On predicting the growth of cultured bivalves

Michael Dowd *
Department of Oceanography, Dalhousie University, Halifax, NS B3H 4J1, Canada

Accepted 3 April 1997

Abstract

A simple, limited ecosystem model focused on bivalve growth in a coastal aquaculture site is presented. The model is based on a system of coupled, nonlinear ordinary differential equations which predict the temporal evolution of the following state variables: individual bivalve weight, bivalve numbers, zooplankton biomass, phytoplankton biomass and non-plankton seast. A limiting nutrient is also included to constrain the overall system. The equations are based on population mass budgets and allow for particle exchange with adjacent regions. The model structure is general and designed to be applicable to a variety of bivalve species or sites. In order to test the feasibility of the model for predicting growth, it is applied to a blue mussel
*Mysidopsis edulis culture site in a coastal inlet near Lunenburg, Nova Scotia, Canada. Idealized forcing functions for the annual cycles of light, temperature and the far-field concentrations of the state variables are used. It is shown that the model is able to reproduce the general features of observed mussel growth in the different regions of the inlet at the relatively low stocking densities found there. Numerical experiments with high stocking densities are carried out in order to estimate carrying capacity for the inlet. Sensitivity analysis shows that predicted mussel growth is highly influenced by small changes in the physiological parameters which describe the mussel energy budget. It is suggested that this feature may prove to be an important limitation in using such models as predictive tools for managing the development of shellfish aquaculture. © 1997 Elsevier Science B.V.

Keywords: Shellfish; Bivalves; Model; Aquaculture

1. Introduction

Increased development of shellfish aquaculture in nearshore regions has resulted in the need for information on the interaction of cultured species with their supporting ecosystem (Smaal, 1991). Quantitative studies of bivalve growth in the culture environment have proved valuable for understanding the ecology of these manipulated systems. However, at present, the ability to provide robust predictive relations for management decisions regarding site selection, expansion of existing operations, and environmental impact is limited.
It is well established that the growth of cultured bivalve species depends on the environmental conditions found at a particular site (e.g. Brown, 1988). However, high densities of suspension feeding bivalves may also alter the prevailing environmental conditions. For example, the filtration activity of large concentrations of bivalves has been shown to affect food dynamics (Smaal et al., 1986; Fréchette et al., 1989; Loo and Rosenberg, 1989) and nutrient cycling (Kautsky and Evans, 1987; Hickman et al., 1991). This provides a potential feedback mechanism whereby bivalve culture can influence its supporting ecosystem, and ultimately the growth rate of its own population. This inverse relation between stocking density and individual growth rate has resulted in the need to reliably assess the carrying capacity of aquaculture sites (Ince et al., 1981; Carver and Mallet, 1990; Raillard and Ménesguen, 1994).

Empirical approaches are often used to assess the interaction of cultured bivalves and their environment. Bivalve growth can be correlated with environmental factors in order to identify important predictive variables (Brown, 1988). Such studies have motivated the construction of habitat suitability indices which measure the ability of a site to support the culture of a given species (Sonait and Brody, 1988). Alternatively, field data may be used to quantify the flow of energy, or mass, through one or more interacting populations (Rodhouse and Roden, 1987). These energy budgets allow the relative importance of the various components in the ecosystem to be assessed. Although these empirical approaches have proven useful, they have fundamental limitations when applied to predicting the behaviour of populations in a dynamically varying environment (Ross and Nisbet, 1990; Vance, 1990).

More recently, studies of bivalve growth have used simulation models to account for the dynamic coupling between a population and its environment. This involves constructing prognostic relationships based on a theoretical perception of how the system operates. The large body of literature on the physiological ecology of cultured bivalve species provides the basis for such models. Models have been developed based on such bivalve energy budgets in which the environment is prescribed (Ross and Nisbet, 1990; Bacher et al., 1991; Hofmann et al., 1992). However, models which dynamically couple bivalves to their environment have been carried out less frequently, and often on a site specific basis (Kremer and Nixon, 1978; Raillard and Ménesguen, 1994).

It is the intention of this paper to offer a general bivalve model which is potentially extensible to a variety of sites, and captures the important aspects of bivalve growth as it relates to its supporting ecosystem. In the thesis of Dowd (1991), such a generic box model for bivalve growth in an aquaculture system was proposed. It included the limited portion of the ecosystem which directly influences bivalve site, and was constructed so as to be a relatively parsimonious description of the culture system. Grant et al. (1993) further examined the relationship between fish data and the structure of this model. In this paper, we present the details of this dynamic model and illustrate it with a simple application to a mussel culture site. The goal here is to assess the feasibility of using this type of model as a management tool in shellfish aquaculture.

The paper is structured as follows. In Section 2, model equations are presented which provide a general framework for assessing bivalve growth. The model is then focused on predicting the growth of a cultured population of the blue mussel *Mytilus edulis*. In Section 3, application of the model to a culture site in a coastal inlet near Lunenburg, Nova Scotia, Canada is carried out. Section 4 presents the results of this simulation, and includes experiments with carrying capacity and sensitivity analysis of the model parameters. Section 5 provides a discussion and conclusions.

2. Model

The limited ecosystem model is focused on describing the growth of cultured bivalves. The general equations presented in this section are intended to be applicable to a variety of bivalve species. However, the application in Section 3 of this paper involves mussel culture and the term 'mussel' will be used henceforth. The ecological interactions in the model include two competing
herbivores, mussels and zooplankton, and two food sources, phytoplankton and non-plankton seston (e.g. bacteria, detritus).

A box model concept is used whereby the coastal inlet is divided into a number of distinct regions (or boxes). As is usual in such models, exchange of suspended particles (phytoplankton, zooplankton, and seston) between adjacent boxes will be assumed proportional to spatial differences in their respective concentrations, scaled by an exchange coefficient, i.e.

$$\frac{dX}{dt} = K(X_\infty - X)$$

where $X$ represents the particle concentration within the box of interest and $X_\infty$ is the corresponding value in an adjacent box. The exchange coefficient is denoted by $K$, with $1/K$ being an e-folding flushing time for the box. (Note that a variety of mixing processes are parameterized by $K$, for a review see Fischer et al. (1979). The above formulation implies that boxes are chosen such that within each box the spatial gradients in the model components are small. A conceptual diagram of the box model is given in Fig. 1.

The population interactions occurring within a box are represented by flux equations which describe the co-evolution of the herbivores (mussels and zooplankton) together with their food sources (phytoplankton and non-plankton seston). For both the mussels and zooplankton, the growth rate depends on the difference between mass gains, through ingestion, and losses, through respiration and mortality. The food sources, phytoplankton and non-plankton seston, are consumed by mussels and zooplankton, but are replenished by phytoplankton growth and exchange. A limiting nutrient for phytoplankton growth is also included as a negative feedback for the system. The basis for the mathematical description of these interactions are mass budgets which include well established functional relationships such as the saturation response of ingestion to increasing food concentration, the exponential $Q_{10}$ response to temperature, the weight-specific allometric relation for physiological rates, and the photosynthesis-irradiance relationship for phytoplankton primary production.

A set of coupled, nonlinear ordinary differential equations is used to describe the growth of cultured mussels in a coastal inlet. The model includes the following state variables: individual mussel weight ($M$); mussel numbers ($N$); zooplankton concentration ($Z$); phytoplankton concentration ($P$); and non-plankton seston concentration ($S$). The mass flux equations for a single box exchanging with an adjacent region and single mussel weight class are

$$\frac{dM}{dt} = \left( \frac{e_{MP}P}{P + \mu_P S} + \frac{e_{MS}M S}{P + \mu_S S} \right) f_{MP} M - f_{MR} R_M M - D_M$$

$$\frac{dN}{dt} = -\lambda_M N - D_N$$

$$\frac{dZ}{dt} = \left( \frac{e_{ZP}P}{P + \mu_P S} + \frac{e_{ZS}Z S}{P + \mu_S S} \right) f_{ZP} Z - f_{ZR} R_Z Z - \lambda_Z Z + K(Z_\infty - Z)$$

Fig. 1. Conceptual diagram of the model components for a single box including two competing herbivores (mussels and zooplankton), and two food sources (phytoplankton and non-plankton seston). The arrows indicate that phytoplankton, zooplankton and seston exchange with adjacent box(es).
\[
\frac{dP}{dt} = \frac{X}{k_x + X} P - \frac{P}{P + \mu_M} f_M I_M Z + \frac{P}{P + \mu_M} f_M I_M M N + K(P_{\infty} - P)
\]

\[
\frac{dS}{dt} = D_S - \frac{\mu_M S}{P + \mu_M} f_M I_M Z - \frac{\mu_M S}{P + \mu_M} f_M I_M M N + K(S_{\infty} - S)
\]

It is assumed, for simplicity, that mass is measured in units of carbon. A nutrient flux equation (e.g. for dissolved nitrogen) is also included to provide a negative feedback on the entire system by limiting phytoplankton growth. The nutrient flux equation is

\[
\frac{dX}{dt} = \xi_Z Z + \xi_M M + D_X - \frac{X}{k_x + X} \gamma P
\]

\[
+ K(x_{\infty} - X)
\]

with \(X\) representing the limiting nutrient. The \(\ast\) subscripting emphasizes that the state variables are expressed here in units of the most limiting nutrient (i.e. the value of the state variable multiplied by the nutrient to carbon ratio of the organism). The various terms in these equations are defined in Table 1 and the details are discussed for the remainder of this section. Note that while these equations are reasonably complex, they represent what is felt to be a minimal description of bivalve growth in a culture site.

To fully specify the problem, the following additional information is required: (i) initial conditions for \(M, N, Z, P, S, X\) all of which must be non-negative; (ii) boundary conditions \(Z_{\infty}, P_{\infty}, S_{\infty}, X_{\infty}\) which for a coastal inlet correspond to the concentration of the state variables in the adjacent open ocean; (iii) forcing functions which consist of time series of temperature and irradiance, and (iv) internal source/sink terms occurring within the area delineated by a box. This last category includes sources or sinks of non-phytoplankton seston \(D_S(t)\), nutrients \(D_N(t)\), harvesting of mussels \(D_M(t)\), and weight losses associated with spawning \(D_M(t)\). Given this information, the flux equations (Eqs. (1)–(6)) can be integrated to yield the temporal evolution of the state variables. Additional weight classes of mussels and multiple boxes can be incorporated into the above framework in a straightforward manner. Note that the equations, as posed, are quite general. To make them specific to a particular shellfish species and site, the dimensionless modulation functions must be chosen. This is described in detail below.

2.1. Mussels

The mussel component provides the focus for the box model and is represented in the greatest detail. The growth rate of an individual mussel is described by Eq. (1) and the population growth rate (the number of individuals) is given by Eq. (2). This separation of the total population
biomass (the product of $M$ and $N$) into individual mussel weight and the number of mussels allows the weight dependence of the physiological rates (Griffiths and Griffiths, 1987) to be included. Below, a relatively simple set of equations governing mussel growth are presented. Willows (1992) and Van Haren and Kooijman (1993), for example, present much more detailed accounts of the mussel energy budget.

The carbon budget for an individual mussel is represented by Eq. (1). The first term on the right hand side of the equation represents the ingestion of phytoplankton and non-plankton seston by mussels. It is composed of an overall assimilation efficiency, given by the quantity in brackets, which is multiplied by a dimensionless function $f_{SI}$, a reference ingestion rate $I_{MR}$ and individual mussel weight $M$. These are each explained below.

The overall assimilation efficiency for mussels is a weighted average of the assimilation efficiencies for phytoplankton $e_{MP}$ and seston $e_{SP}$. The factor $\mu_{M}$ is included to allow for the effect of particle selection by the mussel (Newell et al., 1989; Hawkins et al., 1996). For example, when the selection factor $\mu_{M}$ equal to one, a simple weighted average based on the prevailing composition of the food field ($P, S$) is used to calculate the overall assimilation efficiency. For $\mu_{M}$ between zero and one, mussels preferentially select phytoplankton over non-plankton seston.

The dimensionless function $f_{SI}$ which modulates the reference ingestion rate $I_{MR}$ includes a saturation response to food concentration (Bayne et al., 1989), an exponential $Q_{10}$ response to temperature, and uses an allometric relation to account for increasing weight (Griffiths and Griffiths, 1987). The function is defined as

$$f_{SI} = \frac{P + S}{k_{M} + P + S} \exp(Q_{10}T)M^{b}$$

where $k_{M}$ is the half-saturation constant for mussel ingestion, $Q_{10}$ is the temperature rate constant and $b$ is the allometric exponent. The reference ingestion rate is evaluated at some convenient value ($P + S, T, M$) and the scale factor $c_{MR}$ is chosen such that $f_{SI}$ is unity at this value. This formulation, composed of a dimensionless function multiplying a reference rate, is used throughout.

The second term on the right hand side of (1) represents carbon losses through respiration. It is composed of a dimensionless function $f_{MR}$ multiplied by a reference rate $R_{M}$ and the individual mussel weight $M$. The function $f_{MR}$ includes a standard respiration rate, which depends solely on individual mussel weight, and an active respiration rate which describes the additional mass loss associated with feeding activity and is dependent on body weight, temperature, and food concentration (Bayne et al., 1973; Bayne and Newell, 1983). The function $f_{MR}$ is defined as

$$f_{MR} = c_{MR1}M^{b} + c_{MR2}(P + S)\exp(Q_{MR}T)M^{b}$$

where $b$ is the allometric exponent and $Q_{MR}$ is the temperature rate constant for mussel respiration. The scope for activity coefficient $c_{MR3}$ multiplied by the total food concentration parameterizes the increased metabolic expenditure associated with feeding. The reference respiration rate $R_{2}$ is chosen whereupon the scale factors $c_{MR1}$ and $c_{MR2}$ are determined.

In this formulation, the only provision made for weight losses associated with spawning periods is the term $D_{M}(t)$. In this case, spawning is prescribed as a time dependent mass loss term which serves to reduce individual mussel growth. Models for bivalve growth which includes spawning have been proposed (Ross and Nieb, 1990; Hofmann et al., 1992). These allocate the excess of ingestion over respiration into separate pools for somatic growth and reproduction. When the amount in the reproductive pool exceeds some threshold, spawning then occurs. This calculation imposes irregular and aperiodic fluctuations on body weight which resemble spawning events. This method of representing spawning could be incorporated into the model framework, but due to the complexity of the gametogenic cycle it seems preferable to assess this process on a site-specific basis.

The evolution of the number of mussels is given by Eq. (2). In the aquaculture site this includes stocking, harvesting, natural death and predation. Stocking introduces a given weight class at specific time and is taken into account through the initialization (or re-initialization) of the model. Harvesting removes a known fraction of the muss-
sel population at a given time and is included in the loss term \( D_N(t) \). The remaining terms, natural death and predation, are included in the fractional mortality rate \( \lambda_M \) which varies over time and is determined on a site specific basis (Mallet et al., 1990).

2.2. Zooplankton

Herbivorous zooplankton compete with mussels for the phytoplankton and seston food sources. The zooplankton component of the box model is structured in a similar manner to the mussel component, except that it is not separated based on individual weight and numbers. Rather, the zooplankton component is lumped into a single equation given by Eq. (3) which assumes that a composite individual is representative of the population (Evans and Parslow, 1985; Franks et al., 1986).

The first term on the right hand side of Eq. (3) represents the ingestion of phytoplankton and seston by zooplankton. The overall assimilation efficiency of zooplankton is represented by the quantity in brackets. It includes different assimilation efficiencies for phytoplankton and seston \( \epsilon_{ZP}, \epsilon_{ZS} \) as well as a factor \( \mu_Z \) allowing for particle selection (Poulet, 1983). This overall assimilation efficiency multiplies a dimensionless function \( f_{ZI} \), which includes a saturation response for food ingestion (Frost, 1975), and an exponential \( Q_{10} \) temperature response (Deason, 1980). It is given by

\[
f_{ZI} = \frac{c_{ZI} \left( \frac{P + S}{k_Z + P + S} \right) \exp(Q_{ZI}T)}{k_Z},
\]

where \( k_Z \) and \( Q_{ZI} \) are the rate constants for zooplankton ingestion. The factor \( c_{ZI} \) is determined by the reference rate \( I_Z \) chosen. The second term on the right hand side of Eq. (3) is the respiration term. It is characterized by a modulating function \( f_{ZR} \) which is dependent on temperature alone, i.e.

\[
f_{ZR} = c_{ZR} \exp(Q_{ZR}T).
\]

Here, \( Q_{ZR} \) is the rate constant for the temperature response of zooplankton respiration and \( c_{ZR} \) is the scale factor and set by the choice of the reference rate \( R_Z \). The third term in Eq. (3) represents losses of zoooplankton through mortality and is considered to be a constant fraction \( \lambda_Z \) of the population. The final term of Eq. (3) describes the exchange of zoooplankton with adjacent regions.

2.3. Phytoplankton

The instantaneous growth rate of the phytoplankton population is described by Eq. (4). The phytoplankton are considered without regard to species or individual variation (Steele and Henders, 1981; Evans and Parslow, 1985). The first term on the right hand side of Eq. (4) represents the growth rate of phytoplankton due to photosynthetic production. It is composed of a term representing nutrient limitation \( \chi/(\kappa_Z + \chi) \) (e.g. Dugdale, 1977) which multiplies a light limited growth rate \( y \) and the phytoplankton biomass \( P \).

The growth rate \( y \) is a function of incident light levels as specified by a photosynthesis-irradiance relationship (Platt and Gallegos, 1980). Due to the diurnal variation in light levels, phytoplankton growth has significant variations on time scales less than 1 day. As such scales are of little interest here, a suitable averaging procedure is used. Assuming a uniform distribution of phytoplankton throughout the water column, the growth rate averaged over 1 day \( r \) and a water column of depth \( z = -D \), is

\[
y = \frac{1}{rD} \int_0^r \int_0^D \frac{\text{ch}I(z, t)dz}{C} \] dtdz
\]

where \( z \) is depth, chl/C is the chlorophyll to carbon ratio of the phytoplankton, \( I(z, t) \) is the underwater irradiance field, and \( f(\cdot) \) represents the photosynthesis-irradiance function for phytoplankton (i.e. chlorophyll production as a function of incident light). This daily averaged rate \( y \) is interpreted as the maximum light limited growth rate of phytoplankton representative of the water column.

The remainder of the terms in Eq. (4) represent ingestion by zooplankton, ingestion by the mussel population and the exchange of phytoplankton with adjacent regions. Each of these terms have been dealt with in the preceding sections.
2.4. Non-plankton seston

For the purposes of the box model, seston is defined as non-plankton suspended particulate matter including, for example, bacteria and detritus. The flux equation for seston is given by Eq. (5) and is similar to that of phytoplankton, except for the absence of growth terms. The first term on the right hand side, \( D_S(t) \), represents the internal sources of seston found within the area delineated by the box. This includes resuspension of bottom sediments, decomposition of macrophyte detritus, river input and land runoff. Clearly the values for \( D_S(t) \) are highly site specific. The remainder of the terms in Eq. (5) are ingestion of seston by the zooplankton and mussel populations, and the exchange of seston with adjacent regions.

2.5. Nutrients

The nutrient flux equation Eq. (6) describes the cycling of a single limiting element within the system. This nutrient acts to constrain the growth of the biological components of the system in otherwise favorable conditions by limiting phytoplankton growth. The first two terms on the right hand side of Eq. (6) represent additions to the nutrient pool through excretion by mussels and zooplankton. Consider the excretion term for mussels. According to Eq. (1), respiration is considered as a pure carbon loss. This carbon loss yields a corresponding nutrient excretion, calculated so as to maintain the nutrient to carbon ratio of the mussel (Kremer and Nixon, 1978). Thus, as a first approximation, the excretion rate of nutrients by mussels is

\[ \frac{\\xi_M}{f_{MR}} = R_M. \]

Identical considerations apply to zooplankton excretion. The remainder of the terms in the nutrient flux equation Eq. (6) are uptake by phytoplankton, internal sources of nutrients \( D_N(t) \) such as river input and benthic nutrient regeneration, and exchange with adjacent regions.

3. Application

The box model was applied to a small mussel aquaculture site at Upper South Cove near Lunenburg, Nova Scotia, Canada. At this site, the mussels are mainly *Mytilus edulis* and are cultured in suspension with mussels deployed in mesh sleeves from floating longlines. Upper South Cove, shown in Fig. 2, is a small tidal inlet approximately 3.5 km long and 0.5 km wide with an average depth of 1–2 m. The cove is generally well-mixed in the vertical, has little fresh water input and is ice covered from late December to late March. Gradients in water properties occur mainly along the major axis of the cove. The tidal amplitude is approximately 1 m making the tidal prism a significant proportion of total volume of the cove. Flushing by tides is the dominant mechanism for particle exchange and renewal.

Upper South Cove is connected with Lunenburg Bay by an extremely narrow mouth. Hydrography, drifters, airborne synthetic aperture radar and numerical modelling studies have confirmed that the flushing of Upper South Cove into adjacent Lunenburg Bay occurs through a tight outflow jet on ebb tide and a more uniform inflow on flood tide (Dowd, 1991). Based on this, it is concluded that the water flowing out of Upper South Cove on the ebb tide does not return on the following flood tide. This implies that the concentrations of the state variables in Lunenburg Bay are independent of the concentrations of the state variables in Upper South Cove and thus are taken as model boundary conditions (\( P_\infty, S_\infty, Z_\infty, X_\infty \)).

Upper South Cove has been divided into two spatial boxes (shown in Fig. 2) based on the length of the tidal excursion. The boundary between the two boxes, hereafter referred to as the inner and outer cove, was found to be approximately 1.4 km from the mouth of the inlet which corresponds to the innermost point where the tidal excursion, starting at slack tide, would carry a water parcel into Lunenburg Bay. This boundary also matches the point where observed gradients in the temperature and phytoplankton concentration are largest. Based on these boxes,
tidal exchange coefficients were calculated to be: \( K_1 = 0.5 \text{ day}^{-1} \) for exchange between the inner cove and the outer cove, and \( K_2 = 2 \text{ day}^{-1} \) for exchange between the outer cove and Lunenburg Bay. These numbers were confirmed with a summer heat budget calculation. Note that use of these exchange coefficients implies that the model is averaged over the tidal cycle. Some recent evidence suggests, however, that variations in food concentration within a tidal cycle may prove important to the bivalve growth (Hawkins et al., 1996).

The boundary conditions used for the model consisted of idealized curves for phytoplankton, zooplankton, seston and nitrogen (the most limiting nutrient). These are shown in Fig. 3 and were determined based on observations and typical values for coastal Nova Scotia. For simplicity, the internal source terms for nitrogen \( D_N \) and seston \( D_X \) were set to zero. Similarly, the harvesting rate \( D_W \) and the spawning parameter \( D_M \) were also set to zero. This lack of a spawning cycle makes the box model results interpretable as either: (i) describing the growth of first year mussels for
which no spawning occurs; (ii) averaging over spawning events or (iii) describing only the growth of the somatic pool of body weight.

The two forcing functions required by the box model are time series of light and temperature. A sinusoid was fit to the bi-weekly temperature time series and the result is shown in Fig. 3. Sine curves were also fit to data collected at Upper South Cove for both the daily mean irradiance and the daylength. A separate submodel was used to calculate $\gamma$ in which the underwater irradiance field was specified based on these surface light levels and measured attenuation coefficients for the water column. The integration in Eq. (7) was carried out using the photosynthesis–irradiance curve of Platt et al. (1980) with the parameters of (Platt and Jassby, 1976) and Epply (1972). A carbon to chlorophyll ratio of 40 was assumed. The resulting daily average growth rate $\gamma$ is shown in Fig. 3.

The interactions between the biological components of the model require that a large number of physiological parameters be specified. The values used for the standard model run are given in Table 2. Note that literature values were often reported in a form other than that required for the box model and hence various conversion formulae were used. It is worthwhile to point out that there is considerable uncertainty in the value of many of these parameters, and that furthermore the model results turn out to be highly sensitive to variations in these quantities. The
implications of this are addressed in more detail in the next section.

The model equations (Eqs. (1)–(6)) were numerically integrated for a two box system using a 4th order Runge–Kutta scheme with the parameter values of Table 2 and boundary conditions and forcing functions shown in Fig. 3. The initial conditions for $P$, $S$, $Z$, $\chi$ were taken to be equal to their boundary values at the initial time. For mussels, the initial weights were chosen to be 0.015, 0.045, and 0.09 gC (these correspond to shell lengths of roughly 1.5, 2, and 3 cm, respectively). An initial density $N$ of 1 mussel m$^{-3}$ in each box was used to reflect the approximate stocking density at the site. (It is important to emphasize that the stocking density is the number of mussels divided by the volume of the entire box, not just the regions where the leases are located. The mussel density within the lease area is considerably higher, estimated at 57 mussel m$^{-3}$ in Grant et al., 1993). The integration times reflected the typical stocking-harvesting cycle. Multi-year integrations indicated that a periodic steady state was achieved by the solution after about 4 years.

### 4. Results

Results of the model integration for a calendar year (beginning Jan. 1) are shown in Fig. 4. These indicate that the predicted time series for phytoplankton, zooplankton, seston and nutrients within the cove follow their boundary values fairly closely (compare with Fig. 3). This is largely due to the due to the strong tidal flushing of the cove. However, small but significant deviations from these values do occur, particularly in the fall period. One important feature evident at this time is the difference in the concentration of the phytoplankton, seston and nutrients between the inner and outer cove. This is established due to the combined effect of the biological production within the cove and the differential flushing rates of the inner and outer parts of Upper South Cove.

The phytoplankton series shows an enhanced fall bloom concentrated mainly in the inner cove, which compares well with observations (Mallet and Carver, 1993). This enhancement of the phytoplankton concentration in the fall is a result of high temperatures, high nutrient levels and sufficient light which together serve to maximize the growth rate $\gamma$ at this time. Phytoplankton decreases from the inner cove to the outside due to retention of the high within-cove primary production. Seston and nutrient concentrations follow the opposite pattern, being depleted in the inner cove relative to the outside, in accordance with the differences between supply through exchange and consumption by mussels and zooplankton.

The simulated annual growth trajectories for individual mussel weight in the inner and outer coves are shown in Fig. 5 for a period which matches that of the field study (Fig. 6). The most notable feature is the substantial difference found in the predicted weights of mussels grown in the inner and outer coves. This is primarily due to the

---

### Table 2

Parameter values used in the application of the box model to Upper South Cove and their literature sources

<table>
<thead>
<tr>
<th>Term</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$l_M$</td>
<td>0.1 day$^{-1}$</td>
<td>Bayne et al. (1989), Foster-Smith (1975)</td>
</tr>
<tr>
<td>$l_S$</td>
<td>0.5 day$^{-1}$</td>
<td>Bouguis (1976), Dagg and Grill (1980)</td>
</tr>
<tr>
<td>$k_M$</td>
<td>0.01</td>
<td>Griffiths and Griffiths (1987)</td>
</tr>
<tr>
<td>$k_S$</td>
<td>0.2 day$^{-1}$</td>
<td>Bouguis (1976)</td>
</tr>
<tr>
<td>$c_M$</td>
<td>0.9</td>
<td>Bayne et al. (1976), Winter (1978)</td>
</tr>
<tr>
<td>$c_M$</td>
<td>0.2</td>
<td>Kivrove et al. (1980), Widdows et al. (1979)</td>
</tr>
<tr>
<td>$k_M$</td>
<td>0.9</td>
<td>Bouguis (1976)</td>
</tr>
<tr>
<td>$k_M$</td>
<td>0.1</td>
<td>Conover (1966)</td>
</tr>
<tr>
<td>$k_M$</td>
<td>0.8</td>
<td>Newell et al. (1989)</td>
</tr>
<tr>
<td>$\mu_Z$</td>
<td>0.5</td>
<td>Poulet (1983), Poulet and Marsot (1978)</td>
</tr>
<tr>
<td>$\lambda_M$</td>
<td>0.0–0.002 day$^{-1}$</td>
<td>Mallet et al. (1990)</td>
</tr>
<tr>
<td>$\lambda_S$</td>
<td>0.1 day$^{-1}$</td>
<td>Akins and Magnesan (1988)</td>
</tr>
<tr>
<td>$\kappa_Z$</td>
<td>14 gN m$^{-3}$</td>
<td>Bouguis (1976)</td>
</tr>
<tr>
<td>$\kappa_M$</td>
<td>1000 gC m$^{-3}$</td>
<td>Foster-Smith (1975), Bayne et al. (1989)</td>
</tr>
<tr>
<td>$\kappa_Z$</td>
<td>200 gC m$^{-3}$</td>
<td>Kremer and Nixon (1978)</td>
</tr>
<tr>
<td>$Q_M$</td>
<td>0.07 °C$^{-1}$</td>
<td>Winter (1978)</td>
</tr>
<tr>
<td>$Q_S$</td>
<td>0.11 °C$^{-1}$</td>
<td>Deacon (1980)</td>
</tr>
<tr>
<td>$Q_M$</td>
<td>0.07 °C$^{-1}$</td>
<td>Griffiths and Griffiths (1987)</td>
</tr>
<tr>
<td>$Q_S$</td>
<td>0.07 °C$^{-1}$</td>
<td>Bouguis (1976)</td>
</tr>
<tr>
<td>$b$</td>
<td>−0.4</td>
<td>Bayne and Newell (1983)</td>
</tr>
</tbody>
</table>
enhanced food quality (the P/S ratio) in the inner cove which results in a very high assimilated ration and resultant mussel growth. Both parts of the cove do, however, exhibit similar patterns of predicted growth over time. During the winter months, the mussel growth is slow due to the low concentrations of phytoplankton (poor food quality) together with low temperatures. Tissue weight increases rapidly through the late spring and summer due to increasing temperatures and enhanced food concentrations. After the fall bloom, temperature and food quality drop. Mussel weight then declines over the winter for these larger mussels.

Fig. 4 shows model predictions for the phytoplankton P, zooplankton Z, non-plankton seston S and nitrogen N concentrations over a calendar year (starting Jan. 1). Results are shown for both the inner cove (solid line) and outer cove (dashed line).

count for these processes, but instead averages over their effect.

4.1. Carrying capacity

At the low densities investigated thus far, mussels had little effect on other components of the ecosystem. However, as the mussel density is increased, it is expected that the food field will be altered and ultimately individual mussel growth will be reduced. The box model, validated at low mussel densities, is used to experiment with the effects of increased mussel density and address issues of carrying capacity and maximum yield.

Numerical experiments with the box model at higher mussel densities indicated that similar results were achieved regardless of the mussel distribution between the two boxes. Thus, for simplicity, the model will henceforth be run with equal mussel densities of mussels in each box. In these experiments, zooplankton concentration followed closely its far field values and therefore the zooplankton results are not shown.

The influence of increasing mussel density on phytoplankton, seston and individual mussel weight is shown in Fig. 7 for both the inner cove
and outer cove. The concentrations of phytoplankton and seston decrease as mussel density is increased. Overall, their general temporal patterns are preserved, but shifted to lower values, an effect which is much more pronounced in the poorly flushed inner cove than the well flushed outer cove. Correspondingly, in the inner cove individual mussel growth shows a pronounced decline with increasing mussel density, while little effect is evident in the outer cove. The reason is that, in the outer cove, phytoplankton and seston are replenished rapidly by the strong tidal exchange processes. In the inner cove, tidal exchange is weak and thus phytoplankton and seston can easily be depleted by mussel grazing.

Fig. 8 shows the annual growth of an individual mussel \( M \) as a function of mussel density \( N \) for the inner and outer cove as calculated using the box model. The standard model run is used and the only quantity varied is the initial mussel density. It is seen that predicted mussel growth in the inner cove declines exponentially as stocking density is increased. This region is poorly flushed and therefore re-supply of food is low and easily depleted by mussel grazing. In contrast, mussel growth in the outer cove actually increases slightly
until a density of 30 mussels m\(^{-3}\) is reached whereupon it slowly decreases as expected. The explanation for the slight increase likely lies in the favorable alteration of the food quality under low grazing pressure. As food re-supply is relatively high in the outer cove, depletion of food sources requires significantly higher mussel densities than for the inner cove.

An estimate for the carrying capacity of the inlet can be determined from the information contained in Fig. 8. If the carrying capacity is defined as the stocking density at which a material reduction in the growth rate is found, then the carrying capacity for the inner cove is then certainly less than 5 mussels m\(^{-3}\), and the carrying capacity of the outer cove is near 40 mussels m\(^{-3}\). A more appropriate estimate for carrying capacity might correspond to the maximum yield in population biomass of the system over some time period. Referring to Fig. 8, the maximum yield is defined as the point on each curve where the product of \(M\) and \(N\) is largest. For the inner cove the maximum yield is about 40 mussels m\(^{-3}\) and for the outer cove it is greater than 300 mussels m\(^{-3}\). An appropriate stocking density would likely fall between these two different types of estimates. The important point is that the carrying capacity of the outer cove is nearly an order of magnitude greater than that of the inner cove.

Fig. 6. Observed mussel growth from Upper South Cove during the field study for both the inner and outer cove. The time evolution of tissue weight is shown for mussels of various initial sizes.
5. Sensitivity analysis

Numerical experiments carried out during model development suggested that predicted mussel growth was highly influenced by certain model parameters. Indeed, stability analysis of some simplified, nonlinear versions of the flux equations revealed complex dynamical behaviour as the model parameters were varied (Dowd, 1991). It was felt that, given the uncertainty in many of the model parameters, a systematic sensitivity analysis of the box model equations must be undertaken in order to investigate the influence of small variations in the model parameters on predicted mussel growth. As with any nonlinear system, the degree of sensitivity of the output to parameter variations depends on the base state about which the variations take place. Here, the parameter set given in the previous section was chosen as the standard model run (base state), and the initial mussel weight of 0.045 gC was used (the middle size class).

The sensitivity of the mussel growth to variations in the internal parameters, forcing functions and boundary conditions was measured by the following quantity

\[ S = \frac{\Delta M}{\Delta \text{Parameter}} \]

where \( S \) is a measure of sensitivity, \( M \) refers to mussel weight at the end of the integration period in the standard model run, and \( \Delta M \) is the change...
in the value of $M$ brought about by varying the model parameter. Similarly, the denominator measures the variation in the parameter of interest divided by its standard value. Overall, this equation simply compares the percentage change in mussel weight with a given percentage change in one of the model parameters. Comparing the values of $S$ for every parameter allows an assessment of the relative sensitivity of predicted mussel growth to changes in the parameter values. Here, each parameter in Tables 3 and 4 was varied by $\pm 1\%$ from its standard value. The value of $S$ was averaged for these positive and negative variations and the result tabulated for each parameter in turn. Sensitivity to the boundary conditions and forcing were calculated similarly, with the entire time series varied by a $\pm 1\%$ scaling.

The sensitivity of mussel growth to changes in the physiological parameters characterizing mussels and zooplankton is shown in Table 3. As expected, mussel growth is relatively insensitive to changes in the physiological parameters of zooplankton population, which are only indirectly related to mussel growth. The implication is that direct competition is relatively unimportant and could justifiably be ignored for this case. Zooplankton do, however, partly control phytoplankton dynamics and, in a system less

![Graph](image_url)

**Fig. 8.** Model calculation of maximum mussel weight at the end of the 1-year simulation (Jan. 1–Dec. 31) as a function of mussel density for both the inner and outer cove (upper curve, outer cove; lower curve, inner cove).

<p>| Table 3 | Sensitivity analysis for the physiological parameters for both the inner and outer cove |</p>
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Inner Cove</th>
<th>Outer Cove</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R_z$</td>
<td>0.265</td>
<td>0.0645</td>
</tr>
<tr>
<td>$Q_{ER}$</td>
<td>0.207</td>
<td>0.0418</td>
</tr>
<tr>
<td>$\mu_z$</td>
<td>0.373</td>
<td>0.138</td>
</tr>
<tr>
<td>$\epsilon_{ER}$</td>
<td>0.149</td>
<td>0.0314</td>
</tr>
<tr>
<td>$\epsilon_{ZS}$</td>
<td>0.0345</td>
<td>0.0069</td>
</tr>
<tr>
<td>$\kappa_z$</td>
<td>0.0800</td>
<td>0.0086</td>
</tr>
<tr>
<td>$I_z$</td>
<td>0.415</td>
<td>0.0980</td>
</tr>
<tr>
<td>$Q_{ZI}$</td>
<td>0.568</td>
<td>0.119</td>
</tr>
<tr>
<td>$\lambda_z$</td>
<td>0.0652</td>
<td>0.0182</td>
</tr>
<tr>
<td>$\mu_M$</td>
<td>0.894</td>
<td>0.817</td>
</tr>
<tr>
<td>$\epsilon_{MF}$</td>
<td>1.692</td>
<td>1.382</td>
</tr>
<tr>
<td>$\epsilon_{MS}$</td>
<td>4.416</td>
<td>5.133</td>
</tr>
<tr>
<td>$\kappa_M$</td>
<td>3.172</td>
<td>3.250</td>
</tr>
<tr>
<td>$Q_{MI}$</td>
<td>2.255</td>
<td>2.459</td>
</tr>
<tr>
<td>$b$</td>
<td>2.672</td>
<td>3.231</td>
</tr>
<tr>
<td>$I_M$</td>
<td>6.087</td>
<td>6.563</td>
</tr>
<tr>
<td>$Q_{MB}$</td>
<td>1.4466</td>
<td>1.7249</td>
</tr>
</tbody>
</table>

The quantity $S$ is a measure of parameter sensitivity and is defined in text.

dominated by exchange, would be expected to play a more important role. In contrast, mussel growth is extremely sensitive to changes in the physiological parameters describing the mussel population in both the inner and outer coves. (For instance, a $1\%$ change in $I_M$ is multiplied

<p>| Table 4 | Sensitivity analysis for the environmental parameters for both the inner and outer cove |</p>
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Inner Cove</th>
<th>Outer Cove</th>
</tr>
</thead>
<tbody>
<tr>
<td>$K_1$</td>
<td>0.2472</td>
<td>0.6437</td>
</tr>
<tr>
<td>$K_2$</td>
<td>0.1363</td>
<td>0.2350</td>
</tr>
<tr>
<td>$T$</td>
<td>0.2404</td>
<td>0.3156</td>
</tr>
<tr>
<td>$\xi$</td>
<td>0.2599</td>
<td>0.1255</td>
</tr>
<tr>
<td>$P_m$</td>
<td>0.3604</td>
<td>0.3617</td>
</tr>
<tr>
<td>$Z_{so}$</td>
<td>0.0557</td>
<td>0.0091</td>
</tr>
<tr>
<td>$S_{so}$</td>
<td>0.7934</td>
<td>1.0890</td>
</tr>
<tr>
<td>$\lambda_{so}$</td>
<td>0.2482</td>
<td>0.1059</td>
</tr>
</tbody>
</table>

The quantity $S$ is a measure of parameter sensitivity and is defined in the text.
6-fold in mussel weight). This results from the fact that changing these parameters directly alters the nonlinear equations governing the energy budget of the mussel population. Given the uncertainty in these parameters, this sensitivity has important consequences for the use of the model as a predictive tool.

Table 4 shows the sensitivity of mussel growth to changes in the parameters describing the environment, i.e. the forcing functions, boundary conditions and exchange coefficients. Mussel growth at these low densities is relatively insensitive to the environmental parameters as compared to the mussel physiological parameters. Consider further the exchange parameters $K_1$ and $K_2$. At high densities, it has been shown that exchange plays an important role in determining mussel growth and carrying capacity. However, the sensitivity of mussel growth to variations in $K_1$ and $K_2$ at high densities remains quite stable near the values shown in Table 4.

6. Discussion and conclusions

In this study, a relatively simple, and general, dynamic system has been proposed to model the interaction of a cultured mussel population with the main physical and biological components influencing its growth. Application to an aquaculture site at Upper South Cove was carried out concentrating on the annual variability. The simulation proved reasonably successful and highlighted the relative importance of the internal ecology of the cove versus exchange during different times of the year. In winter and spring, the cold temperatures and low growth rate of phytoplankton combine to suppress the biological cycling of carbon and the system closely follows its boundary values. Mussel growth during this time could be well predicted by using the prescribed far-field values for the phytoplankton and seston. However, as temperature rises in summer, the phytoplankton growth rate increases and the physiological rates of all the biological components are enhanced. Components then deviate significantly from their boundary values and the biological production of the cove dominates over exchange and mussel growth is enhanced. A dynamic model is needed to account for these effects. Overall, the model proved useful as a research tool for which to generate hypotheses on bivalve growth and understand the important ecological interactions occurring in Upper South Cove.

The dynamic model also proved to be a convenient means to experiment with the effects of high density culture. Model predictions show the expected decline in individual mussel growth with increased mussel density. The details of this general relation are, however, modified significantly by differential exchange processes. Food depletion occurs much more rapidly in the poorly flushed inner cove than in the well flushed outer cove, and the carrying capacity of the inner cove is estimated to be an order of magnitude less than that of the outer cove. Particle exchange clearly plays an important role in defining carrying capacity of high density bivalve culture (Carver and Mallet, 1990; Raillard and Ménesguen, 1994).

This study has demonstrated the high sensitivity of the model predicted mussel growth to small changes in the parameters governing mussel ingestion and respiration. This complex behaviour is well known for nonlinear dynamic systems (e.g. May 1976), but is problematic in the sense that it requires specifying physiological parameters with a high degree of accuracy when, in fact, these parameters are poorly known (Bayne and Newell, 1983; Griffiths and Griffiths, 1987). Raillard and Ménesguen (1994) suggest that the important uncertainties in their model of oyster culture lie in the description of particle exchange and mixing processes. In this study, determination of exchange coefficients for Upper South Cove was relatively straightforward. Instead, it is felt that the sensitivity of the model results to the uncertain physiological parameters describing the mussel energy budget is the major limitation of the model in producing robust predictions of bivalve growth.

This parameter sensitivity is largely due to the functional relations used to describe the physio-
logical response of the bivalve to environmental conditions (i.e. the modulating functions $f_{MB}$, $f_{MR}$). These are inherently nonlinear and model sensitivity to parameter changes might be an inseparable property of population models of the sort used to describe bivalve growth. The range of reported values for the parameters means that the model must be ‘tuned’ in order to replicate the observations, resulting in little confidence in its extrapolation ability. For example, it is possible that different parameter sets could give rise to effectively identical model output, but provide quite different results when applied to high density culture or different sites. In realistic cases, it is observed that mussel growth is more stable than that predicted by the model. This is probably not due to a set of underlying, precisely defined physiological parameters, but rather a more linear (or less nonlinear) form for the functional relations. One possible area for improvement for this is a proper accounting of the acclimation of the organisms to prevailing environmental conditions.

In summary, it is suggested that future modeling studies focus on rectifying the uncertainties in bivalve ecology and physiology with the goal of a robust and quantitative description of bivalve growth in a time varying environment. The limited ecosystem, focused on bivalve growth, and represented as a dynamic system does seem to be an appropriate framework for investigating the dynamic of bivalve culture. However, the high sensitivity of this nonlinear system to small parameter changes suggests that alternative parameterizations of the mussel energy balance must be formulated, tested, and refined in both laboratory and field situations before more elaborate and complex predictive models of bivalve growth are constructed.

Acknowledgements

This research was funded by a strategic grant from the Natural Sciences and Engineering Research Council of Canada to Drs J. Grant and K.R. Thompson at Dalhousie University, Halifax, Canada. The author is grateful to these co-investigators for their support throughout the project. I also wish to thank C.E.A. Carver and A. Mailet for making available the observational data, as well as many extremely helpful discussions.

References


