MUSSEL SIMULATION PROGRAM DOCUMENTATION.

PART 1 - DESCRIPTION OF THE MODEL

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1.1 Introduction

The Mussel Model consists of three parts: the Feeding, Physiology and Population models. The Feeding model describes the feeding behaviour of an individual mussel, and finds the energy intake from feeding and the associated costs. The Physiology model partitions this energy between the various activities: growth, reproduction, metabolic costs and storage. A sub-model within the Physiology model determines the spawning behaviour of the model mussel. The Population model uses the reproductive performance of an individual predicted by the Physiology model to estimate the rate of increase of a population composed of such individuals. A control run of the Mussel Model, with no toxic effects, is compared with an impacted but otherwise identical run, to assess the effect of toxins.

The values of parameters for the Mussel Model are taken from a file provided by the user. Food concentrations can be described by a variety of annually periodic functions, or monthly values in a user-supplied file; the food supply is assumed to be the same each year. The effect of toxins on feeding behaviour is entered by the user, and a toxicity routine uses this information to establish toxicity parameters that govern the physiological effects of the toxicant. The Population Model uses a survival schedule in an additional file provided by the user. Section 2.3 gives more detail of user supplied information.

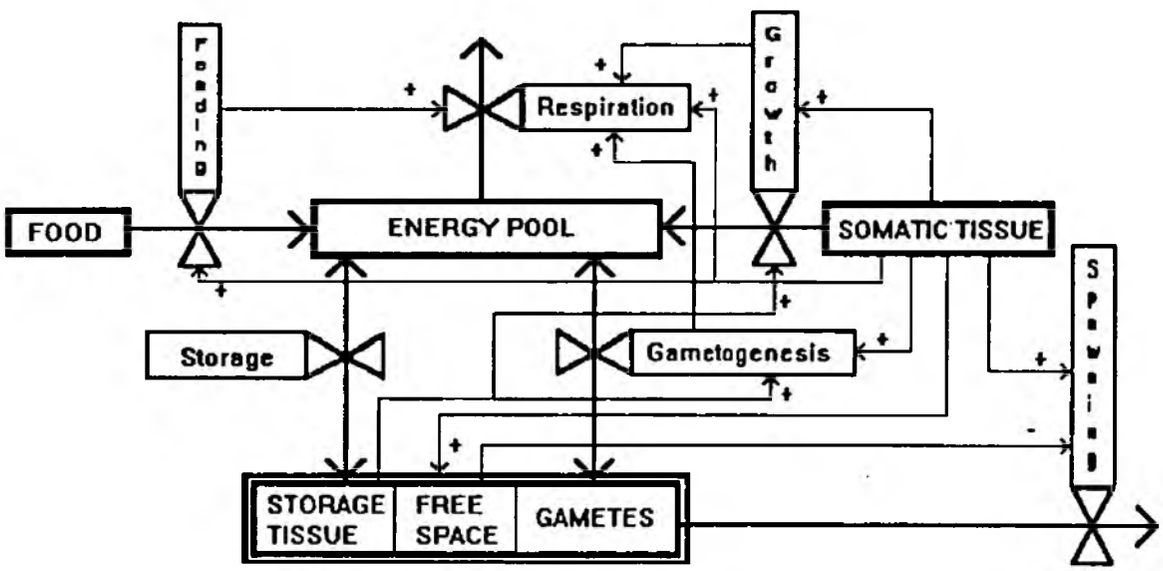

Figure 1.1 Block diagram of the Physiology model.

1.2 The Feeding Model

Background

The Feeding model is based on the assumption that the mussel can adjust its feeding strategy to maximise the net energy gained through the feeding process. The costs of feeding and the absorbed ration are calculated for different feeding strategies. The driving variables for the model are the concentration and composition of available food and the volume of the gut. The strategy that maximises the net energy gained by the mussel is selected. It is assumed that the mussel can adapt its feeding behaviour instantly in response to a change in feeding conditions, or, alternatively, that the feeding conditions in the environment will generally not change more quickly than the response time of the animal. In addition, it is assumed that the gut volume depends only on the somatic dry weight of the animal, and that the gut is kept full. The feeding model is discussed fully elsewhere (Willows, in press); here the effects of the size of the animal and the influence of toxins on feeding strategy and net energy gained through feeding are considered.

In the model, the mussel can change its feeding strategy in three ways:

1) By adjusting the quantity of digestive enzymes produced. Increasing the enzyme production allows more complete digestion of the ingested particles, but also increases the costs of feeding.

2) The food supply will generally consist of a mixture of particles of differing energy content and digestibility. The mussel is assumed to adjust its feeding strategy by selecting more profitable particles, and rejecting others. By rejecting some particles, the mussel must increase the pumping rate in order to keep the gut filled, but the increased cost associated with this can be offset by the greater energy content or rate of digestion of the higher quality particles.

3) By adjusting the pumping rate. The ingested ration increases with increased filtration rate, provided the particle selection remains unaltered, but a higher pumping rate is more expensive. In addition, since the size of the gut is limited, and the model assumes that the gut always remains full, a higher ingestion rate means a shorter gut passage time, and hence less thorough digestion of the ingested particles.

To simplify the use of the model, the food supply is approximated by just two particles, though this limitation is not intrinsic to the model. These are described by parameters whose values are contained in the parameter file. Of these two particles, one represents algae, which have a relatively high energy content, and the other represents suspended sediment which has a lower energetic value. This enables a range of feeding conditions to be represented, for example estuarine or coastal waters, with their different sediment loading (Widdows et al. 1979). At the same time, the information that the user must provide is kept to a minimum.

Model Structure

Absorbed ration:

The rate of energy absorption from particles in the gut is assumed to vary in positive relation with the energy available in the particles, and the concentration of digestive enzymes secreted into the gut. Energy is assumed to be added to the gut contents in the form of digestive enzymes, part of which may be re-absorbed with time. The energy remaining in the gut contents is assumed to decrease exponentially with gut residence time as both food energy and digestive enzymes are absorbed, with the exponential coefficient being proportional to the concentration of digestive enzymes. The concentration of digestive enzymes is proportional to $\frac{ENZYME \cdot T}{V_g}$, so that the exponent is proportional to $\frac{ENZYME \cdot T^2}{V_g}$ giving the following function for the absorbed ration:

$$\text{Absorbed ration} = EI\left[1-\exp\left[\frac{-b \cdot ENZYME \cdot T^2}{V_g}\right]\right] - ENZYME \cdot T \cdot \exp(-a \cdot T)$$

Where:

EI = total available ingested energy ($J \cdot hr^{-1}$)
a = rate coefficient for resorption of digestive enzymes (hr^{-1})
b = rate coefficient for digestion of particles ($ml \cdot J^{-1} hr^{-1}$)
ENZYME = rate of investment in digestive enzymes ($J \cdot hr^{-1}$)
T = gut residence time (hr)
V_g = gut volume (ml)

The above function for the absorbed ration could be negative if the energy loss in digestive enzymes outweighs the energy absorbed from the food. This reflects the metabolic faecal loss that can occur as a transient phenomenon after experimental reduction in the available food (Hawkins and Bayne, 1985). Mussels adjust to the new regime and achieve positive net energy absorption after a period of about 2 weeks.

The available energy in a food, EI, is the energy that could be absorbed at very long (infinite) gut residence times. This may be less than the actual energy content of the particle, depending on the digestive apparatus of the mussel, and it will generally be greater than the actual energy absorbed.

The ingested energy is the product of the food concentration, the filtration rate, and the energy content of the food:

$$\text{Ingested energy, } EI = FR \cdot E \cdot C$$

Where:

FR = Filtration (pumping) rate (litre·hr^{-1})

E = Available energy in food (J·mg^{-1} DW)

C = Food concentration (mg DW·litre^{-1})

Where there are several different particles the total ingested energy is the above multiplied by the selection coefficient, summed over all particles.

$$\text{Ingested energy, EI} = FR \cdot \sum_i S_i \cdot E_i \cdot C_i$$

Where:

S_i = Selection coefficient for particle type *i*

E_i = Energy content of particle type *i* (J·mg^{-1} DW)

C_i = Concentration of particles of type *i* (mg DW·litre^{-1})

The absorbed ration is summed over all particles in a similar way, as follows:

$$RATASS = FR \cdot \sum_i S_i \cdot E_i \cdot C_i \cdot \left[1 - \exp\left[\frac{-b_i \cdot ENZYME \cdot T^2}{V_g}\right]\right] \cdot ENZYME \cdot T \cdot \exp(-a \cdot T)$$

Where:

RATASS = Absorbed ration (J·hr^{-1})

b_i = Absorption rate coefficient for particle type *i* (ml·J^{-1}hr^{-1})

Costs:

The cost of filtration is assumed to be proportional to the square of the water speed through the mussel, based on the expectation of laminar flow (Jorgensen 1976). This gives a cost proportional to (pumping rate)/(cross sectional area). The resistance is assumed to be inversely proportional to the cross sectional area, and proportional to the length. This implies that the water is pumped through a uniform tube, which is far from being the case, but it is assumed that average values for the area and length can be defined, proportional to (somatic size)$^{2/3}$, and to (somatic size)$^{1/3}$ respectively. This gives the following function for the filtration cost:

$$\text{Filtration cost } \alpha \frac{FR^2}{SOMA^{1/3}}$$

Where:

SOMA = somatic dry weight of mussel (mg)

Since the gut volume is assumed to depend only on somatic size, the size can be expressed in terms of the gut volume. This means that the somatic size need not be available to the Feeding model. The relationship between gut volume and size is based on published data (Hawkins et al. 1990).

$$\text{Gut Volume, } V_g \propto SOMA^{2/3}$$

$$\text{Filtration cost} = g_1 \frac{FR^2}{V_g^{1/2}}$$

Where:

g_1 = filtration cost coefficient ($J \cdot hr \cdot ml^{-1.5}$)

The absorption cost is assumed to be proportional to the absorbed ration, RATASS, and the cost of production of digestive enzymes is proportional to the energy invested, ENZYME. There is no cost directly associated with selecting or rejecting particles, (though rejecting particles may necessitate a higher filtration rate to keep the gut filled). So the total cost of feeding is the sum of the filtration, absorption and enzyme production costs. Note that loss of energy in the form of unreclaimed digestive enzymes is not accounted a cost to the mussel, but is taken account of in the evaluation of the absorbed ration.

$$\text{Total feeding costs, FMR} = g_1 \frac{FR^2}{V_g^{1/2}} + g_2 RATASS + g_3 \cdot ENZYME$$

Where:

FMR = Filtration metabolic rate ($J \cdot hr^{-1}$)

g_2 = Absorption cost coefficient (-)

g_3 = Cost of producing digestive enzymes (-)

The net energy gained through feeding is the absorbed ration less the feeding costs:

$$\text{Net energy gained} = RATASS - FMR$$

This is the quantity maximized in the model.

When food is scarce, the feeding costs may be greater than the absorbed ration, leading to negative energy gain. Under these circumstances, it is more advantageous for the mussel to cease to feed, and so costs and energy gain are assumed to be zero and costs are therefore minimized. Metabolic faecal loss, represented by a negative absorbed ration, therefore never occurs in the model.

Filtration rate:

The filtration rate is related to the gut residence time by the assumption that the gut is kept full. The filtration rate is then the gut volume divided by the product of the

effective volume occupied by particles in the gut and the gut passage time. The particle volume may change during digestion, so the effective volume-time of a particle type is the integral of the volume over the gut passage time, T, multiplied by the quantity ingested. For multiple particle types, this is summed over the various particles ingested. This leads to the following relation:

$$\text{Filtration rate} = \frac{V_g}{\sum_i S_i C_i \int_0^T V_i dt}$$

The change in volume of the food particles in the gut is assumed to follow the same function as the energy absorption. The rate constant, b', is assumed to be equal to the rate constant for energy absorption, b. This is a simplifying assumption to reduce the number of parameters, though it is not intrinsic to the model.

$$\text{Particle volume} = V_s - (V_s - V_f)\exp(-b' \cdot ENZYME \cdot T^2)$$

Where:

V_s = Initial volume of particle ($ml \cdot g^{-1}$ DW)

V_f = Final volume of particle ($ml \cdot g^{-1}$ DW)

b' = Rate constant for volume change ($J^{-1} \cdot hr^{-1}$)

Effect of toxicant

The feeding model incorporates two mechanisms of toxicant impact. The first mode represents respiratory chain uncoupling, where the efficiency of metabolic processes is impaired by the action of a toxicant. For this mode of action of a toxin, the model assumes that the metabolic costs of all activities will be increased, and that the feeding strategy will be adjusted to maximize the net energy gain under the new circumstances. The increase in costs is achieved by multiplying the cost coefficients, g_i, by a factor of Q1, the toxicity parameter. The value of Q1 must be greater than one; a value less than one would imply a decrease in costs, and it is assumed that no toxicant would have such an effect. The feeding strategy is optimized in the usual way under the new cost regime. Note that although the unit costs of feeding are increased, the actual feeding cost may decrease as the optimum investment in feeding may be less under the new cost regime; the net energy gained will always be less.

In the second mode, representing the action of narcotics on physiological function, the model first finds the optimum strategy under normal conditions. Filtration rate is then reduced by narcotic action so that, in effect, the animal is feeding sub-optimally. The reduction in filtration rate is achieved by dividing the gut residence time by a factor Q2. A value of Q2 less than one gives a reduction in filtration rate, corresponding to narcotization. The value may be greater than one, leading to an increase in filtration rate; this corresponds to a stimulant action. Narcotization will have the effect of decreasing both costs and ingested ration, while the amount of energy absorbed from each food particle may increase as gut residence

time increases. Some toxicants may cause a stimulation of physiological processes. Such an effect is treated as the opposite to narcotization. Stimulation will increase costs and increase the ingested ration, while decreasing the absorption efficiency. For both stimulation and inhibition, the net energy gained by the mussel will decrease.

Metabolic chain uncoupling and narcotization modes of toxicity may be applied simultaneously; in this case, the optimum strategy is first found with costs increased by a factor of Q1, the metabolic uncoupling factor. The resulting gut residence time is then divided by Q2, the narcotization factor, so that the mussel is operating sub-optimally at increased costs. Narcotization only acts on the Feeding model. Respiratory chain uncoupling is also reflected in the Physiology model, by an increase in respiration costs (see p. 14).

The values of the toxicity parameters, Q1 and Q2 may be determined from information about the short-term effects of the toxin on the feeding behaviour of the mussel. This information is supplied by the user.

Notes on Programming

The Feeding module is run from within the Physiology Model, which supplies the gut volume, the concentration of particles, and estimates of the digestive investment, the selection coefficients, and the gut residence time. The initial and final volumes of the two particle types and their energy contents are parameters in the parameter set, as are the cost coefficients, g_i.

The maximization of the net energy gained is done using NAg library routine E04JAF.

The particle volume is integrated over the gut residence time by substituting $x = T \cdot \sqrt{2 \cdot b' \cdot ENZYME}$ in the particle volume function. In this way, the volume can be re-written as a normal distribution. This standard function is integrated using algorithm AS66 from 'Applied Statistics' (1973), Vol. 223, p424.

1.3 The Physiology Model

Background

The Physiology model simulates the growth and the reproduction of an individual mussel. The energy intake, found using the Feeding Model, is partitioned between growth and reproduction. The partitioning is assumed to depend on the body size and on the energy available to the mussel, which includes stored reserves of energy as well as the amount of absorbed ration. The energy allocations to growth and reproduction are described by Michaelis-Menton type kinetics. The allocation shifts from growth towards reproduction as body size increases. The energy budget has to balance; any excess or shortfall is made up by adding to or taking from the stored reserves. When reserves are zero, the animal is considered to be no longer viable, and death is assumed. The Physiology model is illustrated in Figure 1.1 (p. 3).

A spawning sub-model describes the spawning behaviour of the mussel. The spawning rate depends on the amount of energy available to the mussel and on the amount of gametes accumulated.

The model simulates the growth and reproduction of a single mussel, from an initial state that is set by the user. The output depends on the environmental conditions, in particular, on the available food supply and the impact of pollutants. State variables are somatic size, amount of stored energy, amount of stored gametes, and amount of spawn released.

Model Structure

In the following, α_n, β_n and ϕ_n are parameters whose values are contained in the parameter file supplied by the user.

Energy intake:

The absorbed ration is calculated by the Feeding model. The available food is calculated from data provided by the user, and the gut volume, required by the Feeding model, depends on the somatic size, SOMA:

$$\text{Gut Volume, } V_g = \alpha_1 \text{SOMA}^{\beta_1}$$

The available energy is the absorbed ration, less feeding costs and tissue maintenance costs:

$$\text{Net ration, RATNET} = \text{RATASS} - \text{BMR} - \text{FMR}$$

Where:

RATASS = absorbed ration (from the Feeding model)
BMR = basal metabolic rate (see p. 12)
FMR = feeding metabolic rate (from Feeding model)

Energy allocation:

The rates of growth, G, and gamete production, R, depend principally on a compound variable SDEV, which measures the level of stored energy reserves relative to a target level (Storage DEViation). This target level of reserves is assumed to depend on somatic size.

$$SDEV = STORE - \alpha_{12}SOMA^{\beta 12}$$

When rates of growth or gamete production are non-zero, the rates are determined from SDEV by Michaelis-Menton type equations:

$$|Rate| = \frac{|K_1 K_2 SDEV|}{K_1 + |K_2 SDEV|}$$

Both K_1 and K_2 are functions of somatic size, allowing size-specific changes in allocations between growth and gamete production as size increases (discussed further in Section 1.4, under 'Sensitivity Analysis'). In addition, K_2 is also a function of the net ration, through the use of a compound variable termed POOL (discussed below). Hence, for growth, G:

$$K_1 = \alpha_5 SOMA^{\beta 5}$$

$$K_2 = \alpha_6 SOMA^{\beta 6} POOL^{\phi 1}$$

And for gamete production, R:

When gamete production is positive: $K_1 = \alpha_7 SOMA^{\beta 7}$

And when gametes are re-absorbed: $K_1 = \alpha_9 SOMA^{\beta 9}$

$$K_2 = \alpha_8 SOMA^{\beta 8}\, POOL^{\phi 2}$$

The variable POOL is used to allow growth and gamete production to respond to changes in food supply. Rates of allocation to tissue production are known to be tightly coupled to feeding activity (Widdows and Hawkins, 1989). However, although mussels frequently show evidence of the acclimation of physiological function to environmental changes (e.g. Widdows, 1976, 1985), such physiological adaptation is not usually instantaneous, but can take periods of up to 2 weeks. Hence, POOL is calculated by applying a time-delay to the instantaneous value of the net ration:

$$POOL = RATNET(1 - e^{-wt}) + POOL(t-1)e^{-wt}$$

Where:

POOL = time-delayed energy pool
w = Delay coefficient.

Hence, when both POOL and SDEV are positive, growth and gamete production allocations are positive. When either is negative, growth and gamete production rates are zero, while when SDEV and POOL are both negative growth and gamete production rates are also negative. This represents resorption of body tissues, which is a way of mobilizing energy in addition to the utilization of stored reserves. The rate of resorption of somatic tissue is assumed to depend on the same parameters as growth, while the asymptotic gamete resorption rate can differ from the gamete production rate asymptote.

Energy storage:

The rate of storage, ST, is equal to the ration less all other expenditure, and serves to balance the energy budget:

$$\text{Rate of storage, ST} = \text{RATNET} - \text{Costs} - \text{G} - \text{R}$$

The determination of costs is discussed below.

The mantle is assumed to be the reservoir for both energy stores and accumulated gametes. The capacity of the mantle is assumed to be limited according to the size of the animal, hence:

$$\text{Store capacity} = \alpha_2 \text{SOMA}^{\beta 2}$$

The store capacity influences the rate of spawning, discussed below.

Costs:

Metabolic costs incurred by the mussel can be divided into those due to the maintenance of body tissues, and activity related costs. These activity costs involve feeding, growth, reproductive allocation, spawning and the storage or retrieval of energy reserves. Details of these costs, which contribute to the overall respiration rate, are given below.

Tissue maintenance costs are assumed to depend on the somatic size, SOMA. It is assumed that there are no maintenance costs associated with stored gametes or energy reserves, hence:

$$\text{Basal metabolic rate, BMR} = \alpha_3 \text{SOMA}^{\beta 3}$$

The costs of growth, storage and gamete production are assumed to be proportional to the absolute amount of energy processed through that activity. The resorption of tissue and the release of stored energy are assumed to bear the same costs as positive growth, gamete production and storage; this constitutes a simplification to reduce the number of parameters, and is not intrinsic to the model. The activity costs are thus given by the following relation, where the values of ε_i are provided within the parameter file.

$$\text{Activity costs, SMR} = \varepsilon_1 \cdot |G| + \varepsilon_2 \cdot |R| + \varepsilon_3 \cdot |ST| + \varepsilon_4 \cdot |S|$$

Where the cost parameters, which are dimensionless, are:

ε_1 = Cost of growth/resorption of somatic tissue

ε_2 = Cost of producing/reabsorbing gametes

ε_3 = Cost of creating/utilizing stored reserves

ε_4 = Cost of spawning

And:

G = Growth/resorption of somatic tissue ($J \cdot hr^{-1}$)

R = production/resorption of gametes ($J \cdot hr^{-1}$)

ST = energy put into (or taken from) store ($J \cdot hr^{-1}$)

S = gametes spawned out ($J \cdot hr^{-1}$)

The total respiration costs of the mussel, RESP, are given by the sum of the above components:

$$\text{Respiration, RESP} = \text{BMR} + \text{FMR} + \text{SMR}$$

The feeding costs, FMR, are calculated by the Feeding model (see p. 6).

Spawning sub-model:

An essential assumption of the spawning model is that the capacity for storing accumulated gametes is limited. Therefore a 'trigger level' is set within the model, dependent on the somatic size. Spawning starts when the total amount of stored energy plus accumulated gametes reaches this trigger level, provided that POOL is positive. In general, allowing for the time lag, POOL is positive when the mussel is in positive energy balance. It is assumed that the mussel will not spawn when its energy balance is negative, as perceived by a negative value of POOL. Once spawning has commenced, it continues until the POOL drops to zero or below, or until all the gametes have been released. Therefore while POOL remains positive, spawning will be continuous if the rate of production of gametes is equal to the rate of release, while episodic spawning will occur when the rate of release is greater than the rate of production, allowing the stored gametes to fall to zero. The rate of release of gametes depends on the amount of stored gametes, the amount of storage capacity remaining unused, the somatic size and the value of POOL.

The spawn trigger level is reached, and spawning initiated, when the following condition is satisfied:

$$\text{Spawning triggered when: STORE} + \text{REPRO} > \alpha_{10}\text{SOMA}^{\beta 10}$$

The amount of free space, FREE, is the storage capacity less the amount of store and gametes:

$$\text{Free space, FREE} = \alpha_2\text{SOMA}^{\beta 2} - (\text{STORE} + \text{REPRO})$$

The rate of spawning increases as the amount of stored gametes increases, and also as the amount of free storage space decreases. Hence the spawning rate increases as the levels of stored energy reserves increase. Additionally, the spawning rate increases with increasing POOL, and with increasing somatic size. Size affects the rate both directly and through its effect on the storage capacity and the spawn trigger level:

$$\text{Spawning rate, } S = \mu_1\alpha_7 SOMA^{\beta 7} + \frac{K_1 \cdot REPRO}{REPRO + \mu_2 \cdot FREE}$$

where:

$$K_1 = \alpha_{11} SOMA^{\beta 11} POOL^{\phi 3}$$

and:

μ_1 = Parameter defining the minimum spawning rate

μ_2 = Parameter describing spawning rate variation with free space

Effect of Toxicant:

Toxic effects operate primarily through the Feeding model, by changing the absorbed ration and the feeding costs. In addition, respiratory chain uncoupling is reflected within the Physiology model, by increasing the cost terms BMR and SMR by the factor Q1, as in the Feeding model.

$$\text{Basal metabolic rate, BMR} = Q1 \cdot \alpha_3 \cdot SOMA^{\beta 3}$$

$$\text{Activity costs, SMR} = Q1 \cdot (\varepsilon_1 \cdot |G| + \varepsilon_2 \cdot |R| + \varepsilon_3 \cdot |ST|)$$

Notes on Programming

The Physiology model works in discrete time intervals, calculating the activity pattern of the individual mussel from the conditions and state variables evaluated at the beginning of the interval, and incrementing the state variables by the appropriate amount for the next interval. The interval is set by the integer NPD, the number of iterations per day, which is selected by the user. A large value will give a more accurate result, but will increase the run time. The minimum value of 1 iteration per day will usually be satisfactory since the only process to vary significantly over a day is the spawning activity. The user should be cautious when making direct comparisons between runs where the values of NPD differ.

1.4 The Population Model

Background

The Population module uses the annual spawn production of an individual impacted or unimpacted mussel produced by the Physiology model, together with a mortality schedule supplied by the user, to estimate the rate of increase of an impacted population relative to a control, unimpacted population. Toxicants have no direct effect on the Population model; they only act through the effect they have on the individual's reproductive output calculated within the Physiology model. In calculating the rate of increase it is assumed that the populations are closed to emigration and immigration. Hence all larvae produced are available for recruitment, and there is no exchange with other populations. The effects of larval dispersal and advection away from the population can be included through the use of a larval mortality factor. The loss of larvae is taken from the mortality schedule supplied by the user, and is assumed to be the same for impacted and unimpacted populations. This constitutes the assumption that the toxicant is truly sub-lethal; it has no effect on mortality rates. However, within the Physiology model the toxic impacted mussel can die prematurely relative to the control. This is interpreted in the Population model as 100% mortality at that age, since the Population model is based on the characteristics of a single individual. Runs of the model where this occurs should be treated with caution, since natural populations will contain varying individuals and varying conditions. 100% mortality at a given age due to a sub-lethal toxin would be not be expected in such a situation.

This is a relatively simple model, and there are many environmental and population level processes that are not taken into account, such as temperature and density dependent effects, both on mortality and on the settlement of larvae. The advantage of this simple model is that it can give a qualitative measure of the relative impacts of a toxicant acting under different environmental conditions, or of different toxicants, without the large amount of information necessary to give a detailed quantitative prediction of the productivity of a population. This will be affected in a complex way by other nearby populations, by predation, by toxic impact on larvae, and many other processes.

In the long term, a population would be expected to be near equilibrium, i.e. to have an average population growth rate equal to zero, with birth and immigration balanced by emigration and death. The growth rate found by the Population model reflects the ability of individuals to recover from the impact of natural variations in the environment. This recovery may be adversely affected by the action of a toxicant. The growth rate is thus a measure of the resilience of a population.

The nature of the mussel's environment is determined both by data supplied to the Physiology model, and by the mortality schedule. Mussel populations may be expected to experience differing mortality rates depending on their habitat. Higher

mortality will tend to decrease the resilience of a population. The mortality schedule that is used should be appropriate to the population of interest.

Model Structure

In order to calculate the population growth rate the stable age distribution must first be determined, given the age dependence of individual reproductive output, and the mortality schedule. The stable age distribution is given in terms of the numbers in each age class, N(x,t), where age class x consists of animals of age x-1 to age x at the end of year t.

The model uses the output of the Physiology model for both impacted and control populations, giving population growth rates r_i and r_u respectively. The value of:

$$\text{Relative population growth rate} = \exp(r_i - r_u)$$

is a measure of the impact of the toxicant on individuals within the population.

Stable age distribution:

The number of new recruits to a population in year t is the number of larvae produced in the previous year, multiplied by the larval survival factor, L(0). The number of larvae is the sum of the spawn production over each age class:

$$\text{Number of recruits, } N(0,t) = L(0) \sum_{x=1}^{xmax} N(x,t-1)S(x)$$

Where S(x) is the number of larvae produced in one year by an animal in age class x, and N(x,t) is the number of mussels in age class x in year t. N(x,t) is equal to the number of animals one year younger in the previous year, multiplied by the survival factor for the age class, L(x), as follows:

$$N(x,t) = L(x)N(x-1,t-1)$$

Population growth rate:

The population growth rate in year t is defined as:

$$\text{Growth rate, } R(t) = \ln\left[\sum_{x=1}^{xmax} N(x,t)\right] - \ln\left[\sum_{x=1}^{xmax} N(x,t-1)\right]$$

And the change in rate from year t-1 to year t as:

$$\text{Change in rate, } DELR(t) = \frac{R(t) - R(t-1)}{R(t)}$$

In order to calculate the population growth rate, the routine starts with one animal in each age class, and applies the above equations to find the numbers in the following year. Iteration continues until DELR is less than 0.005 for two successive years, and the stable age distribution and population growth rate are found. It should be noted that the stable age distribution will be heavily dependent on the user-supplied mortality schedule.

1.5 The Parameter Set

Sensitivity analysis

The values of the parameters of the model determine its behaviour. These values can be adjusted to 'tune' the model to match mussels from a particular population, or experiencing particular environmental conditions. This section discusses the effects of changing the parameters from the default values. The analysis of the Feeding model is discussed by Willows (in press); the effect of gut size on feeding is covered here. The Population model has no parameters, but uses a mortality schedule which represents death by age and partly determines the value of the rate of increase, r. This discussion will therefore concentrate on the Physiology model and on the effects of gut size on feeding.

The fundamental structure of the model is determined by the way processes depend on size. The power coefficients, β_i, govern these relationships. Processes are assumed to vary with such quantities as length, area or volume, and the values of the power coefficients are accordingly constrained to multiples of 1/3. As far as feasible they are taken from laboratory or field data. The variation of energy allocation to growth and reproduction with size is chosen so that allocation switches from growth to reproduction as size increases. The values of the power coefficients are considered to provide the essential structure of the model; changing them will produce a different model. The effects of changes in these parameters (β_i) is therefore not considered here.

The consequences of changes in the parameter set depends on the overall structure of the model. First, therefore, the general characteristics of the Physiology model will be considered. A discussion of each parameter will follow, which will refer to the points enumerated in the general discussion.

General features of the Physiology Model

The Physiology model is based on energy budgeting. Energy intake, determined by the feeding model and based on the gut size and food supply, is allocated between growth, gamete production, storage, and respiration. Any change in energy intake or in costs will directly affect the amount of energy available for growth and gamete production.

Both allocation strategy and energy intake depend on somatic size. These dependencies lead to two feedback-loops that dominate the response of the Physiology model, with other effects being relatively minor.

1) *Size dependent allocation.* At small size, energy is allocated primarily to growth. As size increases, the balance shifts towards gamete production. A decrease in the rate of allocation to growth will reduce the somatic size reached in a given time, and hence shift the energy allocations from gamete production to growth. Similarly, an increase in growth allocation will increase the size reached, and hence shift energy

away from growth. Hence the manner in which growth depends on size provides a negative feedback on growth over a period of time. The same mechanism also provides a negative feedback on reproductive investment over a period of time, since the total energy for growth and gamete production together is limited. Increased investment in gamete production will leave less energy available for growth, so that a smaller size is reached in a given time. The reduction in size will lead to increased allocation to growth and decreased allocation to gamete production, compared with the default parameter set. This effect provides a negative feedback on changes to investment in growth or gamete production, and provides a mechanism for 'catch-up' growth to occur after a set-back.

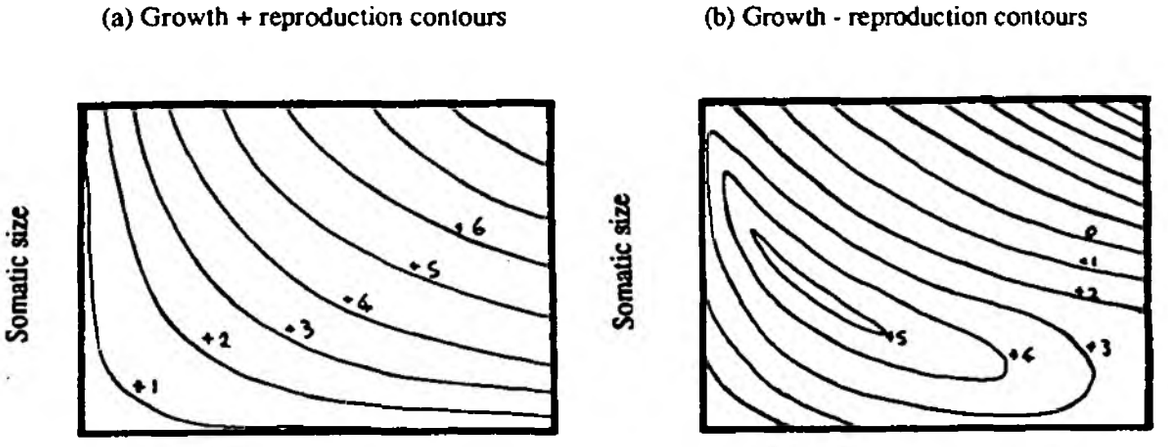

Figure 1.2 Dependence of energy allocations on somatic size and stored energy.

2) *Size dependent intake.* The absolute energy intake increases with increasing size, since larger animals have larger guts. This means that a reduction in growth rate (relative to the default parameter set) will lead to a reduction in energy intake that will have a further negative impact on growth. This provides a positive feedback on energy intake, so that small effects on size may persist through time, and growth may not catch up completely. This can have a disproportionately large effect on gamete production since growth is stabilized by the negative feedback described in (1) above.

Together, the above feedback loops tend to stabilize the asymptotic size in the face of changes in both parameter values and food supply, while destabilizing the reproductive output. In effect, the model resists changes in asymptotic size at the expense of total gamete production. The performance of a population will depend on the total reproductive output of the individuals.

The energy allocations also depend positively on the amount of stored energy. Increases in the total allocation to production lead to decreased store, which in turn decreases growth and reproductive allocation; a negative feedback loop on total production. This means that total allocation to production is stable; the energy gained

from feeding has to go somewhere! A decrease in target store makes the animal more vulnerable to energy shortages when the food supply is low, but the associated increase in size will increase total production through mechanism (2) described above, so there is a trade-off between vulnerability and productivity.

The gut volume is proportional to the 2/3 power of somatic size, so that although the absorbed ration increases with size, the relative absorbed ration decreases. Larger animals also invest more heavily in gamete production. These effects combine so that once significant allocation to gamete production starts the mean level of stored energy tends to remain approximately constant in spite of the continued growth of somatic tissue. Thus as an animal grows, the storage reserves decrease relative to body size, and the animal becomes increasingly vulnerable to low food supplies.

Spawning is assumed to have a high cost but this may be confined to a short period of time. As a result, within the model spawning activity can create a temporary depression in store, and an associated decrease in total productivity while the storage deficit is made up. Effects which reduce the spawning rate and so spread the cost can decrease this effect, and so lead to slight increases in overall production.

Another feature of the Physiology model is the effect that can be produced by an autumn spawning. Both somatic tissue and gametes are resorbed as well as store when the animal is in energy deficit. A late spawning means that there are few stored gametes in winter, and if energy deficit occurs there will be a relatively greater reduction in somatic size and in stored reserves. This will lead to decreased energy intake when positive energy balance is regained, as described in (2) above. This can result in a small persisting reduction in size, as compared with an animal that did not spawn or spawned earlier in the year, and a more significant reduction in total reproductive output. The effect of spawning episode timing can complicate the interpretation of direct comparisons between two runs of the model. For example, a slight improvement in conditions may have the indirect effect of causing a late spawning one year. This could result in the more favoured population performing less well than the control. However, these effects are generally small (<5% over 10 years), but in a marginal case could occasionally make the difference between overwinter survival and death. In all cases where the model mussel 'dies', the cause should be established so that effects such as those just described can be recognized.

The above features account for most of the effects seen when parameters or conditions are changed. The effects of particular parameters are discussed in more detail below.

Gut volume , α_1, and food supply

The energy intake for the Physiology model depends positively on both gut volume and food supply, through the Feeding model. This energy determines the amount of growth and gamete production that can occur. Changes in gut volume or available food will cause changes of the same sign in growth and reproductive allocation, though gamete production will be more affected because of the negative feedback on allocation strategy described in (1) above. The positive feedback on

intake described in (2) above will tend to amplify changes to the gut volume and food supply.

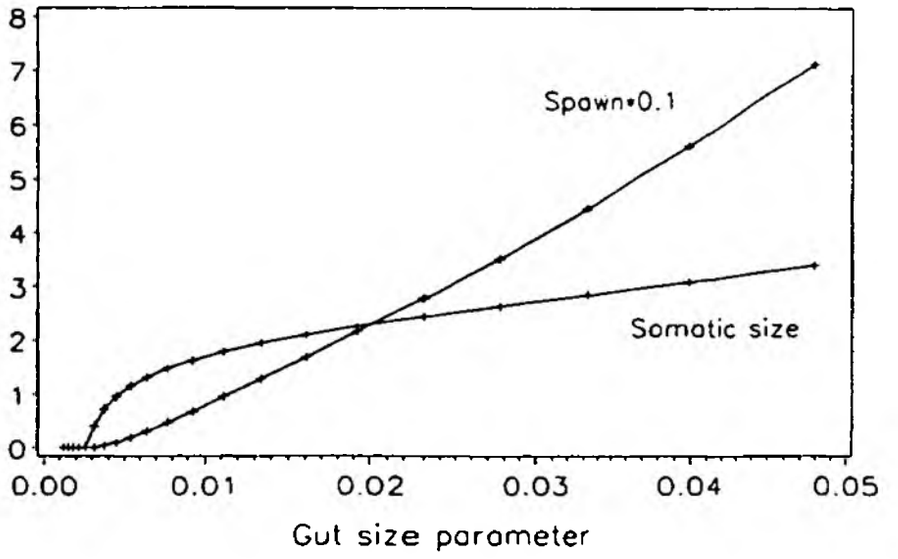

Figure 1.3 Effect of gut volume parameter on growth and gamete production. Mean food concentration = 0.6mg/litre, sine wave. Somatic size reached and total spawn produced in a 5 year run of the model.

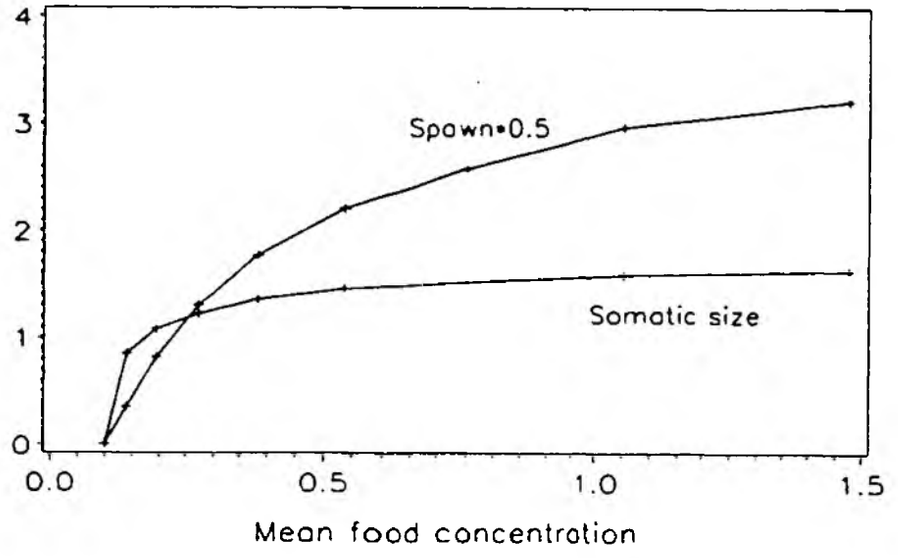

Figure 1.4 Effect of mean food concentration on growth and gamete production. Sine wave food function, variation equal to mean. Somatic size reached and total spawn production in a 5 year period.

The performance of the model is influenced by the seasonal pattern of the food supply as well as the mean value. The feeding model predicts that a mussel will feed less efficiently at high food supply, with absorption efficiency increasing with decreasing food until feeding ceases when the food concentration is near zero.

Because of the variation in behaviour with food concentration, the mussel will perform slightly better on a constant food supply than on one which varies about the same mean value.

The model provides three functions that can be used to describe the food supply. These are (a) constant food, (b) sinusoidal variation and (c) spring and autumn peaks. These functions are described in more detail in Part 2, the User Guide. Of these three functions, a constant food supply will give the best performance, and the spring and autumn peaks function the worst, for the same mean food concentration.

Store capacity, α_2

The default store capacity cannot be reduced enough to have any effect on the model without falling below the default spawn trigger level. Increasing the capacity has the effect of reducing the spawning rate, which slightly increases the long-term productivity. The spawn timing is affected by the changes in rate, and this can lead to unpredictable changes in productivity (Figure 1.5) - these effects are discussed under 'General features' above. The store capacity is assumed to be dependent on the somatic size of the mussel.

Some restrictions must be placed on the store capacity parameters for the model to be viable. Violation of these restrictions, discussed below, does not represent a valid description of the physiological state of a mussel, and should be avoided. Should such conditions be specified, however, the model may still run without an error condition necessarily occuring.

Firstly, the capacity must be sufficient to accomodate all the energy that is allocated to the store. If this condition is not met, and excess energy that would be stored, is lost to the mussel when the capacity is full. This situation does not occur with the default parameter set, even at extremely high food levels, and should be avoided with any user-defined parameter set. If energy is wasted in this way, a message will appear on the screen alerting the user to the situation, but otherwise the model will continue to run normally, with the excess energy being 'lost'.

A second condition is that the store capacity must exceed the spawn trigger level. If this is not the case, spawning will not occur, and the store capacity will be filled with gametes. Energy will then be wasted, as described in the preceding paragraph, and growth and gamete production will be severely reduced. This condition can be expressed:

$$\alpha_2 SOMA^{\beta 2} > \alpha_{10} SOMA^{\beta 10}$$

Finally, the capacity must exceed the target store, otherwise store will always be below target and growth and gamete production will not occur:

$$\alpha_2 SOMA^{\beta 2} > \alpha_{12} SOMA^{\beta 12}$$

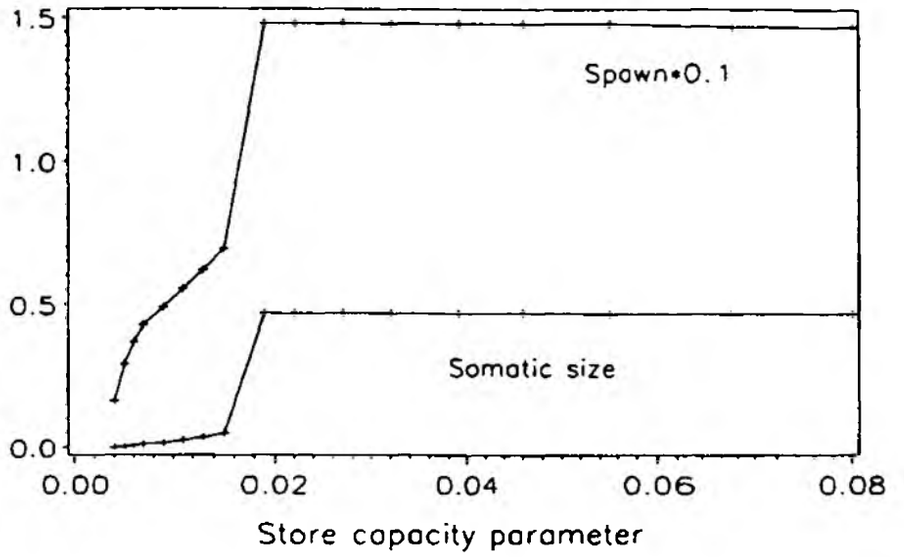

Figure 1.5 Effect of store capacity parameter on growth and gamete production. Sine wave food supply: mean = 0.6mg/litre. Final somatic size and total spawn production in a 10 year run. The points to the left of the discontinuity represent store capacity less than spawn trigger.

Basal metabolic rate, α_3

Under the default parameter set the basal metabolic rate can account for about a third of the respiration costs of the model mussel, an amount of energy roughly equivalent to the scope-for-growth. Changes in this parameter therefore directly affect the energy available for productivity. Feedback loops (1) and (2) above apply, so that asymptotic size is only slightly affected while accumulated gamete production is highly sensitive (Figure 1.6).

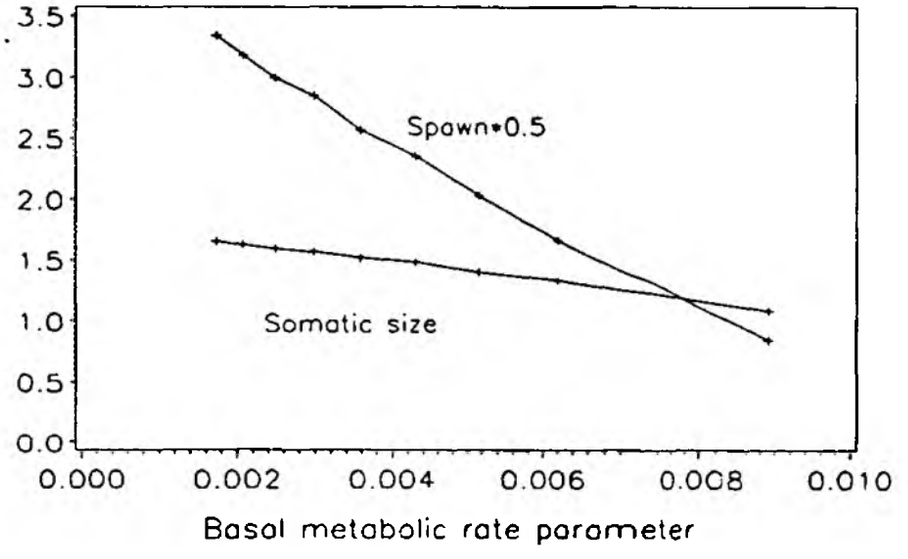

Figure 1.6 Effect of basal metabolic rate parameter on growth and gamete production. Mean food = 0.15mg/litre: somatic size and total spawn production in a 10 year run.

Shell length, α_4

The relation of shell length to somatic size is used only in the output routine, to convert the size data to length prior to fitting a Von Bertalanffy growth equation. The value of this scaling parameter does not affect the performance of the model in any way.

Allocation to growth and gamete production, α_5 to α_8

The Michaelis-Menton equations governing energy allocation to growth and gamete production lie at the heart of the Physiology model:

$$\text{Rate of growth or gamete production} = \frac{|K_1 K_2 SDEV|}{K_1 + |K_2 SDEV|}$$

Where for growth:

$$K_1 = \alpha_5 SOMA^{\beta 5}$$

$$K_2 = \alpha_6 SOMA^{\beta 6} POOL^{\phi 1}$$

And for gamete production, R:

$$K_1 = \alpha_7 SOMA^{\beta 7}$$

$$K_2 = \alpha_6 SOMA^{\beta 6} POOL^{\phi 1}$$

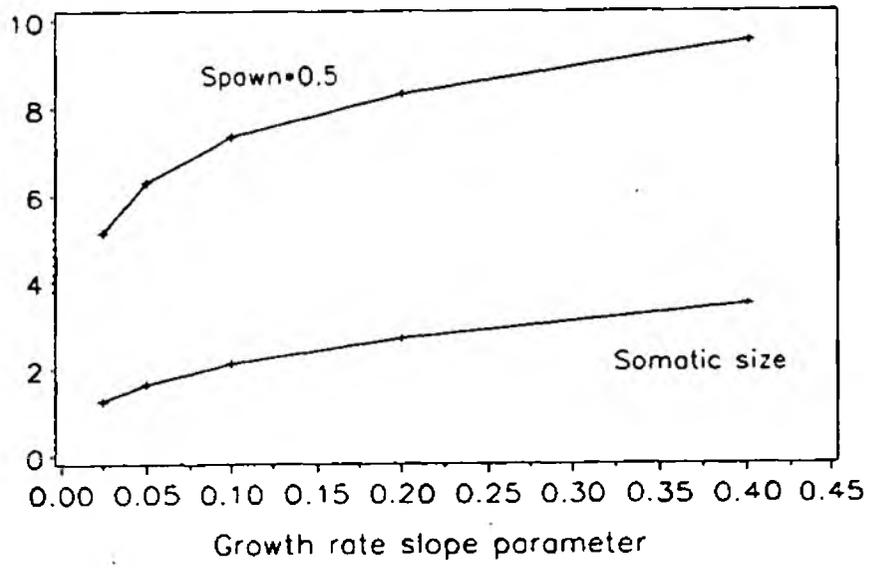

Figure 1.7 Effect of growth allocation rate slope (α_6) on growth and gamete production. Mean food = 0.6mg/litre: size and total spawn production in a 10 year run.

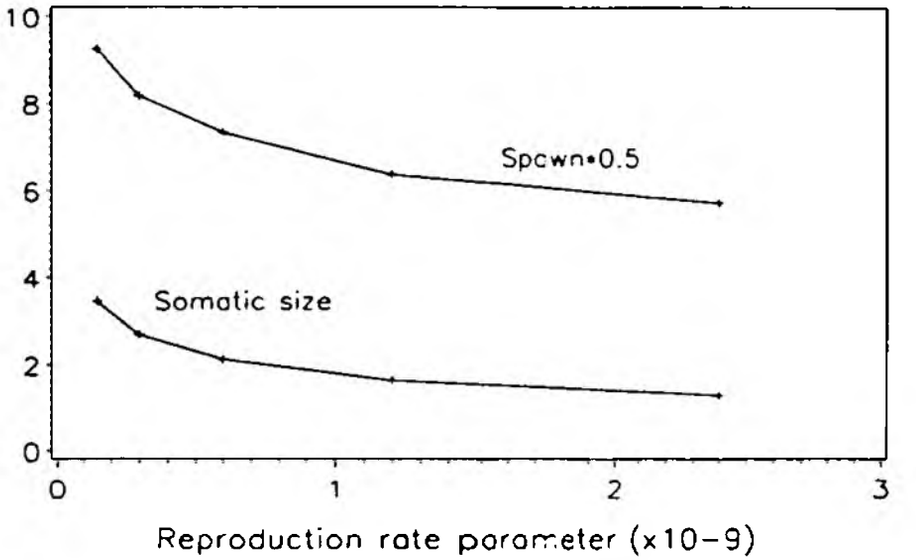

Figure 1.8 Effect of gamete production allocation rate slope (α_8) on growth and gamete production. Mean food = 0.6mg/litre; size and spawn in a 10 year run.

The total allocation to growth and gamete production is stabilized through the dependence on stored energy, so changes in one will cause changes of opposite sign in the other. The general response of the model to the allocation parameters is governed by the feedback mechanisms (1) and (2) discussed at the start of this section.

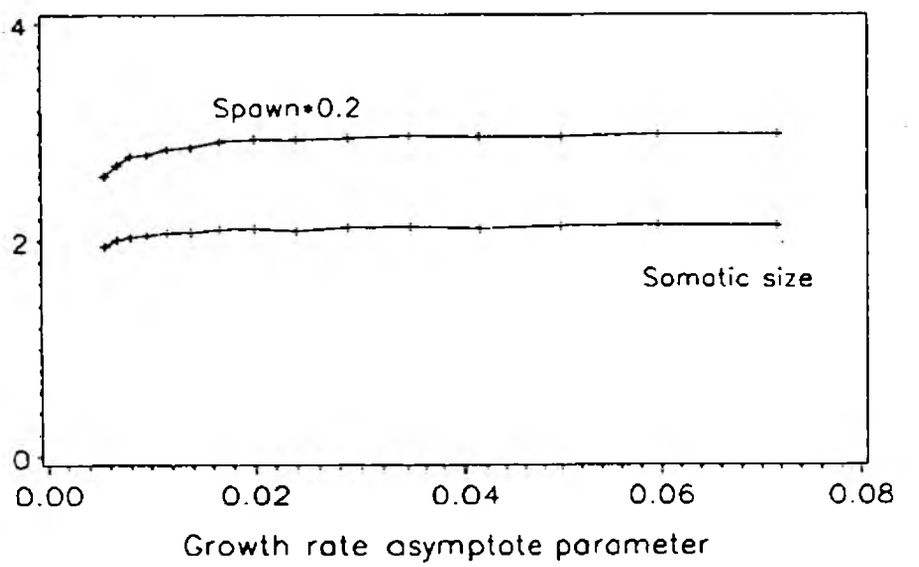

Figure 1.9 Effect of growth allocation rate asymptote (α_5) on growth and gamete production. Mean food = 0.6mg/litre; size and spawn in a 10 year run.

Increasing allocation to growth has a similar effect to decreasing allocation to reproduction. Initially gamete production is lower, compared with data from a run using the default parameter set. Then the greater somatic size leads to greater gamete production, so that after a few years cumulative spawn exceeds that of the control run. Reducing allocation to growth has a similar effect to increasing gamete production; the animal grows less and, because of the smaller size reached, produces less spawn.

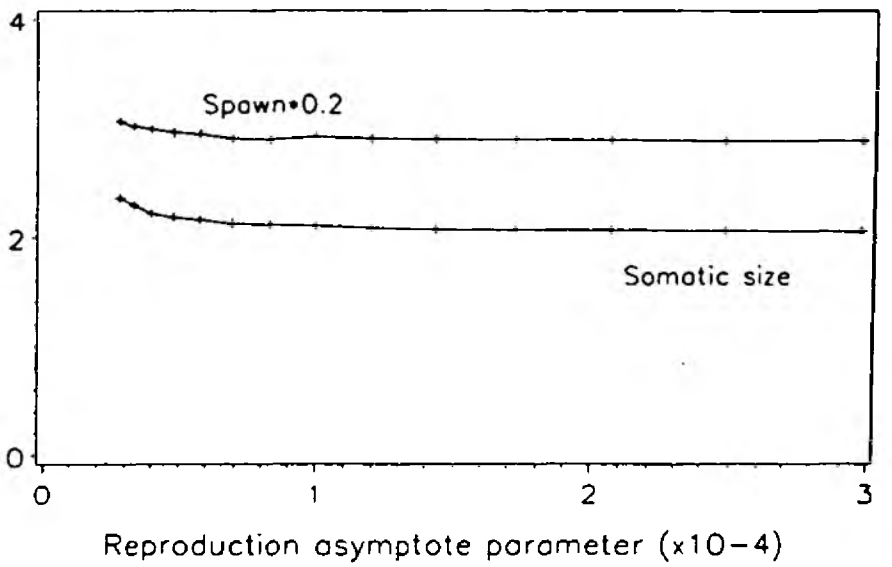

Figure 1.10 Effect of gamete production allocation rate asymptote (α_7) on growth and gamete production. Mean food = 0.6mg/litre; size and spawn in a 10 year run.

With the default parameter set, rates of allocation to both growth and gamete production are normally well below the asymptotic values, so changes in α_5 and α_7, the parameters governing the asymptotes (K1), have less effect than changes to α_6 and α_8, which set the gradients of the Michaelis-Menton equations near the origin (K2·SDEV).

Gamete resorption rate asymptote α_9

The parameter α_9 governs the asymptotic gamete resorption rate, in place of α_7 for the asymptotic gamete production rate. The default values of these two parameters are the same. However, the value of α_9 makes little difference to the performance of the model - less than 5% change in growth and cumulative spawn production over 10 years for a factor 64 increase or decrease in α_9 at low food levels (mean=0.3mg/litre), and virtually no change at all at higher food.

Spawn trigger level α_{10}

The spawn trigger level must be less than the store capacity (see discussion on capacity, p. 22).

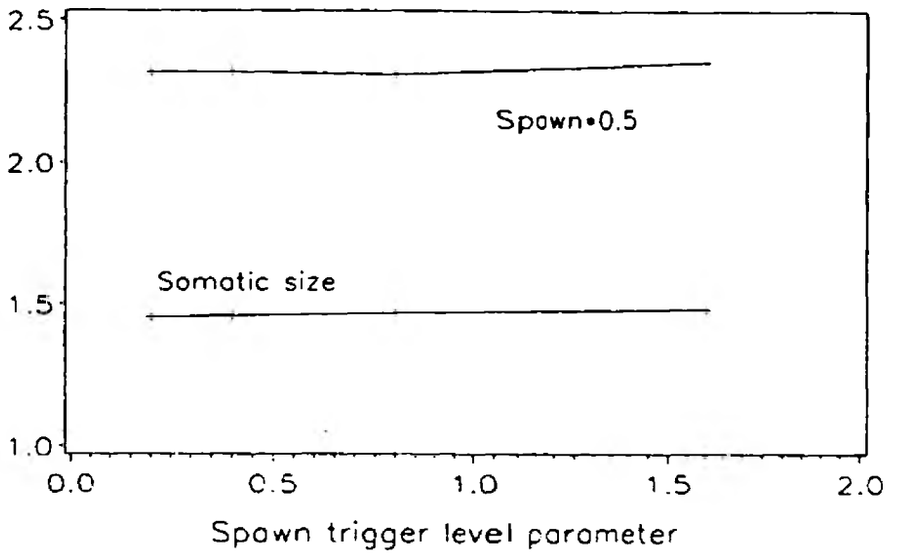

Figure 1.11 Effect of spawn trigger level parameter on growth and gamete production. Mean food = 0.6mg/litre; size and spawn in a 10 year run.

Spawning is triggered when the sum of stored energy and gametes reaches the trigger level. So if the trigger is at or below the level of stored energy, the animal will trickle spawn continuously and will not accumulate gametes. As the trigger is increased above this level, the animal will spawn less frequently and will accumulate increasing amounts of gametes between spawning episodes. The long-term production is indirectly influenced through two opposing processes. Firstly, the cost associated with spawning reduces the store and can lead to a short-term reduction in growth, which can have a long-term effect through feedback loop (2). Reductions in the trigger level act to increase the frequency of spawning, spreading out the cost. This can increase the long-term productivity. Secondly, increased spawning frequency will reduce the mean quantity of gametes stored, and will tend to increase the amount of somatic tissue re-absorbed when food concentration is low. So reductions in α_{10} can also act to reduce productivity.

There is a trade-off between these two factors, depending on the food supply. At high food, the second effect will be negligible, and the first will dominate, while at low food concentration, where re-absorbtion of tissue is significant, the second factor will be more important. In either case, the total energy available is not directly affected, so the sensitivity of long-term performance to this parameter is relatively small.

Maximum spawning rate α_{11}

With the default parameter set, trickle spawning may occur in the first year, but generally spawning episodes last for only a few days; little more than the iteration period, so increases in spawning rate have little effect. In addition to this, the rate is more sensitive to α_{11} at low values, and reaches an asymptote as α_{11} increases. The default values of α_{11} is such that the rate is near the asymptote. So even a factor 10 increase in this parameter makes no difference to the output of a 10 year run of the model.

Decreasing α_{11} reduces the spawning rate and so spreads spawning and its costs over a longer period of time, leading to a slight increase in productivity. However the change in rate will indirectly affect spawn episode timing, and so lead to small changes in production, in either direction, which may mask the overall increase.

Target storage size, α_{12}

The target store is effectively the minimum energy reserve - if store is below target, growth and gamete production cease. If the target is too low, the mussel will be at risk of running out of energy and dying when food supplies are low, particularly after a late autumn spawning when gametes are not available for resorption during winter. The store is energy that could have been used for growth or gamete production. An increase in target store will mean a lower somatic size as compared to data from a control run using the default parameter set. This lower somatic size will mean lower energy intake, and the mussel's development will effectively be delayed compared to the control, owing to feedback mechanism (2) discussed above. However, the animal will be less vulnerable to extended periods of negative energy balance.

Since the spawning is initiated when the sum of store and gametes reaches a trigger level, the level of store affects the number of gametes needed to reach the trigger level, and so has the same effect as changing the trigger level. An increase in target store will effectively reduce the spawn trigger level. The effects of this are discussed under 'Spawn trigger level' above; they depend on food levels. Generally, the effect on somatic size described in the preceding paragraph is more important in terms of long-term productivity, and the effect on spawning is only significant for spawning behaviour.

Relation of growth and gamete production to POOL, ϕ_1 *and* ϕ_2

The variable POOL is calculated by imposing a time-delay on the absorbed ration. The parameters ϕ_i therefore relate physiological processes to the energy intake of the animal. Changes to the default values of these parameters should be undertaken with caution, since changes have widespread repercussions on the growth, gamete production and storage. The values of these parameters may be regarded as a fundamental part of the model.

The parameter ϕ_1 relates growth to POOL. Although ϕ_1 is a power coefficient, the model is not particularly sensitive to its value. Changes of a factor 2 from the default of 0.25 make less than 5% difference to growth or total spawn over a 5 year run of the model, since the dependence on POOL is in any case small. Further increases in ϕ_1 have the effect of reducing growth when somatic size is small and increasing it as size increases, since POOL depends heavily on gut volume and hence on size.

ϕ_2 relates gamete production to POOL. The default value of ϕ_2 is 0.6, and so gamete production has a greater dependence on POOL than growth (ϕ_1 =0.25). Reducing ϕ_2 by a factor of 2 decreases growth and gamete production by about 50% over 5 years. Doubling ϕ_2 increases production by about 40%.

Spawning rate parameters μ_1, μ_2, and ϕ_3

The parameter μ_1 relates the minimum spawning rate to the gametogenesis rate asymptote. μ_2 relates the spawning rate to the amount of free storage space. Spawning rate is positively related to μ_1 and negatively to μ_2. ϕ_3 relates spawning rate to the time-lagged absorbed ration, POOL.

Changes to the default values of the parameters μ_1 and μ_2 which increase spawning rate have no discernible effect on the Physiology model over a 10 year run.

Decreasing spawning rate has effects discussed at the start of this section. Factor 2 changes in μ_1 and μ_2 tending to decrease the rate have no effect on the model; changes of a factor 4 or more affect the timing and duration of spawn episodes, especially after several years into a run, and make a slight difference (about 1%) to growth and production.

Values of defaults

A default parameter set is provided for use with the model. The parameter values in this file have been selected with reference to data from both field and experimental work using individuals taken mainly from populations in the South-West of Britain. The user may wish to amend the default values, or provide a detailed set of values that are appropriate to the particular population that is to be modelled. The default values of the parameters are listed below - see the sensitivity analysis (p. 18) for a discussion of the effects of changes to these, and the User Guide for the limits of acceptable values.

Feeding Model Parameters

Parameter relates to:	Parameter units	Parameter:	Default value:
Enzyme resorption rate	(hr^{-1})	a	0.20
Filtration cost	(J.hr/ml)	g(1)	0.40

Enzyme secretion cost	(J/J)	g(2)	0.15
Initial volume of pcle 1	(ml/mg)	$V_s(1)$	4.00
Initial volume of pcle 2	(ml/mg)	$V_s(2)$	0.50
Final volume of pcle 1	(ml/mg)	$V_f(1)$	2.00
Final volume of pcle 2	(ml/mg)	$V_f(2)$	0.50
Energy content, pcle 1	(J/mg)	E(1)	18.5
Energy content, pcle 2	(J/mg)	E(2)	1.60
Absorption cost	(J/J)	g(3)	0.15
Absorption rate, pcle 1	$(ml \cdot J^{-1} hr^{-2})$	b(1)	0.60
Absorption rate, pcle 2	$(ml \cdot J^{-1} hr^{-2})$	b(2)	0.60
Max. silt concentration	(mg/litre)	msilt	15.0

Physiology Model Parameters

The units of the parameters in the Physiology model are not all well-defined; for example, the units of α_i will depend on β_i. Therefore, the units of the parameters are not given, but rather the units of the process with which that parameter is associated. The units of the parameters can be deduced from the functions in which they appear, described in section 1.2, where the Physiology model is described.

Parameter relates to:	Parameter	Value	Parameter	Value
Gut Volume (ml)	$\alpha(1)$	1.29×10^{-2}	$\beta(1)$	0.66
Store capacity (J)	$\alpha(2)$	$1.80 \times 10^{+1}$	$\beta(2)$	1.00
BMR (J/hr)	$\alpha(3)$	4.30×10^{-1}	$\beta(3)$	0.66
Shell length (cm)	$\alpha(4)$	1.80×10^{-1}	$\beta(4)$	0.33
Growth rate (J/hr): K1	$\alpha(5)$	$2.00 \times 10^{+0}$	$\beta(5)$	0.66
Growth rate (J/hr): K2	$\alpha(6)$	1.00×10^{-1}	$\beta(6)$	-0.66
Gametogenesis (J/hr): K1	$\alpha(7)$	1.00×10^{-2}	$\beta(7)$	1.33
Gametogenesis (J/hr): K2	$\alpha(8)$	6.00×10^{-10}	$\beta(8)$	1.33
Spawn trigger (J)	$\alpha(10)$	$1.60 \times 10^{+0}$	$\beta(10)$	1.00
Max. spawning rate (J/hr)	$\alpha(11)$	$3.64 \times 10^{+1}$	$\beta(11)$	1.10
Target storage size (J)	$\alpha(12)$	$3.00 \times 10^{+1}$	$\beta(12)$	1.00

Growth rate (J/hr)	$\phi(1)$	0.25
Gametogenesis rate (J/hr)	$\phi(2)$	0.60
Spawning rate (J/hr)	$\phi(3)$	2.00
Cost of growth	$\varepsilon(1)$	0.30
Cost of gametogenesis	$\varepsilon(2)$	0.10
Cost of storage	$\varepsilon(3)$	0.03
Cost of spawning	$\varepsilon(4)$	2.00

Energy of SOMA (J/g)	eeq(1)	17.5
Energy of gametes (J/g)	eeq(2)	39.5
Energy of storage (J/g)	eeq(3)	24.0
Energy of a gamete (J)	eeq(4)	1.0×10^{-6}
Min. spawning rate (J/hr)	$\mu(1)$	0.50
Spawn rate variation	$\mu(2)$	1.00

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MUSSEL SIMULATION PROGRAM DOCUMENTATION.

PART 2 - USER GUIDE FOR VAX/VMS

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January 1992

Ammended march 1992

MUSSEL SIMULATION PROGRAM DOCUMENTATION.

PART 2 - USER GUIDE FOR VAX/VMS

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2.1 Outline of the Mussel Simulation Program

Structure of the program

The computer program for the Mussel model consists of four major parts. These are: the input routine, the toxicity routine, the various components of the model itself, and the output routine. At the start of a run, the conditions are established with the input routine. This accepts the parameter file name, and reads in and checks the parameter values, and then prompts the user to enter the run data (see Section 2.3, p.10). Next, the toxicity routine prompts the user for information about the effects of the toxicant on feeding behaviour, and sets the toxicity parameters. The Mussel model then runs with no toxic impact, producing a control data set. The output routine produces a run data file summarizing the run conditions and listing the parameter values, and a report file summarizing the output of the model calculations. The model repeats with toxic effects included, and the output routine produces a report file for the impacted run; the run conditions and parameters are the same as for the control run, so the data file is only produced for the control. The user is then given the option to repeat the run for different toxicity parameters, using the same control conditions. If this option is selected, the toxicity routine is entered, new toxicity parameters are set, and the model is re-run with the new toxic effect. At the end of a sequence of control run and impacted runs, the user may repeat for a new control. If this is chosen, the input routine is entered and the program repeats from the beginning. See flow diagram over page.

Default values exist for much of the keyboard input, and the user may select these by entering a carriage-return character instead of typing a value. When the program is repeated, the default input values will be those used in the previous run. This feature makes it easier for the user to re-run the model for similar but not identical conditions: to examine the effect of changing just one input data value, for example.

Description of the model

The Mussel model consists of the Feeding model, the Physiology model and the Population model. The Physiology model uses the Feeding model to find the energy gained by an individual mussel through feeding, and produces growth curves and a fertility schedule. The Population model uses the fertility schedule to estimate the resilience of a population of similar individuals.

In addition to the above models, there is a toxicity sub-model, which enables the user to establish the toxicity parameters, and a feeding sub-model which enables the user to define the food supply. The individual modules are described briefly below; the user is referred to Part 1 of the documentation for a full description of the model.

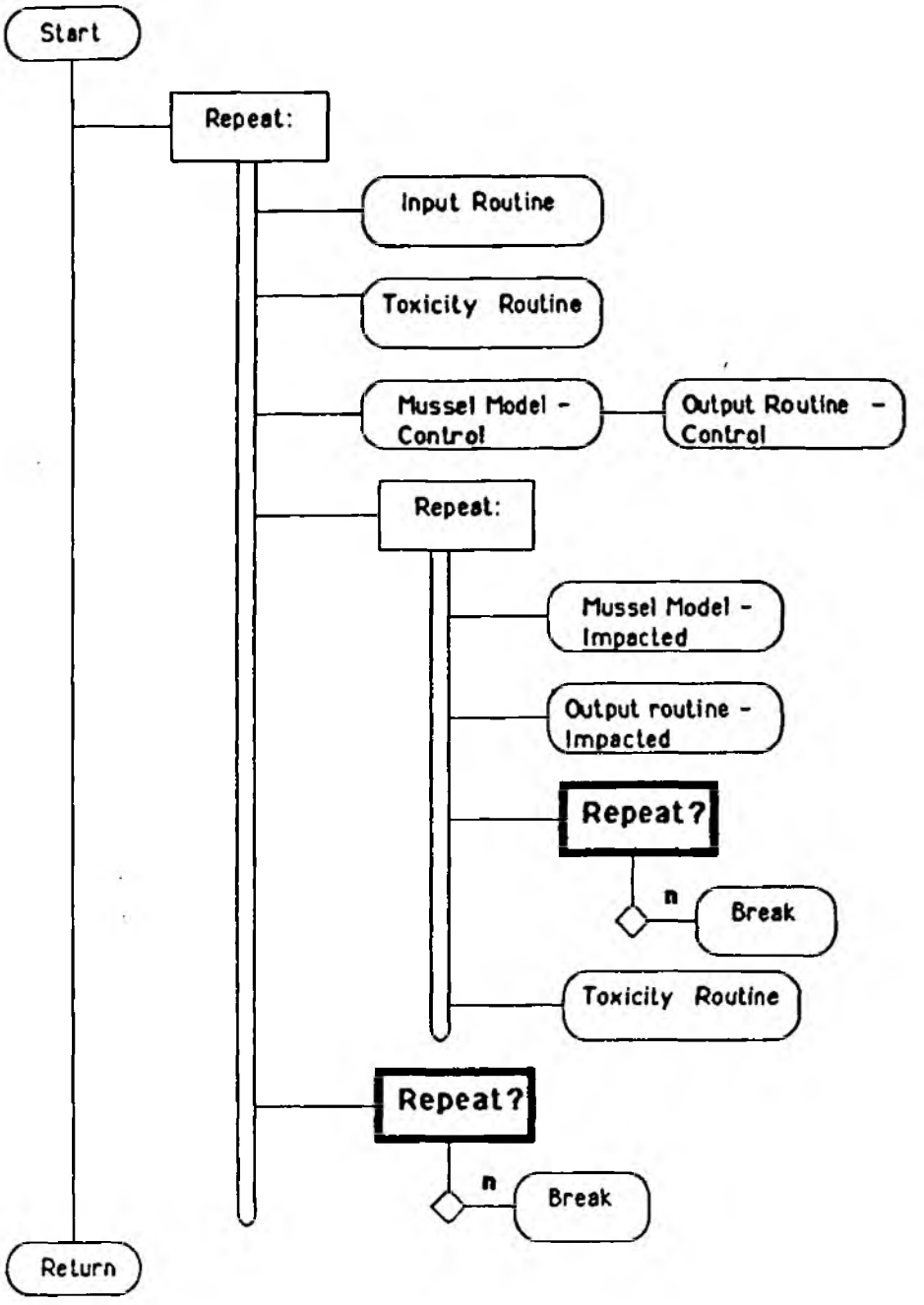

Figure 2.1 Flow chart for the Mussel model program.

The Feeding Model

The Feeding model calculates the absorbed ration of the mussel and the costs of feeding, given the feeding conditions. Assumptions are made about the way food is absorbed, and about the cost functions. The feeding strategy is adjusted, so that the net energy gained through feeding is maximized. The model assumes that the mussel can alter its investment in digestive enzymes and its rate of feeding, and that the mussel can select the more profitable particles out of those available. Costs depend on the pumping rate, the rate of secretion of enzymes and the rate of absorption of energy from food. In addition, some of the digestive enzymes may not be recovered and this constitutes an energy loss to the mussel.

Toxins can affect the Feeding model in two ways. Narcosis acts to reduce the pumping rate so that the feeding strategy is no longer optimal; the selection of particles and investment in digestive enzymes are not affected. In this case, the gut passage time is increased by a 'narcosis factor', which has the effect of reducing the pumping rate, though not necessarily by exactly the same factor. The second way in which toxicants can affect the Feeding model represents respiratory chain uncoupling, where the efficiency of metabolic pathways is impaired. This reduced efficiency results in reduced productivity by the mussel. In this case, the unit cost terms are multiplied by a 'metabolic uncoupling factor', and the optimum feeding strategy is calculated under the new cost regime. If both modes of action operate simultaneously, the model first optimizes the feeding strategy with the increased costs due to metabolic uncoupling, then, secondly, the calculated gut passage time is increased according to the narcosis factor.

The Physiology Model

The Physiology model uses Michaelis-Menton type equations to partition the energy gained through feeding by an individual mussel between growth, reproduction, storage and respiration. The allocations depend on the somatic body size, the amount of stored energy, and the value of a variable POOL. POOL provides an estimate of the energy input to the mussel, and is calculated by applying a time-lag to the energy gained through feeding, on the assumption that the animal cannot immediately change its energy allocations in response to a change in circumstances.

Respiration represents energy utilized for the maintenance of body tissue and activity costs. The cost of maintaining body tissue depends positively on the body size. The costs of activities are proportional to the energy processed through the activity, and are associated with growth, production of gametes, storage of energy and spawning.

A spawning sub-model controls the release of gametes; spawning starts when the sum of storage reserves and gametes reaches a trigger level, which depends on the somatic body size, and when POOL is positive. It continues until all gametes have been released, or until POOL becomes negative. The rate of spawning depends positively on the body size, the value of POOL and the number of gametes remaining, and negatively on the amount of unused storage capacity. In effect, larger and better

fed mussels spawn out more quickly, and mussels initially release spawn more quickly and then slow down as the number of remaining gametes decreases.

Toxins act through the Feeding model, reducing the energy available to the mussel. Metabolic uncouplers also act directly on the Physiology model, increasing the unit costs of all activities (maintenance, growth, reproduction, spawning, energy storage) by the metabolic uncoupling factor.

The Population Model

The Population model uses the fertility schedule for an individual mussel, produced by the Physiology model, to estimate the rate of growth of a population composed of such individuals. A mortality schedule appropriate to the particular environment experienced by the mussel population is provided by the user. It is assumed that the mortality schedule will be the same for toxic impacted populations as for unimpacted ones; this implies the assumption that toxic effects are sub-lethal and so do not affect mortality. The model produces the stable age distribution and an estimate of the growth rate of the impacted population relative to the control, unimpacted population.

The Toxicity sub-model

The Toxicity sub-model enables the user to establish the toxicity parameters, which are used in the Feeding and Physiology models, from information about the toxicants short-term effect on the feeding behaviour of the mussel. The user enters the ambient food concentration that applied during the experiment, and the change in pumping rate resulting from exposure to the toxicant. The mode of action of the toxin must also be known in order to establish the parameter values. If the mode of action is not known, or if the toxicant acts through both modes, the sub-model will try a range of values for the parameters, from purely metabolic uncoupling to purely narcosis. The user then selects a value for the metabolic uncoupling factor to be used in the simulation from the resulting pairs of toxicity factors; the routine finds the corresponding value for the narcosis factor.

The toxicity sub-model uses the Feeding model to calculate the values of the toxicity factors from the data entered by the user. First the Feeding model is used to predict the unimpacted pumping rate. The toxicity sub-model then sets the values of the toxicity factors, in accordance with the mode of action selected by the user, and iterates until a pair of values is found that gives the observed change in pumping rate.

The food supply sub-model

The food supply to the mussel may vary seasonally, but is assumed to be constant between years. The food consists of a mixture of two types of particle, representing algal cells ('food') and suspended sediment ('silt'). The nutritional qualities of these particles are defined by parameters whose values are read from the parameter set file. There is considerable freedom for the user in the specification of the food supply. Most simply, monthly concentrations can be read from a user-supplied file. Alternatively, the concentration of the algal cells can be described by one of three

annually periodic functions, with a corresponding function for the silt. These functions are:

1) The concentrations may both be constant, at values supplied by the user (in the input routine).

2) The concentration of algal cells may vary sinusoidally, from a minimum in December to a maximum in June; in this case the user enters the mean food concentration and the variation about the mean (the half-range), which must be less than the mean. The silt concentration also varies sinusoidally, but is out of phase with the food, so that the maximum is in December when high river flows are likely to carry high suspended sediment. The minimum is in June. The user enters the mean silt concentration; the variation is assumed to be equal to the mean, so that the concentration varies between zero and twice the mean. This option is suitable for the representation of estuarine or coastal populations heavily influenced by freshwater input.

3) The third option available for the food supply function gives a peak in the spring (about March), and a second peak in late summer (about August). The concentration drops to zero in the winter. This function is composed of two superimposed normal distributions, with the second peak being wider than the first. This gives a better approximation to measured patterns of algal concentrations. The user enters the mean concentration and the ratio of the second peak concentration to the first. The silt concentration is assumed to vary sinusoidally, with the maximum in December; the user enters the mean value. This function mimics the situation experienced by coastal populations, less influenced by the land.

The values of the concentration of algal cells are in units of mg dry weight per litre. However, the concentration of silt particles is less important because of their lower nutritional value, so accurate measurement is not necessary. To reflect this, the concentration is entered as a number between 0 (no suspended sediment) and 1 (high suspended sediment). The maximum silt concentration is a parameter, MSILT, whose value is in the parameter set.

2.2 Guidance on use of Model

The MUSSEL simulation model calculates growth curves for an individual mussel given the environmental conditions and the initial state. Data can be produced on the mussel's physiology at intervals of time throughout the run, and, on completion, an estimate is made of the growth rate of a population of such individuals. The output of the model depends on the parameter set that is used, and on the environmental information which the user supplies. The energy intake of the mussel and the partitioning of that energy into growth and reproduction depend on size, so any changes in growth rate will affect the subsequent performance of the model. The results of a single run should not be taken in isolation; the model is properly a comparative tool.

Every run including toxic effects is compared with a control run, made using the same parameter set and environmental conditions, but without the toxicant. The output is assessed relative to the control to give the impact of the toxicant, rather than an absolute value for the performance of mussels under that regime. The impact of different toxicants, characterized by their effect on feeding behaviour and their mode of action, can be compared by repeating the model using the same control conditions.

The Feeding and Physiology modules use parameter values from a parameter file. These values govern the characteristics of the model. Some of these parameters describe the environment, for example, the energy content of the food particles. Other parameters describe the mussel's physiology. The user should set appropriate values for the population in question. Environmental conditions may vary from one population to another, and so may the physiology of individual mussels. The values of parameters describing the physiology may also relate to local environmental conditions not overtly accounted for in the model: for example, salinity and temperature.

The impact of a toxicant will depend on the precise environmental conditions; a population in ideal conditions for growth may be more tolerant of pollution than a population that is barely surviving even when the environment is unpolluted. The model can be used to examine this effect, by comparing runs where the same toxic impact is imposed under different environmental conditions. This may be of assistance in identifying sensitive sites where populations may be particularly vulnerable to anthropogenic stress.

The effect of a toxicant depends not only on its impact on feeding behaviour, but also on the mode of action. For a given reduction in pumping rate, a toxicant that acts through respiratory chain uncoupling will have a more severe impact on the mussels energy budget than one that acts through narcosis alone. This is because the unit costs of activity will be higher in the former case, while the ingested ration will be the same. Note that the absorbed ration may differ, as the investment in digestive enzymes may not be the same. The model can be used to examine the effect of the mode of action of the toxicant, by comparing runs with the same control and the same reduction in pumping rate, but different modes of action. The mode can vary from

purely metabolic uncoupling, through a combination of the two actions, to a purely narcotic effect. This can indicate the possible range of severity of impact where the mode of action of a pollutant is not known.

In addition to chronic toxic effects, the model has the capacity to simulate the effects of an episode of toxic impact on the physiology of an individual mussel. In this case, the output of the population module is no longer appropriate. This is because the output of the physiology model represents a single individual that has experienced an episode of toxic impact at a particular age. In contrast, the population module represents a population of mussels, where individuals in different age classes would experience the toxicant at different stages in their lives. Thus the population module is only applicable to chronic toxic effects.

The response of a mussel to a toxicant will depend on the levels of the toxicant in the tissue, rather that the concentration in the surrounding water. The toxicity routine, which sets the toxicity factors within the model, uses the response of the mussel to a particular toxicant. Provided the mussel has reached equilibrium with its environment, neither the concentration of the toxicant in the tissue nor in the water need be known. Thus for chronic toxic impact, when equilibrium is always maintained, the relationship between the tissue burden and the water concentration is not needed. However, for a toxic episode of limited duration the model assumes that the effects of a toxicant on the mussel will begin immediately at the start of the episode, and will cease immediately at the end. If the time taken for the levels of toxicant in the tissue to reach equilibrium with the concentration in the water is significant, compared to the episode duration, then this asumption may be invalidated. Thus the model is not valid for episodes of toxic impact that are short compared to the uptake time for the toxicant. In the model, the start and end times for an episode are set to the nearest month, and the minimum duration is one month. It is for the user to ensure that the episode duration is long compared with the time required for the feeding behaviour of a mussel to equilibrate on exposure to the toxicant.

2.3 User input

The user must provide information for the model, both as files and as keyboard input. This section describes the information required, the ranges of acceptable values and the form in which they should be supplied.

Two files are essential: the parameter set values, and the survival schedule. The user may also provide a food data file. These files are described in more detail below. The input variables are all declared as 'double precision', and the three files are each read in using unformatted 'read' statements. This means that the values can be expressed in F, E, or D format (e.g. 0.01, 0.1e-01 or 0.1d-01). They are separated by any number of spaces or by a carriage-return.

Keyboard input is entered in response to a request from the program. It is described at the end of this section.

Input files

Examples of the input files are given in Appendix A. They are described below.

The parameter set

The parameter file name must be of the form xxxxxx.PARA, where xxxxxx is a 6-character identifier. The default parameter set file name is MUSSEL.PARA.

The parameters are read in in the following order:

Parameter:	Range of subscript, i:
α_i, β_i	1 - 12
ϕ_i	1 - 3
ε_i	1 - 4
eeq_i	1 - 4
μ_i	1 - 2
a	-
b_i	1 - 2
$V_s(i)$	1 - 2
$V_f(i)$	1 - 2
E_i	1 - 2
g_i	1 - 3
MSILT	-

For details of the meaning of the parameters, please refer to Part 1, the Model Description. Three parameters are not mentioned in the Model Description; these are

α_4, β_4 and MSILT. α_4 and β_4 relate the shell length to the body size. The length is only used in the output routine and does not affect the performance of the model. MSILT specifies the maximum allowed suspended sediment concentration for the food supply sub-model.

The values of the parameters and of data entered at the keyboard are checked to ensure that they are within acceptable limits, to avoid error conditions occurring. These limits are detailed in the tables below. However, this checking may not prevent combinations of parameter or data values leading to error conditions or to invalid run results. Particular caution should be excercised when changing the parameter set (see Part 1, Section 1.4 for a sensitivity analysis).

Physiology Model Parameters - range of values

The limits on β_i are as follows:

$0.1 < \beta_i < 2.0$ for $i = 1$ to 12

The parameters α_i and β_i are all used in allometric relations of the form:

Function $F_i(\alpha_i,\beta_i) = \alpha_i \cdot SOMA^{\beta_i}$

The maximum and minimum values of α_i are set according to the value of F_i, and so depend on the values of β_i. The maximum and minimum values of F are set for a somatic size SOMA = 24000 J (corresponding to 1g at the default value of eeq_3).

Parameters α_i and β_i	Minimum F_i	Maximum F_i
α_1 and β_1	5.0	20.0
α_2 and β_2	1.0×10^{-4}	1.0×10^{-4}
α_3 and β_3	1.0	10.0
α_4 and β_4	1.0	10.0
α_5 and β_5	5.0	30.0
α_6 and β_6	5.0×10^{-5}	3.0×10^{-4}
α_7 and β_7	30.0	120.0
α_8 and β_8	1.0×10^{-4}	2.0×10^{-3}
α_{10} and β_{10}	500·eeq(2)	2000·eeq(2)
α_{11} and β_{11}	0.0	$1.0\times10^{+4}$
α_{12} and β_{12}	$1.0\times10^{+3}$	$1.0\times10^{+4}$

The limits on the other parameters in the Physiology model are as follows:

Parameter	Minimum value	Maximum value
$\phi(i)$, i=1,3	0.1	5.0
$\varepsilon(i)$, i=1,4	0.0	1.0
eeq(1)	5.0	50.0 or eeq(2)
eeq(2)	5.0	50.0
eeq(3)	5.0	50.0 or eeq(2)
eeq(4)	-	-
$\mu(1)$	-	-
$\mu(2)$	-	-

Feeding Model Parameters - range of values

Parameter	Parameter units	Minimum	Maximum
a	(hr^{-1})	0.0	-
b(1)	$(ml \cdot J^{-1} hr^{-2})$	0.0	-
b(2)	$(ml \cdot J^{-1} hr^{-2})$	0.0	-
$V_s(1)$	$(ml \cdot mg^{-1})$	0.0	10.0
$V_s(2)$	$(ml \cdot mg^{-1})$	0.0	10.0
$V_f(1)$	$(ml \cdot mg^{-1})$	0.0	$V_s(1)$
$V_f(2)$	$(ml \cdot mg^{-1})$	0.0	$V_s(2)$
E(1)	$(J \cdot mg^{-1})$	0.0	eeq(2)
E(2)	$(J \cdot mg^{-1})$	0.0	eeq(2)
g(1)	$(J.hr \cdot ml^{-1})$	0.0	-
g(2)	(-)	0.0	-
g(3)	(-)	0.0	-
MSILT	$(mg \cdot l^{-1})$	0.0	-

The survival schedule

The name of the survival schedule data file is not restricted by the Mussel model program. The default is SURV.DATA.

The survival of a year class, L(x), is the proportion of animals of age x-1 surviving into age class x. This will be a number between 0.0 and 1.0, though in fact these numbers are not tested when read in as they will not cause a program error. Survival values greater than 1 should be avoided!

The first value in the file is L(0), the larval survival. This is the proportion of larvae released that settle back into the population. This factor covers larval dispersal from the population, as well as mortality.

Values of L(i) are read in for i = 0 to 20.

Food concentration data file

The name of the food data file is not restricted by the program. The default is FOOD.DATA.

The food data file should contain 24 numbers. These are measurements of 'food' concentration in each month of the year, followed by 12 similar measurements of 'silt' concentration. The units are mg dry weight per litre. The 'food' is particle type 1, as defined by parameters b(1), E(1), $V_s(1)$, and $V_f(1)$, representing algal cells. The silt is particle type 2, defined by parameters b(2), etc., representing suspended sediment.

These values are not checked in any way, as they are unlikely to cause an error; it is for the user to ensure that they are realistic.

Keyboard input

Input is entered in response to prompts from the system. Many of the prompts for input show the default value in brackets. If the default is suitable, then just press 'Enter'. The defaults shown also serve as examples of the type of input required, i.e. whether an integer, a real number, or a character string. If input of the wrong data type is entered (for example, characters when a number is expected) then an error message will appear, and you will be prompted to enter another value.

There are three modules within the Mussel model program that require keyboard input. The Input routine accepts the conditions for the control run, and the Toxicity routine accepts the toxicity parameters. At the end of the run, you will be offered the chance to repeat for a different toxicant using the same control; if you accept this, you will be returned to the Toxicity routine. If you do not wish to repeat with the same control, you will be asked whether to repeat for a new control; if this option is chosen, you are returned to the Input routine. If not, the run ends.

The Mussel Simulation Program is not sensitive to the case of the input. Although some of the input values are upper case in the following discussion, this is merely for clarity in this document, and does not mean that values must be entered as upper case.

An example of the keyboard input and screen output is given in Appendix B.

The Input routine

The questions and answers for the Input routine are described below:

1. **Please enter your name(16 characters):**
   Enter a name of up to 16 characters (including punctuation marks). This name will appear in the report generated by each run of the model. If you do not enter a name, the default, 'Anon.', will be used.

2. **Use default parameter set (y):**
   Press 'Enter' to use the default parameter set (file MUSSEL.PARA) - in this case you will not see 2(a). If you wish to use a different parameter file, enter 'N', and you will be prompted for a name, as follows:

2(a). Enter parameter file name (edulis):
Enter the 6 character file identifier of a user-supplied parameter file; the default is 'EDULIS'. The program assumes the extension is '.PARA', giving a default file name of 'EDULIS.PARA' for a user-supplied parameter set.

3. Food supply types :

0 = Constant food
1 = Sinusoidal variation
2 = Spring and autumn peaks
3 = Monthly values in file

Enter option (1) :

Enter the food supply type, either 0,1,2 or 3; see Section 2.1, p.6 for a description of the food supply sub-model. If you choose options 0 to 2 go to question 4; if you choose option 3, values in file, you will be asked:

3(a). Enter name of food data file (food.data):

Enter the name of the file containing the food data values. This can be up to 16 characters, including filename and extension.

4. Enter mean food concentration in mg dry wt./litre (0.5000) :

Enter the mean food concentration; a positive real number. This is the concentration of particle type 1. If you chose food supply type 0, constant food, you will not be asked any of questions 4(a) to (c); go to question 5.

4(a). Enter variation in food concentration (0.5000) :

If you chose food supply type 1, sine wave, you will be asked:
Enter the variation of the food concentration about the mean (the half-maximum of the sine wave). The default value will be equal to the mean food concentration entered above, and this is also the maximum; the food can never be negative, so the variation cannot exceed the mean.

4(b). Enter ratio of autumn to spring peak (0.5):

If you chose food supply type 2, spring and autumn peaks, you will be asked:
Enter a real number between 0.0 and 1.0. This is the ratio of the maximum food concentration in the autumn peak to that in the spring peak.

5. Silt values range from 0 to 1 :

0 = Open coast; no suspended sediment
1 = High suspended sediment

Enter silt value (0.5000) :

Enter a real number between 0.0 and 1.0. This is the silt concentration, as a proportion of the maximum silt concentration, MSILT, which is in the parameter set.

6. Enter proportion of time for which mussel bed is submerged (1.0000) :

Enter a real number between 0.1 and 1.0. This is the proportion of time that the mussel spends below water level. The mussel cannot feed while out of the water, so the absorbed ration and the feeding costs are scaled down by the number entered here. The maintenance costs, however, are unaffected, so a lower number here will reduce the energy available for growth and reproduction.

7. Start run from settlement of larva (y) ?

This question is concerned with the body size and 'condition index' of the mussel at the start of a run. The default is 1.2mg dry weight of somatic tissue, and condition index of 0.2. The condition index is the proportion of dry body weight made up of energy and gamete stores. The default larval body weight is therefore 1.5mg, of which 0.3mg is energy store. A mussel of under 10mg dry body weight is assumed to have no stored gametes.

If the default is chosen, the next question will be question 8; if not, the size at settlement must be entered, in response to questions 7(a) and (b).

7(a). Enter initial dry body weight in grams (1.0):

Enter a real number between 0.001 and 5.0, for the dry body weight at run start (g).

7(b). Enter initial condition index (0.2):

Enter a real number between 0.0 and 1.0, for the condition index at run start (the proportion of body mass made up of stored energy and gametes).

The model uses the initial body weight and condition index to calculate the energy in somatic tissue, stored gametes and energy stores at the start of the run. The minimum energy in somatic tissue at settlement is 24J; if the body weight and condition index indicate a lower somatic energy, they will be adjusted to give the minimum. If the somatic energy content is less than 10,000J the mussel is deemed to be juvenile, and to have no stored gametes. If it is larger than this, the energy not in somatic tissue is divided equally between store and accumulated gametes. If the energy in gametes is not zero at the run start, the Population model will not run, as the fertility schedule produced by the physiology model may not be complete.

8. Enter survival schedule file name (surv.data) :

Enter a file name for the survival schedule, of up to 16 characters.

9. Write out physiology data in full (n) ?

Choose 'Y' to write out the full data file for the run. (A report file and a summary of parameter values will be produced in any case.) If you choose 'Y', you will be asked question 9(a); otherwise, go to question 10.

9(a). Intervals for data output:

0 = weekly
1 = monthly
2 = quarterly

Enter option (1):

Enter one of the above options. This only affects the frequency with which data is written out; the actual running of the model is not affected.

10. Enter name for output files (mussel) :

Enter a 6-character file identifier for the output files; the names of the output files will be xxxxxxnn.ext, where xxxxxx is the identifier, and nn is the run number; 00 for the control. The extension, .ext, is determined by the file type;

for example, it is .PHY for the physiology data matrix. If you enter fewer than 6 characters, 0's will be appended to make 6 characters.

11. Enter number of iterations of Physiology Model per day (1) :
Enter a positive integer for the number of iterations of the Physiology model per day.

12. Enter start month for food supply (3) :
If you did not choose food supply type 1 (constant food), you will be asked:
Enter an integer between 1 and 12 for the start month of the food supply. This determines the point within the annual food cycle at which settlement occurs. The default is March, when the food concentration is increasing for both sine wave and spring and autumn peaks.

End of Input Routine

The Toxicity routine

There are a number of possible paths through the toxicity routine, depending on the information entered by the user. A flow diagram outlining the various options follows. The questions are listed in detail after this, and routes through the module are indicated.

If this is a repeat run, with a new control, you will be asked question 13 (otherwise go to 14):

13. Are the values the same as before?
Answer 'Y' if the toxicant is the same as for the previous run, and 'N' to enter a different toxicant. If 'Y', go to 14; if 'N', go to 13(a).

13(a) Is the duration the same as before (chronic)?
Answer 'Y' if the duration and timing of the toxicant is the same as before; answer 'N' to enter a different timing. If 'Y', the routine ends here; there are no further questions. If 'N', go to question 18 to enter the duration. The word in brackets indicates whether the default toxic impact is chronic or acute.

14. Do you know the toxicity parameters (y) ?
Answer 'Y' if you already know the toxicity parameters and wish to type them in. Otherwise answer 'N', and questions about the short-term effect of the toxicant will follow.

15. Enter food concentration, mg dry wt./litre (0.5000) :
This question and the following assume that experimental data is available, where a mussel was subjected to the toxicant and the change in pumping rate was observed. Enter the concentration of food (particle type 1) during the experiment, as a positive real number.

16. Enter the impacted pumping rate, as a fraction of the unimpacted rate (0.5000) :

Enter the pumping rate of the impacted mussel, as a fraction of the control; for example, if the rate was reduced to 80% on exposure to the toxicant, then enter 0.8. A stimulant may cause the rate to increase, so the change can be greater than 1. If this is the case, the mode is assumed to be narcotic and the routine calculates and types out the narcotization parameter; go to question 18.

17. Modes of action of toxin :

M = Metabolic uncoupling
N = Narcotization
X = Mode not known

Enter Mode (M) :

Enter 'M' for respiratory chain uncoupling and 'N' for a narcotic or stimulant effect. If the mode is not known, or the toxin acts by both modes, enter 'X'. If 'M' or 'N' is entered, the appropriate toxicity parameter is calculated and displayed; go to question 18. If 'X', a number of possible pairs of toxicity parameters are calculated and displayed (see example screen, Appendix B, p.30); then go to 17(a)

17(a). Enter metabolic uncoupling factor, Q1 (1.0000) :

Enter the respiratory chain uncoupling parameter, using the list of possible values for guidance. The narcotization parameter is then calculated and typed out.

18. Chronic toxic effect? (Y)

Enter 'Y' for chronic toxic impact; 'N' for acute. If 'Y' is entered, go to question 19; if 'N', answer questions 18(a) to (d).

18(a). Enter start year for toxic impact (1):

Enter the year of the run in which toxic impact starts; a positive integer less than or equal to the run duration.

18(b). Enter start month for toxic impact (1):

Enter the month in which the toxic impact starts; an integer from 1 to 12. The impact will start at the *beginning* of this month.

18(c). Enter year for end of toxic impact (1):

Enter the year of the run in which toxic impact ends; a positive integer greater than or equal to the start year, and less than or equal to the run duration.

18(d). Enter month for end of toxic impact (1):

Enter the month in which the toxic impact ends; an integer from 1 to 12. The impact will end at the *end* of this month. The end of impact must be after the start; if not, it is set equal, giving a 1 month duration of impact.

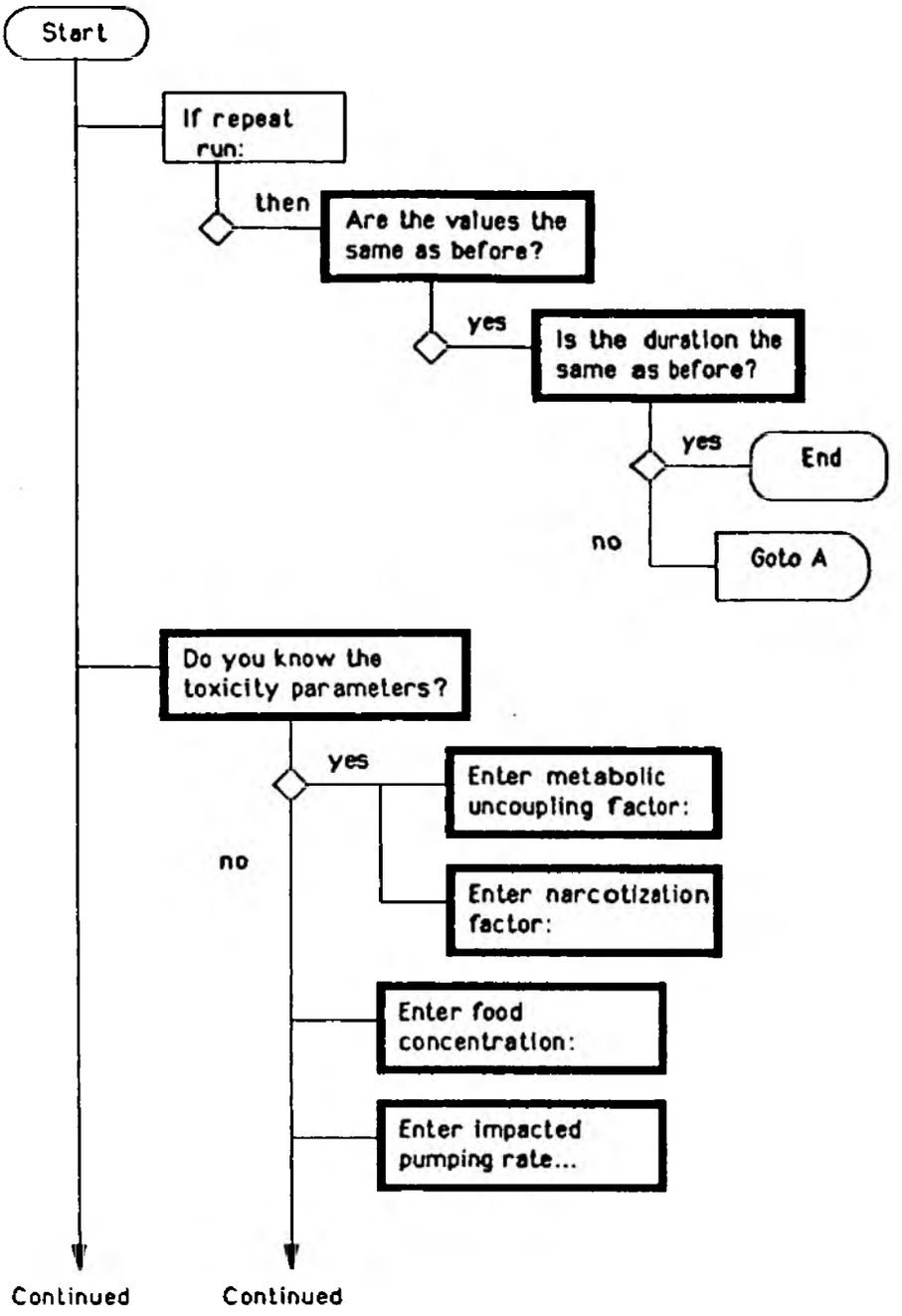

Figure 2.2 Flow diagram for the toxicity routine

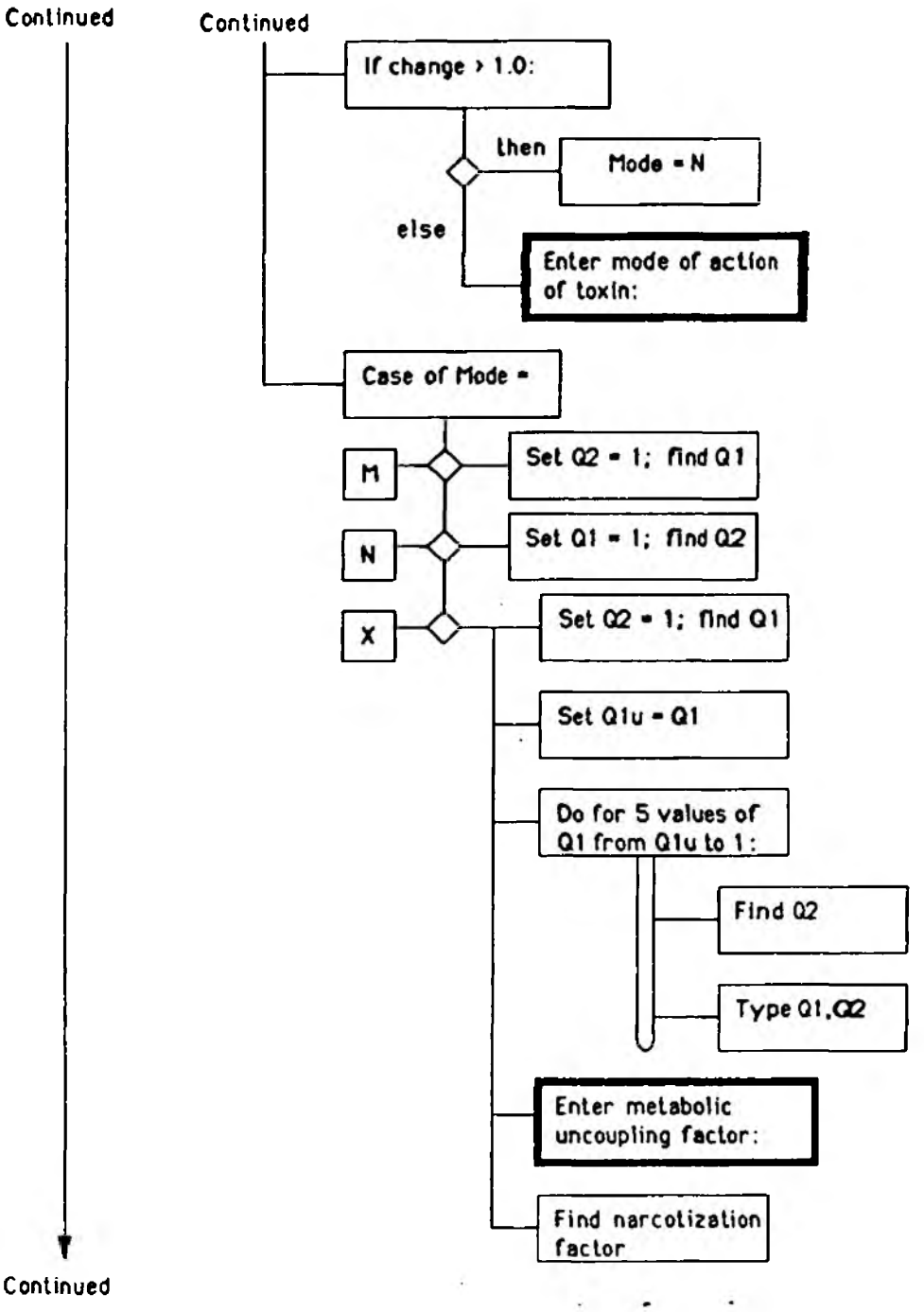

Figure 2.2 Flow diagram for the toxicity routine, continued

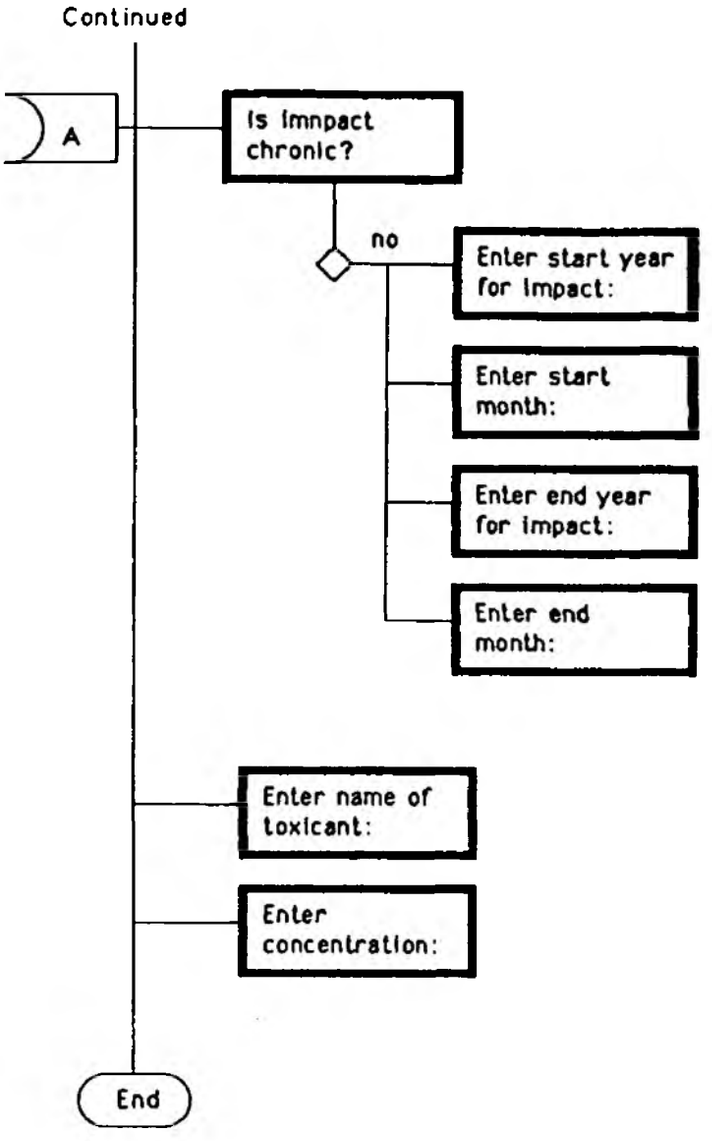

Figure 2.2 Flow diagram for the toxicity routine, continued

19. **Enter name of toxin, 16 characters (<CR> for blank) :**
    Enter the name of the toxicant, in up to 16 characters. This information is for the run report file; it is not used in the model.

20. **Enter concentration of toxin, in mg/l :**
    Enter the concentration of the toxin, a real number. This is for the run report; it is not used in the model.

End of Toxicity Routine

2.4 Output

The Mussel model produces output files summarizing the input to the model, and describing the results of the run. These files provide a record of both the input and output of the model. Three types of file can be produced: run data files, report files and physiology data matrix files. These files are discussed in detail below, and examples of the three file types are given in Appendix c

The naming of the output files follows a convention. The file names are all of the form 'xxxxxxnn.ext'. 'xxxxxx' is the output file name chosen by the user for the control run and its associated impacted runs (see Section 2.3, under 'Keyboard Input', p.14). If the user enters a name of less that 6 characters, it is extended with zeros. 'nn' is the run number; it is 00 for the control run, and is incremented by 1 for every associated impacted run. '.ext' is the file extension; this is set by the Mussel model program, and identifies the output file type. File extensions are .DAT for run data file, .REP for report files, and .PHY for physiology data matrix files.

The run data file

A run data file is produced for every control run. This file summarizes the user input for the run; the information in this file will apply to the corresponding impacted runs as well as to the control.

The run data file lists the Physiology model parameter values and the Feeding model parameter value. Then follows a list of run input data, as follows:

1) Energy in somatic tissue at run start (J).
2) Stored energy at run start (J).
3) Energy in accumulated gametes at run start (J).
4) Total dry body weight at run start (mg).
5) Average food concentration (mg/litre).
6) Suspended sediment concentration as a proportion of the maximum allowed.
7) Proportion of time spent submerged.
8) Output data interval and run length.
9) Start month (for food supply).
10) Number of iterations of Physiology model per day.

The report file

A report file is produced for every run. It provides a summary of the results of the run, and a record of some of the more important input data.

The report file first identifies the run, giving the run name, the user name, and the date. The run name is the 6-character name entered by the user, followed by the run number (see 'Naming Convention', p.23 above). The user name was entered by the user in the Input Routine, and the date is read from the computer system.

Next, the run conditions are summarized. The following information is listed:

1) The parameter file name.
2) The mean food concentration (mg/litre).
3) The proportion of time spent submerged.
4) The initial dry body weight (mg).
5) The initial condition index; this is the proportion of total body weight made up of stored energy and accumulated gametes.
6) The survival schedule file name.

Thirdly, the physiology data is summarized. Von Bertalanffy and Gompertz growth equations are fitted to the size data, and the coefficients are given. A table of spawning data is given, including the start of each spawning episode, the amount of spawn produced in the episode, and the mean body weight (g) during the episode. A fertility schedule is fitted to the spawning data, and the coefficients are given.

Next, the population data is given. This consists of a table giving the shell length of each age class, and the numbers in the age class, out of a total population of 1000 animals. For an impacted population, the length and number are also given as a proportion of the control figures. The growth rate of the impacted population relative to the control is also given.

Finally, a table of physiology data is given. This gives the body weight (g), the condition index, and the number of spawn produced, for each quarter throughout the run.

The physiology data matrix file

The user may choose to output physiology data matrix files for each run in a group. The physiology data matrix file for a run gives data from the physiology model at intervals throughout the run. The interval is either weekly, monthly, or quarterly, as chosen by the user. This data can be plotted out with the user's graphics software. See Section 2.3, under 'Keyboard Input' (p.14), for how to choose to produce this file and how to select the data interval.

The physiology data matrix file contains one record for each data interval. The first record contains the data values at the run start. Each record contains 8 numbers separated by spaces. These are *all* double precision (E10.3 format), except for the first which is an integer (I5 format). They are as follows:
1) The day. (I5).
2) The energy in somatic tissue, Joules. (E10.3)
3) The stored energy, Joules. (E10.3)
4) The energy in accumulated gametes, Joules. (E10.3)
5) The amount of spawn released in the data interval. (E10.3)
6) The pumping rate, litres/hr. (E10.3)
7) The total respired energy in the data interval, Joules. (E10.3)
8) The total scope for growth in the data interval, Joules. (E10.3)

2.5 Program reference

This section gives the information necessary to build the Mussel model program from its component files, and to run it.

Building the Mussel model program

The Mussel model program is written for a VAX VMS system. The following instructions for building the program refer to this system.

The Mussel model main program is in the object module MYMAIN.OBJ. The subroutines are contained in the library MUSSEL.OLB. The program also uses a NAg library routine; you need to know how to access the NAg library on your system.

If the library MUSSEL.OLB does not exist, you can build it from the following object modules:

MYREAD.OBJ
MYPARA.OBJ
MYTOXIN.OBJ
MYQVALS.OBJ
MYFEED.OBJ
MYCONC.OBJ
MYPHYS.OBJ
MYTIL.OBJ
PHYS.OBJ
MYPOP.OBJ
MYOUT.OBJ
LSFIT.OBJ
SPRING.OBJ
PCHECK.OBJ
UTILITY.OBJ
RESET.OBJ
FERTIL.OBJ

The following command file, MSLIB.COM, creates the library MUSSEL.OLB from the above modules.

```
$!  Create library of subroutines for PML Mussel Model:
$!
$library/create mussel myread,mypara,myphys
$library/insert mussel mytil,phys,myconc,mytoxin
$library/insert mussel myqvals,mypop,myout,fertil,lsfit
$library/insert mussel reset,spring,pcheck,utility
```

The following command file, MSLINK.COM, links the Mussel model program. It uses the main program, MYMAIN.OBJ, the library MUSSEL.OLB, and the NAg

library. Note that you may need to change the reference to 'nag/library', as there may be a different procedure for accessing the NAg library on your system

```
$! Link PML Mussel Model:
$!
$link/executable=mussel mymain,myfeed,mussel/library,nag/library
```

The command file MSBUILD.COM combines the function of MSLIB.COM and MSLINK.COM; it creates the library MUSSEL.OLB and then links the Mussel model.

To run the Mussel model

To run the mussel model you need the executable module, MUSSEL.EXE, and the input files described in Section 2.3. The essential input files are the parameter set data file and the survival schedule data file.

Error messages

Table of error codes

Status number:	Meaning:	Action:
1	Error reading parameter file.	Check file is present and in correct format; check file name.
2	Error opening/reading user food data file.	Check as above.
3	Error accepting data entered at the keyboard.	Ensure data is of correct type, ie. real, integer, or character data.
4	Illegal value in parameter set.	Change offending parameter value.
5	Illegal toxicity parameters.	This error should never occur . . .
6	Failure to find toxicity parameters from supplied data.	The toxicity model is unable to simulate the results supplied, and not appropriate to the conditions.
7	Error opening physiology data matrix file for output.	Check file name, disk space, etc.
8	Error calculating food concentration.	This error should never occur . . .
9	NAg routine error - parameter out of range	See discussion below.
10	NAg routine error - minimum not found	See discussion below.
11	NAg routine error - overflow error	See discussion below.
12	NAg routine error - doubt about answer	See discussion below.
13	NAg routine error - variable out of range	See discussion below.

14	Error opening data or report file for output.	Check file names, disk space, etc.
15	Control population growth rate not found.	The control population failed, so no comparison exists for the impacted run. This indicates conditions under which the model is not valid; it is not strictly speaking an error.

NAg routine errors

The Feeding model uses a NAg routine (E02JAF) to maximize the net energy gained through feeding. Errors occasionally occur in this routine, leading to failure of the Feeding model. This can happen when the energy gained through feeding is almost identical for a range of different strategies, so the conditions for a maximum are not well defined. Another cause may be rapidly varying food conditions, when the previous feeding strategy may not provide an appropriate start-point from which the NAg routine can operate. When the NAg routine fails, the Mussel model uses the Feeding model output for the previous iteration of the Physiology model. Inaccurate (or 'out of date') values for feeding costs and energy gain in one iteration of the model will make very little difference in the long term, and the NAg routine generally succeeds the next time round. However, it may happen that the routine fails more than twice in succession, in which case the errors in the costs and energy gained may be significant, and the run is aborted. The failure will depend on the gut volume and the environmental conditions, and is avoided by changing any of these conditions slightly so that the precise combination that caused failure is not encountered. Try small changes to food concentration, metabolic uncoupling factor, start month for food supply, or size of larva at settlement.

APPENDIX A

This Appendix contains examples of the input files for the Mussel model. These files are described in Section 2.3 (p.10).

Example parameter set file

The default parameter set file, MUSSEL.PARA, is given below:

```
0.0129          0.66
1.8             1.00
0.0043          0.66
0.18            0.33
0.02            0.66
0.1             0.66
0.0001          1.33
0.0000000006    .33
0.0001          1.33
1.6             1.00
36.4            0.11
0.30            1.00
0.25    0.60    1.333
0.30    0.10    0.03    0.20
17.5    39.5    24.0    0.000001
0.5     1.0
0.200
0.60            0.60
4               0.5
2               0.5
18.5            1.6
0.400   0.15    0.15
15.
```

Example food data file

The following is an example of a food data file, FOOD.DATA. The values given in this example are approximated from data for the Lynher estuary, Cornwall (Widdows et al. 1979)

```
0.00 0.00 1.00 1.00 0.80 1.20 0.50 0.70 0.50 0.70 0.00 0.00
17.0 37.0 17.0 11.0 3.20 3.80 2.50 5.30 10.5 12.0 25.0 24.0
```

Example survival schedule file

The following is an example of a survival data file, SURV.DATA. The values in this example are arbitrary; they do not reflect the survival schedule of an actual population; it is up to the user to provide values suitable for the population being modelled.

```
0.000000001
0.100
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
0.500
```

APPENDIX B

This section contains an example of the screen display during a run of the Mussel model program, showing screen output from the program and user input. Please see Section 2.3, p.14 for a full description of the keyboard input required by the program.

Example screen

The following is an example of the input and output when the model is run. User input is in **bold** type. In this example, the user chooses not to write out the full physiology data matrix. The toxicity parameters are not known, so details of a toxicity experiment are entered. The mode of action of the toxin is also unknown, so a number of pairs of toxicity parameters are calculated and displayed.

$ run mussel
Running Edulis Simulation Program
Routine to accept run parameters...
Please enter your name (16 characters) : **M.Prestidge**
Use default parameter set (y) ? **y**
Reading parameter file...
Food supply types :
  0 = Constant food
  1 = Sinusoidal variation
  2 = Spring and autumn peaks
  3 = Monthly values in file

Enter option (1) : **1**
Enter mean food concentration in mg dry wt./l (0.5000) : **0.5**
Enter variation in food concentration (0.5000) : **0.5**
Silt values range from 0 to 1 :
  0 = Open coast; no suspended sediment
  1 = High suspended sediment
Enter silt value (0.5000) : **0.5**
Enter proportion of time for which mussel bed is submerged (1.0000) : **1.0**
Start run from settlement of larva (y) ? **y**
Enter survival schedule file name (surv data a1) : **surv data a1**
Run duration is 10 years
Write out physiology data in full (N) ? **n**
Enter name for output files (mussel) : **mussel**
Enter number of iterations of Physiology Model per day (1) : **1**
Enter start month for food supply (3) : **3**
End of input routine.

Routine to establish toxicity parameters...
Do you know the toxicity parameters (y) ? **n**
To evaluate the Toxicity Parameters:

Enter the conditions under which the toxicity measurements
were made, and the effects of the toxicant, in response
to the following questions :

Enter food concentration, mg dry wt./l (0.5000) : **0.5**
Enter the impacted pumping rate, as a fraction of
the unimpacted rate (0.5000) : **0.8**
Modes of action of toxin :
M = Metabolic uncoupling
N = Narcotization
X = Mode not known

Enter Mode (M) : **x**
Some possible pairs of Q1,Q2 values:
Q1 = 1.000 Q2 = 0.727
Q1 = 1.137 Q2 = 0.775
Q1 = 1.275 Q2 = 0.825
Q1 = 1.412 Q2 = 0.880
Q1 = 1.550 Q2 = 0.938
Q1 = 1.687 Q2 = 1.000
NOTE: Metabolic uncoupling will always act to
reduce the filtration rate, but a narcotic may increase
it, so the above list does not cover the full range of
values, and Q1 may be greater than 1.0
Enter metabolic uncoupling factor, Q1 (1.0000) : **1.0**
Q1 = 1.000 Q2 = 0.727
Chronic toxic effect? (Y) **y**
Enter name of toxin, 16 characters (<CR> for blank) : **toxin**
Enter concentration of toxin, in mg/l : **1.0**
End of Toxicity Routine.

Unimpacted...
Running Physiology Model -
End of Physiology Model.

Running Population Model -
Growth rate = 0.517E+00 Number of iterations = 15

End of Population Model.

Running Output Routine

End of run
Impacted...
Running Physiology Model -
End of Physiology Model.

Running Population Model -
Growth rate = 0.368E+00 Number of iterations = 12

End of Population Model.

Running Output Routine

End of run
Repeat for another toxicant, same control (y) ? **n**
Re-run Model, new control (n) ? **n**
$

APPENDIX C

This Appendix contains examples of the output files of the Mussel model program. These files are described in Section 2.4, p.23.

Example run data file

The following is an example of a run data file, produced by the Mussel model for each control run.

Physiology Model Parameter Values

Relation to body size

	ALPHA	BETA
Gut capacity (ml)	0.1290D-01	0.6600D+00
Store capacity (j)	0.1800D+01	0.1000D+01
Basal metabolic rate (soma)	0.4300D-02	0.6600D+00
Basal metabolic rate (gamete)	0.7800D-02	0.6600D+00
Growth rate (K1)	0.2000D-01	0.6600D+00
(K2)	0.1000D+00	0.6600D+00
Gametogenesis rate (K1)	0.1000D-03	0.1330D+01
(K2)	0.6000D-09	0.1330D+01
Gamete reabsorption rate	0.1000D-03	0.1330D+01
Spawn trigger	0.1600D+01	0.1000D+01
Max. spawning rate	0.3640D+02	0.1100D+00
Target storage size (j)	0.3000D+00	0.1000D+01
Shell length	0.1800D+00	0.3300D+00

Relation to scope for growth

	PHI
Growth rate (two)	0.2500D+00
Gametogenesis rate (two)	0.6000D+00
Spawning rate (two)	0.1333D+01

Relation to Activities

	COST
Growth	0.3000D+00
Gametogenesis	0.1000D+00
Storage	0.3000D-01

Spawning	0.2000D+00

Energy Equivalents

	EEQ
Protein	0.1750D+02
Fat	0.3950D+02
Carbohydrate	0.2400D+02
Female Gamete	0.1000D-02

Spawning rate parameter

	MU
Min. rate	0.5000D+00
Initial slope	0.1000D+01

Feeding Model Parameters:

Enzyme resorption rate		0.2000D+00
Filtration cost		0.4000D+00
Enzyme production cost		0.1500D+00
Absorption cost		0.1500D+00
Absorption rate:	Pcle. 1	0.6000D+00
	Pcle. 2	0.6000D+00
Energy Content:	Pcle. 1	0.1850D+02
	Pcle. 2	0.1600D+01
Initial volume:	Pcle. 1	0.4000D+01
	Pcle. 2	0.5000D+00
Final volume:	Pcle. 1	0.2000D+01
	Pcle. 2	0.5000D+00

Variable initial values

Somatic tissue (j)	0.2880D+02
Storage tissue (j)	0.5250D+01
Gametes (j)	0.0000D+00
Total body mass (mgs)	0.1500D-02
Av. food conc. (mgs per l)	0.3000D+00
Silt Parameter (0 to 1)	0.0000D+00
Time submerged (0 to 1)	0.1000D+01
Time interval	30.42 days over 10 years
Start month	March
Iterations per day	1

Example report file

The following is an example of the report file generated by the Mussel model each run. This is the report of a control run, i.e., without toxic impact.

REPORT OF RUN "tst02r01" (Control)
User name: Batch run 02 .
Date: 15-Dec-91

RUN CONDITIONS:

Parameter file name	= bmussel para a1 (default)
Mean food concentration	= 0.30 (sine wave)
Silt level	= 0.000
Proportion of time spent below water	= 1.00
Initial body weight	= 0.0015
Initial condition index	= 0.200
Survival schedule file name	= surv data a1

PHYSIOLOGY DATA:

Standard growth equations were fitted to the results of
the Physiology Model, using a least-squares fitting routine
written by M.R.Carr of Plymouth Marine Laboratory.

Von Bertalanffy growth equation:

Shell length = Lmax(1-exp(-a(t+t0)))

Coefficients are:	Lmax	= 0.601E+01	St. error = 0.384E-01
	a	= 0.489E+00	St. error = 0.194E-01
	t0	= 0.375E+00	St. error = 0.537E-01

Standard deviation of points from fitted curve = 0.121E+00

Gompertz growth equation:

Somatic size = Smax*exp(-exp(-a(t+t0)))

Coefficients are:	Smax	= 0.181E+01	St. error = 0.327E-01
	a	= 0.448E+00	St. error = 0.251E-01
	t0	= -0.239E+01	St. error = 0.738E-01

Standard deviation of points from fitted curve = 0.640E-01

Spawning episodes:

The following table gives the times at which the Model predicts spawning episodes to start, the number of gametes produced in each episode, and the mean somatic size (in grams) of the mussel during spawning.

Year	Month	Gametes	Mean size (g)
3	2	0.143E+08	0.66
4	1	0.247E+08	0.91
4	6	0.287E+08	1.08
5	5	0.337E+08	1.23
6	4	0.380E+08	1.36
7	4	0.422E+08	1.48
8	4	0.458E+08	1.59
9	3	0.492E+08	1.69
10	3	0.524E+08	1.78

A curve was fitted to the spawning data, using a least squares routine by M.R.Carr, which gives the variation in the number of gametes produced in a spawning episode with the somatic size (in grams), as follows:

Spawn produced = a+(b*(Size**c))

Coefficients are:	a	= -0.846E+07	St. error = 0.519E+07
	b	= 0.348E+08	St. error = 0.532E+07
	c	= 0.962E+00	St. error = 0.125E+00

Standard deviation of points from fitted curve = 0.622E+06

POPULATION DATA:

The age distribution of the population is given below. The number of mussels of each age expected in a random sample of 1000 animals, and the shell length of each age class, are given, together with the values relative to the control (unimpacted) run.

Age	Length	Rel. Length	Number	Rel. Number
1	2.75	1.000	586.42	1.000
2	4.17	1.000	242.72	1.000
3	4.85	1.000	100.54	1.000

4	5.18	1.000	41.71	1.000
5	5.44	1.000	17.27	1.000
6	5.63	1.000	7.14	1.000
7	5.79	1.000	2.96	1.000
8	5.92	1.000	1.23	1.000

Relative per capita productivity = 0.784E+00

TABLE OF PHYSIOLOGY DATA

Quarter	Size (g)	Index	Spawn
1	0.0183	0.43	0.000E+00
2	0.0762	0.46	0.000E+00
3	0.1581	0.40	0.000E+00
4	0.1622	0.31	0.000E+00
5	0.2567	0.49	0.000E+00
6	0.4286	0.59	0.000E+00
7	0.5653	0.61	0.000E+00
8	0.5693	0.59	0.000E+00
9	0.6676	0.32	0.143E+08
10	0.8051	0.61	0.000E+00
11	0.8993	0.68	0.000E+00
12	0.8993	0.66	0.000E+00
13	0.9411	0.41	0.247E+08
14	1.0548	0.65	0.000E+00
15	1.1014	0.30	0.287E+08
16	1.1014	0.18	0.000E+00
17	1.1428	0.52	0.000E+00
18	1.2318	0.19	0.337E+08
19	1.2719	0.44	0.000E+00
20	1.2719	0.36	0.000E+00
21	1.3080	0.59	0.000E+00
22	1.3715	0.31	0.380E+08
23	1.4160	0.51	0.000E+00
24	1.4160	0.45	0.000E+00
25	1.4462	0.63	0.000E+00
26	1.4992	0.38	0.422E+08
27	1.5396	0.55	0.000E+00
28	1.5396	0.49	0.000E+00
29	1.5656	0.65	0.000E+00
30	1.6122	0.42	0.458E+08
31	1.6485	0.57	0.000E+00
32	1.6485	0.52	0.000E+00
33	1.6715	0.66	0.000E+00
34	1.7133	0.44	0.492E+08
35	1.7463	0.57	0.000E+00
36	1.7463	0.52	0.000E+00

37	1.7669	0.66	0.000E+00
38	1.8051	0.43	0.524E+08
39	1.8353	0.57	0.000E+00
40	1.8353	0.51	0.000E+00

Example physiology data matrix file

Below is an example physiology data matrix file. This is from a control run of 2 years duration. The default parameter set was used, and all input data was set to the default values. The data is output at intervals of about 1 month (the default data interval). Please note that the last number in each record has been wrapped onto a new line, as the records are too long to print on a single line.

```
  0 0.288E+02 0.525E+01 0.000E+00 0.000E+00 0.000E+00 0.000E+00
0.000E+00

 30 0.884E+02 0.831E+02 0.115E-02 0.000E+00 0.108E+00 0.192E+00
0.191E+00

 61 0.233E+03 0.237E+03 0.277E-01 0.000E+00 0.137E+00 0.400E+00
0.401E+00

 91 0.468E+03 0.501E+03 0.263E+00 0.000E+00 0.175E+00 0.679E+00
0.692E+00

122 0.827E+03 0.922E+03 0.164E+01 0.000E+00 0.237E+00 0.102E+01
0.105E+01

152 0.130E+04 0.150E+04 0.707E+01 0.000E+00 0.341E+00 0.143E+01
0.147E+01

182 0.192E+04 0.225E+04 0.243E+02 0.000E+00 0.534E+00 0.189E+01
0.192E+01

213 0.270E+04 0.318E+04 0.715E+02 0.000E+00 0.956E+00 0.245E+01
0.237E+01

243 0.358E+04 0.405E+04 0.168E+03 0.000E+00 0.182E+01 0.313E+01
0.256E+01

274 0.443E+04 0.418E+04 0.290E+03 0.000E+00 0.887E+00 0.324E+01
0.149E+01

304 0.503E+04 0.399E+04 0.377E+03 0.000E+00 0.239E+00 0.222E+01
0.693E+00

335 0.557E+04 0.396E+04 0.472E+03 0.000E+00 0.883E+00 0.233E+01
0.807E+00

365 0.615E+04 0.463E+04 0.629E+03 0.000E+00 0.255E+01 0.392E+01
0.195E+01

395 0.703E+04 0.632E+04 0.105E+04 0.000E+00 0.180E+01 0.500E+01
0.415E+01

426 0.824E+04 0.813E+04 0.189E+04 0.000E+00 0.140E+01 0.537E+01
0.521E+01

456 0.961E+04 0.969E+04 0.325E+04 0.000E+00 0.127E+01 0.591E+01
0.593E+01
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487	0.111E+05	0.110E+05	0.531E+04	0.000E+00	0.130E+01	0.653E+01	0.659E+01
517	0.127E+05	0.119E+05	0.803E+04	0.000E+00	0.150E+01	0.718E+01	0.719E+01
547	0.141E+05	0.113E+05	0.216E+04	0.887E+07	0.194E+01	0.103E+02	0.521E+01
578	0.154E+05	0.121E+05	0.582E+04	0.000E+00	0.286E+01	0.842E+01	0.786E+01
608	0.167E+05	0.120E+05	0.960E+04	0.000E+00	0.436E+01	0.932E+01	0.687E+01
639	0.177E+05	0.107E+05	0.123E+05	0.000E+00	0.136E+01	0.768E+01	0.316E+01
669	0.183E+05	0.984E+04	0.138E+05	0.000E+00	0.559E+00	0.518E+01	0.179E+01
700	0.188E+05	0.939E+04	0.152E+05	0.000E+00	0.129E+01	0.518E+01	0.193E+01
730	0.194E+05	0.983E+04	0.168E+05	0.000E+00	0.482E+01	0.773E+01	0.363E+01

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