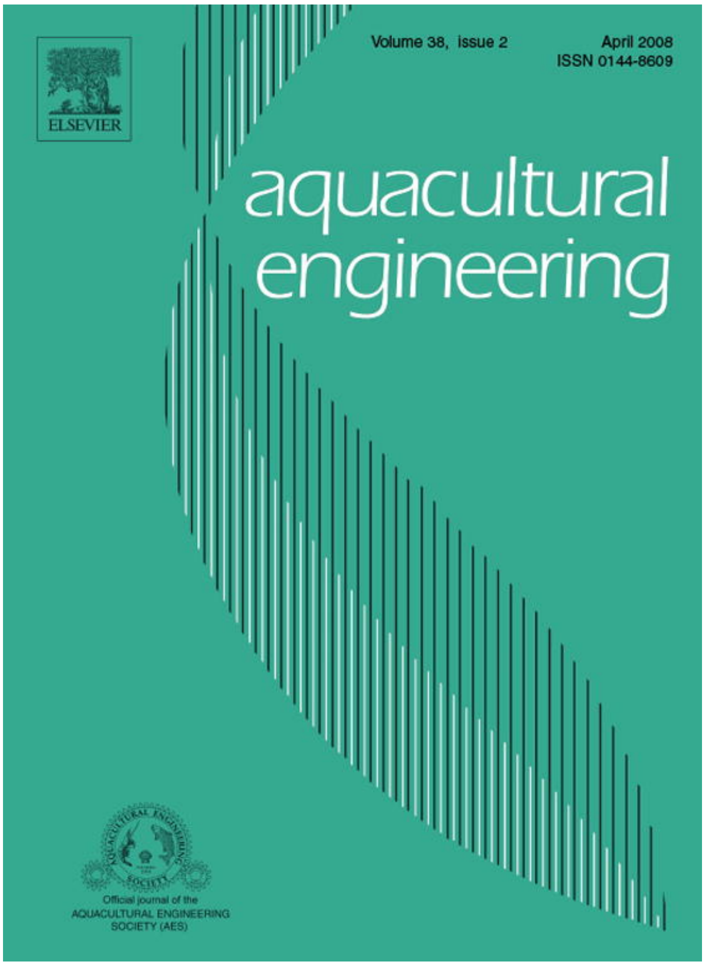
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A mesocosm fish farming experiment and its implications for reducing nutrient load on a regional scale

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Abstract

This work presents results from a mesocosm fish farming experiment. The main aim of the work was to put the results from the experiment into a wider context dealing with an approach to get zero – or even – negative nutrient fluxes from fish cage farms on a regional scale. To quantify the nutrient loading of phosphorus and nitrogen from net cage aquaculture, a standard dynamic mass-balance model approach was used. A comparison was made between responses from two feeding scenarios with rainbow trout (*Oncorhynchus mykiss*). One set was given a commercial pelleted fish food the other food with fresh herring inclusion. We have shown that on a regional scale, a zero nutrient load situation may be achievable if the wild fish from the given region account for about 11% of the fish food. In the mesocosm experiment, we also tested different approaches to calculate the growth of the cultivated fish and one can conclude that there are no major differences in using the different sub-models for the interpretations to get zero emissions but different growth functions do give different dynamic responses for the fish growth. We have also tested if it is important to account for denitrification. Under the given conditions this is not the case. Critical testing of the modelling has been performed with uncertainty and sensitivity analyses and the major uncertainties were identified in the growth pattern of the fish and the mesocosm biomass nutrient uptake rate. We argue that these results imply that, from an eutrophication point of view, fish farming in open net cages can be viewed as an environmental sustainable industry, if the fish feed includes nutrients that originate from the surrounding waters.

Keywords: Fish farming; Rainbow trout; Fish growth; Herring; Nutrient load; Phosphorus; Nitrogen; Mesocosm; Dynamic modelling; Baltic Sea

1. Introduction and aim

The cultivation of fish in net cages in open water has environmental effects related to overuse of antibiotics, escaping fish, spreading diseases to and causing genetic drift on natural fish populations (Dar, 1999; FAO, 2001). Open net farming is also a contributor of nutrients to its surroundings (Read and Fernandez, 2003, and references herein). The ecological effects of such emissions depend on the location of the farm (Nordvarg, 2001; Johansson, 2001). However, in many coastal areas, total nutrient load calculations show that fish farm emissions often are of minor magnitude compared to other nutrient fluxes (Enell, 1995; Helminen et al., 1998; FEI, 2002). The Rio declaration (Anon., 1993), following the United Nations conference on environment and development, states that unsustainable patterns of production should be reduced and eliminated. Hence, there is a

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great symbolic value if the fish farm could become more ''environmentally sustainable''.

The amount of nutrients released to the aquatic environment depends on the cultivation technique, feed composition and local environmental factors (Stigebrandt et al., 2004). One way to reduce the nutrient loading to a given coastal region with fish farms is to include wild fish produced in this region. This has been subject to studies by Ruohonen (1994) and Ruohonen et al. (1998), who examined the physiological effects of inclusion of fresh herring in rainbow fish feed. At present, the fishmeal, which constitutes the major nutrient supply in the commercial feed used in fish farming in the Baltic region, originates mainly from Atlantic Ocean and North Sea catches (Vihervuori, A., personal communication by email. 16 January 2004). By replacing some of that fishmeal with wild fish, e.g., Baltic herring or sprat, one could theoretically achieve a zero, or even negative net nutrient load from fish farming. The idea is to view the system in a larger perspective, not limited to the fish farm (the local scale), but also incorporate the surrounding area from where the fish that is used for fish meal is caught. This is how we define regional scale in this study.

This is not a new strategy (Mäkinen, 1991) but dynamic modelling has not before been used to study such effects. This type of modelling gives the possibilities to account for seasonal variations and thereby predict the environmental impacts more realistically.

To test how different feeding scenarios could affect the nutrient loading from fish farms, we will use a standard dynamic mass-balance model (see Håkanson and Peters, 1995) which will be briefly explained and critically tested. The model is run with data from a mesocosm experiment, where rainbow trout (*Oncorhynchus mykiss*) was reared under conditions comparable to those of a coastal fish farm. Since both phosphorus and nitrogen can be limiting for primary production in coastal areas (e.g., Kirkkala et al., 1998), the model will be used for simulations using both nutrients. After critical testing, the idea is to study different inclusion levels of locally fished herring and simulate the nutrient flows.

In short, the aim of this work is to:

- Use a dynamic mass-balance model to simulate phosphorus and nitrogen flows in a fish farming mesocosm.
- Quantify and rank how different variables influence uncertainties in model predictions.
- Test different sub-models for rainbow growth and their effects on the simulation results.
- Seek the threshold value when the wild fish inclusion in fish feed creates a zero nutrient load from a fish farm at a regional scale.

2. Materials and methods

The nutrient flows to, within and from the mesocosm were quantified by different sub-models (Fig. 1). The overall dynamic model has been calibrated with data from the mesocosm experiment. The experiment was performed by the Finnish Environmental Research Group, MFG, at their Baltic Sea Laboratory at Lillandet (60°13′N, 22°5′E), Finland in 1994 (Lehtinen et al., 1998). A presentation of the mesocosm setup has been published by Tana et al. (1994). The cultivation time was 3 months and two sets of 15 rainbow trout were reared. For model variables, see Appendix B. In the experiment, three feeding scenarios were tested and the effects on the system studied.

- COM: A feeding scenario where a *com*mercial fish feed was used.

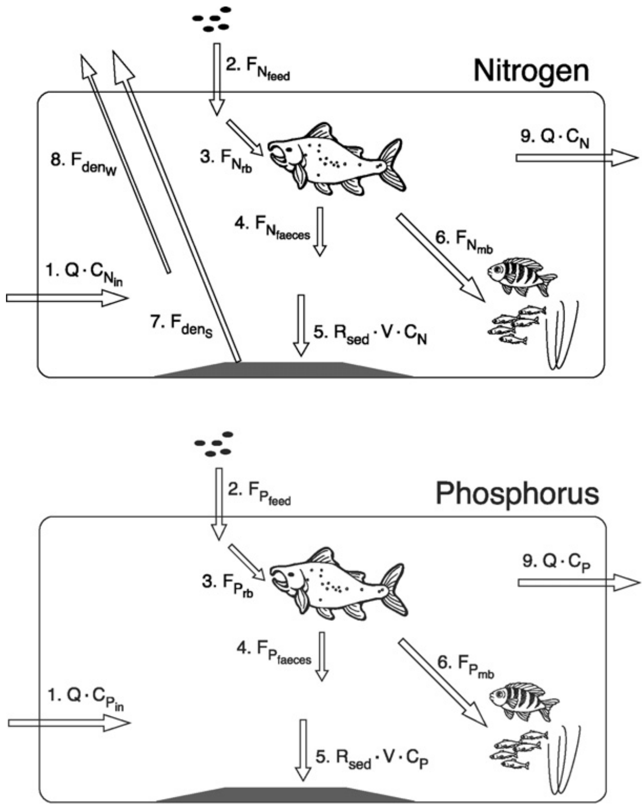

Fig. 1. A schematic illustration of the mesocosm and the modelled processes. (a) Nitrogen and (b) phosphorus. 1, inflow; 2, added feed; 3, uptake in cultivated fish; 4, faeces from cultivated fish; 5, net sedimentation; 6, uptake in biota in mesocosm; 7, denitrification from sediments (evidently only from N); 8, denitrification from water; 9, outflow.

- HER: A feed containing 30% inclusion of Baltic *her*ring.
- CON: A *con*trol mesocosm with no fish farming.

The COM and HER feed had comparable levels of lipids, proteins and dry matter. Initial and final measurements were made on fish size and abundance of other introduced species, e.g., sticklebacks (*Gasterosteidae*), blue mussels and algae. Daily measurements of water temperature and nutrient concentrations in inflowing water were made. In the following section, we will present (i) basic nutrient flow equations, (ii) five different approaches to quantify rainbow growth and (iii) sub-models for nutrient flows related to feeding, biota and denitrification.

2.1. Basic nutrient flow equations

The amount of nutrient X in water (M_X; where X = g nitrogen or phosphorus) has been calculated from the basic mass-balance model for a defined water body (Håkanson and Peters, 1995). $C_{x\text{in}}$ is the concentration of the nutrient in the inflow (μg/l) and C_X the concentration in the mesocosm water and the outflow. To account for fish farming, the nutrient fluxes related to feeding and uptake in different biota in the mesocosm were also calculated. Furthermore, to test the relative importance of denitrification, a sub-model for that process was added. This gives

$$V\frac{\partial C_X}{\partial t} = \underset{\text{in}}{QC_{X\text{in}}} - \underset{\text{out}}{QC_X} + \underset{\text{added}}{F_{X_{\text{feed}}}} - \underset{\text{fish}}{F_{X_{\text{rb}}}} - \underset{\text{biota}}{F_{X_{\text{mb}}}} - \underset{\text{sedimentation}}{R_{\text{sed}}VC_X} - \underset{\text{denitrification}}{F_{\text{den}}} \quad (1)$$

F is the flow (mass/time), C the concentration (mass/volume), Q the water flow (volume/time), R the rate (1/time) and V is the volume. Other processes than those given by Eq. (1) are considered to be of minor importance in this context, e.g., the atmospheric deposition constituted only about 0.25% of the total phosphorus load and about 0.37% of the total nitrogen load on the mesocosm system (Lehtinen et al., 1998). For simplicity, the resuspension from sediments in the mesocosm is not included as a separate flow and therefore the model gives the net sedimentation (R_{sed} is the net sedimentation rate).

2.2. Sub-models

2.2.1. Growth sub-model

Five different approaches to model rainbow growth were tested. The sub-models were calibrated with initial and final fish weights. The rainbow growth model was, in turn, used to estimate the mesocosm biomass growth calculation by means of a simple calculation constant (K_{MBNU}). Two growth models were developed by us for this study and compared to other fish growth models published in the scientific literature. All growth models are compiled in Appendix A.

2.2.2. The biomass sub-model

The calculations concerning fish and feed nutrient conversions and feed composition are collected in this sub-model together with the algorithm for the theoretical removal of nutrients due to the fishing of herring. The central nutrient pool is M_{exch}. This mathematical construction of a fish stomach is an intermediate nutrient exchange pool between the feed nutrient supply (F_{feed}) and the rainbow biomass (M_{rb}). With this solution, one can achieve a buffer time between feeding and fish growth and also catch the effects of increased nutrient releases following a feeding event. From this pool, nutrients are transferred to the fish and mesocosm biomass pool according to (F for flow):

$$\frac{\partial M_{\text{exch}}}{\partial t} = F_{\text{feed}} - F_{\text{rb}} - F_{\text{mb}} - F_{\text{faeces}} \quad (2)$$

The rainbow trout nutrient excretion is calculated as

$$F_{\text{faeces}} = M_{\text{exch}}R_{\text{excr}} \quad (3)$$

where R_{excr} is the nutrient excretion rate (1/time). F_{feed} is either given empirically or calculated from the feed conversion ratio (FCR):

$$\text{FCR} = \frac{\text{amount of feed utilised (kg ww)}}{\text{weight of produced fish (kg ww)}} \quad (4)$$

The amount of herring used to produce 1 g of feed (DC_{her}) is a key factor. For practical feed production reasons, this value should vary from 0 to about 6 g ww per g dw. If the value is 6 g ww, the herring constitutes about 60% of the feed. With this factor, and the knowledge of the feed supply to the farm (F_{feed}), the amount of herring that needs to be fished (F_{herfish}) can be calculated as

$$F_{\text{herfish}} = \text{DC}_{\text{her}}F_{\text{feed}} \quad (5)$$

2.2.3. Denitrification sub-model

According to Larsson et al. (1985), denitrification accounts for about 70% of the total nitrogen removal in the Baltic Sea. Note that this value is very uncertain. To see if denitrification could be of importance in the mesocosm setup, a method for calculating denitrification was implemented. The method was originally developed in a mesocosm study by Seitzinger and Nixon (1985). They showed a strong logical relationship between the mass of dissolved inorganic nitrogen (M_{IN}) and the N_2-flux from the sediments. The flux is calculated as

$$F_{\mathrm{dens}} = N_2\mathrm{flux} = R_{\mathrm{den}} M_{\mathrm{IN}} \quad (6)$$

where the denitrification rate (R_{den}) is 0.16, which means that 16% of the inorganic nitrogen (M_{IN}) is removed per time unit by denitrification. However, the data set used to derive this relationship was small ($n = 4$) and therefore the results should be interpreted with caution. In this model, that is done by assigning the variable a large uncertainty in the sensitivity and uncertainty analyses. M_{IN} was calculated from total nitrogen in the mesocosm water and DC_N, a distribution coefficient that regulates how much of the nitrogen (M_N) that is in dissolved inorganic form.

$$M_{\mathrm{IN}} = \mathrm{DC_N} M_{\mathrm{N}} \quad (7)$$

Since no measurements on nitrogen fractionation were made in the mesocosm experiment, the values were taken from Foy and Rosell (1991), who made such measurements in a Northern Ireland fish farm over a 1-year period. DC_N can then be calculated as

$$\mathrm{DC_N} = \frac{\mathrm{NH_4 + NO_2 + NO_3}}{N_{\mathrm{TOT}}} \quad (8)$$

These results should be comparable to the conditions in the mesocosm setup where ammonium excretion constituted about 70% of the total fish nitrogen excretion (Lehtinen et al., 1998). For simplicity, the same equations (Eqs. (6)–(8)) were used to calculate denitrification from the water body (F_{denW}).

3. Results

To rank the influences of the variable uncertainties in predicting a target variable, a sensitivity analysis was performed according to procedures discussed by Håkanson and Peters (1995). The nitrogen removal in the mesocosm at day 100 was chosen as the target y-variable. All x-variables were assigned realistic coefficients of variation (CV, see Fig. 2) and normal distributions were assumed for all tested x-variables. The x-variables that contributed most to total model uncertainty (see Fig. 2) were the nutrient uptake rate to the mesocosm biomass, the nutrient concentration in the food and the feed conversion ratio.

The rainbow trout growth, as calculated with the different approaches, is shown in Fig. 3. Although these approaches give different results (Fig. 4) no sub-model can easily be rejected. However, the METAMOD approach performed very well when feeding data was provided (Fig. 5). Therefore, in this study the METAMOD sub-model is used in the following simulations. Sub-models TGC, METABOLIC, METAMOD and TEMPMOD depend on mesocosm temperature and/or feeding rate (Fig. 5).

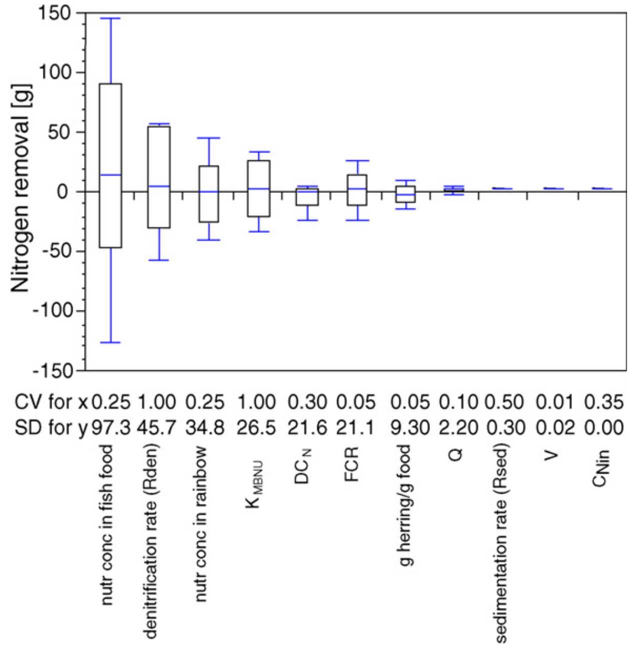

Fig. 2. Box plot of model sensitivity for parameter variations. The target y-variable is the nitrogen removal (g) from the system at simulation day 100. Standard deviation, S.D., in percent of the mean, CV is the coefficient of variation (CV = S.D./MV; MV, the mean value). The CV-values are our best estimates of the inherent uncertainties associated with the given x-variables.

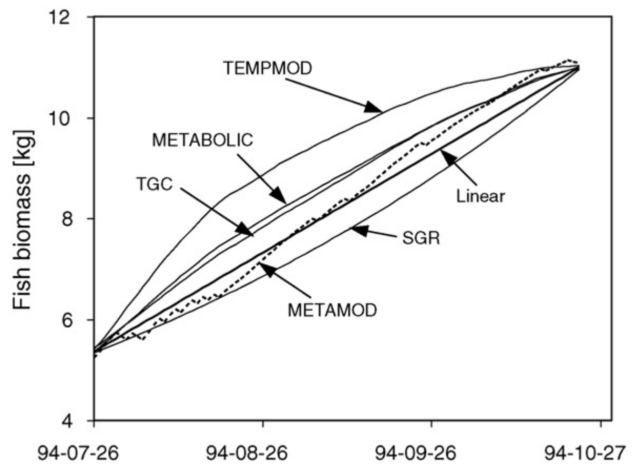

Fig. 3. Rainbow trout growth patterns as calculated using different sub-models.

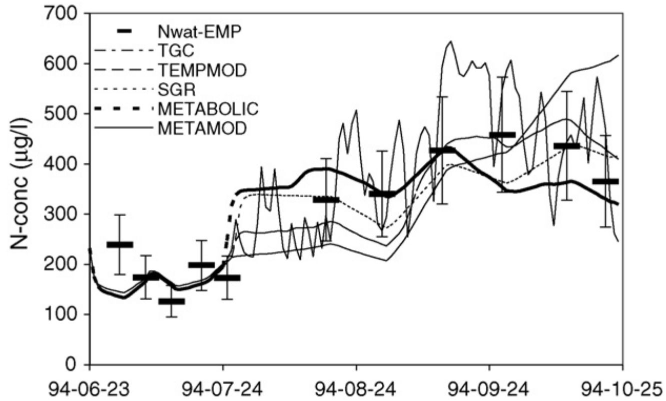

Fig. 4. Simulation results show nitrogen concentrations in mesocosm water for different rainbow trout growth sub-models.

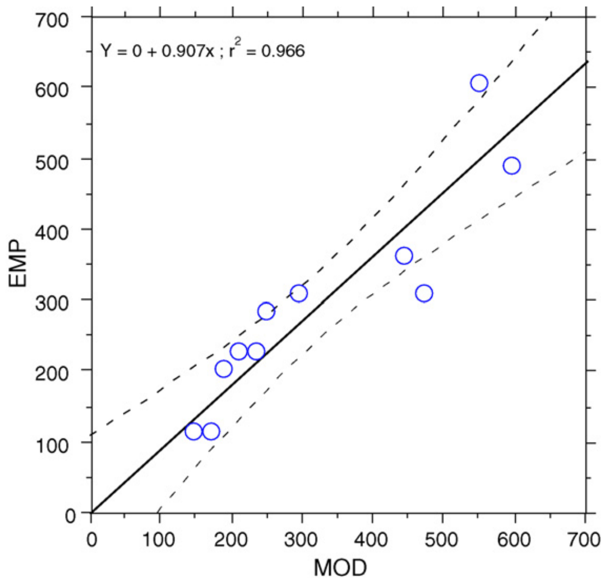

Fig. 5. Modelled values vs. empirical data. 95% confidence bands are shown as dotted lines. (Setup: phosphorus modelling, feeding data provided, METAMOD rainbow growth sub-model.)

The temperature decreased steadily during the experiment (Fig. 6). Note that all growth sub-models are included in the overall mesocosm model and one can easily switch between them. The results of the calibrated model can be seen in Fig. 7.

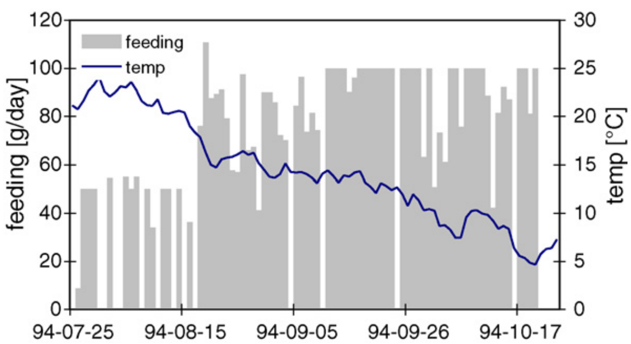

Fig. 6. Rainbow trout feeding and mesocosm temperature.

One of the main goals of this study was to find the zero load threshold value for the fish farm (Fig. 8). The breaking point is reached when 10.6% herring is included in the fish feed. At that point there is no net phosphorus load from the fish farm and a balance of the phosphorus fluxes to and from the fish farm. The corresponding threshold value for nitrogen is 11.0%. The HER feed scenario results in a removal of both nitrogen and phosphorus from the system.

4. Discussion and conclusions

The sensitivity analyses ranked the importance of the various model variables in the model. The flow to the cultivated fish accounts for 1/3 of the total phosphorus output (Table 1). This means that the model is sensitive to the rainbow growth process. From these simulations (Fig. 4), it is not, however, a simple task to identify the best sub-model setup. Partly, this is due to lack of data for model calibrations. Since rainbow growth is a metabolic process (Fig. 3), it is likely that the inclusion of feed data and temperature would give a more realistic estimation of the real growth pattern. The METAMOD model seems to be preferable to the METABOLIC model since the feeding rate varies with time (in accordance with the mesocosm experiment).

The nutrient uptake rate by the mesocosm biota (except rainbow trout) is of great importance for two reasons. Firstly, it directly influences the nutrient concentration in water. Secondly, it is the single most contributing factor to total model uncertainty. In this study, this flow was estimated via a constant related to the rainbow growth. This is evidently a simplification, since different aquatic organisms in the mesocosm (e.g., plankton, periphyton, mussels and sticklebacks) have different growth patterns. Furthermore, while the fish nutrient uptake probably is more or less instantaneous, the nutrient uptake by other mesocosm biota may have

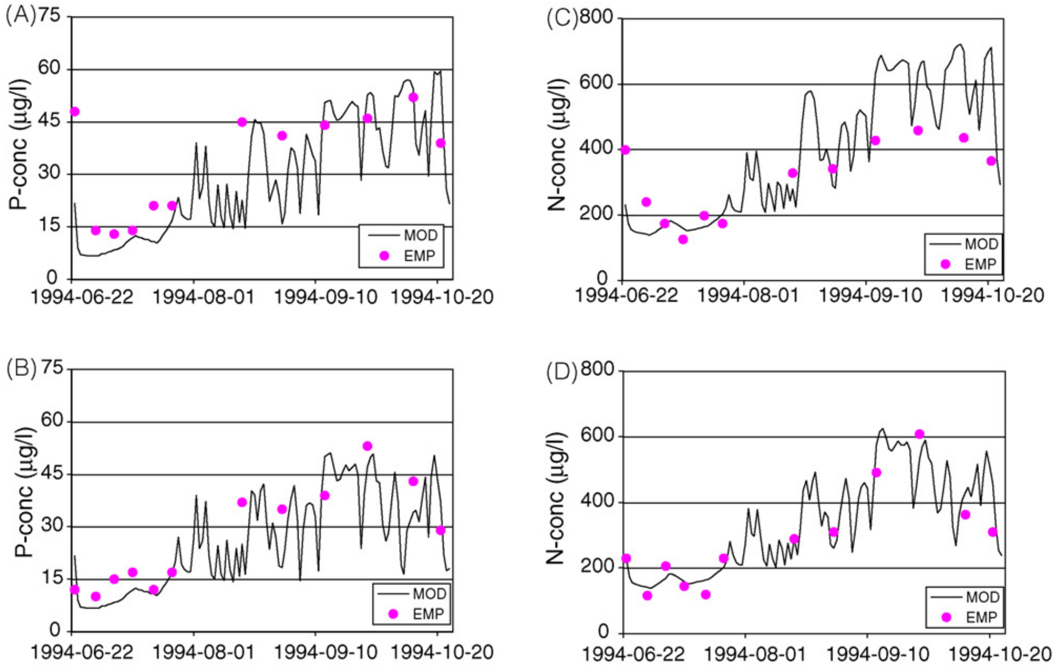

Fig. 7. Model results after calibrations of the model. (A) Phosphorus concentration, HER feed scenario; (B) phosphorus concentration, COM feed scenario; (C) nitrogen concentration, HER feed scenario; (D) nitrogen concentration, COM feed scenario.

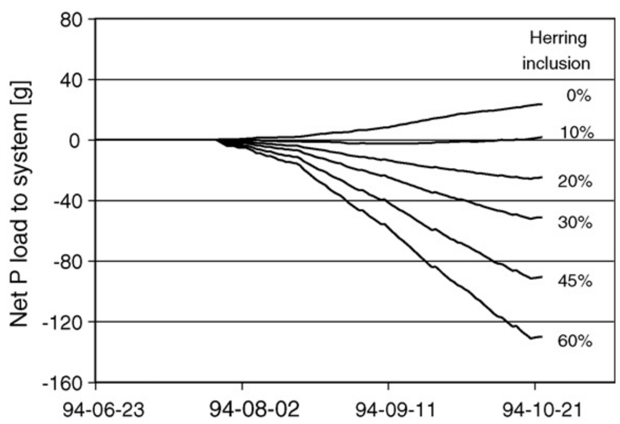

Fig. 8. Simulations using different herring inclusions in fish feed.

different uptake patterns. Due to lack of more detailed information from the experiment, these modelling processes could not, as we understand, be further improved.

Denitrification is probably of more importance in real aquatic systems than in the mesocosm. In the mesocosms with a high water circulation and high concentrations of dissolved oxygen, denitrification will be low. Rönner (1985) estimated that denitrification in the Baltic Sea accounted for up to 55% of the total nitrogen input.

In order to estimate the implications for the Archipelago Sea fish farming industry, the following simple calculation could serve as a rough example: The fish farming industry in the Archipelago Sea produced ≈4000 tonnes of rainbow trout in 2001 (HELCOM, 2002). To estimate the amount of fish food needed for this production, a FCR of 1 can be used. The inclusion of 11% locally fished herring or sprat in the fish food would then require a catch of 4000*1*0.11 = 440 tonnes of locally fished herring or sprat. The landings for 2001 of sprat in ICES subdivision 29, which includes the Archipelago Sea and can be considered as its closest fishing grounds, was 38,700 tonnes (ICES, 2006). Hence, it would

Table 1
Simulated mesocosm nutrient flows (total flow, HER feed scenario)

No. (in Fig. 1)	Nutrient flows	Phosphorus		Nitrogen	
		(g)	% of total	(g)	% of total
Input					
1	Incoming water	17.4	22.9	197.4	30.7
2	Farm → water	58.5	77.1	444.6	69.3
	Total	75.9	100	642	100
Output					
9	Water outflow	25.7	33.9	345.3	54.3
3	Water → fish	24.6	32.5	151.4	23.8
5	Water → sediment	19.6	25.9	45.8	7.2
7	Sediment → atmosphere	0	0	41.7	6.6
8	Water → atmosphere	0	0	13.0	2.0
6	Water → biomass	5.9	7.8	39.1	6.1
	Total	75.8	100	636.3	100

theoretically only require about 1% of the total sprat catch for the closest fishing grounds in order to fill the need for locally included fish in the fish feed. The present phosphorus load from fish farming activities in the Archipelago Sea was estimated to 55 tonnes (Gyllenhammar and Håkanson, 2005). Following the theory outlined in this paper, this would equal the phosphorus load reduction for the ICES subdivision 29. However, since fish farming activities only accounts for 7% of the anthropogenic load of phosphorus to the Archipelago Sea (Gyllenhammar and Håkanson, 2005) the corresponding reductions would be correspondingly small.

The main results from this study are:

- With this dynamic mass-balance model, it is possible to follow the nutrient dynamics of a fish farming mesocosm.
- The fish food nutrient concentration is the single most important source of the model uncertainty.
- The rainbow growth pattern is important for the nutrient concentration in the water.
- More than 11% inclusion of locally fished herring in rainbow food creates a zero nutrient load scenario.
- If the model is to be used in a real fish farming scenario, the process of denitrification needs to be studied further since the mesocosm environment probably underestimates the nitrogen removal compared to a real net cage fish farm.

Appendix A. Growth models from the literature (SGR, TGC and METABOLIC) or developed in this study (TEMPMOD and METAMOD)

(Since the fish growth equations are valid for both nitrogen and phosphorus, the subscript X is omitted for clarity in this section.)

A.1. The SGR approach

SGR (specific growth rate) is a standard method used in fish weight calculations (e.g., Parker and Larkin, 1959; Nortvedt et al., 1992). The growth rate is then defined as the absolute rate divided by the current size of the fish:

$$\mathrm{SGR} = \frac{(\partial W/\partial t)}{W}$$

where W is the fish weight and t is the time. The mean specific growth rate over the time interval t_1–t_2 is, after integration, given by

$$R_{\mathrm{rb,SGR}} = \mathrm{e}^{(\ln W_2 - \ln W_1)/(t_2 - t_1)} - 1.$$

A.2. The TGC approach

The TGC (thermal-unit growth coefficient) method of calculating fish growth was developed by Cho (see Cowey, 1992) to predict growth in nutritional experiments. The TGC is first calculated from growth data according to

$$\mathrm{TGC} = \frac{(W_2^{1/3} - W_1^{1/3})}{\sum \mathrm{temp} \cdot \mathrm{days}}$$

where the influences from the accumulated temperature is accounted for. The expected weight increase in living fish may then be obtained from

$$W_2 = \left(W_1^{1/3} + \sum (\mathrm{TGC} \cdot \mathrm{temp} \cdot \mathrm{days})\right)^3$$

and the rainbow growth calculated as

$$R_{\mathrm{rb,TGC}} = \frac{W_2 - W_1}{t_2 - t_1}.$$

A.3. The TEMPMOD approach

In our approach (called TEMPMOD), the mesocosm water temperature was used to moderate the fish growth. The initial and final fish weights were used as boundary values and the square of the temperature chosen to influence the pattern. This moderator operates on the linear growth factor and the rainbow growth (g/day) is calculated as

$$R_{\mathrm{rb,TEMPMOD}} = \left(\frac{W_2 - W_1}{t}\right)\left(\frac{T}{\overline{T} + K_1}\right)^2$$

where K_1 is the calibration constant, T the mesocosm water temperature (°C), $\overline{T}$ the mean mesocosm water temperature (°C), t the cultivation time (days) and W_2 and W_1 are the final and initial fish weights (g), respectively.

A.4. The METABOLIC approach

Extensive work by From and Rasmussen (1984) and Rasmussen and From (1991) has resulted in an empirical growth model for salmonids, where the basic equation is

$$R_{\mathrm{rb,METABOLIC}} = \frac{\partial W}{\partial t} = H\left(\frac{\partial R_{\mathrm{feed}}}{\partial t}\right) - K\left(W_t, \left(\frac{\partial R_{\mathrm{feed}}}{\partial t}\right)\right)$$

where $\partial W/\partial t$ is the weight change (g/day), W_t the weight of fish at time t (g), $\partial R_{\mathrm{feed}}/\partial t$ the weight of food consumed per unit time (feeding rate) (g/day), $H(\partial R_{\text{feed}}/\partial t)$ the an anabolic term (what is accumulated in fish biomass) and $K(w_t, H(\partial R_{\text{feed}}/\partial t))$ is a catabolic term (sum of ‘‘break down’’).

Every term is then divided into its physiological process and the resulting equation, with calibrated constants, for Danish conditions, is given by

$$\frac{\partial W}{\partial t} = f0.0822\,e^{0.0762T}W^{0.6738} - 0.00969\,f^{1.3783}\,e^{0.0522T}W^{0.7426} - (0.0132\,e^{1.2228\cdot f} - 1)\,e^{0.0799T}W^{0.4850} - 7.4295 \times 10^{-3}(e^{1.0208f} - 1)\,e^{0.0659T}W^{0.7010} - 1.7611 \times 10^{-4}(e^{2.3690f} - 1)\,e^{0.1025T}W^{0.7066} - 0.00607\,e^{0.0888T}W^{0.8260}$$

where f is the feeding rate (between 0 and 1). In the mesocosm model, the factor f is used to calibrate the growth to achieve the measured final weights.

A.5. METAMOD approach

The most complex rainbow growth rate simulation method tested in this study is the METAMOD approach ($R_{\text{rb,METAMOD}}$). It is constructed by combining the METABOLIC approach and the use of the existing feeding data to calibrate the feeding rate. The fish at each feeding occasion were given a full meal (feeding rate = 1). For the days without feeding, the feeding rate was calibrated to give the measured final weights. Note that with the METAMOD approach, it is possible to achieve ‘‘negative growth’’ during periods of low or zero feeding.

Appendix B. Mesocosm model parameters and constants

	Value	Remark
Dates		
Simulation start date, 01 June 1994		
Fish farming start date, 25 July 1994		
Simulation stop date, 24 October 1994		
Physical constants		
Water volume (V)	7600 l	
Water flow (Q)	5 l/min	
Initial nutrient values		
Sediment nutrient content	0 g	
Mesocosm water phosphorus content	0.166 g	Calculated from the mean phosphorus concentration of the incoming water
Mesocosm water nitrogen content	1.76 g	Calculated from the mean phosphorus concentration of the incoming water
Nutrient constants		
Kd for phosphorus	0.875	Calibrated value
Kd for nitrogen	0.1	Calibrated value
DC_N	0.8	From Foy and Rosell (1991)
Initial fish weights		
Weight of fish given commercial food (COM)	350 g	Mean weight of all 15 fishes in the pool
Weight of fish given herring enriched food (HER)	353 g	Mean weight of all 15 fishes in the pool
Final fish weights		
Weight of fish given COM food	737 g	Mean weight of all 15 fishes in the pool
Weight of fish given herring enriched food	737 g	Mean weight of all 15 fishes in the pool
Fish nutrient constants		
Phosphorus content in rainbow	0.45%	From Håkanson and Wallin (1991)
Nitrogen content in rainbow	3%	From Håkanson and Wallin (1991)
Phosphorus content in herring	0.45%	Rainbow data was used since no measurements were available
Nitrogen content in herring	3%	Rainbow data was used since no measurements were available
Feed parameters		
Phosphorus content in COM	1%	

Appendix B. (*Continued*)

Phosphorus content in HER	1%	
Nitrogen content in COM	7%	
Nitrogen content in HER	7.6%	
Feed added in the COM food pool	5402 g	During the experiment (25 July 1994–24 October 1994)
Feed added in the HER food pool	5866 g	During the experiment (25 July 1994–24 October 1994)
Amount of herring in HER food (DC_{her})	3 g ww herring/g ww food	
Various rates		
Phosphorus sedimentation rate (R_{sed_P})	0.55	Calibrated value
Nitrogen sedimentation rate (R_{sed_N})	0.6	Calibrated value
Mesocosm biomass nutrient uptake coefficient (K_{MBNU})	0.4	Estimated from mesocosm final biomass data
Nutrient excretion rate from fish stomach (K_{excr})	0.9	Calibrated value

If no other source is given, data come from Lehtinen et al. (1998).

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