THE INFLUENCE OF SIZE-SELECTIVE MORTALITY ON GROWTH BACK-CALCULATION OF HARD CALCIFIED STRUCTURES SUCH AS OTOLITHS.

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Abstract

Otolith samples that are collected routinely at fisheries laboratories for many decades have been widely utilized to reconstruct the changes in the somatic growth rates over long time periods. Fishing, as well as other mortality agents, may be size selective and may affect the composition of a fish population with regard to the growth types. In the context of a study of the changes in growth rate of various demersal fish (plaice, cod, haddock and saithe) between the present time period and time periods before the era of industrialized fishing, this paper explores the effects of size selective fishing on the back-calculated growth rates from otoliths collected from the exploited population. The decay of the population numbers due to size-selective exploitation is simulated for different growth types, and the changes in the population composition with regard to the growth types is explored for various levels of exploitation. The simulation results are used to explore the possible bias in back-calculated growth rate of fish species exploited at levels typical for the North Sea demersal fish.

Introduction

Fishing is a process which selectively removes particular size classes from the population (Policansky, 1993). The relationship between fishing mortality and size (exploitation pattern) depends on the selectivity characteristics of the gear and on the overlap in distribution between the fishery and the fish. In demersal fisheries using towed gears, the fishing mortality will generally increase sharply around the size at which the fish are retained in the net and will be flat-topped beyond this size. This exploitation pattern is typical for present day trawl fisheries on flatfish and roundfish (ICES, 1999). A dome shaped exploitation pattern, however, may also occur in towed demersal gear when the larger size classes have a higher chance to escape from the approaching gear, or when the larger size classes have a different spatial distribution pattern (Rijnsdorp and Millner, 1996).

Size selective fishing will affect the population composition with regard to its growth rate. Growth rates of individual fish generally varies substantially. This variability will have a phenotypic and a genetic component. The contribution of the genetic component to the variability in growth is estimated at about 10% (Policansky, 1993a; 1993b). In a system where fishing mortality only starts at a particular size, the faster growing growth types will be selectively removed from the population once the recruit to the fishery. This may lead to genetical selection for particular genotypes. Hence, Ricker (1981) interpreted the decrease in the mean size at age in salmon populations to be due to the size selective mortality generated

by the fisheries. Also this process is one of the possible explanations of the apparent decrease in growth rate as observed from the back-calculation of otolith in fish populations (Jones, 1958, Ricker, 1969).

In the context of a study of the changes in growth rate of various demersal fish (plaice, cod, haddock and saithe) between the present time period and time periods before the era of industrialized fishing, this paper explores the effects of size selective fishing on the back-calculated growth rates from otoliths collected from the exploited population. We will focus on the changes in population composition with regard to growth types due to exploitation and its potential bias in the reconstruction of changes in growth rate using a numerical simulation model. In addition, the data base of back-calculated plaice otoliths (Rijnsdorp, 1992; 1996) will be employed to analyze the effects off sampling length on back-calculated growth.

Material and methods

The model

The objective of the model was used to simulate a population of individual fish at the start of the year by calculating the size at age as well as the probability to be alive at that age. The steps in the simulation is summarized in Table 1. The numbers refer to the equations given below.

The population comprised of different growth types (G). Growth was assumed to follow the von Bertalanffy growth equation:

$$L_i = L_\infty \left(1 - e^{(-K(t-t_0))}\right)$$

Different growth types were modeled assuming either K or L_{inf} to be normally distributed. In total 21 growth types were modeled in the range of $K \pm 2\sigma_k$ and $L_{inf} \pm 2\sigma_{Linf}$. The variation in growth rate represents the intrinsic (genetic) variation. The relative number of each growth type in the population at time zero (N_G) is given by the normal probability density function.

$$N_G = n \, \exp(\frac{-(K_G - mean/s)^2}{2}) \tag{1}$$

where K_G is the growth parameter for growth type G, mean is the mean growth parameter for the population and s is the standard deviation. N is a scaling factor set at 100.

For each growth type the growth trajectory was simulated given the specified growth parameters. At the start of each year the annual growth increment (ΔL) was calculated from the growth parameters and the size attained.

$$t_i = t_0 - K^{-1} \ln(1 - (L_i / L_\infty)) \tag{2a}$$

$$\Delta L = r(L_\infty (1 - e^{(-K(t_i - t_0))}) - L_i) \tag{2b}$$

The number of surviving fish of each growth type ($_iN_G$) was calculated given the level of natural mortality (M) and fishing mortality (F) giving a pre-defined exploitation pattern. With Z=F+M:

$$_{i+1}N_G = {}_iN_G e^{-Zdt} \tag{3}$$

The time step (dt) in the model was 0.25 year. The population numbers of each growth type decreases over time due to the natural mortality and fishing mortality and the effect on the population composition of growth types was explored.

The two basic growth models are shown in Figure 2. In order to model the effect of environmentally induced variability in growth, the intrinsic annual growth (ΔL) was multiplied by a random variable from a normal distribution with a pre-defined coefficient of variation (CV).

The set of parameters, shown in the Table 1, were chosen to mimic plaice. Three different levels of fishing mortality were explored: F=0.0, F=0.5 and F=1.0. Fishing mortality was applied to fish >20cm onwards. The environmentally induced variation in annual growth were simulated for a CV=0%, 10%, 20%, 30%, 40% and 50%.

Analysis from the simulated population

From the simulated population, the mean growth parameters were estimated as a function of the size of the fish in the population. The second analysis focussed on the annual length increments in the population in relation to fish size. Thus, we calculated the mean length increment of fish of 5cm size classes. To mimic a length stratified sample, the length increments were weighted over the survival probability of each growth type at each length class (cm group), so that each length class was equally represented in the sample of the simulated population.

Back-calculations of real otoliths

For back-calculation of growth rates, otoliths were sampled from the market sampling data at RIVO-DLO. This market sampling data base contains otoliths of fish that were randomly selected by market category from fish landed by commercial fishermen. From these market samples, otolith sets were selected either from specific cohorts at successive years (YCLS samples) or of cm-size classes in a particular year (Length stratified samples). In the length stratified sample, up-to 4 otoliths per cm-group was sampled from the available material. The data base of otolith back-calculations of female North sea plaice was updated by length stratified samples collected in the first quarter in the southern North Sea in 1997, 1998 and 1999.

Results

Simulation of population composition

The length frequency distributions of the simulated populations at three different levels of fishing mortality rate are shown in Figure 1. Without exploitation the population comprises mainly of large sized individuals. Due to the nature of the growth model used, model-2 populations show a larger maximum body size than the model-1 populations. At exploitation rates of F=0.5 and F=1.0, starting at a body size of 20 cm, the number of large sized fish decreased substantially. Among the small fish two cohorts of 1- and 2-group fish can be recognized.

In the first simulation run (Figure 2), the change in the growth parameter was explored at three levels of fishing mortality rate and six levels of environmental variability in growth (CV). The results are expressed in standard deviation units above or below the mean. In model-1 and model-2 populations the mean growth parameter showed a sawtooth pattern at smaller sizes. This sawtooth pattern is due to the distinct cohorts where the smaller individuals have shown a slower growth rate than the larger individuals. At older age, the size distributions of various age group will start to merge reducing the amplitude of the sawtooth. The amplitude of the sawtooth is also reduced at higher levels of environmentally induced variation in growth.

At zero exploitation, the mean growth parameter in the population is close to the mean intrinsic growth parameter. The shift in the proportion of growth types by cm-class was solely due to the differences in growth rate. Faster growth types were slightly more numerous in the larger size classes, while slower growth types dominated the smallest size classes. In model-1 populations, a larger bias is apparent only at very small sizes and at sizes close to Linf. In model-2 populations, the mean growth parameter Linf in the population shows some bias at almost all sizes. At small sizes there is a negative bias, reflecting the predominance of slow growth types. At intermediate size classes a small positive bias develops. At sizes between 40 and 50cm, however, a negative bias is again visible. Only in the population of larger fish (>50cm) a dominance of faster growth types is apparent.

Comparison of the curves between different levels of exploitation shows that exploitation leads to a positive bias in the population composition of growth types at the exploited part of the population. The bias increases with size. At the small size classes a negative bias is apparent. Environmentally induced variability in growth reduces the bias. The order of magnitude of the bias is well below one SD-unit, except in the largest size classes in the population where it may reach 2 SD-units.

Simulation of back-calculation of annual growth increments.

From the simulated populations, the annual length increment was estimated per 5cm size classes. The approach adopted mimics a back-calculation study where otoliths of individual fish provide information of the growth (length increments) at successive age. These length increments can be related to the size at the start of the year. Hence, from the simulated population fish were sampled in equal numbers per cm size class of 1-cm. The length increments (ΔL_{ij}) were expressed relative to the length increment at F=0 and CV=0 (ΔL_{00}): Bias = (ΔL_{ij}- ΔL_{00}) / ΔL_{00}. A positive value indicates that the growth is overestimated.

In the unexploited situation, a negative bias in the back-calculated growth rate occurs in the smallest size class of <10cm, whereas at size classes above 15-20cm a positive bias is apparent. This bias is due to the change in relative proportion of growth types with increasing fish size in the population.

The heavy lines in Figure 3, shows the bias due to the variation in intrinsic growth rate within the population (CV=0) at fishing mortality rates of F=0, F=0.5 and F=1.0. At increasing levels of exploitation, a small positive bias develops in both population models. The bias is less than 5% in model-1 populations. In model-2 populations, a larger bias develops.

With environmental variation in annual growth, the bias in back-calculated growth increases. This is due to the way in which annual variability in growth was modeled: a multiplier of the intrinsic growth rate. In general, the magnitude of the bias in the modeled populations is less than 15% at intermediate levels of environmental variation (CV=0.3). Maximum bias of about 50% was observed at a F=1.0 and CV=0.5 in model-1 population, whereas a maximum bias of 75% was observed in model-2 populations.

Back-calculation of length increments from otolith samples

To analyze the effect of the sampling length on the back-calculated growth, the data set of otolith back-calculations was re-analyzed by sub-sets of sampling length >50cm, 40-50cm and 30-40cm. In each sub-set, the annual length increments were analyzed by 5cm size class (Figure 4). The time series of back-calculated length increments since 1950 clearly shows that the estimates obtained from larger sized fish are higher than those of fish sampled at a smaller size. A scatter plots of the back-calculated growth estimates suggests that there is generally a positive relationship between the estimates obtained from the different size classes (Figure 5).

Analysis of variance of the annual length increment as a function of year (YR) and sampling size class (S) was carried out with the model: dL = α + YR + S + YR*S + ϵ, with year and sampling size class being class variables. The results of the ANOVA shows that in all size classes, year and sampling size class contribute significantly to the variance in growth. The parameter estimates of the ANOVA model for the effect of sampling size class on the bias in back-calculated growth shows that the bias is larger is plotted in Figure 6. The bias in growth increases with sampling size class.

In some of the size classes there is also a significant interaction of sampling size class and year, indicating that the effect of sampling size is stronger in some years than in other years. Such an effect may occur when fishing mortality rate increases of varies over the time period during which otolith samples have been collected, as indeed is the case in plaice. For size class <10 cm, Figure 4 suggests that the difference in growth rates back-calculated from the three sampling size classes has increased over the time period between 1950 and 1998. In the other size classes this seems less obvious. However, the statistical result could also be an artifact without a biological meaning.

Discussion

The present preliminary exploration of the effects of selective fishing on the changes in the population composition of growth types has clearly illustrated that it is impossible to take a representative sample of the initial growth types in the population. At any size, the population composition differs from the one at time zero. The magnitude of distortion increases with the level of exploitation. The difference in results of the two growth models is due to the difference in the size range where the main differences in growth occur. In model-1 populations, these differences occur at intermediate sizes, whereas in model-2 populations this mainly occurs at larger sizes.

No data are available on the variability in the intrinsic growth rate (σK and $\sigma Linf$) nor on the annual variability in growth in natural populations. Heritability studies showed that a 10-30% of the variability in growth could be ascribed to genetic variation and the remaining proportion to environmental variation (Policansky, 1993). The simulation approach could be used to explore the contribution of intrinsic variation and annual variation to the simulated variability in size at age and compare this with the observed variability in size at age or growth, in order to determine the envelope of likely levels of intrinsic and environmentally induced variability in growth.

The results of the analysis of the effect of sampling size on the back-calculated growth from the otolith data set is in general agreement with the results of the simulation study. A positive bias in growth was apparent. The level of magnitude indicated by the empirical study was 10%-40% (Figure 6), whereas the simulation study indicated a bias of less than 25% at moderate levels of CV (0.3) and at the level of fishing mortality on North Sea plaice (F=0.5). This positive sampling bias may explain the increase in growth rate apparent in the larger size classes of the otolith study (Rijnsdorp and van Leeuwen, 1996), and which was also apparent in Figure 4 (40-44.9cm). Further investigations of the effect of sampling bias is needed to detect the influence it may have on the reconstructed changes in growth.

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Table 1. Steps in the simulation of a population of individual fish varying in growth rate and exploited according to a specific exploitation pattern. The population was sampled to estimate growth rates in relation to fish size. The numbers between parenthesis refer to the equations in the text.

Loop for Growth Type (G)
    Loop for Individual Fish (N)
        Determine number of fish for growth type (**1**)
        Loop for Age (YR)
            Determine annual growth rate (length increment) (**2a, 2b**)
            Apply annual growth variability (CV)
            Loop time step within year (T)
                Determine new length
                Calculate number of survivors Ni (**3**)
            End T-loop
            Output (growth type, length, age, Ni)
        End YR-loop
    End N-loop
End G-loop

Table 2. Parameter setting of the simulation model of a population of fish with a normally distributed intrinsic growth parameter K or Linf, at different levels of fishing mortality and different levels of annual variation in growth (environmentally driven).

|		
K	0.20	$year^{-1}$
σ_k	0.02	$year^{-1}$
L_{inf}	60	Cm
σ_{linf}	6	Cm
t_0	0	Year
$L_{recruitment}$	20	Cm
M	0.10	$year^{-1}$
YR_{max}	25	Year
Number of growth types	21	
Number of fish per growth type	normally distributed	
CV (coefficient of variation in annual growth)	0%-50%	Year
F (fishing mortality coefficient)	0.00-1.00	Year

Table 3. Results of the ANOVA of the effect of year (YR) and sampling length-class (S) on the growth estimates by 5-cm size-class as obtained from otolith back-calculations. The model tested was dL = Y + S, where Y and S were class variables. In the SS column the entry for total is the total SS. The SS for the YR, S and YR*S entries are the explained SS.

|	SS	df	MSexplained	MSerror	F	P
<10cm						
Total	9578.36	1468				
YR	1802.46	45	40.055	5.464	7.330	<0.01
S	511.89	5	102.377	5.123	19.985	<0.01
YR*S	979.34	159	6.159	4.992	1.234	n.s.
10-14.9cm						
total	7224.46	1001				
YR	1579.79	45	35.106	5.904	5.946	<0.01
S	496.23	5	99.245	5.414	18.332	<0.01
YR*S	861.45	147	5.860	5.332	1.099	n.s.
15-19.9cm						
total	6536.68	1317				
YR	1384.31	46	30.094	4.054	7.424	<0.01
S	303.77	5	60.753	3.830	15.863	<0.01
YR*S	794.19	159	4.995	3.663	1.364	<0.05
20-24.9cm						
total	5325.68	1334				
YR	1091.93	47	23.233	3.290	7.062	<0.01
S	302.83	5	60.566	3.066	19.753	<0.01
YR*S	506.20	162	3.125	3.058	1.022	n.s
25-29.9cm						
total	5039.69	1601				
YR	784.74	48	16.349	2.740	5.967	<0.01
S	463.20	5	92.640	2.449	37.821	<0.01
YR*S	663.13	172	3.855	2.274	1.696	<0.01
30-34.9cm						
total	5100.24	1897				
YR	465.70	48	9.702	2.507	3.871	<0.01
S	590.99	4	147.747	2.192	67.414	<0.01
YR*S	580.93	156	3.724	2.050	1.816	<0.01
35-39.9cm						
total	4272.75	2235				
YR	488.39	49	9.967	1.731	5.757	<0.01
S	422.67	3	140.891	1.540	91.491	<0.01
YR*S	347.93	135	2.577	1.472	1.751	<0.01
40-44.9cm						
total	2491.93	1941				
YR	262.07	49	5.348	1.179	4.538	<0.01
S	233.72	2	116.861	1.056	110.647	<0.01
YR*S	152.92	92	1.662	1.025	1.621	<0.01
45-49.9cm						
total	857.19	1185				
YR	155.30	49	3.169	0.618	5.129	<0.01
S	49.73	1	49.728	0.575	86.544	<0.01
YR*S	16.91	43	0.393	0.582	0.676	Ns

Figure 1. Simulation. Panels left: the two models of intrinsic growth variation employed. The intrinsic variability in growth was modeled through a normal distribution of parameter $K \pm \sigma_k$ (model 1) and $L_{inf} \pm \sigma_{Linf}$ (model 2). Panels right: the size distribution of the modeled populations with no fishing mortality (F=0) and two levels of fishing mortality rate (F=0.5 and F=1.0 for fish >20cm).
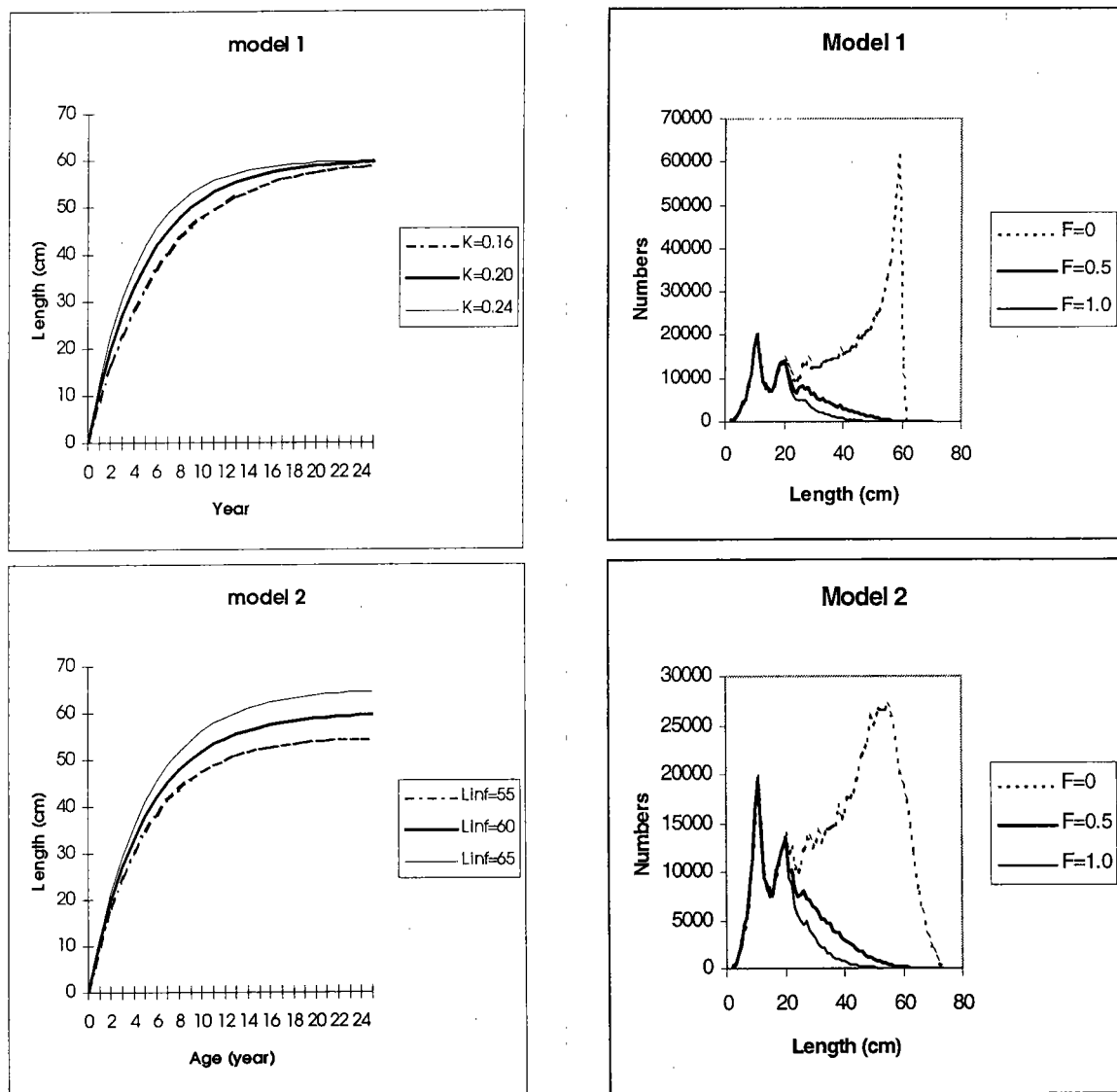
Figure 2. Simulation. Change in the mean growth parameter of a population fish surviving to a particular fish size (cm) for three levels of fishing mortality (F=0, F=0.5 and F=1.0) and different levels of environmental variability in the annual growth (CV=0, CV=0.1, CV=0.2, CV=0.3, CV=0.4 and CV=0.5). The left hand panels presents simulation results for a model-1 population with K=0.20 (sd=0.02). The right hand panels presents results for a model-2 population with Linf=60cm (sdev=6)
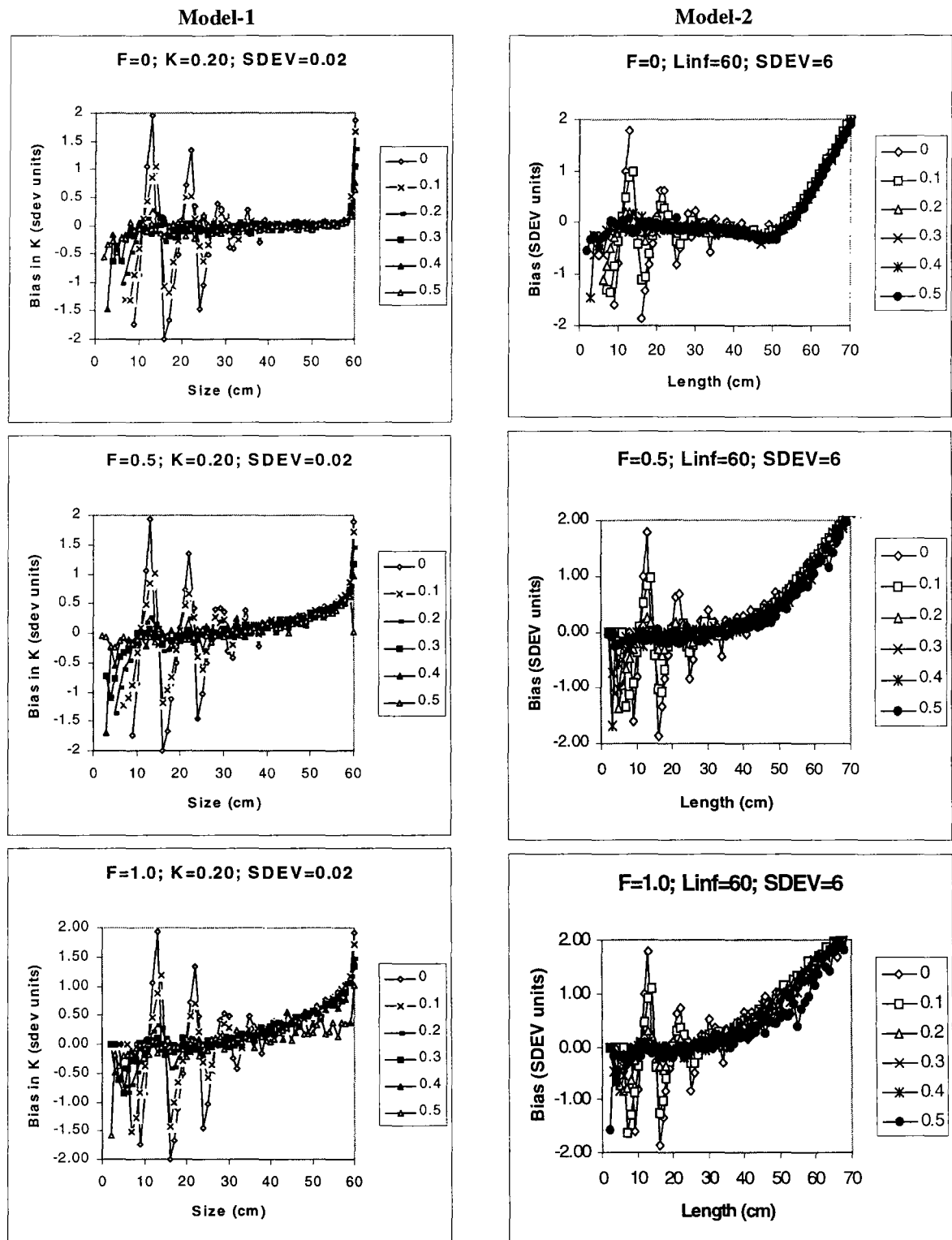
Figure 3. Simulation: Bias in growth estimates of 5cm size classes obtained by back-calculation of otoliths at fishing mortality rates of F=0, F=0.5 and F=1.0, upper, middle and lower panel, respectively, and at various levels of environmental variability: CV=0, 0.1, 0.2, 0.3, 0.4 and 0.5. The bias in growth is expressed as the difference between the simulated growth and the growth at zero mortality and CV=0. Righthand panels: Model-1 with K=0.20 (sdev=0.02); Lefthand panels: Model-2 with Linf=60 (sdev=6).
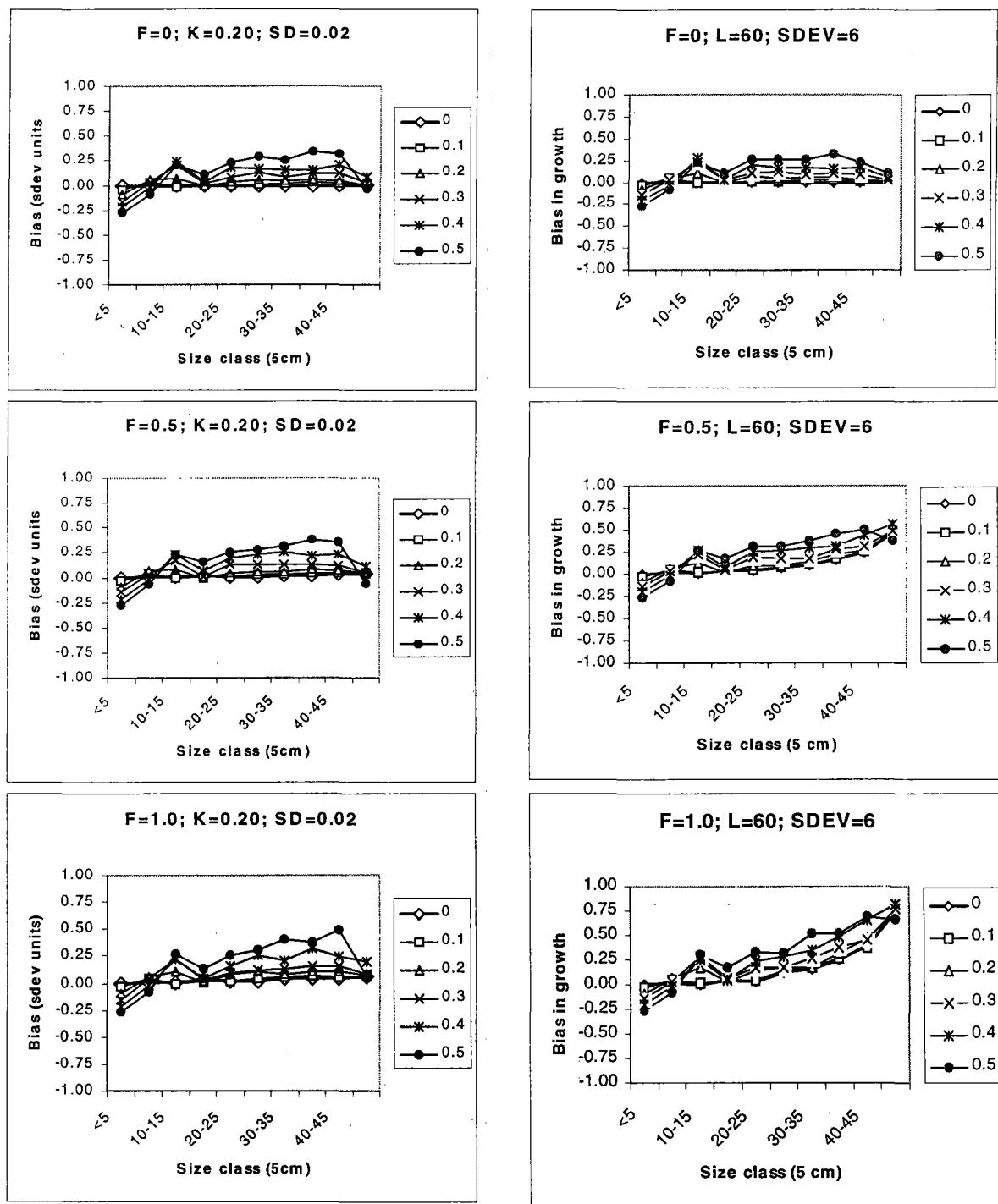
Figure 4. Otolith samples of plaice: Effect of sampling lengths of otoliths on the back-calculated growth (cm). The back-calculated length increment by 5cm size class (<10cm, 20-24.9cm, 30-34.9cm and 40-44.9cm) is compared from otolith samples of 30-40cm fish, 40-50cm fish and >50cm fish. Data used: Length stratified otolith samples off female plaice otolith.
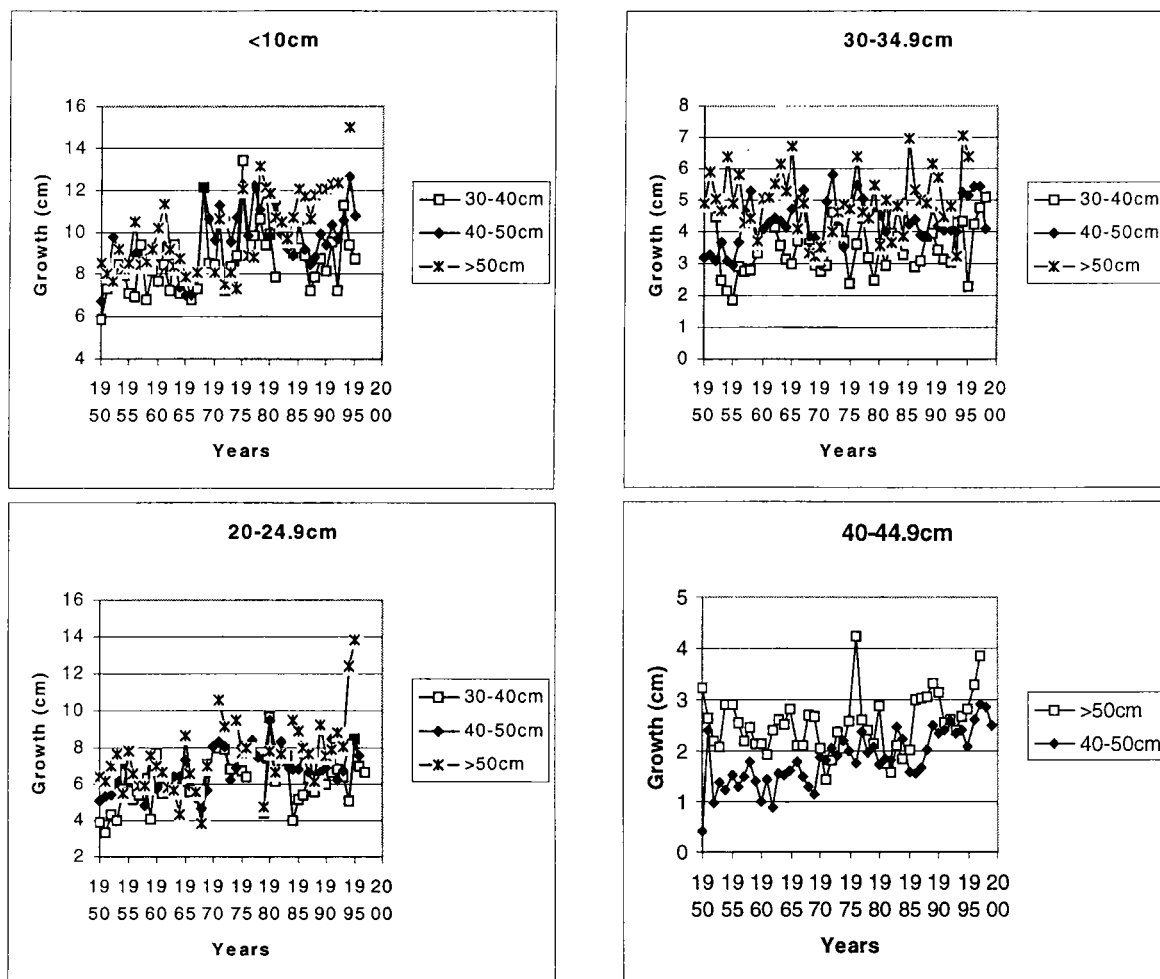
Figure 5. Scatter plots of the back-calculated growth of 4 size classes of plaice as obtained from otolith sampled from fish of >50cm, 40-50cm or 30-40cm.
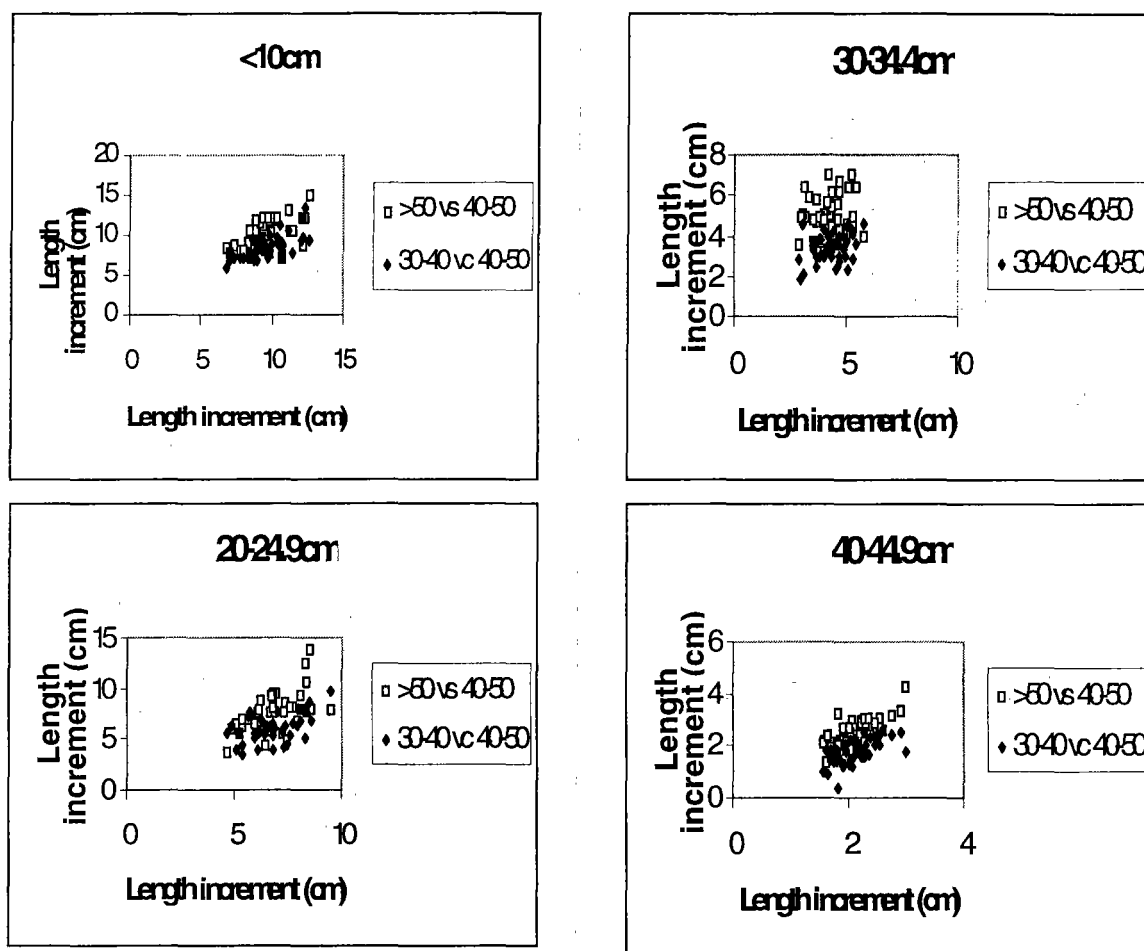
Figure 6. Otolith samples of plaice: Relative bias in back-calculated length increment, expressed as proportion of the difference between the back-calculated length increment from sampling size class >50cm, for different fish sizes (10-14.9, 20-24.9, 30-34.9, 40-44.9cm). Data: otolith samples of plaice collected in the period 1950-1999.