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Stochastic simulation of size variation in turbot: possible causes analysed with an individual-based model

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Causes of size variation in a population of juvenile turbot were studied using an individual-based model (IBM). Each simulation started with 800 (divided into eight groups of 100 each) 120-day-old (posthatch) juveniles and was run for 140 days, and the data gained from model simulations compared directly with the result of a laboratory study with size-graded turbot. Stochastic growth with memory, which was included in the models as an individual genetical growth rate variation, is important in explaining size variation, and the combination between individual genetic growth rate and social interactions related to size-dependent hierarchies also contributes to size variation. The use of size-dependent growth rate alone fails to explain size variation, and is of little value in predicting size variation in turbot culture. Further, the results indicate formation of different types of size hierarchies for different sizes of juvenile turbot.

Key words: growth; individual-based model; size hierarchy; genetic variation; juvenile turbot; *Scophthalmus maximus*.

INTRODUCTION

Variation in individual growth rates can lead to high variation in sizes of individual fishes of the same age, which is a typical feature seen in natural fish populations (e.g. DeAngelis *et al.*, 1993; Letcher *et al.*, 1996) and in laboratory studies with many fish species (e.g. Folkvord, 1991; Carmichael, 1994; Forsberg, 1996; Aune *et al.*, 1997) including turbot *Scophthalmus maximus* (Rafinesque) (Rosenberg & Haugen, 1982; Nijhof, 1994; Imsland *et al.*, 1995, 1996). From an ecological viewpoint it is important to gain a better insight into the factors that govern these size variations, as variations in growth and hence fish sizes within a population can have a dramatic effect on the dynamics of a cohort (Chambers & Leggett, 1992; DeAngelis *et al.*, 1993; Rice *et al.*, 1993). In an aquaculture situation such large variation in sizes of similar aged fish has a negative impact on the production control and the profitability of the fish farm, as there exist large price variations between different sizes of fish (Lavens & Remmerswaal, 1994; Sutherland, 1997).

Many different factors have been put forward to explain observed size variation in a cultured fish population; e.g. genetic differences producing size variability (Huston & DeAngelis, 1987; Forsberg, 1995, 1996) and social interactions (Brett, 1979; Jobling, 1982; Jobling & Koskela, 1996). Social

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interactions can lead to decreased growth in low ranking individuals (Wirtz, 1974; Jobling, 1985; Koebele, 1985; Jobling & Reinsnes, 1987; Huntingford *et al.*, 1990; McCarthy *et al.*, 1992; Jobling & Koskela, 1996), and to the establishment of a size hierarchy. The establishment of a size hierarchy may be caused by direct competition for food (McCarthy *et al.*, 1992; Jobling & Koskela, 1996) or by other, less well-understood, social interactions (Jobling, 1982). Large differences in individual growth performance have been noted in juvenile turbot (Nijhof, 1994; Imsland *et al.*, 1996), as have stable size hierarchies (Gaumet, 1994; Imsland *et al.*, 1996, 1997*b*), and there is a need to optimize production characteristics (Lavens & Remmerswaal, 1994). In order to achieve more homogeneous growth one needs to control factors that contribute significantly to growth variation in turbot. A first step is to analyse which factors contribute most to the observed growth variation. One way to do this is to analyse possible causes with a model simulation of a population where individual growth trajectories are followed and the causes of variation are analysed.

Earlier simulation studies with wild populations have highlighted the importance of better understanding of the mechanisms behind growth variation in fish (e.g. DeAngelis *et al.*, 1993; Letcher *et al.*, 1996), as this will contribute to our understanding of survival and fish population dynamics. In their study Letcher *et al.* (1996) analysed variation in survival of larval fish with an individual-based model and found that, of the intrinsic variables analysed, growth variation explained 70% of variance in survival and had at least equally strong impact on survival in the fish population as extrinsic variables (predator size and density, prey density) did. Further, DeAngelis *et al.* (1993) showed that formulation of individual growth rates that are to some extent correlated over time (i.e. individual growth with memory) could cause dramatic changes in the dynamics of a fish cohort causing the distribution of growth rates in the population to broaden, which resulted in larger size variation in the population.

The present study designed an individual-based simulation model to analyse the contribution of different growth governing factors to the observed variation in juvenile weights reared under constant environmental conditions. Individual-based models (IBMs) have gained popularity in recent years (DeAngelis & Gross, 1992; Judson, 1994; Letcher *et al.*, 1996; Rose *et al.*, 1996) as they simulate a population as a collection of individual organisms each with its own life history. The IBM model applied here is aimed at studying the effect of size-dependent growth, individual genetic growth function and size hierarchy-dependent growth, as well as the combinations between these factors, on size variation in turbot. Further, to study the effect of different initial size variation each simulation was run using the initial weights (see below for details) from the laboratory study of Sunde *et al.* (1998). In their study, juvenile turbot were size graded into three size groups: small, medium and large, i.e. individuals from each size group were grown independently from individuals of other size groups, and additional fish were held in ungraded (control) groups. Each simulation started with a total of 800 juveniles [divided into eight groups of 100 fish as in the Sunde *et al.* (1998) experiment] and was run for the same period of time (140 days) as the Sunde *et al.* (1998) study so that the data from the model simulations could be compared directly with the results of the Sunde *et al.* (1998) study. In this way, our model predictions could be tested with an existing independent data set.

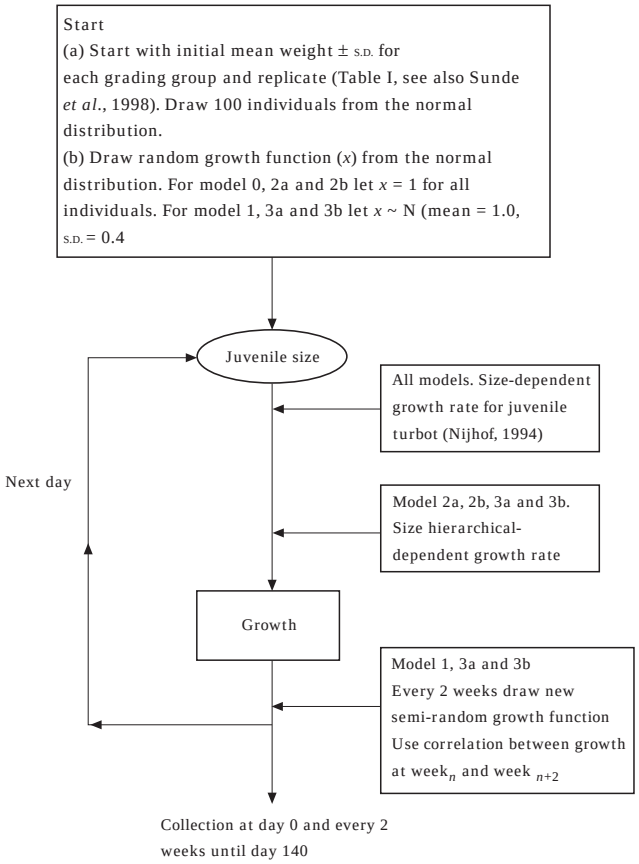

FIG. 1. Flow diagram of the individual-based growth model applied in the present study. The model calculates growth rates for each juvenile every day of the simulation. Parameters for growth and correlation of growth between week$_n$ and week$_{n+2}$ are based on laboratory experiments with juvenile turbot (Nijhof, 1994; Imsland *et al.*, 1997*a*, *b*, *c*) and halibut (Hallaråker *et al.*, 1995). Each simulation started with 100 juveniles using initial mean weight ± S.D. of the four grading groups in the study of Sunde *et al.* (1998).

MATERIALS AND METHODS

MODEL DESCRIPTION

General

The model simulated growth in juvenile turbot starting at the age of 4 months (posthatch) and varied over 140 days. A constant temperature (19° C) was applied. Each fish was defined by its weight, no fish died during the simulated growth trial, and the fish were fed *ad libitum*. To simulate growth every fish passed through the growth simulation model every day (Fig. 1). The model included three major state-specific growth factors of juvenile turbot, namely size-dependent growth rate, individual genetic growth function and size hierarchical-dependent growth. Each state-specific growth function depended on the weight of each juvenile. These growth functions are described in detail below. Function parameters were determined in two ways. Where available functions from previously published experiments on juvenile turbot were used (size-dependent growth: Nijhof, 1994; Imsland *et al.*, 1995, 1996), whereas in some cases published data were recalculated to arrive at function parameters (individual growth function with memory: Gaumet, 1994; Hallaråker *et al.*, 1995; Imsland *et al.*, 1996, 1997*b*). Two different

TABLE I. Initial mean weight (g), standard deviation (S.D.), and minimum and maximum weight (g) in each group of size graded juvenile turbot used in the individual-based model simulation of growth in turbot

Grading group	Replicate	Mean weight (g)	S.D. (g)	Minimum (g)	Maximum (g)
Small	1	3·47	0·81	1·55	5·22
	2	3·51	0·83	1·95	5·96
Medium	1	6·83	1·57	3·26	9·90
	2	6·99	1·82	3·49	10·77
Large	1	10·30	1·23	7·30	12·80
	2	10·55	1·82	7·66	14·94
Ungraded	1	6·50	2·67	1·64	12·20
	2	6·72	2·61	2·38	12·97

Each grading group consisted of two replicate tanks. See Sunde *et al.* (1998) for further details of the grading groups.

variants of size hierarchy were tested based on previously published literature (Jobling, 1982, 1995; Huntingford *et al.*, 1990; McCarthy *et al.*, 1992; Jobling & Bardvik, 1994; Jobling & Koskela, 1996).

To study the effect of different initial size variations each simulation was run using initial weight ± S.D. from the laboratory study of Sunde *et al.* (1998). In their study juvenile turbot reared at 19° C and fed *ad libitum* were size graded into three size groups (mean initial size ± S.D., Table I): small (3·4 ± 0·9 g), medium (7·0 ± 1·7 g) and large (10·5 ± 1·4 g), and additional fish were held in ungraded (6·6 ± 2·6 g) groups to give a total of four experimental groups, each being replicated. Each simulation started with 800 [divided into eight groups as in the Sunde *et al.* (1998) experiment] 120-day-old (posthatch) turbot juveniles and was run for the same period of time as the Sunde *et al.* (1998) study (140 days) so that the data from the model simulations could be compared directly with the results of the Sunde *et al.* (1998) study.

GROWTH

General growth model

The initial weight (W_0 in g) of each individual fish was drawn from a normal distribution, $\sim N(\mu, \sigma)$ where μ is the mean weight and σ is the standard deviation, and where initial μ and σ are taken from the study of Sunde *et al.* (1998) (Table I). The growth of individual i at time t was modelled as:

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)]\ X_i(t)\ Z_i(t) \quad (1)$$

where $W_i(t+1)$ is the weight of fish i at time $(t+1)$; $W_i(t)$ is the weight of fish i at time t; $G_i(t)$ is the size specific growth rate of individual i at time t; Δt is the length of the time interval under study (here $\Delta t = 1$ as the model simulates growth on a 1-day basis); $X_i(t)$ is an individual stochastic growth factor (see below); and $Z_i(t)$ is a size dependent hierarchical growth factor (see below).

Size-dependent growth rate [$G_i(t)$]

In many fish species growth rates are related inversely to size (Pedersen & Jobling, 1989; Fonds *et al.*, 1992; Rijnsdorp, 1993; Björnsson & Tryggvadóttir, 1996; Imsland *et al.*, 1996). To include this relationship in the growth model, the equation given by Nijhof

(1994) was used, which is based on calculations from a number of growth studies on juvenile turbot in the size range 3–3000 g:

$$G_i(t) = 0{\cdot}1148 \times W_i(t)^{-0{\cdot}5} \tag{2}$$

where $G_i(t)$ and $W_i(t)$ are the specific growth rate and weight, respectively, of individual i at time t. In the model simulation, size dependent growth rate was calculated for each fish on each day according to the weight of the individual fish on that day.

Individual stochastic growth function [$X_i(t)$]

Every individual was assigned an individual growth factor X_i that indicated the relative growth rate of the individual i in relation to average growth rate in the population. Further, X_i for each individual was time dependent, as every individual was assigned a new X_i every 2nd week (see details below). As X_i is a continuous random variable the central limit theorem assures that X will follow a normal distribution with $E(X) = 1$ and S.D.(X) = known. The probability distribution function of X is thus given as:

$$f(X) = \frac{1}{\sigma_X \sqrt{2\pi}} e^{-0{\cdot}5\left[\frac{1-X}{\sigma_X}\right]^2} \tag{3}$$

To find the X_i for each individual the cumulative distribution function $F(X)$ was estimated:

$$F(X) = \int_0^x f(\rho)\,d\rho \tag{4}$$

A random number (r) is drawn from the uniform distribution on section [0, 1] and set $F(X) = r$ to calculate X_i. An estimation of S.D.(X) was used which was based both on the available literature (Forsberg, 1995, 1996) and recalculations from earlier studies (Hallaråker *et al.*, 1995; Imsland *et al.*, 1995, 1996, 1997*b*). The recalculations were done using data on individually tagged fish so that individual growth can be tracked. An individual growth factor and its variance based were recalculated on the relative growth rate of the individual in relation to average growth rate in the population and the variance of these growth rates. A total of 920 individual growth trajectories was analysed and, based on these data, an estimate for S.D.(X) was found and accordingly S.D.(X) was set = 0·4 in the model simulations.

Correlation between growth factors in week$_n$ and week$_{n+2}$

There are three possible scenarios in the correlation between individual growth rate in time: deterministic growth rate, random growth rate and random growth rate with memory. Deterministic growth would mean that, once chosen, the value of X for each individual would not alter in the time period studied. One way to study if this is the case or not is to study growth rates of tagged fish over a given time period. In Fig. 2 the standardized growth (G_S) rates of 20 individually tagged turbot were followed over a period of 168 days (recalculated from Imsland *et al.*, 1996). G_S was found using the formula:

$$G_S = \frac{G_i(t) - \bar{G}(t)}{\text{S.D.}_{G(t)}} \tag{5}$$

where $G_i(t)$ is growth of individual i at time t, $\bar{G}(t)$ is the average growth of all n individuals at time t, and S.D.$_{G(t)}$ is the standard deviation of the 20 growth rates at time t. As growth rates of the individuals cross extensively (Fig. 2), a deterministic growth rate for each individual seems unlikely. As pointed out by DeAngelis *et al.* (1993), correlated

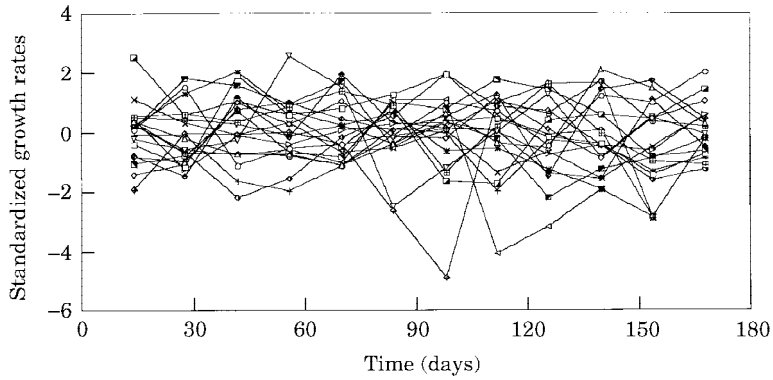

FIG. 2. Individual standardized growth rate trajectories of 20 individually tagged turbot. Data are recalculated from Imsland *et al.* (1996). See Materials and Methods for details of recalculations.

growth rates cause the distribution of growth rates in the population to broaden, whereas the outcome of growth simulations with random individual growth rates without memory is similar to the outcome of simulations with no random variation. To study the correlation between growth rates in one period with the growth rate in an adjacent period, Spearman's rank correlation (r_{SP}) coefficient was calculated from a number of laboratory studies with turbot (Gaumet, 1994; Imsland *et al.*, 1995, 1997*a*, *b*) and halibut *Hippoglossus hippoglossus* (L.) (Hallaråker *et al.*, 1995). In all of these studies the fish were weighed every 2 weeks so that individual growth could be estimated for a number of 2-week periods. The correlation between individual growth rates in week$_n$ and week$_{n+2}$ was then tested for all of these studies. There was an overall positive correlation between adjacent (i.e. between week$_n$ and week$_{n+2}$) growth rates ($r_{SP}=0{\cdot}4$). Therefore, this study used a stochastic growth rate with memory, and a new growth factor (X_i) was assigned to each individual every 2 weeks and this factor was positively correlated ($r_{SP}=0{\cdot}4$) with the previous one.

Size hierarchy-dependent growth rate [$Z_i(t)$]

The formation of size hierarchies in fish is generally found to have negative effects on overall biomass gain, and leads to inconsistency of growth among groups and heterogeneity in growth among individuals within a group (Jobling, 1995; Jobling & Koskela, 1996). Two variants of size hierarchies [$Z_i(t)$] were included in the model. Different size hierarchy variants have been postulated based on experimental studies. One variant was a dominance hierarchy in which every fish is subordinate to a larger individual (McCarthy *et al.*, 1992; Jobling, 1994). Another postulated variant of size-related dominance was the division of a fish group into dominant (the largest fish) and subordinates (the smallest fish) (Jobling, 1982; Huntingford *et al.*, 1990). In both cases the dominant fishes will eat a disproportionately high percentage of food provided (Huntingford *et al.*, 1990; McCarthy *et al.*, 1992; Jobling & Bardvik, 1994). However, although accepted to influence growth of farmed fish (Jobling, 1982, 1995; Huntingford *et al.*, 1990; McCarthy *et al.*, 1992; Jobling & Koskela, 1996) it is difficult to obtain direct information about the importance of social interactions on size variation in fishes. Thus size hierarchy was included in our models to investigate to what extent the formation of size hierarchy influences observed size variation. Two variants were tried (Z_a and Z_b) which simulate two postulated variants of size hierarchies in fishes (see above). These variants simulate a size hierarchy in which every fish is subordinate to all fish that are larger than that individual (Z_a), and a size hierarchy among the subordinate fish (Z_b). As the model results were compared with experimental results (Sunde *et al.*, 1998), the same experimental set-up was followed namely, eight groups of 100 fish in separate tanks.

Initially, several different modulation strengths of size hierarchy were tested, and based on these initial trials, 0·1 was chosen as the difference between the highest and lowest position.

(Z_a) decreasing sequence of 0·001 from 1·0 to 0·9 for all individuals in the same tank (n=100 for each tank), i.e. for the largest fish at time t, Z_i=1·0, for the second largest fish at time t, Z_i=0·999, the third largest fish at time t, Z_i=0·998, . . ., the smallest fish at time t, Z_i=0·900.

(Z_b) decreasing sequence of 0·002 from 1·0 to 0·9 for the 50 smallest (subordinates) fish in every tank, i.e. Z_i=1·0 for the dominants (n=50, the largest, second largest, . . ., fish no. 51) at time t, for fish no. 50 at time t, Z_i=0·998, for fish no. 49 at time t, Z_i=0·996, for fish no. 48 at time t, Z_i=0·994, . . ., for fish no. 1 (the smallest fish) at time t, Z_i=0·900.

MODEL TESTING AND APPLICATION

Six different versions of the general growth model (1) were tested in the present study. Model 0: size-specific growth

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)] \tag{6}$$

Model 1: stochastic growth factor and size-specific growth

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)]\ X_i(t) \tag{7}$$

Model 2a: hierarchical growth factor Z_a and size-specific growth

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)]\ Z_{ai}(t) \tag{8}$$

Model 2b: hierarchical growth factor Z_b and size specific growth

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)]\ Z_{bi}(t) \tag{9}$$

Model 3a: hierarchical growth factor Z_a, stochastic growth factor, and size specific growth

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)]\ X_i(t)\ Z_{ai}(t) \tag{10}$$

Model 3b: hierarchical growth factor Z_b, stochastic growth factor, and size specific growth

$$W_i(t+1) = W_i(t)\ \exp[G_i(t)(\Delta t)]\ X_i(t)\ Z_{bi}(t) \tag{11}$$

All models were tested using the statistical package S-PLUS (Venables & Ripley, 1994), and every model testing with every 100 fish replicated in order to simulate replicated tanks so that model simulations could be compared directly to the Sunde *et al.* (1998) study.

DATA ANALYSIS AND STATISTICAL METHODS

A Kolmogorov–Smirnov goodness-of-fit two-sample test (Zar, 1984) was applied to compare the weight distribution from each model simulation at every collection date (every 2 weeks) with the corresponding data from laboratory studies (Sunde *et al.*, 1998). For each measurement the observed freqency was recorded. Then the cumulative observed frequencies were determined from which the cumulative related frequencies were obtained. Next for each measurement the corresponding expected frequency was determined. In this context the expected frequency was set to be the laboratory data of Sunde *et al.* (1998). Then the test statistic in this test was based on the largest disparity between the observed and the expected data (Zar, 1984). Hence, if the Kolmogorov–Smirnov test was not significant, the distributions tested were not different (Zar, 1984).

For every weight distribution the skewness (γ_1) of weight was calculated (Zar, 1984). The Bonferroni correction (Johnson & Field, 1993) for the significance level (α) was applied when comparing the different models at each collection date. Coefficient of variation (CV) of weight for each replicate tank of the grading groups was regressed against time (days) and analysed with linear regression (Zar, 1984). Separate regressions were made for each model. The regression coefficients from these regressions were tested for homogeneity with laboratory data using analysis of covariance (ANCOVA, Sokal & Rohlf, 1995). In cases of homogeneity (i.e. parallel regression lines) a common regression coefficient was calculated.

RESULTS

MODEL EVALUATION

The models were evaluated in two ways: (1) the weight distribution and skewness gained from the different models at each collection date were compared with laboratory data (Table II); and (2) the corresponding time pattern of CV of the size–frequency distribution of the different models (Table III, Fig. 3) were compared with laboratory data (Sunde *et al.*, 1998).

WEIGHT DISTRIBUTIONS

The initial weight distribution of all models did not differ from the laboratory data for all grading groups (Kolmogorov–Smirnov two sample test, $P>0{\cdot}7$, Table II). As the experiment proceeded there was, however, a large variation in the fit of the different model data with corresponding laboratory data (Kolmogorov–Smirnov two sample test, Table II). Overall, models 1, 3a and 3b displayed the best fit to laboratory data (Table II). For the ungraded group, models 3a and 3b were the only ones that displayed similar fits to those of the corresponding laboratory data [Table II(d), Fig. 4].

The weight distribution gained by model 1 did not differ from that of the laboratory data (Kolmogorov–Smirnov two sample test, $P>0{\cdot}05$) from day 0 until day 28 for the small grading group [Table II(a)], from day 84 onwards for the medium grading group (Table II(b)], and from day 56 to day 112 for the large grading group [Table II(c)]. The weight distribution from model 3a did not differ from corresponding laboratory data from day 84 onwards for the small grading group [Table II(a)], from day 56 to 84 for the medium grading group [Table II(b)], from day 28 to 56 for the large group [Table II(c)], and from day 42 to 70 for the ungraded group [Table II(d)].

Model 3b displayed the best fit of all models for the medium, large and ungraded groups (Table II). For the small grading group, however, model 3a displayed the best overall fit [Table II(a)]. The weight distribution from model 3b did not differ from corresponding laboratory data from day 126 onwards for the small grading group [Table II(a)], from day 56 onwards for the medium grading group [Table II(b)], from day 42 to 126 for the large group [Table II(c)], and from day 70 to 126 for the ungraded group [Table II(d)].

Mean weight of the distributions gained by model 0 was similar to that of the laboratory data, especially for the medium and ungraded groups [Table II(b) and (d), respectively]. However, although displaying similar mean weights, model 0 explained the observed size variation in the laboratory data poorly,

TABLE II. Mean weights (g) for all experimental categories (small, medium, large and ungraded) for both experimental data (see Sunde *et al.*, 1998) and all IBMs throughout the study

(a) Small group

Data	Day 0	Day 14	Day 28	Day 42	Day 56	Day 70	Day 84	Day 98	Day 112	Day 126	Day 140
Exp. data	3·5 (0·8)	5·8 (1·3)	8·6 (2·1)	13·1 (3·5)	19·7 (5·5)	26·9 (7·8)	36·6 (11·8)	47·7 (15·4)	60·3 (20·3)	73·1 (25·4)	88·3 (31·7)
γ_1	0·407	− 0·050	− 0·183	− 0·142	− 0·001	− 0·009	0·051	0·180	0·176	0·399	0·722
Model 0	*3·4 (0·9)**	7·1 (1·2)	12·1 (1·6)	18·3 (1·9)	25·9 (2·7)	34·7 (2·3)	44·9 (3·1)	56·4 (3·4)	69·1 (3·8)	83·2 (4·2)	98·5 (4·5)
γ_1	0·060	0·270	0·199	0·157	0·130	0·111	0·097	0·085	0·077	0·069	0·063
Model 1	*3·5 (0·8)**	*7·2 (1·8)**	*12·2 (3·6)**	18·5 (5·7)	26·0 (8·4)	34·9 (11·5)	44·9 (14·4)	56·5 (17·8)	69·4 (21·4)	83·7 (25·0)	99·1 (28·8)
γ_1	− 0·088	0·100	0·318	0·446	0·503	0·507	0·582	0·714	0·809	0·749	0·572
Model 2a	*3·5 (0·8)**	7·0 (1·3)	11·4 (1·9)	16·8 (2·7)	23·1 (3·7)	30·1 (4·9)	*37·9 (6·5)**	*46·4 (8·3)**	55·6 (10·5)	65·3 (13·0)	75·6 (15·8)
γ_1	− 0·303	− 0·243	− 0·149	− 0·061	0·010	0·068	0·115	0·153	0·185	0·214	0·239
Model 2b	*3·5 (0·8)**	7·1 (1·3)	11·8 (2·0)	17·6 (2·8)	24·6 (3·9)	32·6 (5·3)	41·6 (7·1)	51·7 (9·1)	62·7 (11·6)	74·7 (14·5)	87·6 (17·9)
γ_1	− 0·058	− 0·282	− 0·427	− 0·529	− 0·601	− 0·649	− 0·681	− 0·700	− 0·712	− 0·718	− 0·721
Model 3a	*3·4 (0·7)**	6·7 (1·9)	11·5 (3·8)	17·6 (6·3)	24·6 (9·3)	32·7 (12·7)	*41·6 (16·4)**	*51·0 (19·9)**	*61·2 (23·9)**	*72·0 (28·7)**	*83·6 (33·7)**
γ_1	− 0·185	0·187	0·363	0·406	0·558	0·640	0·660	0·580	0·552	0·572	0·616
Model 3b	*3·5 (0·8)**	7·2 (2·1)	12·0 (4·1)	18·1 (6·8)	25·3 (9·9)	33·8 (13·5)	43·3 (17·4)	54·0 (21·2)	65·7 (25·6)	*78·5 (30·9)**	*91·8 (36·5)**
γ_1	0·091	0·276	0·364	0·438	0·382	0·367	0·296	0·192	0·146	0·175	0·199

Results are given as mean (S.D.); number of fish in each experimental category varied from 192 to 200 in each grading group, number of fish in each IBM was 200 at all times. All results consist of two replicate tanks (n=100 in each replicate). Results of statistical analysis (Kolmogorov–Smirnov two-sample test, P<0·05) for comparison of the sampling distribution of experimental data *v.* each model are given for each date. Model distributions significantly different from experimental data (P<0·05) are not marked.

Non-significant results are marked * and in *italics*. Skewness (γ_1) of all weight distributions is also given.

TABLE II(b). Medium group

Data	Day 0	Day 14	Day 28	Day 42	Day 56	Day 70	Day 84	Day 98	Day 112	Day 126	Day 140
Exp. data	6·9 (1·7)	10·4 (2·6)	15·4 (4·2)	21·6 (6·1)	30·9 (8·9)	40·3 (12·2)	52·4 (16·5)	66·1 (21·4)	82·0 (27·9)	97·8 (33·2)	119·0 (40·9)
γ_1	0·211	0·404	0·631	0·656	0·564	0·681	0·595	0·518	0·530	0·531	0·603
Model 0	*7·0 (1·6)**	11·9 (2·1)	18·1 (2·6)	25·6 (3·1)	34·4 (3·6)	44·5 (4·1)	55·9 (4·6)	68·7 (5·1)	82·7 (5·6)	98·0 (6·1)	114·5 (6·6)
γ_1	− 0·179	− 0·248	0·292	− 0·321	− 0·343	− 0·359	− 0·371	− 0·382	− 0·390	− 0·397	− 0·403
Model 1	*6·8 (1·7)**	11·6 (2·8)	18·1 (4·7)	26·1 (7·3)	35·2 (10·1)	45·5 (13·1)	*56·9 (15·7)**	*69·7 (18·4)**	*84·4 (22·1)**	*99·8 (25·9)**	*116·2 (29·6)**
γ_1	0·081	0·171	0·414	0·563	0·553	0·479	0·395	0·288	0·244	0·265	0·287
Model 2a	*6·9 (1·9)**	11·4 (2·7)	16·7 (3·7)	*23·0 (4·8)**	*30·1 (6·2)**	*37·8 (7·9)**	46·4 (9·8)	55·5 (12·1)	65·3 (14·6)	75·6 (17·6)	86·4 (20·9)
γ_1	− 0·190	− 0·142	− 0·081	− 0·021	0·049	0·102	0·147	0·186	0·220	0·249	0·276
Model 2b	*6·7 (1·6)**	11·3 (2·3)	17·1 (3·2)	23·9 (4·3)	31·9 (5·8)	*40·8 (7·5)**	*50·8 (9·7)**	61·8 (12·1)	73·7 (15·1)	86·5 (18·4)	100·3 (22·2)
γ_1	0·097	− 0·102	− 0·262	− 0·387	− 0·479	− 0·547	− 0·594	− 0·627	− 0·649	− 0·664	− 0·673
Model 3a	*7·1 (1·6)**	11·6 (3·1)	17·4 (5·5)	24·0 (8·2)	*31·5 (12·0)**	*40·0 (16·5)**	*49·2 (20·7)**	59·3 (25·4)	69·9 (30·5)	81·2 (35·5)	93·0 (40·8)
γ_1	0·009	0·563	0·584	0·568	0·667	0·794	0·891	0·867	0·783	0·763	0·764
Model 3b	*7·1 (1·6)**	12·0 (3·1)	17·9 (5·5)	24·9 (8·3)	*33·0 (11·4)**	*42·1 (14·6)**	*52·4 (18·5)**	*64·2 (23·2)**	*77·2 (28·5)**	*90·9 (33·9)**	*105·6 (40·0)**
γ_1	0·266	0·340	0·426	0·352	0·282	*0·164*	0·084	0·106	0·188	0·222	0·179

TABLE II(c). Large group

Data	Day 0	Day 14	Day 28	Day 42	Day 56	Day 70	Day 84	Day 98	Day 112	Day 126	Day 140
Exp. data	10·4 (1·5)	14·6 (2·2)	20·8 (3·9)	28·6 (6·3)	39·9 (9·3)	51·6 (12·6)	68·9 (17·7)	85·0 (22·8)	103·1 (29·3)	121·8 (34·4)	146·4 (40·6)
γ_1	0·147	0·388	0·378	0·561	0·359	0·141	0·099	0·101	0·143	0·332	0·312
Model 0	*10·3 (1·3)*	*16·2 (1·6)	23·3 (2·0)	31·8 (2·3)	41·5 (2·6)	52·6 (2·9)	64·9 (3·3)	78·5 (3·6)	93·5 (3·9)	109·7 (4·2)	127·2 (4·6)
γ_1	0·160	0·120	0·091	0·072	0·057	0·047	0·037	0·030	0·024	0·019	0·014
Model 1	*10·5 (1·2)*	*16·6 (3·0)	24·3 (5·9)	32·9 (8·7)	*42·7 (12·0)*	*54·2 (15·2)*	*67·0 (18·6)*	*80·2 (21·6)*	*94·6 (24·7)*	110·8 (28·0)	128·6 (31·3)
γ_1	0·218	0·424	0·729	0·506	0·261	0·266	0·298	0·290	0·295	0·341	0·298
Model 2a	*10·3 (1·3)*	*15·4 (2·0)	*21·5 (2·9)*	*28·3 (4·0)*	36·0 (5·4)	44·3 (7·1)	53·2 (9·1)	62·8 (11·5)	72·9 (14·2)	83·5 (17·3)	94·6 (20·7)
γ_1	− 0·063	0·003	0·057	0·099	0·133	0·163	0·189	0·212	0·235	0·256	0·276
Model 2b	*10·4 (1·2)*	*16·0 (1·9)	22·6 (2·8)	30·3 (4·0)	39·1 (5·6)	48·8 (7·5)	59·5 (9·8)	71·2 (12·6)	83·8 (15·7)	97·4 (19·4)	111·8 (23·5)
γ_1	0·131	− 0·169	− 0·378	− 0·513	− 0·597	− 0·649	− 0·681	− 0·700	− 0·710	− 0·715	− 0·717
Model 3a	*10·3 (1·2)*	*16·2 (3·4)	*22·7 (6·3)*	*30·3 (9·5)*	*38·5 (13·2)*	47·2 (17·3)	56·5 (21·1)	66·3 (25·0)	75·9 (29·2)	86·8 (33·9)	98·1 (39·1)
γ_1	0·013	1·070	0·667	0·528	0·482	0·508	0·537	0·501	0·476	0·502	0·586
Model 3b	*10·4 (1·3)*	*16·1 (3·0)	23·0 (5·5)	*31·1 (8·6)*	*40·2 (12·0)*	*50·1 (15·7)*	*61·7 (20·4)*	*73·8 (25·4)*	*87·3 (30·6)*	*102·2 (36·1)*	117·8 (41·6)
γ_1	0·032	0·108	0·075	0·005	− 0·048	− 0·106	− 0·097	− 0·008	0·035	− 0·010	− 0·013

TABLE II(d). Ungraded group

Data	Day 0	Day 14	Day 28	Day 42	Day 56	Day 70	Day 84	Day 98	Day 112	Day 126	Day 140
Exp. data	6·6 (2·6)	9·9 (3·5)	14·7 (5·6)	20·8 (8·0)	29·9 (11·8)	39·8 (15·5)	52·0 (20·0)	65·8 (24·8)	81·1 (30·6)	95·3 (36·3)	116·6 (42·4)
γ_1	0·386	0·484	1·015	1·057	1·068	1·096	0·987	0·981	0·984	0·980	1·102
Model 0	*6·6 (2·7)**	11·4 (3·6)	17·4 (4·5)	24·7 (5·3)	33·4 (6·2)	43·3 (7·1)	54·6 (8·0)	67·1 (8·9)	80·9 (9·8)	96·1 (10·7)	112·5 (11·6)
γ_1	0·073	− 0·089	− 0·189	− 0·256	− 0·304	− 0·368	− 0·391	− 0·409	− 0·424	− 0·437	− 0·340
Model 1	*6·6 (2·5)**	11·3 (3·9)	17·4 (6·3)	24·9 (8·9)	33·8 (11·7)	44·1 (15·1)	55·7 (19·0)	68·5 (22·9)	82·1 (26·6)	97·4 (30·8)	114·1 (35·9)
γ_1	0·090	0·252	0·332	0·446	0·524	0·504	0·359	0·134	0·265	0·252	0·339
Model 2a	*6·9 (2·7)**	11·3 (3·7)	16·7 (4·8)	22·9 (6·2)	30·0 (7·7)	37·9 (9·5)	46·4 (11·6)	55·6 (13·9)	65·4 (16·6)	75·7 (19·7)	86·6 (23·0)
γ_1	0·124	0·023	0·015	0·045	0·090	0·136	0·179	0·218	0·253	0·284	0·311
Model 2b	*6·7 (2·5)**	11·4 (3·5)	17·2 (4·6)	24·1 (6·0)	32·1 (7·7)	41·4 (9·6)	51·1 (11·9)	62·1 (14·6)	74·1 (17·6)	87·0 (21·1)	100·9 (25·0)
γ_1	− 0·289	− 0·434	− 0·515	− 0·565	− 0·598	− 0·622	− 0·636	− 0·652	− 0·660	− 0·665	− 0·668
Model 3a	*6·6 (2·7)**	12·8 (5·4)	16·8 (6·8)	*23·1 (9·3)**	*30·6 (12·4)**	*38·8 (15·8)**	47·6 (19·1)	56·5 (22·6)	66·1 (26·4)	76·1 (31·3)	87·1 (36·3)
γ_1	0·348	1·148	0·508	0·608	0·738	0·860	0·860	0·773	0·764	0·746	0·789
Model 3b	*6·6 (2·7)**	11·2 (4·1)	17·1 (6·3)	23·9 (8·9)	32·0 (12·1)	*41·6 (15·9)**	*51·9 (20·1)**	*63·7 (25·0)**	*76·2 (30·7)**	*90·1 (36·5)**	104·9 (42·6)
γ_1	0·178	0·319	0·224	0·264	0·401	0·455	0·443	0·429	0·437	0·431	0·403

TABLE III. Results from regression analysis of coefficient of variation (CV) for weight regressed against time (days)

Grading group	Data	β	$t(\beta)$	P for $\beta=0$
Small	LD	0·087	7·94	<0·01
	M0	−0·112	−5·98	<0·01
	M1	0·037	1·82	0·10
	M2a	0·009	0·61	0·56
	M2b	−0·001	−0·08	0·94
	M3a	0·108	4·85	<0·01
	M3b	0·095	3·65	<0·01
Medium	LD	0·077	17·22	<0·01
	M0	−0·101	−7·41	<0·01
	M1	0·002	0·23	0·82
	M2a	−0·009	−0·67	0·52
	M2b	0·003	0·28	0·78
	M3a	0·152	7·48	<0·01
	M3b	0·146	6·15	<0·01
Large	LD	0·106	8·95	<0·01
	M0	−0·058	−8·17	<0·01
	M1	0·064	2·21	0·04
	M2a	0·069	20·64	<0·01
	M2b	0·069	23·42	<0·01
	M3a	0·167	5·85	<0·01
	M3b	0·150	6·94	<0·01
Ungraded	LD	0·001	0·12	0·90
	M0	−0·189	−7·60	<0·01
	M1	−0·038	−8·08	<0·01
	M2a	−0·065	−3·12	0·01
	M2b	−0·062	−3·07	0·01
	M3a	−0·002	−0·59	0·56
	M3b	0·017	1·56	0·15

LD, Laboratory data; M0, Model 0; M1 = Model 1, etc. β is the regression coefficient in the regression equation $Y=\alpha+\beta X$ where Y is CV and X is time. The t statistic and corresponding P value for the hypothesis $\beta=0$ are individual.

and, apart from the initial weight distribution, model 0 always displayed a significantly different weight distribution compared to the laboratory data (Kolmogorov–Smirnov, $P<0{\cdot}01$, Fig. 4).

Models 2a and 2b also displayed a poor fit to the laboratory data especially for the large [Table II(c)], and ungraded [Table II(d), Fig. 4] groups.

On average, the laboratory data were skewed positively (i.e. skewed to the right) around their mean value for all grading groups (Table II, Fig. 4). Models 1, 2a and 3a displayed the closest similarity to the distribution symmetry of the laboratory data, as on average these models were also skewed positively for all grading groups (Table II, Fig. 4). However, models 0 and 3b displayed in most cases a symmetrical distribution about their mean value (Table II). The only model displaying an average negative skewed distribution for all grading groups was model 2b (Table II).

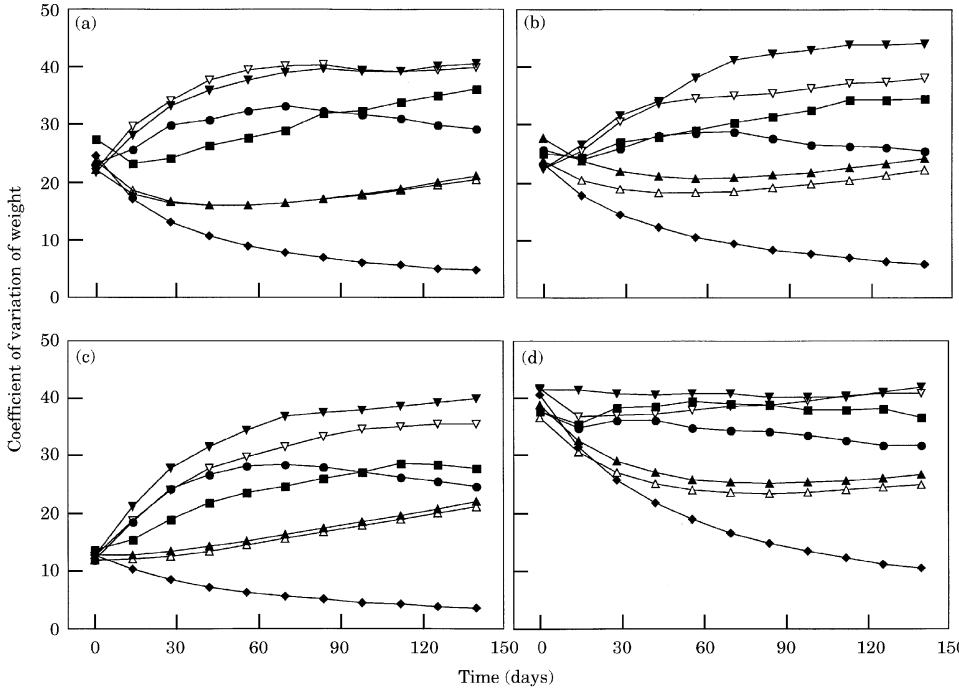

FIG. 3. Coefficient of variation (CV) of weight plotted against time (days) for four different grading groups: (a) small, (b) medium, (c) large, (d) ungraded. The result from laboratory data (Sunde *et al.*, 1998) and all simulation models run in the present study are shown. ■, Laboratory data; ◆, model 0; ●, model 1; ▲, model 2a; △, model 2b; ▼, model 3a; ▽, model 3b.

CAUSES OF SIZE VARIATIONS

For the laboratory data, the CV of weight increased in all grading groups [linear regression, $P<0{\cdot}01$, Table III, Fig. 3(a), (b), (c)] except the ungraded one, where the CV was unaltered over time [$P=0{\cdot}9$, Table III, Fig. 3(d)]. Models 3a and 3b displayed the same pattern for CV as did the laboratory data although these models had higher CV values for small, medium and large grading groups [Fig. 3(a), (b), (c), respectively] compared with laboratory data. Further, models 3a and 3b had parallel regression lines with laboratory data for the small (ANCOVA, $F_{2,27}=0{\cdot}26$, $P>0{\cdot}75$), large ($F_{2,27}=2{\cdot}02$, $P>0{\cdot}15$) and ungraded ($F_{2,27}=1{\cdot}60$, $P>0{\cdot}20$) groups so that a common regression coefficient (β) could be calculated. Hence, the CV increased with time for the small and large grading groups for the laboratory data and models 3a and 3b (common $\beta=0{\cdot}097$, $P<0{\cdot}01$, $\beta=0{\cdot}013$, $P<0{\cdot}01$, respectively), but was unaltered in the ungraded group (common $\beta=0{\cdot}005$, $P>0{\cdot}20$).

For model 1, CV increased in all grading groups (Table III), but in contrast to laboratory data CV decreased [$P<0{\cdot}01$, Table III, Fig. 3(d)] over time for the ungraded group. Model 1 and laboratory data had parallel regression lines ($F_{1,18}=1{\cdot}84$, $P>0{\cdot}15$) for the large grading group (common $\beta=0{\cdot}085$, $P<0{\cdot}01$). The CV values in models 2a and 2b always were lower than in the laboratory data (Fig. 3). The time dependent pattern of CV was different between models 2a and 2b and laboratory data in all grading groups except for the large group, where CV increased in both model and laboratory data [$P<0{\cdot}01$, Table III,

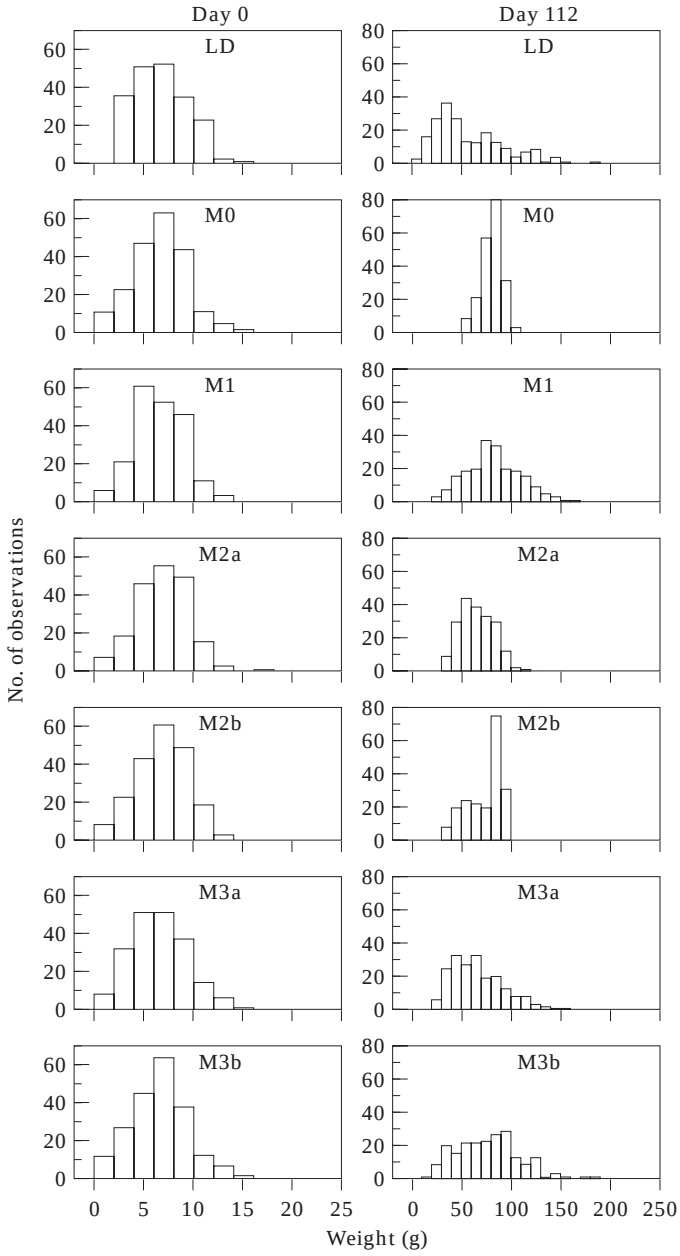

FIG. 4. Weight-frequency histogram for the ungraded group at two selected dates: day 0 and day 112. The weight frequencies from laboratory data (Sunde *et al.*, 1998) and all simulation models run in the present study are shown.

Fig. 3(c)], whereas the regression lines were not parallel (ANCOVA, $F_{2,27}=8{\cdot}42$, $P<0{\cdot}01$). In the other grading groups CVs for the models 2a and 2b data were unaltered [small and medium groups, $P>0{\cdot}50$, Fig. 3(a) and (b)], or decreased with the passage of time [ungraded group, $P<0{\cdot}05$, Fig. 3(d)].

The CV for model 0 data decreased in all grading groups ($P<0{\cdot}01$, Table III, Fig. 3), and was always much lower during the latter part of the experiment than found for corresponding laboratory data (Fig. 3).

DISCUSSION

THE MODEL APPROACH

To our knowledge this is the first published paper where individual-based simulations were used to study fish growth in aquaculture. Earlier model predictions in aquaculture have been based on modelling growth for a group of fish, but not including day-to-day individual stochastic factors (Cuenco *et al.*, 1985; Forsberg, 1995; Rosa *et al.*, 1997).

The major difference between previous IBM approaches and the one presented in this paper is that our models are aimed at explaining size differences in culture of a species, whereas earlier approaches have been aimed more generally at explaining population dynamics in natural populations (e.g. Chambers & Leggett, 1992; DeAngelis *et al.*, 1993; Rice *et al.*, 1993; Letcher *et al.*, 1996; Rose *et al.*, 1996; Kristiansen & Svåsand, 1998). Another difference is the time scale under study. The present paper studied growth of size graded turbot for a period of 140 days during the juvenile stage with a simple simulation model including only three growth governing factors and the combination between these factors. In contrast modelling population dynamics of many marine fishes requires long-term (multigenerational) simulations (Rose *et al.*, 1996) where feeding, growth, and mortality of every fish is simulated each day (DeAngelis *et al.*, 1991; Letcher *et al.*, 1996; Rose *et al.*, 1996) using detailed IBMs. The advantage of the detailed model approach is a much greater flexibility in the questions that can be addressed (Rose *et al.*, 1996) whereas the main drawback can be the lack of comparison between model simulations and experimental data. The present study provided a realistic analysis of the findings by comparing directly the results of our models with existing laboratory data (Sunde *et al.*, 1998) giving a realistic estimation and evaluation of our findings. DeAngelis (1988) pointed out that perhaps the best approach in model simulations is to attempt to fractionate the problem being studied into a large number of simpler ones that might be addressed individually. The IBMs used in this paper are very simple and use only a few equations derived mainly from existing literature (Gaumet, 1994; Nijhof, 1994; Hallaråker *et al.*, 1995; Imsland *et al.*, 1995, 1996, 1997*b*), but simulate events in the culture of turbot which are quite similar to the farming situation. This is only the first step towards a better understanding of the factors that govern size variation of cultured turbot. Important biotic variables such as the metabolic cost of each individual (Nijhof, 1994), food consumption and feeding efficiency (Devesa, 1994) are not included in the model applied here. Later versions might include other growth governing factors, e.g. temperature (Jones *et al.*, 1981; Danielssen *et al.*, 1990; Burel *et al.*, 1996), photoperiod (Fonds, 1979; Imsland *et al.*, 1995, 1997*c*), salinity (Gaumet, 1994; Gaumet *et al.*, 1995), genotype specific growth (Nævdal *et al.*, 1992; Torrissen & Shearer, 1992; Imsland *et al.*, 1997*a*), and sexual dimorphism in growth (Devauchelle *et al.*, 1988; Déniel, 1990; Imsland *et al.*, 1997*b*), and the duration of the study

might be extended to cover fully the period from early juvenile stage to sexual maturation.

CAUSES OF SIZE VARIATION IN THE CULTURE OF TURBOT

Size variation in cultured turbot was related mainly to individual genetic growth factors (model 1), and the combination of individual genetic growth factors and social interactions related to size-dependent hierarchies (models 3a and 3b). The use of size-dependent growth alone (model 0, Nijhof, 1994) failed to explain the observed size variation (Figs 3 and 4) in all grading groups (Tables II and III), and was of little value to predict size variation in turbot culture. Further, our modelling efforts suggested that the individual genetical variation in growth must be taken into account when designing future IBMs. This is of vital importance in model studies of natural populations as growth may have a large effect on survival (Letcher *et al.*, 1996), and including individual genetically based growth variations can increase the predicting power of IBMs. Forsberg (1995, 1996) included a normally distributed genetical growth index in his model assumptions, and found that his models followed closely data gained from commercial-scale empirical results. For turbot, initial trials (Gjerde *et al.*, 1997) indicated that the heritability for body weight in turbot is large, and that there is a substantial additive genetic variation in growth rate in turbot which is promising for genetic improvement of the growth rate through selective breeding.

The genetic growth factor alone (model 1) failed to explain observed size variation in ungraded turbot [Tables II(d) and III], whereas the combination of genetic growth factor and size-dependent hierarchy (models 3a and 3b) fitted laboratory data well for ungraded turbot [Table III(d), Fig. 4]. This might indicate that a size hierarchy influencing the growth of individual fish formed to a larger extent in ungraded groups of turbot. Further, the increase in CV observed in the present study amongst the small, medium and large groups [Fig. 3(a), (b) and (c), respectively] might suggest some form of competition for food or social interactions among juvenile turbot, because in populations where the growth of some individuals was suppressed by food competition, CV increased (Jobling, 1982). In some fish species dominant individuals exhibit higher growth rates compared to subordinate individuals when reared together (Brown, 1946; Magnuson, 1962; Jobling, 1985; Koebele, 1985). Different factors have been proposed to explain why larger individuals suppress growth in smaller individuals (Wirtz, 1974; Wallace *et al.*, 1988), but food competition seems to be particularly important (Magnuson, 1962; Wallace & Kolbeinshavn, 1988). Further, Doyle & Talbot (1986) introduced the term resource-dependent competition, to describe the process where resource competition, e.g. for food, controls the relative growth rates. The fish in the study of Sunde *et al.* (1998) were size graded (Table I) to test the effect of different initial size variation on subsequent growth, and to test whether the separation of small and large individuals from each other resulted in less negative effects of social interactions (Jobling, 1982, 1995; Knights, 1987) on growth. They found no negative effect of size grading on growth and biomass gain, but pointed out that feeding every 6 min and feeding in excess during those studies may have been important factors in reducing aggression, so that the growth of the smallest individuals was not heavily

suppressed by the larger individuals. This was indicated also in the study of Jobling & Koskela (1996). They analysed interindividual variation in growth in rainbow trout *Oncorhynchus mykiss* (Walbaum) during restricted feeding and in a subsequent period of full feeding, and suggested that feeding hierarchies were established under feed restriction but were broken down rapidly under full feeding. However, there are cases in which size hierarchies develop in the presence of excess food (Ehrlich *et al.*, 1976; Jobling, 1982; McCarthy *et al.*, 1992). In these cases it is suggested that a size hierarchy (with larger fish dominating smaller ones) forms where the dominant fish consumes a greater proportion of the group meal (Huntingford *et al.*, 1990; McCarthy *et al.*, 1992; Jobling, 1995). It follows that, although reduced under excess feeding, food competition and aggression might still contribute to the formation of size hierarchies under such conditions. Our findings support this as there are indications that size variation in turbot is partly a consequence of size hierarchy formation.

There was a difference in the sensitivity of models 3a and 3b to the different grading groups at different times, indicating formation of different types of size hierarchies in different size groups. In the small grading group model 3a showed the best fit to laboratory data [Table II(a)], whereas model 3b fitted the medium, large and ungraded groups better than did model 3a [Table II(b), (c), and (d), respectively]. This indicates a formation of size hierarchy in the medium, large and ungraded groups where growth of the subordinates (here the 50 smallest fish) was influenced negatively by the dominants, but whereas the size rank order within the dominants (the 50 largest fish) was less important (factor Z_b). In contrast, the results indicate formation of a dominance hierarchy including all the fish (factor Z_a) in the small grading group. Further, there was a shift from factor Z_a towards factor Z_b during the latter stages of the experiments (Table II) for all grading groups, which might suggest formation of different types of size hierarchies for different sizes of juvenile turbot.

CONCLUSIONS

The present modelling study indicates that there are two main causes for size variation in laboratory studies with turbot:

(a) an individual genetical growth rate variation, which is stochastic in the population and changes with time (stochastic growth with memory);
(b) the combination of individual genetical growth rate and social interactions related to size-dependent hierarchies.

The use of size-dependent growth alone fails to explain size variation, and is of little value in predicting size variation in turbot culture.

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