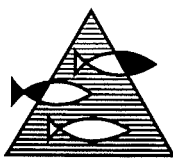


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A general fish model is described and deals simultaneously with all fundamental aspects of fish metabolism and growth. The model conserves energy and matter, resolved in protein, fat, carbohydrates, nitrogen and phosphorus. Here the main application is to derive output from the model of interest for water quality in and around salmon fish farms. The model can be adapted to other fish species.

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2. Fiskemodell
3. Miljø

Emneord - engelsk:

1. Fish farm
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ABSTRACT

The fish model described in this paper is quite general and deals simultaneously with all fundamental aspects of fish metabolism and growth. The model conserves energy and matter, resolved in protein, fat, carbohydrates, nitrogen and phosphorus. Here the main application is to derive output from the model of interest for water quality in and around fish farms. Thus, oxygen consumption due to fish respiration and emissions of various biologically active dissolved substances from a fish farm are derived for given fish stock, food composition, feeding rate and temperature. The fluxes of particulate organic matter (uneaten food and faeces) from a farm are also derived. The model can be used for many purposes. It can be used to find food compositions fulfilling different objectives, for instance, minimising the emission of plant nutrients or food costs. It should be possible to adapt the model to other fish species for use in, for instance, models of natural populations of fish interacting with each other.

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1. INTRODUCTION

The MOM system (Monitoring - Ongrowing fish farms - Modelling) is designed for observation, prediction and regulation of the local environmental impact of intensive marine fish farming, see Ervik et al (1993, 1997). The final mathematical model of the MOM system will cover all major aspects of the interaction between fish farms and the environment. We have already developed a dispersion model that computes the spreading of particulate organic matter from a fish farm with specified size and separation between cages (Stigebrandt, 1995). We have also developed a benthic model computing the critical load of the bottom sediment with respect to viable benthic animals (Stigebrandt & Aure, 1995). Used together these models may compute the critical emission of particulate organic matter from a farm located in an area with specified current conditions and water depth (Stigebrandt & Aure, 1995). To complete the model of the MOM system we need to include a fish model computing the metabolism and growth of a specified fish stock. A quite general fish model is presented in this paper. Given feeding rate, food properties and temperature, the fish model computes the emission of particulate organic matter from the net pens, which is necessary input to the dispersion model. The fish model also computes the emission of dissolved substances and oxygen consumption due to respiration. This information is necessary to compute water quality in the pens, i.e. concentrations of oxygen and emitted dissolved substances potentially harmful for the fish, under different current and other environmental conditions. A water quality model for the cages in fish farms remains to be developed but the essentials of such a model are briefly discussed in this paper. An overview of the MOM model is given in Fig. 1.

The state variable of the mathematical fish model is the weight of the fish. For the application of the model on the farm level, the distribution of fish with respect to weight can be looked upon as the state variable. In practice, this is described as the mean weight and number of fish in different weight classes. Food composition, the rate of food supplies and ambient water temperature are important external variables in the model. The basic fish model has existed for more than one decade as an unpublished computer program and model results were described in, e.g. Stigebrandt (1986) and Stigebrandt & Molvær (1986). In this paper the basic model is slightly revised by tuning of some model constants using recent data on farmed Norwegian salmon obtained from Einem et al. (1995). Modern food composition used in the Norwegian fish farm industry is adopted from Åsgård and Hillestad (1998).

The outline of the paper is as follows. The compositions of fish and food are described in

section 2. The fish model is presented in section 3 and model results are displayed and validated in section 4. Emissions of dissolved substances and oxygen consumption due to fish metabolism are derived from the model in section 5. A short description of the fish model as implemented in the MOM model system is given in section 6. The paper is concluded in section 7 with a short discussion including the mentioning of other possible applications of the model.

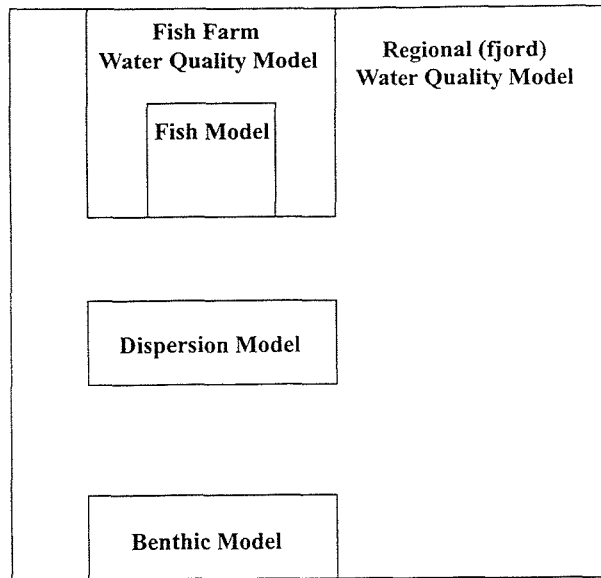


Fig. 1. Overview of the model system in MOM. The fish model is described in the present paper.

2. COMPOSITION OF FISH AND FOOD

The food is composed of protein (fraction by mass, F_p), fat (F_f) and carbohydrates (F_c). In addition, the food contains minerals and water. Protein, fat and carbohydrates have different roles in the metabolism and anabolism of fish and have different energy content and chemical composition. For computations of appetite, oxygen consumption and emissions of organic matter, nitrogen and phosphorus, it is necessary to know the actual composition of food. The specific energy content of fat, protein and carbohydrates are $C_f=9450$ cal/g, $C_p=5650$ cal/g and $C_c=4100$ cal/g, respectively, see e.g. Parsons et al. (1979) (1 cal=4.187 J). The specific energy content of the food then is $\delta = F_p C_p + F_f C_f + F_c C_c$ (cal/g). The fraction of food energy contributed by the proteins is $E_p = F_p C_p / \delta$. The fractions contributed by fat and carbohydrates, E_f and E_c , are defined analogously. The specific energy of the fish is $C_n = P_p C_p + P_f C_f$ where P_p (P_f) is the protein (fat) fraction by mass of the fish. P_f and P_p may change during the life cycle of the fish.

3. A MODEL FOR THE ENERGY FLOW IN FISH

To compute the environmental impact of a fish farm it is necessary to know the emissions of different biochemically active substances from the farm. These are determined by the rate of food supply, properties of the food and how the food is processed by the fish and can be computed from a fish model including the appetite, metabolism and growth. The fish model starts from the energy equation for fish that may be written (e.g. Webb, 1978)

$$Q_r - (Q_f + Q_N) = Q_s + Q_l + Q_{sda} + Q_g + Q_p \quad (1)$$

The terms on the left-hand side describe the sum of energy metabolised by the fish and the terms on the right-hand side are the energy costs due to the different metabolic activities. In Eq. (1) Q_r is food consumed, Q_f faecal loss, Q_N excretory (nitrogen) loss or non-faecal loss, Q_s standard metabolism, Q_l locomotor (activity) metabolic cost, Q_{sda} apparent specific dynamic action, Q_g growth (anabolism) and Q_p reproductive cost for gamete synthesis. All terms have the dimension energy per day, e.g. cal day⁻¹ or J day⁻¹. The different terms in Eq. (1) are briefly described in section 3.1 below. For a thorough discussion, see e.g. Webb (1978). A discussion of abiotic effects upon the energetics of fish, i.e. temperature effects, is postponed to section 3.2. Some properties of the fish model are presented and validated in section 4.

3.1 Descriptions of the terms in the energy equation

Maximum food consumption $Q_r(\max)$ (cal day⁻¹) is defined as appetite when food is unrestricted. The appetite App, also called maximum voluntary food intake is thus the maximum food consumption Q_r divided by the specific energy content of the food, δ , thus $\text{App} = Q_r / \delta$ (g day⁻¹). The energy requirement $Q_r(\max)$ increases with the mass (weight) of a fish. Below we will provide estimates of all terms in Eq. (1) except Q_r and by that we may calculate $Q_r = Q_r(\max)$.

For optimum conditions, the maximal or potential growth rate of a fish, $G_{\max} = dW/dt$ (g day⁻¹), of weight W can be described by the following equation

$$\frac{dW}{dt} = G_{\max} = aW^b \quad (2)$$

Here the parameters a (g^{1-b} day⁻¹) and b (non-dimensional) are constants (possibly with some genetic variation) for a given species and a is also a function of temperature and possibly also other abiotic factors, see section 3.2 below. A prerequisite for maximal

growth is that the fish is given maximal ration $Q_r(\text{max})$. When growing the mass of protein (fat) built into the fish is the fraction P_p (P_f) of the total fish growth. To attain maximal growth the food must thus have a minimum content of protein as further discussed in section 4.4 below. The growth under reduced food supply is briefly discussed later in this paper.

The fish growth given by Eq. (2) can be expressed in energy terms using the mean specific energy content C_f (cal/g) of the actual fish. Since $Q_g = C_f dW/dt$ (cal/day) we then obtain

$$Q_g = a C_f W^b \quad (3)$$

for the rate of energy "stored" in the fish during conditions of maximum growth.

Some of the ingested food is not assimilated but leaves the fish with the faeces. The assimilated fraction of protein (fat, carbohydrates) is denoted by A_p (A_f , A_c). We thus obtain for the faecal energy loss, Q_f

$$Q_f = FL Q_r \quad (4)$$

Here $FL = (1-A_p)E_p + (1-A_f)E_f + (1-A_c)E_c$. In the first version of this model (Stigebrandt, 1986), the following values were used for the assimilated fractions $A_p = 0.97$, $A_f = 0.90$ and $A_c = 0.60$. However, the values of these parameters depend on the quality of food. Einem et al (1994) used the following values for farmed salmon in Norway $A_p = 0.89$, $A_f = 0.92$ and $A_c = 0.50$ and these values will be adopted for computations in the present paper.

Assimilated amino acids in excess of growth requirements are metabolised. However, approximately 15% of the metabolised protein energy are excreted, mainly as ammonia. This energy loss Q_N is thus given by

$$Q_N = 0.15 C_p (F_p A_p \frac{Q_r}{\delta} - P_p a W^b) \quad (5)$$

Here the expression between parentheses is the amount of assimilated amino acids in excess of growth requirements (g day^{-1}). The assimilated food energy (i.e. $Q_r - Q_f$) minus nitrogenous losses after assimilation (Q_N) is the energy available for metabolism and growth.

The lower limit of metabolism is Q_s which approximates the energy required to maintain a non-stressed fish at rest. The metabolism is satisfied first and will deplete stored energy when food ration is very low whereby the fish is losing weight. There appears to be an

upper metabolic limit $Q_m(\max)$. The metabolic scope is defined as $Q_m(\max)$ minus Q_s . This is a measure of the energy that can be made available for all activities over and above basic maintenance, e.g. digestion, absorption, locomotion, regulation under stress and growth.

There is a well-established empirical relationship between the body mass W and Q_s

$$Q_s = \alpha W^\gamma \quad (6)$$

Here α ($\text{cal day}^{-1} \text{g}^{-0.8}$) and γ (non-dimensional) are constants for a given species (there is however some genetic variation) and α is a function of temperature and other abiotic factors as discussed in section 3.2 below. It appears that γ is about 0.8 for many species. In Stigebrandt (1986) α was taken equal to 15 but a comparison with results presented by Einem et al (1994) suggests that α equals 11. One reason for the difference may be that Stigebrandt (1986) used data from farms in running river water to estimate α . Energy loss due to locomotion Q_l may have been substantial in this case as discussed below.

A feeding fish must process the food through digestion, assimilation, transportation, biochemical treatment and incorporation and this requires energy. The sum of these energy requirements is the apparent specific dynamic action, Q_{sda} . Specific dynamic action alone, SDA, represents the biochemical energy costs of food treatment and is considered to be the major portion of apparent specific dynamic action. SDA is 30% of energy intake for protein. We assume that the biochemical energy cost is 5% of the energy intake for fat and carbohydrates. Thus, we write

$$Q_{SDA} = BC Q_r \quad (7)$$

Here $BC = 0.3A_p E_p + 0.05(A_f E_f + A_c E_c)$. The fraction of food energy assimilated by the fish minus the fraction that is used for biochemical food treatment is $\epsilon = 1 - FL - BC$. The metabolisable energy content of food is $\epsilon \cdot \delta$ minus the fraction excreted by nitrogenous waste. The latter varies with the amount of protein in excess of growth requirements, see E. (5).

The locomotor energy cost, Q_l , is probably rather small for fish kept in cages in inshore areas. In cages anchored in rivers and other environments with strong currents, however, the velocity of the water flowing through the cage may be quite large and this may lead to appreciable Q_l -values as mentioned above. In the model, Q_l is included in Q_s , thus raising the value of α . The final term in the energy equation (1) is the reproductive energy cost, Q_p . This is neglected in the model because fishes normally are removed for slaughter before they become sexually matured.

Finally, we insert the expressions for the different energy terms given above into Eq. (1). We then obtain the following equation for the maximal ration $Q_r = Q_r(\max)$ to be used in this paper

$$\varepsilon^* Q_r = \alpha W^\gamma + a C_{fi}^* W^b \quad (8)$$

Here $\varepsilon^* = \varepsilon - 0.15E_p A_p$ and $C_{fi}^* = 0.85C_p P_p + C_f P_f = C_n - 0.15C_p P_p$. Q_r is the rate of energy (cal day⁻¹) ingested by the fish. The weight of this food is the appetite A_{pp} which thus equals Q_r / δ (g day⁻¹).

3.2. Abiotic effects on appetite and growth

Growth and metabolism, and thereby appetite, are not only functions of weight and genetic background but also of temperature and possibly also of other environmental parameters. Among these one may mention duration and intensity of natural light (illumination) and concentrations of oxygen, ammonium and carbon dioxide in the ambient water. Typically, biochemical rates in fish double when temperature increases by about 8-9°C.

Mathematically this can be described by an exponential function by which we multiply the right side of Eq. (8). We then obtain for the appetite

$$Q_r = \frac{1}{\varepsilon^*} (\alpha W^\gamma + a C_{fi}^* W^b) e^{\tau T} \quad (9)$$

and for maximum growth

$$\frac{dW}{dt} = a W^b e^{\tau T} \quad (10)$$

Here T is temperature (°C) and τ is an inverse temperature scale (°C⁻¹) equivalent to the well-known Q_{10} . Thus, when temperature increases by $1/\tau$, appetite and growth increase by a factor e (=2.718). In this paper τ is taken equal to 0.080 (°C⁻¹). This τ -value implies that biochemical rates in the fish double by a temperature increase of about 8.6°C.

For many species, there is an optimal temperature interval for growth. For e.g. rainbow trout, this is around 16°C. Higher temperatures stress the fish whereby Q_s increases faster than described by the (constant) τ . In order to reduce fish metabolism at high temperatures, it appears to be common practice among fish farmers to supply smaller rations than those calculated from Eq. (9). The maximum fish growth at temperatures close to 0°C appears to be less than given by Eq. (10). This may be accounted for in the model

by decreasing the value of the parameter "a" at low temperature (not implemented in the model so far due to lack of data). However, the reduced growth at low temperatures may possibly be due to influence from other factors correlated to temperature. On such factor at high latitudes is natural illumination.

Maximum growth occurs only if the external (abiotic) conditions are favourable. In winter, the growth at high latitudes is usually less than optimal. This has led to extensive use of artificial illumination, stimulating the production of anabolic hormones, in Norwegian salmon farms in winter, c.f. Oppedal et al. (1997).

Decreasing the upper metabolic limit $Q_m(\max)$ at the same time as Q_s is constant or increasing means that the growth Q_g decreases. Thus, to obtain an efficient fish production the environmental conditions in a farm must be good, with satisfactory oxygen concentrations and low concentrations of metabolic waste products and other toxicants. Reduced oxygen concentrations decrease the appetite for many species. $Q_m(\max)$ tends to decrease almost in proportion to reduced dissolved oxygen levels. Q_s is relatively independent of ambient oxygen levels but is elevated at very low concentrations. Elevated concentration levels of carbon dioxide and ammonium also decrease $Q_m(\max)$ while Q_s is relatively insensitive. Other environmental toxicants may also act as limiting factors on Q_m . In future when quantitative knowledge on these abiotic effects possibly becomes available they may be implemented in the model, e.g. by letting the parameters a and α be functions of the concentrations of the actual substances. In the present version of the fish model, temperature is the only abiotic factors included. Readers are referred to, e.g. Webb (1978) for a review of the subject.

4. PRESENTATION AND VALIDATION OF MODEL RESULTS

With known values of the coefficients a , b and τ we may compute the maximal rate of growth for a certain temperature. If we also know α , γ , C_{fi} we may compute the appetite of the fish with respect to a specific composition of the food. In order to demonstrate the model we use $\alpha=11$, $\gamma=0.8$, $a=0.038$, $b=2/3$, $\tau=0.080$ ($^{\circ}\text{C}^{-1}$) and $C_{fi}=2000$ (cal g^{-1}), values that should apply to salmon in present day Norwegian fish farms. In the computations below the fish is fed on "standard food" with $F_p=0.45$, $F_f=0.30$ and $F_c=0.07$ if not otherwise stated. The protein and fat content of the fish is given by $P_p=0.18$ and $P_f=0.18$. Both food and fish compositions might of course be changed arbitrarily in the computer model. This is done in the present paper to study consequences of different food compositions.

4.1. Growth rates

From Eq. (2) it is easily seen that with $b=2/3$ the relative growth rate (the daily growth divided by the body weight) decreases with increasing weight as $W^{-1/3}$.

The fish growth from time $t=t_0$ to time $t=t_1$ is readily obtained by integration of Eq. (10). Using $b=2/3$ one obtains the following analytical solution for the weight W_1 at $t=t_1$

$$W_1 = [W_0^{1/3} + \frac{a}{3} \int_{t_0}^{t_1} e^{\tau T} dt]^3 \quad (11)$$

Here W_0 is the fish weight at $t=t_0$. To compute the value of the integral one has to know the temperature T as function of time. The fish growth is non-linear in temperature. This is evident from the series expansion of the integrand by which one may approximate the integral

$$\frac{a}{3} \int_{t_0}^{t_1} e^{\tau T} dt \approx \frac{a}{3} (1 + \tau T_m + \frac{1}{2} (\tau T_m)^2 + \dots) (t_1 - t_0) \quad (12)$$

Here T_m is the mean temperature during the period (t_1-t_0) . Einem et al (1995) used the so-called temperature-unit growth model by which the integral is approximated in the following way

$$\frac{a}{3} \int_{t_0}^{t_1} e^{\tau T} dt \approx TGC (t_1 - t_0) T_m \quad (13)$$

They considered TGC to be constant. Comparison between Eqs. (12) and (13) shows that this assumption hardly is fulfilled for the wide span in temperature occurring in Norwegian coastal waters. The TGC model should therefore be used with great caution. With present day's extremely fast PC's there seem to be no reason at all to approximate the integral in Eq. (11) in such a simplified way as done in Eq. (13).

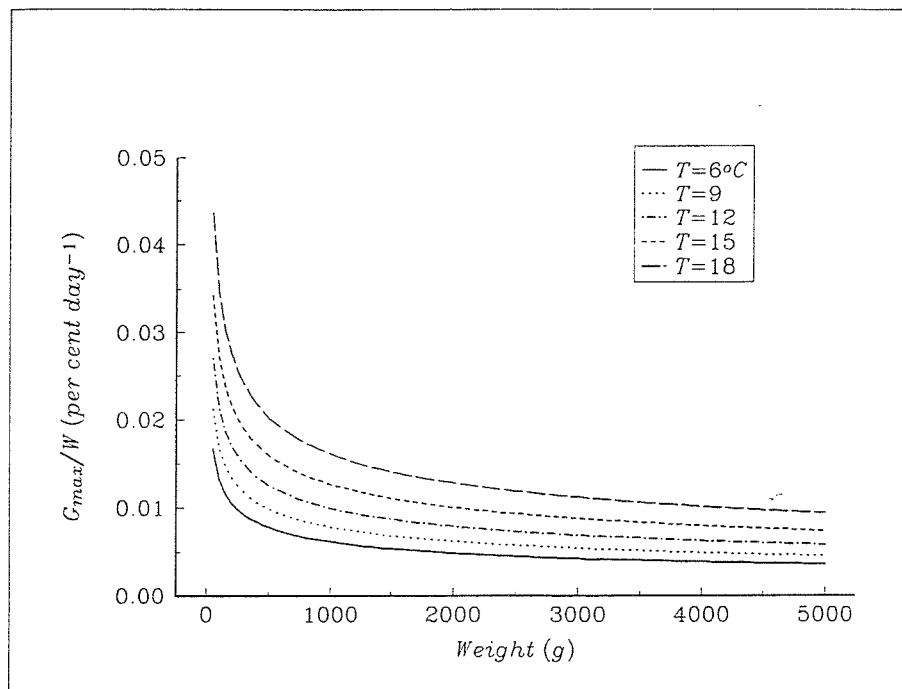


Fig. 2. Normalised maximal growth rates G_{\max}/W of fish vs fish weight W for some temperatures.

Maximal normalised growth rates G_{\max}/W of a fish as a function of fish weight W , computed using Eq. (10), are given in Fig. 2 for some temperatures T . This graph clearly demonstrates the non-linear behaviour of the relative growth rate with respect to both temperature and weight. The development of the weight of a fish with time in a specific location is readily obtained by integration of Eq. (10) using temperature from the actual location. Results for a one-year-long integration, starting 1 May with a smolt of weight 80 gram, for some locations along the Norwegian coast are shown in Fig. 3. Monthly mean temperatures used in the computations were obtained from Midttun (1975). Comparison between the growth in Fig. 3 for Korsfjorden with the growth in Einem et al (1994) for SW Norway shows that the growth presented by the latter authors is obtained with the present model using $a=0.038$. Stigebrandt (1986) estimated $a=0.033$ and increase the growth coefficient may indicate that breeding work might have increased growth rates by about 15% in about ten years. However, it is possible that also other factors have contributed to the increased growth rate of salmon.

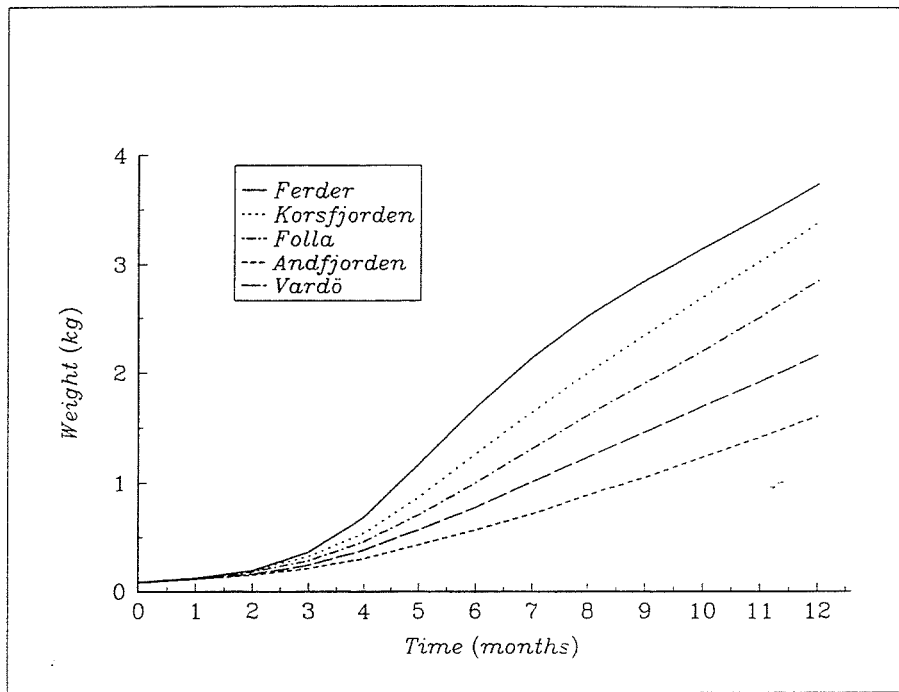


Fig. 3. The increase in weight of fish during one year of maximal growth at different locations along the Norwegian coast. The computations started in April with fishes of weight 80 g.

4.2. Fish appetite and retention of energy

The theoretical food conversion ratio FCR_t , which is the quotient between $App=Q_r/\delta$ and the growth rate dW/dt , is shown in Fig. 4 for different fish weight for three different types of fish food. It is quite evident that FCR_t decreases with increasing fat content of the food. Theoretically, FCR_t does not vary with temperature. The major use of FCR_t is for computations of the amount of surplus food (wasted food). This is computed as $FCR-FCR_t$, where FCR equals the amount of food given to the fish divided by the resulting increase in fish mass.

In Einem et al. (1995) it was assumed that the energy retention in the fish ($=Q_g/Q_r$) has a fix value. However from Eqs. (3) and (8) with $b=2/3$ and $\gamma=0.8$ it is obvious that energy retention decreases with increasing fish weight, see also Fig. 5. This figure also shows that energy retention varies with food composition with highest energy retention for low protein content (high protein retention, see Fig. 6) so only little protein is used for non-growth purposes.

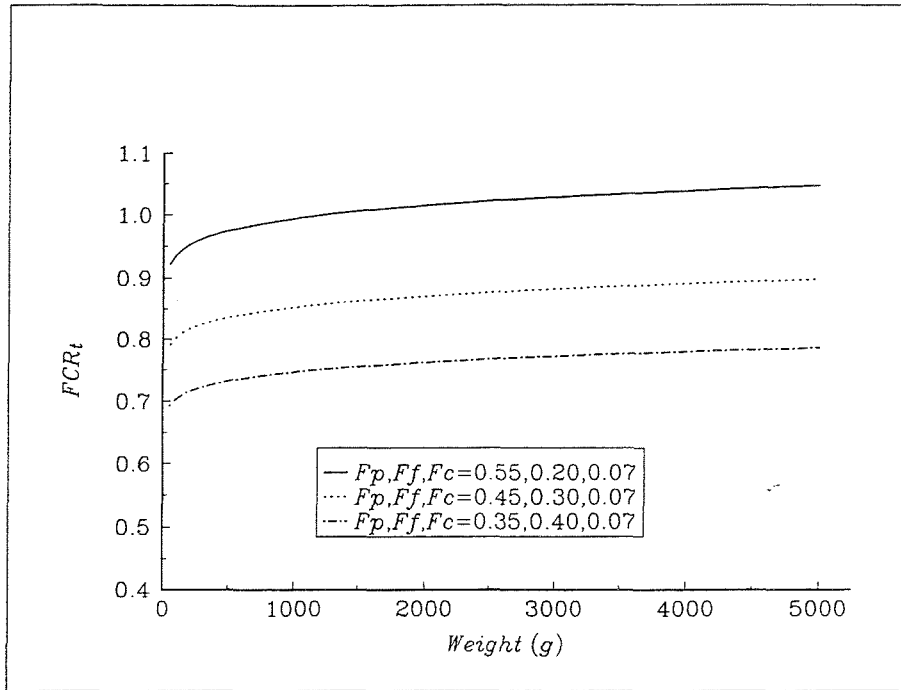


Fig. 4. The theoretical food conversion ratio FCR_t as a function of fish weight ($> 50g$) for three different types of fish food specified in the legend.

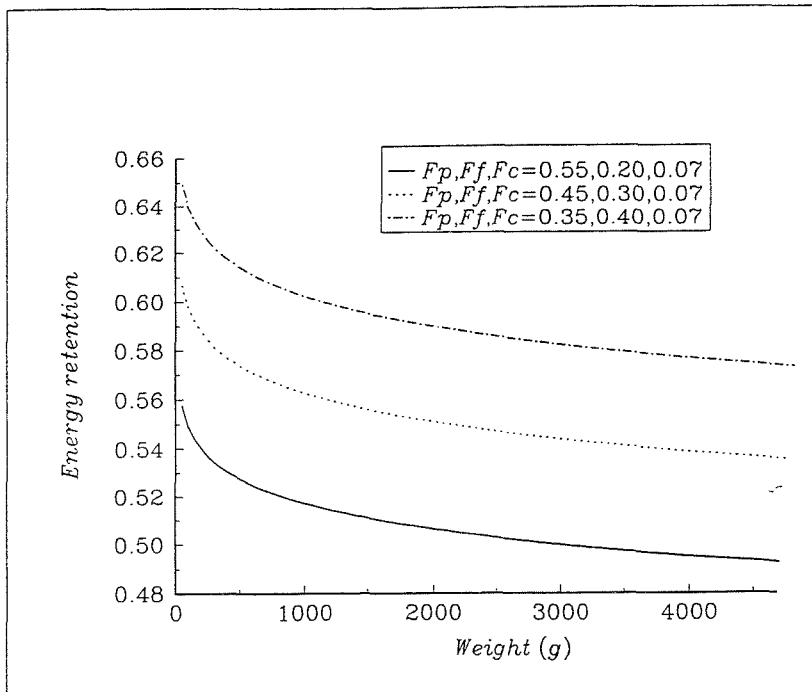


Fig. 5. The ratio between Q_e and Q_r (the energy retention) as a function of fish weight ($> 50 g$) for three different types of fish food specified in the legend.

4.3. Retention of protein by the fish

The fish needs proteins and fat for bodybuilding. However, the composition of proteins should be well balanced in relation to the needs of the fish and proteins and fat are of course not interchangeable in anabolic processes. This put constraints on the optimal food composition. The theoretical retention of protein in the fish, R ($0 \leq R < 1$), is defined as the ratio between the amount used for growth and the amount given with the food according to appetite, thus

$$R = \frac{P_p a W^b}{\frac{Q_r}{\delta} F_p} \quad (14)$$

It is obvious that retention of protein strongly depends on the protein content of food in relation to growth requirements. Maximum retention is obtained when all assimilated protein is used for growth, thus $R(\max) = A_p$ (≈ 0.89). Fig. 6 shows theoretical protein retention as a function of the protein content of the food for three different types of food under the assumption that the fish eats the maximal ration. It is obvious from the graph that giving the fish food of high protein content is a waste of economic resources. Food with high protein content also gives rise to large emissions of ammonium and phosphate because assimilated protein in excess of growth requirements is metabolised, see section 5.3 below.

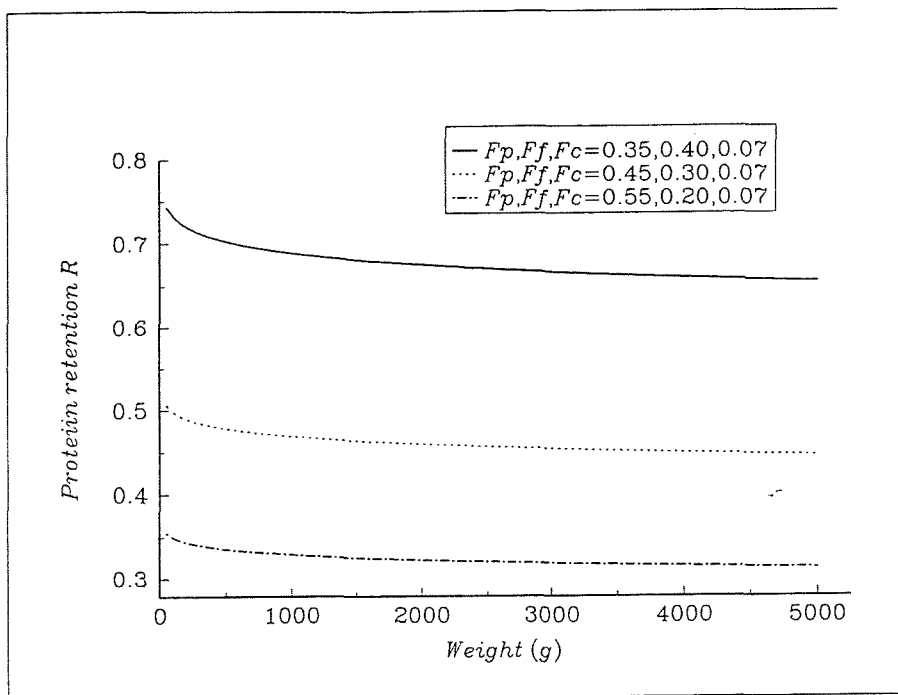


Fig. 6. Protein retention in fish as function of fish weight (> 50 g) for three different types of fish food specified in the legend (the composition of the fish is $P_p=0.18$, $P_f=0.18$).

4.4 Integrated demands of food to produce a fish of a certain weight

The total (integrated) amount of food needed to produce a fish, fed according to appetite, of a certain weight depends on the composition of food but is independent of temperature. The time it takes to produce the fish, however, depends on temperature as demonstrated in Fig. 2. The dependence of the integrated needs of food upon food composition is clearly demonstrated by a comparison of the results in Tables 1 and 2 which are for standard food and low protein food, respectively. It is again demonstrated that the fatter food with less protein (Table 2) has lower food conversion factor and a higher protein conversion factor than standard food (Table 1).

Table 1. The total demands of food to produce a fish of a certain weight, starting from fish weight 50 gram.

Also shown is the mass of protein stored in the fish and given by the food, respectively. The food is described by $F_p=0.45$, $F_f=0.30$, $F_c=0.07$.

Fish weight (kg)	1.000	2.000	3.000	4.000	5.000
Fish protein (kg)	0.180	0.360	0.540	0.720	0.900
Food (kg)	0.792	1.655	2.532	3.419	4.313
Food protein (kg)	0.356	0.744	1.139	1.539	1.940

Table 2. The total demands of food to produce a fish of a certain weight, starting from fish weight 50 gram.

Also shown is the mass of protein stored in the fish and given by the food, respectively. The food is described by $F_p=0.35$, $F_f=0.40$, $F_c=0.07$.

Fish weight (kg)	1.000	2.000	3.000	4.000	5.000
Fish protein (kg)	0.180	0.360	0.540	0.720	0.900
Food (kg)	0.693	1.449	2.217	2.993	3.775
Food protein (kg)	0.243	0.507	0.776	1.048	1.321

5. THE FISH FARM AS A SOURCE/SINK FOR THE ENVIRONMENT.

The energy model for fish developed in the previous section may seem to be exceedingly general and detailed since it, unlike other fish models, also resolves protein, fat and carbohydrates. However, to follow the flow of energy and matter in a fish farm it is necessary to use a model with this resolution. In this section, we will compute the dissolved and particulate emissions of organic matter and plant nutrients from a fish farm. In addition, the fish respiration and the potential consumption of oxygen to oxidise the emitter matter will be estimated.

5.1 Emission of ammonia and phosphate and oxygen consumption in the cages

The protein fraction (by weight) of the fish is P_p and the rate of protein storage in fish is $P_p dW/dt$. The rate of protein assimilation by the fish is $F_p A_p Q_r / \delta$ where Q_r is given by Eq. (9). Nitrogen constitutes the fraction N_p (about 1/6) of the protein and, as already mentioned in connection with Eq. (5) protein in excess of growth requirements, i.e. $F_p A_p Q_r / \delta - P_p dW/dt$, is metabolised. The nitrogen from the excess protein is excreted as ammonia (NH_3) and we can compute the ammonia excretion, EN (expressed by its content of N, thus $g\ N\ day^{-1}$), from fish using the following expression

$$EN = \left\{ \frac{F_p A_p Q_r}{\delta} - P_p \frac{dW}{dt} \right\} N_p \quad (15)$$

Results of the computations, with $P_p = 0.18$, are shown Fig. 7.

Since the nitrogen to phosphorus ratio (by weight) is about 6 in commonly used fish food (i.e. phosphorus P constitutes about $N_p/6$ of the weight of the protein), we can directly or use the following formula

$$EP = \left\{ \frac{F_p A_p Q_r}{\delta} - P_p \frac{dW}{dt} \right\} \frac{N_p}{6} \quad (16)$$

If the fat fraction (by weight) of fish is P_f the rate of fat storage in fish is $P_f dW/dt$. The rate of fat assimilation by the fish is $F_f A_f Q_r / \delta$. The amount of fat, used for non-growth metabolic processes, is $F_f A_f Q_r / \delta - P_f dW/dt$. All assimilated carbohydrate, i.e. $F_c A_c Q_r / \delta$, is used for non-growth metabolic processes.

The oxygen demands for the chemical breaking down of organic matter are 1.89 $g\ O_2/g$ protein, 2.91 $g\ O_2/g$ fat and 1.07 $g\ O_2/g$ carbohydrate, e.g. Karlgren (1981). We denote

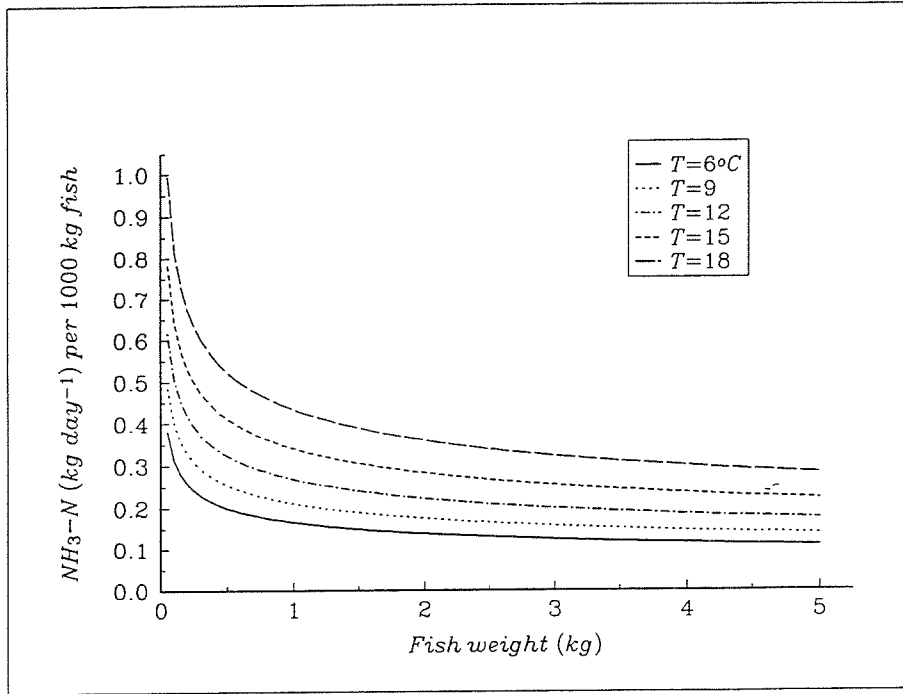


Fig. 7. Emission of $\text{NH}_3\text{-N}$ (kg day^{-1}) from 1000 kg of fish of different individual weight (>50 g) for some temperatures. The food is described by $F_p=0.45$, $F_f=0.30$, $F_c=0.07$.

these oxygen demands by O_p , O_f , O_c and O_a , respectively. Thus the respiratory oxygen demand of fish, DO_2 (gO_2/day), is

$$\text{DO}_2 = (F_p A_p Q_r / \delta - P_p \frac{dW}{dt}) O_p + (F_f A_f Q_r / \delta - P_f \frac{dW}{dt}) O_f + F_c A_c Q_r / \delta O_c \quad (17)$$

Oxygen consumption due to respiration, as computed from Eq. (17) with $P_p=P_f=0.18$, is given in Fig. 8. The oxygen for fish respiration is taken from the water in the cage. Equations (15) and (17) were tested in Molvær & Stigebrandt (1989). They used data obtained from a large fish farm located in a partly quite narrow strait between islands. The water exchange was controlled by pumping so the flushing of the farm was rather well known. Using budgets for oxygen, nitrogen and phosphorus, they found reasonable agreement between model predictions and field data.

In addition to the oxygen demand by the fish itself, there is also a demand of 0.47 ($\text{g O}_2/\text{g protein}$) to oxidise the excreted ammonia to nitrate. Oxygen is also needed to oxidise faeces and excess food deposited at the bottom sediment as further discussed in the following section. Connected to the oxygen consumption is production of carbon dioxide. An approximate estimate of the emission of carbon dioxide into the cages can be calculated from the oxygen consumption (respiration) by the fish.

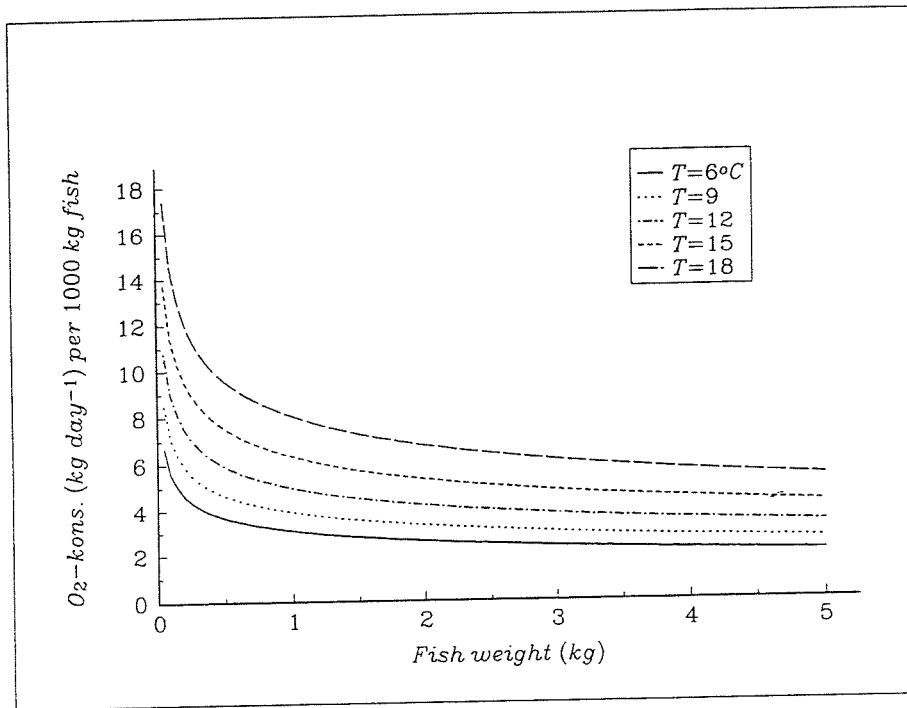


Fig. 8. Oxygen consumption at different temperatures ($\text{kg O}_2 \text{ day}^{-1}$) by 1000 kg of fish of different individual weight ($> 50 \text{ g}$) for some temperatures. The food is described by $F_p=0.45$, $F_f=0.30$, $F_c=0.07$.

The excreted ammonia is non-faecal and goes directly into the water in the cage. This is also believed to be the case for the fraction p_w (about 50%) of the accompanying releases of phosphate

5.2. The flow of matter to and from the bottom

Faeces and excess food added to the fish cages have negative buoyancy and will therefore sink through the water column and reach the bottom before being oxidised. In Stigebrandt and Aure (1995) we developed a benthic model computing the critical load of the bottom sediment with respect to viable benthic animals. Here we are interested in estimating the source of organic matter produced by the fish farm.

From each fish the faecal mass loss is

$$E_{fae} = FL \frac{Q_r}{\delta} \quad (18)$$

The excess food may be expressed by the food conversion ratio FCR_r . This is given by the difference between the amount of food supplied for production and the food really used by the fish. The latter may be estimated by the fish model as the theoretical food conversion ratio FCR_t . As demonstrated in this paper, estimates of $FCR - FCR_t$ depend on FCR_t which

varies with the food composition. The loss of food (the difference between the supplied food ration and the ingested food) is thus

$$E_{food} = \frac{Q_r}{\delta} (FCR - FCR_t) \quad (19)$$

This is information that will be used in the dispersion model (Stigebrandt, 1995) computing the organic load on the bottom sediment.

In earlier days, it was usual that faeces and excess food accumulated on the bottom beneath fish farms. The oxidation of some of the organic matter was thus postponed to future. If there is no accumulation of organic matter on the bottom the integrated oxygen demand to oxidise faeces and excess food can be estimated as in Eqs. (20) and (21) below. This oxygen consumption is of interest on a regional scale and is thus important input for the regional water quality model in the MOM model system.

The contribution to the total oxygen demand by faeces is

$$DO_2(fe) = \{F_p(1 - A_p)O_p + F_f(1 - A_f)O_f + F_c(1 - A_c)O_c\}Q_r/\delta \quad (20)$$

In addition comes the oxygen demand of the sedimenting food. If the actual food conversion ratio is FCR and the theoretical food conversion ratio is FCR_t, the oxygen demand to oxidise the excess food is

$$DO_2(fo) = (F_pO_p + F_fO_f + F_cO_c)(FCR - FCR_t)Q_r/\delta \quad (21)$$

5.3 Integrated oxygen demand and emissions of particulate and dissolved organic matter to produce a fish of a certain weight

The total emissions of faeces, ammonium and phosphorus to produce a fish of a certain weight, fed according to appetite, is independent of the temperature and by that the time taken to produce the fish. However, the total emissions depend on the composition of the food. This is evident from a comparison of Tables 3 and 4. The fatter food with less protein leads to less respiration and smaller emissions of plant nutrients in the cages (Table 4) than standard food (Table 3). Production of faeces is rather similar in the two cases. As already mentioned, the emission of ammonium can be minimised using the fish model in this paper to find a composition of food attaining this objective.

Table 3. The total demand of oxygen (row2) to produce a fish of a certain weight, starting from fish weight 50 gram. Also shown are the mass of excreted nitrogen (row3), phosphorus (row4), emitted mass of faeces (row5). The oxygen demand to oxidise faeces (row 6) and nitrogen (row7) and phosphorus (row8) in faeces. Oxygen demand to oxidise excess food, with $FCR-FCR_i=0.3$, (row 9) and its content of nitrogen (row10) and phosphorus (row11) are also shown. The food is described by $F_p=0.45$, $F_f=0.30$, $F_c=0.07$.

Fish weight (kg)	1.000	2.000	3.000	4.000	5.000
Oxygen resp. (kg)	0.445	0.956	1.496	2.049	2.614
NH ₃ -N (kg)	0.024	0.052	0.080	0.110	0.139
PO ₄ -P (kg)	0.004	0.009	0.013	0.018	0.023
Faeces (kg)	0.091	0.190	0.290	0.393	0.495
Oxygen:faeces (kg)	0.159	0.333	0.508	0.687	0.866
N in faeces (kg)	0.015	0.030	0.046	0.063	0.079
P in faeces (kg)	0.002	0.005	0.008	0.010	0.013
Oxy:ex.food (kg)	0.428	0.893	1.366	1.845	2.327
N in ex.food (kg)	0.018	0.037	0.057	0.077	0.097
P in ex.food (kg)	0.003	0.006	0.009	0.013	0.016

Table 4. The total demand of oxygen (row2) to produce a fish of a certain weight, starting from fish weight 50 gram. Also shown are the mass of excreted nitrogen (row3), phosphorus (row4), emitted mass of faeces (row5). The oxygen demand to oxidise faeces (row 6) and nitrogen (row7) and phosphorus (row8) in faeces. Oxygen demand to oxidise excess food, with $FCR-FCR_i=0.3$, (row 9) and its content of nitrogen (row10) and phosphorus (row11) are also shown. The food is described by $F_p=0.35$, $f=0.40$, $F_c=0.07$.

Fish weight (kg)	1.000	2.000	3.000	4.000	5.000
Oxygen resp. (kg)	0.356	0.774	1.212	1.666	2.130
NH ₃ -N (kg)	0.008	0.017	0.027	0.037	0.047
PO ₄ -P	0.001	0.003	0.004	0.006	0.008
Faeces (kg)	0.076	0.159	0.243	0.329	0.414
Oxygen:faeces (kg)	0.141	0.295	0.450	0.609	0.767
N in faeces (kg)	0.013	0.027	0.041	0.055	0.069
P in faeces (kg)	0.002	0.004	0.007	0.009	0.012
Oxy:ex.food (kg)	0.396	0.827	1.263	1.706	2.152
N in ex.food (kg)	0.012	0.025	0.039	0.053	0.066
P in ex.food (kg)	0.002	0.004	0.006	0.009	0.011

6. IMPLEMENTATION OF THE FISH MODEL IN THE MOM SYSTEM

For computations of water quality in a fish farm, it is necessary to know the physical configuration of the farm (number and size of cages and separation between cages). It is also necessary to know the current in the upper layers from measurements from which one may calculate the variance of the current. For the moment, it is not clear how to compute the critical current conditions from current measurements and the importance of horizontal dispersion processes for the flushing of a farm. Furthermore, one needs to know temperature and concentrations of ammonia and oxygen in the water flushing the farm.

Provided the numbers of fishes in different weight classes in the farm are known, Eqs. (15) and (17) may be used to compute the emission of ammonia and oxygen consumption by respiration, respectively, in the farm. For computations of water quality in the cages, the volume spanned by the farm and the critical (worst) current conditions must be known from measurements. The volume spanned by the farm may be increased by increasing the separation of cages and the flushing may be made more efficient by orienting the farm perpendicular to the main current direction. A water quality model for the cages, including details of the computations of maximum concentrations of ammonium and minimum concentrations of oxygen, will be described in a planned paper.

The total oxygen demand and the total emission of ammonium for a given fish production are given by Tables 3 and 4 for two different types of food. It can be seen that these vary quite a lot with the composition of food. This may be important in critical cases. There is a seasonal variation in emission rates and respiration due to variations in daily production, which in turn are due to variations in biomass and temperature. For computations of water quality in a farm, typical seasonal variations of the daily fish production have to be estimated. One may then assume that the maximum daily production is a certain factor greater than the mean daily production given by the annual production.

For given fish production the MOM model computes the loading of the bottom with faeces and excess food. The production of faeces is given by Eq. (18). It is about 0.1 times the fish production and varies relatively little with food composition, cf. Tables 1 to 4. The "production" of excess food is given by Eq. (19), which requires that the actual FCR be known. The loading of the bottom with faeces and excess food may be computed by the dispersion model (Stigebrandt, 1995). That model requires that the current have been measured for a sufficiently long period so the variance of the current in two perpendicular directions can be calculated. The dispersion computations also require that the sinking speeds of food and faeces be known. In the dispersion model, the size of the cages and the

distance between cages is important for the pattern of sedimentation of faeces and excess food on the bottom.

For the coupled regional model (Fig. 1) it is important at which depths plant nutrients are introduced. According to Kremer and Nixon (1978) also the phosphorus mineralised by metabolic processes in zooplankton is excreted (as phosphate). If ammonium and phosphorus are excreted simultaneously, this will secure that the nutrients may be fully used for further production of plant plankton. However, Persson (1987) found from experiments that about 50% of the phosphorus mineralised by metabolic processes are excreted and the rest is exported by faeces, thus indicating that nitrogen and phosphorus are partly separated by the fish. In the present fish model we assume that the fraction p_w of phosphorus is excreted in dissolved form together with the ammonium-nitrogen and the rest, $1-p_w$, is exported by faeces. At present we thus put $p_w=0.5$ for model computations.

7. DISCUSSION.

The fish model presented in this paper is put together in a logical way and deals simultaneously with all fundamental aspects of fish metabolism and growth. To do this, the model has to handle the energetics of fish as well as to perform a detailed accounting of protein, fat, carbohydrates, nitrogen and phosphorus. The model may therefore be used for many purposes and may be adapted to other fish species using appropriate values of the model parameters. It is believed that one area of application would be in models of natural multi-species populations of fish interacting with each other. However, the application in the present paper focuses on salmon in fish farms.

When fish is fed according to appetite, maximal growth rate is obtained provided there are no adverse environmental conditions. The growth decreases with reduced feed and when the ration corresponds to the energy needed for maintenance the growth is zero. For still lower rations the fish starves and loses weight. This will of course have tremendous consequences for the protein retention that in the latter case is negative. For feeding at maintenance level or less, all proteins supplied by the food are wasted. Thus, from this point of view it should be advantageous to use cheap food with quite low protein content for maintenance feeding. This should also reduce the emissions of nitrogen and phosphorus to the surrounding environment.

To compute the interaction between a fish farm and the surrounding environment the fish farm model has to be coupled to a hydrodynamic - biochemical model for the surrounding water system. Such a coupled model computes both the impact of the fish farm upon the

state of the environment and the impact of the state of the environment (possibly influenced by the farming) upon water quality in the farm (feedback). It should be of great value for the management of a farm to do such computations, showing possible adverse environmental effects on the fish in a farm. In the model of the MOM system, it will be possible to perform this kind of computations after having merged the local MOM model and a model for the regional environment. We will use a regional environment model called Fjordmiljø. This is widely used in Norway and fully described in Stigebrandt (1992). A crucial part of Fjordmiljø is based on results presented in Aure and Stigebrandt (1990).

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