DEVELOPMENT OF A COMPUTER SIMULATION MODEL OF A CULTURED BLUE MUSSEL (*Mytilus edulis*) POPULATION

Final Report

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SUMMARY

This document describes the formulation, construction, performance, and evaluation of a computer model designed to simulate energy flow in the blue mussel, *Mytilus edulis*. The model was developed in the belief that it would be useful in addressing a number of problems and questions associated with the commercial cultivation of this organism.

Construction of the model involved synthesizing current ideas and hypothesis on the major biophysical factors thought to control the growth, spawning and mortality of *Mytilus*, and expressing this information mathematically in a form that could be solved over time with the aid of a computer. Inputs to the model include water temperature and particulate inorganic and organic matter concentration. The model outputs shell and meat growth rates, condition indices, biofeces production, spawn production and spawning times. Validation of the model against several independent data sets suggests the model to have significant predictive capability and that it can provide a useful framework for investigating problems such as site selection, summer mortality, carrying capacity and the environmental impact of mussel culture.

The report is divided into three main sections. The first documents the formulation of the model in terms of the theoretical background upon which it is based and the data base available for its construction. The second section describes the model's behavior in general, presents the results of a sensitivity analysis, and compares output of the model with data obtained from field studies. The final section discusses the model in terms of its potential and limitations in addressing some of the problems associated with shellfish culture.

RESUME

CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

Culture of the blue mussel, *Mytilus edulis*, is one of the fastest growing food-related industries in Canada. It is viewed as potentially one of the most valuable of coastal industries and has been selected as a development of major national importance by the Science Council of Canada (Anon., 1985). Successful mussel culture operations have now been established in Prince Edward Island, Nova Scotia, New Brunswick and, to a limited extent in Newfoundland, and there is great interest among many people in its further development.

Despite the optimistic outlook for the future of this industry, a number of important problems have developed that are essentially biological in nature and for which solutions are not readily available. One example is the widespread occurrence of post-spawning mortality in recent years. There is also concern that in some areas the carrying capacity of some sites may be near the limit and further expansion may have detrimental effects on mussels as well as the environment in which they are grown.

In response to such concerns a number of environmental monitoring programs have been established. The overall objective of these programs is to obtain baseline information that will allow a better understanding of the interaction of the physical, chemical, and biological variables that control the settlement, growth, spawning, and survival of cultured mussels, and to assess the potential environmental impact of mussel culture.

Analysis of the data obtained in these programs is, however, somewhat limited without a model that synthesizes this information in a meaningful way. As an aid to this task, we have developed, based on information presently available in the scientific literature, a dynamic simulation model that describes the energetics, growth, spawning, and survival of cultured mussels over the two to three year period required for individual organisms to reach marketable size, and have validated this model using data obtained from existing monitoring programs. More specifically, the objective was to develop a model that could be used to:

(1) explore the relationships between environmental variables and growth, spawning, and survival of mussels;

(2) evaluate the relevance of variables presently being monitored with respect to their predictive value;

(3) determine criteria for site selection;

(4) identify areas of uncertainty with respect to our understanding of mussel ecology and physiology under culture conditions and to make recommendations for future research needs and;

(5) make estimates of carrying capacity of particular sites.

There have been a number of attempts to develop a simulation model of *Mytilus*. The first published model (Radford *et al.*, 1981) attempted to describe the behavior of a natural intertidal population. Its usefulness for testing hypotheses and understanding the behavior of *Mytilus* is somewhat limited because many processes are simulated by regression and data-fitting techniques that provide little insight into the underlying mechanisms that control the various rate processes. Another model, by Verhagen (1983), also simulates a natural population and is essentially an extension of the model by Radford *et al.* (1981) and suffers from the same limitations. A third model, developed by Incze *et al.* (1980), attempts to predict the carrying capacity of a suspended mussel population in an aquaculture situation. Although useful for obtaining crude estimates of carrying capacity, it provides little insight into the dynamics of *Mytilus*. A forth model, recently developed by Bayne *et al.* (1988) to test the optimization strategy of *Mytilus*, takes a more realistic approach to describing the behavior of *Mytilus*. Although general in nature, the more important physiological processes are simulated and the model allows for optimization of certain processes. This approach, and the formulations presented, were a valuable aid in developing the present model. A fifth model, developed by Klepper and Scholten (1988), was prepared as part of a larger ecosystem model of the Oosterschelde Estuary located in southwest Netherlands. This model is perhaps the best presently available in the literature and, although it deals with a benthic population of *Mytilus* and is less detailed, has a number of similarities to the model presented here. More recently a dynamic simulation model of *Mytilus* was presented by Ross and Nesbet (1990). This model is also less detailed than the one presented here, but shares many of the same underlying concepts.

2. MODEL DEVELOPMENT

2.1. Introduction

Development of a simulation model involves four basic tasks; (1) formulation of the theoretical background of the model; (2) identification of driving variables, state variables, and input-output relationships; (3) expressing the input and output relationships in mathematical terms; and (4) determining the values of parameters in the mathematical formulations.

Depending on the kind of questions being addressed, a number of model formulations are possible for any one particular system. A "general" model, although sometimes lacking in resolution and limited in terms of the precision of its answers, is often the first choice in model development. The main advantage of a general model is that the data requirements for its construction are minimal and its behavior is relatively easy to interpret and understand. A more "reductionist" model on the other hand allows more questions to be addressed, gives more precise answers, and potentially allows greater insight into the behavior of a system, but requires considerably more information for its construction and greater effort to understand its behavior. Our approach to this problem was to begin with a relatively simple and general model and to then add complexity as our understanding of the system increased. This resulted in the formulation of a suite of models varying in complexity. Our ultimate goal was to identify a single model that would answer as many questions as possible and yet still be realistic in the sense that the model be limited to concepts and parameters that have an ecological or physiological interpretation and that can be measured in either the laboratory or field.

The following sections document the theoretical basis upon which the model was formulated and the subsequent development of the model in terms of the processes and parameters that were eventually incorporated into the model.

2.2. Theoretical Background

The theoretical framework of the model is the energy budget equation commonly used to express the growth rate of an organism. For an animal this is most commonly expressed mathematically as follows:

$dB/dt = I - (R + E + Rp)$ where,

dB/dT = Change in Biomass with time (i.e., growth)
B = Biomass
t = Time
I = Ingestion
R = Respiration
E = Egestion
Rp = Reproduction

The units of the model are grams dry weight. The time scale of the model is days and simulations were run for time periods of up to three years.

The model is written in FORTRAN and was run using the ACSL (Advanced Continuous Simulation Language) software package (Mitchell and Gauthier, 1987).

2.3. Model Overview

The factors controlling growth and reproduction in *Mytilus* depend to a large extent on its physiological state at a particular time. The various components of an individual mussel increase or decrease at different times and at different rates relative to one another. This is especially true of shell growth in relation to meat growth as well as of the production and release of gametes. In addition, the "triggers" associated with some processes, such as the build-up of glycogen reserves, gonads, and gametes, and the release of gametes, appear to depend on the relative biomass of these components at any one particular time. In order to model these processes it thus becomes necessary to divide an individual mussel into a number of components, each of which represents a separate state variable. These include (1) somatic tissue, which is further divided into protein, carbohydrate, and lipid; (2) shell material, both organic and inorganic; (3) carbohydrate reserves; (4) gonadal tissue; and (5) gametes.

The sole input to the mussel is particulate matter, which is formulated as time series data and input as a driving variable. Total particulate matter is divided into unassimilable material (particulate inorganic matter) and potentially assimilable material (particulate organic matter). Losses include respiration, egestion (true feces), pseudofeces (particulate material filtered but not ingested) and spawn.

The rate at which particulate matter is ingested depends on ventilation rate (volume of water filtered per unit of time), particulate matter concentration, and the maximum potential ingestion rate. Ventilation rate is a function of body size and temperature. The maximum ingestion rate is a function of body size. Pseudofeces production occurs only when the minimum ventilation rate and particulate matter concentration are so high that the amount of material filtered exceeds what can be ingested.

Ingested materials are assimilated in proportion to the ratio of inorganic to organic matter in the filtered particulate matter. The assimilated matter is then apportioned into either somatic tissue, glycogen reserves, or shell organic matter according to a number of criteria, the most important of which is the relationship between the amount of particulate matter assimilated and the maximum growth rate. If the amount of assimilated matter is greater than the maximum growth rate of somatic tissue, the difference between the two is allocated to glycogen reserves. The proportion of assimilated matter

allocated to shell organic matter is simply a fixed percentage of the total amount of assimilation allocated to somatic growth. Shell growth, however, is also a function of the rate at which inorganic material is incorporated into the shell which depends on both temperature and the rate of input of organic matter into the shell.

The conversion of glycogen reserves into gonads is assumed to occur as a discrete input. The trigger for this conversion is the ratio of total carbohydrate to total protein content, which increases as glycogen reserves accumulate. Accumulated gonadal material immediately begins to be converted into gametes at a rate proportional to temperature and, after most of the gonads are converted into gametes, spawning occurs.

The loss due to respiration is the sum of standard respiration and active respiration. Standard respiration is simply a function of body size and active respiration is a function of both the amount of particulate material ingested and the amount that is subsequently assimilated. Respiration losses are assumed to come first from glycogen reserves and, if this component is depleted, then from somatic tissue. There are no respiration losses from either gonads or gametes.

Figure 1 presents a diagram indicating the model components and the inputs and outputs associated with each component.

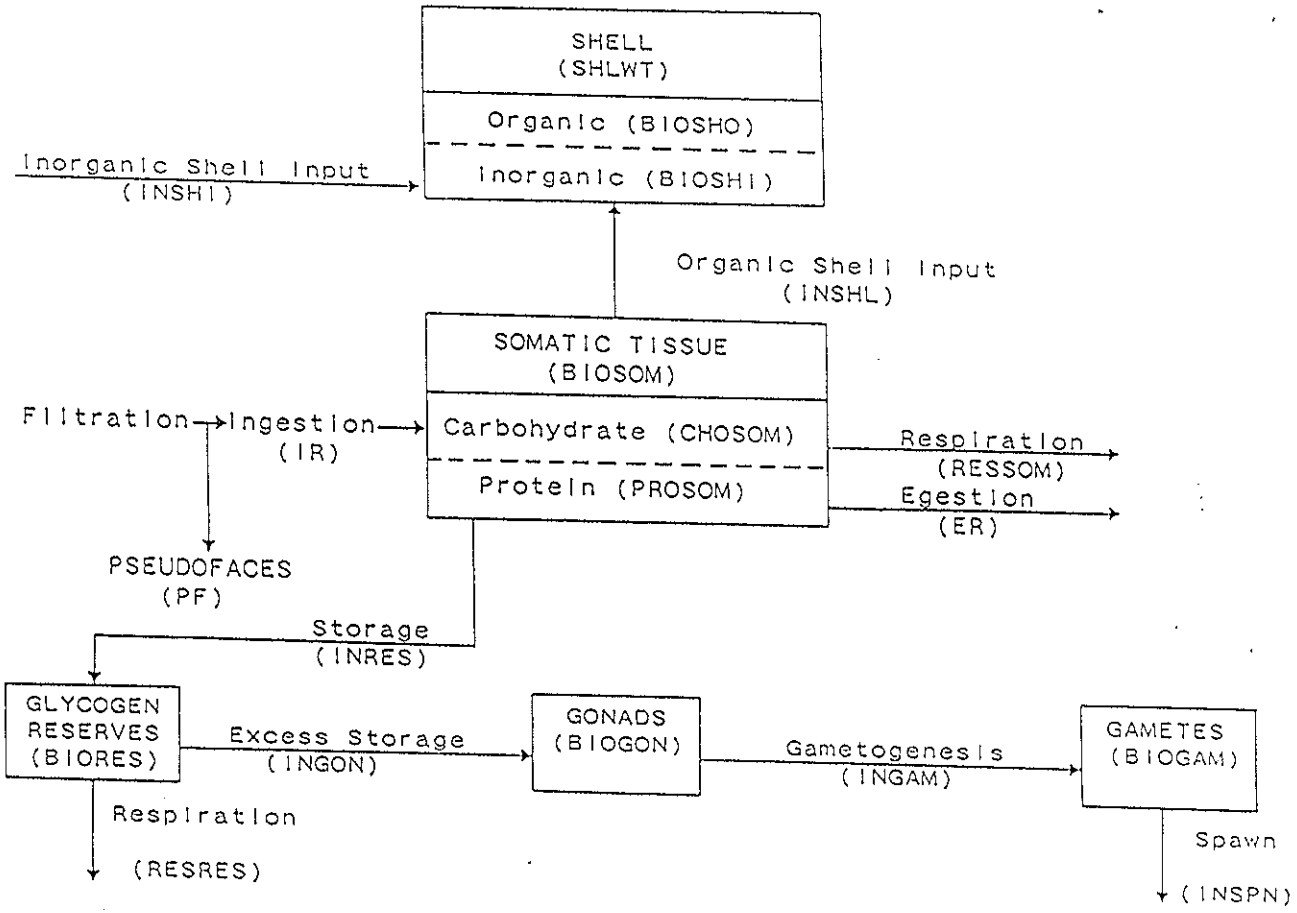


Figure 1. Block diagram of mussel components showing inputs and outputs

3. MODEL DOCUMENTATION

3.1. Introduction

The following section documents the structure of the model. The mathematical formulations defining the driving variables and the inputs and losses of each state variable are presented and the theory upon which each formulation is based is described.

3.2. Variable Name Conventions

The following conventions are used in assigning variable names:

a. The biomass of each state variable begins with the prefix BIO and the remaining suffix indicates the particular state variable:

BIOSOM	-	Biomass of Somatic Tissue
BIORES	-	Biomass of Glycogen Reserves
BIOGON	-	Biomass of Gonadal Tissue
BIOGAM	-	Biomass of Gametes
BIOSHO	-	Biomass of Shell Organic Matter
BIOTOT	-	Total Organic Biomass (sum of all of the above)
BIOSHI	-	Biomass of Shell Inorganic Matter

b. The initial conditions of each state variable (i.e., the value of a state variable at the beginning of a model run) is prefixed by IC:

ICSOM	-	Initial Conditions of Somatic Tissue
ICRES	-	Initial Conditions of Glycogen Reserves
ICGON	-	Initial Conditions of Gonadal Tissue
ICGAM	-	Initial Conditions of Gametes
ICSHO	-	Initial Conditions of Shell Organic Matter
ICSHI	-	Initial Conditions of Shell Inorganic Matter

c. The summation of inputs and outputs of each state variable, which represents the rate of change, or growth rate, of biomass is denoted by the prefix GRO:

GRORES	-	Growth of Glycogen Reserves
GROGON	-	Growth of Gonadal Tissue
GROGAM	-	Growth of Gametes
GROSHO	-	Growth of Shell Organic Matter
GROSHI	-	Growth of Shell Inorganic Matter

d. The summation of inputs to each state variable is denoted by the prefix IN:

INSOM	-	Input to Somatic Biomass
INRES	-	Input to Glycogen Reserves
INGON	-	Input to Gonadal Tissue
INGAM	-	Input to Gametes
INSPN	-	Input to Spawn
INSHO	-	Input to Shell Organic Matter

INSHI - Input to Shell Inorganic Matter

e. The summation of losses from each state variable is denoted by the prefix LOS:

LOSSOM	-	Loss from Somatic Tissue
LOSRES	-	Loss from Glycogen Reserves
LOSGON	-	Loss from Gonadal Tissue
LOSGAM	-	Loss from Gametes

f. Weight specific functions are denoted by the prefix SP:

SPMGR	-	Specific Maximum Growth Rate
SPMIR	-	Specific Maximum Ingestion Rate
SPVR	-	Specific Ventilation Rate
SPRESP	-	Specific Respiration Rate

g. Model parameters are denoted by lower case letters, weight specific parameters by the prefix sp, their constants by the suffix c, and their exponents by the suffix x:

spmgrc	-	weight constant for specific maximum growth rate
spmgrx	-	weight exponent for specific maximum growth rate
spmirc	-	weight constant for specific maximum ingestion rate
spmirx	-	weight exponent for specific maximum ingestion rate
spvrc	-	weight constant for specific ventilation rate
spvrx	-	weight exponent for specific ventilation rate
spresc	-	weight constant for specific respiration rate
spresx	-	weight exponent for specific respiration rate
spgam	-	specific rate of gametogenesis

h. Model parameters formulated as Q10 functions are denoted by the prefix QTF:

QTFLT	-	Low Temperature Correction for Filtration Rate
QTFHT	-	High Temperature Correction for Filtration Rate
QTFGAM	-	Temperature Correction for Rate of Gametogenesis
QTFSHI	-	Temperature Correction for Rate of Inorganic Shell Growth

3.3. Driving Variables

Driving variables are those environmental variables that make the system being modelled go. Their behavior with time is not simulated by the model but is instead input using either an analytical equation or time series data obtained from measurements

made in the field. Two driving variables are required for the model; (1) temperature and; (2) particulate matter concentration.

3.3.1. Temperature

Daily temperature for any particular model run can be input using either field data or by conversion of field data into a sine wave formulation. The latter is formulated as follows:

```
TEMP = med - dev * COS (PI / 180 * (T + ps))    where,

     TEMP  =  Temperature
     med   =  median annual temperature
     dev   =  maximum deviation from median
     COS   =  Cosine
     PI    =  3.1415927
     T     =  Day of Year (Julian)
     ps    =  phase shift (180 - day of maximum temp)
```

3.3.2. Particulate Matter Concentration

Particulate matter concentration represents the amount of particulate material, both organic and inorganic, that is contained within the water column and which is potentially filterable by *Mytilus*. *Mytilus* has been reported to effectively filter with almost one hundred percent efficiency all suspended particles larger than about 2 microns (Bayne *et al.*, 1977; Hildreth and Mallet, 1980; Kiorbe and Mohlenberg, 1981; Wright *et al.*, 1982). Although this size range does not include most free-living bacteria, as well as some of the smaller phytoplankton, there is little reason to suppose that either of these constitute a significant proportion of total particulate matter in most coastal systems. As a result, information on total particulate matter fulfills this data requirement. This information is entered into the model as time series data using the following conventions:

```
TPM = TPOM + TPIM  where,

     TPM   =  Total Particulate Matter
     TPOM  =  Total Particulate Organic Matter
     TPIM  =  Total Particulate Inorganic Matter
```

3.4. State Variables

3.4.1. Somatic Tissue

BIOSOM represents the biomass of somatic tissue. The general formulation describing its rate of change is:

```
BIOSOM = integ(GROSOM, ICSOM)
  if(NETGRO .GE. 0.0) GROSOM = NETGRO .ELSE. GRSOM
    NETGRO = INSOM - LOSSOM
  GRSOM = INSOM - RESSOM    where,
```

BIOSOM = Biomass of Somatic Tissue
GROSOM = Growth of Somatic Tissue
ICSOM = Initial Biomass of Somatic Tissue
NETGRO = Net Growth of Somatic Tissue (with input to shell)
GRSOM = Net Growth of Somatic Tissue (without input to shell)
LOSSOM = Sum of Outputs from Somatic Tissue
INSOM = Inputs to Somatic Tissue
RESSOM = Respiration Loss from Somatic Tissue

3.4.1.1. Inputs

INSOM represents the input of particulate organic matter to somatic biomass. It is calculated as the lesser of the maximum growth rate and assimilation rate:

INSOM = min(MAXGRO, AR) where,

MAXGRO = Maximum Growth Rate
AR = Assimilation Rate

The maximum growth rate varies with body size according to the following formulation:

MAXGRO = SPMGR * BIOSOM
SPMGR = spmgrc * (BIOSOM ** spmgrx) where,

SPMGR = Specific Maximum Growth Rate
spmgrc = weight constant
BIOSOM = Biomass of Somatic Tissue
spmgrx = weight exponent

Assimilation rate is calculated as the product of ingestion rate, assimilation efficiency and food quality:

AR = IR * ae * fq where,

AR = Assimilation Rate
IR = Ingestion Rate
ae = assimilation efficiency
fq = food quality

Although there is some evidence that *Mytilus* can select organic from inorganic matter (Kiorbe *et al.*, 1980; Kiorbe and Molenberg, 1981; Newell and Jordan, 1983), the mechanism by which this occurs, as well as its quantitative importance, is poorly understood and not included in the model. Food quality, for the purpose of the model, is defined as the ratio of organic to inorganic material in the ingested particulate matter:

```
FQ = TPOM / TPM    where,

     FQ   =  Food Quality
     TPOM =  Total Particulate Organic Matter
     TPM  =  Total Particulate Matter
```

Ingestion rate is the product of particulate matter concentration and ventilation rate. Body size, however, sets an upper limit on ingestion rate and, along with temperature, determines the ventilation rate. Mathematically, ingestion rate is calculated as the lesser of the maximum ingestion rate and the temperature corrected ingestion rate. The maximum ingestion rate and ventilation rates are considered to be a function of the biomass of somatic tissue only since it is unlikely that an increase of other biomass components, such as reserves or gametes, contribute to a mussel's ability to ingest greater amounts of particulate matter or filter greater amounts of water. The mathematical formulation is as follows:

```
IR =  min(IRMAX, FRTC)
 IRMAX = SPMIR * BIOSOM
  SPMIR = spmirc * (BIOSOM ** spmirx)    where,

     IR       =    Ingestion Rate
     IRMAX    =    Maximum Ingestion Rate
     FRTC     =    Filtration Rate Corrected for Temperature
     SPMIR    =    Specific Maximum Ingestion Rate
     spmirc   =    Maximum Ingestion Rate weight constant
     spmirx   =    Maximum Ingestion Rate weight exponent
     BIOSOM   =    Biomass of Somatic Tissue
```

It should be noted that this formulation treats the maximum ingestion rate solely as a function of body size. Although temperature probably also influences ingestion rate, since it increases the assimilation rate, there exist no data in the literature that allows this affect to be quantified and it is not included in the formulation. It has also been suggested that there exists a threshold particle concentration below which stimulation of ventilation rate does not occur (Tenore and Dunstan, 1973; Widdows, 1978). However, the threshold concentrations reported are so low it is unlikely that this is ever important under natural conditions of suspension culture. As a result, a threshold particle concentration is not included in the ingestion formulation.

The temperature corrected filtration rate is formulated as follows:

```
FRTC = SPVR * BIOSOM * TC * TPM
 SPVR = spvrc * (BIOSOM ** spvrx)  where,

     SPVR     =    Specific Ventilation Rate
     BIOSOM   =    Biomass of Somatic Tissue
     TC       =    Temperature Correction Factor
     TPM      =    Total Particulate Matter
```

spvrc	=	weight constant
spvrx	=	weight exponent

A number of studies (Ali, 1970; Schulte, 1975; Vahl, 1973; Widdows, 1976; Winter, 1978) have shown that filtration rate increases with temperature between 0 and 10 C, and decreases with temperature between 20 and 30 C. Between 10 and 20 C temperature appears to have little influence on filtration rate. The temperature correction factor consists of three separate formulations each corresponding to one of three temperature ranges:

```
if (TEMP .LT. 10.0) TC = QTFLT
      QTFLT = exp((TEMP - 10.0) * q10tcl)

if (TEMP .GT. 10.0 and TEMP .LT. 20.0) TC = QTFMT
      QTFMT = 1.0

if (TEMP .GT. 20.0) TC = QTFHT
 QTFHT = exp((10.0 - TEMP) * q10tch)    where,
```

TEMP	=	Temperature
QTFLT	=	Low Temperature Correction
q10tcl	=	Q10 Factor For Low Temperature Correction
QTFMT	=	Midrange Temperature Correction
QTFHT	=	High Range Temperature Correction
q10tch	=	Q10 Factor for High Temperature Correction

This formulation limits ventilation rate, and thus filtration rate, at both low and high temperatures; between 0 and 10 C ventilation rate increases according to a Q10 factor; between 10 and 20 C ventilation rate is unaffected by temperature; above 20 C the ventilation rate is again controlled by temperature, but in this case decreases as temperature increases.

3.4.1.2. Losses

There are two losses from somatic tissue; respiration and input to shell organic matter:

```
LOSSOM = RESSOM + INSHO    where,
```

LOSSOM	=	Sum of Inputs to Somatic Tissue
RESSOM	=	Respiration Loss from Somatic Tissue
INSHO	=	Input to Shell Organic Matter

Respiration losses deplete somatic tissue only when the biomass of glycogen reserves is inadequate to meet the respiration requirement. The formulation is as follows:

```
if (BIORES .LT. TRESP) RESSOM = TRESP    where,
```

BIORES	=	Biomass of Glycogen Reserves
TRESP	=	Total Respiration
RESSOM	=	Respiration Loss from Somatic Tissue

The input to shell organic matter is documented in Section 3.4.6. Respiration loss is documented in Section 3.5.

3.4.2. Glycogen Reserves

BIORES represents the biomass of glycogen reserves. The general formulation describing its rate of change is:

```
BIORES = integ(GRORES, ICRES)
 GRORES = INRES - LOSRES    where,

   BIORES    =    Biomass of Glycogen Reserves
   ICRES     =    Biomass of Glycogen Reserves at Start
   GRORES    =    Growth of Glycogen Reserves
   INRES     =    Sum of Inputs to Glycogen Reserves
   LOSRES    =    Sum of Output from Glycogen Reserves
```

3.4.2.1 Inputs

The only input to glycogen reserves is assimilated organic matter above that required to attain maximum growth of somatic tissue. As a result, glycogen reserves accumulate only when both filtration rate and assimilation are optimal. The formulation is as follows:

```
INRES = AR - INSOM    where,

   AR      =    Assimilation Rate
   INSOM   =    Input to Somatic Tissue
```

3.4.2.2 Losses

Losses from glycogen reserves include respiration and input to gonads:

```
LOSRES = RESRES + INGON    where,

   RESRES    =    Respiration Loss from Glycogen Reserves
   INGON     =    Input to Gonads
```

The respiration loss from glycogen reserves occurs only if the reserves are sufficient to meet this requirement:

```
if (BIORES .GE. TRESP) RESRES = TRESP    where,

   TRESP     =    Total Respiration Loss
   RESRES    =    Respiration Loss from Glycogen Reserves
```

The input to gonads is documented in section 3.4.3. Respiration losses are documented in Section 3.5.

3.4.3. Gonadal Tissue

BIOGON represents the biomass of gonadal tissue. The general formulation representing its rate of change is as follows:

```
BIOGON = integ(GROGON, ICGON)
 GROGON = INGON - LOSGON    where,

   BIOGON    =    Biomass of Gonadal Tissue
   ICGON     =    Biomass of Gonadal Tissue at Start
   GROGON    =    Growth of Gonadal Tissue
   INGON     =    Sum of Inputs to Gonadal Tissue
   LOSGON    =    Sum of Losses from Gonadal Tissue
```

3.4.3.1. Inputs

The input to gonadal tissue comes from glycogen reserves. The trigger for this transfer is the ratio of carbohydrate to protein content of the mussel, the assumption being that reserve glycogen is the precursor of gametes, and that gametes are formed only when there is an accumulation of glycogen reserves over and above that required to satisfy the respiratory requirements of the mussel. This input is formulated as follows:

```
if(CPR .gt. tres) BIOGON = BIORES
 CPR = TOTCHO / PROSOM
  TOTCHO = CHOSOM + BIORES
   CHOSOM = pcc * BIOSOM
  PROSOM = pcp * BIOSOM    where,

   CPR    = Ratio of Carbohydrates to Protein
   tres   = trigger for transfer of glycogen reserves
   TOTCHO = Total Carbohydrate Content of the Mussel
   CHOSOM = Carbohydrate Content of Somatic Tissue
   PROSOM = Protein Content of Somatic Tissue
   pcc    = percent carbohydrate of somatic tissue
   pcp    = percent protein of somatic tissue
```

3.4.3.2. Losses

The loss from gonadal tissue is the conversion of gonads into gametes (INGAM). This is described in Section 3.4.4.

3.4.4. Gametes

BIOGAM represents the biomass of gametes. The general formulation representing its rate of change is as follows:

```
BIOGAM = integ(GROGAM, ICGAM)
 GROGAM = INGAM - LOSGAM    where,

   BIOGAM    =    Biomass of Gametes
   ICGAM     =    Biomass of Gametes at Start
```

INGAM = Input to Gametes
LOSGAM = Loss from Gametes

3.4.4.1. Inputs

The input to gametes comes from the gonads, the biomass of which determines the amount of gametes produced. The rate at which gametes are formed is assumed to be controlled primarily by temperature (Kautsky, 1982; Seed, 1976). The formulation is as follows:

INGAM = spgam * BIOGON * QTFGAM where,

INGAM = Input to Gametes
spgam = Specific Rate of Gametogenesis
BIOGON = Biomass of Gonads
QTFGAM = Q10 Factor for Gametogenesis

3.4.4.2. Losses

The loss of gametes is a result of spawning. Spawning is assumed to occur when most of the gonads are converted to gametes and is triggered by the ratio of gonadal biomass to gamete biomass:

if(GGR .LT. tspn) LOSGAM = BIOSPN
GGR = BIOGON / BIOGAM where,

GGR = Gonad to Gamete Ratio
tspn = spawn trigger
BIOSPN = Biomass of Spawn

3.4.5. Spawn

BIOSPN represents the biomass of gametes that have been spawned. It is the loss from gametes:

BIOSPN = LOSGAM

The formulation for LOSGAM is described in Section 3.4.4.

3.4.6. Shell Organic Matter

BIOSHO represents the biomass of shell organic matter. Its growth is formulated as follows:

BIOSHO = integ(GROSHO, ICSHO)
GROSHO = INSHO where,

BIOSHO = Biomass of Shell Organic Matter
ICSHO = Biomass of Shell Organic Matter at Start
GROSHO = Growth of Shell Organic Matter
INSHO = Input to Shell Organic Matter

Input to BIOSHO comes from somatic tissue at a rate that is proportional to the growth rate of somatic tissue, provided that the

latter is positive. If growth of somatic tissue is zero or less , the input to shell organic matter is zero:

```
if(NETGRO .GT. 0.0) GROSHO = INSHO .ELSE. 0.0
 INSHO = pssom * INSOM    where,

   NETGRO  =  Net Growth of Somatic Tissue
   GROSHO  =  Growth of Shell Organic Biomass
   pssom   =  Proportion of Somatic Growth into Shell
              Organic Biomass
```

3.4.7. Shell Inorganic Matter

The total weight of a mussel's shell is determined by the inorganic as well as the organic content of the shell. It was considered essential that total shell weight be included as a model output since this variable is often used for the calculation of condition indices. There exists very little quantitative information available with regard to the factors that control the rate at which inorganic matter is synthesized into the shell, but that which does exist suggests temperature to be the prime factor (Almada-Villela *et al.*, 1982). The formulation for growth of shell inorganic matter assumes that this occurs in proportion to the growth of shell organic matter but modified according to a Q10 factor:

```
BIOSHI = integ(GROSHI, ICSHI)
 GROSHI = roi * GROSHO * Q10SHI    where,

   BIOSHI =  Weight of Shell Inorganic Matter
   ICSHI  =  Weight of Shell Inorganic Matter at Start
   GROSHI =  Growth of Shell Inorganic Matter
   roi    =  ratio of organic to inorganic input
   GROSHO =  Growth of Shell Inorganic Matter
   Q10SHI =  Q10 factor for shell inorganic matter input
```

3.5. Total Respiration

Respiration losses can be divided into two components: standard respiration and active respiration. Standard respiration is that associated with an inactive animal and represents the cost of minimal ventilation, as well as any stress associated with unfavorable conditions, such as exceptionally low or high temperatures or salinities. Active respiration represents the cost of particle capture, transport, ingestion, absorption and digestion of organic matter, and perhaps, gametogenesis. Despite a major amount of research effort, there is a great deal we do not understand about the relative importance of these various factors in terms of their overall effect on respiration. Many of the early studies, for example, concentrated on establishing a relationship between the standard respiration rate and temperature since temperature seems to be a major controlling factor in most animals. However, more recent studies (Newell and Pye, 1970a, 1970b; Widdows, 1973a, 1973b) suggest that mussels have an enormous capacity for acclimation, and that temperature, unless in the range that produces stress, has relatively

little long-term influence on standard respiration rate. The model therefore assumes that standard respiration rate is simply an exponential function of body size:

```
SRESP = SPRESP * (BIOTOT - BIOSHO)
 SPRESP = spresc * (BIOTOT - BIOSHO) ** spresx   where,

   SRESP   =  Standard Respiration Rate
   SPRESP  =  Specific Standard Respiration Rate
   BIOTOT  =  Total Organic Biomass
   BIOSHO  =  Biomass of Shell
   spresc  =  weight constant
   spresx  =  weight exponent
```

The active respiration rate, because it depends on a large number of factors, has been much more difficult to characterize. An extensive survey of the literature failed to produce a formulation based on the level of activity of a mussel. After considerable attempts to relate active respiration to factors related to the rate at which particulate material is filtered and assimilated, the following formulation appeared to be most suitable:

```
ARESP = (irres * IR) + (arres * AR)   where,

   ARESP  =  Active Respiration Rate
   irres  =  ingestion rate factor
   IR     =  Ingestion Rate
   arres  =  assimilation rate factor
   AR     =  Assimilation Rate
```

This formulation simply assumes that the loss due to active respiration is a constant proportion of ingestion and assimilation.

Total respiration is then the sum of standard and active respiration:

```
TRESP = SRESP + ARESP
```

3.6. Other Variables

This section documents a number of variables that are routinely output by the model and which are for the most part simply calculated from the formulations documented above. Their formulation thus requires little theoretical discussion.

3.6.1. Pseudofeces Production

The production of pseudofeces occurs when filtration rate (the product of ventilation rate and particulate matter concentration) exceeds the maximum ingestion rate:

```
PF = max(0.0, FRXTRA)
 FRXTRA = FRTC - IRMAX    where,

   PF      =  Pseudofeces Production
   FRXTRA  =  Filtration Above that Potentially Ingestable
   FRTC    =  Temperature Corrected Filtration Rate
   IRMAX   =  Maximum Ingestion Rate
```

3.6.2. Egestion

Egestion represents the excretion of unassimilated ingested particulate matter, both organic and inorganic. It is calculated as the difference between ingested and assimilated particulate matter:

```
ER = IR - AR    where,

   ER  =  Egestion Rate
   IR  =  Ingestion Rate
   AR  =  Assimilation Rate
```

3.6.3. Shell Length

The growth of a mussel is sometimes measured as an increase in shell length. This variable is particularly important in determining the length of time required for a mussel to attain marketable size. It can be calculated from the shell weight based on information obtained from shell length-weight relationships. Data sets presented for cultured mussels by Brylinsky (1989) and Sephton (unpublished) were analyzed to obtain the following relationship:

```
SHLLGT = 35.0 * (SHLWT ** 0.29)
 SHLWT = BIOSHO + BIOSHI    where,

   SHLLGT  =  Shell Length (millimeters)
   SHLWT   =  Shell Weight
   BIOSHO  =  Biomass of Shell Organic Matter
   BIOSHI  =  Mass of Shell Inorganic matter
```

The relationship between shell weight and shell length for the data set analysed is illustrated in Figure 2.

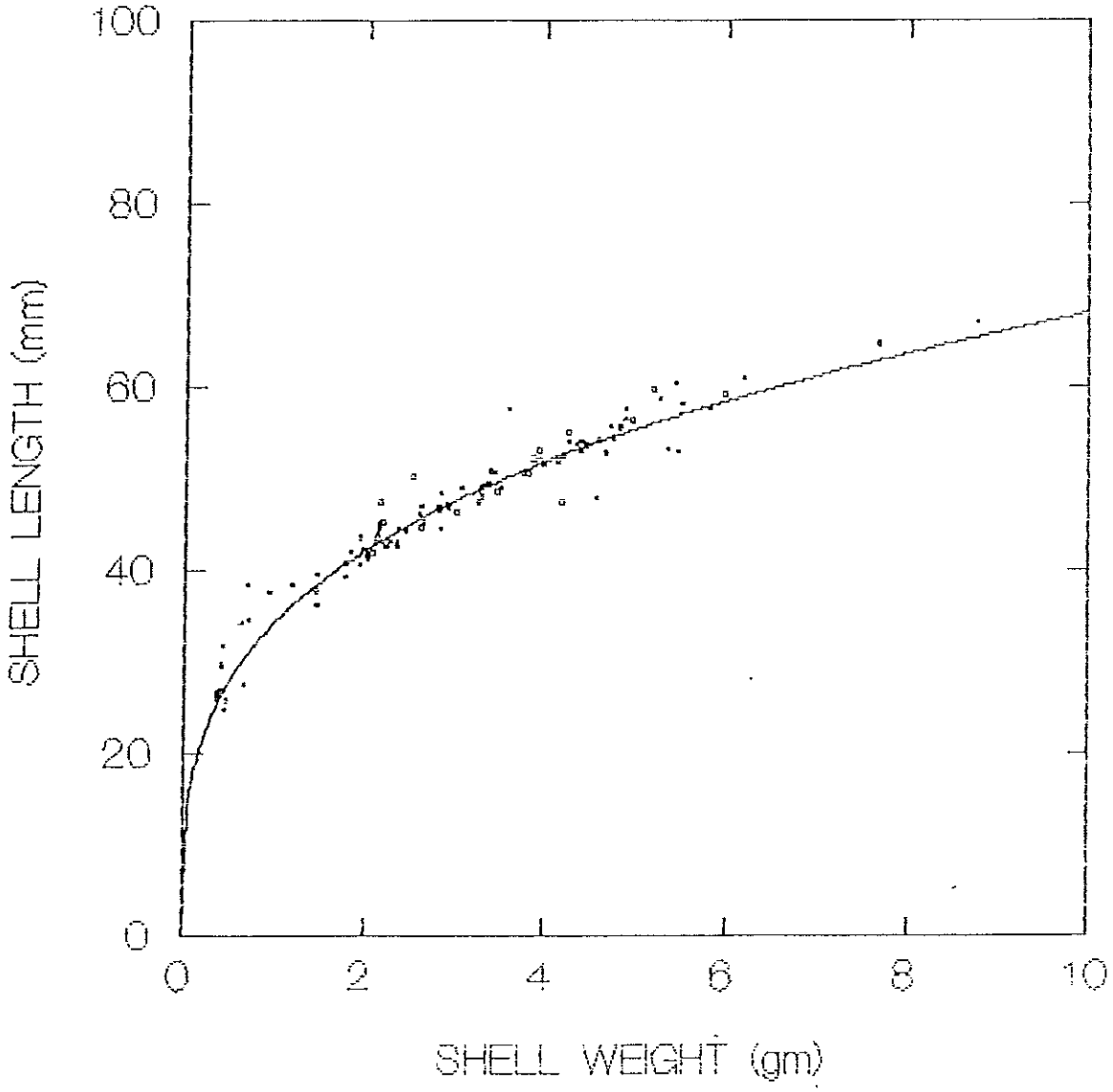


Figure 2. Relationship between shell weight and shell length for data presented by Brylinsky (1989) and Sephton (unpublished); n = 107, r = -0.91

3.6.4. Condition Index

It was considered important to have the model output some measure of the condition of a mussel at any particular time. Although there are numerous formulae for calculation of condition indices, all involve comparing some measure of shell size with meat size. For the purpose of the model the following formula was used:

CI = (BIOTOT - BIOSHO) / SHLWT where,

CI	=	Condition Indice
BIOTOT	=	Total Organic Biomass
BIOSHO	=	Biomass of Shell Organic Matter
SHLWT	=	Shell Weight

3.6.5. Cumulative Variables

It is often instructive to examine the total amount of biomass, or of any other variable, that accumulates over the time span of a model run. If, for example, this is done for each state variable together with its inputs and outputs, it provides the information required to construct an annual energy budget. The following are routinely output by the model:

CUMSOM	=	integ(INSOM, 0.0) - Cumulative Somatic Biomass
CUMRES	=	integ(INRES, 0.0) - Cumulative Glycogen Reserves
CUMGON	=	integ(INGON, 0.0) - Cumulative Gonadal Tissue
CUMGAM	=	integ(INGAM, 0.0) - Cumulative Gametes
CUMFR	=	integ(IRPOT, 0.0) - Cumulative Filtration
CUMIR	=	integ(IR, 0.0) - Cumulative Ingestion
CUMAR	=	integ(AR, 0.0) - Cumulative Assimilation
CUMER	=	integ(ER, 0.0) - Cumulative Egestion
CUMPF	=	integ(PF, 0.0) - Cumulative Pseudofeces
CUMSRP	=	integ(SRESP, 0.0) - Cumulative Standard Respiration
CUMARP	=	integ(ARESP, 0.0) - Cumulative Active Respiration
CUMTRP	=	CUMSRP + CUMARP - Cumulative Total Respiration

3.7. Parameter Estimates

3.7.1. Introduction

Numerous parameters are required in the mathematical formulation of the model. The approach adopted in assigning values to each parameter was to first consider the most appropriate value on the basis of theoretical concepts, and to then compare this value with emperically derived values presented in the literature based on laboratory and field studies. In those instances where theory and experimental findings do not agree, an attempt was made to resolve the difference by carefully reevaluating theory and observations. Where insufficient information is available to resolve differences, results from experimental studies were used. For some parameters an extremely wide range of values is reported in the literature. In

these cases determination of the amount of effort to devote to refining the estimate depended on the results of a sensitivity analysis on that particular parameter, those parameters having a large effect on model output receiving the most further study and reevaluation.

Table 1 presents a summary of the parameters required for the model along with their values.

TABLE 1. Summary of Model Parameters

Parameter	Value
spmirc	0.12
spmirx	-0.32
ae	0.50
spvrc	2.75
spvrx	-0.40
q10tcl	0.1386
q10tch	0.1386
tres	0.60
pcc	0.15
pcp	0.60
spmgam	0.015
q10gam	0.0639
tspn	0.01
pssom	0.05
roi	15.0
q10shi	0.1386
spresc	0.072
spresx	-0.30
irres	0.05
arres	0.15

3.7.2. Specific Maximum Ingestion Rate

The specific maximum ingestion rate is an exponential function of the biomass of somatic tissue:

SPIMAX = spmirc * (BIOSOM ** spmirx) where,

spmirc = ingestion rate weight constant
BIOSOM = Biomass of Somatic Tissue
spmirx = ingestion rate weight exponent

The values of spmirc and spmirx were derived from data reported by Widdows *et al.* (1979) for a study in which the maximum ingestion rate was determined as the ingestion rate at which pseudofeces production is observed to just begin. The derived relationship is illustrated in Figure 3.

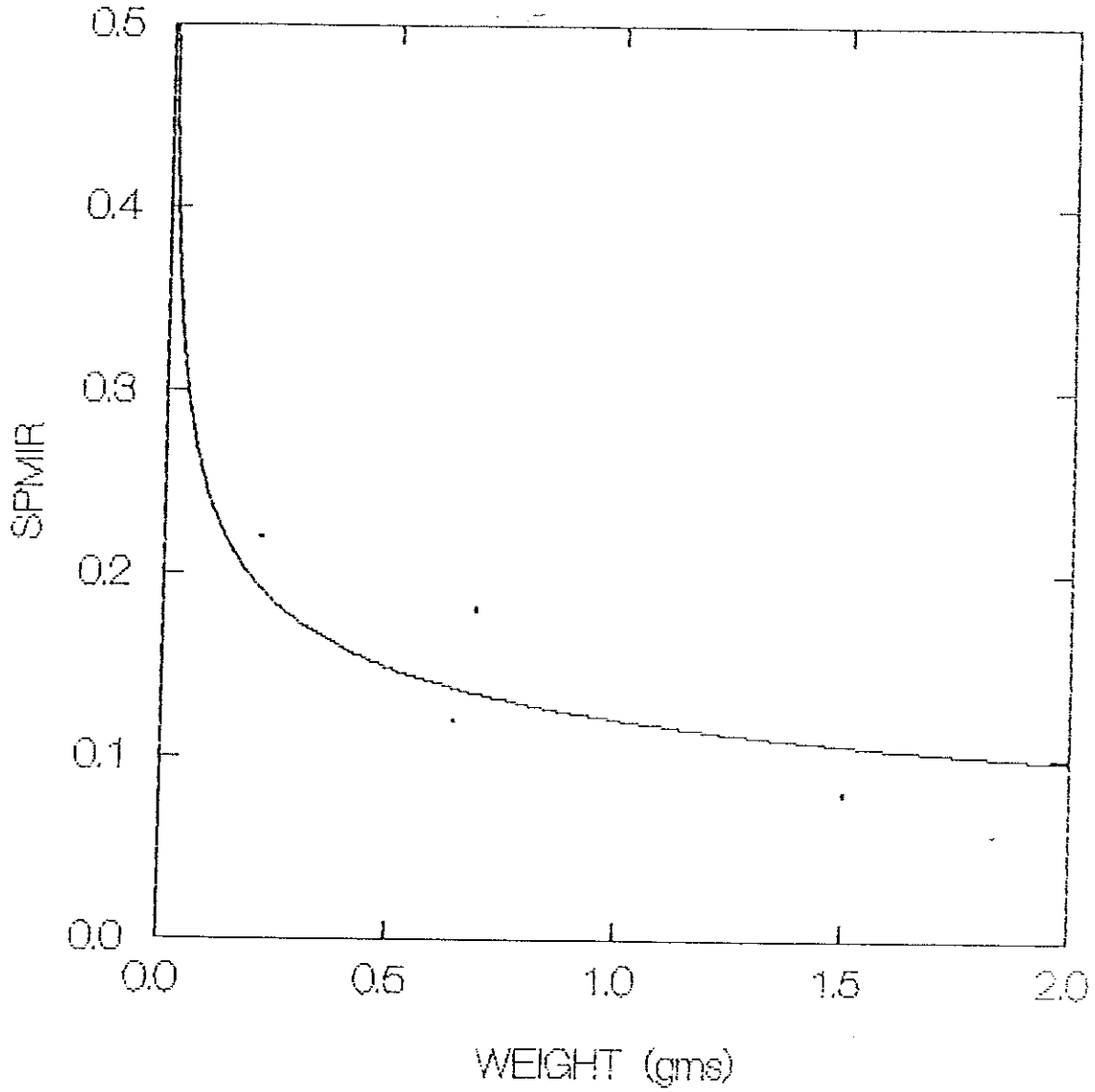


Figure 3. Relationship between weight and specific maximum ingestion rate derived from data presented by Widdows, et al. (1979). Fitted line represents the equation SPMIR = 0.012 WEIGHT $^{-0.32}$

3.7.3. Assimilation Efficiency

The assimilability of naturally occurring particulate matter is an exceptionally difficult variable to quantify. Although no one has yet devised a suitable measure of assimilability, a number of investigators estimate that about 40 to 60 percent of naturally occurring particulate organic matter is potentially assimilable by *Mytilus* (Bayne *et al.*, 1988; Hawkins *et al.*, 1985; Navarro and Winter, 1982). As a compromise, the model assumes an average of 50 percent. The formulation also assumes that the ratio of organic to inorganic matter in the total particulate matter has no influence on the assimilation efficiency of organic particulates, and that assimilation efficiency is not affected by the rate at which particulate matter is ingested. Both of these assumptions are subject to debate (Bayne *et al.*, 1988; Griffiths and Griffiths, 1987; Vahl, 1973; Widdows, 1978; Winter, 1976).

3.7.4. Specific Ventilation Rate

The specific ventilation rate is an exponential function of the biomass of somatic tissue:

```
SPVR = spvrc * (BIOSOM ** spvrx)    where,

   spvrc   =  ventilation rate weight constant
   BIOSOM  =  Biomass of Somatic Tissue
   spvrx   =  ventilation rate weight exponent
```

Very few investigators have attempted to obtain direct estimates of ventilation rates. In most cases it is filtration rate, the product of ventilation rate and particle concentration that is measured. Fortunately, this measurement also provides the parameter estimates required to characterize ventilation rates. A large number of investigators have measured these parameters and there is now good agreement on the value of the weight exponent (Bayne *et al.*, 1976; Bayne and Newell, 1983; Griffiths and Griffiths, 1987; Winter, 1978). Estimates of the weight constant, however, tend to vary because of the influence of particle concentration on filtration rate. A value of 2.75 is used in the model.

3.7.5. Q10 Factors for Filtration Rate

As discussed in Section 3.4.1.1 filtration rate is affected by temperatures between 0 and 10 C, where it increases with temperature, is unaffected at temperatures between 10 and 20 C, and decreases with temperature between 20 and 30 C. Assuming an exponential rate of increase and decrease at the low and high temperature ranges respectively, the following formulations are used in the model:

```
QTFLT = exp((TEMP - 10) * q10tcl
QTFHT = exp((20 - TEMP) * q10tch    where,

   QTFLT     =     Low Temperature Correction Factor
```

q10tcl	=	0.1386
QTFHT	=	High Temperature Correction Factor
q10tch	=	0.1386

3.7.6. Specific Maximum Growth Rate

The specific rate of maximum growth is modelled as a function of the biomass of somatic tissue:

SPGMAX = spmgrc * (BIOSOM ** spmgrx) where,

spmgrc	=	weight constant
BIOSOM	=	Biomass of Somatic Tissue
spmgrx	=	weight exponent

There are surprisingly few studies that attempt to estimate the maximum growth rate of *Mytilus*. There is, however, considerable data on growth rates under optimal conditions for mussels of various sizes (Ceccherelli and Barboni, 1983; Ceccherelli and Rossi, 1984; Gabbott and Bayne, 1973; Hilbish, 1986; Thompson, 1984). This data was analysed to obtain the parameters listed in Table 1. The derived relationship between specific maximum growth rate and biomass is illustrated in Figure 4.

3.7.7. Trigger for Transfer of Glycogen Reserves

The transfer of glycogen reserves to gonadal tissue occurs when the ratio of carbohydrate to protein reaches a specific value (discussed in section 3.4.3):

if(CPR .gt. tres) BIOGON = BIORES where,

CPR	=	Ratio of Carbohydrate to Protein
tres	=	transfer trigger
BIOGON	=	Biomass of Gonadal Tissue
BIORES	=	Biomass of Glycogen Reserves

The parameter tres represents the ratio of carbohydrate to protein that must be exceeded for the transfer to occur. Its value (0.60) was estimated from data on the biochemical composition of mussels that were in the very initial stage of gametogenesis. Table 2 presents a summary of the data and sources used.

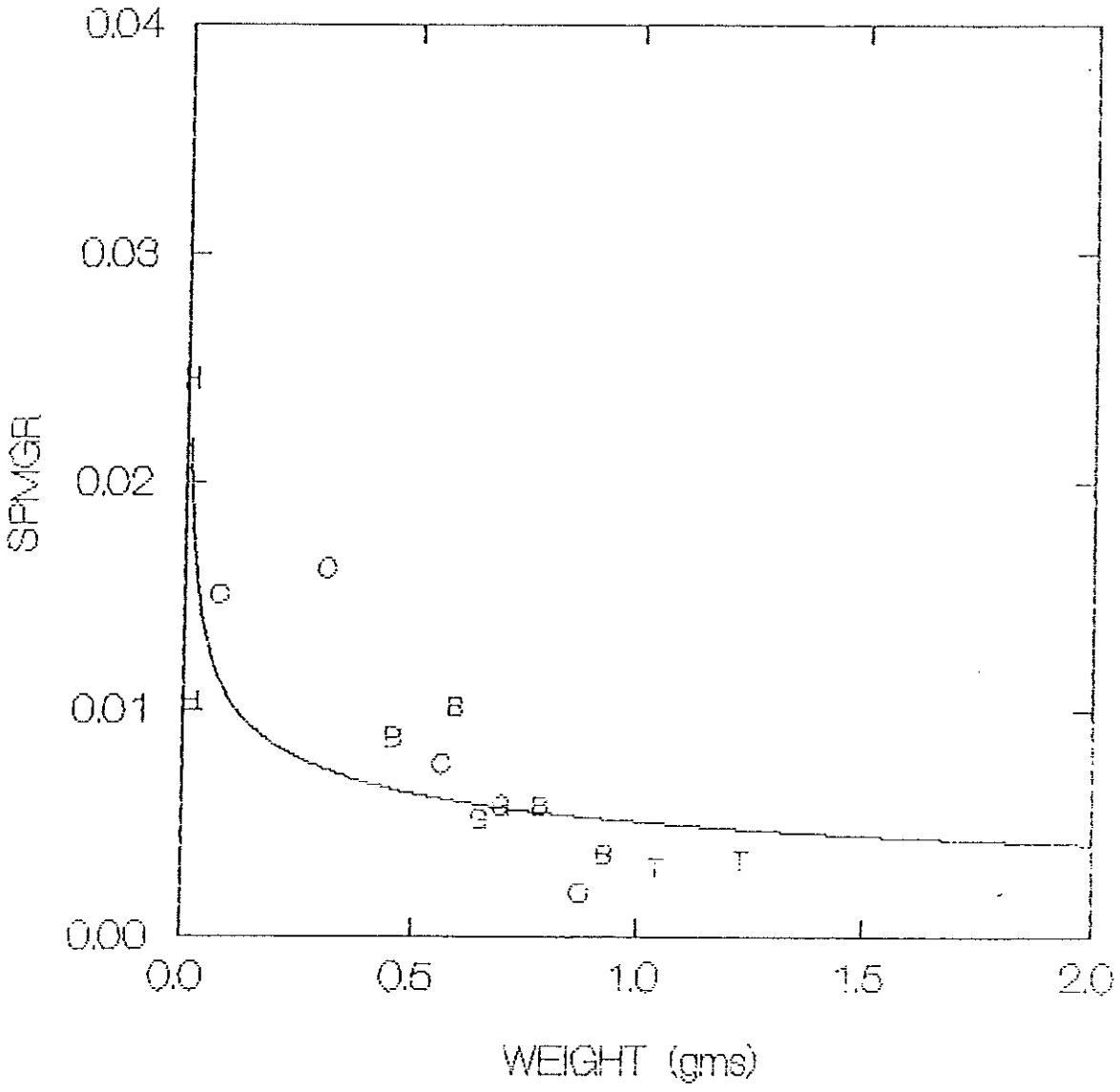


Figure 4. Relationship between weight and specific maximum growth rate. (Letters represent data sources: B - Ceccherelli and Barboni, 1983; C - Ceccherelli and Rossi, 1984; G - Gabbott and Bayne, 1973; H - Hilbish, 1986; T - Thompson, 1984.) Fitted line represents the equation SPMGR = 0.005 WEIGHT $^{-0.003}$; n = 15, r = 0.85

Table 2. Summary of data used to estimate tres.

Source	Ratio
Bressin and Marin (1985)	0.70
Dare and Edwards (1975)	0.49
Emmett *et al.* (1987)	0.46
Hawkins *et al.* (1985)	0.61
Zandee *et al.* (1980)	0.68

3.7.8. Proportion of Carbohydrate and Protein in Somatic Tissue

As noted above, the trigger for transfer of glycogen reserves to gonads is based on the ratio of total carbohydrate to protein. It thus becomes necessary to determine the proportion of carbohydrate (pcc) and protein (pcp) in somatic tissue. This was estimated from data presented for mussels that had just spawned and therefore contained minimal amounts of either glycogen reserves or gametes (Bressin and Marin, 1985; Dare and Edwards, 1975; Emmett *et al.*, 1987; Gabbott, 1983; Hawkins *et al.*, 1985; Pieters *et al.*, 1980; Thompson, 1984; Zandee *et al.*, 1980). Table 3 summarizes the data and sources used to estimate these parameters.

Table 3. Summary of data used to estimate pcc and pcp.

Source	% Protein	% Carbohydrate
Bressin and Marin (1985)	84	9
Dare and Edwards (1975)	82	12
Emmett *et al.* (1987)	66	22
Gabbott (1983)	67	29
Hawkins *et al.* (1985)	76	11
Pieters *et al.* (1980)	75	20
Thompson (1984)	71	16
Zandee *et al.* (1980)	79	8

3.7.9. Specific Maximum Rate of Gametogenesis

The rate at which gametes are formed was estimated from data presented in studies measuring the accumulation of gametes over time (Bayne *et al.*, 1978; Bressin and Marin, 1985; Emmett *et al.*, 1987;

Hawkins *et al.*, 1985; Kautsky, 1982; Lowe *et al.*, 1982; Newell *et al.*, 1982; Pieters *et al.*, 1979; Rodhouse *et al.*, 1984a, 1984b; Seed and Brown, 1975; Thompson, 1984; Zandee *et al.*, 1980; Zurburg *et al.*, 1979). The maximum rates, which occur at temperatures above 10 C, were used to estimate this parameter.

3.7.10. Q10 Factor for Gametogenesis

The maximum rate of gametogenesis is modified by a Q10 factor. Although there are numerous studies that relate degree-days to rate of gametogenesis, there are no data that allow calculation of a Q10 factor. A value of 2.0 is assumed in the model and is formulated as follows:

```
QTFGAM = exp((TEMP - 10) * q10gam)
  q10gam = 0.0639
```

3.7.11. Spawning Trigger

This parameter (tspn) represents the ratio of gonads to gametes that must be exceeded to cause spawning to occur. Very few studies have attempted to provide estimates of this parameter, but it appears that spawning is initiated when almost all gonadal material has matured. It is assigned a value of 0.01.

3.7.12. Proportion of Assimilation Into Shell Biomass

There is virtually no data that allows an estimate of the proportion of assimilation that is subsequently incorporated into the organic matter component of the shell. The value of 0.05 used in the model is based on optimization to fit real data.

3.7.13. Ratio of Organic to Inorganic Input to the Shell

Growth of the inorganic component of the shell is assumed to be proportional, in part, to the growth of the organic component. The parameter roi represents this proportion. There is no data in the literature that allows this parameter to be determined and, unfortunately, it could only be estimated after analysis of a number of model runs in which the model output was compared with field data. A value of 15 was arrived at which is modified by temperature as described in Sections 3.4.7 and 3.7.12.

3.7.14. Q10 Factor for Inorganic Shell Growth

QTFSHI corrects the rate at which inorganic material is added to the shell as a result of the influence of temperature. Estimates of Q10 values for this process range between three and five (Almada-Villela *et al.*, 1982). An average of four is assumed and formulated as follows:

```
QTFSHI = exp(TEMP * q10shi)
  q10shi = 0.1386
```

3.7.15. Specific Standard Respiration Rate

The specific standard respiration rate (spresp) is a function of total biomass and is formulated as follows:

SPRESP = spresc * (BIOTOT - BIOSHO) ** spresx where,

spresc	=	weight constant
BIOTOT	=	Total Biomass
BIOSHO	=	Biomass of Shell
spresx	=	weight exponent

Of all parameters spresc and spresx have been the most intensively studied. The values presented in Table 1 are based on a large number of studies (summarized by Bayne *et al.*, 1976; Bayne and Newell, 1983; Griffiths and Griffiths, 1987; Winter, 1978).

3.7.16. Active Respiration Parameters

Unlike standard respiration, active respiration, which is the cost of particle capture, transport, ingestion and assimilation, despite numerous attempts (Bayne and Scullard, 1977; Bayne *et al.*, 1976; Hamburger *et al.*, 1983; Hawkins *et al.*, 1983), has been very difficult to quantify. Most studies suggest that active respiration amounts to somewhere between 10 and 20 percent of assimilation. The model assumes that active respiration is a function of both ingestion (irres) and assimilation (arres). These parameters have been assigned values of 0.05 and 0.15 respectively.

There is also some evidence that the rate of gametogenesis influences respiration rate (Bayne, 1973; Bayne and Newell, 1983; Gabbott and Bayne, 1973; Widdows, 1978), but this also has not been quantified and is not included in the model.

3.8. Summary of Model Formulations

The following section presents a summary of the model formulations.

```
TEMP = med - dev * COS(PI/180 * (T + ps))

TPM = TPOM + TPIM

BIOSOM = integ(GROSOM, ICSOM)
     if(NETGRO .GE. 0.0) GROSOM = NETGRO .ELSE. GRSOM
          NETGRO = INSOM - LOSSOM
               INSOM = min(MAXGRO, AR)
                    MAXGRO = SPMGR * BIOSOM
                         SPMGR = spmgrc * (BIOSOM ** spmgrx)
                    AR = IR * ae * FQ
                         IR = min(IRMAX, FRTC)
                              IRMAX = SPMIR * BIOSOM
                               SPMIR = spmirc * (BIOSOM ** spmirx)
                         FRTC = SPVR * BIOSOM * TC * TPM
                              SPVR = spvrc * (BIOSOM ** spvrx)
                              if(TEMP .LT. 10.0) TC = QTFTL
                                QTFTL = exp((TEMP - 10) * q10tcl)
                              if(TEMP .GT. 10.0 AND .LT. 20.0) TC =
                                        QTFMT
                                QTFMT = 1.0
                              if(TEMP .GT. 20.0) TC = QTFHT
                                QTFHT = exp((10.0 - TEMP) * q10tch)
                         FQ = TPOM / TPM
               LOSSOM = RESSOM + INSHO
                    if(BIORES .LT. TRESP) RESSOM = TRESP
          GRSOM = INSOM - RESSOM

BIORES = integ(GRORES, ICRES)
     GRORES = INRES - LOSRES
          INRES = AR - INSOM
          LOSRES = RESRES + INGON
               if(BIORES .GE. TRESP) RESRES = TRESP

BIOGON = integ(GROGON, ICGON)
     GROGON = INGON - LOSGON
          if(CPR .GT. tres) INGON = BIORES
               CPR = TOTCHO / PROSOM
                    TOTCHO = CHOSOM + BIORES
                         CHOSOM = pcc * BIOSOM
                    PROSOM = pcp * BIOSOM
          LOSGON = INGAM
```

```
BIOGAM = integ(GROGAM, ICGAM)
     GROGAM = INGAM - LOSGAM
          INGAM = spmgam * BIOGON * QTFGAM
               QTFGAM = exp((TEMP - 10.0) * q10gam)
          LOSGAM = BIOSPN
               if(GGR .LT. tspn) BIOSPN = BIOGAM
                    GGR = BIOGON / BIOGAM

BIOSHO = integ(GROSHO, ICSHO)
     GROSHO = INSHO
          if(GROSHO .LTE. 0.0) INSHO = 0.0)
          if(GROSHO .GT. 0.0) INSHO = pssom * INSOM

BIOSHI = integ(GROSHI, ICSHI)
     GROSHI = roi * GROSHO * QTFSHI
          QTFSHI = exp(TEMP - q10shi)

TRESP = SRESP + ARESP
     SRESP = SPRESP * (BIOTOT - BIOSHO)
          SPRESP = spresc * (BIOTOT - BIOSHO) ** spresx
     ARESP = (irres * IR) + (arres * AR)

CUMSOM     =     integ(INSON, 0.0)
CUMRES     =     integ(INRES, 0.0)
CUMGON     =     integ(INGON, 0.0)
CUMGAM     =     integ(INGAM, 0.0)
CUMFR      =     integ(IRPOT, 0.0)
CUMIR      =     integ(IR, 0.0)
CUMAR      =     integ(AR, 0.0)
CUMER      =     integ(ER, 0.0)
CUMPF      =     integ(PF,0.0)
CUMSRP     =     integ(SRESP, 0.0)
CUMARP     =     integ(ARESP, 0.0)
CUMTRP     =     CUMSRP + CUMARP

PF = max(0.0, FRXTRA)
     FRXTRA = IRTC - IRMAX

ER = IR - AR

SHLLGT = 30 * (SHLWT ** 0.33)

SHLWT = BIOSHO + BIOSHI

CI = (BIOTOT - BIOSHO) / SHLWT
```

4. MODEL OUTPUT

4.1. Standard Model Run

A standard model run was made to evaluate the general behavior of the model. Driving variables for the standard model were generated using values for temperature and particulate organic matter concentration characteristic of Atlantic Canada coastal waters (Figure 5). Seasonal variations in particulate organic matter were set to follow the trends typical for a system having a spring and fall phytoplankton bloom. The model was run for three years using initial condition values appropriate for a mussel having been spawned in the fall prior to time zero. The general behavior of the standard model in terms of how each state variable varies with time is presented in Figures 6 to 10.

In general, model behavior agrees well with what is found in nature. Both biomass and shell length increase at rates and reach sizes similar to those observed under culture conditions. There is also a spawning event that occurs in the fall of each year. The seasonal trend in growth rate follows closely the trend in particulate matter concentration but is modified by the limitation placed on filtration rate by temperature. This results in highest growth rates occurring during the spring, when both particulate matter and temperature are increasing; a decrease in growth rate during the summer when particulate matter is low; and an increase in the fall when particulate matter again increases. The later increase in growth rate is less than what occurs in the spring, partly because it is terminated by a spawning event and partly because both particulate matter concentration and temperature are lower than in the spring. The condition index follows the same seasonal trend as growth rate; an increase during the spring bloom period and a decline immediately after spawning.

Figure 11 illustrates the relationship between the maximum ingestion rate and filtration rate. During those periods when both food concentration and temperature are high the filtration rate is also high. However, because body size places a constraint on the amount of particulate matter that can be ingested, the actual ingestion rate is less than the filtration rate. Under this condition the excess filtered particulate material is channeled into pseudofeces (Figure 10).

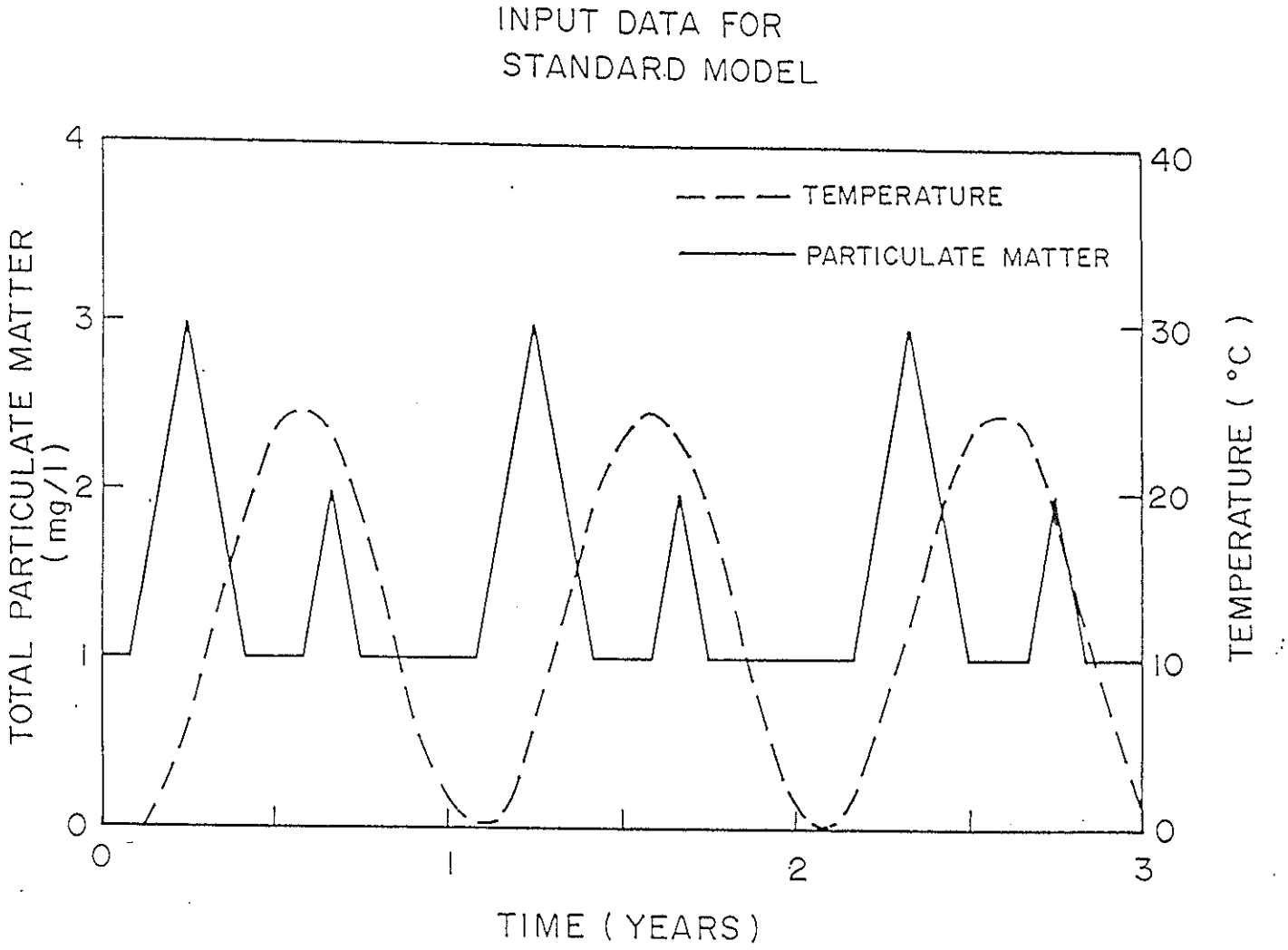


Figure 5. Seasonal variation in driving variables used as input for standard model simulations

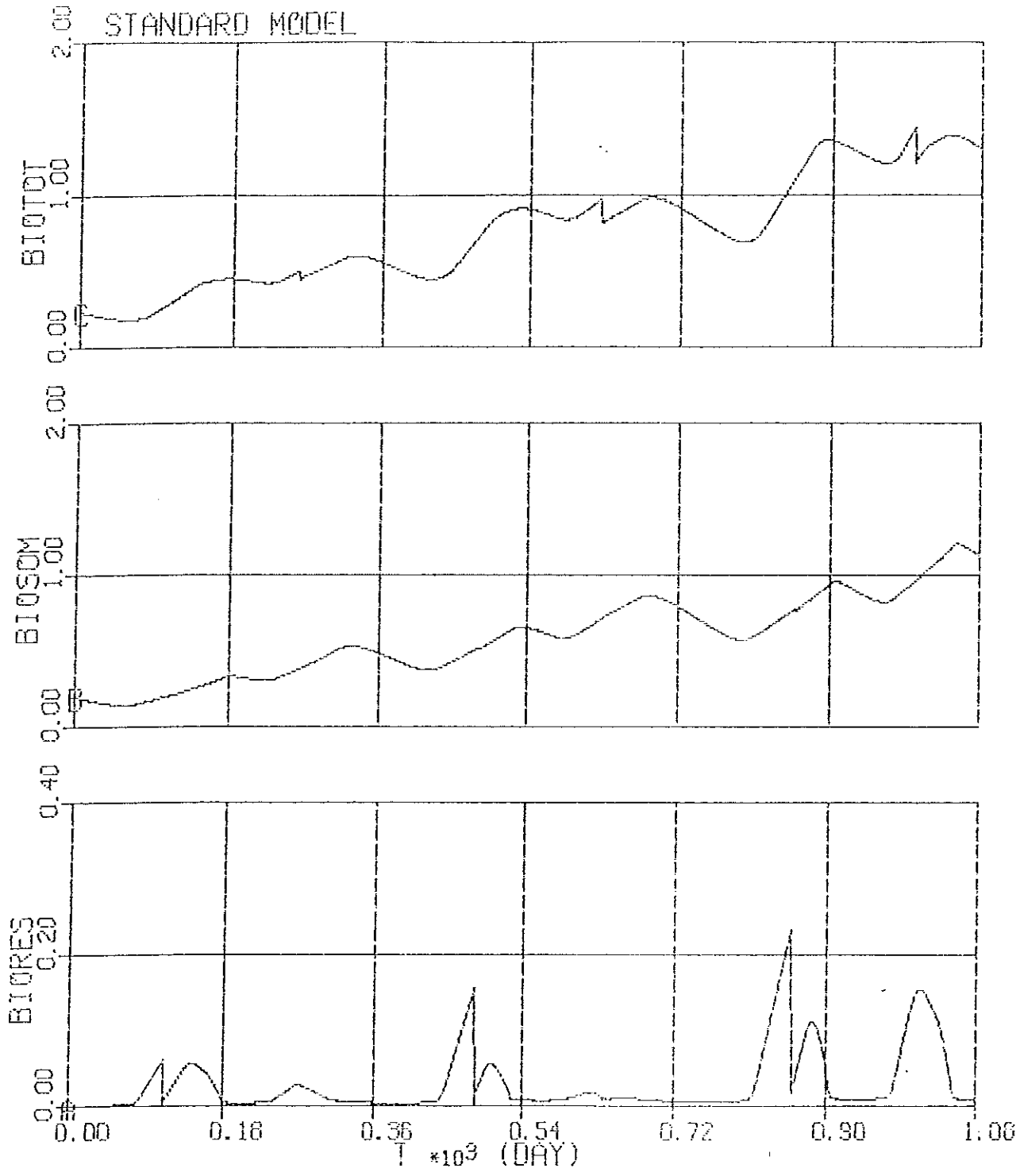


Figure 6. Standard model output for Total Biomass (BIOTOT), Biomass of Somatic Tissue (BIOSOM) and Biomass of Glycogen Reserves (BIORES)

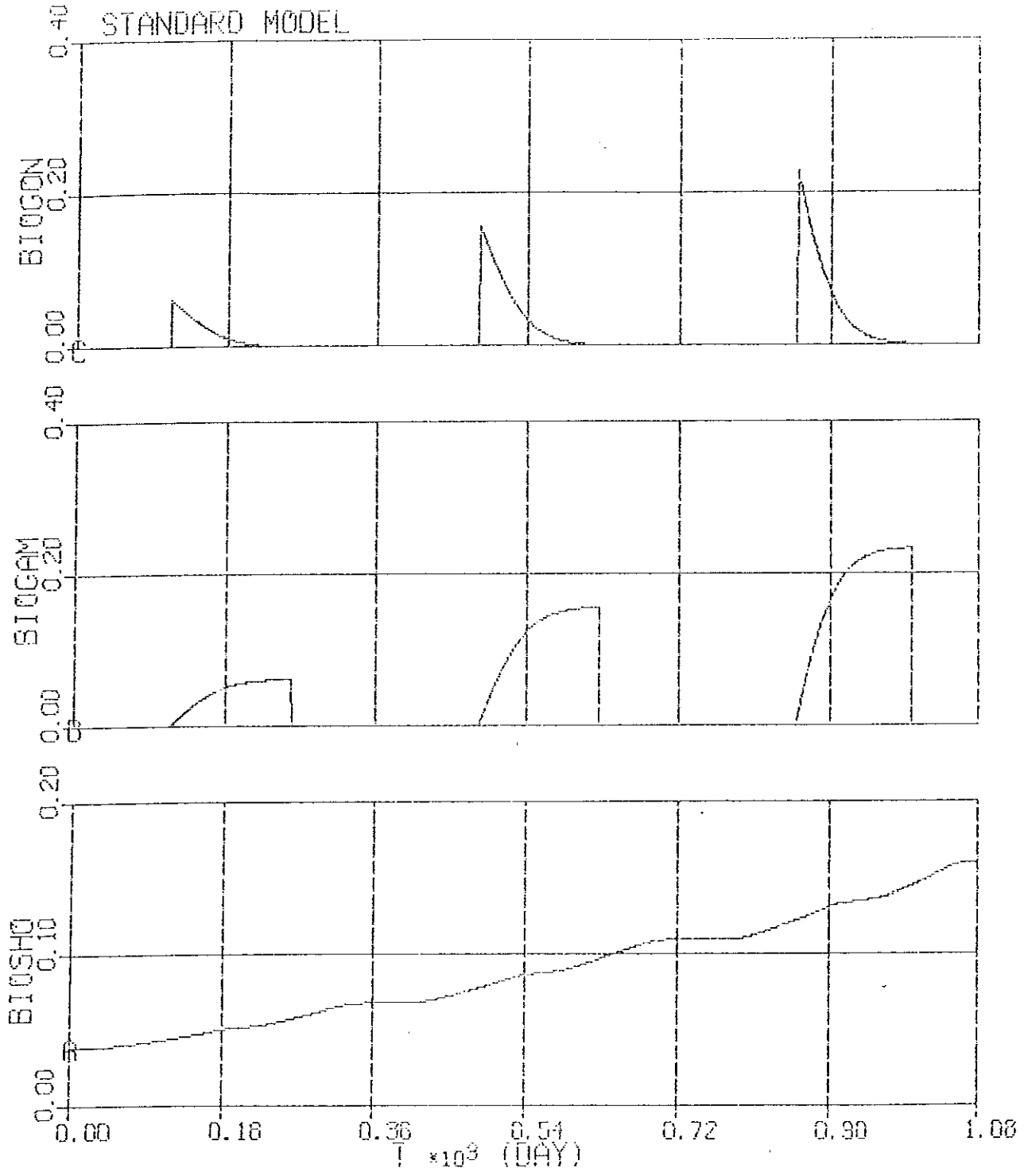


Figure 7. Standard model output for Biomass of Gonads (BIOGON), Biomass of Gamets (BIOGAM) and Shell Organic Biomass (BIOSHO)

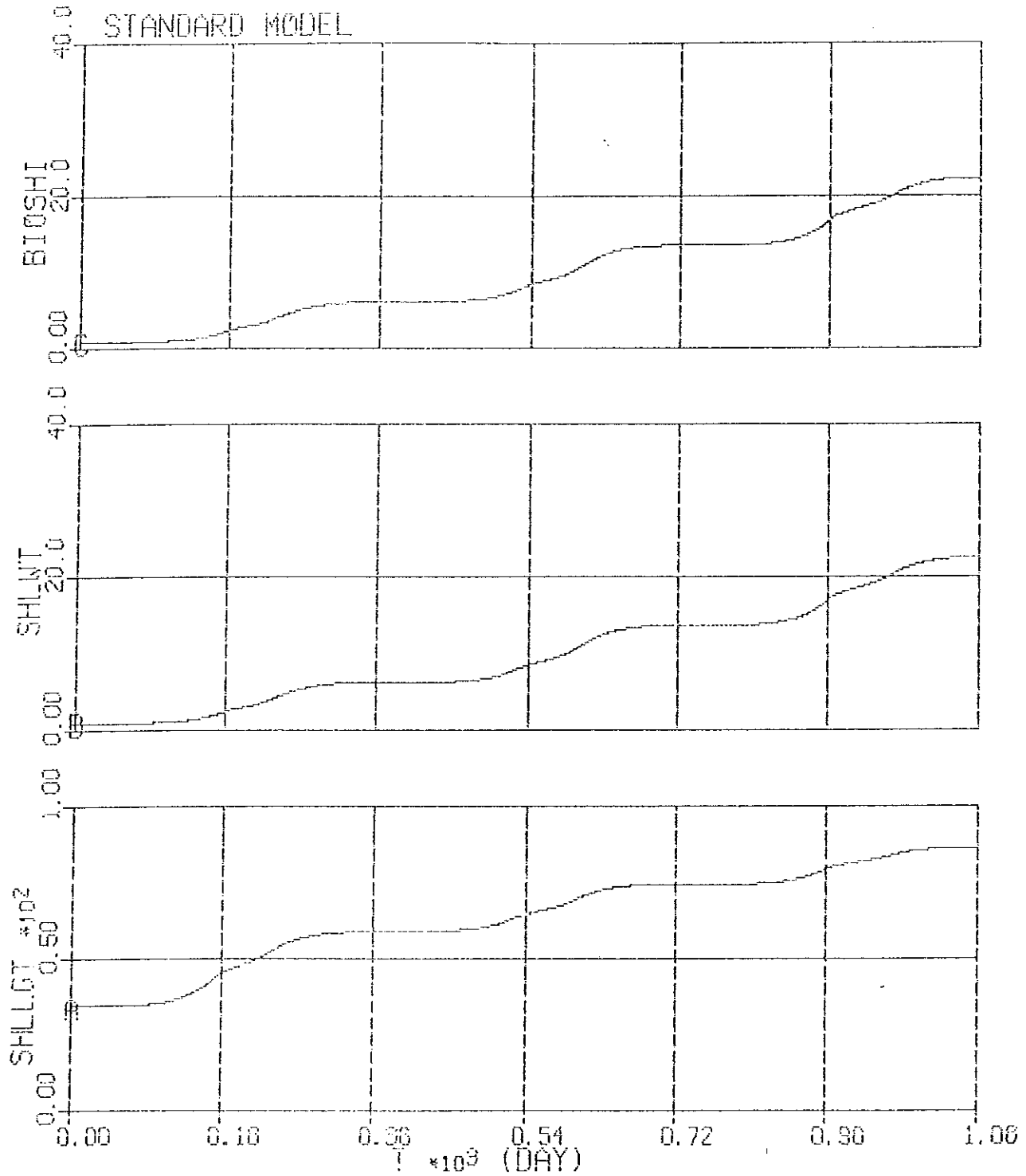


Figure 8. Standard model output for Shell Inorganic Weight (BIOSHI), Shell Weight (SHLWT) and Shell Length (SHLLGT)

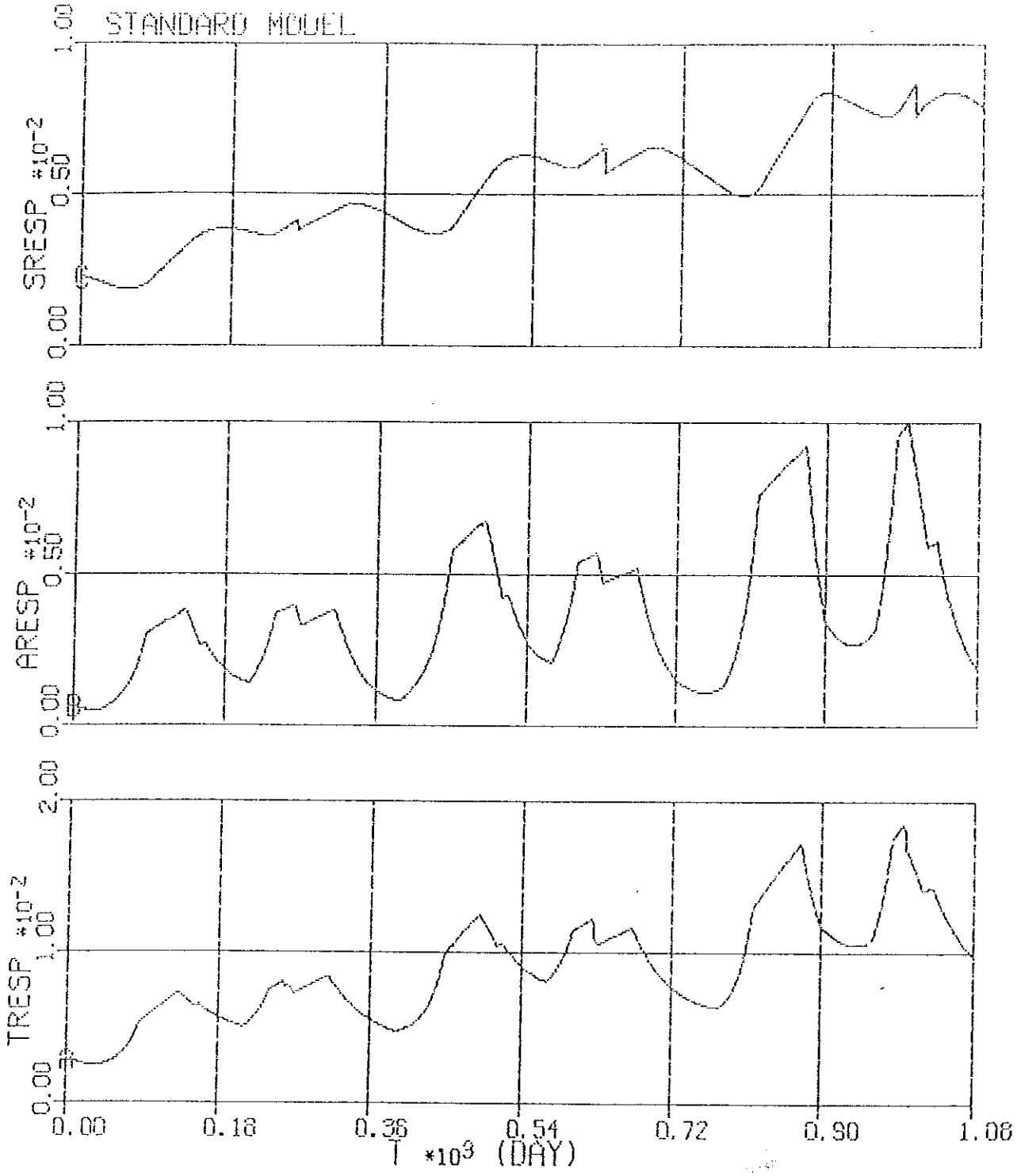


Figure 9. Standard model output for Standard Respiration (SRESP), Active Respiration (ARESP) and Total Respiration (TRESP)

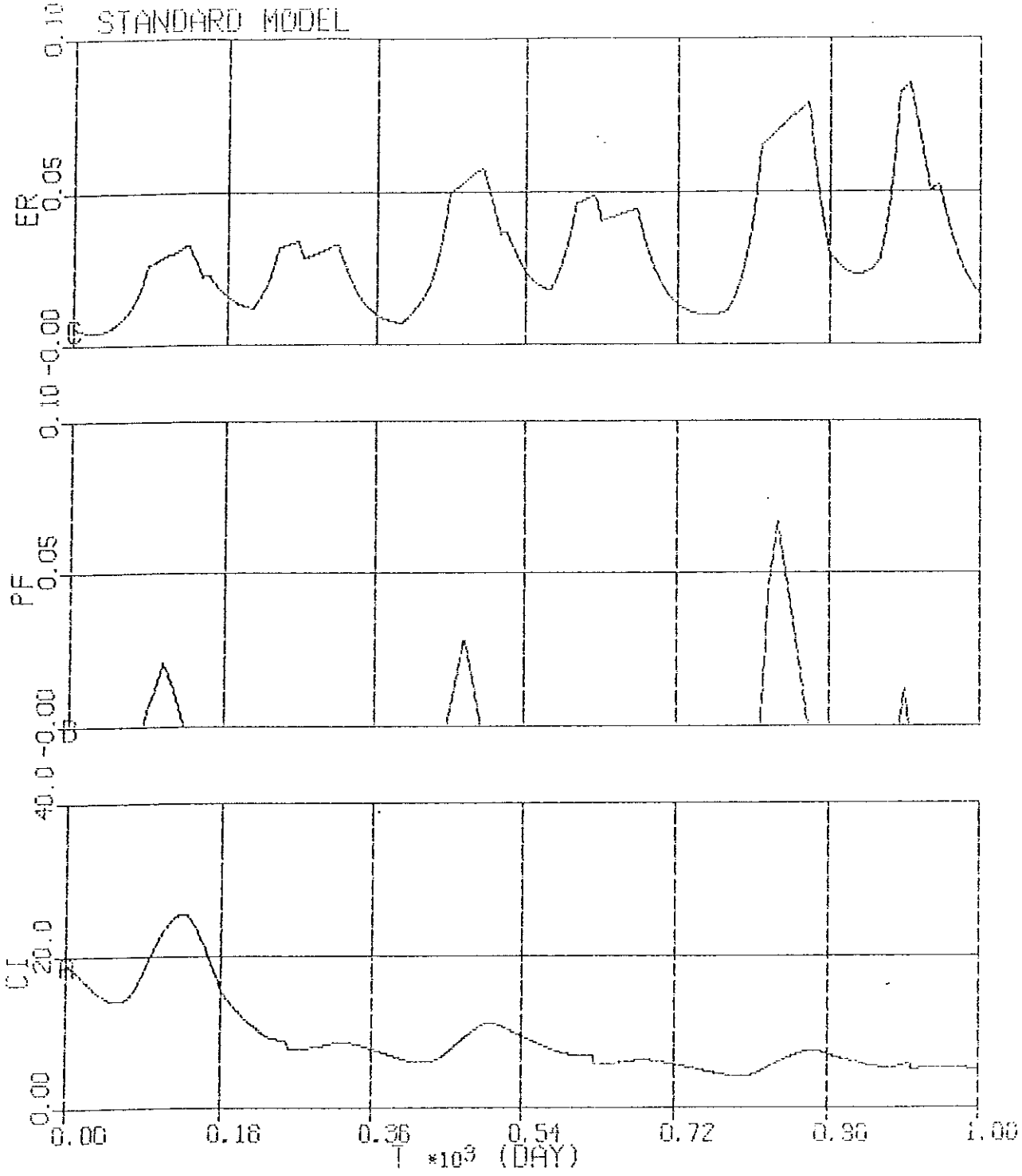


Figure 10. Standard model output for Egestion Rate (ER), Pseudofeces Production (PF) and Condition Index (CI)

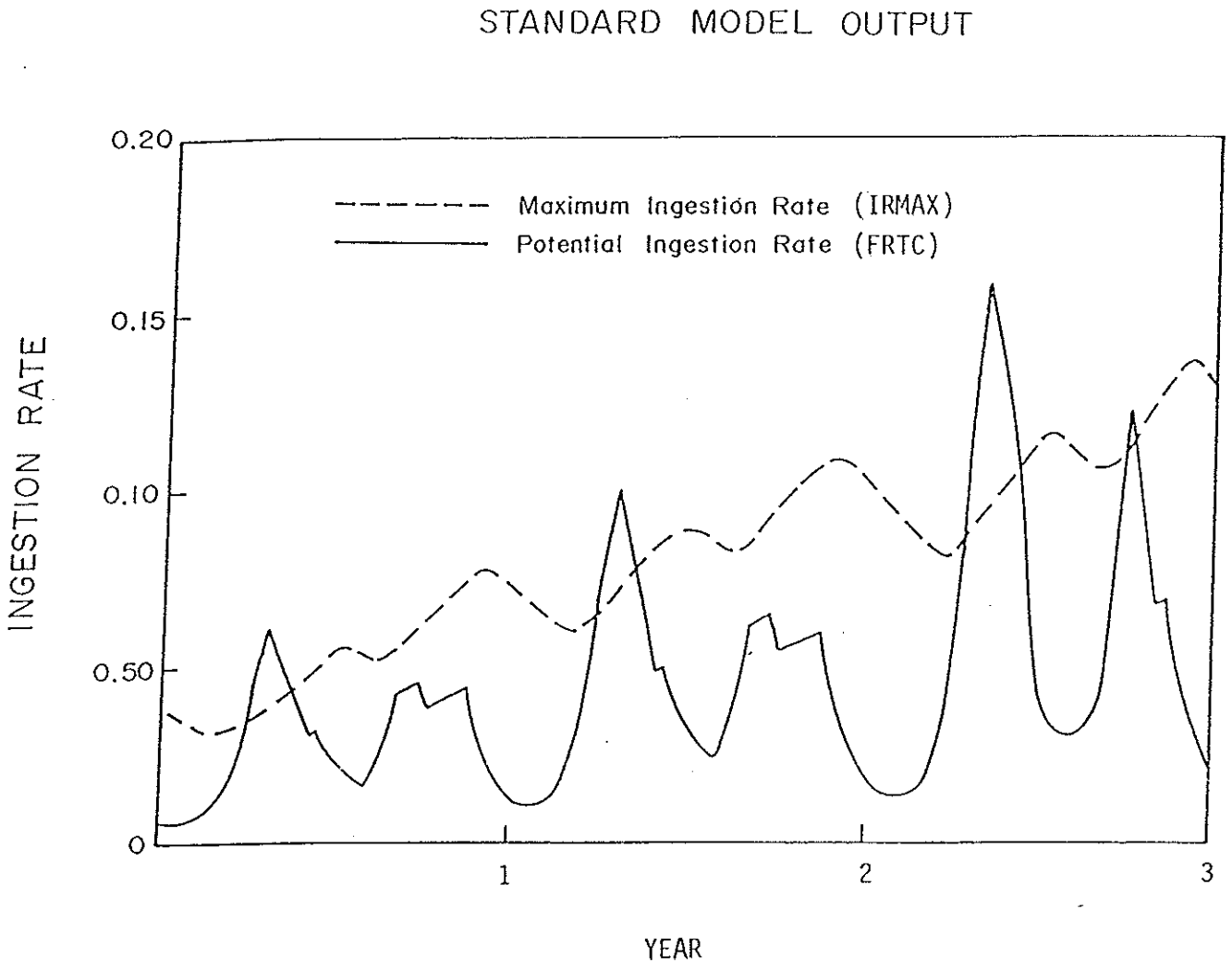


Figure 11. Standard model output for Maximum Ingestion Rate (IRMAX) and Potential Filtration Rate (FRTC)

4.2. Energy Budgets

In order to evaluate the degree to which the various energy partitioning processes of the model represent what is known to occur in nature, an energy budget was calculated for each year of a three year model run. The results, presented in Table 4, compare favorably with energy budgets presented for natural mussel populations (Bayne and Newell, 1983; Dare, 1975; Deslous-Paoli, 1985; Navarro and Winter, 1982; Riisgard and Randlov, 1981; Rodhouse *et al.*, 1984a, 1984b; Rosenberg and Loo, 1983; Thompson, 1984). As is typical of most organisms, the model predicts that most of the ingested material is respired and that the proportion of ingestion respired increases with age. Approximately 60 percent of the total respiration is due to standard respiration, the remainder being accounted for by active respiration. The model output also shows an increase with age, from 16 percent during year one to 38 percent during year three, in the amount of assimilated material that is partitioned into reproductive products. Numerous studies have shown that for *Mytilus* this usually amounts to somewhere between 10 and 40 percent for younger mussels and nearly 100 percent for older mussels (Griffiths and Griffiths, 1987).

Table 4. Annual energy budget for standard model.

	Year I		Year II		Year III	
	gms Carbon	%	gms Carbon	%	gms Carbon	%
Filtration	10.4680		15.9940		21.7799	
Ingestion	9.9500	95.1	15.3858	96.2	19.6058	90.1
Pseudofeces	0.5179	4.9	0.6085	3.8	2.1741	9.9
Ingestion	9.9500		15.5120		19.4796	
Assimilation	2.4875	25.0	3.8465	25.0	4.9014	25.0
Egestion	7.4625	75.0	11.5394	75.0	14.7043	75.0
Assimilation	2.4875		3.8465		4.9016	
Growth	0.3865	15.5	0.3117	13.3	0.6185	12.6
Respiration	2.1011	84.5	3.3346	86.7	4.2831	87.4
Growth	0.3865		0.3117		0.6185	
Biosho	0.0282	7.3	0.4190	8.2	0.0505	8.2
Biosom	0.2899	75.0	0.3095	60.6	0.3315	53.7
Biores	0.0054	1.6	0.0023	0.4	0.0022	0.3
Spawn	0.0623	16.1	0.1571	30.8	0.2236	37.8
Respiration	2.1011		3.3346		4.2831	
Standard	1.2304	58.6	1.9884	59.6	2.5676	60.0
Active	0.8706	41.4	1.3463	40.4	1.7155	40.0

5. MODEL VALIDATION

Model validation consists of comparing model output from simulations using data on driving variables obtained from field measurements and then comparing model output with real data on state variables. The model was validated against four data sets, three of which were obtained from the results of a monitoring program carried out by mussel growers at various sites in the Atlantic Provinces (Brylinsky, 1989), and one of which was obtained by T. Sephton (unpublished) of the Gulf Region Department of Fisheries and Oceans, for a site in Prince Edward Island. Three of these sites are located in Prince Edward Island and one is located in Nova Scotia. All are quite different from one another in terms of physical characteristics, amounts and seasonal variation of particulate matter and age of mussels. This diversity provides a good test of the model's ability to simulate mussel growth under a wide variety of conditions.

The one Nova Scotia site (SFT) is located in a relatively exposed area in an open bay on the south shore and is characterised by relatively low temperatures, low amounts of particulate matter, and mussels less than one year old. Of the Prince Edward Island sites, one is located on the Cardigan River (CARD), an estuary along the northeast coast characterised by moderate temperatures, high particulate matter concentrations and mussels greater than one year old. The remaining two Prince Edward Island sites (TRA1 and TRA2) are both located in Tracadie Bay, a relatively well-protected bay along the northcentral coast. Both of the Tracadie Bay sites are characterised by high temperatures but TRA1 has considerably lower levels of particulate matter. In addition, TRA1 contained mussels less than one year old while TRA2 contained mussels greater than one year old.

All of the validation data sets spanned time periods of less than one year, the shortest being about six months and the longest about eight months. Figure 12 presents the data used for driving variables in the validation simulations. Temperature was input as a sine wave formulation and total particulate organic and inorganic matter as time series data. The state variables used for model validation include total biomass (BIOTOT), shell weight (SHLWT), shell length (SHLLGT) and condition index (CI).

The results of the validation runs are presented in Figures 13 to 16. In general model output agrees with the validation data quite well, both in terms of the rate of growth of biomass and shell and in the timing of spawning events. The best agreement is for the Cardigan River site and the poorest is for Tracadie Bay Site 2. For the latter, model output and field data for BIOTOT, and as a result CI, differ considerably. SHLWT and SHLLGT, however, agree quite well.

The model also appears to be quite successful in predicting spawning events. The validation data for the SFT and TRA1 sites

suggest the occurrence of spawning events and these are predicted by the model. The time of spawning at the SFT site, however, is predicted to be about one month later than that suggested by the validation data.

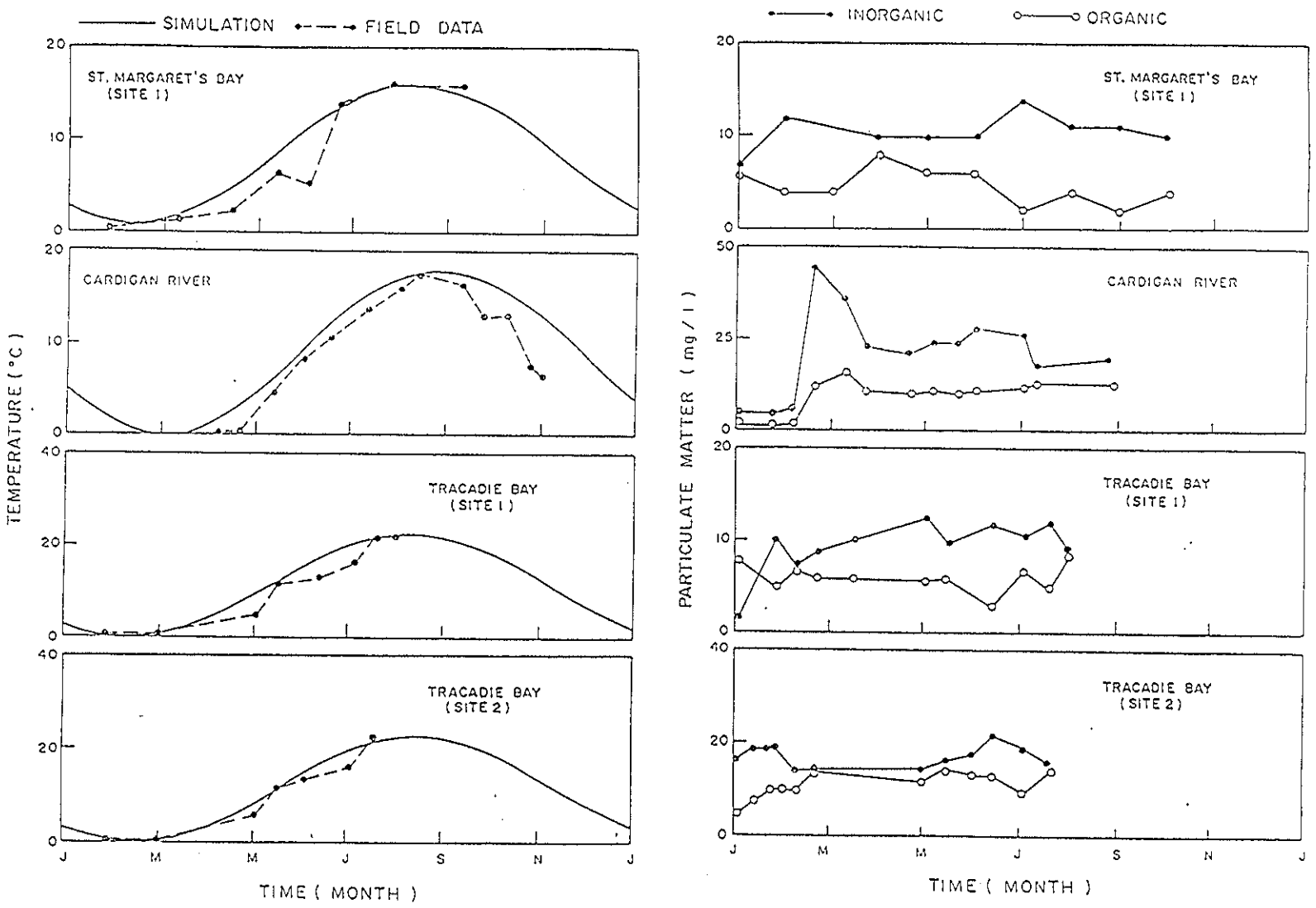


Figure 12. Time series data for driving variables used in model validation

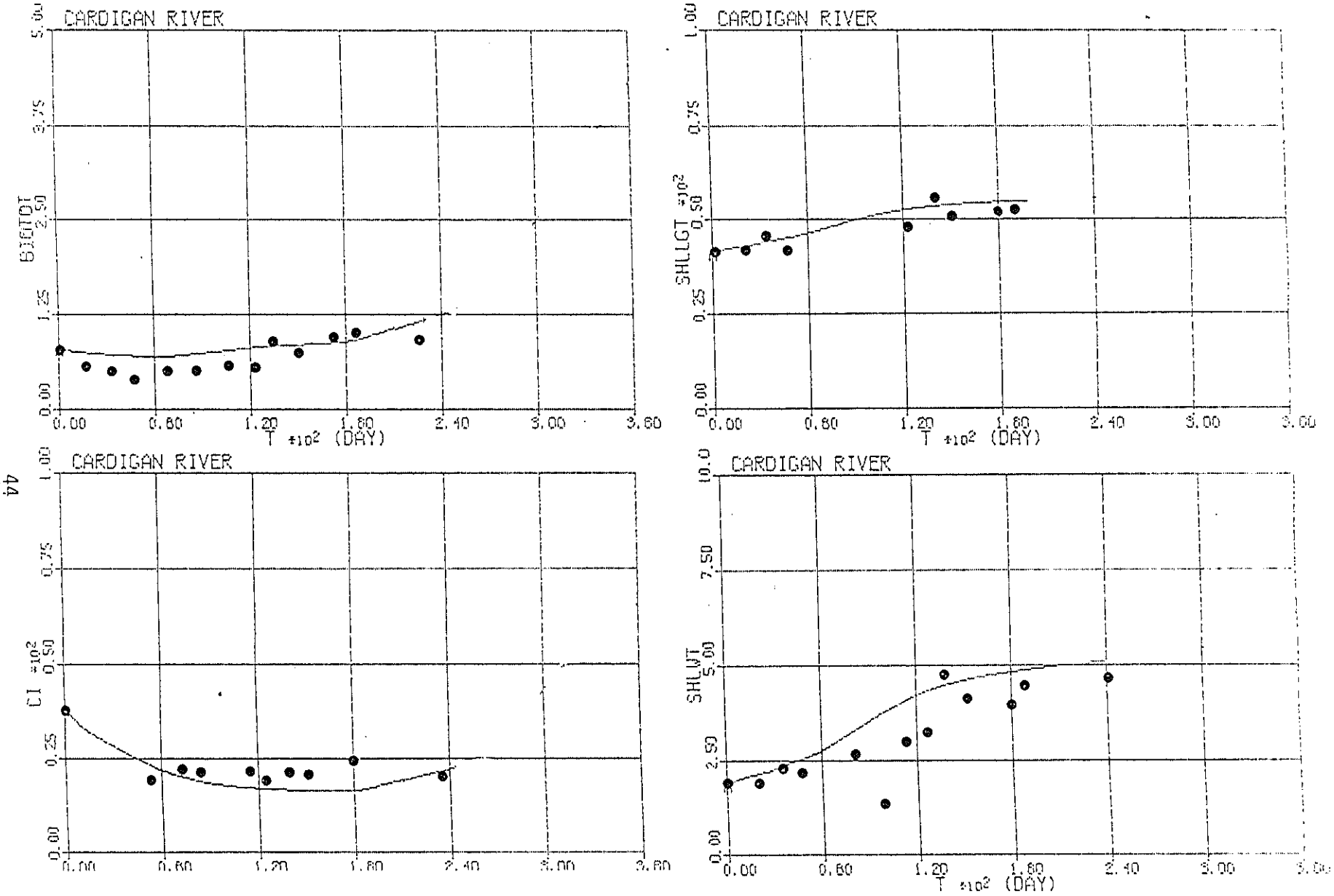


Figure 13. Comparison of model output with validation data for Cardigan River site

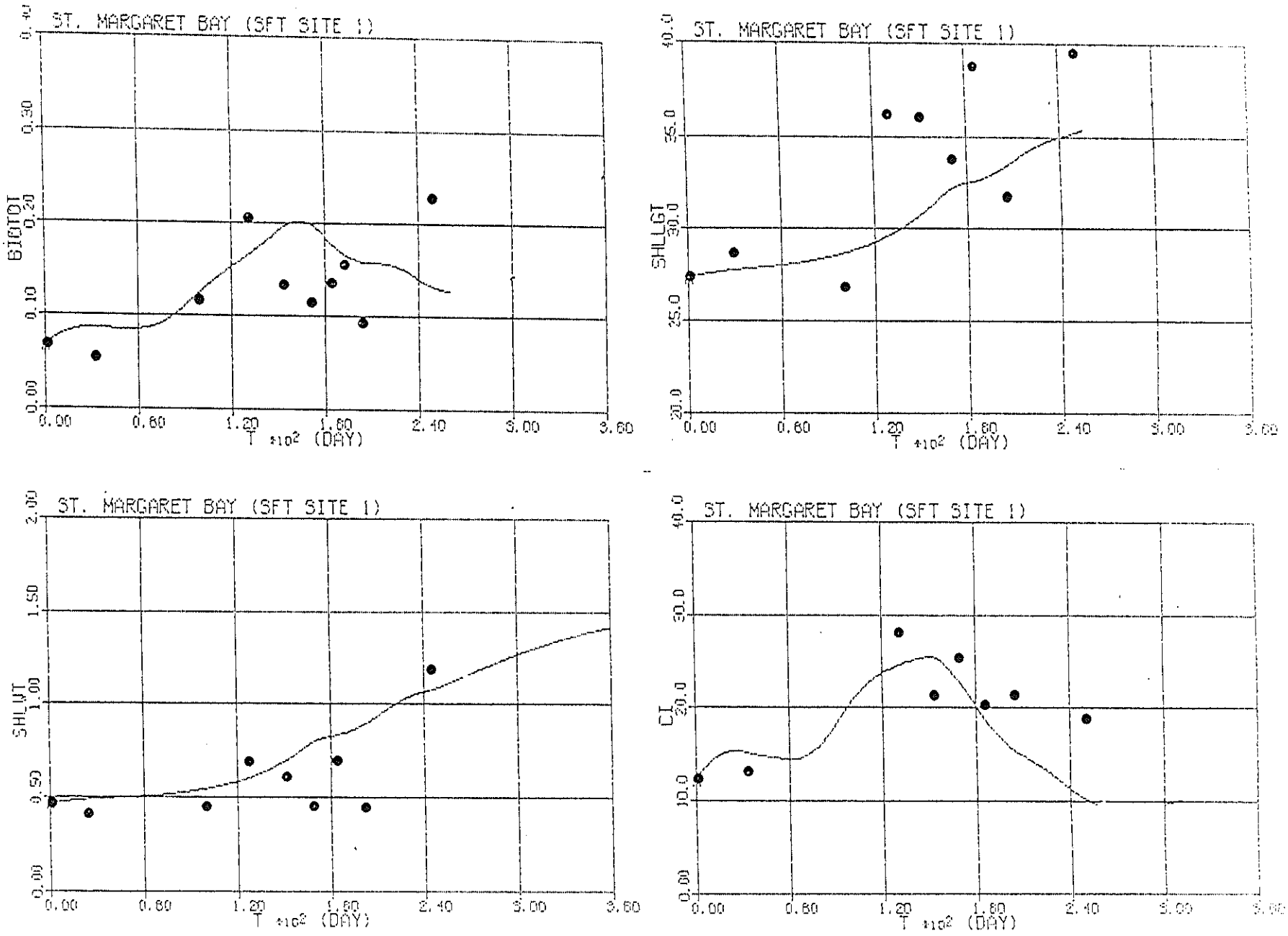


Figure 14. Comparison of model output with validation data for St. Margaret's Bay site

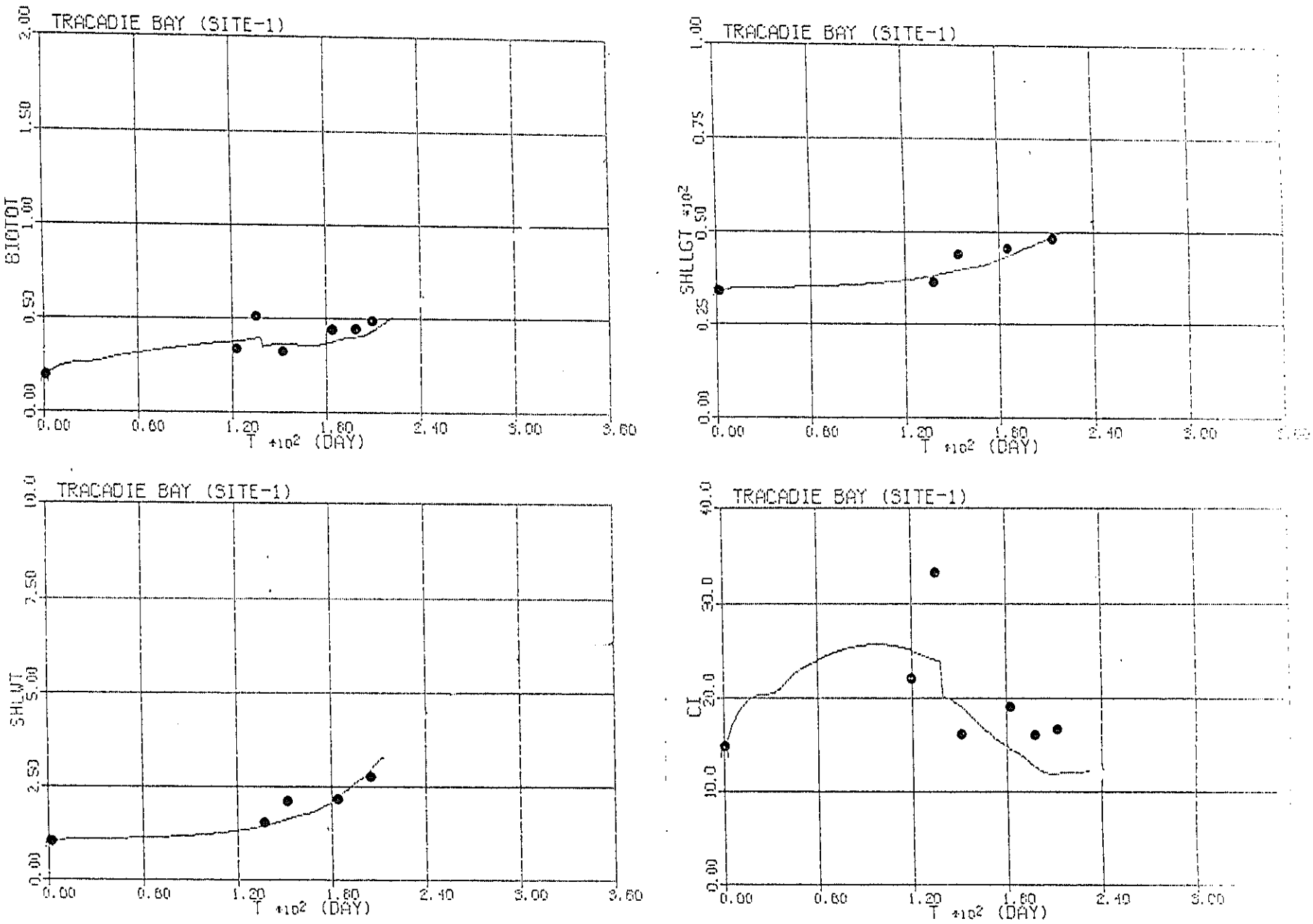


Figure 15. Comparison of model output with validation data for Tracadie Bay Site-1

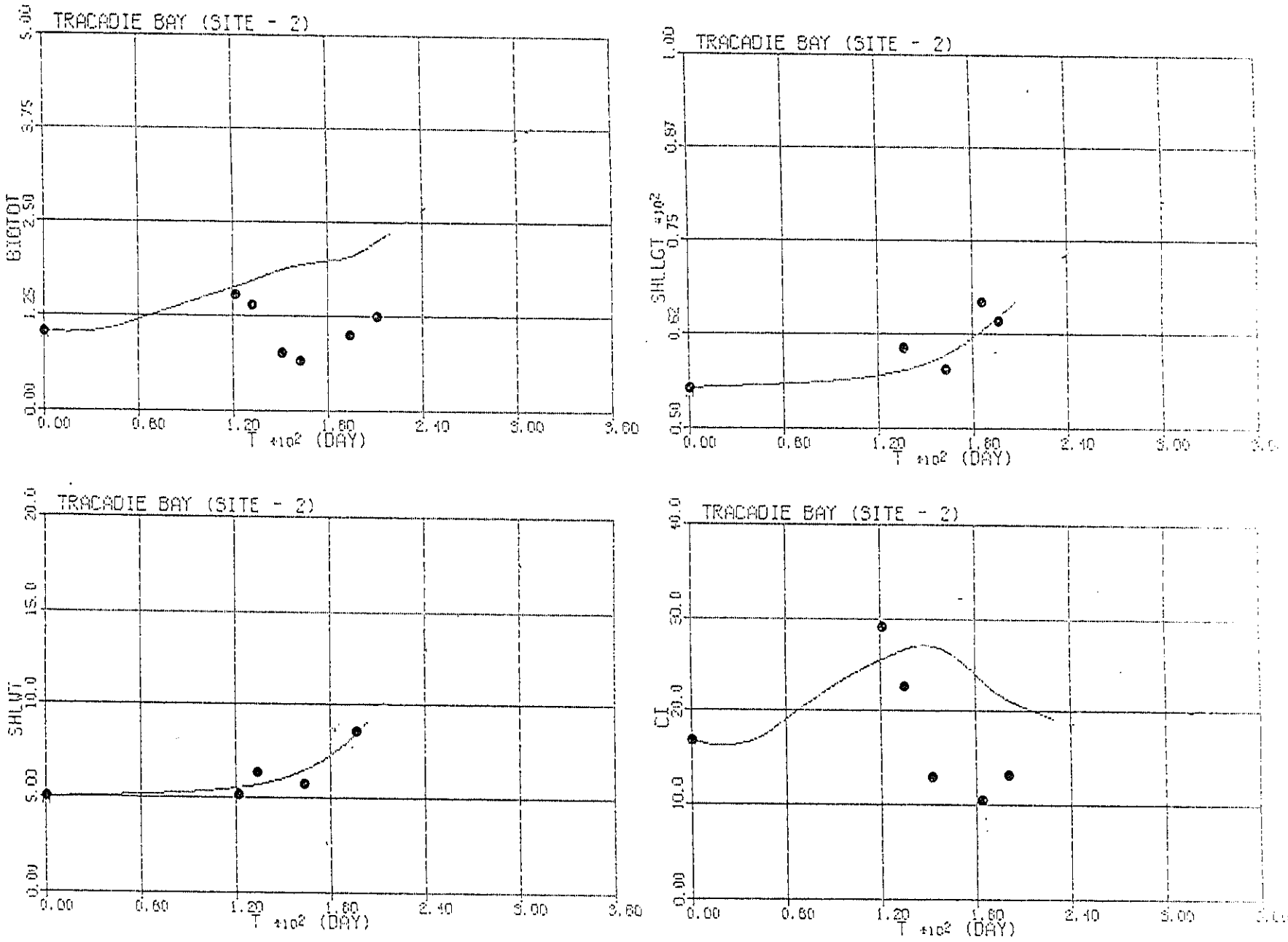


Figure 16. Comparison of model output with validation data for Tracadie Bay Site-2

6. SENSITIVITY ANALYSES

A sensitivity analysis was performed to determine which model parameters have the greatest influence on model output. The procedure was to alter each model parameter by a factor of 10 percent, both positively and negatively, and to compare the resulting output with the output of a standard model run. The amount of change produced in a number of selected state variables at the end of a two year simulation was expressed as both absolute and relative sensitivities. Absolute sensitivities represent the actual amount of change that occurs whereas relative sensitivities represent the proportional amount of change occurring (Brylinsky, 1972). Table 5 presents a summary of relative sensitivities resulting from a 10 percent increase in each parameter. Other sensitivities are presented in Appendix I.

Almost all of the state variables examined are most sensitive to those parameters associated with the direct inputs and losses of organic material, particularly ventilation rate constant (spvc), assimilation efficiency (ae) and standard respiration rate constant (spresc). A 10 percent change in these parameters produces changes on the order of 20 to 45 percent in most state variables. The rate at which gametogenesis occurs as determined by temperature (q10gam) also produces relatively large changes, on the order of 10 to 30 percent, in most state variables. Shell growth is most sensitive to the Q10 function (q10shi) that controls the degree to which temperature influences shell growth. In contrast, parameters associated with weight exponents show relatively small sensitivities, most being on the order of 10 percent or less.

Surprisingly, the median temperature (med) has a significant effect only on the rate at which pseudofeces is produced, a 10 percent increase resulting in almost a 50 percent increase in pseudofeces production. The important influence temperature has on pseudofeces production has been documented by others (Haven and Morales-Alamo, 1966; Tsuchiya, 1980).

Table 5. Relative Sensitivities based on a ten percent increase in each parameter.

	BIOTOT	BIOSOM	CUMSON	CUMIR	CUMAR	CUMER	CUMPF	CUMTRP	CUMSRP	CUMARP	SHLWT	SHLLGT
spvrc	0.387	-0.421	0.221	0.234	0.447	0.234	0.387	0.198	0.221	0.234	0.156	0.049
spvrx	-0.115	-0.123	-0.103	-0.091	-0.091	-0.091	0.237	-0.082	-0.076	-0.091	-0.059	-0.020
spresc	-0.323	-0.351	-0.203	-0.158	-0.158	-0.158	-0.349	-0.121	-0.096	-0.158	-0.127	-0.044
spresx	0.063	0.068	0.074	0.044	0.044	0.044	0.010	0.038	0.033	0.044	0.032	-0.011
spmirc	-0.092	-0.095	0.117	-0.087	-0.087	-0.087	-0.379	-0.091	-0.093	-0.087	-0.069	-0.023
spmirx	-0.034	-0.036	0.002	-0.024	-0.024	-0.024	0.136	-0.022	-0.021	-0.024	-0.016	-0.005
spmgrc	0.002	-0.002	0.078	0.0132	0.013	0.013	0.005	0.012	0.011	0.013	0.031	0.010
spmgrx	0.005	0.004	0.026	0.007	0.007	0.007	0.003	0.006	0.006	0.007	0.011	0.004
spmgam	0.015	0.017	0.005	0.003	0.003	0.003	<0.001	0.001	<0.001	0.003	0.005	0.002
tspn	0.004	0.004	0.001	0.008	0.001	0.001	<0.001	<0.001	<0.001	0.001	0.001	<0.001
ae	0.474	0.520	0.410	0.1149	0.226	0.079	0.016	0.167	0.170	0.163	0.156	0.049
q10tcl	-0.085	-0.090	-0.091	-0.067	-0.067	-0.067	-0.078	-0.060	-0.055	-0.067	-0.045	-0.015
q10tch	-0.054	-0.058	-0.029	-0.034	-0.034	-0.034	-0.003	-0.030	-0.026	-0.034	-0.024	-0.008
q10gam	0.319	0.346	0.162	0.194	0.194	0.194	0.010	0.166	0.146	0.194	0.131	0.041
q10shi	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.299	0.081
irres	-0.140	-0.153	-0.059	-0.061	-0.061	-0.061	-0.010	-0.045	-0.071	-0.007	-0.054	-0.018
arres	-0.106	-0.116	-0.045	-0.046	-0.046	-0.046	-0.007	-0.034	-0.053	-0.005	-0.041	-0.014
mcd	-0.030	-0.035	0.042	-0.009	-0.009	-0.009	0.461	-0.008	-0.006	-0.010	-0.001	<0.001

7. POTENTIAL APPLICATIONS

A major objective of this project was to produce a simulation model that would be useful in addressing a wide range of concerns of interest to both practicing mussel culturists and those involved in development of the mussel aquaculture industry. There are numerous applications to which the model can be put. The following section illustrates three possibilities; one dealing with the estimation of the carrying capacity of a culture site, one dealing with an evaluation of a potential management strategy, and another dealing with the biological problem of understanding the possible causes of summer mortality. Other potential applications include combining the present model with an economic model to perform various types of economic analyses, or combining the model with an ecosystem model to address problems associated with the potential environmental impacts of mussel culture.

7.1. Estimation of Carrying Capacity

Of major interest to those involved in mussel aquaculture is determination of the carrying capacity of a particular site. Carrying capacity is usually broadly defined as the number or biomass of mussels that can be stocked before growth rates become reduced. A number of researchers have attempted to develop models that could be used to estimate carrying capacity. Incze *et al.* (1981) developed the first model to estimate carrying capacity. The assumption underlying their model was that the carrying capacity of a system would be reached when the filtration demand equalled one-half of the ambient seston concentration. The parameters required by their model are maximum filtration rate, current velocity and seston concentration. Rosenberg and Loo (1983) extended this approach to provide estimates of the carrying capacity of a natural mussel culture site. More recently, Carver and Mallet (1990) estimated the carrying capacity of a small coastal inlet in Nova Scotia using data obtained from field measurements of filtration rates and exchange ratios and the assumption that carrying capacity equalled the biomass of mussels required to ingest one-half of the food supply.

Common to all of these studies is the assumption that carrying capacity depends on the relationship between food supply and food demand, and that food supply is determined by seston concentration and the rate at which seston is delivered (expressed as either current velocity or exchange ratio). Under conditions of low particle delivery rates seston will be filtered faster than it is supplied resulting in the depletion of particulate matter as water flows through a culture site. Incorporation of these ideas into the present model requires altering the model to include the effect of this competition for available food between mussels. Theoretically this can be done using the following mathematical formulation:

$$CIR = PIR * (1 - e^{-PDR/PIR})$$

$$PDR = CV * TPM \qquad \text{where,}$$

CIR = Corrected Population Ingestion Rate
PIR = Uncorrected Population Ingestion Rate
PDR = Particle Delivery Rate
CV = Current Velocity
TPM = Total Particulate Matter

This formulation corrects the ingestion rate by a factor proportional to the rate at which food is delivered and the rate at which it would be ingested if there were no food limitation. Figure 17 illustrates how the magnitude of the correction factor (expressed as CIR/PIR) changes in relation to the ratio of particle delivery rate and ingestion rate. If current velocity is low and filtering rate high, the correction factor is large because the potential ingestion rate is much greater than the rate at which food is being delivered thus resulting in a high level of double filtration (i.e., filtration of water that has been partially filtered by competing mussels). Generally, as long as the ratio of particle delivery rate and ingestion rate remains above about five, the correction factor is very small. At a ratio of two (the value used in the previously mentioned studies of carrying capacity) the reduction in ingestion rate is about 86.5 percent.

The above formulation was incorporated into the standard model to illustrate how it may be applied to estimate the carrying capacity of a culture site. Carrying capacity is here defined as the number of mussels that can be supported per cubic meter of water flow before the ratio of corrected population ingestion rate to uncorrected population ingestion rate falls below a critical value. The critical value was set at 0.9 and is based on the assumption that a reduction of 10 percent in ingestion rate would not seriously decrease the time required for a mussel to reach marketable size. The mathematical formulation used in the model is developed as follows:

$$0.9 = (1 - e^{-PDR/PIR})$$

taking the ln of both sides and rearranging,

$$PIR = PDR / 2.3$$

substituting N*IR for PIR where N = Number of Mussels,

$$N = PDR / 2.3 * IR$$

substituting Q*TPMCM for PDR where Q = Cubic Meters d^{-1} and TPMCM = Grams Particulate Organic Matter m^{-3},

$$N = Q * TPMCM / 2.3 * IR$$

and substituting Q = CV * 864 where CV = Current Velocity in cm sec^{-1},

$$N = CV * 864 * TPCM / 2.3 * IR$$

This formulation was used in the standard model to estimate carrying capacity in terms of the numbers of mussels that could be supported per cubic meter of water flow for a system with average daily current velocities of .1 , .5 and 1 cm sec^{-1}. The results are presented in Figure 18 and illustrate that carrying capacity, when expressed in terms of numbers of mussels, will vary seasonally as a result of the influence of seasonal variations in total particulate matter and water temperature on ingestion rates, and decrease annually as a result of the increase in mussel size.

To evaluate carrying capacity in terms of total biomass N was multiplied by BIOTOT. The results (Figure 19) illustrate that in this case, although the seasonal variations in carrying capacity are still evident, the total biomass that can be supported increases annually as a result of the underlying allometric relationships that allow a greater biomass to be supported per unit of ingestion as an individual mussel increases in size.

To produce estimates of carrying capacity in terms of the number of mussel lines that could be supported per cubic meter of water flow it was assumed that the distance between mussel socks was 0.5 m and that each meter of mussel line contains 200 mussels. The results of a standard model run are presented in Figure 20. The seasonal and annual trends are the same as those for mussel biomass but the units are in number of tiers per cubic meter of flow.

All of the above simulations were run based on mean daily current velocities. Currents in most mussel aquaculture systems, however, are tidally generated and vary on an hourly as well as a daily basis. Although for any specific culture site a data base could be developed for daily variations in tidally induced currents and could easily be incorporated into the model, it would be difficult to incorporate hourly based variations since the model is based on a daily time scale. The main problem in using daily averages of current velocity is that this assumes the mussels are able to integrate the hourly changes in particle delivery rate. In reality, for a system dominated by tidally induced currents, a mussel would be subjected to periods of low delivery rates during slack tide and high delivery rates during high tide. During the former the mussel population may become food limited. This problem is discussed by Incze *et al.* (1981) who point out that there is little available information that allows us to determine how long a mussel population can withstand sub-optimal food concentrations before growth is significantly reduced.

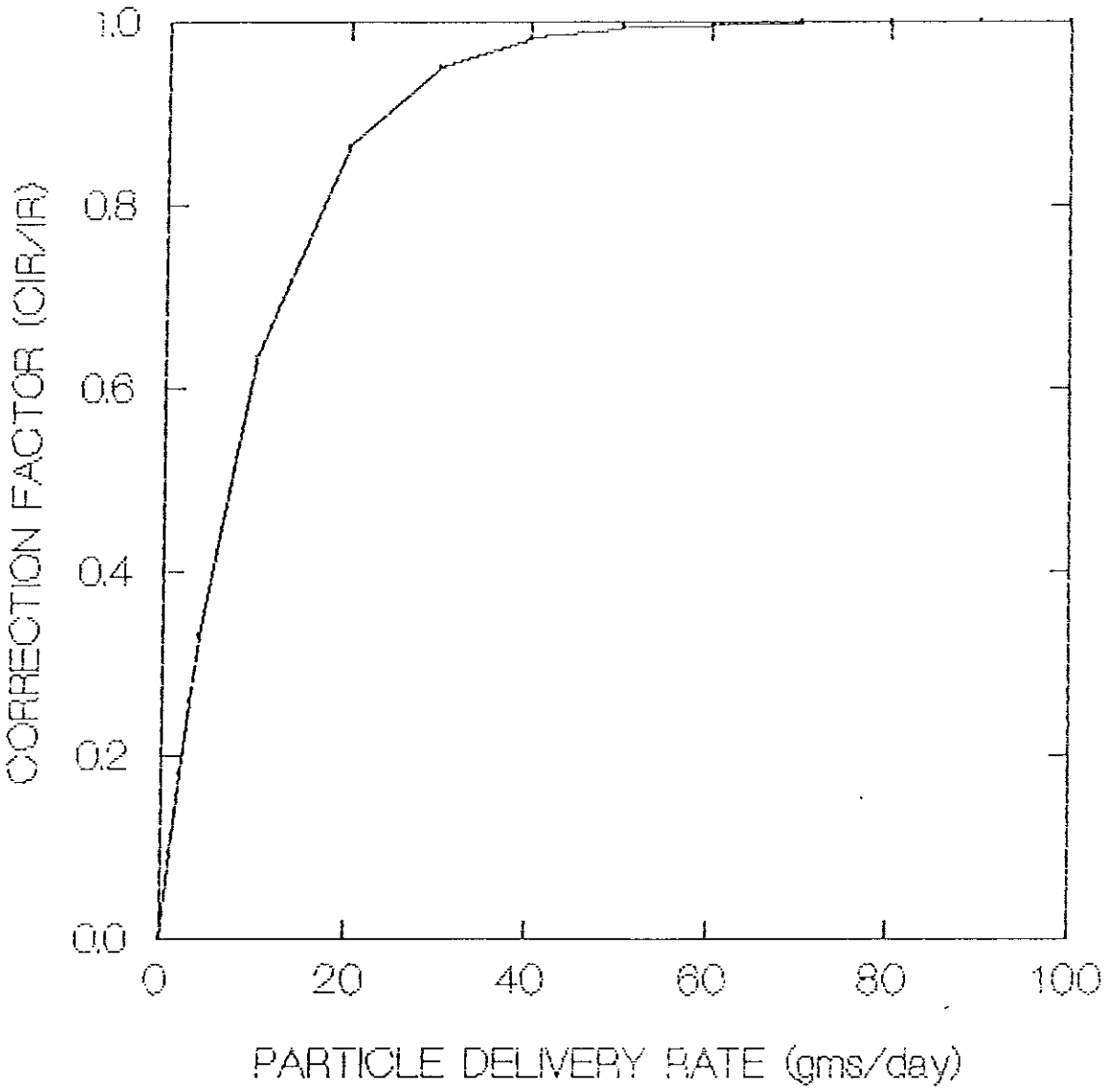


Figure 17. Relationship between correction factor (CIR/IR) and particle delivery rate

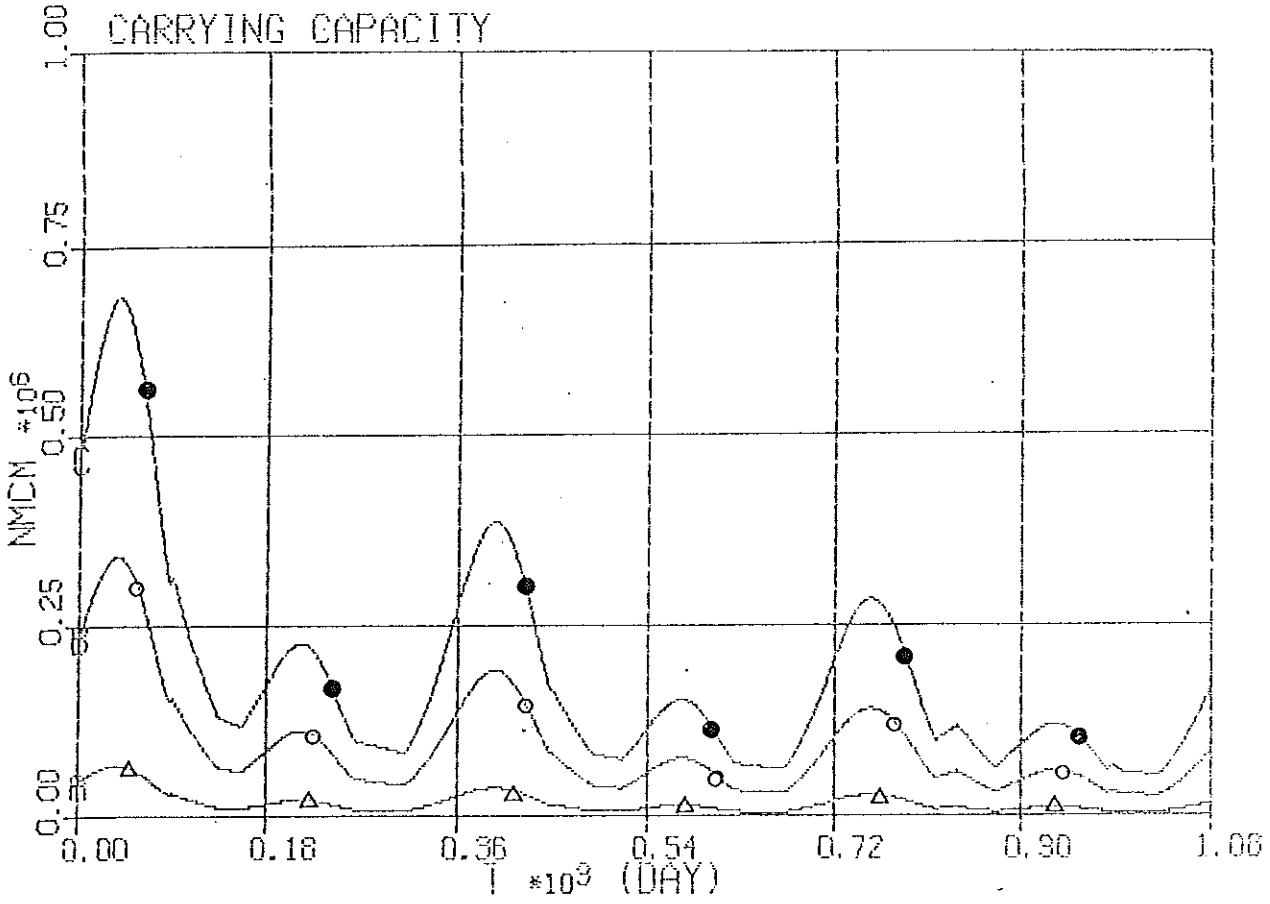


Figure 18. Seasonal and annual variation in carrying capacity, expressed as number of mussels per cubic meter of water flow, for a system with average daily current velocities of 0.1 (△), 0.5 (○) and 1.0 (●) CM SEC^{-1}

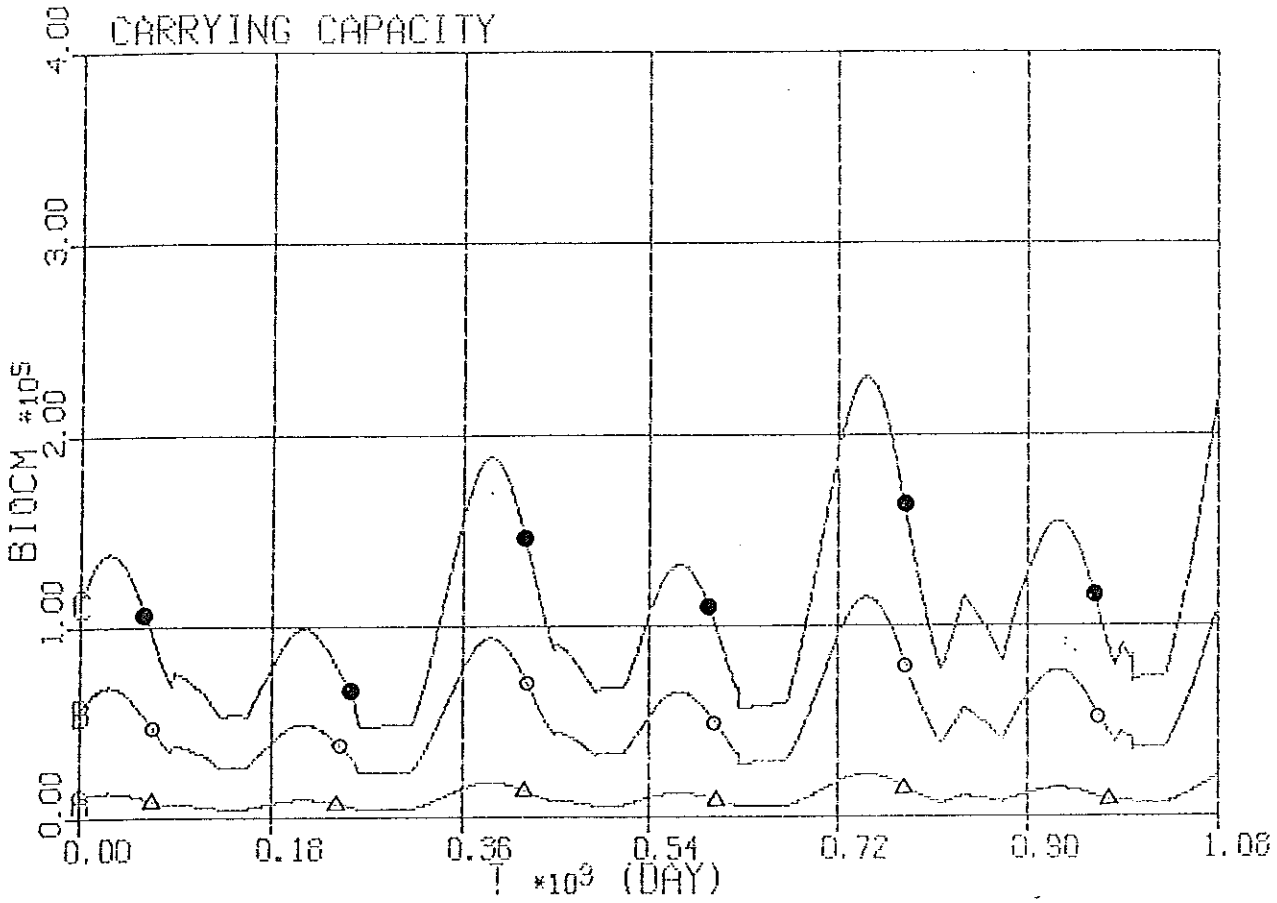


Figure 19. Seasonal and annual variation in carrying capacity, expressed as biomass of mussels per cubic meter of water flow, for a system with average daily current velocities of 0.1 (△), 0.5 (○) and 1,0 (●) CM SEC^{-1}

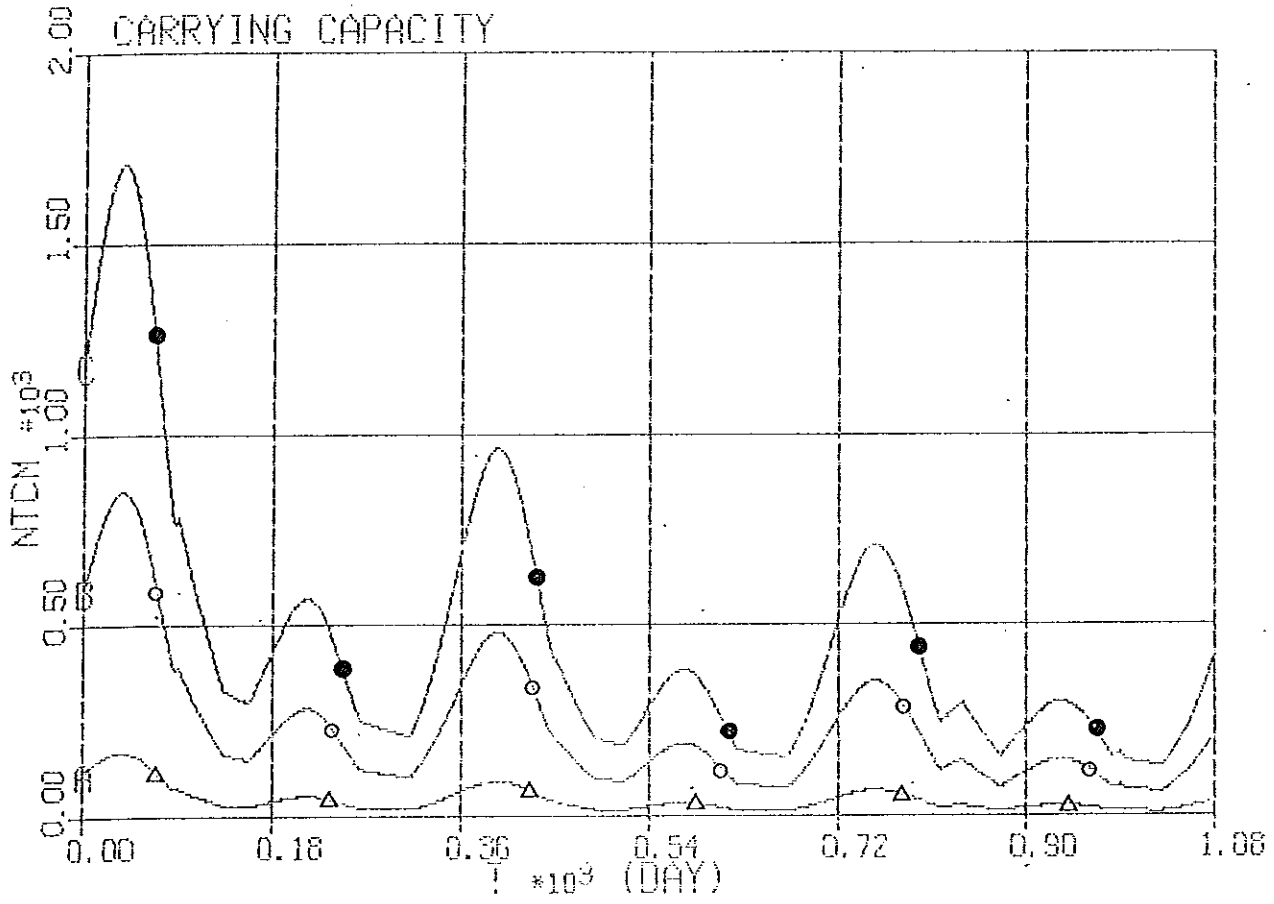


Figure 20. Seasonal and annual variation in carrying capacity, expressed as number of lines per cubic meter of water flow, for a system with average daily current velocities of 0.1 (△), 0.5 (o) and 1.0 (●) CM SEC^{-1}

7.2. Evaluation of Management Strategies

Numerous undocumented observations suggest that, at culture sites exhibiting thermal stratification, mussels often seem to perform better when grown in the cooler lower waters as opposed to the warmer upper waters. If true, this places some doubt as to the usefulness of raising mussel lines previously sunken to avoid ice damage. To evaluate the practice of leaving mussels permanently below the thermocline the results of two model runs having different temperature characteristics were compared. One model run was made in which water temperature varied seasonally from 0 to 30 C. This represents what might occur in surface waters. The other model run was made using a temperature range of 0 to 10 C. This represents the variation that might be typical of lower waters. Seasonal variation and concentration of particulate matter were the same in both model runs.

The results of the two model runs are presented in Figure 21. Surprisingly, the mussels grown in the cooler waters grew more rapidly and, after three years, attained a final biomass almost twice that of the mussels subject to the higher temperatures. The reason for the increased growth at lower temperatures is that, although filtration rates are lower because of their dependence on temperature, there are no losses from either pseudofeces production or, more importantly, spawning.

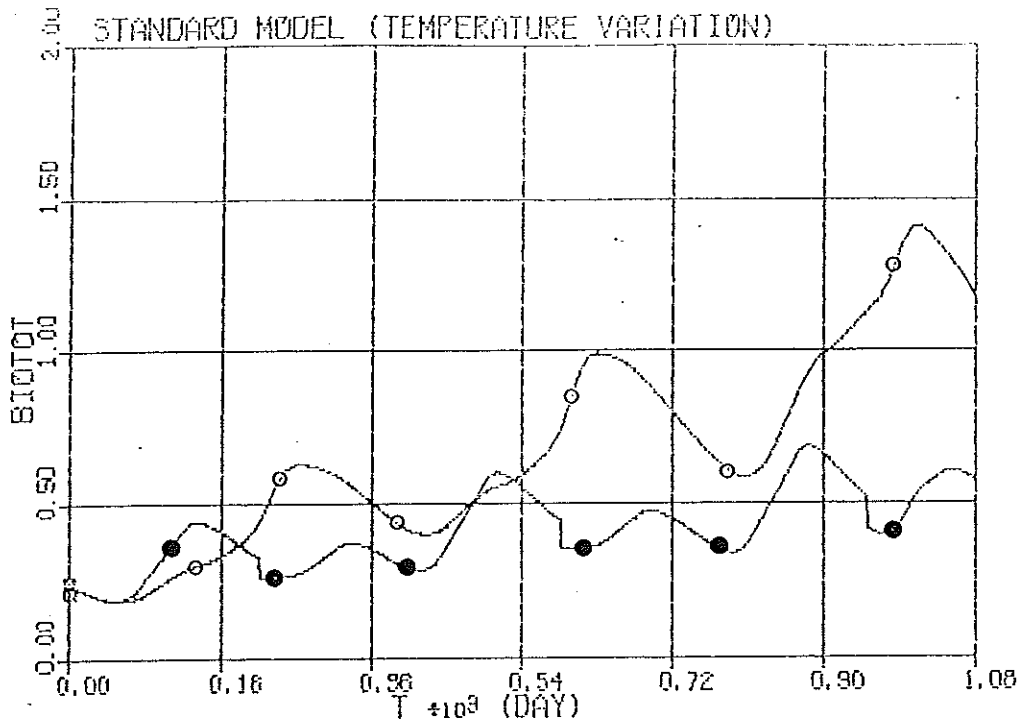
Shell size, however, exhibited the opposite trend. Mussels grown in the cooler waters attained lower shell weights and lengths than those grown in the warmer waters (Figure 21). The difference, however, was not as dramatic as for biomass.

7.3. Understanding Summer Mortality

At some mussel culture sites the mortality of mussels during late summer is often a problem. Usually the larger, market-sized mussels are most seriously affected. Although the present model does not actually predict when or if mortality will occur, if the possibility of mortality can be defined in terms of a critical condition index (e.g., if the condition of a mussel falls below a certain critical value the mussel will die), then the model can be used to evaluate potential mortality. Since the model routinely outputs condition indices all that is required is to run simulations under specified conditions and observe the trends in condition index.

The results of the previously described simulations to evaluate the differences in growth rates under different temperature regimes can be used to illustrate this approach. Figure 22 compares the seasonal variations in the condition index. At the lower temperatures, the condition index never falls below a value of about 12 while at the higher temperatures, excepting for a short period at the beginning of the simulation, the condition index never attains a value greater than 12. These results support the concept that high temperatures may cause stress leading to mortality because of the

losses that are incurred as a result of the increased probability of spawning events that essentially deplete food reserves (Thompson, 1987).



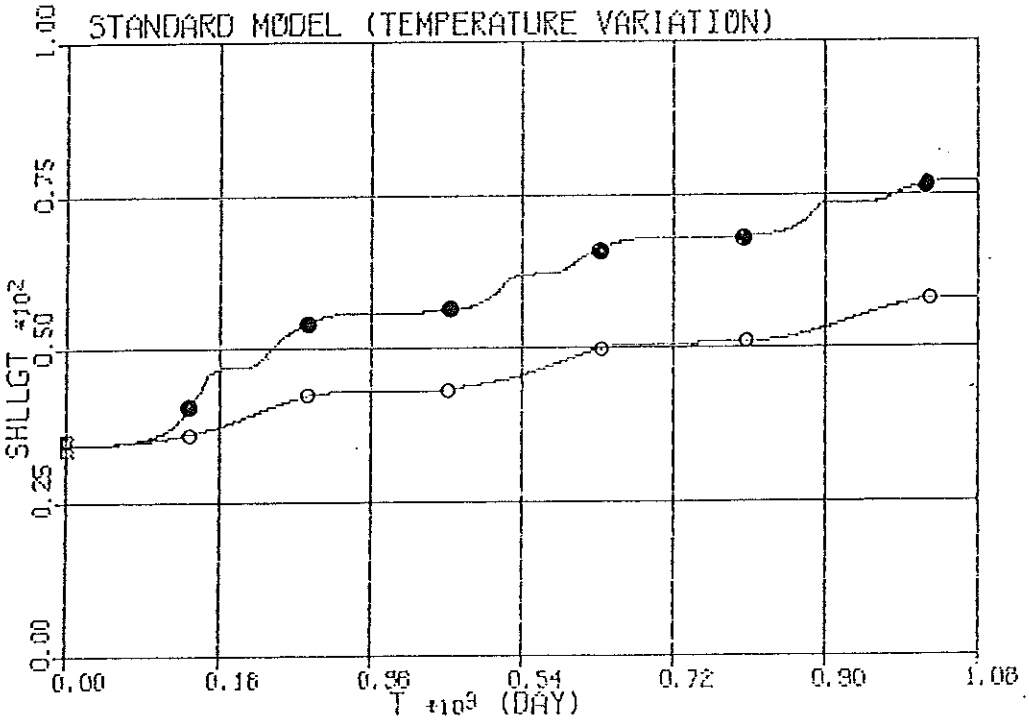


Figure 21. Comparison of growth characteristics for mussels grown under different temperature regimes (o- 0 to 10 C; ● - 0. to 30 C)

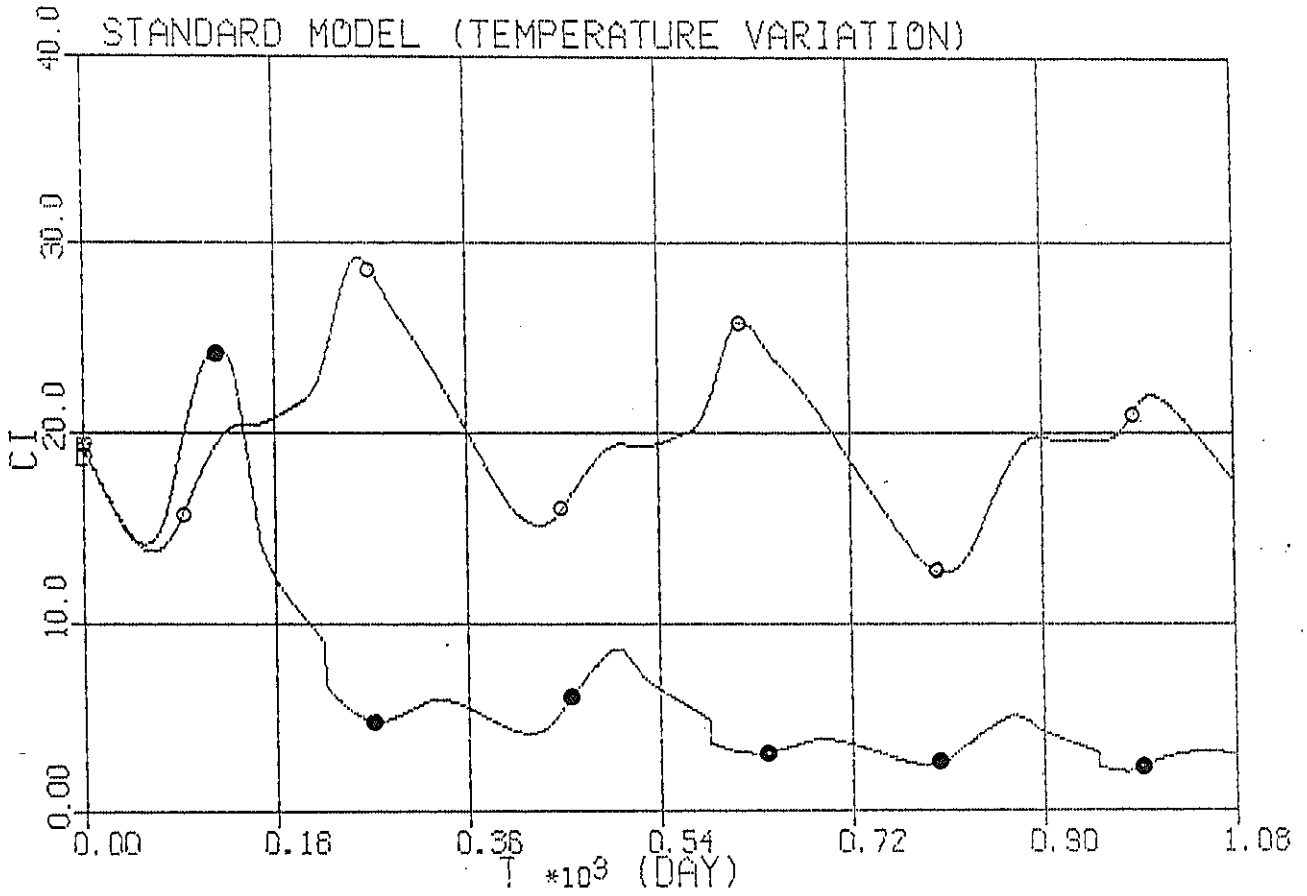


Figure 22. Comparison of condition indices for mussels grown under different temperature regimes (o- 0 to 10 C; ●-0 to 30 C)

8. FUTURE DEVELOPMENT

Although there has been substantial laboratory and field study devoted to understanding the factors controlling growth, spawning and mortality of *Mytilus*, there still exist serious gaps in our knowledge of the important processes involved, as well as of the magnitudes and nature of the rate parameters that control these processes. Much of the information used to develop the present model was obtained from studies having quite different objectives than to provide information to be used in model development. Despite this shortcoming in available data, the model presented here does appear to have considerable ability to describe the general behavior of *Mytilus* under a wide variety of culture conditions. This is encouraging, especially since all of the parameters required by the model are both biologically interpretable and experimentally measurable. Further development of the model to increase its resolution and provide more accurate estimates will probably have to await studies designed specifically to test the assumptions underlying the model and to provide better estimates of parameter values. In this respect, the areas of study most likely to result in significant improvements of the model are those that deal with the processes and parameters to which the model is most sensitive. Based on the results of the sensitivity analyses, these include the processes and parameters associated with the control of filtration, assimilation, respiration and spawning.

It is interesting to note that most of these processes have been in the past and are presently the topic of much debate. With regard to the filtration process there is currently a good deal of confusion as to the ability of *Mytilus* to control its ventilation rate to optimize growth efficiency under conditions of varying food availability (Bayne *et al.*, 1988; Foster-Smith, 1975; Jorgensen *et al.*, 1988, 1990; Navarro and Winter, 1982). The present model does not allow for optimization but could easily be modified to include this concept. The assimilability of natural seston is also poorly understood, both in terms of food quality (which has proved difficult to define quantitatively) and the possible effect of ingestion rate on assimilation efficiency (Bayne and Newell, 1983; Bayne and Worrall, 1980; Deslouis-Paoli *et al.*, 1990;). Providing some means of allowing food quality to vary seasonally, perhaps in relation to the ratio of living organic to non-living organic material is one approach towards dealing more reasonably with this factor. Although there have been numerous estimates of the parameters associated with standard respiration rates, there is conflicting evidence on the ability of *Mytilus* to acclimate its standard respiration rate under varying temperatures (Newell and Branch, 1980; Widdows, 1973a; Widdows and Bayne, 1971). Perhaps our poorest understanding of the energetics of *Mytilus* lies in the nature of the relationship between active respiration and feeding, assimilation and absorption processes (Bayne *et al.*, 1976; Bayne and Scullard, 1977; Hawkins *et al.*, 1985; Navarro and Winter, 1982 refs). The role of endogenous versus exogenous factors in controlling spawning events is also poorly understood (Seed, 1976).

Further development of the model requires additional data bases that can be used to more rigorously test the model. Very little of this kind of information is available in the published literature and, although some data collection and monitoring programs that can supply this data presently exist, most do not include information on many of the more important variables, particularly current velocity, glycogen reserves and spawning condition.

For the model to be useful in understanding the impact of mussel culture on marine environments, it must eventually be incorporated into a larger ecosystem model. This is particularly true for culture systems that tend to be relatively closed since this would increase the likelihood that the mussel population itself will have an effect on the processes controlling food availability.

In summary, although the model presented here offers considerable potential for dealing with a number of problems faced by the mussel aquaculture industry, it requires further validation to more completely evaluate its potential and limitations. This will most likely come about only from studies designed specifically to test its underlying assumptions and to provide better estimates of its quantitative elements.

9. ACKNOWLEDGEMENTS

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10. REFERENCES

Ali, R.M. 1970. The influence of suspension density and temperature on filtration rate of *Hiatella artica*. Mar. Biol. 6:291-303.

Almada-Villela, P.C., J. Davenport, and L.D. Gruffydd. 1982. The effects of temperature on the shell growth of young *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 59:275-288.

Anon. 1985. Aquaculture: An opportunity for Canadians. Science Council of Canada. Ottawa.

Bayne, B.L. 1973. Physiological changes in *Mytilus edulis* L. induced by temperature and nutritive stress. J. Mar. Biol. Ass. U.K. 53:39-58.

Bayne, B.L. and R.C. Newell. 1983. Physiological energetics of marine molluscs, p. 407-515. *In* K.M. Wilbur and A.S.M. Saleuddin [eds.], The Biology of Molluscs: Physiology. Academic Press.

Bayne, B.L. and C. Scullard. 1977. An apparent specific dynamic action in *Mytilus edulis* L. J. Mar. Biol. Assoc. U. K. 57:371-378.

Bayne, B.L. and C.M. Worrall. 1980. Growth and production of mussels *Mytilus edulis* from two populations. Mar. Ecol. Prog. Ser. 3:317-328.

Bayne, B.L., J. Widdows, and R.J. Thompson. 1976. Physiological integrations, p. 261-291. *In* B.L. Bayne [ed.], Marine mussels. International Biological program 10. Cambridge University Press.

Bayne, B.L., D.L. Hollard, M.N. Moore, D.M. Lowe, and J. Widdows. 1978. Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. J. Mar. Biol. Ass. U.K. 58:825-841.

Bayne, B.L., J. Widdows, and R.E.I. Newell. 1977. Physiological measurements on estuarine bivalve molluscs in the field, p. 57-58. *In* B.F. Keegan, P.O. Ceidgh and P.J.S. Boaden [eds.], Biology of Benthic Organisms. Pergamon Press.

Bayne, B.L., A.J.S. Hawkins, and E. Navarro. 1988. Feeding and digestion in suspension-feeding bivalve molluscs: the relevance of physiological compensations. Am. Zool. 28:147-159.

Bressin, M. and M.G. Marin. 1985. Seasonal variation in biochemical composition and condition index of cultured mussels (*Mytilis galloprovincialis*) in the lagoon of Venice (North Adriatic). Aquaculture 48(1):13-21.

Brylinsky, M. 1972. Steady-state sensitivity analysis of energy flow in a marine ecosystem, p. 88-101. *In* B.C. Patten [ed.], Systems analysis and simulation in ecology. Academic Press.

Brylinsky, M. 1989. Final report on the water quality monitoring program for mussel growers. Publication No. 11, Acadia Centre for Estuarine Research.

Carver, C.E.A. and A.L. Mallet. 1990. Estimating the carrying capacity of a coastal inlet for mussel culture. Aquaculture 88:39-53.

Ceccherelli, V.N. and A. Barboni. 1983. Growth, survival and yield of *Mytilus galloprovincialis* Lamk. on fixed suspended culture in a bay of the Po River delta. Aquaculture 34:101-114.

Ceccherelli, V.V. and R. Rossi. 1984. Settlement, growth and production of the mussel *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 16:173-184.

Dare, P.J. 1975. Settlement, growth and production of the mussel *Mytilus edulis* L. in Morecambe Bay. Fish. Invest. Min. Agric., Fish and Food, London. Ser. II.

Dare, P.J. and D.B. Edwards. 1975. Seasonal changes in flesh weight and biochemical composition of mussels (*Mytilus edulis* L.) in the Conway estuary, North Wales. J. Exp. Mar. Biol. Ecol. 18:89-97.

Deslous-Paoli, J.M. 1985. Assessment of energetic requirements of reared molluscs and their main competitors, p. 319-346. *In* Shellfish culture and management. International Seminar in LaRochell, France.

Deslous-Paoli, J.M. S. Boromathanarat, M. Heral, W. Boromathanarat, and D. Razet. 1990. Energy budget of a Mytilus edulis L. population during its first year on bouchots in the bay of Marennes-Oleron. Aquaculture 91:49-63.

Emmett, B., K. Thompson, and J.D. Popham. 1987. The reproduction and energy storage cycles of two populations of *Mytilus edulis* (Linne) from British Columbia. J. Shell. Res. 6:29-36.

Foster-Smith, R.L. 1975. The effect of concentration of suspension on the filtration rates and pseudofecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu). J. Exp. Mar. Biol. Ecol. 17:1-22.

Gabbott, P.A. 1983. Developmental and seasonal metabolic activities in marine molluscs, p. 165-217. *In* The Mollusca, Vol. 2, Environmental biochemistry and physiology. Academic.

Gabbott, P.A. and B.L. Bayne. 1973. Biochemical effects of temperature and nutritive stress on *Mytilus edulis* L. J. Mar. Biol. Assoc. U. K. 53: 269-286.

Griffiths, C.L. and R.J. Griffiths. 1987. Bivalvia, p. 1-89. *In* T.J. Pandian and F.J. Vernberg [eds.], Animal Energetics, Vol. 2. Academic.

Hamburger, K., F. Mohlenberg, A. Randlov, and H.V. Riisgard. 1983. Size, oxygen consumption and growth in the mussel *Mytilus edulis*. Mar. Biol. 75:303-306.

Haven, D.S. and R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. Limnol. Oceanogr. 11:487-498.

Hawkins, A.J.S. and B.L. Bayne. 1985. Seasonal variation in the relative utilization of carbon and nitrogen by the mussel *Mytilus edulis*. Mar. Ecol. Prog. Ser. 25:181-188.

Hawkins, A.J.S., B.L. Bayne, and K.R. Clarke. 1983. Co-ordinated rhythums of digestion, absorption and excretion in *Mytilus edulis* (Bivalvia: Mollusca).

Hawkins, A.J.S., P.N. Salkeld, B.L. Bayne, E. Gnaiger, and D.M. Lowe. 1985. Feeding and resource allocation in the mussel *Mytilus edulis*: evidence for time-averaged optimization. Mar. Ecol. Prog. Ser. 20:273-287.

Hilbish, T.J. 1986. Growth trajectories of shell and soft tissue in bivalves: seasonal variation in *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 96:103-113.

Hildreth, D.I. and A. Mallet. 1980. The effect of suspension density on the retention of 5 um diatoms by the *Mytilus edulis* gill. Biol. Bull. 158:316-323.

Incze, L.S., R.A. Lutz, and L. Watling. 1980. Relationships between effects of environmental temperature and seston on growth and mortality of *Mytilus edulis* in a temperate northern estuary. Mar. Biol. 57:147-156.

Incze, L.C., R.A. Lutz, and E. True. 1981. Modelling carrying capacity for bivalve molluscs in open, suspended-culture systems. J. World Mar. Soc. 12:143-155.

Jorgensen, C.B., P.S. Larsen, F. Mohlenberg and H.U. Riisgard. 1988. The mussel pump: properties and modelling. Mar. Ecol. Prog. Ser. 45:205-216.

Jorgensen, C.B., P.S. Larsen, and H.V. Riisgard. 1990. Effects of temperature on the mussel pump. Mar. Ecol. Prog. Ser. 68:89-97.

Kautsky, N. 1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. Mar. Biol. 68:143-160.

Kiorbe, T. and F. Mohlenberg. 1981. Particle selection in suspension feeding bivalves. Mar. Ecol. Prog. Ser. 5:291-296.

Kiorbe, T., F. Mohlenberg and O. Nohr. 1980. Feeding, particle selection and carbon adsorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. Ophelia. 19:193-205.

Klepper, O. and H. Scholten. 1988. A model of carbon flows in relation to macrophyte food supply in the Oosterschelde Estuary (S.W. Netherlands). Balans nota 42. Delta Institute for Hydrobiological Research.

Lowe, D.M., M.N. Moore, and B.L. Bayne. 1982. Aspects of gametogenesis in the marine mussel *Mytilus edulis* L. J. Mar. Biol. Assoc. U. K. 62:133-145.

Mitchell, J. and J. Gauthier. 1987. Advanced Continuous Simulation Language Reference Manual. Mitchell and Gauthier Assoc. Concord, Mass.

Navarro, J.M. and J.E. Winter. 1982. Ingestion rate, assimilation efficiency and energy balance in *Mytilus chilensis* in relation to body size and different algal concentrations. Mar. Biol. 67:255-266.

Newell, R.C. and G.M. Branch. 1980. The effects of temperature on the maintenance of energy balance in marine invertebrates. Adv. Mar. Biol. 17:329-326.

Newell, R.E.I. and S.J. Jordan. 1983. Preferential ingestion of organic material by the American oyster *Crassostera virginica*. Mar. Ecol. Prog. Ser. 13:47-53.

Newell, R.C. and V.I. Pye. 1970a. Seasonal changes in the effect of temperature on the oxygen consumption of the winkle *Littorina littora* L. and the mussel *Mytilus edulis* L. Comp. Biochem. Physiol. 34:367-383.

Newell, R.C. and V.I. Pye. 1970b. The influence of thermal acclimation on the relation between oxygen consumption and temperature in the winkle *Littorina littorea* L. and *Mytilus edulis* L. Comp. Biochem. Physiol. 34:385-397.

Newell, R.E.I., T.J. Hilbish, R.K. Koehn, and C.J. Newell. 1982. Temporal variation in the reproductive cycle of Mytilus edulis L. (Bivalvia, Mytilidae) from localities on the east coast of the United States. Biol. Bull. Mar. Biol. Lab., Woods Hole. 162:299-310.

Pieters, H., J.H. Kluytmans, W. Zurburg, and D.I. Zandee. 1979. The influence of seasonal changes on energy metabolosm in *Mytilus edulis* (L.) I. Growth rate and biochemical composition in relation to environmental parameters and spawning, p. 285-293. *In* E. Naylor and R.G. Hartnoll [eds.], Cyclic phenomena in marine plants and animals. Pergamon Press.

Pieters, H., J.H. Kluytmans and D.I. Zandee. 1980. Tissue composition and reproduction of *Mytilus edulis* in relation to food availability. Neth. Joun. Sea Res. 14:349-361.

Radford, P.J., I.R. Joint, and A.R. Hiby. 1981. Simulation models of individual production processes, p. 677-700. *In* A.R. Longhurst [ed.], Analysis of marine ecosystems. Academic.

Riisgard, H.V. and A. Randlov. 1981. Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar. Biol. 61:227-234.

Rodhouse, P.G., C.M. Roden, G.M. Burnell, M.P. Hensey, B. Ottway, and T.H. Ryan. 1984a. Food resource, gametogenesis and growth of *Mytilus edulis* on the shore and suspended culture: Killary Harbour, Ireland. J. Mar. Biol. Ass. U.K. 64:513-529.

Rodhouse, P.G., C.M. Roden, M.P. Hensey, and T.H. Ryan. 1984b. Resource allocation in *Mytilus edulis* on the shore and in suspended culture. Mar. Biol. 84:27-34.

Rosenberg, R. and L. Loo. 1983. Energy-flow in a *Mytilus edulis* culture in western Sweden. Aquaculture 35:151-161.

Ross, A.H. and R.M. Nesbet. 1990. Dynamic models of growth and reproduction of the mussel *Mytilus edulis* L. Funct. Ecol. 4:777-787.

Schulte, E.H. 1975. Influence of algal concentrations and temperature on the filtration rate of *Mytilus edulis*. Mar. Biol. 30:331-341.

Seed, R. 1976. Ecology, p. 13-65. *In* B.L. Bayne [ed.], Marine Mussels, their Ecology and Physiology. Cambridge University Press.

Seed, R. and R.A. Brown. 1975. The influence of reproductive cycles, growth, and mortality on population structure in *Modiolus modiolus* (L.), *Cerastroderma edule* (L.), and *Mytilus edulis* (L.), (Mollusca: Bivalvia), p. 257-274. *In* H. Barnes [ed.], Proc. 9th European Marine Biology Symposium. Aberdeen University Press.

Tenore, K.R. and W.M. Dunstan. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. Mar. Biol. 21:190-195.

Thompson, R.J. 1984. The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subartic, non-estuarine environment. Mar. Biol. 79:277-288.

Thompson, R.J. 1987. Post-spawning mortality in the blue mussel, *Mytilus edulis*, p. 98-103. *In* J.F. Roach [ed.], Atlantic Canada Aquaculture Workshop - Proceedings. General Education Series #5, Vol. 1. Fisheries and Oceans Canada.

Tsuchiya, M. 1980. Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. J. Exp. Mar. Biol. Ecol. 47:203-222.

Vahl, D. 1973. Pumping and oxygen consumption rates of *Mytilus edulis* L. of different sizes. Ophelia. 12:45-52.

Verhagen, J.H.G. 1983. A distribution and population model of the mussel *Mytilus edulis* in Lake Grevelingan, p. 373-383. *In* W.K. Lavanroth, G.V. Skogerbac and M. Flung [eds.], State of the Art in Ecological Modelling. Elsevier Press.

Widdows, J. 1973a. The effects of temperature on the metabolism and activity of *Mytilus edulis*. Neth. J. Sci. Res. 7:387-398.

Widdows, J. 1973b. Effect of temperature and food on the heart beat, ventilation rate and oxygen uptake of *Mytilus edulis*. Mar. Biol. 20:269-276.

Widdows, J. 1976. Physiological adaptation of *Mytilus edulis* L. to cyclic temperatures. J. Comp. Physiol. 105:115-128.

Widdows, J. 1978. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J. Mar. Biol. Ass. U.K. 58:109-124.

Widdows, J. and B.L. Bayne. 1971. Temperature acclimation of *Mytilus edulis* with reference to its energy budget. Mar. Biol. Ass. U.K. 51:827-843.

Widdows, J., P. Fieth, and C.M. Worrall. 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. 50:195-207.

Winter, J.E. 1976. Feeding experiments with *Mytilus edulis* L. at small laboratory scale. II. The influence of suspended silt in addition to algal suspension on growth, p. 585-602. *In* G. Persoone and E. Jaspers [eds.], Proc. 10th Europ. Mar. Biol. Symp., Vol. 1. Universa Press.

Winter, J.E. 1978. A review of the knowledge of suspension-feeding in Lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture 13:1-33.

Wright, R.T., R.B. Coffin, C.D. Ersing, and D. Pearson. 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. Limnol. Oceanogr. 27:91-98.

Zandee, D.I., J.H. Kluytmans, and W. Zurburg. 1980. Seasonal variations in biochemical composition of *Mytilus edulis* with reference to energy metabolism and gametogenesis. Neth. J. Sea. Res. 14:1-29.

Zurburg, W., J.H. Kluytmans, H. Pieters, and D.I. Zandee. 1979. The influence of seasonal changes on energy metabolism in *Mytilus edulis* L. II. Organ specificity, p. 293-300. *In* E. Naylor and R.G. Hartnoll [ed.], Cyclic phenomena in marine plants and animals. Pergamon Press.

11. APPENDIX

Sensitivity Analysis of BIOTOT

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.3028	-0.3296	0.3558	0.3873
spvrx	0.0865	0.0941	-0.1060	-0.1153
spresc	0.3865	0.4206	-0.2965	-0.3227
spresx	-0.0721	-0.0785	0.0582	0.0634
spmirc	0.1501	0.1634	-0.0849	-0.0924
spmirx	0.0268	0.0291	-0.0313	-0.0340
spmgrc	-0.0173	-0.0188	0.0017	0.0018
spmgrx	-0.0032	-0.0035	0.0043	0.0047
spmgam	-0.0228	-0.0248	0.0140	0.0152
tspn	-0.0041	-0.0044	0.0034	0.0037
ae	-0.1567	-0.1706	0.4354	0.4739
q10tcl	0.0903	0.0982	-0.0778	-0.0847
q10tch	0.0535	0.0582	-0.0493	-0.0537
q10gam	-0.0154	-0.0167	0.2930	0.3189
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.1359	0.1479	-0.1290	-0.1404
arres	0.1013	0.1102	-0.0975	-0.1061
med	0.0055	0.0060	-0.0277	-0.0302

Sensitivity Analysis of BIOSOM

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.2841	-0.3554	0.3363	-0.4206
spvrx	0.0802	0.1003	-0.0986	-0.1233
spresc	0.3683	0.4607	-0.2804	-0.3508
spresx	-0.0674	-0.0843	0.0544	0.0680
spmirc	0.1474	0.1843	-0.0761	-0.0952
spmirx	0.0252	0.0316	-0.0290	-0.0363
spmgrc	-0.0124	-0.0156	-0.0017	-0.0021
spmgrx	-0.0021	-0.0026	0.0029	0.0036
spmgam	-0.0218	-0.0273	0.0136	0.0170
tspn	-0.0037	-0.0046	0.0033	0.0042
ae	-0.1451	-0.1815	0.4154	0.5196
q10tcl	0.0837	0.1047	-0.0721	-0.0902
q10tch	0.0506	0.0632	-0.0464	-0.0581
q10gam	-0.0147	-0.0184	0.2765	0.3459
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.1290	0.1614	-0.1222	-0.1529
arres	0.0964	0.1206	-0.0924	-0.1156
med	0.0065	0.0082	-0.0278	-0.0347

Sensitivity Analysis of SHLWT

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.4226	-0.1476	0.4466	0.1560
spvrx	0.1448	0.0505	-0.1681	-0.0587
spresc	0.4213	0.1472	-0.3627	-0.1267
spresx	-0.1083	-0.0378	-0.0920	0.0321
spmirc	0.0874	0.0305	-0.1982	-0.0692
spmirx	0.0392	0.0137	-0.0455	-0.0159
spmgrc	-0.1212	-0.0423	0.0898	0.0314
spmgrx	-0.0287	-0.0099	0.0303	0.0107
spmgam	-0.0201	-0.0070	0.0129	0.0045
tspn	-0.0036	-0.0012	0.0032	0.0011
ae	-0.2320	-0.0811	0.4456	0.1556
q10tcl	0.1525	0.0533	-0.1288	-0.0450
q10tch	0.0720	0.0251	-0.0679	-0.0237
q10gam	-0.0135	-0.0047	0.3746	0.1309
q10shi	-3.0570	-0.2220	4.1090	0.2990
irres	0.1561	0.0545	-0.1543	-0.0539
arres	0.1171	0.0409	-0.1163	-0.0406
med	-0.0197	-0.0069	-0.0017	-0.0006

Sensitivity Analysis of SHLLGT

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-2.1794	-0.2840	2.0803	0.0490
spvrx	0.6954	0.0164	-0.8362	-0.0198
spresc	1.9675	0.0464	-1.8561	-0.0437
spresx	-0.5366	-0.0126	-0.4454	-0.0105
spmirc	0.4236	0.0110	-0.9933	-0.0234
spmirx	0.1910	0.0045	-0.2240	-0.0053
spmgrc	-0.6017	-0.0142	0.4350	0.0102
spmgrx	-0.1399	-0.0033	0.1488	0.0035
spmgam	-0.0984	-0.0023	0.0629	0.0015
tspn	-0.0174	-0.0004	0.0157	0.0004
ae	-1.1678	-0.0275	2.0755	0.0489
q10tcl	0.7333	0.0173	-0.6402	-0.0151
q10tch	0.3492	0.0082	-0.3351	-0.0079
q10gam	-0.0661	-0.0016	1.7583	0.0414
q10shi	-5.3820	-0.0720	6.040	0.0810
irres	0.7505	0.0177	-0.7690	-0.0181
arres	0.5652	0.0133	-0.5769	-0.0136
med	-0.0967	-0.0023	-0.0081	-0.0002

Sensitivity Analysis of CUMSPN

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.0460	-0.2100	0.0486	0.2214
spvrx	0.0211	0.0963	-0.0226	-0.1029
spresc	0.0533	0.2430	-0.0445	-0.2029
spresx	-0.0176	-0.0801	0.0162	0.0737
spmirc	-0.1479	-0.6740	0.0257	0.1172
spmirx	0.0001	0.0002	0.0005	0.0022
spmgrc	-0.0153	-0.0700	0.0171	0.0779
spmgrx	-0.0057	-0.0254	0.0055	0.0259
spmgam	-0.0019	-0.0086	0.0011	0.0051
tspn	-0.0001	-0.0005	0.0001	0.0006
ae	-0.2194	-1.0000	0.0900	0.4104
q10tcl	0.0227	0.1033	-0.0199	-0.0909
q10tch	0.0066	0.0302	-0.0064	-0.0290
q10gam	-0.0011	-0.0052	0.0354	0.1615
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.0135	0.0614	-0.0129	-0.0586
arres	0.0101	0.0459	-0.0099	-0.0451
med	-0.0107	-0.0488	0.0091	0.0417

Sensitivity Analysis of CUMIR

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-5.6072	-0.2213	5.9271	0.2339
spvrx	1.9947	0.0787	-2.3034	-0.0909
spresc	4.2318	0.1670	-4.0042	-0.1580
spresx	-1.2998	-0.0513	1.1180	0.0441
spmirc	-0.3584	-0.0141	-2.2143	-0.0874
spmirx	0.5317	0.0210	-0.6104	-0.0241
spmgrc	-0.5367	-0.0212	0.3334	0.0132
spmgrx	-0.1586	-0.0062	0.1769	0.0070
spmgam	-0.1455	-0.0057	0.0842	0.0033
tspn	-0.0237	-0.0009	0.0200	0.0008
ae	-1.9846	-0.0783	2.9117	0.1149
q10tcl	1.9115	0.0754	-1.6894	-0.0667
q10tch	0.9224	0.0364	-0.8644	-0.0341
q10gam	-0.0948	-0.0037	4.9180	0.1941
q10shi	0.0001	0.0000	0.0001	0.0000
irres	1.4915	0.0589	-1.5477	-0.0611
arres	1.1227	0.0443	-1.1606	-0.0458
med	-0.0298	-0.0012	-0.2385	-0.0094

Sensitivity Analysis of CUMAR

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-1.4018	-0.4226	1.4818	0.4466
spvrx	0.4987	0.0787	-0.5759	-0.0909
spresc	1.0580	0.1670	-1.0011	-0.1580
spresx	-0.3250	-0.0513	0.2795	0.0441
spmirc	-0.0896	-0.0141	-0.5536	-0.0874
spmirx	0.1329	0.0210	-0.1526	-0.0241
spmgrc	-0.1342	-0.0212	0.0833	0.0132
spmgrx	-0.0396	-0.0062	0.0442	0.0070
spmgam	-0.0364	-0.0057	0.0210	0.0033
tspn	-0.0059	-0.0009	0.0050	0.0008
ae	-1.0799	-0.1705	1.4341	0.2264
q10tcl	0.4779	0.0754	-0.4224	-0.0667
q10tch	0.2306	0.0364	-0.2161	-0.0341
q10gam	-0.0237	-0.0037	1.2295	0.1941
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.3729	0.0589	-0.3869	-0.0611
arres	0.2807	0.0443	-0.2902	-0.0458
med	-0.0075	-0.0012	-0.0596	-0.0094

Sensitivity Analysis of CUMER

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-4.2055	-22.13	4.4453	0.2339
spvrx	1.4960	0.0787	-1.7276	-0.0909
spresc	3.1738	0.1670	-3.0032	-0.1580
spresx	-0.9749	-0.0513	0.8384	0.0441
spmirc	-0.2689	-0.0141	-1.6608	-0.0874
spmirx	0.3987	0.0210	-0.4578	-0.0241
spmgrc	-0.4025	-0.0212	0.2500	0.0132
spmgrx	-0.1189	-0.0062	0.1327	0.0070
spmgam	-0.1092	-0.0057	0.0631	0.0033
tspn	-0.0178	-0.0009	0.0150	0.0008
ae	-0.9047	-0.0476	1.4775	0.0778
q10tcl	1.4336	0.0754	-1.2671	-0.0667
q10tch	0.6917	0.0364	-0.6484	-0.0341
q10gam	-0.0711	-0.0037	3.6884	0.1941
q10shi	0.0000	0.0000	0.0000	0.0000
irres	1.1186	0.0589	-1.1608	-0.0611
arres	0.8420	0.0443	-0.8705	-0.0458
med	-0.0224	-0.0012	-0.1789	-0.0094

Sensitivity Analysis of CUMPF

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.3028	-0.3296	0.3558	0.3872
spvrx	0.2657	0.2360	0.2670	0.2371
spresc	0.0257	0.0228	-0.3933	-0.3492
spresx	-0.0139	-0.0124	0.0110	0.0097
spmirc	0.5041	0.4476	-0.4269	-0.3791
spmirx	-0.1473	-0.1308	0.1533	0.1361
spmgrc	-0.0074	-0.0066	0.0057	0.0051
spmgrx	-0.0031	-0.0027	0.0032	0.0028
spmgam	-0.0008	-0.0007	0.0005	0.0004
tspn	-0.0001	-0.0001	0.0001	0.0001
ae	-0.0305	-0.0271	0.0182	0.0162
q10tcl	0.1054	0.0936	-0.0875	-0.0777
q10tch	0.0028	0.0024	-0.0029	-0.0025
q10gam	-0.0005	-0.0004	0.0116	0.0103
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.0088	0.0078	-0.0111	-0.0098
arres	0.0068	0.0060	-0.0082	-0.0073
med	-0.4673	-0.4149	0.5191	0.4610

Sensitivity Analysis of CUMTRP

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-1.0529	-0.1937	1.0773	0.1982
spvrx	0.3910	0.0719	-0.4473	-0.0823
spresc	0.6181	0.1137	-0.6600	-0.1214
spresx	-0.2353	-0.0433	0.2051	0.0377
spmirc	-0.0918	-0.0169	-0.4944	-0.0910
spmirx	0.1061	0.0195	-0.1218	-0.0224
spmgrc	-0.1015	-0.0187	0.0646	0.0119
spmgrx	-0.0307	-0.0056	0.0344	0.0064
spmgam	-0.0117	-0.0022	0.0060	0.0011
tspn	-0.0018	-0.0003	0.0015	0.0003
ae	-0.7038	-0.1295	0.9086	0.1672
q10tcl	0.3649	0.0671	-0.3246	-0.0597
q10tch	0.1704	0.0314	-0.1604	-0.0295
q10gam	-0.0072	-0.0013	0.9011	0.1658
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.2233	0.0411	-0.2450	-0.0451
arres	0.1693	0.0311	-0.1828	-0.0336
med	-0.0022	-0.0004	-0.0411	-0.0076

Sensitivity Analysis of CUMSRP

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.5622	-0.2099	0.5587	0.2214
spvrx	0.2165	0.0673	-0.2458	-0.0764
spresc	0.2478	0.0770	-0.3096	-0.0962
spresx	-0.1215	-0.0378	0.1072	0.0333
spmirc	-0.0604	-0.0188	-0.3007	-0.0934
spmirx	0.0596	0.0185	-0.0684	-0.0213
spmgrc	-0.0546	-0.0169	0.0354	0.0110
spmgrx	-0.0168	-0.0052	0.0188	0.0059
spmgam	0.0010	0.0003	-0.0014	-0.0004
tspn	0.0003	0.0001	-0.0003	-0.0001
ae	-0.4426	-0.1375	0.5479	0.1702
q10tcl	0.1977	0.0614	-0.1768	-0.0549
q10tch	0.0897	0.0279	-0.0848	-0.0263
q10gam	0.0011	0.0003	0.4707	0.1462
q10shi	0.0000	0.0000	0.0000	0.0000
irres	0.2270	0.0705	-0.2286	-0.0710
arres	0.1703	0.0529	-0.1719	-0.0534
med	0.0004	0.0001	-0.0202	-0.0063

Sensitivity Analysis of CUMARP

	Decrease		Increase	
Parameter	Absolute	Relative	Absolute	Relative
spvrc	-0.4906	-0.2213	0.5186	0.2339
spvrx	0.1745	0.0787	-0.2016	-0.0909
spresc	0.3703	0.1670	-0.3504	-0.1580
spresx	-0.1137	-0.0513	0.0978	0.0441
spmirc	-0.0314	-0.0142	-0.1938	-0.0874
spmirx	0.0465	0.0210	-0.0534	-0.0241
spmgrc	-0.0470	-0.0212	0.0292	0.0132
spmgrx	-0.0139	-0.0062	0.0155	0.0070
spmgam	-0.0127	-0.0057	0.0074	0.0033
tspn	-0.0021	-0.0009	0.0017	0.0008
ae	-0.2612	-0.1178	0.3607	0.1627
q10tcl	0.1672	0.0754	-0.1478	-0.0667
q10tch	0.0807	0.0364	-0.0756	-0.0341
q10gam	-0.0083	0.4303	-0.0037	0.1941
q10shi	0.0000	0.0000	0.0000	0.0000
irres	-0.0036	-0.0016	-0.0165	-0.0074
arres	-0.0009	-0.0004	-0.0109	-0.0049
med	-0.0026	-0.0012	-0.0209	-0.0094