#### THE UNIVERSITY OF CALGARY

### A computer simulation model of the growth and life history of the aquatic predator <u>Nephelopsis</u> obscura

by

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#### A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGY

CALGARY, ALBERTA

AUGUST, 1985

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#### THE UNIVERSITY OF CALGARY

#### 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 <u>Nephelopsis</u> obscura" submitted by Larry Ralph Linton in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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#### Abstract

A computer model was written to simulate a simple conceptual bioenergetics model of the growth and life history of the aquatic predator <u>Nephelopsis</u> <u>obscura</u> 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 <u>N. obscura</u>. 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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

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and body size. No data were available on the intensity of specific mortality factors except post-reproductive mortality, which was considered to be complete, making <u>N. obscura</u> 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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#### Acknowledgments

I would first of all like to thank Dr. R. W. Davies for being my supervisor, friend and colleague. My association with him has been pleasant and fruitful. The members of my supervisory committee, Drs. McRae, Owen, Chinnappa and Pritchard read and criticized the manuscript, as did Dr. Calow. Financial support for this research was provided by the Killam Foundation, NSERC (grant to R. W. Davies) and a Dissertation Fellowship from the University of Calgary.

Many genial and stimulating conversations with Dr. Donald Baird made the thesis research a pleasurable task. Conversations with Sandra Walde, Drs. Wrona, Culp and Rasmussen and Mr. Larry Powell and Mr. Bill Parsons were of considerable help in clarifying concepts and generating new ideas.

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.

Dr. Gordon Fick generously provided statistical advice on regression analysis. He also suggested the proportional hazards analysis.

Above all, I wish to thank my parents and Ann Ross for their continuing love and support. Without their encouragement and optimism, I probably would not have finished.

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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° 16'W, 51° 9'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.

<u>Nephelopsis</u> 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  $300 \text{ m}^{-2}$  (Wrona 1982).

The eggs of  $\underline{N}$ . <u>obscura</u> 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, <u>N. obscura</u> 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 (eq. 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): .

$$\Delta B = C - F - U - R \qquad [1.1]$$

where  $\triangle B$  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 <u>et al.</u> 1982), and its components have been thoroughly reviewed by Calow (1981). This formulation of growth has a number of important features. It integrates (Bayne <u>et al.</u> 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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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 - <u>sensu</u> 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 <u>et al.</u> 1982), and its components have been thoroughly reviewed by Calow (1981). This formulation of growth has a number of important features. It integrates (Bayne <u>et al.</u> 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 <u>et al.</u> (1976) describe a model of the growth of the mussel <u>Mytilus edulis</u> 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 <u>Daphnia</u> by Paloheimo <u>et al.</u> 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 modelled as power functions of swimming speed and body weight. A fixed temperature of  $10^{\circ}$ 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 (<u>Salmo</u> <u>truta</u> 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 <u>et al.</u> (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 <u>et al.</u> 1977) that functional feeding response estimates of ingestion rates are not generally included in simulation models because they are too difficult to obtain.

Stewart <u>et al.</u> (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 1.1) 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 Body size is allowed to vary up or down, depending upon the size. 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 <u>N. obscura</u> 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 <u>Nephelopsis</u> 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 results 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 <u>N. obscura</u> 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 [2.1]

and the new body size as:

new	body	size	=	old	body	size	+	production		
-	- ene	ergy	to	o re	eprod	lucti	on	•	[2.	.2]

### 2.3 Data entry

Data are entered into the simulation from the data file FILE11 (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

#### Maximal assimilation rates

# 3.0 Introduction

The respiration rate of <u>N. obscura</u> is known to be a function of nutritional state, with animals fed <u>ad libitum</u> 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

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 <u>ad libitum</u> food conditions (fully satiated), and was defined as the sum of growth in calories under <u>ad libitum</u> food conditions plus calories respired under these conditions. Thus

$$MASS = GROWTH + RESPIRATION [3.2]$$

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

$$W_{t} = a \exp(rt)$$
 [3.3]

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 <u>ad libitum</u> food, resulted in an individual that weighed about 11 kg, which is approximately four orders of magnitude larger than any known specimens of <u>N. obscura</u>. Therefore, the only available equations for growth of <u>N. obscura</u> were rejected as appropriate general models for ad libitum growth.

Figure 3.1 Weekly mean temperature (<sup>o</sup>C) at 1 m depth in Stephenson's Pond from 80-11 to 82-04.



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# 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 <u>ad libitum</u> 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  $10^{\circ}$ C or  $5^{\circ}$ C is apparent, however growth did occur at  $20^{\circ}$ C and  $15^{\circ}$ C.

Inspection of Figure 3.2 suggests that growth at  $20^{\circ}$ C and  $15^{\circ}$ 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 The data show marked fluctuations in growth rate, weighing times. 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

$$pwc = W_{t+1} / W_t$$
 [3.4]

Figure 3.2 Wet weights (mg) of <u>Nephelopsis obscura</u> under experimental ad <u>libitum</u> food conditions at 5°C, 10°C, 15°C and 20°C.

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20°C	15°C	10°C	5°C	
Age Mean (wk) Wet Wt (mg)	Age Mean (wk) Wet Wt (mg)	Age Mean (wk) Wet Wt (mg)	Age Mean (wk) Wet Wt (mg)	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	0 0.9 1 1.6 2 1.4 3 1.2 4 1.9 5 1.5 6 2.0 7 1.6	

Table 3.1 Weekly mean wet weights (mg) of cohorts of <u>Nephelopsis</u> obscura raised at four different temperatures with <u>ad libitum</u> food (<u>Enchytraeus</u> sp).

Figure 3.3 Weight gain (mg wk<sup>-1</sup>) for <u>Nephelopsis</u> obscura with ad libitum food at 15°C and 20°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  $20^{\circ}C$  and  $15^{\circ}C$  data were:

$$pwc_{20} = 2.05 \exp(-0.1106wt)$$
 [3.5]

$$pwc_{15} = 1.78 exp(-0.0859wt)$$
 [3.6]

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  $20^{\circ}$ C and  $15^{\circ}$ 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  $20^{\circ}$ C and 819 mg at  $15^{\circ}$ C were used when simulated weights exceeded these values (an extrapolation).

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

Figure 3.4 Proportional weight change versus wet weight (mg) for <u>Nephelopsis</u> obscura with <u>ad libitum</u> food at 15°C and 20°C.





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



Table 3.2 Proportional growth rates of different weight classes of <u>Nephelopsis</u> obscura at 15°C and 20°C. Details of the method of calculation are given in the text.

		· ···· ···· ···· ···· ···· ···· ···· ····	، عليه الحيد الجب البرب المنه الحد الحد الحد الحد	یند میں سے بہت ہے۔ جب خدہ اس ایے جب خدہ ا	
20°C		15°C			
Weight Class		Prop	Weight	Prop	
Lower Boundary (mg)	Upper Boundary (mg.)	Rate	Lower Boundary (mg)	Upper Boundary (mg)	Rate
0.05 0.1 0.2 0.4 0.8 1.6 3.2 6.4 12.8 25.6 51.2 102.4 204.8 409.6 819.2	0.1 0.2 0.4 0.8 1.6 3.2 6.4 12.8 25.6 51.2 102.4 204.8 409.6 819.2 1638.4	0.000 0.000 3.800 1.864 2.077 1.940 1.693 1.437 1.239 1.234 1.171 1.153 1.149 1.115	0.05 0.1 0.2 0.4 0.8 1.6 3.2 6.4 12.8 25.6 51.2 102.4 204.8 409.6	0.1 0.2 0.4 0.8 1.6 3.2 6.4 12.8 25.6 51.2 102.4 204.8 409.6 819.2	0.000 0.000 2.500 2.026 1.802 1.546 1.436 1.518 1.391 1.290 1.279 1.154 1.094 1.085

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





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while at  $15^{\circ}$ 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  $20^{\circ}$ C and 819 mg at  $15^{\circ}$ 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  $20^{\circ}$ C and 204 mg at  $15^{\circ}$ C. From Figure 3.3 it would appear that the ages 14 wk at  $20^{\circ}$ C and 22 wk at  $15^{\circ}$ 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.

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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  $20^{\circ}$ C and 1000 mg at  $15^{\circ}$ 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  $20^{\circ}$ C and 30 wk at  $15^{\circ}$ C). These weekly weight gains (WWG) (76.3 mg for  $20^{\circ}$ C and 26.5 mg for  $15^{\circ}$ C) were introduced into the following formula:

$$pwc = W_{t} + WWG / W_{t} \qquad [3.7]$$

where  $W_t$  is weight at time t from the generating function

$$W_{t} = W_{t-1} + WWG$$
 [3.8]

with t starting from 14 wk or 22 wk for 20°C and 15°C respectively

using  $W_{14} = 102$  mg and  $W_{22} = 204$  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°C and 204 mg at 15°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.

	. 20 <sup>0</sup> C			15°C	· · · · · · · · · · · · · · · · · · ·
Weight	Class	Prop Growth	Weight	Class	Prop
Lower Boundary (mg)	Upper Boundary (mg)	Rate	Lower Boundary (mg)	Upper Boundary (mg)	Rate
102.0 178.3 254.6 330.9 407.2 483.5 559.8 636.1 712.4 788.7 865.0 941.3 1017.6 1093.9 1170.2 1246.5 1322.8 1399.1 1475.4 1551.7 1628.0 1704.3 1780.6 1856.9 1933.2 2009.5 2085.8 2162.1 2238.4 2314.7 2391.0 2467.3 2543.6 2619.9 2696.2 2772.5 2848.8 2925.1	178.3 254.6 330.9 407.2 483.5 559.8 636.1 712.4 788.7 865.0 941.3 1017.6 1093.9 1170.2 1246.5 1322.8 1399.1 1475.4 1551.7 1628.0 1704.3 1780.6 1856.9 1933.2 2009.5 2085.8 2162.1 2238.4 2314.7 2391.0 2467.3 2543.6 2619.9 2696.2 2772.5 2848.8 2925.1 3001.4	1.748 $1.428$ $1.300$ $1.231$ $1.187$ $1.158$ $1.136$ $1.120$ $1.097$ $1.088$ $1.075$ $1.070$ $1.065$ $1.061$ $1.075$ $1.061$ $1.058$ $1.055$ $1.061$ $1.058$ $1.055$ $1.061$ $1.047$ $1.045$ $1.047$ $1.045$ $1.047$ $1.045$ $1.047$ $1.045$ $1.041$ $1.039$ $1.037$ $1.035$ $1.034$ $1.035$ $1.034$ $1.035$ $1.034$ $1.035$ $1.034$ $1.035$ $1.034$ $1.035$ $1.032$ $1.031$ $1.030$ $1.029$ $1.028$ $1.027$ $1.026$	204.0 230.5 257.0 283.5 310.0 336.5 363.0 389.5 416.0 442.5 469.0 495.5 575.0 601.5 628.0 654.5 681.0 707.5 734.0 760.5 787.0 813.5 840.0 866.5 893.0 919.5 946.0 972.5 999.0	230.5 257.0 283.5 310.0 336.5 363.0 389.5 416.0 442.5 469.0 495.5 522.0 548.5 575.0 601.5 628.0 654.5 681.0 707.5 734.0 760.5 787.0 813.5 840.0 866.5 893.0 919.5 946.0 972.5 999.0 1025.5	1.130 1.115 1.093 1.085 1.079 1.073 1.068 1.064 1.057 1.053 1.051 1.048 1.046 1.044 1.044 1.042 1.040 1.037 1.036 1.035 1.034 1.035 1.031 1.030 1.029 1.027 1.027

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

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



AGE (weeks)

# 3.3 Summary

Estimates of the maximum number of calories assimilated by an individual under <u>ad libitum</u> 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 <u>N. obscura</u>. Continuing these experiments until the specimens die of old age would also provide information about the maximum life span of <u>N. obscura</u>, 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 15oC and 102 mg at 20oC.

### 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 The factors include species differences, temperatures, oxygen (1982).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 <u>N. obscura</u> under anoxia at various temperatures. At  $20^{\circ}$ C 100% mortality occurred within 4 d, however at  $5^{\circ}$ C, only 40% mortality had occurred after 30 d. These results suggest that <u>N. obscura</u> 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 <u>N. obscura</u> 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 - 1-2 mg, 20-30 mg, 80-120 mg and approximately 350 mg; ration level - fed to satiation versus starved; and temperature -  $5^{\circ}$ C,  $10^{\circ}$ C,  $15^{\circ}$ C and  $20^{\circ}$ 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 ( $F_{(6,192)} = 0.74$ , p>>0.05) while treatment effects were highly significant ( $F_{(2,198)}=58.19$ , p<0.001). <u>A posteriori</u> testing using Scheffe comparisons showed ventilating uptake and random movement uptake to be not significantly different (geometric means being 20.87 ul hr<sup>-1</sup> and 20.77 ul hr<sup>-1</sup> respectively) but, the resting uptake rates were significantly smaller (geometric mean = 11.85 ul hr<sup>-1</sup>). 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 it does not make biological sense to discuss an individual of zero (ea. 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 ( $\mu$ l hr<sup>-1</sup>) by <u>Nephelopsis</u> 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). SD = standard deviation of regression coefficient, t = regression coefficient/SD.

·			Coded		Uncoded	
Variable		Coefficient SD		t	 Coefficient	
Intercept Temperature	(т)	16.9496	0.4610	36.7	5.20593	
( <sup>0</sup> C)		1.11370	0.08159	13.6	-0.58043	
Ration	(R)	10.641	1.173	9.0	1.2433	
Net Wt (mg)	(W)	0.044819	0.003435	13.0	-0.0105431	
Activity	(A)	10.4791	0.9298	11.2	-7.0275	
ГхR		0.7229	0.2111	3.4	0,7229	
Γ×W		0.0037529	0.000636	5.9	0,0037529	
ΓхΑ		1.0938	0.1677	6.5	1,0938	
N x 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 (15°C) (Wrona 1982) and is assumed to apply for all temperatures at which reproduction Furthermore, it is assumed that there is an instantaneous occurs. 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:

، جان ہوں، جس قصر خط ملک فلے جس مالو کری کے خط ملک جون ایک قلید کری کے بھی بھی ک	برمه بين حق جود التار اليار من التار الذا عنه جود بين عند التار إلى التار أن التار بين التار بين التار بين الت
Substrate	cal µl <sup>-1</sup> of
	O <sup>2</sup> Consumed
Glucose	0.005007
Fat	0.004686
Protein	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 <u>N. obscura</u> 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  $(20^{\circ}C)$  these data were insufficient for the purposes of the model. Laboratory experiments were therefore performed to measure feeding rates of <u>N. obscura</u> 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 N. 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 (<u>Glyptotendipes</u> <u>paripes</u> (Edwards) and <u>Chironomus riparius</u> 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  $5^{\circ}$ C for no longer than 1 wk prior to the experiments. When experimental temperatures were greater than  $5^{\circ}$ C, the Chironomidae were acclimated to the experimental temperatures in steps no greater than  $5^{\circ}$ 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 mg, 5.4 mg, and 5.7 mg.

# 5.1.2 Nephelopsis obscura collection and acclimation

<u>Nephelopsis</u> <u>obscura</u> collection and acclimation procedures were the same as for Chironomidae, however, individuals of <u>N. obscura</u> were acclimated to the experimental temperature for a minimum of 1 wk. <u>N. obscura</u> was acclimated to the experimental prey density for a minimum of 3 d (Anholt, 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 <u>N. obscura</u> 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) <u>N. obscura</u> egestion of whole prey which may be missed in the count of numbers captured; 3) <u>N. obscura</u> 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  $\mu$ m sieve. Chironomidae that passed through the 450  $\mu$ m sieve and were thus entrained within the experimental substrate were eliminated by heating the sieved mud to 50°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 cm<sup>2</sup> of bottom area and 2 cm depth of mud, (approximately the same arena size used by Anholt (1982)). This container was maintained at  $20^{\circ}$ 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°C (the experimental temperature at which it was assumed that tube building rate would be minimum). After 29 hr 87.5% of the Chironomidae had built tubes. Extrapolation of this result suggested that after 34 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

<u>N. obscura</u> 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 <u>N. obscura</u>, initially maintained in substrate containing a high density of Chironomidae, was placed in a petri dish with 20 Chironomidae and no substrate, thus enabling <u>N. obscura</u> 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 <u>Chironomus</u>: <u>Glyptotendipes</u> and very rare occurrences of <u>Cryptochironomus</u>. One <u>N. obscura</u>, 13 <u>Chironomus</u> and 7 <u>Glyptotendipes</u> were placed in a petri dish with no substrate. After 24 hours at  $20^{\circ}$ C one <u>Chironomus</u> and five <u>Glyptotendipes</u> 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  $20^{\circ}$ C, in 28 cm<sup>2</sup> arenas each with 2 cm depth of mud, 56 Chironomidae identified to genus, and one <u>N. obscura</u> (mean wt = 366.8 mg, SD = 41.5 mg)

per arena. Five replicate controls without <u>N. obscura</u> 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 2x2 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 (df=1) suggesting discrimination by <u>N. obscura</u>, 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 <u>Chironomus</u> and <u>Glyptotendipes</u> were established and after 1 wk (a period longer than the experiment) <u>Chironomus</u> pupated whereas <u>Glyptotendipes</u> did not. Under the assumption that all the pupae in the original experiment were <u>Chironomus</u>, 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 <u>Nephelopsis</u> obscura on <u>Chironomus riparius</u> (Chir.) and <u>Glyptotendipes</u> 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.	Gly	p. Pupa	e Eate	n X <sup>2</sup>
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
				المن ويرد والدر البري البري البري ال		d f	×2	
Independence of Classification				(1)	11.094***			
Heterogeneity				(4)	5.819**			
Т	otal					(5)	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<sup>-1</sup>  $d^{-1}$ ) and those of the above experiment (1.73 Chironomidae leech<sup>-1</sup>  $d^{-1}$ ). However, after observing the behaviour of <u>N. obscura</u> 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 cm<sup>2</sup> and 227 cm<sup>2</sup>). There were two <u>N. obscura</u> used in the 60 cm<sup>2</sup> arenas, and eight in the 227 cm<sup>2</sup> (mean <u>N. obscura</u> wet wt = 335 mg, SD = 46 mg) arenas, providing a constant predator density of approximately one <u>N. obscura</u> per 29 cm<sup>2</sup> of substrate. The prey density used was 2 Chironomidae cm<sup>-2</sup>. Both predator and prey densities were comparable to field densities (Rasmussen 1983). Experiments were conducted at 20°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 <u>Nephelopsis</u> <u>obscura</u> versus experimental arena size (prey density 2 cm<sup>-2</sup>).



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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, <u>N. obscura</u> does not egest whole prey which might decrease the estimate of predation rate.

Anholt (1982) reported that <u>N. obscura</u> has different predation rates upon <u>Chironomus</u> and <u>Glyptotendipes</u>, 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 cm<sup>-2</sup>, 2 cm<sup>-2</sup> and 0.5 cm<sup>-2</sup>; predator size - small (100 mg to 130 mg), medium (300 mg to 400 mg) and large (500 mg to 600 mg) and temperature -  $5^{\circ}$ C, 12.5°C and 20°C. The prey densities of 0.5 cm<sup>-2</sup> and 3.0 cm<sup>-2</sup> were above and below ambient field prey densities for Chironomidae of the size used in the experiments (Rasmussen 1983). <u>N.'obscura</u> sizes used approximately spanned the range in the field. The minimum <u>N. obscura</u> body size used was based upon a preliminary experiment that showed that individuals <80 mg wet wt took none of the large Chironomidae used in these experiments.

The arenas used were 227 cm<sup>2</sup> (section 5.1.3.6) and contained previously heated pond mud for substrate (section 5.1.3.1). Control arenas with no <u>N. obscura</u> 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°C) or warm (>12.5°C) with intermediate temperatures being transitional and brief in spring and fall. The experiments at  $5^{\circ}$ C approximated field winter temperature, and 12.5°C and 20.0°C, represented the approximate summer minimum and maximum temperatures respectively For a series of experiments using large N. obscura, high (Figure 3.1). prey densities and all three experimental temperatures there was no detectable prey consumption at 5°C after 48 hours. Extrapolation of the 20<sup>0</sup>C and 12.5<sup>0</sup>C rates for these initial experiments suggests that feeding stops at about 11°C. Thus the 5°C temperature in the experimental design was changed to 15°C, intermediate in the range of summer temperatures.

#### 5.1.4.2 Results

The rates of capture of prey by small, medium and large <u>N.</u> 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 (d-1) of Chironomidae prey by small 100-130 mg) <u>Nephelopsis</u> obscura, versus Chironomidae prey density (cm<sup>-2</sup>) at 12.5°C, 15°C and 20°C.



Figure 5.3 Capture rates (d<sup>-1</sup>) of Chironomidae prey by medium (300-400 mg) <u>Nephelopsis</u> <u>obscura</u>, versus Chironomidae prey density (cm<sup>-2</sup>) at 12.5°C, 15°C and 20°C.



Figure 5.4 Capture rates  $(d^{-1})$  of Chironomidae prey by large (500-600 mg) <u>Nephelopsis</u> <u>obscura</u>, versus Chironomidae prey density  $(cm^{-2})$  at 12.5°C, 15°C and 20°C.



Table 5.2 Regression of the functional feeding response of <u>Nephelopsis</u> 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. SD = standard deviation of the regression coefficient, t = regression coefficient/SD.

<i>,</i>	Coded			Uncoded
	Coefficient	SD	t	Coefficient
Intercept Prev density (P)	-0.0270	0.1855	-0.15	-1.3854
Temperature (T)	0.89518	0.09038	9.90	1.16518
( <sup>o</sup> C) Wet wt (mg) (B) P x T P x B T x B	-0.0242 0.001175 0.05849 0.0009645 -0.0003042	0.05660 0.001053 0.03028 0.0005282 0.0003340	-0.43 1.12 5.23 1.83 -0.91	0.06706 0.005738 -0.03729 -0.0088245 -0.0003042
P x T x B 	0.0006526  2 = 0.939	0.0001900	3.43	0.0006526

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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 cal mg<sup>-1</sup>) was obtained from D. J. Baird (pers. comm.).

### 5.1.4.3 Discussion

In experiments in which N. 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 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 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  $8.8^{\circ}$ C Field data show that <u>N. obscura</u> does feed at a low rate under winter ice-covered conditions (Davies, Wrona and Everett 1978). The estimate of  $8.8^{\circ}$ 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  $8.8^{\circ}$ 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  $8.8^{\circ}$ 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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  $ml^{-1}$ ) 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 <u>N. obscura</u> feed on Chironomidae and Cladocera/Copepoda (Davies, Wrona and Everett 1978). Since small individuals (< 80 mg) of <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> used in the experiments were collected from Stephenson's Pond and acclimated to the experimental temperatures for 1 wk. The experimental temperatures used were  $15^{\circ}$ C and  $20^{\circ}$ C. Cladocera densities in the sewage lagoon were estimated to be approximately 1 ml<sup>-1</sup>, so prey density in the experiments were set at  $0.25\times$ ,  $1\times$ ,  $4\times$  and  $8\times$ this field density. <u>N. obscura</u> used in the experiments were 5-10 mg, 20-30 mg and 40-70 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 <u>N. obscura</u> so that the diameter of the arena was always at least three times the length of the largest leech. <u>N. obscura</u> 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  $ml^{-1}$  (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  $ml^{-1}$  versus capture rate at prey density 8  $ml^{-1}$  was not significant. Prey capture rate was fit to the variables temperature, prey density (with the 8X 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.

Wet Wt of 50 Cladocera (mg)	Mean Wet Wt Per Individual (mg)	Dry Wt of 50 Cladocera (mg)	Mean Dry Wt Per Individual (mg)	
50.87 48.14 45.79	1.0170 0.9628 0.9158	2.69 2.43 2.30	0.0538 0.0486 0.0460	
Dry wt (mg)	= 0.0	513 wet wt (r	 mg )	
Cal	= 3.1	39381 dry wt	(mg)	
Cal per Clad	iocera = 0.1	73		

Figure 5.5 Cladocera prey capture rate  $(hr^{-1})$  by <u>Nephelopsis</u> <u>obscura</u> versus prey density  $(ml^{-1})$  at 15<sup>o</sup>C and 20<sup>o</sup>C.





PREY DENSITY (cm -2)

Figure 5.6 Cladocera prey capture rate  $(hr^{-1})$  by <u>Nephelopsis</u> obscura versus <u>Nephelopsis</u> obscura wet weight (mg) at 15<sup>o</sup>C and 20<sup>o</sup>C.



Table 5.4 Regression of the functional feeding response of <u>Nephelopsis</u> 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. SD = standard deviation of the regression coefficient, t = regression coefficient/SD.

		Coded			Uncoded	
· · ·		Coefficient	SD	t	Coefficient	
Intercept Prev densitv	t sitv (P)	. 0.2772	0.0334	2.08	-1.31212	
(cm <sup>-2</sup> ) Temperature	(T)	0.54582	0.06468	8.44	0.32205	
(°C) Wetwt(mg) PxB	(B)	0.09191 0.000895 0.007459	0.03663 0.006144 0.002498	2.51 0.15 2.99	0.09191 0.000895 0.007459	

## 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 <u>Aphanizomenon flos-aquae</u> (L) Ralfs are not present. Until data are available, Cladocera prey density data will be simulated using an equation for a downward facing parabola:

 $PD_t = -at^2 + b$  [5.1] where  $PD_t$  is previously 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

$$a = b / t_0^2$$
 [5.2]

where  $t_0$  is the number of weeks from the mean at which it is desired that  $PD_t$  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 <u>N. obscura</u> ranging in size from approximately 90 mg to 380 mg were acclimated to  $10^{\circ}$ C and  $15^{\circ}$ C for 1 wk while being fed <u>Tubifex tubifex</u> (Linn.) <u>ad libitum</u>. Each <u>N. obscura</u> 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 <u>T. tubifex</u> using the relationship

calories = 1.066 T. tubifex wet wt - 0.528 [5.3]

(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 cal mg<sup>-1</sup> (determined using a Phillipson (1964) microbomb calorimeter), which was then converted into equivalent wet wt of <u>T</u>. 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  $\underline{T}$ . 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°C and 15°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 mean = 0.773, SE= 0.0018; method two: mean = 0.807, (method one: SE = 0.024).Since no justification could be seen for choosing one method over the other, the mean of all 32 estimates (0.79, SE = 0.028) was used to estimate assimilation efficiency in subroutine ACTASS.

### 5.4 Discussion

The feeding rates of <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> populations on Chironomidae populations the <u>N. obscura</u> used in his experiment ranged from 20 mg to 250 mg. The present study has shown that <u>N. obscura</u> <80 mg wet wt are unable to consume the large 4<sup>th</sup> 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 <u>N. obscura</u> 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 ml<sup>-1</sup> 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 <u>N. obscura</u> and Cladocera. There was no detectable increase in capture rate between prey densities of 4 ml<sup>-1</sup> and 8 ml<sup>-1</sup>, possibly suggesting that <u>N. obscura</u> became satiated at a prey density in the region of 4 ml<sup>-1</sup>, 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 Those which have been incorporated into the Chapters 3 through 5. model appear to be reasonable representations of the underlying conceptual model (Figure 1.1), 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 necessary 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 <u>N. obscura</u>. 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. Тο 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: 1) 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 (cm<sup>-2</sup>) (solid line) and mean individual wet weight (mg) (broken line) in Stephenson's Pond in 1980-1981. After Rasmussen (1983).





Cladocera densities were simulated using equation 5.1, with parameters b=3.0, a=0.1875 and  $t_0=4$  centered at the  $3^{rd}$  wk in May, and b=2.5, a=0.2778 and  $t_0=3$  centered at the  $2^{nd}$  wk of September. These values provide for a 7 wk spring bloom with maximum density of three Cladocera  $ml^{-1}$  and a fall bloom of 5 wk duration with a maximum density of 2.5  $ml^{-1}$ .

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 12.50C,

Table 6.1 Coefficients for the fit of <u>Nephelopsis</u> <u>obscura</u> 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	
Respirat	tion equation	· - · · · · · · · · · · · · · · · · · ·		
	Intercept Temperature	-0.0385	0.0113	3.41
	(°C)	0.0043	0.0007	6.31
	state Body size (n (exponent) Activity r <sup>2</sup> = 76.3%	0.0184 ng) 0.3427 -0.0147 0.0669	0.0097 0.0209 0.0017 0.0077	1.90 16.40 8.65 8.69
Cladocer	ra capture rat	e equations		
15°C	Intercept Prey density (cm <sup>-2</sup> ) r <sup>2</sup> = 68.7%	0.2470	0.1686 0.0729	1.47 7.26
20 <sup>0</sup> C .	Intercept Prey density (cm <sup>-2</sup> ) r <sup>2</sup> = 76.3%	0.3651	0.1740 0.0830	1.86 8.43

	Variable	Coefficient	SD	t
Chironom	nidae capture r	ate equation	S	
12.5°C				
	Intercept Dray depaity	0.2438	0.3674	0.6
	$\begin{array}{r} \text{Prey density} \\ (cm^{-2}) \\ r^2 = 43.0\% \end{array}$	0.4016	Q.1748	2.3
15°C				
-	Intercept	-0.1606	0.5361	0.3
	$r^{2} = 69.8\%$	1.0258	0.2551	4.03
20°C				
0	Intercept Prev density	-0.1002	0.7467	-0.13
	$r^2 = 72.4\%$	1.8133	0.3734	4.80

Table 6.1 continued

15oC and 20<sup>o</sup>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  $12.5^{\circ}C$  (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 6.2 50 wk of simulated <u>Nephelopsis</u> 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.

 (	 Chiron	nomidae c	apturë r	ates `	
	Temp (°C)	o Coef	SD	Adj Coef	Maximum Difference (cal)
Intercept	12.5	0.2438	0.3674	0.6112	71
Prey density	12.5	0.4016	0.1748	0.5764	-16 61 -33
Intercept	15	-0.1606	0.5361	0.3755	16 -24
Prey density	15	1.0258	0.2551	1.2809	29
Intercept	20	-0.1002	0.7467	0.6465	8-8
Prey density	20	1.8133	0.3737	2.1867	15 -15

### Cladocera capture rates

Intercept	15	0.2470	0.1686	0.4156	39
Prey density	15	0.52898	0.07285	0.60183	-41 36
Intercept	20	0.3651	0.1740	0.45613 0.5391	-38 -3
Prey density	20	0.62821	0.08299	0.1911 0.71120	15 -2
				0.54522	15

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Respiration	rate			
	Coef	SD	Adj Coef	Maximum Difference (cal)
Intercept	-0.0385	0.0113	-0.0272	-15 24
Temperature ( <sup>o</sup> C)	0.0043	0.0007	0.0050	60 73
Nutritional state	0.0184	0.0097	0.0281	0
Wet wt (mg)	0.3427	0.0209	0.3636	- 2
(exp)	-0.0147	-0.0017	-0.0130 -0.0164	-9 5
Acțivity	0.0669	0.0077	0.0745 0.0592	-48 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 1.1) 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°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.

Chironomidae capture i	rates		
Term Co	oef	Adjusted Coef	% Diff.
12.5°C intercept 0.2 15.0°C intercept -0.3 20.0°C intercept -0.3 12.5°C prey 0.4 density $(cm^{-2})$ 15.0°C prey 1.6 density $(cm^{-2})$ 20.0°C prey 1.8 density $(cm^{-2})$ Total Chironomidae co	2438 1606 1002 1016 0258 3133 onsumption	0.366 0.122 -0.242 -0.081 -0.151 -0.050 0.603 0.201 1.545 0.515 2.715 0.905 +50% -50%	$ \begin{array}{r} 1.7\\ 0.0\\ -0.6\\ 0.7\\ 0.0\\ 0.2\\ 8.2\\ -6.6\\ 5.1\\ -11.1\\ 6.1\\ -4.1\\ 7.4\\ -29.0\\ \end{array} $
Cladocera capture rațe	9 5		
15.0°C intercept 0.2 20.0°C intercept 0.3 15.0°C prey 0.5 density (cm <sup>-2</sup> ) 20.0°C prey 0.6 density (cm <sup>-2</sup> ) Total Cladocera consum	2470 5651 52898 52821 aption	0.371 0.124 0.54765 0.18255 0.79347 0.26449 0.942315 0.314105 +50%	3.6 -3.5 -2.8 2.9 8.2 0.0 -7.0 6.8 4.5
	,	- 50%	-8.8

Respiration rate		-	
	Coef	Adjusted Coef	% Diff.

	م چنهه اختبار مربعه نصبه محبه اجبه (جد اجدا اختبار 100 فالله الله الله ا		
Intercept	-0.0385		8.6
Temperature ( <sup>0</sup> C)	0.0043	0.0086	-11.0
Nutritional s	tate 0.0184	0.0368	-2.9
Body size (mg)	0.3427	0.6854	-16.4
	-0.0147	-0.0294	7.8 -13.4
Activity	0.0669	0.1338 0.03345	-6.8 3.0
Total respira	tion	+ 5 0% - 5 0%	-12.0 10.6

#### 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 (1150 10' W, 510 4'N), and were acclimated for 1 wk at either 10<sup>0</sup>C, 15<sup>0</sup>C or 20<sup>0</sup>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 <u>N. obscura</u> 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  $20^{\circ}$ 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  $20^{\circ}$ 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  $10^{\circ}$ C and  $15^{\circ}$ C but deviates at higher temperatures.

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

	10°C			15°C			20 <sup>0</sup> C	
W	PC	PF	 WW	PC	PF	· ww	PC	PF
358.9 413.7 424.3 432.8 437.2 440.6 542.0 556.9 576.8 623.2 648.4 672.5 699.0 720.3 984.1 740.7 248.6 343.3 334.0 Me an SD	7.7 $0.6$ $-11.8$ $-15.6$ $9.6$ $-7.0$ $-17.2$ $-11.8$ $-18.7$ $-17.1$ $-16.5$ $2.8$ $12.6$ $-15.2$ $1.5$ $2.6$ $-12.6$ $8.8$ $1.7$ $-3.6$ $6.8$	100 100 60 75 100 60 71 100 52 83 42 100 100 46 100 61 100 61 100	146.8 178.1 351.3 408.2 411.1 417.3 503.4 506.1 577.2 630.6 821.0 883.5 920.9 1194.7 2215.3 2585.2 2960.3 3734.9	$\begin{array}{c} 0.0\\ 17.1\\ 21.7\\ -10.9\\ -1.5\\ -6.5\\ -3.3\\ -5.5\\ -2.8\\ -0.4\\ -2.9\\ -6.0\\ 0.0\\ -1.1\\ -18.5\\ -18.0\\ -19.8\\ -22.4\\ \end{array}$	$     \begin{array}{r}       100\\       100\\       100\\       100\\       100\\       100\\       100\\       100\\       100\\       100\\       100\\       100\\       24\\       66\\       38\\       54   \end{array} $	120.6 370.3 411.5 601.8 673.2 688.9 1369.3 1639.6 1890.0 2207.0 2728.6 Mean SD	$ \begin{array}{r} -15.4\\ 31.6\\ 22.3\\ 24.4\\ 28.1\\ 27.1\\ 3.5\\ 14.0\\ -1.0\\ 3.4\\ -13.2\\ \hline 16.9\\ 15.9\\ \end{array} $	100 100 100 100 100 42 100 92 100 21

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 cal (234.5 mg) to a minimum of 3.5 cal. Gates (1984) has shown that under laboratory conditions mortality at 10°C and 20°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 winter 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 cm<sup>-2</sup>) (solid line) and mean individual Chironomidae wet weight (mg) (broken line) in Stephenson's Pond from 84-06-13 to 84-10-25.



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Figure 6.4 Weekly mean temperature (°C) at 1 m depth in Stephenson's Pond from 84-06-13 to 84-10-25.



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may contribute significantly to the energy budget of <u>N. obscura</u>. 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-1. 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 cal (680 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 <u>Nephelopsis</u> <u>obscura</u>, using 1980 Chironomidae data and 1980 temperature data from Stephenson's Pond.



Table 6.5 Simulated <u>Nephelopsis</u> 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:

Temp Data			Simulated		Chironomidae Brov Data	
Week		Body Size	As s imi	lation	Density	
	(ºC)	(cal)	Maximal (cal)	Actual (cal)	( cm <sup>-2</sup> )	(mg)
197 198 199 200 201 202 203 204 205 206 207 208 209 210 211 212 213 214 215 216 217	11.8 13.2 11.7 10.7 12.2 16.1 18.9 16.0 17.1 17.5 16.7 16.8 16.1 13.6 14.4 13.4 12.0 12.0 12.0 11.3 9.1	465.8 467.6 471.1 483.4 500.2 508.3 502.5 487.3 458.6 433.8 415.4 408.6 411.1 415.6 411.1 414.8 429.9 444.8 461.9 472.9 469.7	85.9 75.0 87.6 98.1 88.6 76.1 103.4 72.4 81.4 81.0 73.2 73.6 67.1 65.4 59.7 66.6 78.7 81.0 89.3 88.2	29.4 36.3 41.4 43.5 40.2 38.4 34.4 9.1 14.0 20.2 29.8 40.2 41.3 26.9 34.6 46.9 42.9 46.3 37.9 15.7	1.135 0.286 0.212 0.139 0.065 5.203 4.871 4.545 4.216 4.013 3.796 3.579 3.247 2.915 2.768 2.486 2.182 2.129 2.076 2.065	4.2 4.3 4.2 4.1 0.1 0.4 0.1 0.4 0.8 1.0 2.5 3.6 7 3.6 7 3.9 4.0

		using	1980	4 prey da O tempera	ta with ture data	:	
[	Temp Data			Simulated		Chironom Prev Da	nidae ta
Week		Boo	dy re	Assimi	lation	Density	 
	(°C)	(ca	al)	Maximal (cal)	Actual (cal)	( cm <sup>-2</sup> )	(mg)
201 202 203 204 205 206 207 208 209 210 211 212 213 214 215 216 217 218	12.2 16.1 18.9 16.0 17.1 17.5 16.7 16.8 16.1 13.6 14.4 13.4 12.0 12.0 11.3 9.1	455 494 520 563 588 588 588 588 588 588 588 588 578 578	5.2 .7 .2 .4 .8 .8 .8 .8 .8 .8 .5 .1 .9 .7 .5 .8 .9 .7 .6 .5 .8 .9 .7 .5 .8 .9 .7 .2 .4 .8 .9 .2 .8 .9 .5 .9 .7 .0 .0 .0 .0 .0 .0 .0 .0 .0 .0	81.2 74.5 102.9 80.8 93.6 97.7 89.3 90.0 85.4 88.6 78.3 88.6 102.2 100.1 104.5 98.8 98.8	73.5 74.5 102.9 80.8 56.4 51.9 52.2 77.8 46.9 25.0 43.6 33.6 19.3 16.2 13.0 0.0	4.000 2.167 4.400 5.733 12.800 11.733 7.533 6.933 10.533 5.333 12.133 9.200 5.267 9.400 9.600 5.800	5.5 3.9 5.4 2.4 2.1 2.3 2.0 2.9 2.9 3.0 2.9 3.0 2.5 2.0

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 wk yr<sup>-1</sup>. 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 <u>Nephelopsis</u> <u>obscura</u>, using 1984 Chironomidae data and 1980 temperature data from Stephenson's Pond.



AGE (weeks)

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  $cm^{-2}$  to 2.5  $cm^{-2}$ , while in the second, they range from 9.6  $cm^{-2}$  to 5.3  $cm^{-2}$ .

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 <u>N. obscura</u> 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 <u>N. obscura</u> shows prey selectivity between <u>T. tubifex</u> 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 <u>Nephelopsis</u> <u>obscura</u>, using 1984 Chironomidae data and 1984 temperature data from Stephenson's Pond.



AGE (weeks)

Table 6.6 Simulated <u>Nephelopsis</u> 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:

Temp Data			Simulated		Chironomidae Bray Data	
Waak	Bata	Body	Assimi	lation	Prey Da	
	( ⁰C )	(cal)	Maximal (cal)	Actual (cal)	( cm <sup>-2</sup> )	51ze (mg)
203 204 205 206 207 208 209 210 211 212 213 214 215 216 217 218 219 220	7.2 8.7 9.4 8.5 9.8 9.1 9.5 0.0 8.9 7.5 3.1 2.2 9.6 9.7 4.5 0.8 9.9 0.1	570.5 604.3 653.3 695.6 694.6 684.2 681.7 711.5 703.3 687.5 672.7 654.8 629.6 605.0 599.0 575.2 552.1 560.2	89.4 106.5 119.9 115.8 134.1 126.5 128.8 133.5 127.4 111.0 107.2 116.5 132.5 129.4 31.5 120.0 121.9 5.3	89.4 97.4 119.9 115.8 74.9 61.5 70.9 109.2 65.0 50.0 29.8 20.7 0.0 0.0 0.0 3.7 0.0 0.0	4.000 2.167 4.400 5.733 12.800 11.733 7.533 6.933 10.533 5.333 12.133 9.200 5.267 9.400 9.600 5.800 5.267 5.267 5.267	5.5 3.9 5.4 5.4 2.3 3.4 2.3 2.0 2.9 2.9 3.0 2.6 3.5 2.0 2.8 2.7

## Table 6.6 (continued)

# Simulation using 1980 prey data with 1980 temperature data:

Temp Data Week	Simulated			Chironomidae Data Data	
	Body Size	Assimilation		Prey Data	
		Max ima l	Actual	Density	Size
( °C)	(cal)	(cal)	(cal)	( cm <sup>-2</sup> )	(mg)
	414.0	، سے پی پی جن بھ بے اس کے پر ان ا	<u>ہے</u> ہید بند جند <del>میں</del> دی جوہ دند ا		
17.2	418.5	78.0	43.7	0.065	4.0
18.7	419.8	89.3	43.6	5.203	0.1
19.4	412.2	95.8	35.4	4.871	0.3
18.5	386.6	91.0	12.2	4.545	0.4
19.8	366.3	97.5	18.5	4.216	0.6
19.1	354.3	93.1	23.9	4.013	0.8
19.5	35/./	94.1	40.4	3.796	1.4
20.0	5/4.6	99.8	56.4	3.579	2.0
10.9	)92.Z	86./	5/.5	3.247	2.5
17.7	400.)		22.U	2.915	ン・U フ・フ
12.1	400.0	77 9	24.7	2.760	2.2
96	414.0 /19 /	83 8	24 2	2.400	).0 7 7
9.7	427.9	86 2	28.2	2.102	3 9
4.5	423.7	22.3	0.0	2.076	39
10.8	427.4	85.7	26.0	2.065	4.0
9.9	412.7	90.6	2.8	2.054	4.0
0.1	418.8	4.0	0.0	2.043	4.1
	Temp Data (°C) 17.2 18.7 19.4 18.5 19.8 19.1 19.5 20.0 18.9 17.5 13.1 12.2 9.6 9.7 4.5 10.8 9.9 0.1	Temp Data Body Size ( $^{\circ}C$ ) (cal) (cal) 17.2 418.5 18.7 419.8 19.4 412.2 18.5 386.6 19.8 366.3 19.1 354.3 19.1 354.3 19.5 357.7 20.0 374.6 18.9 392.2 17.5 406.3 13.1 403.6 12.2 414.0 9.6 419.4 9.7 427.9 4.5 423.7 10.8 427.4 9.9 412.7 0.1 418.8	$\begin{array}{c c} Temp & Simulated \\ Data & \\ \hline Body & Assimi \\ Size & \\ \hline Maximal \\ (^{O}C) & (cal) & (cal) \\ \hline \\ & & & & & \\ & & & \\ & & & & \\ & & & $	$\begin{array}{c c c} Temp \\ Data \\ \hline \\ Body \\ Size \\ \hline \\ Maximal \\ Actual \\ (^{O}C) \\ (cal) \\ (c$	$\begin{array}{c c c c c c c c c c c c c c c c c c c $
Figure 6.8 A 220 wk simulation of body size (cal) of <u>Nephelopsis</u> obscura, using 1980 Chironomidae data and 1984 temperature data from Stephenson's Pond.



AGE (weeks)

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 <u>N. obscura</u> growth rates than temperature. From Figure 6.5 through 6.8, it would appear that <u>N. obscura</u> 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 <u>N. obscura</u> would be found to be much larger there.

In Lac des Arcs, a shallow pond in the foothills of Alberta, specimens of <u>N. obscura</u> 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 <u>N. obscura</u> 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  $10^{\circ}$ C and  $15^{\circ}$ C, but may overestimate at  $20^{\circ}$ 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 <u>N. obscura</u> 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 <u>N. obscura</u> growth patterns than are differences in thermal regimes.
 3) Periods of <u>N. obscura</u> shrinkage occur in Stephenson's Pond following the spring Chironomidae emergence.

4) If periods of shrinkage do not occur when mean prey size is small,
 <u>N. obscura</u> 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 <u>N. obscura</u>, 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°C with no food supplied. Wrona (1982) showed the mean number of cocoons and embryos produced per individual to range from zero at 5°C to 7.29 and 26.54 respectively at 20°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 mg, and large: 300 - 450 mg. Two temperatures (15°C and 20°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 OX (starvation), 1X (the entire weekly maintenance ration at one feeding), 2X (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 <u>N. obscura</u>. If the <u>N. obscura</u> 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:

calories = 
$$0.66$$
 wet wt +  $2.72$ . [7.1]

### 7.1.2 Collections

Specimens of <u>N. obscura</u> were collected from Stephenson's Pond in May 1984 shortly after the beginning of the ice free period, when water temperature was  $8^{\circ}$ C. Field observations at the time of collection confirmed that these <u>N. obscura</u> 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 <u>ad libitum</u> food (<u>T. tubifex</u>), then assigned to one of the cells of the experimental design. Before any <u>N. obscura</u> were assigned to the experiment, 20 specimens were dissected to assess the state of gonad development.

# 7.2 Results

Of the 180 <u>N.</u> 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 coccoons) 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 <u>Nephelopsis</u> <u>obscura</u> on temperature ( $^{O}C$ ), 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	-			
		ded		Uncoded
	Coefficient	SD	 t	Coefficient
Intercept Wet wt (mg) Temperature ( <sup>o</sup> C)	21.5364 0.07315 1.6998	0.9578 0.01433 0.3877	22.49 5.11 4.38	27.49758 0.07315 1.6998
df = 109	$r^2 = 31.8\%$		، جند خند است النام التار اليار جرب التار	

Cocoon calories

	Coded		Uncoded	
	Coefficient	SD	 t	Coefficient
Intercept Wet wt (mg) Temperature ( <sup>O</sup> C)	38.601 0.16123 1.4672	1.352 0.02022 0.5471	28.56 7.97 2.68	-25.875 0.16123 1.4672
df = 109	$r^2 = 41.2\%$		<u>`</u>	

## 7.3 Discussion

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 Equations describing these variations in age specific mortality factors. 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 <u>N. obscura.</u> 1) Deformed cocoons that do not hatch are occasionally deposited, and laboratory observations suggest that over the range of  $5^{\circ}$ C to 20°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°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 <u>N. obscura</u> (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

<u>Nephelopsis</u> 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 m<sup>2</sup>, while Ekman dredge samples (0.0225 m<sup>2</sup>) 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°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 <u>Nephelopsis</u> <u>obscura</u> raised at 20°C under <u>ad libitum</u> 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).

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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 Several factors contributed to this failure: rates. 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 This problem appeared most prominent after ice among the zones. 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 <u>Nephelopsis obscura</u> frequency of occurrence in Stephenson's Pond versus time (1979-1980) and leech weight.



Figure 8.3 <u>Nephelopsis</u> 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

$$S(t) = p_1 e^{p_2 t} + p_3 e^{p_4 t}$$
 [8.1]

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
P1	85.62	4.22
P2	-2.38	1.84
P3	14.38	3.72
P4	-0.11	0.04

with residual mean square of 0.043 (Figure 8.4A).

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

$$h(t) = hp(ht)^{p-1}$$
[8.2]

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]).



$$S(t) = exp - (ht)^{P}$$
 [8.3]

The parameters were estimated by least squares regression of  $\ln$  [- $\ln$  S(t)] versus ln 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:

Coef SD p = 0.187 0.0877 intercept = 0.598 0.1832 h = 24.509

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

### Post-reproductive mortality

### 9.0 Introduction

Observations of reproductive <u>Nephelopsis obscura</u> (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

 $h = e^{r}$ 

[9.1]

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  $(z_i)$  which is varying, there is a regression parameter  $(B_i)$  that can be used to predict r as:

$$r = m + B_1 z_1 + B_2 z_2 + \cdots B_p z_p$$
 [9.2]

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:

$$h(\underline{z}) = e^{(m + B_1 z_1 + B_2 z_2 + \cdots B_p z_p)} [9.3]$$
  
=  $e^{m_e B' z}$ 

where <u>B</u> and <u>z</u> 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 e<sup>m</sup> a function of time ( $h_0(t)$ ). Thus equation [9.3] becomes:

$$h(t;\underline{z}) = h_0(t)e\underline{B'\underline{z}}$$
 [9.4]

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  $\underline{B}$  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  $e\underline{b'z}$  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 z. Based upon a priori arguments (Calow 1983) all variables except temperature were

Table 9.1 The variables used to fit <u>Nephelopsis</u> <u>obscura</u> mortality to the proportional hazards model. T = temperature;  $B_r$  = body size in calories at the start of cocoon deposition;  $dB_r$  = change in body size during cocoon deposition; C = total calorific value of cocoons produced;  $n_r$  = the number of meals offered during the cocoon deposition period;  $I_i$  = calorific value of the food consumed at each meal;  $B_i$  = 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 Initial size Proportional energy loss during reproduction Proportional reproductive output	T B <sub>r</sub> arcsin(dB <sub>r</sub> /B <sub>r</sub> ) arcsin(C/B <sub>r</sub> )	
Proportional daily feeding rate during reproduction	$(1/n_r) * \sum_{i=1}^{n_r} I_i/B_i/t_i$	
Proportional daily feeding rate after reproduction	$(1/n_p) * \sum_{i=1}^{n_p} I_i/B_i/t_i$	

Table 9.2 Regression equation from the fit of <u>Nephelopsis</u> <u>obscura</u> mortality to the proportional hazards model. t = regression coefficient/ standard deviation of the coefficient. Variables defined in Table 9.1.

Variable	Coefficient	t
Temperature	0.3319	7.49***
Initial size	-0.0034	-2.34**
Proportional energy	1.5316	2.43**
loss during reprodu	ction	
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		
Variable	Coefficient	t
Temperature	0.3366	8.00 ***
Initial size	-0.0038	-2.78 **
Proportion1 energy	1.4570	2.52 **

\*\*\*=p<0.001 \*\*=p<0.01 n.s.=not significant at alpha=0.05

-4.17 \*\*\*

loss during reprod.

Feeding rate after -23.7670

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 <u>Nephelopsis obscura</u> mortality when temperature (<sup>O</sup>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 <u>Nephelopsis</u> obscura mortality when temperature (°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 <u>N. obscura</u>, 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  $15^{\circ}$ C the metabolic rate of <u>N. obscura</u> 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 <u>Chironomus riparius</u> (Rasmussen 1983). The consequent loss of their brood caused a crash in Chironomidae prey density which was followed by a marked decline in the <u>N. obscura</u> population size, the numbers of which are presently below peak densities recorded before 1983. The fact that <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 m<sup>\$</sup>-2<sup>s</sup> - 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:

$$1 = \sum_{X} e^{-r_{X}} l_{X} m_{X}$$
 [10.1]

where x is age in weeks,  $l_x$  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  $(l_x)$  schedule and natality  $(m_x)$  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 <u>N. obscura</u> when life-history parameters are varied, or when certain habitat variables are changed. An attempt was made to predict the optimum life history for <u>N. obscura</u> 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 1.1) so that varying one will produce a change in other variables.

# 10.2.2 Longevity

#### 10.2.2.0 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 <u>Nephelopsis</u> <u>obscura</u> 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. mo, 24 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 yr.

#### 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 <u>Nephelopsis</u> 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).



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Age	Proportional	Body Size
(yr)	Satiation	(mg)
1	0.8301	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 <u>N. obscura</u> feeding in habitats containing larger Chironomidae or switching from Chironomidae to some larger prey item. Age at first reproduction was set to 1 yr, 2 yr and 3 yr.

### 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 <u>Nephelopsis obscura</u> using observed field Chironomidae prey sizes and <u>Nephelopsis</u> <u>obscura</u> age at first reproduction of 1 yr (solid line), double observed field prey sizes with <u>Nephelopsis obscura</u> age at first reproduction at 1 yr (long dashed line), and double observed field prey sizes with <u>Nephelopsis obscura</u> age at first reproduction at 2 yr (short dashed line) versus time (weeks).



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Figure 10.4 Simulated population sizes of <u>Nephelopsis</u> 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 <u>ad libitum</u>.



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 <u>Nephelopsis</u> 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 (long dashed line).



# 10.2.6 Iteroparity versus semelparity

### 10.2.6.0 Introduction

Some populations of <u>N. obscura</u> have been reported (eg. Peterson 1983) to contain much larger individuals (>2000 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 yr, 2 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 10.6A), 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 <u>Nephelopsis</u> 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 <u>Nephelopsis</u> 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 <u>ad libitum</u> 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).



Figure 10.8 Simulated population sizes of <u>Nephelopsis</u> obscura with <u>ad</u> <u>libitum</u> 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 yr (10.8B) or 3 yr (10.8C).



that careful examination of the life history of  $\underline{N}$ . <u>obscura</u> 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 <u>N. obscura</u> (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 <u>N. obscura</u> 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 calories 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 <u>N. obscura</u> 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 <u>N.</u> 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 <u>Nephelopsis</u> 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.

AAFR	, MNB	PI
		<u>میں بین میں زیر ملت بین بین بین بین میں ایم ملت م</u>
2	no limit 3	2.54
3	no limit	>10
-		/10
2	no limit	2.09
3	no limit 3	>10 >10
2	no limit	1.25
• 3	n'o limit 3	>10 >10
	AAFR 2 3 2 3 2 2 3	AAFRMNB2no2no3no2no2no3no3no2no1 $\frac{3}{3}$ 3no1 $\frac{3}{3}$ 3no1 $\frac{3}{3}$

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 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 <u>N. obscura</u>). 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 <u>ad libitum</u> 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 <u>N. obscura</u> 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) <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>N. obscura</u> 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 <u>ad libitum</u> 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 their applicability to circumstances other than those in results i. e. 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°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 <u>N. obscura</u> 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 <u>N. obscura</u> in habitats which produce large specimens.

The model at its present stage of development is unable to address questions regarding the population dynamics of <u>N. obscura</u> since no data are available regarding density-dependent feedback on population size. Evidence exists for inter-specific competition for food between. <u>N. obscura</u> and <u>Erpobdella</u> <u>punctata</u> (Leidy) (Davies, Wrona and Linton 1982). It is also possible that regulation of <u>N. obscura</u> 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 <u>N. obscura</u>. The individual growth rates of the prey would have to be investigated as functions of prey population density since cropping by <u>N. obscura</u> 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 <u>N. obscura</u> cropping, the impact of <u>N. obscura</u> 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 <u>N. obscura</u> (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 density-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 <u>N. obscura</u>, 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 <u>N. obscura</u> 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.

#### Literature Cited

- Anholt, B. R. 1982. A test of alternative models of prey selection by <u>Nephelopsis obscura</u> Verrill (Hirudinoidea). M. Sc. Thesis. University of Calgary, Alta. (129 pp).
- Bayne, B. L., J. Widdows and R. J. Thompson. 1976. Physiological integrations. In: Marine mussels: their ecology and physiology. (Ed. B. L. Bayne). Cambridge University Press, Cambridge, G. B.
- Calow, P. 1976. Biological machines. Edward Arnold, London, G. B.
- Calow, P. 1978. Life cycles; an evolutionary approach to the physiology of reproduction, development and aging. John Wiley and Sons, Inc., N. Y., U. S. A.
- Calow, P. 1981. Invertebrate biology a functional approach. John Wiley and Sons, Inc. N. Y., U. S. A.
- Calow, P. 1983. Resource utilization and reproduction. In: Physiological ecology. (Ed. P. Calow and C. R. Townsend). Blackwell Scientific Publications. Edinburgh, G. B.
- Calow, P. and H. Riley. 1980. Leeches: an adaptational approach to their ecology and physiology. J. Biol. Educ. 14: 279-289.
- Caswell, H. 1979. The validation problem. In: Systems analysis and simulation in ecology. Vol. IV, (Ed. B. C. Patten). Academic Press, N. Y.
- Cole, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103-137.
- Cox, D. R. 1972. Regression models and life-tables. J. R. Stat. Soc. B. 34: 187-220.
- Dall, P. C. 1979. Ecology and production of the leeches <u>Erpobdella</u> <u>octoculata</u> and <u>Erpobdella</u> <u>testacea</u> in Lake Esrom Denmark. Arch. Hydrobiol. Suppl. 57: 188-220.
- Davies, R. W. 1973. The geographic distribution of freshwater Hirudinoidea in Canada. Can. J. Zool. 51: 531-545.
- Davies, R. W. and R. P. Everett. 1977. The life history, growth, and age structure of <u>Nephelopsis</u> obscura Verrill, 1872 (Hirudinoidea) in Alberta. Can. J. Zool. 55:620-627.
- Davies, R. W., T. B. Reynoldson and R. P. Everett. 1977. Reproductive strategies of <u>Erpobdella punctata</u> (Hirudinoidea) in two temporary ponds. Oikos 29: 313-319.

- Davies, R. W., F. J. Wrona and R. P. Everett. 1978. A serological study of prey selection by <u>Nephelopsis</u> obscura Verrill (Hirudinoidea). Can. J. Zool. 56:587-591.
- Davies, R. W., F. J. Wrona and L. Linton. 1982. Changes in numerical dominance and its effect on prey utilization and inter-specific competition between <u>Erpobdella</u> <u>punctata</u> and <u>Nephelopsis</u> <u>obscura</u> (Hirudinoidea): an assessment. Oikos 39: 92-99.
- Davies, R. W., F. J. Wrona, L. Linton and J. Wilkialis. 1981. Inter- and intra-specific analysis of the food niches of two sympatric species of Erpobdellidae (Hirudinoidea) in Alberta, Canada. Oikos. 37:105-111.
- Dawkins, R. 1982. The extended phenotype. Oxford University Press, Oxford, G. B.
- Dixon, W. J., 1981. BMDP statistical software. University of California Press, Berkley, Calif., U. S. A.
- Driver, E. A. 1977. Chironomid communities in small prairie ponds: some characteristics and controls. Freshwat. Biol. 7: 121-134.
- Elliott, J. M. 1973. The life cycle and production of the leech <u>Erpobdella octoculata</u> (Hirudinea: Erpobdellidae) in a Lake District stream. J. Anim. Ecol. 42: 435-448.
- Elliott, J. M. 1976. The energetics of feeding, metabolism and growth of brown trout (Salmo trutta L.) in relation to body weight, water temperature and ration size. J. Anim. Ecol. 45:923-948.
- Everett, R. P. 1974. An ecological study of Hirudinoidea native to Alberta. M. Sc. Thesis. University of Calgary, Alta. (151 pp).
- Gates, T. E. 1984. Influences of temperature on the distribution and abundance of two sympatric Erpobdellidae (Hirudinoidea). M. Sc. Thesis. University of Calgary, Alta. (114 pp).
- Giese, A. C. 1968. Cell physiology, third edition. W. B. Saunders and Co. Toronto.
- Granger, C. W. J. and P. Newbold. 1973. Some comments on the evaluation of economic forecasts. Applied Econ. 5: 35-47.
- Hamilton, W. D. 1966. The modelling of senescence by natural selection. J. Theor. Biol. 12:12-45.
- Holling, C. S. 1959a. The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. Can. Entomol. 91: 293-320.

- Holling, C. S. 1964. The functional response of predators to prey density and its role in mimicry and population, regulation. Mem. Entomol. Soc. Can. 45: 1-60.
- Hopkins, A. 1981. Regression with incomplete survival data. in: BMDP statistical software. (Ed. W. J. Dixon). University of California Press, Berkley, Calif., U. S. A.
- Hubbell, S. P. 1971. Of sowbugs and systems: the ecological bioenergetics of a terrestrial isopod. In: Systems analysis and simulation in ecology. Vol. I. (Ed. B. C. Patten). Academic Press, N. Y., U. S. A.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54: 187-211.
- Iwama, G. K. and A. F. Tautz. 1981. A simple growth model of salmonids in hatcheries. Can. J. Fish. Aquat. Sci. 38:649-656.
- Kalbfleisch, J. D. and R. L. Prentice 1980. The statistical analysis of failure time data. John Wiley and Sons, Toronto.
- Kirkendall, L. R. and N. C. Stenseth. 1985. On defining "breeding once". Am. Nat. 125:189-204.
- Kerr, S. R. 1971a. Prediction of growth efficiency in nature. J. Fish. Res. Board Can. 28:809-814.
- Kerr, S. R. 1971b. A simulation model of lake trout growth. J. Fish. Res. Board Can. 28:815-819.
- Kitchell, J. F. and J. E. Breck. 1980. Bioenergetics model and foraging hypothesis for a sea lamprey (<u>Petromyzon marinus</u>). Can. J. Fish. Aquat. Sci. 37:2159-2168.
- Kitchell, J. E., D. J. Stewart and D. W. Weininger. 1977. Applications of a bioenergetics model to yellow perch (<u>Perca</u> <u>flavescens</u>) and walleye (<u>Stizostedion</u> <u>vitreum</u> <u>vitreum</u>). J. Fish. Res. Board Can. 34:1922-1935.
- Kruger, F. 1968. Contributions to the energetics of animal growth. In: Quantitative biology of metabolism. (Ed. A. Locker). Springer-Verlag New York Inc., N. Y., U. S. A.
- Linton, L. R., R. W. Davies and F. J. Wrona. 1983. The effects of water temperature, ionic content and total dissolved solids on <u>Nephelopsis obscura</u> and <u>Erpobdella punctata</u> (Hirudinoidea: Erpobdellidae): II Reproduction. Holarctic Ecology 6:64-68.

- Majkowski, J. and K. G. Waiwood. 1981. A procedure for evaluating the food biomass consumed by a fish population. Can. J. Fish. Aq. Sci. 38: 1199-1208.
- Makorova, N. P. and V. Ye. Zaika. 1971. Relationship between animal growth and quantity of assimilated food. Hydrobiol. J. 7:1-8.
- Mann, A. H. 1962. Leeches (Hirudinea) their structure, physiology, ecology and embryology. Pergamon Press, Oxford, G. B.
- Mertz, D. B. 1971. Life history phenomena in increasing and decreasing populations. In: Statistical Ecology. (Ed. G. P. Patil, E. C. Pielou and W. E. Watters) Pennsylvania State University Press, Penn., U. S. A.
- Mihram, G. A. 1971. Some practical aspects of the verification and validation of simulation models. Oper. Res. Quart. 23: 17-29.
- Miller, D. R. 1979. Model validation through sensitivity analysis. in: Benchmark papers in Ecology, Vol. 9, pp 292-295. (Ed. Shugart, H. H. and R. V. O'Neil). Dowden, Hutchinson and Ross, Inc., Stroudsburg, Penn, U. S. A.
- Minton, J. W. and R. B. McLean. 1982. Measurement of growth and consumption of sauger (<u>Stizostedion canadense</u>): implications for fish energetics studies. Can. J. Fish. Aquat. Sci. 39:1396-1403.
- Murphy, P. M. and M. A. Learner. 1982. The life history and production of the leech <u>Erpobdella octoculata</u> (Hirudinea Erpobdellidae) in the River Ely, South Wales. J. Anim. Ecol. 51: 57-67.
- Nagahbushanam, R. and G. K. Kulkarni. 1977. The effects of some extrinsic factors on the respiratory metabolism of the freshwater leech <u>Poecilobdella</u> <u>viridis</u>: oxygen tension, pH and salt concentrations. Hydrobiol. 56(2):181-186.
- Paloheimo, J. E., S. J. Crabtree and W. D. Taylor. 1982. Growth model of <u>Daphnia</u>. Can. J. Fish. Aquat. Sci. 39:598-606.
- Parker, R. E. 1979. Introductory statistics for biology. 2nd Edition, (Institute of Biology. Studies in Biology; no 43.) Edward Arnold (Publishers) Ltd., London, G. B.
- Parker, R. P. and P. A. Larkin. 1959. A concept of growth in fishes. J. Fish. Res. Board Can. 16:721-745.

- Peterson, D. L. 1983. Life cycle and reproduction of <u>Nephelopsis</u> obscura Verrill (Hirudinea: Erpobdellidae) in permanent ponds of northwestern Minnesota. Freshwat. Invert. Biol. 2: 165-172.
- Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos 15:130-139.
- Prosser, C. L. 1973. Comparative animal physiology. W. B. Saunders Company, Toronto, Canada.
- Rasmussen, J. B. 1983. An experimental analysis of competition and predation and their effects on growth and coexistence of chironomid larvae in a small pond. Ph. D. Thesis. University of Calgary, Alta. (216 pp).
- Ricker, W. E. (Ed.). 1971. Methods for assessment of fish production in fresh waters. 2nd edn. I. B. P. handbook No. 3. Blackwell Scientific Publications, Oxford, G. B.
- Ryan, T. A. Jr., B. L. Joiner and B. F. Ryan. 1981. Minitab reference manual. On line system documentation, Honeywell installation, University of Calgary.
- Sibly, R. and P. Calow. 1983. An integrated approach to life-cycle evolution using selective landscapes. J. Theor Biol. 102: 527-547.
- Sokal, R. R. and Rohlf, F. J. 1969. Biometry. W. H. Freeman and Co., San Francisco, Calif., U. S. A.
- Solomon, D. J. and A. E. Bradfield. 1972. The energetics of feeding, metabolism and growth of perch (Perca flaviatilis L.). J. Anim. Ecol. 41:699-718.
- Stewart, D. J., D. Weininger, D. V. Rottiers and T. A. Edsall. 1983. An energetics model for the lake trout, <u>Salvelinus</u> <u>nomaycush</u>: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40:681-698.
- Townsend, C. R. and P. Calow. 1981. Physiological ecology. Blackwell scientific publications. Oxford, G. B.
- Ursin, E. 1967. A mathmatical model of some aspects of fish growth, respiration and mortality. J. Fish. Res. Board Can. 24:2355-2453.
- Verrill, A. E. 1874. Synopsis of the North American fresh-water leeches. In: U. S. Fisheries Commission report for 1872-73. Pt. II. 666-689.
- Ware, D. M. 1975. Growth, metabolism and optimal swimming speed of a pelagic fish. J. Fish. Res. Board Can. 32:33-41.

- Ware, D. M. 1978. Bioenergetics of pelagic fish; theoretical change in swimming speed in relation with body size. J. Fish. Res. Board Can. 35:220-228.
- Wrona, F. J. 1982. The influence of biotic and abiotic parameters on the distribution and abundance of two sympatric species of Hirudinoidea. Ph. D. Thesis. University of Calgary, Calgary, Alta. (168 pp).
- Wrona, F. J. and R. W. Davies. 1984. An improved flow-through respirometer for aquatic macroinvertebrate bioenergetic research. Can. J. Fish. Aq. Sci. 41: 380-385.
- Yourdon, E. 1975. Techniques of program structure and design. Prentice-Hall, Inc. Englewood Cliffs, N. J., U. S. A.

# Appendix A

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# The simulation model and its subroutines

c program grow	grow	1
C This program computes the size of an individual to see a	grow	2
the size of an individual as a function of:	grow	3
c 1) - temperature	grow	4
2) - oxygen concentration (as of 85-05-27 yet	grow	5
c to be installed)	grow	6
c 3) - food availability	grow	7
	grow	8
cdeclare arrays	grow	9
	grow	10
almension prey(100,3), temp(100), o2(1), growth(5), rep(52),	grow	11
<pre>L conort(50,6), nweeks(5), wdgr(80,10), nd(5)</pre>	worp	12
real meter(35),mindif,maxdif,minb,maxb,nstate(2),mass	voip	13
integer year	grow	14
	grow	15
cthe array nweeks contains the following information:	grow	16
	grow	17
c nweeks(1) - the number of weeks for which the simulation is to ru	ungrow	18
c nweeks(2) - the number of the week in the temperature data	grow	19
c and prey density data from which simulation	arow	20
c is to start. this is analagous to specifying	grow	$21^{-1}$
c hatching time if body is initialized at a very	grow	22
c small value	grow	23
c nweeks(3) - the number of the week presently being simulated	grow	24
c nweeks(4) - the number of weeks of valid temperature data	grow	25
	grow	26
cthe array meter is used for debugging and i/o. its contents are:	grow	27
	grow	28
c meter(1) - the week being simulated (loaded in grow.fortran)	grow	29
c meter(2) - temperature (loaded in maxass.fortran)	grow	30

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meter(3) - temperature
С
                                             (loaded in actass.fortran)
                                                                            arow
                                                                                   31
      meter(4) - temperature
С
                                            (loaded in respir.fortran)
                                                                                   32
                                                                            WOID
      meter(5) - body size in calories at the beginning of the week.
С
                                                                            arow
                                                                                   33
C
                                             (loaded in maxass.fortran)
                                                                            qrow
                                                                                   34
      meter(6) - body
С
                                             (loaded in actass.fortran)
                                                                                   35
                                                                            arow
      meter(7) - body
С
                                             (loaded in respir.fortran)
                                                                            arow
                                                                                   36
      meter(8) - body size at the end of the week
С
                                                                            arow
                                                                                   37
С
                                             (loaded in grow.fortran)
                                                                                   38
                                                                            arow
      meter(9) - maximal assimilation
С
                                             (loaded in maxass.fortran)
                                                                                   39
                                                                            arow
      meter(10) - actual assimilation
С
                                             (loaded in actass.fortran)
                                                                            arow
                                                                                   40
      meter(11) - chironomid prey density
С
                                             (loaded in actass.fortran)
                                                                            qrow
                                                                                   41
     meter(12) - chironomid prey wet wt
С
                                             (loaded in actass.fortran)
                                                                                   42
                                                                            worp
      meter(13) - Cladocera prey density
С
                                             (loaded in actass.fortran)
                                                                            qrow
                                                                                   43
      meter(14) - respiration
C-
                                            (loaded in respir.fortran)
                                                                            arow
                                                                                   44
      meter(15) - maximal growth rate
С
                                            (loaded in mgainl.fortran
                                                                            grow
                                                                                   45
С
                                                     or mgain2.fortran)
                                                                            grow
                                                                                   46
С
      meter(16) - calories invested in reproduction
                                                                                   47
                                                                            qrow
С
                                             (loaded in effort.fortran)
                                                                            qrow
                                                                                   48
      meter(17) - embryo production
С
                                             (loaded in effort.fortran)
                                                                            qrow
                                                                                   49
      meter(18) - growth efficiency
С
                                            (loaded in grow.fortran)
                                                                            drow
                                                                                   50
С
                                                                                   51
                                                                            qrow
c...the array cohort is used to keep track of different cohorts
                                                                                   52
                                                                            qrow
        which may be present simultaneously in the population
С
                                                                                   53
                                                                            qrow
        (up to a maximum of 50 without resetting the dimension
С
                                                                            qrow
                                                                                   54
        statement above). its contents are as follows:
С
                                                                            qrow
                                                                                   55
С
                                                                                   56
                                                                            qrow
         the rows each represent a cohort, the index of the last cohort grow
С
                                                                                   57
           being stored below in "lc", and the cohort counting
С
                                                                            qrow
                                                                                   58
С
           index is "ic".
                                                                            Qrow
                                                                                  59
С
         the columns are:
                                                                            worp
                                                                                  60
             column 1 - the age of the cohort in weeks
С
                                                                            worp
                                                                                  61
С
             column 2 - the size of the cohort in numbers.
                                                               these
                                                                            qrow
                                                                                  62
С
                         values may be fractional.
                                                                                  63
                                                                            worp
             column 3 - the average size of an individual of the
С
                                                                            arow
                                                                                  64
```

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С cohort grow 65 column 4 - the body size at the commencement of С worp 66 С reproduction 67 worp С column 5 - a switch set to the week of the beginning 68 grow of reproduction and 0.0 at the end. С 69 grow С 70 **Qrow** .. the array rep is used to control breeding. its contents are c. grow 71 zero or unity and are read from the input data. it contains С 72 **vo** 1p C 52 elements, on for each week of the year. in any week 73 qrow С in which the correspond element of rep is set to 1.0, 74 **QLOM** breeding will occur. С 75 grow С qrow 76 77 qrow 78 grow 79 qrow c...open data input file qrow 80 grow 81 open(11, mode="in", access="sequential", form="formatted") 82 WOID 83 qrow c...open output file **d**L OM 84 grow 85 open(12,mode="out",access="sequential",form="formatted") qrow 86 qrow 87 c...open input file for input of base line run results. The results of grow 88 simulations under different environmental conditions С qrow 89 are compared to these bench mark results read in from this С 90 qrow file to investigate the effects of varying environmental С qrow 91 conditions or model parameters. С 92 grow 93 grow open(13,mode='in',access='sequential',form='formatted') 94 **VO1**D qrow 95 sensitivity analysis output is to file14 С qrow 96 97 grow open(14,mode='out',access='sequential',form='formatted') qrow 98

```
grow 99
 c...call data initialization routine
                                                                               grow 100
                                                                               grow 101
       call datain(prey, temp, o2, growth, wdgr, nweeks, body, igcd, nd, rep)
                                                                               grow 102
       cohort(1,3) = body
                                                                               grow 103
       cohort(1,2) = 1.0
                                                                              grow 104
       lc = 1
                                                                               grow 105
       mindif = 10.**7
                                                                               grow 106
       maxdif = -10.**7
                                                                               grow 107
                                                                              grow 108
 С
                                                                              grow 109
 c********* main loops through years, weeks and cohorts ********
                                                                              grow 110
 С
                                                                              grow 111
 С
                                                                              grow 112
 С
                                                                              grow 113
 c...loop through years
                                                                              grow 114
 С
                                                                              grow 115
       ny = 15
                                                                              grow 116
       do 510 year = 1 , ny
                                                                              grow 117
 С
                                                                              grow 118
 c...loop through weeks
                                                                              grow 119
 С
                                                                              grow 120
       do 500 nweeks(3) = nweeks(2) , nweeks(2) + nweeks(1) - 1
                                                                              grow 121
 С
                                                                              grow 122
 c...loop through cohorts
                                                                              grow 123
 C
                                                                              grow 124
       do 490 \text{ ic} = 1 , lc
                                                                              grow 125
С
                                                                              grow 126
c...age the cohort
                                                                              grow 127
С
                                                                              grow 128
      (cohort(ic, 1) = cohort(ic, 1) + 1.0)
                                                                              grow 129
. C
                                                                              grow 130
c... if the cohort is dead, skip to next one
                                                                              grow 131
C
                                                                              grow 132
```

```
if(cohort(ic,2).lt. 0.0) go to 490
                                                                             arow 133
С
                                                                             grow 134
c... if the cohort can breed, set the breeding condition flag
                                                                             grow 135
С
                                                                             grow 136
      if((rep(nweeks(3)) .gt. 0.5 .and. rep(nweeks(3)-1) .lt. 0.5
                                                                             arow 137
         .and. cohort(ic,3) .ge. 80.0).or.
     1
                                                                             grow 138
       (rep(nweeks(3)).gt. 0.5 .and. cohort(ic,5).gt.0.0))then
     1
                                                                             grow 139
       if(rep(nweeks(3)).gt.0.5.and.cohort(ic,1).ge.52)then
С
                                                                             grow 140
         bf1 = 1.0
                                                                             grow 141
         bf2 = 1.0
                                                                             grow 142
      else
                                                                             grow 143
         bf1 = 0.0
                                                                             grow 144
      end if
                                                                             grow 145
С
                                                                             grow 146
c...growth
                                                                             grow 147
С
                                                                             grow 148
      call maxass(nweeks(3), temp, growth, wdgr, cohort(ic, 3), mass,
                                                                             grow 149
          igcd,nd,meter,bfl)
     1
                                                                             grow 150
      call actass (temp, nweeks(3), prey, cohort(ic, 3), nstate,
                                                                             grow 151
         mass, aass, meter)
     1
                                                                             grow 152
      call respir (nweeks(3), temp, nstate, cohort(ic, 3), resp, meter, bfl)
                                                                             grow 153
      prod = aass - resp
                                                                             grow 154
С
                                                                             grow 155
c...reproduction
                                                                             grow 156
С
                                                                             grow 157
      if (bfl .gt. 0.5) then
                                                                             grow 158
         call breed(nweeks(3), cohort, ic, lc, aass, meter, temp, repeff)
                                                                             grow 159
      else
                                                                             grow 160
         repeff = 0.0
                                                                             grow 161
         meter(16)=0.0
                                                                             grow 162
         meter(17) = 0.0
                                                                             grow 163
      end if
                                                                             grow 164
      cohort(ic,3) = cohort(ic,3) + prod - repeff -
                                                                             grow 165
С
                                                                             grow 166
```

```
c...compute growth efficiency
                                                                             grow 167
С
                                                                             grow 168
    if (aass .gt. 0.0) then
                                                                             grow 169
          meter(18) = prod / aass.
                                                                             grow 170
       else
                                                                             grow 171
          meter(18)=0.0
                                                                             grow 172
      end if
                                                                             grow 173
      meter(1) = nweeks(3)
                                                                             grow 174
      meter(8) = cohort(ic, 3)
                                                                             grow 175
С
                                                                             grow 176
c...mortality
                                                                             grow 177
С
                                                                             grow 178
С
                   set maximum longevity
                                                                             qrow 179
С
                                                                             grow 180
       if(cohort(ic,1).ge. 112.)then
С
                                                                             grow 181
           cohort(ic,2)=-1.0
С
                                                                             grow 182
С
       else
                                                                             grow 183
С
                                                                             grow 184
С
          proportional feeding rate after reproduction
                                                                             grow 185
С
                                                                             grow 186
          if(cohort(ic,5) .ne. 0.0 .and.
                                                                             grow 187
     1
            nweeks(3) .gt. cohort(ic,5)+3 .and.
                                                                             grow 188
     1
            nweeks(3) .lt. cohort(ic,5)+10)then
                                                                             grow 189
              cohort(ic,6)=cohort(ic,6)+aass/0.79/cohort(ic,3)/7.0
                                                                            grow 190
              far = cohort(ic, 6)/(cohort(ic, 5) + 3. - nweeks(3))
                                                                            grow 191
         else
                                                                            grow 192
              cohort(ic, 6) = 0.
                                                                            grow 193
              far = 0.
                                                                            grow 194
         end if
                                                                            grow 195
                                                                            grow 196
         call surviv(nweeks(3), temp, cohort, ic, far, p)
                                                                            grow 197
         cohort(ic,2) = cohort(ic,2) * p
                                                                            grow 198
С
       end if
                                                                            grow 199
С
                                                                            grow 200
```

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c...call for sensitivity analysis
                                                                           grow 201
C
                                                                           grow 202
    call sensit(nweeks(3), cohort(ic, 3), mindif, maxdif)
С
                                                                           grow 203
С
                                                                           grow 204
490
      continue
                                                                           grow 205
С
                                                                           grow 206
C******
                end cohort loop
                                    ******
                                                                           grow 207
С
                                                                           grow 208
С
                                                                           grow 209
c...incriment the index of the last cohort (lc) if
                                                                           grow 210
        reproduction is finished and breeding has ocurred.
С
                                                                           grow 211
C
                                                                           grow 212
      if(rep(nweeks(3)) .gt. 0.5 .and. rep(nweeks(3)+1).lt.0.5
                                                                           grow 213
          .and. bf2 .gt. 0.5)then
     1
                                                                           grow 214
         lc = lc + l
                                                                           grow 215
         bf2 = 0.0
                                                                           grow 216
      end if
                                                                           grow 217
С
                                                                           grow 218
c...reset the reproduction marker in column 5 if 10 weeks
                                                                           grow 219
        have elapsed since the commencement of reproduction.
С
                                                                           grow 220
С
                                                                           grow 221
      do 492 i = 1, lc - 1
                                                                           grow 222
         if(cohort(i,5).gt. 0.0 .and. nweeks(3) .eq. cohort(i,5)+9)
                                                                           grow 223
                cohort(i,5)=0.0
     1.
                                                                           grow 224
492
      continue
                                                                           grow 225
С
                                                                           grow 226
c...write out total population at the end of each week
                                                                           grow 227
С
                                                                           grow 228
      total = 0.0
                                                                           grow 229
      do 495 i = 1, lc
                                                                           grow 230
          write(12,1002)(cohort(i,j),j=1,6)
С
                                                                           grow 231
         if(cohort(i,2).gt. 0.)total = total + cohort(i,2)
                                                                           grow 232
495
      continue
                                                                           grow 233
      tweek = (year - 1) * 52 + nweeks(3)
                                                                           grow 234
```

```
write(12,1008)tweek, total
С
                                                                            grow 235
       total = logl0 (total)
                                                                           grow 236
      write(12,1009)tweek,total
                                                                            grow 237
500
       continue
                                                                           grow 238
С
                                                                           grow 239
c******
                 end weeks loop
                                                                           grow 240
С
                                                                           arow 241
c...the weeks loop may not cover a complete 52 week period.
                                                                It is thus grow 242
          necessary to compute the probability of surviving
С
                                                                           grow 243
С
          to the beginning of the next simulation cycle
                                                                           grow 244
С
                                                                           grow 245
      if (year .lt. ny) then
                                                                           grow 246
          diff = 52. - nweeks(1)
                                                                           grow 247
           do 494 i = 1, lc
                                                                           grow 248
               if(cohort(i,2) .lt. 0.0) go to 494
                                                                           grow 249
               sp = exp(-(24.509*cohort(i,1)/4.0)**0.187)
                                                                           grow 250
               sn = exp(-(24.509*(cohort(i,1)+diff)/4.0)**0.187)
                                                                           grow 251
              cohort(i,2)=cohort(i,2)*sn/sp
                                                                           grow 252
              cohort(i,1)=cohort(i,1)+diff
                                                                           grow 253
494
          continue
                                                                           grow 254
      end if
                                                                           grow 255
510
      continue
                                                                           grow 256
С
                                                                           grow 257
C******
                end years loop
                                    ******
                                                                           grow 258
С
                                                                           grow 259
С
                                                                           grow 260
С
                                                                           grow 261
c...write out minimum and maximum differences obtained during
                                                                           grow 262
С
       sensitity anaysis
                                                                          grow 263
С
                                                                           grow 264
       write(14,1011)mindif,minb,minwk,maxdif,maxb,maxwk
С
                                                                           grow 265
С
                                                                           grow 266
c...close files
                                                                           grow 267
С
                                                                           grow 268
```

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	do 600 i = 11,14 close(i)	grow	269 270
600	continue	grow	271
	stop	ğrow	272
		grow	273
1000	format('week',4x,'body',4x,'max. assim.',4x,'assim',4x,'resp',4x,	grow	274
	1 'prod',4x,'rep. eff.')	grow	275
1001	format(i4,2x,f6.0,4x,fll.5,2x,f7.1,2x,f7.1,2x,f7.1,2x,f7.1)	qrów	276
1002	format(f6.0,f10.5,2f7.1,f6.0,f7.1)	arow	277
1006	format(' run terminated in grow.fortran - body size negative')	grow	278
1008	format(f6.0,f10.1/)	arow	279
1009	format(f5.0,f12.6)	arow	280
1011	format(' mindif = ',fl0.5,' minb=',fl0.5,' minwk=',i4,/	arow	281
	1 'maxdif = ',f10.5,' maxb=',f10.5,' maxwk=',i4)	arow	282
		arow	283
	end	grow	284

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<pre>subroutine datain (prey,temp,o2,growth,wdgr,nweeks,body,igcd,nd, data 1     rep)     data 2     data 3     dimension prey(100,3),temp(100),o2(1),growth(5),rep(52)     data 4     dimension nweeks(5),wdgr(80,10),nd(5)     data 6 cget the number of weeks for which the simulation is to run     and the week within which simulation is to run     c and the week within which simulation is to commance.     data 9     read(11,)nweeks(2)     data 10     read(11,)nweeks(2)     data 12     call preyin(prey)     data 15     call temperature data         call tempin (temp,nweeks(4))     data 20     cget the growth data         call growth dat</pre>				
<pre>l rep) data 2 dimension prey(100,3),temp(100),o2(1),growth(5),rep(52) data 3 dimension nweeks(5),wdgr(80,10),nd(5) cget the number of weeks for which the simulation is to run c and the week within which simulation is to commence. data 9 read(11,)nweeks(1) read(11,)nweeks(2) data 11 cget the prey density data. data 13 call preyin(prey) data 15 cget the temperature data call tempin (temp,nweeks(4)) data 19 cget the growth data call growth,wdgr,nd,igcd) data 22 cget initial body size in calories read(11,)body data 32 data 33 data 32 data 33 data 43 data 14 data 15 data 15 data 16 data 17 data 22 data 32 data 34 data 35 data 35 data 35 cload array of breeding weeks</pre>	subroutine datain (prey,temp,o2,growth,wdgr,nweeks,body,igcd,nd,	data	1	
dimension prey(100,3),temp(100),o2(1),growth(5),rep(52)data 3dimension nweeks(5),wdgr(80,10),nd(5)data 4cget the number of weeks for which the simulation is to rundata 7cand the week within which simulation is to commence.data 9read(11,)nweeks(1)data 10read(11,)nweeks(2)data 12cget the prey density data.data 13call preyin(prey)data 15cget the temperature datadata 17call tempin (temp,nweeks(4))data 20cget the growth datadata 21c2(1) = 10.data 23cget the growth datadata 23cget the growth datadata 23cget the oxygen concentration in mg/1data 23o2(1) = 10.data 25cget initial body size in caloriesdata 26read(11,)bodydata 30data 23data 23cload array of breeding weeksdata 33cload array of breeding weeksdata 33	l rep)	data	2	
dimension prey(100,3),temp(100),o2(1),growth(5),rep(52) data 4 dimension nweeks(5),wdgr(80,10),nd(5)data 5 data 5 data 6cget the number of weeks for which the simulation is to run c and the week within which simulation is to commence.data 7 data 7cand the week within which simulation is to commence.data 8 data 9 data 10 read(11,)nweeks(2)data 11 data 11cget the prey density data.data 13 data 14 data 15 data 16data 19 data 16cget the temperature data call tempin (temp,nweeks(4))data 20 data 21 data 22 data 22data 22 data 22 data 22cget the growth data call grwin (growth,wdgr,nd,igcd)data 22 data 24data 25 data 31 data 32 data 31 data 32 data 31 data 32 data 32 data 32 cload array of breeding weeks%		data	3	
dimension nweeks(5),wdgr(80,10),nd(5)data 5cget the number of weeks for which the simulation is to rundata 7cand the week within which simulation is to commence.data 8read(11,)nweeks(1)data 10read(11,)nweeks(2)data 11cget the prey density data.data 12call preyin(prey)data 15call tempin (temp,nweeks(4))data 18call tempin (temp,nweeks(4))data 20cget the oxygen concentration in mg/1data 23co2(1) = 10.data 23call grwin (growth,wdgr,nd,igcd)data 26call grwin (growth,wdgr,nd,igcd)data 31call tenjin tial body size in caloriesdata 31call array of breeding weeksdata 32cload array of breeding weeksdata 32	dimension prey(100,3),temp(100),o2(1),growth(5),rep(52)	data	4	
<pre>cget the number of weeks for which the simulation is to run data 7 c and the week within which simulation is to commence. data 8 read(11,)nweeks(1) data 10 read(11,)nweeks(2) data 11 cget the prey density data. data 14 call preyin(prey) data 15 cget the temperature data data 17 call tempin (temp,nweeks(4)) data 19 cget the oxygen concentration in mg/l data 20 cget the growth data data 23 cget the growth data data 24 call grwin (growth,wdgr,nd,igcd) data 25 cget initial body size in calories data 29 read(11,)body data 31 cload array of breeding weeks</pre>	dimension nweeks(5),wdgr(80,10),nd(5)	data	5	
<pre>Cget the number's of weeks for which the simulation is to run data 7 c and the week within which simulation is to commence. data 8 read(11,)nweeks(1) data 10 read(11,)nweeks(2) data 11 cget the prey density data. data 13 call preyin(prey) data. data 15 cget the temperature data call tempin (temp,nweeks(4)) data 19 cget the oxygen concentration in mg/1 data 22 cget the growth data call growth,wdgr,nd,igcd) data 25 call grwin (growth,wdgr,nd,igcd) data 26 cget initial body size in calories data 30 read(11,)body data 32 cload array of breeding weeks</pre>		data	6	
c       and the week within which simulation is to commence.       data 8         read(11,)nweeks(1)       data 10         read(11,)nweeks(2)       data 11         cget the prey density data.       data 12         call preyin(prey)       data 16         cget the temperature data       data 17         call tempin (temp,nweeks(4))       data 20         cget the oxygen concentration in mg/1       data 23         o2(1) = 10.       data 25         call grwin (growth,wdgr,nd,igcd)       data 26         call grwin (growth,wdgr,nd,igcd)       data 30         cget initial body size in calories       data 31         cload array of breeding weeks       data 33	cget the number of weeks for which the simulation is to run	data	7	
$\begin{array}{c} \mbox{read}(11,)\mbox{nweeks}(1) & data & 9 \\ \mbox{read}(11,)\mbox{nweeks}(2) & data & 11 \\ \mbox{data} & 12 \\ \mbox{data} & 12 \\ \mbox{data} & 13 \\ \mbox{data} & 14 \\ \mbox{data} & 15 \\ \mbox{data} & 16 \\ \mbox{data} & 19 \\ \mbox{data} & 20 \\ \mbox{cget the oxygen concentration in mg/l} & \mbox{data} & 21 \\ \mbox{model} & \mbox{data} & 22 \\ \mbox{model} & \mbox{data} & 22 \\ \mbox{model} & \mbox{data} & 22 \\ \mbox{cl} & \mbox{data} & 22 \\ \mbox{cl} & \mbox{data} & 25 \\ \mbox{model} & \mbox{data} & 26 \\ \mbox{call grwin (growth,wdgr,nd,igcd)} & \mbox{data} & 28 \\ \mbox{model} & \mb$	c and the week within which simulation is to commence.	data	8	
$\begin{array}{c} read(11,)nweeks(1) \\ read(11,)nweeks(2) \\ data 10 \\ data 11 \\ data 12 \\ data 13 \\ data 14 \\ data 14 \\ data 15 \\ data 16 \\ data 16 \\ data 16 \\ data 16 \\ data 17 \\ data 18 \\ data 19 \\ data 20 \\ data 21 \\ data 22 \\ data 22 \\ data 22 \\ data 22 \\ data 23 \\ data 24 \\ data 25 \\ data 25 \\ data 25 \\ data 25 \\ data 26 \\ call grwin (growth,wdgr,nd,igcd) \\ data 28 \\ cget initial body size in calories \\ read(11,)body \\ cload array of breeding weeks \\ data 31 \\ data 32 \\ data 30 \\ data 31 \\ data 31 \\ data 30 \\ data 31 \\ data 30 \\ \end{array}$		data	9	
read(11,)nweeks(2)       data 11         cget the prey density data.       data 13         call preyin(prey)       data 16         cget the temperature data       data 17         call tempin (temp,nweeks(4))       data 20         cget the oxygen concentration in mg/1       data 21         o2(1) = 10.       data 23         call grwin (growth,wdgr,nd,igcd)       data 25         call grwin (growth,wdgr,nd,igcd)       data 27         cget initial body size in calories       data 30         read(11,)body       data 31         cload array of breeding weeks       data 34	read(11,)nweeks(1)	data	10	
cget the prey density data. call preyin(prey) cget the temperature data call tempin (temp, nweeks(4)) cget the oxygen concentration in mg/l o2(1) = 10. cget the growth data call grwin (growth, wdgr, nd, igcd) cget initial body size in calories read(11,)body cload array of breeding weeks data	read(11,)nweeks(2)	data	11	
call preyin(prey)       data 13         call preyin(prey)       data 15         cget the temperature data       data 17         call tempin (temp,nweeks(4))       data 19         cget the oxygen concentration in mg/l       data 21         o2(1) = 10.       data 25         call grwin (growth,wdgr,nd,igcd)       data 27         call grwin (growth,wdgr,nd,igcd)       data 28         cget initial body size in calories       data 29         read(11,)body       data 31         cload array of breeding weeks       data 33		data	12	
call preyin(prey)data14call preyin(prey)data15cget the temperature datadata16call tempin (temp, nweeks(4))data19cget the oxygen concentration in mg/ldata20o2(1) = 10.data21call grwin (growth datadata24call grwin (growth, wdgr, nd, igcd)data25cget initial body size in caloriesdata26read(11,) bodydata30datacload array of breeding weeksdata33	cget the prey density data.	data	13	
call preyin(prey)data 15cget the temperature datadata 17call tempin (temp,nweeks(4))data 18call tempin (temp,nweeks(4))data 19cget the oxygen concentration in mg/ldata 21o2(1) = 10.data 23cget the growth datadata 24call grwin (growth,wdgr,nd,igcd)data 25call grwin (growth,wdgr,nd,igcd)data 29cget initial body size in caloriesdata 30read(11,)bodydata 31cload array of breeding weeksdata 34		data	14	
cget the temperature datadata16call tempin (temp, nweeks(4))data19cget the oxygen concentration in mg/ldata21 $o2(1) = 10.$ data22cget the growth datadata23call grwin (growth,wdgr,nd,igcd)data25cget initial body size in caloriesdata28read(11,)bodydata31cload array of breeding weeksdata30	call preyin(prey)	data	15	
<pre>data 17 data 18 data 18 data 19 data 20 cget the oxygen concentration in mg/l</pre>		data	16	
call tempin (temp,nweeks(4))data 18cget the oxygen concentration in mg/ldata 21o2(1) = 10.data 22cget the growth datadata 24call grwin (growth,wdgr,nd,igcd)data 26cget initial body size in caloriesdata 29read(11,)bodydata 31cload array of breeding weeksX	cyei ine temperature data	data	17	
call tempin (temp, nweeks(4))data 19cget the oxygen concentration in mg/ldata 21o2(1) = 10.data 22cget the growth datadata 24call grwin (growth,wdgr,nd,igcd)data 26call grwin (growth,wdgr,nd,igcd)data 28cget initial body size in caloriesdata 29read(11,)bodydata 31cload array of breeding weeksdata 33	$\mathbf{coll}  \mathbf{torr} := (\mathbf{t} \mathbf{corr} + \mathbf{corr}$	data	18	
<pre>cget the oxygen concentration in mg/l o2(1) = 10. data 22 data 23 data 24 cget the growth data call grwin (growth,wdgr,nd,igcd) call grwin (growth,wdgr,nd,igcd) data 26 call grwin (growth,wdgr,nd,igcd) data 28 cget initial body size in calories data 29 cget initial body size in calories data 30 cload array of breeding weeks data 33 </pre>	Call Lempin (Lemp, nweeks(4))	data	19	
<pre>data 21 data 22 data 22 data 23 data 24 cget the growth data call grwin (growth,wdgr,nd,igcd) cget initial body size in calories read(11,)body cload array of breeding weeks</pre>	a set the everes second statistics ()	data	20	
o2(1) = 10.data 22 data 23 data 24cget the growth datadata 25 data 25 data 26call grwin (growth,wdgr,nd,igcd)data 27 data 27 data 28 data 29 data 30 data 31 data 31 data 32cload array of breeding weeksdata 33 W	cget the oxygen concentration in mg/l	data	21	
<pre>data 23 data 24 data 24 cget the growth data     call grwin (growth,wdgr,nd,igcd) cget initial body size in calories     read(11,)body cload array of breeding weeks</pre>	$a^{2}(1) = 10$	data	22	
cget the growth data call grwin (growth,wdgr,nd,igcd) cget initial body size in calories read(11,)body cload array of breeding weeks data 32 data 33 N data 34 data 32 data 34 data 34 V	02(1) = 10.	data	23	
<pre>call grwin (growth,wdgr,nd,igcd) cget initial body size in calories read(11,)body cload array of breeding weeks</pre> data 25 data 26 data 27 data 28 data 29 data 30 data 31 data 32 data 32 data 33 V	c get the growth data	data	24	
call grwin (growth,wdgr,nd,igcd) cget initial body size in calories read(11,)body cload array of breeding weeks data 32 data 33 N data 34 data 33 N M data 34 M M M M M M M M M M M M M	cget the growth data	data	25	
cload array of breeding weeks data 30 cload array of breeding weeks data 30 cload array of breeding weeks data 32 cload array of breeding weeks data 33 cload array of breeding weeks data 34 v	call anwin (anouth udan ad ired)	data	26	
cget initial body size in calories read(11,)body cload array of breeding weeks data 31 data 32 data 33 v data 33 v data 33 v data 30 data 30 v	carr grwin (growin,wugr,nu,igeu)	data	27	
cget initial body size in calories   data 29     read(11,)body   data 31     cload array of breeding weeks   data 33	C get initial body size is colonies	data	28	
read(11,)body cload array of breeding weeks data 32 data 33 data 33 data 34 V	cget initial body size in calories	data	29	
cload array of breeding weeks data 31 data 32 data 33 data 34	read(11) body	data	30	
cload array of breeding weeks data 32 data 33 N data 34 V	reau(II,)body	data	31	
data 33 N data 34 V	c load array of brooding works	data	32	
data 3/ V	cioad array of breeding weeks	data	33	N
4 40 40		data	34	34

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read(11,)(rep(i),i=1,52)	data	35
return	data	36
end	data	37

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subroutine grwin (growth,wdgr,nd,igcd)	grwi	1
	grwi	2
C ************************************	grwi	3
C * *	grwi	4
c * input growth data *	grwi	5
C * *	grwi	6
C ************************************	grwi	7
	grwi	8
ctransfered parameters:	grwi	9
c growth - an array within which the parameters	grwi	10
c of a growth equation are transferred to the	grwi	11
c calling routine	grwi	12
c wdgr - an array within which Weight Dependent Growth	grwi	13
c Rates are transfered to the calling routine.	grwi	14
c nd - an integer vector containing the number of	grwi	15
c valid rows of data in wdgr for each temperature	. grwi	16
c igcd - integer growth code specifying within which	grwi	17
c array the growth data are being transfered back	grwi	18
c to the calling routine.	grwi	19
c igcd = 1 => transfer in growth	grwi	20
c igcd = $2 \Rightarrow$ transfer in wdgr	grwi	21
	grwi	22
	grwi	23
	grwi	24
cthis subroutine enters growth parameters	grwi	25
c growth parameters may be entered in one of two forms:	grwi	26
c 1) parameters of an exponential growth equation of the form	grwi	27
Wt = a exp(r)	grwi	28
c The parameter r is entered into the array growth for each	grwi	29
c celcius temperature 0, 5, 10, 15 and 20	ąrwi	30
c and is the instantaneous weekly growth rate.	grwi	31
c The parameter a is the body size at the beginning	grwi	32
c of the week.	grwi	33
c It this method of computation is used, the computations	grwi	34

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c made in subroutine MGAIN1 should be checked by the	arwi	35
c user and altered if necessary.	arwi	36
c 2) parameters may be weight dependent growth rates per week.	arwi	37
c These are stored in array wdgr. The columns of this	arwi	38
c array are set off in pairs, each pair for one of the celciu	sarwi	39
c temperatures 0, 5, 10, 15, and 20. The first column in eac	harwi	40
c pair is the upper bound of the weight for which the	grwi	41
c parameter in the adjacent (right) column applies.	grwi	42
c If this method of entering the growth function is used	grwi	43
c the user must be sure that the algorithm in subroutine	grwi	44
c mgain2 is compatable with the series of temperatures .	grwi	45
c at which measurements were made.	grwi	46
C .	grwi	47
	grwi	48
dimension growth(5),wdgr(80,10),nd(5)	grwi	49
	grwi	50
	grwi	51
cread data type code	grwi	52
	grwi	53
read(11,)igcd	grwi	54
	grwi	55
if(igcd .eq. 1) then	grwi	56
	grwi	57
center the coefficients for the exponential growth equation.	grwi	58
c each element contains the exponent for the equation	grwi	59
c for a different temperature, from 0 C to	grwi	60
c ZUC by 5 C intervals.	grwi	61
$        -$	grwi	62
growtn(1) = -0.10	grwi	63
growtn(2) = 0.02	grwi	64
yrow(n(j)) = 0.14	grwi	65
yrowin(4) = 0.26	grwi	66
yrowin(z) = 0.22	grwi	67
	grwi	68

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	else if (igcd .eq. 2) then	grwi	69
<b>c</b>	this section enters weight and temperature dependent growth	grwi	70
C	ratee	grwi	/ 1
с с	loop through the temperatures 0 5 10 15 and 20 reading first	grwi	72
	the number of weight ranges for each temporature	grwi	77.
	then pairwise the upper weight boundary and its oc	grwi	74
0	weekly growth note	yrwi	75
C	weekiy growth late.	grwi	70
	do 20 itemp:→ 1 5	yrwi grwi	77
•	$\frac{1}{20} \frac{1}{100} = 1$	grwi	78
L	· i - itemp * 2	grwi	/9
		grwi	80
<u> </u>	read number of data points for this temperature	grwi	81
L	read number of data points for this temperature	grwi	82
	read(11) nd(itema)	grwi	85
		grwi	84
•	****	grwi	85
	* *	grwi	86
C C	* WARNING the following loop converse *	grwi	87
	$^{\circ}$ wavelet $G = C = C = C = C = C = C = C = C = C = $	grwi	88
	* however the error is transed (as) to $*$	grwi	89
	* opp3	grwi	90
	* errj. *	grwi	91
	· · · · · · · · · · · · · · · · · · ·	grwi	92
L	······································	grwi	93
	$d_{0} = 10$ ; $1 = \frac{1}{2} d(\frac{1}{2} + \frac{1}{2})$	grwi	94
	ao io i = 1, $aa(itemp)$	grwi	95
		grwi	96
	IT(nd(itemp) .eq. U) call errs	grwi	97
	read (11,) wdgr(1, $j-1$ ),wdgr(1, $j$ )	grwi	98
10		grwi	99
10	CONTINUE	grwi	100
20		grwi	101
2 U	CONTINUE	arwi	102

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	· ·		
	· · · ·		
		arwi 103	
С	write out the weight dependent growth rates	arwi 104	
		arwi 105	
С	write(12,1000)	arwi 106	
1000	format(" temperature and weight dependent growth rates - ",/,	grwi 107	
	1 10x,"0 C"11x,"5 C"11x,"10 C"11x,"15 C"11x,"20 C")	grwi 108	
		grwi 109	
	do 30 i = 1 , 80	grwi 110	
Ċ	write(12,1001)(wdgr(i,j),j=1,10)	grwi 111	
1001	format(2x,5(f8.0,1x,f5.3))	grwi 112	
30	continue	grwi 113	
		grwi 114	
	else	grwi 115	
		grwi 116	
	call errz(igcd)	grwi 117	
	ond if	grwi 118	
		grwi 119	
	return	grwi 120	
	iotain	grwi 121	
	end	$\begin{array}{c} \text{grw}_{1} \\ \text{z}_{2} \\ \text{z}_{3} \\ \text{z}_{4} \\ $	
		grwi 125	
			/

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•
	subroutine tempin (temp,jweek)	t emp	1
С	** * * * * * * * * * * * * * * * * * * *	temp	2
С	* *	t emp	3
С	* input temperature data *	t emp	4
С	* * *	t emp	5
С	**********************************	t emp	6
	·	t emp	7
	dimension temp(100)	t emp	8
	real mx, my	t emp	9
ctl	his subroutine is used to input temperature data.	t emp	10
С	the transfered parameters are:	t emp	11
С	temp – a vector array within which the temperatures are	t emp	12
С	returned to the calling routine	t emp	13
С	jweek – the number of weeks of valid temperature	t emp	14
С	data (returned)	t emp	15
cte	emperature data can be entered to the model either as measured	t emp	16
С	field data or by digitizing a graph of temperature versus time.	t emp	17
С		t emp	18
С	if the data to be used are digitized data, then the first record	t emp	19
С	of the temperature data must be a 1 while if the data are	t emp	20
С	obtained by measurement, then the first record of the	t emp	21
С	temperature data must be a 2. These codes are used to transfer	t emp	22
С	control to the appropriate sections of the temperature input	t emp	23
С	routine.	t emp	24
-		t emp	25
cf	ill the temperature array with 999.	t emp	26
		t emp	27
	do 10 i = 1 , 100	t emp	28
	temp(i) = 999.	t emp	29
10	continue	t emp	30
С	read the data type code	t emp	31
		t emp	32
	read (11,)icode	t emp	33
	•	t emp	34

if(icode .eq. 1) then

t emp 36 c...For this section of the program to be executed, the temperature 37 temp data are being entered as values digitized from a plot of С 38 temp temperature versus time. The following read will input the С 39 temp C the information required to transform digitized readings into temp 40 temperatures'. . C 41 temp С jweek - the number of weeks of temperature data 42 temp - the temperature, in degrees celcius, С t. temp 43 equivalent to the maximum value on the abscissa C t emp 44 on the plot from which digitized readings С t emp 45 С are being obtained. temp 46 ox & oy - the origin of the co-ordinate system from which temp С 47 the readings were taken. these values should С temp 48 С both be 0.0 49 t emp mx - the length of the abscissa in centimeters. С 50 temp this length is that which is equivalent to С 51 temp jweek number of weeks. note - type is real C temp 52 - the y displacement in centimeters of the right С Y temp 53 С end of the abscissa. temp 54 С this value should of course be 0.0 55 t emp it is included as a check to the accuracy of the temp Ċ 56 С digitizing process temp 57 - the x displacement in centimeters of the upper entemp С х 58 С of the ordinate. this value is analagous to 59 temp С y above, and should also be 0.0. 60 temp my - the length of the ordinate in cm which is С 61 temp С equivalent to t degrees centigrade. temp 62 С note - type is real temp 63 temp 64 read(11,)jweek,t,ox,oy,mx,y,x,my temp 65 temp 66 if(ox .ne. 0.0 .or. oy .ne. 0.0 .or. y .ne. 0.0 .or. x .ne. 0.0) temp 67 l call errorl temp 68

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temp

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t emp
                                                                                    69
         read the digitized x, y coordinates in cm and transform
С
                                                                              temp
                                                                                    70
            them to degrees celcius and store in vector temp
С
                                                                              temp
                                                                                    71
С
         if an end of file mark is encountered, an error has ocurred
                                                                                    72
                                                                              temp
С
            since there are fewer data than specified by JWEEK.
                                                                              temp
                                                                                    73
                                                                             temp
                                                                                    74
      do 20 i = 1', jweek
                                                                                    75
                                                                             temp
            read(11,,end=40,err=40)ir,x,y
                                                                                    76
                                                                             temp
            temp(ir) = t*y/my
                                                                             temp
                                                                                    77
20
      continue
                                                                             temp
                                                                                    78
С
                                                                                    79
                                                                             temp
                                                                                    80
                                                                             t emp
С
                                                                                    81
                                                                             temp
С
       write out the computed temperatures
                                                                             temp
                                                                                    82
С
                                                                                    83
                                                                             temp
                                                                                    84
                                                                             temp
       write(12,1000)(temp(i), i=1, jweek)
С
                                                                                    85
                                                                             temp
1000
      format(8f9.1)
                                                                             temp
                                                                                    86
                                                                             temp
                                                                                    87
      else if (icode .eq. 2) then
                                                                                    88
                                                                             temp
                                                                             temp
                                                                                    89
c...for this section of the program to be executed, the temperature
                                                                             temp
                                                                                    90
       data are in the form of measured field values that can be
С
                                                                             temp
                                                                                    91
       read directly. In the read below, j is the week of the
С
                                                                                    92
                                                                             temp
       data being read.
С
                                                                             temp
                                                                                    93
С
       First read the number of weeks of data being provided
                                                                                    94
                                                                             temp
С
       in the file, then read the data.
                                                                                    95
                                                                             temp
                                                                                   96
                                                                             temp
      read(11,,end=40,err=40) jweek
                                                                                    97
                                                                             temp
                                                                             temp
                                                                                   98
С
                                                                                   99
                                                                             temp
c...write header
                                                                             temp 100
С
                                                                             temp 101
С
       write(12,1001)
                                                                             temp 102
```

100	<pre>1 format(///lx,"week",lx,"temp"/)</pre>	temp 103 temp 104
•	do $3U$ i = 1, jweek	temp 105
_	read(11,)), temp(j)	temp 106
· C	write(12,1002), temp(j)	temp 107
100.	2 format(14,15.1)	temp 108
30	continue '	temp 109
C		temp 110
	else	temp 111
		temp 112
	call errl	temp 113
		temp 114
	end if	temp 115
		temp 116
	return	temp 117
		temp 118
40	continue	temp 119
	call err9('tempin',jweek,i)	temp 120
		temp 121
	end	temp 122

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د د				
subroutine	previn (prev) .	Drev	1	
с	F) (F),	prey	2	
cfunction:		prey	3	
c this su	broutine reads orev density and	prey	) //	
c mean pr	ev biomass data for various weeks of the	prey	5	
c simulat	ion.	prey	6	
ctransfered pa	rameters:	prey	7	
c prey -	a two dimensional array containing chironomid densiti	esprev	8	
c	in column 1. mean individual chironomid wet	Drev	9	
С	biomass in column 2 and Cladocera numbers	nrev	10	
с	per cubic centimeters in column 3.	préy	11	
С	The index of each row is the week of the	prey	12	,
С	simulation(iweek) for which the data are to be used.	prev	13	
cinput file fo	rmat:	prev	14	
c the input d	ata file for prey density has two record types.	brev	15	
c record type	1 : one field containing as an integer,	prev	16	
с	the number of weeks of prey density data.	prey	17	
С	format - freefield.	prey	18	
c record type	2 : four fields - freefield	prey	19	
С	field one - integer index of the week	prey	20	
с	associated with the remaining data on	prey	21	•
С	the record, in ascending order, with no	prey	22	
c ·	weeks missing between the first and	prey	23	
С	last week of data.	prey	24	
С	field two – Chironomidae prey density – real	prey	25	
С	field three – mean chironomid wet biomass – real	prey	26	
С	field four - Cladocera density per cubic cm.	prey	27	
С		prey	28	
C		prey	29	
dimension p	rey (100,3)	prey	30	
		prey	31	
cput 999. into	column 1 of prey.	prey	32	
J- 10 ( )	100	prey	33	2
ao 10 j = 1	, 100 ·	prey	34	4

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	nrev(i, 1) = 999	
10		prey
с С		. prey
0	read the number of weeks of data	prey
0		prey
C		, prey
-	read(11,) IW	prey
С		prey
C	read the data	prey
С		prey
	do $20^{\circ}j = 1$ , iw	prey
	read(11,,end=30,err=30)ir,(prey(ir,k),k=1,3)	prey
20	continue	prey
С		prey
-	return	prey
С		prey
30	continue	prey
	call err9('preyin',j,iw)	prey
	end	prev

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subroutine maxass (iweek, temp, growth, wdgr, body, mass, igcd, nd, meter, maxa
                                                                                      1
     1
          breed)
                                                                                      2
                                                                              maxa
С
                                                                                      3
                                                                              maxa
       dimension temp(100), growth(5), wdgr(80, 10), nd(5), dummy(2)
                                                                                      4
                                                                              maxa
С
                                                                                      5
                                                                              maxa
      real mass, mg, meter (35)
                                                                                      6
                                                                              maxa
С
                                                                                      7
                                                                              maxa
   .load metering array with temperature and body size at the
с.
                                                                              maxa
                                                                                      8
      beginning of the week.
С
                                                                                      9
                                                                              maxa
С
                                                                                     10
                                                                              maxa
      meter(2)=temp(iweek)
                                                                                     11
                                                                              maxa
      meter(5) = body
                                                                                     12
                                                                              maxa
С
                                                                              maxa
                                                                                     13
С
                                                                              maxa
                                                                                     14
c...call for maximal respiration requirements, which will occur when
                                                                              maxa
                                                                                     15
        satiated (the second element in the third transfered parameter
С
                                                                                     16
                                                                              maxa
         equals 1.0). This is accomplished by transfereing a
С
                                                                                     17
                                                                              maxa
         dummy array with 1.0 in element 2 to subroutine respir.
С
                                                                                     18
                                                                              maxa
С
                                                                                     19
                                                                              maxa
        dummy(2) = 1.0
                                                                              maxa
                                                                                     20
С
                                                                              maxa
                                                                                     21
С
                                                                                     22
                                                                              maxa
      call respir(iweek, temp, dummy, body, resp, meter, breed)
                                                                                     23
                                                                              maxa
С
                                                                                     24
                                                                              maxa
  .. compute maximum number of calories gained due to growth under
с.
                                                                                     25
                                                                              maxa
      ad libitum food conditions
С
                                                                              maxa
                                                                                     26
С
                                                                                     27
                                                                              maxa
      if (igcd .eq. 1) call mgainl(growth, body, iweek, temp(iweek),
                                                                                     28
                                                                              maxa
     1 meter,calgan)
                                                                                     29
                                                                              maxa
      if (igcd .eq. 2) call mgain2(wdgr,body,temp,iweek,nd,
                                                                                     30
                                                                              maxa
     1 meter, calgan)
                                                                                     31
                                                                              maxa
С
                                                                              maxa
                                                                                     32
С
                                                                                     33
                                                                              maxa
c...compute maximal assimilation rate as the maximal growth plus
                                                                                     34
                                                                              maxa
```

	,			
			•	a
		·		
	2 A	c maximal respiration	maxa	35
		C	maxa	36
		mass = resp + calgan	maxa	37
		C	maxa	38
		C	maxa	39
		C	maxa	40
		cload metering array	maxa	41
		C (a)	maxa	42
		meter(9) = mass	maxa	43
		return	maxa	44
-			maxa	45
		end	maxa	46
		·		
				· ·

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```
subroutine mgainl(growth, body, iweek, temp, meter, calgan)
                                                                                mqai
                                                                                        1
С
                                                                                mgai
                                                                                         2
      dimension growth(5)
                                                                                         3
                                                                                 mqai
С
                                                                                         4
                                                                                mqai
       real mg, meter(35)
                                                                                         5
                                                                                mgai
С
                                                                                mga i
                                                                                         6
c...compute maximal weight gain under ad libitum food conditions.
                                                                                        7
                                                                                mqai
       the equation is obtained by re-arranging those of Dr. F. J. Wrona mgai
С
                                                                                        8
      1982. Ph. D. thesis - p 129. These equations are applicable to
С
                                                                                        9
                                                                                mqai
      only small individuals
С
                                                                                mgai
                                                                                       10
С
                                                                                       11
                                                                                mqai
С
                                                                                       12
                                                                                mgai
c...check that temperature data are valid.
                                                                                mqai
                                                                                       13
С
                                                                                       14
                                                                                mqai
       if (temp .eq. 999.) call err5(iweek,"mgainl")
                                                                                       15
                                                                                mqai
С
                                                                                mgai
                                                                                       16
        this equation requires body size in mg wet weight
С
                                                                                mgai
                                                                                       17
С
                                                                                mqai
                                                                                       18
С
        the conversion to calories from wet weight of 0.6577 cal/mg wet
                                                                                mgai
                                                                                       19
       weight was determined by D. J. Baird.
С
                                                                                mqai
                                                                                       20
      mg = body / 0.6577
                                                                                mgai
                                                                                       21
С
                                                                                       22
                                                                                mqai
c...compute the exponential growth rate (interpolate between
                                                                                       23
                                                                                mgai
         temperatures)
С
                                                                                mgai
                                                                                       24
С
                                                                                       25
                                                                                mgai
      if (temp .le. 5.0) then
                                                                                       26
                                                                                mgai
          r = (\operatorname{qrowth}(2) - \operatorname{qrowth}(1)) \times \operatorname{temp}/5.0 + \operatorname{qrowth}(1)
                                                                                       27
                                                                                mgai
          if (r.lt. 0.0) then
                                                                                       28
                                                                                mgai
             calgan = 0.0
                                                                                mgai
                                                                                       29
             return
                                                                                       30
                                                                                mqai
          end if
                                                                                mqai
                                                                                       31
      else if (temp .gt. 5 .and. temp .le. 10.0) then
                                                                                       32
                                                                                mgai
          r = (growth(3) - growth(2))*(temp-5.0)/5.0 + growth(2)
                                                                                       33
                                                                                mqai
      else if (temp .gt. 10 .and. temp .le. 15.0) then
                                                                                       34
                                                                                mgai
```

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```
r = (growth(4) - growth(3))*(temp-10.0)/5.0 + growth(3)
                                                                                  35
                                                                           mgai
      else if(temp .gt. 15 .and. temp .le. 20) then
                                                                           mqai
                                                                                  36
         r = (growth(5) - growth(4))*(temp-15.0)/5.0 + growth(4)
                                                                           mqai
                                                                                  37
                                                                                  38
                                                                           mgai
      else
         call err7(iweek,temp)
                                                                           mgai
                                                                                  39
      end if
                                                                           mgai
                                                                                  40
                                                                           mgai
                                                                                  41
С
c...load metering array with maximal growth rate.
                                                                           mgai
                                                                                  42
                                                                           màai
                                                                                  43
С
      meter(15)=r
                                                                           mgai
                                                                                  44
      wtgain = mg * exp(r)
                                                                           mgai
                                                                                  45
                                                                           mgai
                                                                                  46
С
c...weight gain is in mg wet weight.
                                                                           mgai
                                                                                  47
                                                                           mgai
                                                                                  48
С
      calgan = wtgain * 0.6577
                                                                           mgai
                                                                                  49
                                                                           mgai
                                                                                  50
С
      return
                                                                           mgai
                                                                                  51
                                                                                  52
                                                                           mgai
C.
                                                                           mg a i
                                                                                  53
      end
```

```
subroutine mgain2(wdgr,body,temp,iweek,nd,meter,calgan)
                                                                                  1
                                                                           mqai
c...this subroutine computes maximal caloric requirements using weight
                                                                                  2
                                                                          mgai
      and temperature dependent growth rates.
                                                                                  3
C
                                                                           mgai
С
                                                                           mqai
                                                                                  4
      integer cl.cu,rl,ru
                                                                                  5
                                                                           maai
      real mg.meter(35)
                                                                                  6
                                                                           mqai
      dimension wdgr(80,10), nd(5), temp(100)
                                                                                  7
                                                                           mqai
С
                                                                                  8
                                                                           mqai
c...the array wdgr contains columns of weight dependent growth rates
                                                                           mgai
                                                                                  9
       and their associated weights. Each pair of columns is for
С
                                                                           mgai
                                                                                 10
       a different temperature. The indices of the columns associated
C
                                                                          mqai
                                                                                 11
       with the temperatures at which measurements were made above and
                                                                                 12
С
                                                                          mqai
       below the present working temperature (temp) must be computed
С
                                                                                 13
                                                                           mgai
       and the temperature dependent growth rate determined by
C
                                                                                 14
                                                                           mqai
       interpolation.
С
                                                                          mgai
                                                                                 15
С
       Growth rates are in the even numbered columns.
                                                                          mqai
                                                                                 16
С
                                                                                 17
                                                                          mqai
                ******
С
                                                                                 18
                                                                          mgai
            NOTE: this subroutine assumes that measurements in
С
                                                                           mqai
                                                                                 19
                  wdgr are at 0 C, 5 C, 10 C, 15 C and 20 C.
С
          ×
                                                                  ¥
                                                                                 20
                                                                          mgai
С
                  If the user has growth rates measured at
                                                                                 21
                                                                  ¥
                                                                           maai
                  different temperatures the following algorithm*
С
                                                                                 22
                                                                           mgai
С
                  must be appropriately modified.
                                                                                 23
                                                                           mqai
С
                      **********************
                                                                          mqai
                                                                                 24
С
                                                                                 25
                                                                          mgai
  ...variables used in this subroutine:
C.
                                                                                 26
                                                                          mgai
С
                                                                          mgai
                                                                                 27
         cl - (column lower) - column of wdgr associated with the lower mgai
С
                                                                                 28
                                part of the temperature range spanned
С
                                                                          mgai
                                                                                 29
                                by the growth data which cover the
С
                                                                          mqai
                                                                                 30
                                present temperature being used
С
                                                                                 31
                                                                          mqai
С
                                                                          mgai
                                                                                 32
С
         cu - (column upper) - column of wdgr associated with the upper mgai
                                                                                 33
С
                                t emp
                                                                                 34
                                                                          mgai
```

2 5 C

C	mgai	35
c rl – (row lower) – row of wdgr associated the the next	mgai	36
c higher weight for which growth rate is	mgai	37
c available at the lower of the two	mgai	38
c boundary temperatures	mgai	39
C	mgai	40
c ru - (row upper) - row of wdgr associated the the next	mgai	41
c higher weight for which growth rate is	mgai	42
c availale at the higher of the two	mgai	43
c boundary temperatures	mgai	44
C	mgai	45
C	mgai	46
C	mg a i	47
ccheck for valid temperature data	mg a i	48
	mg a i	49
if (temp(iweek) .eq. 999.) call err5(iweek,"mgain2")	mg a i	50
C	mgai	51
	mg a i	52
c write(12,1000)body, temp(iweek)	mg a i	53
1000 format(" subroutine mgain2 - paramters transfered in - body =",	mgai	54
$1 \ f10.4," \ temperature = ", f10.4)$	mg a i	55
c compute index of lower column	mg a i	56
	mg a i	57
cl = temp(lweek) / 5.0	mg a i	58
c1 = c1 + 2 + 2	mg a i	59
C .	mg a i	60
c compute index of upper column	mg a i	61
	mg a i	62
c the following assumes that the highest temperature	mg a i	63
c associated with the data in wdgr is 20 C. If higher	mg a i	64
c temperatures have been used to fill wdgr, then	mgai	65
c appropriate changes must be made to the following	mgai	66
c it statements.	mg a i	67
c the algorithm for finding the values of cu and cl will	mg a i	68

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also fail if temperature exceeds 20 C, unless appropriately
С
                                                                            mqai
                                                                                   69
           modified.
С
                                                                            mqai
                                                                                   70
С
                                                                            maai
                                                                                   71
      if(temp(iweek) .eq. 20.) cu = 10
                                                                                   72
                                                                            mgai
С
                                                                            mgai
                                                                                   73
      if(temp(iweek) .1t. 20) cu = c1 + 2
                                                                                   74
                                                                            mgai
                                                                                   75
С
                                                                            mqai
         compute the temperatures associated with these indices
С
                                                                            mqai
                                                                                   76
С
                                                                                   77
                                                                            mgai
      tl = (float(cl) / 2.0 - 1.0) * 5.0
                                                                            mgai
                                                                                   78
      tu = tl + 5.0
                                                                            mqai
                                                                                   79
С
                                                                            mqai
                                                                                   80
         convert body from calories to mg
С
                                                                            mqai
                                                                                   81
С
                                                                                   82
                                                                            mqai
     mg = body / 0.6577
                                                                            mqai
                                                                                   83
С
                                                                            mgai
                                                                                   84
c...check whether the size of the individual has exceeded the
                                                                                   85
                                                                            mgai
         maximum for which data are available.
С
                                                                            mgai
                                                                                   86
С
                                                                            mgai
                                                                                   87
      if(mg .gt. wdgr(nd(cl/2),cl-1) .or. mg .gt. wdgr(nd(cu/2),cu-1))
                                                                            mqai
                                                                                   88
         call err4(mg,temp(iweek))
     1
                                                                                   89
                                                                            mqai
С
                                                                            mgai
                                                                                   90
         search the array wdgr for the rows associated with this
С
                                                                            mgai
                                                                                   91
            weight at both temperatures tl & tu
С
                                                                                   92
                                                                            mqai
С
                                                                                   93
                                                                            mqai
С
                                                                                  94
                                                                            mgai
      do 10 i = 1,50
                                                                            mgai
                                                                                   95
           if (wdgr(i,cl-1) .gt. mg) then
                                                                            mgai
                                                                                  96
              rl = i
                                                                            mqai
                                                                                  97
              qo to 15
                                                                            mqai
                                                                                  98
           end if
                                                                                  99
                                                                            mqai
10
      continue
                                                                            mgai 100
15
      continue
                                                                            mqai 101
C
                                                                            mgai 102
```

```
mgai 103
      do 20 i = 1, 50
           if (wdgr(i,cu-1) .gt. mg) then
                                                                            mgai 104
                                                                            mgai 105
               \mathbf{r}\mathbf{u} = \mathbf{i}
               ao to 25
                                                                            mgai 106
           end if
                                                                            mgai 107
20
      continue
                                                                            mgai 108
25
                                                                            mgai 109
      continue
С
                                                                            mqai 110
         interpolate between these growth rates to find the rate to
                                                                            mqai 111
С
            be used.
                                                                            mgai 112
С
                                                                            mgai 113
С
      scale = (temp(iweek) - tl) / (tu - tl)
                                                                            mqai 114
      rate = wdgr(rl,cl) + (wdgr(ru,cu) - wdgr(rl,cl)) * scale
                                                                            mgai 115
                                                                            mgai 116
С
c...load metering array
                                                                            mgai 117
                                                                            mgai 118
С
      meter(12) = rate
                                                                            mgai 119
                                                                            mgai 120
С
С
          compute weight gain
                                                                            mgai 121
                                                                            mgai 122
С
      wtgain = mg * rate - mg
                                                                            mqai 123
                                                                            mgai 124
С
          convert to calories
                                                                            mgai 125
С
                                                                            mgai 126
С
      calgan = wtgain * 0.6577
                                                                            mgai 127
                                          ۷
                                                                            mgai 128
С
c...write out computed theoretical maximal caloric gain
                                                                            mgai 129
                                                                            mgai 130
С
       write(12,1003)calgan
                                                                            mgai 131
С
     format("maximal theoretical growth in calories = ",f10.5)
                                                                            mgai 132
1003
                                                                            mgai 133
      return
                                                                            mgai 134
      end
```

```
subroutine actass(temp, iweek, prey, body, nstate, mass, aass, meter)
                                                                                     1
                                                                             acta
                                                                                     2
С
                                                                             acta
                                                                                     3
С
                                                                             acta
С
                                                                             acta
                                                                                     4
c...function:
                                                                                     5
                                                                             acta
        this subroutine computes ACTual ASSimilation rate
                                                                                     6
С
                                                                             acta
        as a function of temperature, nutritional state, and
                                                                                     7
С
                                                                             acta
        prey density.
                                                                                     8
С
                                                                             acta
                                                                             acta
                                                                                     9
С
c...transfered parameters:
                                                                                    10
                                                                             acta
        temp - the temperature - input
                                                                                   11
С
                                                                             acta
        iweek - the week of the simulation - input
                                                                             acta
                                                                                   12
С
        prey - a two dimensional array of prey density and
С
                                                                             acta
                                                                                   13
С
                 mean prey wet biomass. - input
                                                                             acta
                                                                                   14
        body - the body size of the predator in calories - input
                                                                             acta
                                                                                   15
С
        nstate - a one dimensional array with two elements containing
                                                                             acta
                                                                                   16
С
                  the nutritional state in the previously simulated
                                                                                   17
С
                                                                             acta
                  week and the week presently being simulated.
                                                                                   18
                                                                             acta
С
С
                  - output.
                                                                             acta
                                                                                   19
        mass - maximal assimilation rate. - input
С
                                                                             acta
                                                                                   20
        aass - actual assimiltion rate. - output
                                                                                   21
С
                                                                             acta
                                                                                   22
С
                                                                             acta
С
                                                                                    23
                                                                             acta
      dimension temp(100), prey(100,3)
                                                                             acta
                                                                                    24
      real nstate(2)
                                                                             acta
                                                                                    25
      real meter(35), ingest, mass
                                                                                   26
                                                                             acta
                                                                             acta
                                                                                   27
С
c...load metering array
                                                                             acta
                                                                                   28
                                                                                    29
С
                                                                             acta
      meter(3) = temp(iweek)
                                                                             acta
                                                                                   30
      meter(6)=body
                                                                                   31
                                                                             acta
                                                                             acta
                                                                                   32
С
c...check for valid prey densities (see subroutine datain
                                                                                   33
                                                                             acta
         for explanation of 999. code)
                                                                                   34
С
                                                                             acta
```

		acta	35	
	if (prey(iweek,1) .eq. 999.) call err6 (iweek,"actass")	acta	36	
	C	acta	37	
	C shark for wall d towns a twins.	acta	38	
	ccheck for valid temperatures	acta	39	
	C if (topp(iwank) or 000 ) and or 5(iwank Wantara W)	acta	40	
	11 (temp(iweek) .eq. 999.) call err5(iweek, "actass")	acta	41	
		acta	42	
	u n compute estuel essimilation note of Chinesemides	acta	43	
	ccompute actual assimilation rate of Chirohomidae	acta	44	
	c note 1: since reading is assumed to stop at 0.8 degrees	acta	45	
	c cercius, aass is assigned zero for temperatures	acta	46	
	note 2: the variable body transfored in it in calculation	acta	47	
	C note 2: the variable budy transfered in is in calories,	acta	40 40	
	c so must be converted to my in the consumption	acta	49	
	c opte 3: numbers consumed are converted into calcries by	acta	20 51	
•	c multiplying the number of prev consumed by their	acta	52	
	c mean wet higmass in mg and by calories per mg	acta	52	
	wet weight, the conversion factor of 0.801564	acta	54	
	C calories per ma wet biomass of chironomids is	acta	55	
	c compliments of Mr. T. Gates	acta	56	
	c note 4: the regression equation below estimates number of	acta	57	
	C prev taken per day, so consumption must be multiplied	acta	58	
	c by 7.0 to make per week estimates.	acta	59	
	C	acta	60	
	if (temp(iweek), le, 8,8) then	acta	61	
	aass = 0.0	acta	62	
•	else	acta	63	
	С	acta	64	
	cChironomidae prey capture	acta	65	
	C	acta	66	
	C****************	acta	67	
	С	acta	68	

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```
NOTE: the following equation was found to produce unacceptable
С
                                                                         acta
                                                                               69
         results since its first derivitive was negative within
С
                                                                         acta
                                                                               70
         some of the region of the independent variable. It
С
                                                                         acta
                                                                               71
         sould be stricity positive. The data
С
                                                                              72
                                                                         acta
         for each temperature were refit, and it was found that body
С
                                                                         acta 73
         size had no significant effect, so was eliminated.
С
                                                                         acta
                                                                               74
         Only prey density was used as an independent variable,
С
                                                                         acta
                                                                              75
         and, slope is estimated for temperatures other than
С
                                                                              76
                                                                         acta
         those at which experiments were conducted by interpolation.
С
                                                                               77
                                                                         acta
С
                                                                         acta
                                                                               78
С
       consum = -1.3854 + 1.16518*prey(iweek,1)
                                                                               79
                                                                         acta
                + 0.06706 * temp(iweek)
      1
С
                                                                               80
                                                                         acta
      2
                + 0.005738 * body / 0.6577
С
                                                                               81
                                                                         acta
С
      3
                -0.03729 * \text{prey(iweek,1)} * \text{temp(iweek)}
                                                                               82
                                                                         acta
                - 0.0088245 * prey(iweek,1) * body / 0.6577
С
      4
                                                                         acta
                                                                               83
      5
                - 0.0003042 * temp(iweek) * body / 0.6577
С
                                                                         acta
                                                                               84
                + 0.0006526 * prey(iweek,1) * body / 0.6577 * temp(iweekacta
      6
С
                                                                               85
С
                                                                         acta
                                                                               86
C***
          acta
                                                                               87
С
                                                                               8.8
                                                                         acta
С
                                                                               89
                                                                         acta
    at 12.5 C consum = 0.244 + 0.402 prey density
С
                                                                         acta
                                                                               90
    at 15.0 C consum =-0.161 + 1.03 prey density
С
                                                                               91
                                                                         acta
    at 20.0 C consum =-0.100 + 1.81 prey density
С
                                                                         acta
                                                                               92
С
                                                                         acta
                                                                               93
         if(temp(iweek).le. 15)then
                                                                         acta
                                                                               94
            a=0.2438-(0.2438-(-0.1606))*(temp(iweek)-12.5)/2.5
                                                                         acta
                                                                               95
            b=0.4016-(0.4016-(1.0258))*(temp(iweek)-12.5)/2.5
                                                                         acta
                                                                               96
         else
                                                                         acta
                                                                               97
            a=-0.1606-(-0.1606-(-0.1002))*(temp(iweek)-15.0)/5.0
                                                                         acta
                                                                               98
            b=1.0258-(1.0258-(1.8133))*(temp(iweek)-15.0)/5.0
                                                                               99
                                                                         acta
         end if
                                                                         acta 100
С
                                                                         acta 101
         consum=a + b * prey(iweek,1)
                                                                         acta 102
```

acta 103 acta 104 this is chironomid prey capture per day. convert to calories acta 105 per week acta 106 acta 107 acta 108 acta 109 using simple linear regression of all capture rates acta 110 on temperature suggested feeding ceases as approximately acta 111 8.8 C. However, the above equation for consumption acta 112 can produce negative capture rates at temperatures acta 113 slightly above 8.8 C, depending upon prey density. acta 114 Therefore, if consum is negative, simply set it acta 115 to zero. acta 116 acta 117 if (consum .gt. 0.0) then acta 118 ingest = consum \* prey(iweek,2) \* 0.801564 \* 7.0 acta 119 else acta 120 consum = 0.0acta 121 ingest = 0.0acta 122 end if acta 123 acta 124 if prey density is large, and mean prey size is large; acta 125 the above feeding equation may produce estimates acta 126 of ingestion which are greater than the maximal acta 127 rate determined in subroutine maxass. acta 128 On the assumption that when these conditions prevail acta 129 the leech would stop feeding when it bacame satiated, acta 130 set the ingestion rate to the maximal ingestion acta 131 rate. Since food is 'super-abundant' and acta 132 the animal is satiated simply return to acta 133 the calling routine, and don't bother acta 134 going through the Cladocera section of this acta 135 routine. acta 136

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```
acta 137
С
        if(ingest *0.79 .gt. mass)then
                                                                      acta 138
           aass = mass
                                                                      acta 139
                                                                      acta 140
С
                                                                      acta 141
С
c...compute nutritional state as the proportion actual
                                                                      acta 142
       assimilation to maximal assimilation
                                                                      acta 143
С
С
                                                                      acta 144
           nstate(1) = nstate(2)
                                                                      acta 145
           nstate(2) = 1.0
                                                                      acta 146
                                                                      acta 147
С
                                                                      acta 148
С
c...load metering array
                                                                      acta 149
                                                                      acta 150
С
           meter(10)=aass
                                                                      acta 151
           meter(11)=prey(iweek,1)
                                                                      acta 152
           meter(12)=prey(iweek,2)
                                                                      acta 153
           meter(13)=prey(iweek,3)
                                                                      acta 154
           return
                                                                      acta 155
        end if
                                                                      acta 156
                                                                      acta 157
С
c...Cladocera as prey
                                                                      acta 158
                                                                      acta 159
С
        if(prey(iweek,3) .ne. 0.0) then
                                                                      acta 160
                                                                      acta 161
С
                                                                      acta 162
С
                                                  C*****
       acta 164
С
          the following equation was generated from the Cladocera
С
   NOTE:
                                                                      acta 165
          consumption data using all interaction terms. It doesn't
                                                                      acta 166
С
          work.
                                                                      acta 167
С
                                                                      acta 168
C.
      consum = -1.31212 + 0.32205*prey(iweek,3) + 0.09191*temp(iweek)
С
                                                                      acta 169
            +0.000895*body/0.6577 + 0.007459*prey(iweek,3)*body/0.6577 acta 170
С
  1
```

(

```
acta 171
С
С
                                                                           acta 172
c**
                                                                           acta 173
С
                                                                           acta 174
                                                                           acta 175
С
    at 15 C consum = 0.247 + 0.52898 * prey(iweek)
С
                                                                           acta 176
    at 20 C consum = 0.3651 + 0.62821 * prey(iweek)
С
                                                                           acta 177
                                                                           acta 178
С
            a = 0.2470-(0.2470 - 0.3651)*(temp(iweek)-15.)/5.0
                                                                           acta 179
            b = 0.52898 - (0.52898 - 0.62821)*(temp(iweek) - 15.)/5.0
                                                                           acta 180
С
                                                                           acta 181
         if(prey(iweek,3) .le. 4.) then
                                                                           acta 182
            consum = a + b * prey(iweek,3)
                                                                           acta 183
         else
                                                                           acta 184
            consum = a + b * 4.0
                                                                           acta 185
         end if
                                                                           acta 186
                                                                           acta 187
С
                                                                           acta 188
С
                                                                           acta 189
        this is consumption per hour, so convert it to
С
                                                                           acta 190
С
          consumption per week (*168) and multiply by the caloric
                                                                           acta 191
          value of a single Cladocera (*0.173 cal).
C
                                                                           acta 192
С
                                                                           acta 193
            ingest = ingest + consum * 168. * 0.173
                                                                           acta 194
С
                                                                           acta 195
         end if
                                                                           acta 196
С
                                                                           acta 197
        now convert total calories ingested to calories assimilated
С
                                                                           acta 198
          using an assimilation efficiency of 0.79.
С
                                                                           acta 199
С
                                                                           acta 200
         aass = ingest * 0.79
                                                                           acta 201
С
                                                                           acta 202
      end if `
                                                                           acta 203
С
                                                                           acta 204
```

```
As explained above, the these equations may result
С
                                                                           acta 205
            in ingestion rates above satiation (mass). If this
С
                                                                          acta 206
            occurs, set actual assimilation to the satiation
С
                                                                           acta 207
            value.
С
                                                                           acta 208
С
                                                                           acta 209
      if(aass .gt. mass) aass = mass
                                                                           acta 210
С
                                                                           acta 211
С
                                                                           acta 212
c...compute nutritional state as the proportion actual
                                                                           acta 213
        assimilation to maximal assimilation
С
                                                                           acta 214
С
                                                                          acta 215
      nstate(1) = nstate(2)
                                                                          acta 216
      nstate(2) = aass/mass
                                                                           acta 217
C
                                                                           acta 218
      write(10,1000)iweek,aass
С
                                                                           acta 219
cl000 format(" subroutine actass - week =",i3," actual assimilation=", acta 220
      1 f6.3)
С
                                                                           acta 221
С
                                                                          acta 222
c...load metering array
                                                                           acta 223
С
                                                                           acta 224
      meter(10)=aass
                                                                           acta 225
     meter(ll)=prey(iweek,l)
                                                                          acta 226
     meter(12)=prey(iweek,2)
                                                                          acta 227
     meter(13)=prey(iweek,3)
                                                                          acta 228
      return
                                                                          acta 229
      end
                                                                           acta 230
```

```
subroutine respir(iweek, temp, nstate, body, resp, meter, breed)
                                                                            resp ,
                                                                                    1
С
                                                                                    2
                                                                            resp
      dimension temp(100)
                                                                                    3
                                                                            resp
      real meter(35)
                                                                                    4
                                                                            resp
      real nstate(2),mq,n
                                                                                    5
                                                                            resp
С
                                                                                    6
                                                                            resp
С
                                                                                    7
                                                                            resp
c...load metering array
                                                                                    8
                                                                            resp
С
                                                                                    9
                                                                            resp
      meter(4)=temp(iweek)
                                                                                   10
                                                                            resp
      meter(7)=body
                                                                                   11
                                                                            resp
С
                                                                            resp
                                                                                   12
c...This subroutine computes the oxygen uptake rate for an
                                                                                   13
                                                                            resp
      individual of the size, nutritional state and at the
С
                                                                                   14
                                                                            resp
      temperature specified in the transfered parameters
С
                                                                            resp
                                                                                   15
      and then converts this oxygen uptake rate to its calorific
С
                                                                            resp
                                                                                   16
С
      equivalent.
                                                                                   17
                                                                            resp
      the returned parameter resp will be the caloric uptake equivalent resp
С
                                                                                   18
          to the computed oxygen uptake.
С
                                                                                   19
                                                                            resp
                                                                            resp
С
                                                                                   20
c...internally used variables are:
                                                                                   21
                                                                            resp
       a = activity => the proportion of time for which an individual
C
                                                                                   22
                                                                            resp
                        is active.
С
                                                                                   23
                                                                            resp
                        This variable has not been measured, so has
С
                                                                            resp
                                                                                   24
                        been arbitrarily assigned a value of 0.4 for
С
                                                                            resp
                                                                                   25
                        baseline runs. Its impact upon growth rate
С
                                                                                   26
                                                                            resp
С
                        will be assess using sensitivity analysis.
                                                                                   27
                                                                            resp
       u = oxygen uptake in microlitres per hour
С
                                                                                   28
                                                                            resp
С
                                                                            resp
                                                                                   29
С
                                                                            resp
                                                                                   30
c...check for valid temperature data.
                                                                                  31
                                                                            resp
С
                                                                                  32
                                                                            resp
      if (temp(iweek) .eq. 999.) call err5(iweek, "respir")
                                                                                   33
                                                                            resp
C
                                                                            resp
                                                                                  34
```

 $\sim$ σ

С		resp	35
cinitiali:	ze the internal variables	resp	36
С	·	resp	37
a = 0.4	b and the second se	resp	38
С		resp	39
ccompute (	otal oxygen uptake per hour (mo2).	resp	40
C		resp	41
c oxygen up	take = 5.2059 - 0.58043(temperature) + 1.24533(ration)	resp	42
C	- 0.01054131(wet weight) - 7.0275(activity level)	resp	43
С	+ 0.7229(temperature)(ration)	resp	44
С	+ 0.0037529(temperature)(wet weight)	resp	45
С,	+ 1.0938(temperature)(activity level)	resp	46
С	+ 0.016436(wet weight)(activity level)	resp	47
С		resp	48
c  u = 5	20593 - 0.58043*temp(iweek) + 1.2433*nstate(2)	resp	49
c 1 - 0.	0105431*body/0.6577 - 7.0275*a	resp	50
c 2 + 0.	7229*temp(iweek)*nstate(2)	resp	51
c 3 + 0	0037529*temp(iweek)*body/0.6577	resp	52
c : 4 + 1	0938*temp(iweek)*a	resp	53
c 5 + 0.	016436*body/0.6577*a	resp	54
C		resp	55
cthe above	equation has first derivitives = 0.0 within the	resp	56
c regior	define by ecological constraints, so was discarded	resp	57
c and th	e following equation derived from the data using	resp	58
c RWDA b	rogram PAR	resp	59
c the fo	llowing equation computes qo2, so uptake must be	resp	60
c multip	lied by body size to obtain mo2.	resp	61
C		resp	62
u = -0.	U385 + U.UU43*temp(iweek) + 0.0184*nstate(2)	resp	63
1 +	U.342/*exp(-U.014/*body/0.6577) + 0.0669*a	resp	64
		resp	65
u=u*DOC	y/U.62//	resp	66
		resp	67
cnow conve	ri inis oxygen uptake rate to its caloric equivalent	resp	68

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```
С
                                                                             resp
                                                                                    69
      cal = u * 0.004731
                                                                             resp
                                                                                    70
С
                                                                             resp
                                                                                    71
c...this is the caloric expenditure in respiration per hour.
                                                                                    72
                                                                             resp
      compute the caloric uptake per week (24 * 7 hours per week)
С
                                                                                    73
                                                                             resp
С
                                                                                    74
                                                                             resp
      resp = cal * 168
                                                                                    75
                                                                             resp
С
                                                                                    76
                                                                             resp
c...increase this value if reproduction is occurring
                                                                                    77
                                                                             resp
С
                                                                                    78
                                                                             resp
      if (breed .gt. 0.5) resp = resp * 2.0
                                                                                    79
                                                                             resp
С
                                                                                    80
                                                                             resp
С
                                                                                    81
                                                                             resp
c...write out report for this pass throught the subroutine
                                                                                    82
                                                                             resp
С
                                                                                    83
                                                                             resp
С
                                                                                    84
                                                                             resp
       write(12,1000)temp(iweek),mg,n,a,u
С
                                                                                    85
                                                                             resp
      format(/" subroutine respir: temp =",f5.1," wet weight=",
1000
                                                                                    86
                                                                             resp
     1 f7.1," nutritional state=",f5.2," activity=",f5.2,
                                                                                    87
                                                                             resp
     2 / 20x," oxygen uptake=",f5.1," microlitres per hour")
                                                                                    88
                                                                             resp
С
                                                                                    89
                                                                             resp
С
                                                                                    90
                                                                             resp
c...load metering array
                                                                             resp
                                                                                    91
С
                                                                                    92
                                                                             resp
      meter(14) = resp
                                                                                    93
                                                                             resp
      return
                                                                                    94
                                                                             resp
      end
                                                                             resp
                                                                                    95
```

```
subroutine breed(iweek, cohort, ic, lc, aass, meter, temp, repeff)
                                                                             bree
                                                                                    1
      dimension cohort(50,6), temp(100)
                                                                                    2
                                                                             bree
      real meter(35)
                                                                                    3
                                                                             bree
С
                                                                             bree
                                                                                    4
С
            if the cohort has not yet bred then
                                                                             bree
                                                                                    5
           save the week in which reproduction starts and
С
                                                                             bree
                                                                                    6
            the body size.
С
                                                                             bree
                                                                                    7
С
                                                                             bree
                                                                                    8
      if(cohort(ic,5).lt.0.5)then
                                                                             bree
                                                                                    9
            cohort(ic, 4) = cohort(ic, 3)
                                                                             bree
                                                                                   10
            cohort(ic.5) = iweek
                                                                             bree
                                                                                   11
      end if
                                                                                   12
                                                                             bree
С
                                                                             bree
                                                                                   13
           compute reproductive effort and embryo production
С
                                                                             bree
                                                                                   14
С
                                                                             bree
                                                                                   15
С
                                                                            bree
                                                                                   16
          The ingestion rate used in the regression equation for
C
                                                                            bree
                                                                                   17
С
              caloric reproductive output is calories ingested per day
                                                                            bree
                                                                                   18
             per calorie of the body. The transferred parameter AASS
С
                                                                            bree
                                                                                   19
              is ASSIMILATION PER WEEK, so must be converted to INGESTIONbree
С
                                                                                   20
             PER DAY, then taken as a ratio to body size.
С
                                                                            bree
                                                                                   21
С
                                                                            bree
                                                                                   22
       consumption = AASS / assimilation efficiency/ 7 days / body size bree
С
                                                                                   23
С
                                                                            bree
                                                                                   24
      consum = aass / 0.79 / 7.0 / cohort(ic,3)
                                                                            bree
                                                                                   25
С
                                                                            bree
                                                                                   26
        the variable for body size used in the regression is in caloric bree
С
                                                                                   27
             so does no have to be converted.
С
                                                                            bree
                                                                                   28
С
                                                                            bree
                                                                                   29
c...compute cocoon calories
                                                                           bree
                                                                                   30
С
                                                                            bree
                                                                                   31
      ccal = -25.875 + 0.16123*cohort(ic, 3) + 1.4672*temp(iweek)
                                                                            bree
                                                                                   32
С
                                                                                   33
                                                                            bree
c...report an error if ccal is negative
                                                                                  34
                                                                            bree
```

```
С
                                                                             bree
                                                                                    35
       if(ccal .lt. 0.0) then
                                                                             bree
                                                                                    36
         write(12,1000)iweek,ccal
                                                                             bree
                                                                                    37
          ccal=0.0
                                                                             bree
                                                                                    38
          return
                                                                             bree
                                                                                    39
      end if
                                                                             bree
                                                                                    40
С
                                                                             bree
                                                                                    41
С
                                                                             bree
                                                                                   42
  .. compute cocoon calories per week. the value calculated above
c.
                                                                             bree
                                                                                    43
        is for the entire reproductive period. assume that cocoon
C
                                                                             bree
                                                                                    44
        deposition lasts 4 weeks.
С
                                                                             bree
                                                                                    45
С
                                                                             bree
                                                                                    46
      repeff = ccal / 4'.0
                                                                             bree
                                                                                    47
      meter(16) = repeff
                                                                             bree
                                                                                    48
С
                                                                             bree
                                                                                    49
c...compute number of embryos
                                                                             bree
                                                                                    50
С
                                                                             bree
                                                                                    51
      embro = -27.4975 + 0.07315*cohort(ic, 3) + 1.6998*temp(iweek)
                                                                             bree
                                                                                    52
С
                                                                             bree
                                                                                    53
c...compute embryos per week. the value calculated above
                                                                             bree
                                                                                    54
        is for the entire reproductive period. assume that cocoon
С
                                                                             bree
                                                                                    55
С
        deposition lasts 4 weeks.
                                                                             bree
                                                                                    56
С
                                                                             bree
                                                                                    57
      if (embro .qt. 0) then
                                                                             bree
                                                                                   58
         embro = embro / 4.0
                                                                                   59
                                                                             bree
      else
                                                                             bree
                                                                                   60
         embro = 0.0
                                                                             bree
                                                                                   61
      end if
                                                                             bree
                                                                                   62
С
                                                                             bree
                                                                                   63
      meter(17) = embro
                                                                             bree
                                                                                   64
С
                                                                             bree
                                                                                   65
      cohort(lc+1,2) = cohort(lc+1,2) + embro*cohort(ic,2)
                                                                             bree
                                                                                   66
      cohort(lc+1,1) = cohort(lc+1,1) + 1.0
                                                                             bree
                                                                                   67
С
                                                                             bree
                                                                                   68
```

	cohort(1c+1,3) = 15.3	bree	6
		bree	71
1000		bree	7.
1000	format(15,18.4)	bree	7:
1001	format(50x,4f13.6)	bree	7
	end	bree	7
4			

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subroutine sensit(iweek, body, mindif, maxdif) 1 sens С 2 sens c...this subroutine does comparisons for sensitivity analysis. It is sens 3 broken into two section, depending upon what type of analysis С sens 4 is desired. the first section searches for the minimum С 5 sens and maximum absolute difference over an entire simulation run, C 6 sens while the second section determines a percentage difference С 7 sens on one particular week. С 8 sens С 9 sens c...to run the subroutine, a file (13) is required which contains 10 sens on each record a week number followed by the base line С 11 sens body size in that week. С 12 sens C 13 sens c...to run the two different sections, simply comment out sens 14 c that which is not needed and compile. 15 sens С sens 16 c...read in bench mark data and compare 'body' in this run with 17 sens С the benchmark result. sens 18 С sens 19 Ċ 20 sens read the benchmark week and bench mark body size С 21 sens С 22 sens read(13,)week,bmsize С 23 sens С sens 24 compute proportional variation of the present run relative С 25 sens to bench mark (check first for correct week) С 26 sens С 27 sens the first section searches for maximum difference С 28 sens (positive = maxdiff, negative = mindiff) over the С 29 sens entire run. С 30 sens С 31 sens if(iweek .eq. int(week)) then С 32 sens diff = body - bmsizeС 33 sens С pvar = diff/bmsizesens 34

cc	write(14,1009)week,bmsize,body,pvar	sens	35
cc1009	9 format(3f6.0, f10.5)	sens	36
С	if(diff .lt. mindif)then	sens	37
С	mindif = diff	sens	38
с	minwk = iweek	sens	39
С	minb = bmsize	sens	40
С	end if ,	sens	41
С	if(diff .gt. maxdif)then	sens	42
С	maxdif = diff	sens	43
С	maxwk = iweek	sens	44
С	maxb = bmsize	sens	45
с <sub>.</sub> .	end if	sens	46
С	else	sens	47
С	call errl0	sens	48
C	end if	sens	49
C		sens	50
С	this section determines the difference at week 47 of the	sens	51
С	run	sens	52
С	if(iweek .eq. 47) then	sens	53
С	diff = body - bmsize	sens	54
С	<pre>pct = 100.0 * diff / bmsize</pre>	sens	55
C	write(14,1010)pct	sens	56
c1010	format(f5.1)	sens	57
С	end if	sens	58
	return	sens	59
	end	sens	60

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	subroutine surviv(iweek,temp,cohort,ic,far,p)	surv	1	
	cthis subroutine computes survival probability to next week,	surv	2	
	c using one of two functions, depending upon whether	surv	3	
	c the animal is reproducing (or has recently reproduced).	surv	4	
	C	surv	5	
	ctransfered parameters are:	surv	6	
	c iweek - the number of the current week being simulated	surv	7	
	c temp – a vector of weekly temperatures	surv	8	
	c cohort - an array of information about the cohorts in the	surv	9	
	c population. (see grow.fortran)	surv	10	
	c ic - an integer identifying which row in array cohort	surv	11	
	c is to be used.	surv	12	
	c far - feeding rate after reproduction (set to zero if	surv	13	
	c reproduction has not ceased).	surv	14	
	c p - probability of surviving to next week.	surv	15	
	C	surv	16	
	dimension temp(100),hot(10),cohort(50,6)	surv	17	
	C	surv	18	
•	cdefine underlying post-reproductive hazard function	SUrv	19	
	C	surv	20	
	data (hot(i),i=1,10)/1.1970e-5, 1.970e-5, 1.1970e-5, 3.0144e-5,	surv	21	
	1 8.0997e-5, 1.5063e-4, 3.5832e-4, 4.1416e-4, 2.1826e-4,	surv	22	
	2 1.5815e-4/	surv	23	
	С	surv	24	
	ctest whether the animal is reproducing or has reproduced within	surv	25	
	c the last 10 weeks (the period for which values of the Ho(t)	surv	26	
	c function exist).	surv	27	
	C	surv	28	
	if(iweek.ge.cohort(ic,5).and.iweek.le.cohort(ic,5)+9)then	surv	29	
	C	surv	30	
	c use the proportional hazards model	surv	31	
	C	surv	32	
	c compute proportional energy loss during reproduction	surv	33	N
		SHEV	3/1	6

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		<pre>pelrep = (cohort(ic,4)-cohort(ic,3))/cohort(ic,4)</pre>	surv	35
		compute the rick factor portion of the propertional becords	SULV	26
	0	model	surv	27
			SULV	28
	L	$p_i = p_i = p_i = (0.33((*+i)) + (i)) = (0.39(*+i)) = (0$	surv	29 60
	1	113k = exp(0.5566 + temp(1week) = 0.0056 + conort(10.4) + 1.457 + perrep	surv	40
		-20.16/*iar)	SULV	41
	C C	compute which were after the second state of the t	surv	42
	C .	compute which week after the commencement of reproduction	surv	43
	C	the animal is presently at	surv	44
	С		surv	45
		1 = 1  week - cohort(10,5) + 1	surv	46
	С		surv	47
	С	multiply the risk factor by the underlying hazard	surv	48
	С		surv	49
		risk = hot(i) * risk	surv	50
	С	· · · · · · · · · · · · · · · · · · ·	surv	51
	С	compute probability of survival	surv	52
	С		surv	53
,		p = 1.0 - risk	surv	54
	С		surv	55
	С	this is the probability of survival for one of the 7	surv	56
	С	days of the week, so calculate probability of surviving	surv	57
	C	the entire week	surv	58
	С		surv	59
		p = p * * 7.0	surv	60
	С		surv	61
		return	surv.	62
	С		SHEV	63
	el	Se	SULV	64
	C		SULLY	65
	cthe	animal is not reproducing, so compute probability of survival	surv	66
	с	based upon age. this section should be revised when data	surv	67
	с	come available, to permit prediction of survival as a	SULV	68
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С	function of habitat and physiological variables.	surv	69
С		surv	70
С	the regression equation predicts survival as a function	SULV	71
С	of age in months, so convert age from weeks to months	surv	72
С		surv	73
	t = cohort(ic, 1) / 4.0	surv	74
С		surv	75
С	compute probability of surviving to the present age	surv	76
С		surv	77
	sp = exp(-(24.509*t)**0.187)	surv	78
С		surv	79
С	compute probability of surviving to one week older	surv	80
С		surv	81
	· ·	surv	82
	sn = exp(-(24.509*(t+0.25))**0.187)	surv	83
C		surv	84
С	compute probability of surviving the week	surv	85
С		surv	86
	p = sn / sp	surv	87
		surv	88
	return	surv	89
	end if	surv	90
	end .	surv	91

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·	subroutine errl	errl	1	•
	write(12,1000)	errl	2	
1000	) format("error in temperature input data")	errl	3	
	do 10 i = 11 , 14	errl	4	
	close(i)	errl	5	
10	continue	errl	6	
•	stop '	errl	7	
	end	errl	8	
	subroutine err2 (icode)	err2	ĩ	
	write(12,1000)icode	err2	2	
1000	format(" error in growth data type code. code = ",i5)	err2	3	
	do 10 i = 11 , 14	err2	`4	
	close(i)	err2	5	
10	continue	err2	6	
	stop	err2	7	
	end	err2	8	
• • •	subroutine err3	err3	1	
	write(12,1000)	err3	2	
1000	format(" the assumption of a zero trip do loop in subroutine",/,	err3	3	
	l " grwin is not supported - fatal error.",/,	err3	4	
	2 " exit via subroutine err3")	err3	5	
		err3	6	
	do 10 i = 11 , 14	err3	7	
	close(i)	err3	8	
10	continue	err3	9	
		err3	10	
	stop	err3	11	
	end	err3	12	
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	subroutine err4(body,temp)	err4	1
	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
		erŗ4	6
	do 10 i = 11, 14	err4	7
	close (i)	err4	8
10	continue	err4	9
		err4	10
	stop	err4	11
	, end	err4	12
	subroutine err5(iweek, subr)	err5	1
	character*6 subr	err5	2
1000	write(12,1000)subr,iweek	err5	3
1000	format(" error exit from ", a6," via err5 - temperature at week",	err5	4
		err5	5
	do $10 \ i = 11$ , 14	err5	6
10	Close(1)	err5	7
10	continue	err5	8
	stop	errs	.9
	end aubrouting ang((iuggle autr)	err5	10
	subroutine erro(iweek, subr)	err6	Ţ
	$w_{\text{nito}}(12, 1000)$ subring $w_{\text{not}}$	err6	2
1000	format(" opport ovit from " of " via opp( and	err6	5
1000	i i/)	err6	4
	$d_{0} = 11 = 14$	erro	2
	close(i)	erro	67
10	continue	orro	/
10	ston		O Q
	end	erré	10
		0110	τU

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	subroutine err7(i,t)	err7	1
•	write(12,1000),t	err7	2
	1000 format(' error exit from mgain1, temperature at week', i4,	err7	3
	1 + exceeds 20 C. temperature = ', f4.0)	err7	4
	do 10 i = 11 , 14	err7	5
	close(i)	err7	6
•	10 continue	err7	7
	stop	err7	8
	end	err7	9
	subroutine err8(ccal,c,b,t,w)	err8	1
	writel2,1000)ccal,c,b,t	err8	2
	1000 format(' reproductive effort negative in subroutine EFFORT',/,	err8	3
	1 'cocoon calories = ',fl0.2,/,	err8	4
-	2 'consumption = ',fl0.4,/,	err8	5
	3 'body = ',fl0.5,/,	err8	6
	4 / temperature = ',f5.1	err8	7
	5 'week = ', i5)	err8	8
	do 10 i = 11 , 14	err8	9
	close(i)	err8	10
	10 continue	err8	11
	stop	err8	12
	end	err8	13
	subroutine err9(name, j, i)	err9	1
	character*6 name	err9	2
	write(12,1000)name, j, i	err9	3
	1000 format(' read error in subroutine ',a,' for week ',i5,	err9	4
	1 'out of ',15,' weeks.')	err9	5
٠	do 10 = 11, 14	err9	6
	Close(1)	err9	7
		err9	8
	stop	err9	9
	ena	err9	10

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	subroutine errl0	errlO	1		
1000	write(12,1000)	errlO	2		-
	iormat(' bench mark week and simulation week do not match in'	err10	3	•	
T	1 ' program grow.fortran.')	err10	4		
	00 10 1 = 11, 14	errlO	5		
10	Close(1)	err10	6 <sup>.</sup>		
10	continue	errlO	7		
	stop	errlO	8		
	end	err10	9		
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## 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 <u>Nephelopsis</u> obscura is presented. Columns of dots represent data which have been excluded 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.

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 $18 \Rightarrow$  this is the number of weeks that the simulation is to run  $32 \Rightarrow$  this is the week where simulation is to start  $55 \Rightarrow$  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 1.3 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 3) chironomid individual biomass 32 0.065 4.013 2.8 06/10/80 4) Cladocera density (numbers per ml) 33 5.203 0.148 2.3 06/17/80 5) date (not read) 80 0.897 4.299 1.3 05/13/81 81 0.046 4.336 2.3 05/20/81

2 => code for measured, not digitized, temperature data 18 => 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) 47 10.8 04/10/84 48 9.9 12/10/84 49 0.1 25/10/84 2 => the code for weight dependent growth rates 1 => the number of weight dependent growth rates for 0 C 10000 1.0 => the maximum weight and growth rate  $1 \Rightarrow$  the number of weight dependent growth rates for 5 C 10000 1.020201 => the maximum weight and growth rate 1 => the number of weight dependent growth rates for 10 C 10000 1.150274 => the maximum weight and growth rate

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 $41 \Rightarrow$  the number of weight dependent growth rates for 15 C 0.400 2.500 The data fields are: 0.800 1) - bottom of weight range 2.026 1.600 1.802 2) - proportional growth rate . . • . • • 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 1.026 2.0 => the initial body size from which the simulation is to start. 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 This array contains one entry for each week to be simulated. A 1 in the array represents a week in which reproduction is to occur while a O codes for no breeding.

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