the field is:
    33 18.7 20/06/84 1) - week
    34 19.4 27/06/84 2) - temperature
    35 18.5 04/07/84 3) - date (not read)
        \bullet. ..
        47 10.8 04/i0/84
    48 9.9 12/10/84
    49 0.1 25/10/84
2 => the code for weight dependent growth rates
l => the number of weight dependent growth rates for 0 C
10000 1.0 => the maximum weight and growth rate
l => the number of weight dependent growth rates for 5 C
10000 l.020201 => the maximum weight and growth rate
l => the number of weight dependent growth rates for l0 C
10000 l.l50274 => the maximum weight and growth rate
```

```
4l }=>\mathrm{ the number of weight dependent growth rates for 15 C
0.400 2.500 The data fields are:
0.800 2.026 1) - bottom of weight range
1.600 1.802 2) - proportional growth rate
    \bullet -
    999.0 1.027
10000.0 1.027
46 =>> the number of weight dependent growth rates for 20 C
0.800 3.800
1.600 : 1.864
    . .
10000.0 i.026
2.0 m the initial body size from which the simulation is to start.
```



```
01lll l 0 0 0 0 0 0 0 0 0 0 0 0 This array contains one entry
    for each week to be simulated. A l in the array represents
    a week in which reproduction is to occur while a O codes
    for no breeding.
```

