EFFECT OF SIZE-SELECTIVE MORTALITY ON GROWTH OF COASTAL COD (*Gadus morhua* L) ILLUSTRATED BY TAGGING DATA AND AN INDIVIDUAL-BASED GROWTH AND MORTALITY MODEL

by

Tore S. Kristiansen and Terje Svåsand

Institute of Marine Research,
Division of Aquaculture, PO Box 1870,
N-5024 Nordnes-Bergen, Norway

ABSTRACT

Since 1983 more than one million reared cod juveniles have been tagged and released in different areas along the Norwegian coast. The goal of the programme is to evaluate the ecological and economical potential in sea ranching with cod. In this evaluation use of correct growth rates and growth models are essential to estimate optimum yield and fishing patterns. In one of the release areas the apparent growth rates of 3 year old cod, calculated by sampling the population at different ages, were very slow (0.08 mm/day). However, when measuring individual growth rates of individual tagged cod of the same size, the mean growth rates were much faster (0.24 mm/day). These observations were attributed to size-selective fishing mortality and were illustrated by an individual based simulation model of a population of cod with variable individual growth rates. The effects on mean length at age of the surviving population of increasing fishing intensity and mesh sizes were demonstrated. The model showed that size selective fishing with the observed individual growth variation, removed the fastest growing individuals at proportionally higher rates than the slower growing ones, leading to decreased mean population growth rate. Also the fishing mortality values which gave the largest yields, changed when individual variation was included, and when we used the apparent growth rate in the model the yield per recruit was dramatically reduced. This study has shown that individual growth variation and size selective mortality are factors which should be considered in future fisheries management and ecosystem models.

INTRODUCTION

After a cohort of cod has recruited to the fisheries, its fishing mortality is usually much larger than its natural mortality. In many cod stocks the fishing mortality (F) may exceed 40% a year (e.g. North Sea cod F>0.7, Anon., 1995a; North Atlantic cod, F>0.6, Anon., 1995b). In most fish populations, the fish of each year-class are subject to differential mortality in relation to size (Ricker, 1969). When mortality rates increase with size, the fastest growing individuals will be removed at proportionally higher rates than the slower growing membersof the same year class. The slowest growing individuals would then be over-represented at older ages ("Lee's Phenomenon": first discovered by Sund, 1911, and discussed in detail by Lee, 1912). Further, size-selective fishing mortality will cause an apparent reduction in population growth rate (increase in mean length/weight of the population with age), which may lead to serious errors in estimation of important population parameters such as production and yield per recruit, if not corrected for (Ricker, 1969; Myers 1989, Parma and Deriso, 1990; Laevastu, 1992). Size-selective mortality will only have an effect on a cohort when individual size at age and growth rates vary. However, the natural occurring variance in individual growth rates within cohorts, and the extent to which this variance magnifies the effects of size selective fishing has been little explored. The main reason for this has probably been lack of appropriate models and field data.

A coastal cod enhancement programme was initiated in western Norway in 1983, and since then more than a million tagged cod juveniles have been released at several locations on the Norwegian coast (Svåsand, 1994). The goal of the programme is to evaluate the ecological and economical potential of ocean ranching of cod. The reared cod will recruit to the fishery in the release areas, and the yield from the releases will depend on the growth of the released fish and natural mortality and fishing mortality in these areas. The observed returns of the tagged fish and samples from fishing surveys give us a picture of survival and yield under the present conditions, but this is not necessarily the optimum yield and may be a result of suboptimal size selective fishing mortality. To obtain insight into this problem we need models that can simulate the effects of changing conditions (e.g fishing mortality, size selection, growth variation) on growth and yield.

In one of the release areas in particular, we observed a very slow rate of population growth in both released and wild III+ cod (Svåsand and Kristiansen, 1990b). In the same area we also tagged wild cod to estimate mortality rates and recapture rates of "large" cod, and found a very high fishing intensity. The cod were fitted with individually numbered tags and individual lengths were measured at tagging and recapture. When we calculated the individual growth rates, we found much higher growth rates than the apparent population growth rate of the same group. In this paper these observations are studied in more detail, and to the extent to wich this can be explained by size selective fishing will be discussed.

To simulate the effects of size selective fishing, we have chosen to use an individual-based model (DeAngelis and Gross, 1992; Judson 1994). The model "creates" each individual and keeps track of size at age and cause of mortality of each fish. We can therefore calculate for example mean size and standard deviation of the surviving population at any time. The model can also simulate the effects on the population and yield of increased fishing mortality, selection length, individual growth variation, and combinations of these. The importance of these results in the management of commercial fisheries is discussed.

MATERIALS AND METHODS

Release area

From 1983 to 1987 almost 20,000 reared 0- and I-group cod were released in Heimarkspollen (60°3'N 5°14'E), a small, nearly land-locked fjord (2.9 km^2) at Huftarøy, the largest island of the Austevoll archipelago. The connection to the outside fjord is through three narrow inlets, of which the largest is about 3 m deep and 30 m wide. Topographical and hydrographical descriptions of Heimarkspollen are given in Kristiansen and Svåsand (1990).

Released reared 0-group cod.

The released juveniles had been reared in a enclosed seawater pond (Øiestad *et al.*, 1985) and all fish were tagged with individual numbered Floy anchor tags or internal steel tags. In this paper the recapture data from the releases of 0-group Floy-tagged cod in the autumns of 1983-1986 are used (Table 1).

Table 1. Number of reared cod tagged with Floy tags released in autumn 1983, 84 and 85, sizes at release, number and percentage recaptured, and yield per released cod.

Group	Number	Mean length	St. dev	No. recaptured	% Recaptured	Y/R (g/released cod)
H83	2923	182	20	688	23,5 %	181
H84	3754	171	30	751	20,0 %	81
H85	7790	162	16	1216	15,6 %	61
All	14467	168	24	2655	18,4 %	108

Tagging of "large" cod

A total of 1067 large cod were captured alive between December 1986 and February 1988, measured and tagged and released back into the sea (Svåsand 1991)(Table 2). This group is referred to as "large" cod. Of these 121 were previously released fish, which were released again with the same tag after tag number and size had been registered.

Table 2. Number of "large" cod released 1986-88 of the four size groups, mean length and standard deviation at release, number and percentage recaptured.

Group	Number	Mean length	St. dev	No. recaptured	% Recaptured
L1 (<25cm)	128	206	27	47	36,7 %
L2 (25.0-34.9 cm)	467	304	27	270	57,8 %
L3 (35.0-44.9 cm)	342	389	27	197	57,6 %
L4 (>= 45.0 cm)	130	522	81	62	47,7 %
All	1067			576	54,0 %

Sampling and analysis of tagging data

The sampling programme was based on tag returns from local fishermen in Austevoll and other areas (Svåsand and Kristiansen, 1990b; updated unpublished results) and experimental fishing surveys in Heimarkspollen with small meshed trammel nets and trout nets (Kristiansen and Svåsand, 1990).

Population growth rates

Most of the data were acquired by fishermen and anglers, and most of the tag returns included information on both length and weight. However, the weight information was assumed to be

inaccurate, and length was therefore used to describe growth. Daily length increment (DLI, mm/day) was chosen as the unit of growth rate. Date of hatching was defined as 1 April (Svåsand and Kristiansen, 1990a). The population growth rate is defined as the increase in mean length of a cohort (here: group of fish of the same age) with age.

Mean individual growth rate

Mean individual growth rate is defined as the mean daily length increment measured from individual fish in a given time period. In order to obtain information on mean individual growth and growth variation in different size intervals, the group of "large" cod were divided in 4 size intervals at release and mean individual growth rates and standard deviations for each size interval were estimated (Table 2 & 3). All recaptures outside the release area (Heimarkspollen), and recaptures less than 30 days and more than one year after tagging were excluded.

The model

The model is an individual-based model (IBM), in which we simulate the release of a group of N cod juveniles, who live through their lives (one at a time) independent of each other (Fig. 3). The life of a fish is modelled in time steps of 90 days (one quarter). In each time step the fish has a size-dependent probability of survival and if it survives it grows according to an individual growth function. If the fish does not die the loop stops at a maximum age. If a fish dies it has either been "fished", "predated" or has "died" from unknown causes, according to length-dependent probability functions. The resulting set of data consists of lengths and weights of the surviving cod, the fished cod and the cod dead from other causes in each time step, which can then be analysed and compared.

The growth model

The length at release for an individual cod is drawn at random from a normally distributed population. The expected mean and standard deviation chosen were 170 mm and 17 mm, respectively, which are similar to those of the released reared cod (Table 1). The expected mean length of the population in the next time step, when there is no mortality is given as:

$$L_{t+\Delta t} = L_t + DLI(L_t)\Delta t,$$

where $DLI(L_t)$ is a length-dependent function for daily length increment and L_t is mean length at the previous time step. The individual length-dependent growth rates are assumed to be normally distributed, $\sim N(DLI(L_t), \sigma)$. At release each cod was given a constant deviation, $s(i)$, from the mean growth rate, which was drawn randomly from the distribution $\sim N(0, \sigma)$. The standard deviation (σ) was chosen to be independent of fish length. The growth function for an individual is:

$$L_{i,t+\Delta t} = L_{i,t} + (DLI(L_{i,t}) + s(i))\Delta t.$$

The fish was not allowed to decrease in length $(If\ (DLI(L_{i,t}) + s(i)) < 0\ then\ (DLI(L_{i,t}) + s(i)) = 0)$.

The mean length-dependent growth rates ($DLI(L_t)$), were chosen as constants within four length intervals (< 250 mm, [250,350 mm>, [350,450mm>, $\geq$450). The chosen constants were equivalent to the observed mean individual growth rates in the same length intervals

calculated from recaptured "large" cod (Tabel 3). The standard deviation was chosen equal to the weighted mean of the standard deviation of DLI observed in each group (0.19 mm/day, Table 3). To avoid «super cod» in the cohort maximum size was set to 1400 mm.

Length (mm) was tranformed to ungutted weight (g) by the function (Kristiansen 1987):

$Weight = 1.11(0.006((Length/10)^{3.1}) + 5.6$

The mortality model

The size-dependent total rate of instantaneous mortality (yr^{-1}), $Z(L_i)$, is the sum of the fishing mortality, $F(L_i)$, predation mortality $M(L_i)$ and residual natural mortality, M_0, i.e

$Z(L_i) = F(L_i) + M(L_i) + M_0,$

To describe the size dependency of the predation mortality we have chosen a linear function, in which the predation mortality decreases linearly as prey size increases up to a maximum:

$M(L_i) = a - bL_i$, when $L_i < 30$ cm, else $M(L_i) = 0$.

Chosen parameters for predation mortality (only cod ≤ 30 cm) were M(Li) = 4.125 - 0.1375L$_i$. and residual mortality was set to $M_0 = 0.2$ independant of size. These values gave mortality rates which seemed reasonable on the basis of earlier estimates from the same area (Svåsand and Kristiansen 1990b, Kristiansen and Svåsand, in prep) (Fig. 1).

Figure 1. Length-dependent function for natural mortality (predation and residual mortality) used in the simulations.
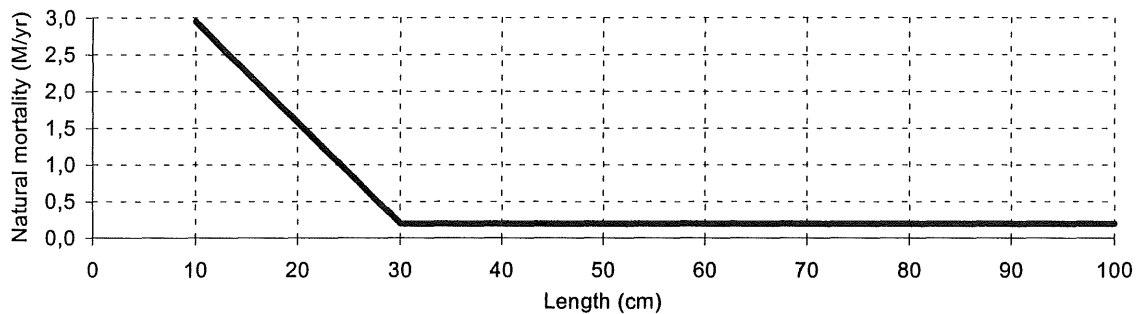
Size-dependent fishing mortality is modelled as a S-shaped logistic curve (Fig. 2), as usually used to quantify retention in a trawl fishery (e.g Sparre and Venema 1992):

$R(L_i) = 1/[1 + exp(-r(L_i - L_{50}))]$; $r = 2ln3/(Selection\ range)$; $L_{50} = (selection\ factor * mesh\ size)$;

where L_{50} denotes the length at 50% selection. The fishing mortality is expressed as:

$F(L_i) = F_{max}R(L_i).$

F_{max} is fishing mortality at 100% recruitment. The size-dependent probability of survival through one time step (quarter), S, is then modelled as:

$$S(L_i)=exp(-Z(L_i)/4)$$

when $Z(L_i)$ is expressed in instantaneous length-dependent mortality per year. At the beginning of each time step a random number is drawn from the uniform distribution [0,1]. If the number is less than or equal to $S(L_i)$ the fish survives this quarter, otherwise it dies. If the fish dies it is either fished or dead from other causes. The conditional probability of being fished, given that the fish is dead:

$$p(fished|dead)=F(L_i)/Z(L_i).$$

To decide if the fish was fished a new random number is drawn from the uniform distribution [0,1], and if the number is less or equal to $p(fished|dead)$ the fish was fished, otherwise the fish died from natural causes.

Figure 2. Examples of trawl selection curves used in the model. Selection range = 50 mm. 50% selection range 35 cm, 55 cm and 75 cm.
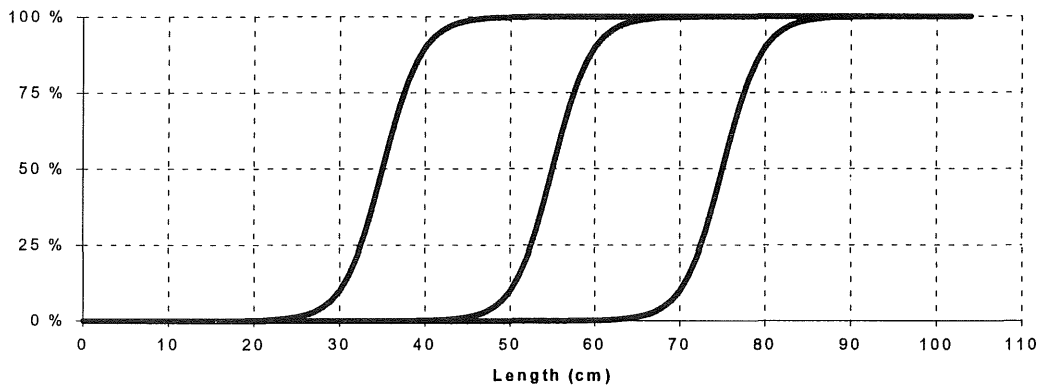
The model was programmed in SAS 6.10 (Sas Institute Inc.). Random numbers were drawn by the functions RANNORM (normal distributions) and RANUNI (uniform distributions), using the computer time as seed, to avoid predetermined sequences of random numbers.
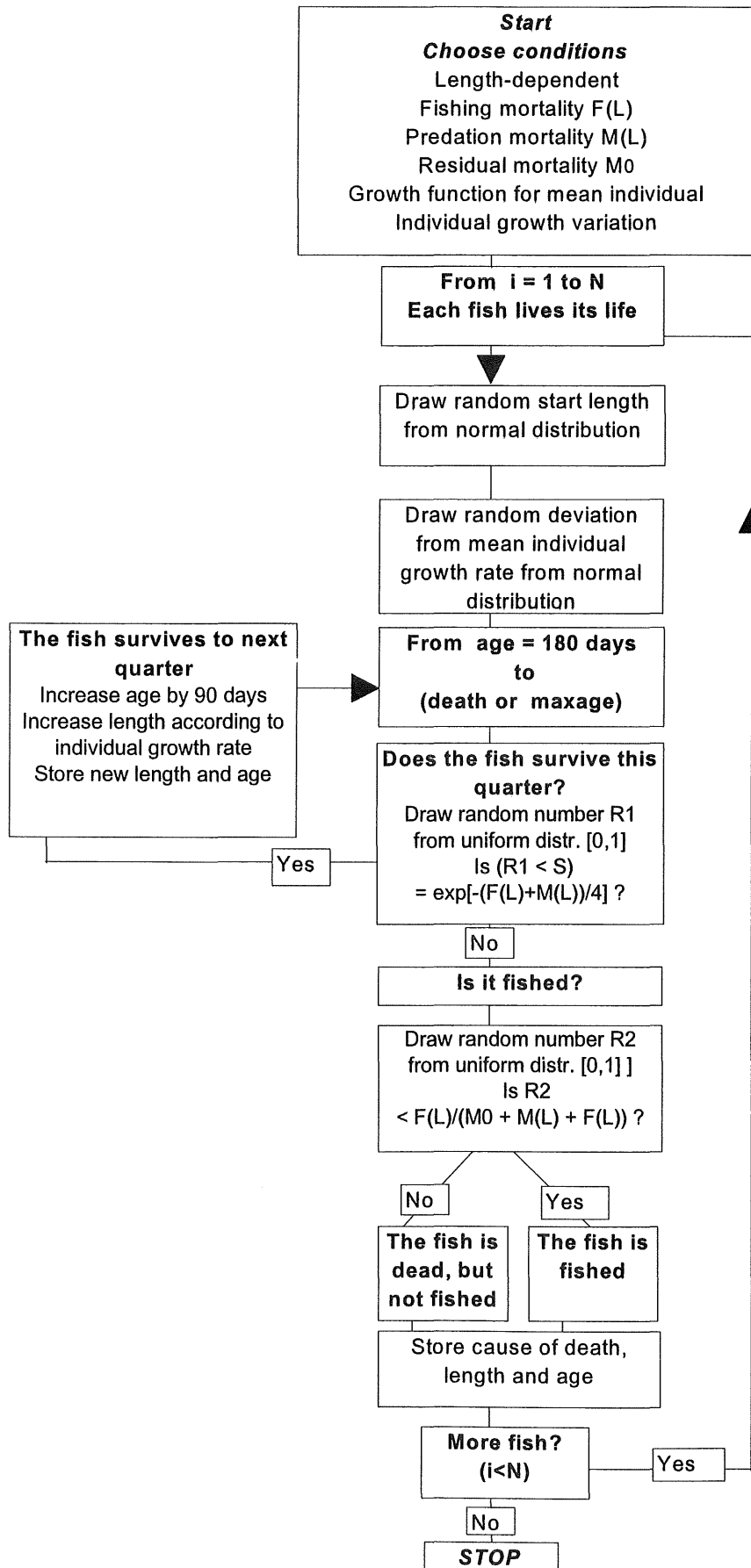
Model runs and analysis
The effect of growth variation on mean lengths at age in the population and in the catch were simulated with standard deviations of the DLI equal to 0.0, 0.1 and 0.2 mm/day, with fishing mortality F=1.0 and 50% selection length = 550 mm. Each set of values was run on two simulated releases of 10,000 cod. The mean length of the population and in the catch were calculated in each quarter, and the mean of the two simulations was used in the presentation.

To study the effect of increasing fishing mortality and increasing 50% selection length on the mean length at age and mean growth rate of the population and in the catch, the model were ran with 4 different values of fishing mortality (0, 0.5, 1.0, 1.5) and 4 different 50% selection lengths (100, 350, 550, 750 mm). Each set of values were ran on 2

simulated releases of 10,000 cod. Mean length in the population and in the catch were calculated in each quarter, and the mean of the two simulations was used in the presentation.

To study the effect of increasing fishing mortality and increasing 50% selection length on the yield pr relased fish (yield/recruit), the model was run using 10 different values of fishing mortality (0.25 - 2.5, step 0.25) and 10 different 50% selection lengths (0-1350 mm, step 150 mm). Each set of values was run on 10 simulated releases of 1,000 cod, and yield per recruit was calculated as the sum of the weight of the fished cod in all releases, divided by the number of fish released (10,000).

Figure 3. Flow chart of the individual-based growth and mortality model

Start
Choose conditions
Length-dependent
Fishing mortality F(L)
Predation mortality M(L)
Residual mortality M0
Growth function for mean individual
Individual growth variation

From i = 1 to N
Each fish lives its life

Draw random start length
from normal distribution

Draw random deviation
from mean individual
growth rate from normal
distribution

The fish survives to next
quarter
Increase age by 90 days
Increase length according to
individual growth rate
Store new length and age

From age = 180 days
to
(death or maxage)

Does the fish survive this
quarter?
Draw random number R1
from uniform distr. [0,1]
Is (R1 < S)
= exp[-(F(L)+M(L))/4] ?

Yes

No

Is it fished?

Draw random number R2
from uniform distr. [0,1]]
Is R2
< F(L)/(M0 + M(L) + F(L)) ?

No

Yes

The fish is
dead, but
not fished

The fish is
fished

Store cause of death,
length and age

More fish?
(i<N)

Yes

No

STOP

RESULTS

Growth of recaptured reared cod

The recaptured reared cod showed large variations in size at age, as shown in the scatterplott (Fig. 4). The apparent mean growth of two-year-old and older fish was slow and seemed to stagnate at a very low asymptotic length, as shown by the von Bertalanffy growth curve fitted to the data (Fig. 4, $L\infty$ =437 mm). The slope of the curve at age two was 6.9 cm/yr (DLI= 0.19 mm/day) and at age three only 3.0 cm/yr (DLI=0.08 mm/day). The same trend is apparent when we look at the mean length at age from the recaptures in nets, by hook and line and fishing surveys (Fig. 5). The mean lengths from recaptures from the fishing surveys are assumed to be closer to the true mean length at age in the population, and we can see that the catches from the fishermens nets are size selective, especially during the first two years after release. When we compare the observed mean lengths with the "true"growth curve, based on mean individual growth rates (Tabel 3), the apparent growth rate deviates strongly from the individual growth rate from about quarter 10.

Figure 4. Scatterplott of length at age of recaptured reared cod, and von Bertalanffy curve fitted to the data ($L\infty$ =437 mm, K=0.835, t_0=.0076), from the release groups in Table 1.
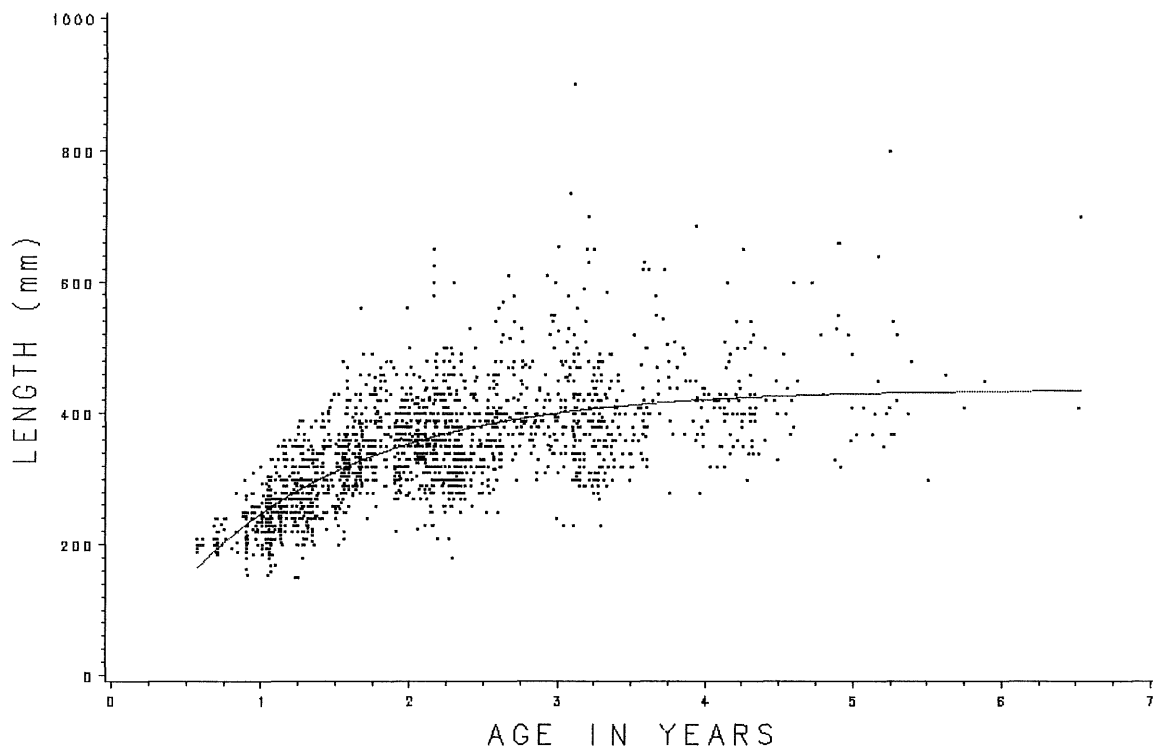
Figure 5. Mean length at age of recaptured cod caught in nets, on hook and line and in research surveys. The "true" growth curve calculated from "large" cod and the von Bertalanffy growth curve (Fig 4.) are shown to illustrate the difference between individual growth rate and apparent population growth rate.

Legend:
- ◆ Fishing nets
- ◈ Researv surveys
- ◇ Hook and line
- —— Mean individual growth (model)
- ········ Von Bertelanffy
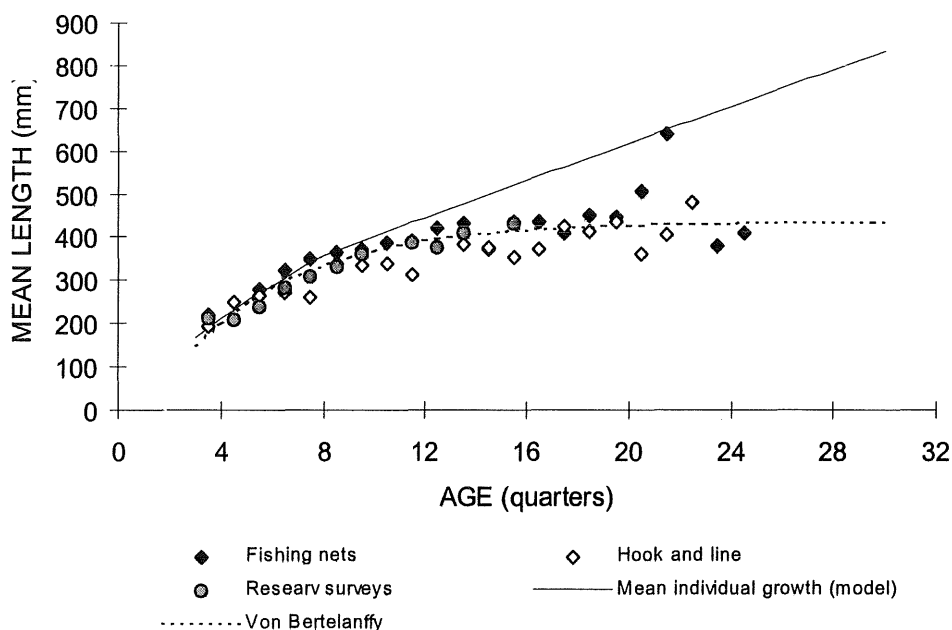
Growth of recaptured "large" cod

Mean growth rate and growth variation in the various size groups is shown in Table 3. The growth rate decreased with increasing size, but seemed to be stable (linear) for cod larger than 350 mm. The individual growth variation was rather stable, with an estimated weighted mean of standard deviation of DLI equal to 0.19 mm/day. The distribution of DLI within the groups is shown i Figure 6.

Table 3. Growth of tagged "large" cod, recaptured in the release area more than 30 days and less than one year after release.

Group	Number	Mean length at release	Mean length at recapture	Mean DLI	St.dev DLI	Days in sea
L1 (<25cm)	17	215	304	0.47	0.23	205
L2 (25.0-34.9 cm)	118	311	373	0.39	0.19	176
L3 (35.0-44.9 cm)	96	392	429	0.24	0.18	150
L4 (>= 45.0 cm)	25	550	577	0.25	0.18	129
All	256	358*	409*	0.33*	0.19*	

* weighted mean

Treating the whole group of "large" cod as a "cohort" and plotting length at recapture against days after release (Fig. 7a), linear regression on the points gives a population growth rate of 0.15 mm/day, which is about half the mean individual growth rate (0.33 mm/day, Table 3). The plot of daily length increment against days after release shows a trend towards decreasing growth rate with time (Fig. 7b), indicating that the fastest growing fish has a higher probability of recapture. The decreasing trend in mean number of days in the sea before recapture by increasing size at release, also strongly indicates size-dependant mortality (Table 3). Using all recaptures from the release area, the mean numbers of days in the sea were 295 s in L1, 209 in L2, 181 in L3 and 148 in L4.

Figure 6. Histograms of individual growth variation (DLI) in the four release groups of "large" cod, recaptured between 30 and 365 days after release.
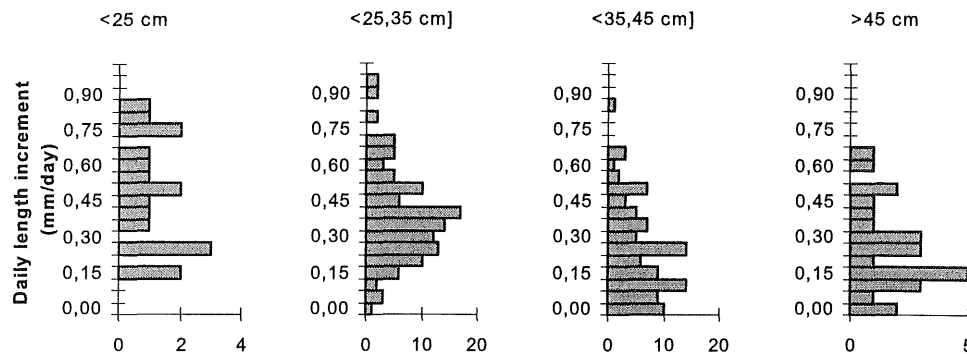
Most of the recaptures (477 of 576) were reported within one year after release, which together with the high recapture ratio (54%), showed that the fishing mortality in the area was very high. Using only recaptures from the release area (Heimarkspollen), estimated mortality was Z=1.54/yr. (Linear regression on ln(recaptures), time until recapture, unit half a year) Assuming natural mortality about 0.2, this gives a fishing mortality of F=1.34. Using all recaptures the estimated mortality was Z=1.70/yr.

Model simulations

Our main aims in using the model was to investigate what happened when we fished with size-selective gear on a cohort of unique individuals with variable size and growth rate similar to the observed values in the release area, and tto find out whether size-selective fishing could explain the oberved growth pattern in the area. One or many groups of cod with normal length distribution (mean 170 mm, st.dev. 17 mm), were "released" in the fishing area, and each cod was given an individual predetermined growth curve at release.

Effects of increased growth variation

First we wanted to simulate the effects of individual growth variation on the mean length in the population and in the catch, when we fished with size selective fishing mortality. To illustrate this we ran the model with no size and growth variation (all individuals have the same size at age) and with variable size and standard deviation of DLI equal to 0.1 and 0.2 mm/day. The highest value was similar to the observed values in the release area (Table 3). The fishing mortality was set at F=1.0 and 50% selection length was set at 550mm.

The effects on mean length at age in the surviving cohort and in the catch under the different conditions is shown in Fig. 8. When there was growth variation, the mean length in the population decreased strongly when the fishing mortality increased, and the growth curve changed from linear (when no variation) to a "von Bertalanffy like" curve (Fig. 8a) . The effect increased with increased growth variation. In the catch, increasing individual growth variation led to earlier recruitment and increased mean size at age for the first five years (20 quarters). Later, the mean mean length were about constant (Fig. 8b). The jumping curves at older ages arise from random effects in the simulation, due to a few old fish in the catches when the fishing mortality is high.

Figure 7. Length at recapture of the group of large cod (a) and mean individual daily length increment from release to recapture (b). Mean length and stadard deviation at release are indicated in (a). The lines are least square linear regression on all points on the plot. The equations are (a): length=0.153(days after release)+384 (b): DLI=-0.000164(days after release)+ 0.355. Recaptures within 30 days after release are excluded.

(a)

(b)
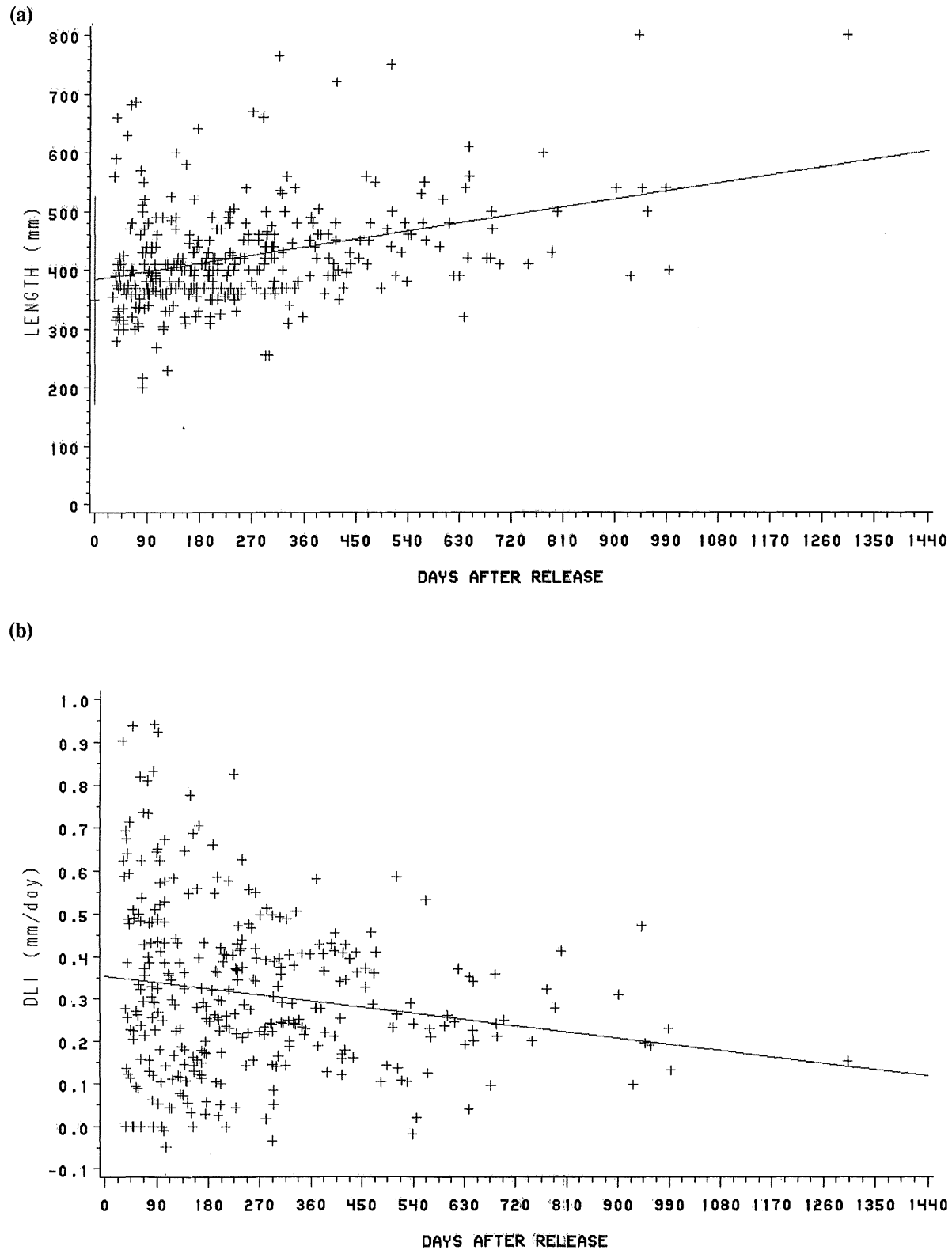
Effects on population mean lengths of increased 50% selection length and increased fishing mortality

The effect of increasing 50% selection length (50% SL) on the mean length at age of the cohort is shown in Fig. 9. The smallest selection length is set to 100 mm, which means that there is no size selection on our fish. In general size-selective fishing mortality leads to decreased mean size at age in the cohort, compared no size-selection or no fishing (Fig. 9a-d.). At F=0.5 (Fig. 9b), the effect is smallest at 50% SL = 350 mm, because the time the cohort needs to grow through the size selection interval is shortest for the smallest selection lengths, caused by faster mean growth at small sizes. At low mortality many fast growing fish survives and can contribute to the mean lengths at older age, where there is no size seletivity. The reduction of mean length at age increases with increased fishing mortality (Fig. 11a). In the catch (Fig. 10) the mean length at age increase with increasing 50% selection length, but the differences decrease with age of the fish. Here too the effects increase with increasing fishing mortality, and at F=1.5 there is almost no apparent growth in mean length at age in the catch (Fig. 10b).

Effects on mean DLI at age of size-selective fishing

The mechanisms which lead to the decreased mean size of the population are clearly demonstrated in Fig. 12. The fastest growing fish are fished first, and the average growth rate of the fish in the catch lies far above the average when there is no fishing. This leads to decreased mean growth rate in the cohort, and the effect increases with increasing fishing mortality (Fig. 13).

Effects of size-selective fishing mortality and fishing intensity on yield per recruit, using three different growth models.

As shown above, size-selective fishing can have major effects on a cohort with variable individual growth and size, and this must obviously also have an effect on the yield of the cohort. This is demonstrated in Fig. 14, where we ran the model with different combinations of fishing mortality and 50%SL and three different growth models. In Fig. 14a, we have used the growth model used above with growth variations as observed in the release area. In Fig. 14b we have used the same model, but with no growth or length variation (all fish with same length at age), and in Fig 14c the von Bertalanffy growth curve from Fig. 4, (L∞ =437 mm K=0.835 t_0=.0076), estimated from recaptured reared cod.

The three methods gave large differences, with maximum yield/recruit of 1109 g with growth variation (Fig 14a), 632g (57%) with mean individual growth (Fig 14b) and only 115 g (10%) with the von Bertalanffy growth model (Fig 14c). These are results from a stochastic model (10 runs of 1000 fish) and the results will show some variation between runs, but the trend is very clear. The fishing moralities and mesh sizes (50% SL) which gave the maximum values were also very different between the models. This shows that use of individual groeth rates and individual growth variation is very important factors in yield calculations, when there is size-selective fishing mortality. Use of apparent population growth may lead to large underestimation of the optimum yield and give wrong optimal mesh sizes and fishing moralities. The errors will increase as size-selection increases in intensity, as shown above (e.g. Fig. 10).

Figure 8. Effect of increasing individual growth variation on the mean length at age in the cohort (a) and in the catch (b) .

a) Mean length at age in the cohort
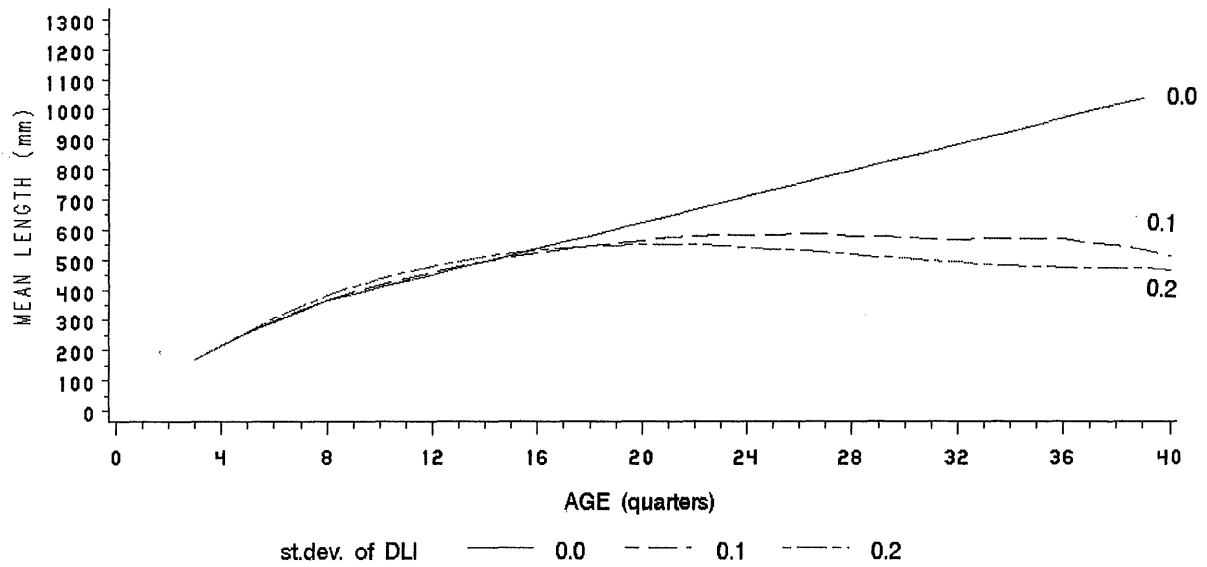
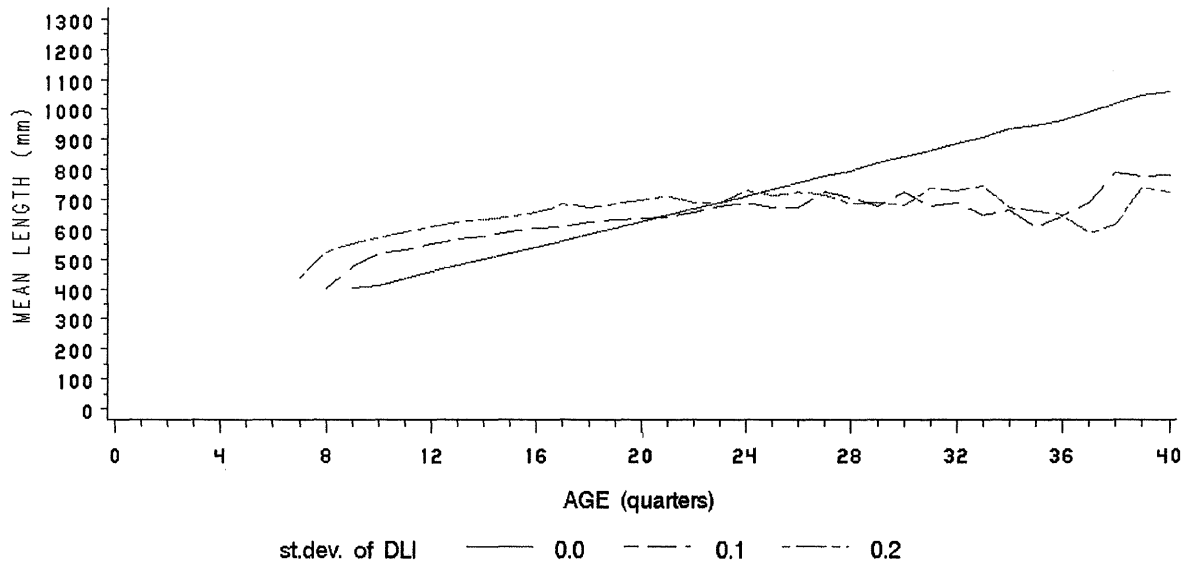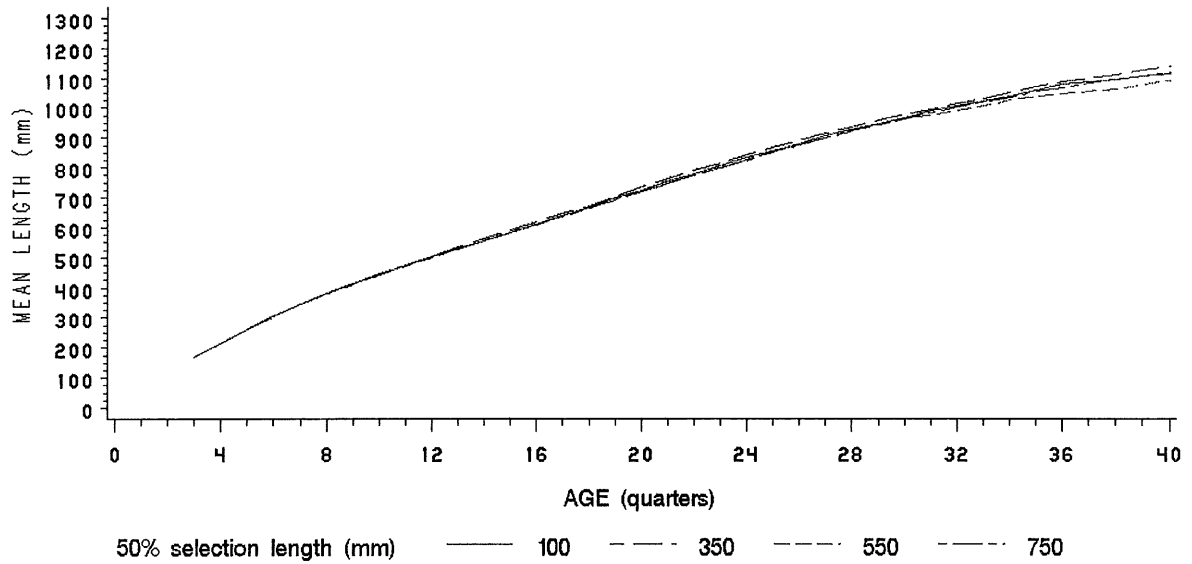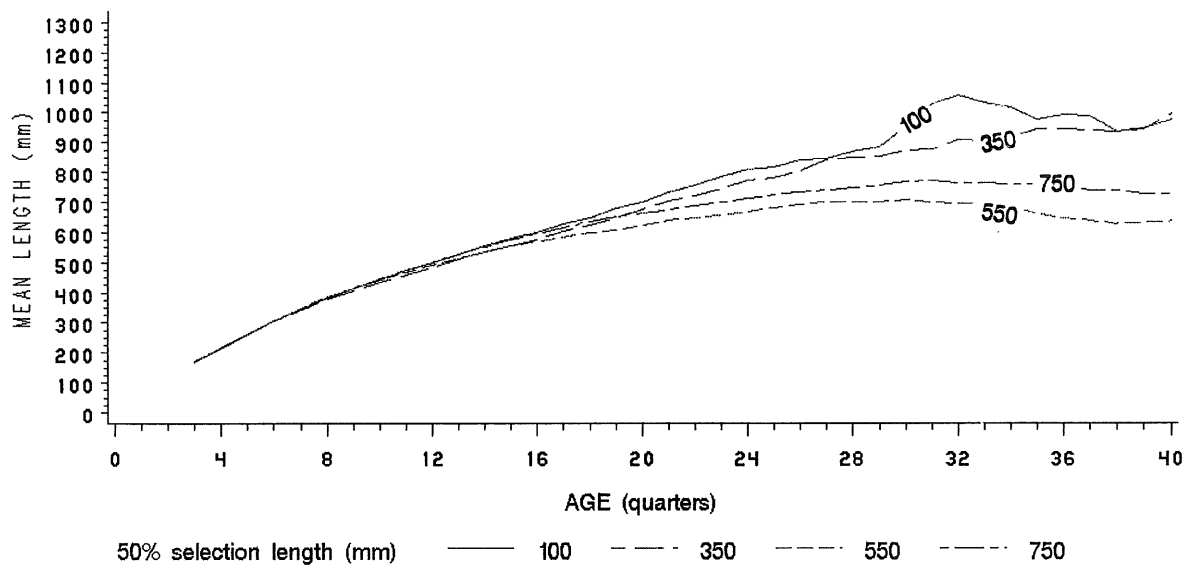**b) Mean length at age in the catch**

Figure 9. Effect on mean length in the population of increasi ng 50% selection length
(150mm, 350 mm, 550 mm and 750 mm) .

a) No fishing (F=0)

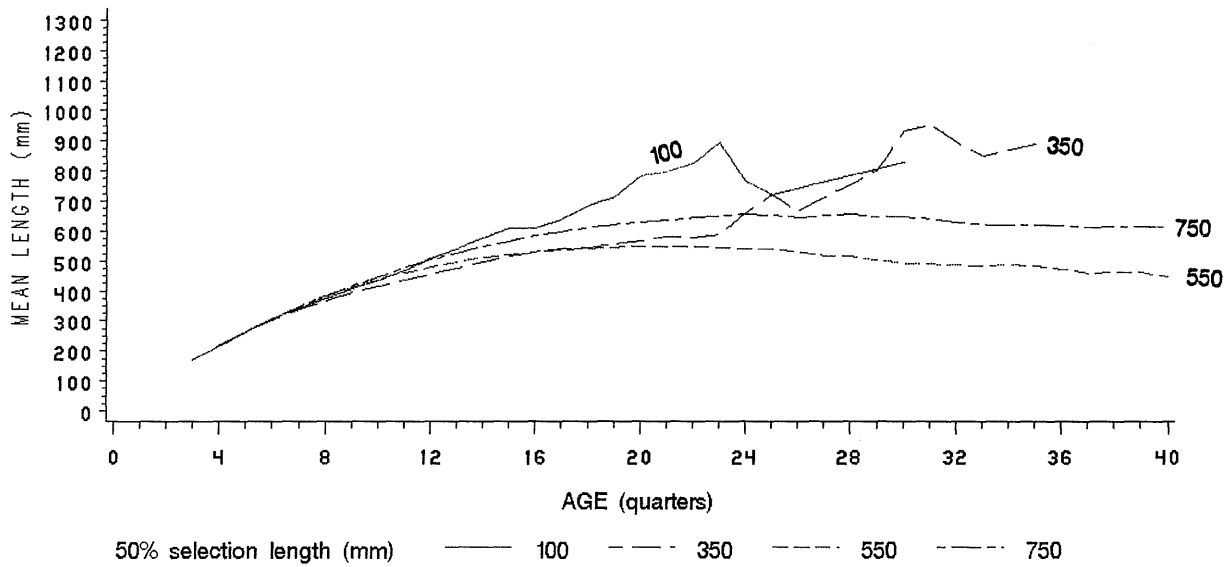

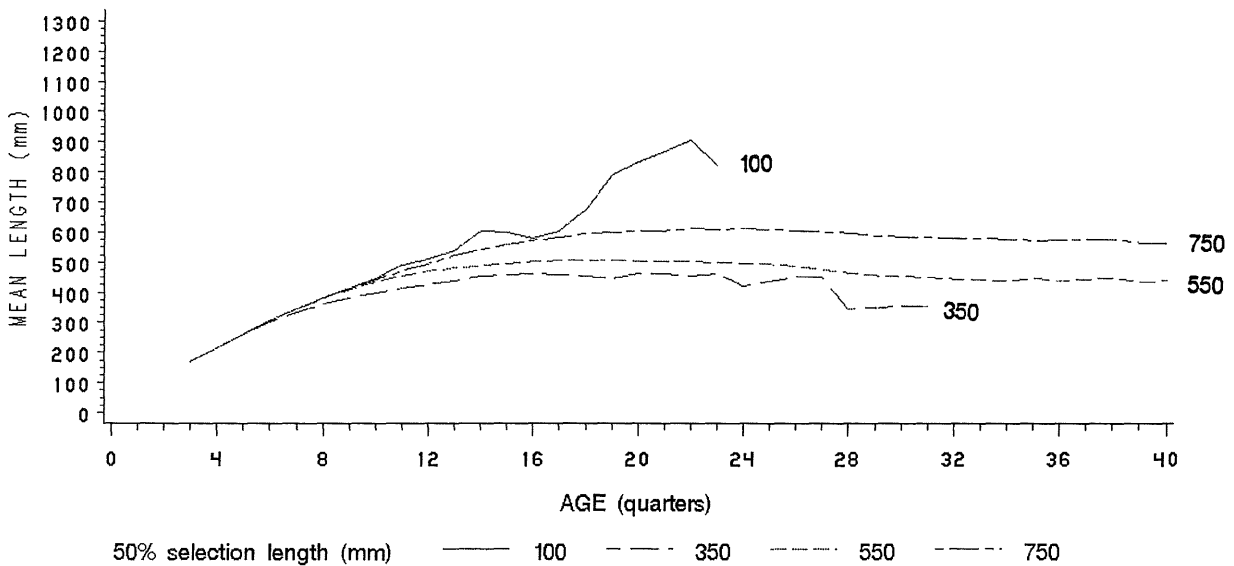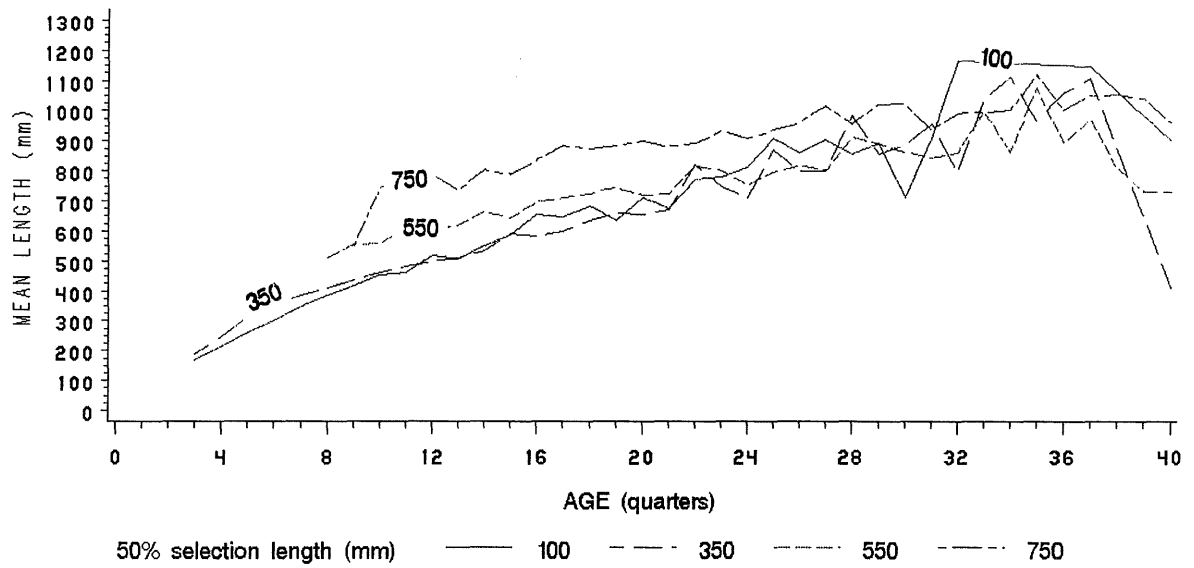**b) Fishing mortality = 0.5**

c) Fishing mortality = 1.0.

MEAN LENGTH (mm) vs AGE (quarters)

50% selection length (mm) —— 100 — —· 350 ———· 550 ——·· 750

d) Fishing mortality = 1.5.

MEAN LENGTH (mm) vs AGE (quarters)

50% selection length (mm) —— 100 — —· 350 ········ 550 ——·· 750

Figure 10. Effect on mean length in the catch of increasing 50% selection length
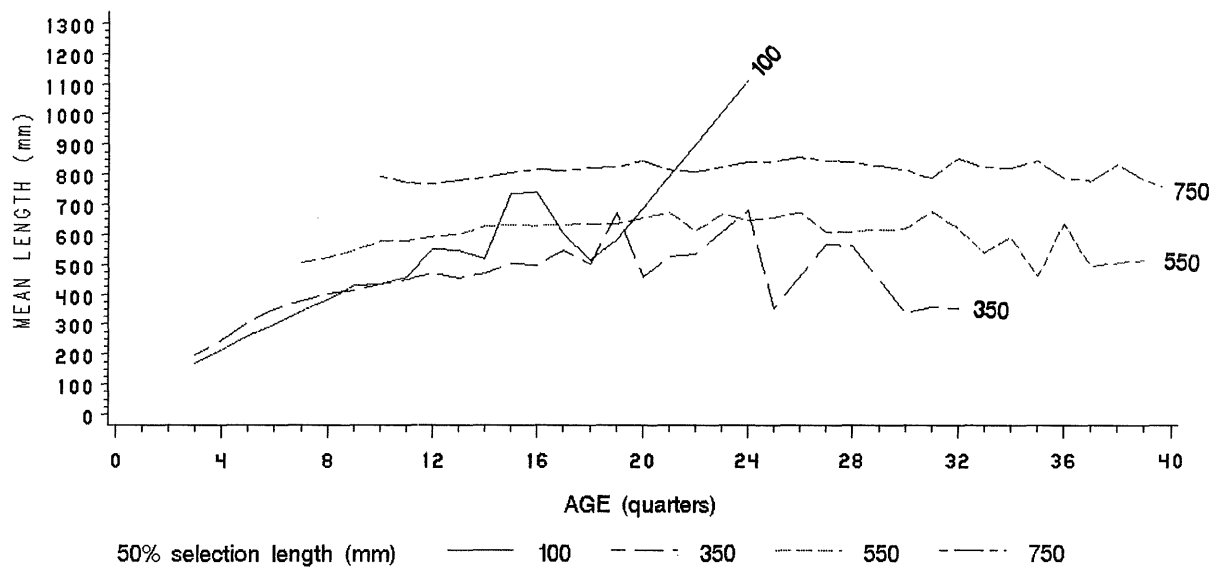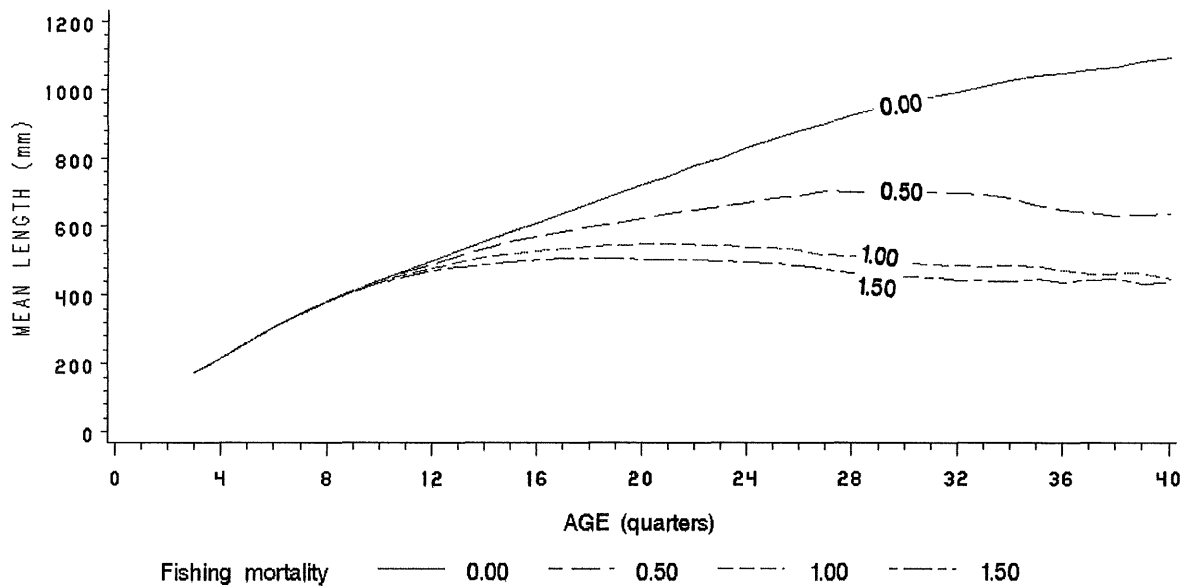(100mm, 350 mm, 550 mm and 750 mm) .

a) Fishing mortality = 0.5.

50% selection length (mm)   ——— 100   — — · 350   ·——·—· 550   ·—·—·· 750

b) Fishing mortality = 1.5.

50% selection length (mm)   ——— 100   — — · 350   ·——·—· 550   ·—·—·· 750

Figure 11. Effect on mean length in the cohort (a) and in the catch (b) of increasing fishing mortality, when 50% selection length is 550 mm.

(a) Mean length at age in the cohort

(b) Mean length at age in the catch. Mean length of the cohort when no fishing (F=0) is shown to illustrate the difference.
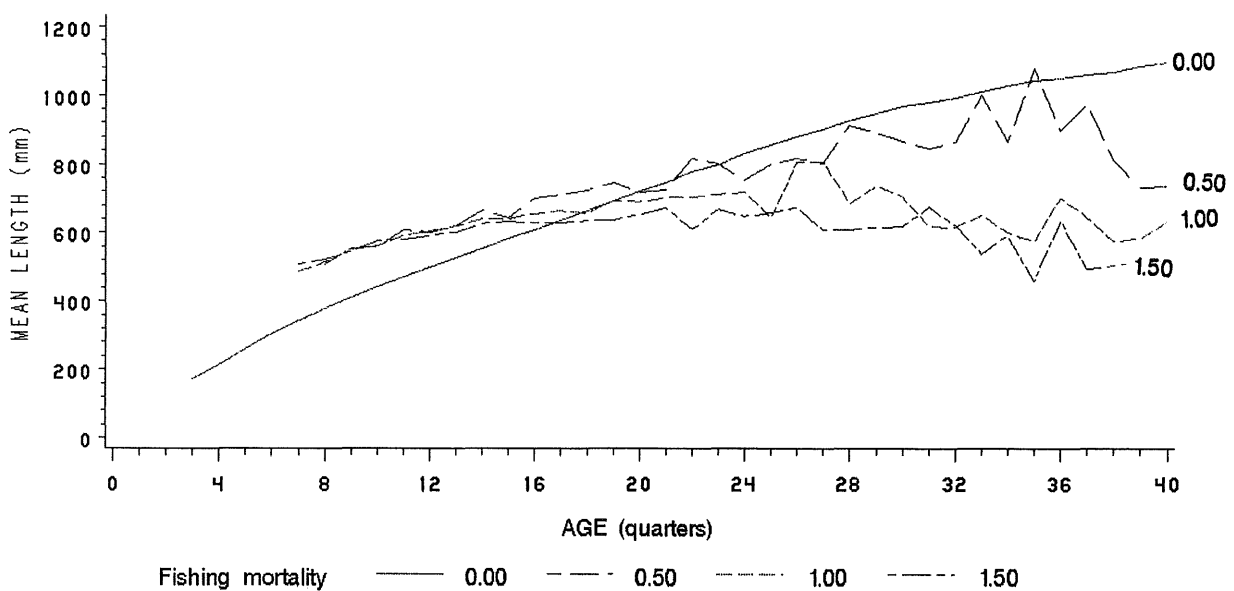
Figure 12.   Effect on mean daily length increment (DLI) in <u>the catch</u> of increasing fishing
mortality, when 50% selection length is 550 mm. Mean DLI in the population
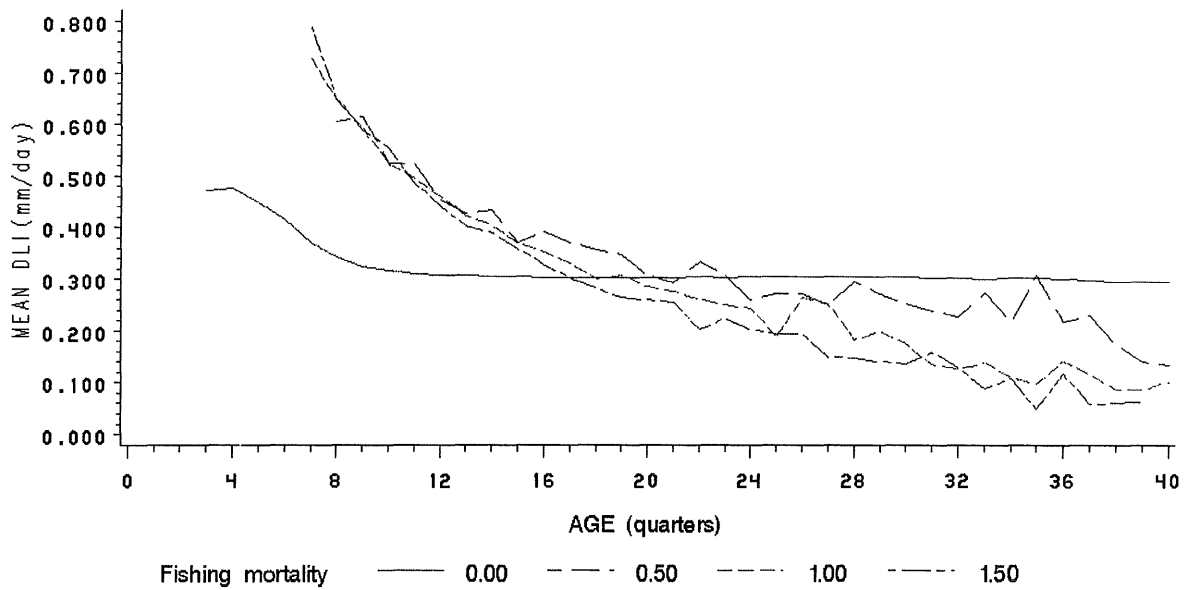when no fishing is shown to illustrate the selective removal of fast growing fish

Figure 13.   Effect on mean daily length increment (DLI) in <u>the population</u> of increasing   fishing
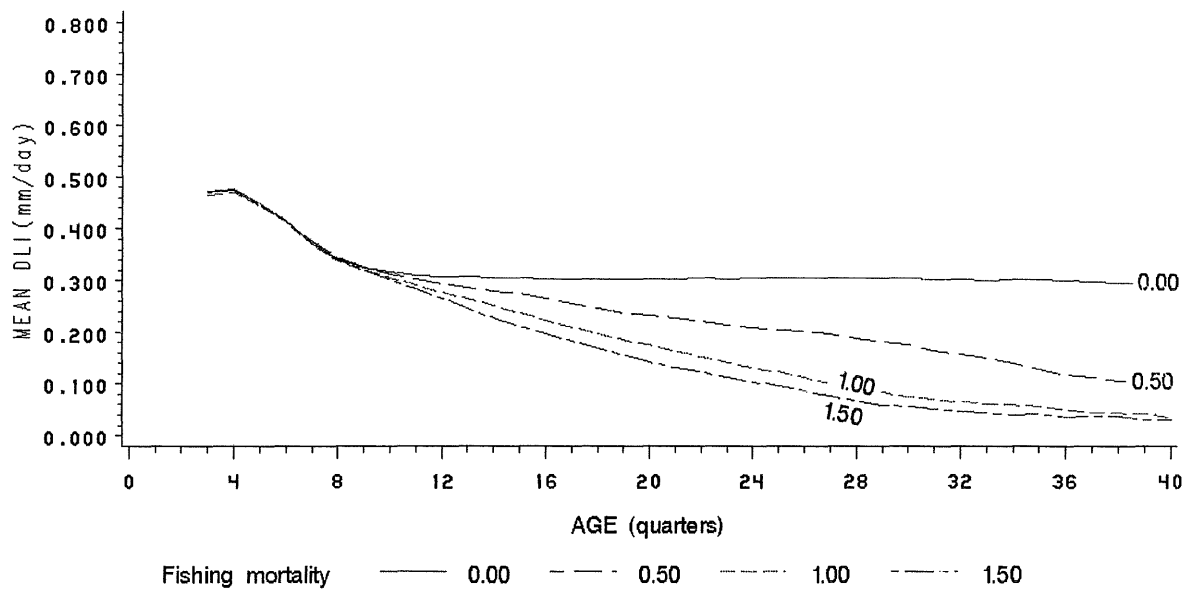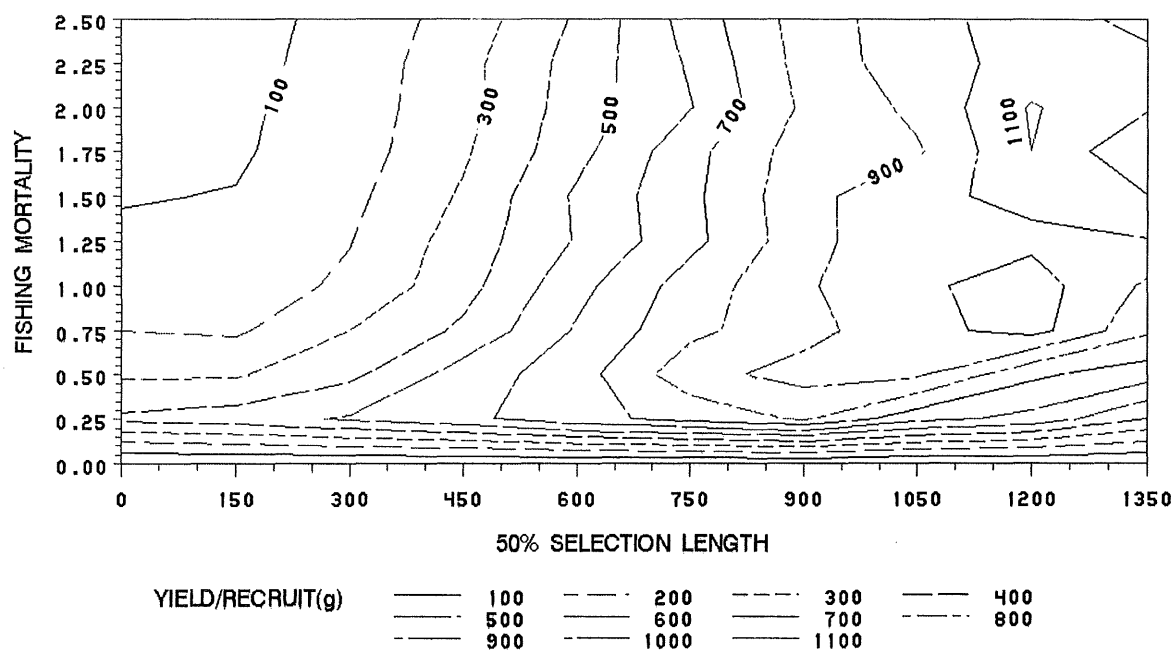mortality, when 50% selection length is 550 mm

Figure 14. Effect of growth model, fishing mortality and 50% selection length (mesh size) on yield pr
recruit (released cod) in a simulated release of 10x1000 cod.

a) Individual growth variation. Mean individual growth rate as observed from "large" cod and.

b) No individual growth- or size-variation. Mean individual growth rate as observed from "large" cod.
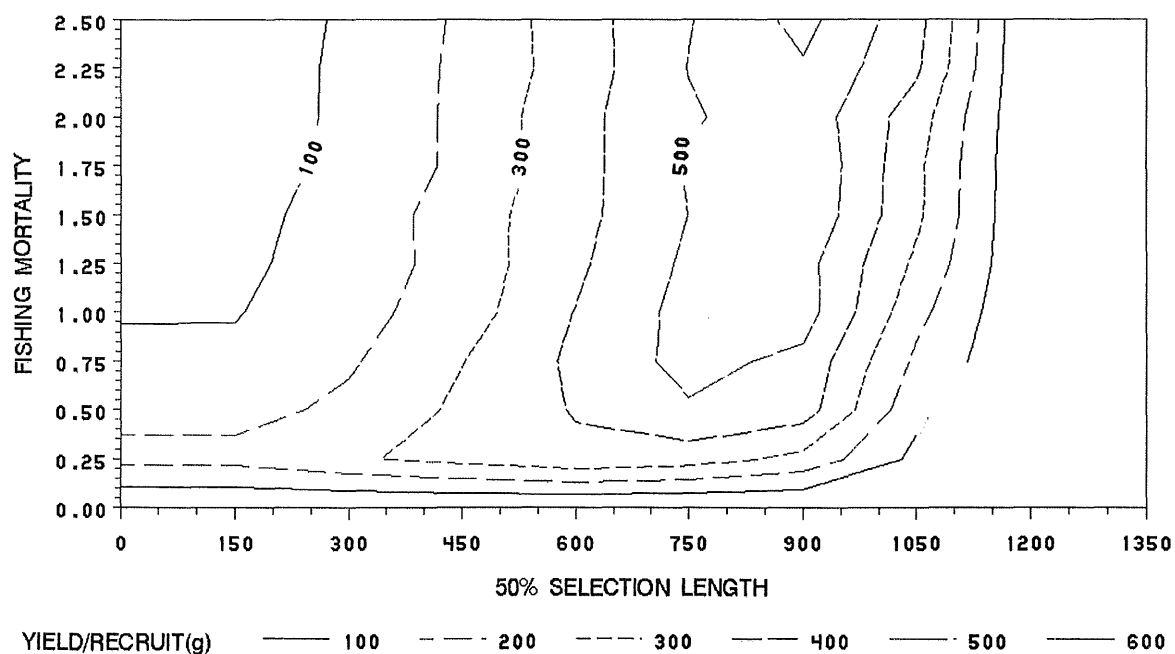
c)   No individual growth- or size-variation. Mean population growth rate (von Bertelanffy equation estimated from all recaptures of the released cod groups). Note the change in contour levels.
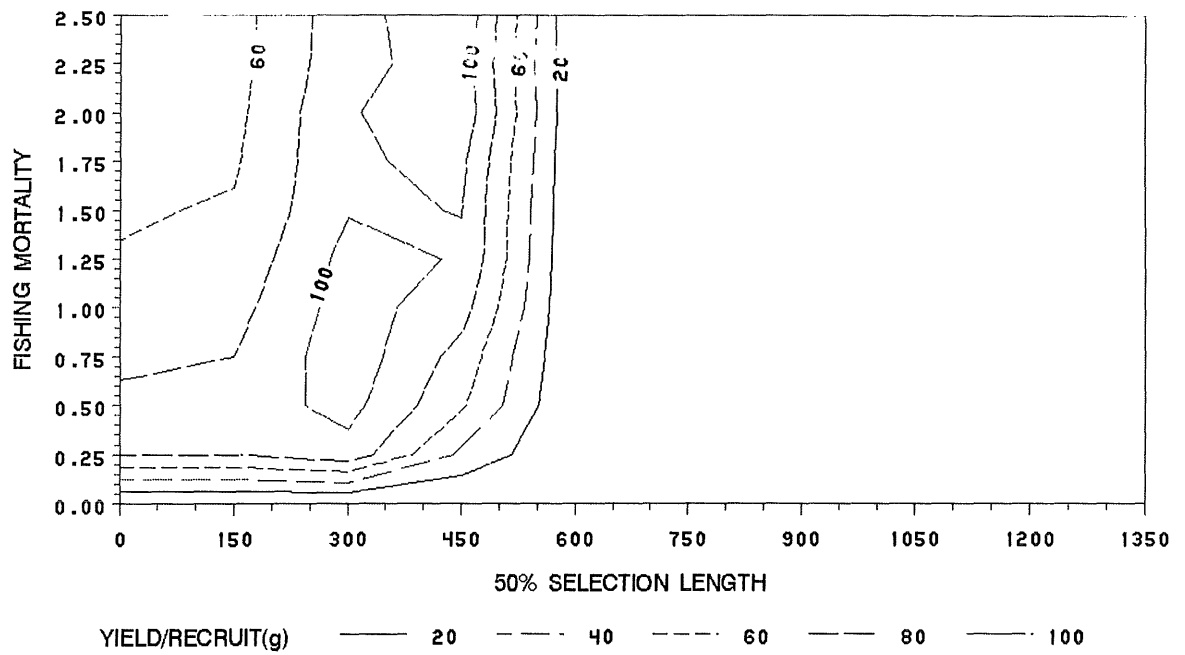
DISCUSSION

The length at age of recaptured reared cod showed that the cohorts seemed to stop growing at around the age of three. However, when we tagged individual cod of different lengths and compared mean individual growth with the "population" growth rate of the same group, the mean individual growth was about twice as high. By using the observed mean individual growth in the different length intervals, we made a "true" growth curve for the cod population in the release area, with linear growth in each length interval. The large difference between the apparent population growth rate of the released cohorts and the "true" growth rate was illustrated clearly in Fig. 6. A likely explanation of these observations was size- selective fishing mortality, which was indicated both by the decreasing mean time until recapture with increasing size at release and by the clear trend towards earlier recapture of the fastest growing fish.

By design most fishing gear is selective of larger, older fish, and in most fisheries young fish recruit to the fishery by size, and not by age (Laevastu 1992). The fastest growing fish will recruit earlier to the fishery, and at a given age the cumulative risk of being fished is largest for fast-growing individuals. The difference in cumulative mortality between different size (growth) fractions of the cohort will then decide how much size-selective mortality affects size distribution in the cohort and in the catch. These mechanisms were shown clearly in the modelled cohort, where size-selective fishing led to decreased population growth and selective removal of large fast-growing fish. The model also showed that with fishing mortality as high as observed in the release area, size-selective fishing mortality was capable of reducing the apparent growth of the cohort to almost zero. Size-selective fishing could therefore have produced the observed growth pattern of the released cohorts, when the cohorts had a mean individual growth rate equal to the "true" growth curve used in the model, when unselectively fished.

The model assumed all growth variability to be endogenous and independent of size at release. In a cohort fish will be of different size for many reasons, e.g. date of birth, feeding conditions, temperature, etc. (Laevastu 1992), and future growth is not necessarily correlated with the size at the end of the larval stage for example. However if a positive correlation existed the effects of size selective mortality would increase. We have not looked at such effects in the model runs, but this can easily be done.

The "true" growth curve was based on the mean individual growth of groups of cod within the same length intervals, and the slope of the curve gives the mean growth at length., rather than growth at age, which is not the same (Francis 1988). The "true" growth curve at age in Fig 5 is the growth of an individual with mean length at release and mean length-dependant growth rate. The calculations of the "true" curve were based on fish sampled in the release area which had been exposed to selective fishing, and the mean growth rate of the individuals may have been biased compared to the mean growth of an unselectively fished population mortality. The fastest growing fish may also have had a larger probability of being caught and tagged, which could have led to an overestimation of the growth rate in the population. As a whole it is therefore not possible to say how close the"true" growth curve is to the growth curve of the cohorts have had without size selective mortality .

A method much used to calculate the"true"growth rate is back calculation of length at age by use of the proportionality between length at age and the radius of rings in scales or otoliths (see Francis 1990). To do this we need a relative large and representative sample of otoliths

or scales of all ages; this is a labour intensive method. This method often shows that old fish had a slower growth rate at lower ages than the fish sampled at lower ages (Lee's Phenomenon). However, this method can not estimate the growth curve the cohort would have had if there had been no selective mortality. However, it does give a truer growth rate than the population growth rate (Ricker 1969).

This paper uses the mean individual growth curve to illustrate the growth of an unfished population, and the slope of this curve is not very important in the illustration of the effects of selective mortality. However, the actual values of the simulated yield per recruit are influenced by growth rate, and to estimate the true maximum yield of a cohort the growth function should be as true as possible.

In the model initial size and length-dependant growth were given at "release". The growth rate depended only on length, and the given "inherited" growth factor given at "release" (6 mnd). The deviations from the mean "true" growth function (growth factors) were modelled equal to the observed deviations within the "large" size groups, with normal distribution of the deviations. In nature growth variation is a combined effect of genetic factors, ecological conditions such as biomass of prey and predators, temperature, fishing pattern, and stochastic factors. If we had wished to model the conditions in the release area more exactly, more of these conditions would have had to be considered. However, the point of using the model was to describe the effects of size selective fishing mortality on a cohort similar to the released cohorts, and not to come as close as possible to the observed values.

Much of the observed effect depended on the individual growth variation. When we looked at recaptures of wild cod tagged in Masfjorden about 100 km north of our release area (unpublished data), the individual growth and growth variation were similar to the values observed in Heimarkspollen (std. of DLI: 0.16 in Masfjorden, cod >250 mm at tagging), which indicated that the observed variation in this study was not unusual. The simulation also showed that a standard deviation of DLI of 0.10 also had a relatively large effect on a size-selective fishery, so the conclusions also seem to be valid in a population with less growth variation. The initial length distribution will obviously also influence the effect of selective fishing and should be investigated.

Individual growth variation within cohorts is seldom estimated or published, but there should be a large qantity of tagging data and otoliths for back-calculation available from many cod stocks, that could be used to estimate this variation. In our own projects and in the other projects participating in the Norwegian ocean ranching programme (Anon. 1990), many thousand of reared and wild individual tagged cod of different sizes, have been released along the Norwegian coast. This will be very good material for the stydy of individual growth variation, and we will continue our studies of individual variation using these and other available data sets.

The individual-based model used in this paper is very simple and uses only familiar equations, but simulates events in the cod's life in quite similar way to real life. The model is stochastic and it is possible to study the effects of stochastic events. The model can also be easily developed to handle more complex conditions. The main drawback of this type of model may be the large computer capacity needed for the calculations. However, the very rapid development of computing capacity makes this a vanishing problem.

All individuals alive are used in the calculations of the population mean length and these show the real mean length of the modelled cohort. As the cohorts grow older and the mortality is high, there will be few fish left alive or in the catch in a given time interval, and random effects may lead to different means in different runs under the same conditions. This may be counteracted by taking the means of several runs or using more fish in the simulations. The resulting data set for the catch from the model runs is of the same type as the real set of recaptures, and may be compared by statistical methods.

The most important results obtained from the model were the large differences in yield per recruit when we used the different growth models. When using the apparent population growth rate (von Bertalanffy model) the maximum yield per recruit was only 10% of the maximum yield in the variable individual growth model, and the optimum fishing pattern was very different. Furthermore, the yield per recruit with the "true" growth model without size and growth variation was only 57% of the yield given by the same model with variation. In the release area there were very high fishing mortality (F>1.3) and strong size selection, so the difference will not be so large in most areas. The model does not have any feedback mechanisms, e.g. density-dependant growth or increased natural mortality due to survival of many large fish, which also would reduce the yield in a real population.

To sum up, size-selective fishing does have a large influence on the size distribution and the growth rates of a cohort when there is growth and size variability. Under such conditions use of apparent growth rate in yield calculations will lead to underestimation of optimum yield and an less thanoptimal fishing pattern. Variability in growth rate is an important factor in the study of fish populations, and should to a much larger extent be considered in fisheries management models and in ecological studies. It is published several other models that treat the aspects of selective mortality in different ways (e.g. Favro et al. 1979, Myers 1989, Parma and Deriso 1990, DeAngelis et. al 1991, Beyer and Lassen 1994), so lack of appropriate models should not be an excuse to not take the problem of variable size and growth within cohorts seriously in fisheries assessment. The possibility of selection for slow growth rate and negative change in the genetic composition of the populations leading to lower long time production should also be considered (see Favro et al. 1979, Law and Grey 1989, Sutherland 1990, Altukov 1994).

REFERENCES

Anon. 1995a. Extract of the report of the Advisory Committee on Fishery Management, stocks in the North Sea, to the North-East Atlantic Fisheries Commission. ICES November 1994.

Anon. 1995b. Extract of the report of the Advisory Committee on Fishery Management, Stocks in the North-East Arctic, to the North-East Atlantic Fisheries Commission. ICES, November 1994.

Altukov, Yu. P. 1994. Genetic consequences of selective fishing. Russian Journal of Genetics, 30: 5-21.

Beyer, J.E. and Lassen, H. 1994. The effect of size selective mortality on the size-at age of baltic herring. Dana, vol 10: 203-234.

DeAngelis, D.L., Godbout, L. and Shuter, B.J., 1991. An individual-based approch for predicting density-dependant dynamics in smallmouth bass populations. Ecol. Modelling, 57:91-115.

DeAngelis, D.L. and Gross, L.J. (eds). 1992. Individual-based Models and Approaches in Ecology. Populations, Communities and Ecosystems. Chapman and Hall.

Favro., L.D., Kuo, P.K. and McDonald, J.F., 1979. Population-genetic study of the effects of sselective fishing on the growth rate of trout.

Francis, R.I.C.C. 1988. Are growth parameters estimated from tagging and age length data comparable? Can. J. Fish. Aquat. Sci. 45:936-942.

Francis, R.I.C.C. 1990. Back calculation of lef fish length: a critical review. J. Fish.Biol. (1990) 36: 883-902.

Judson, O.P. 1994. The rise of the individual-based model in ecology. TREE, 9(1): 9-14.

Kristiansen, T.S. 1987. Vekst og ernæring til utsatt oppdrettet torskeyngel og villtorsk (*Gadus morhua* L.) i Heimarkspollen Austevoll. Cand. scient. oppgave. Institutt for fiskeribiologi. Universitetet i Bergen. 1987, 134 pp.

Kristiansen, T.S. and Svåsand, T. 1990. Enhancement studies on coastal cod in western Norway III. Inter-relationships between reared and indigenous cod in a nearly land-locked fjord. J. Cons. int. Explor. Mer, 47: 23-29.

Laevastu, T. 1992. Interactions of size-selective fishing with variation in growth rates and effects on fish stocks. ICES C.M.1992/G:5.

Law, R. and Grey, D.R., 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology, 1989, 3:343-359.

Lee, R.M. 1912. An investigation into the methods of growth determination in fishes. Conseil. Perm. Intern. Exploration Mer, Publ. Circonstance 63. 35 pp.

Myers, R.A.M. 1989. Estimatinf bias in growth caused by size-selective fishing mortality. ICES C.M. 1989/D:8

Parma, A., and Deriso, R.B. 1990. Dynamics of age and size composition in a population subject to size-selective mortality: Effects of phenotypic variability in growth. Can. J. Fish. Aquat. Sci. 47: 274-289.

Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Bd. Can. 26: 479-541.

Sparre, P. and Venema, S.C. 1992. Introduction to tropical fish stock assessment. Part 1. Manual. - FAO Fish. Techn. Pap. 306/1 Rev.1 376 pp.

Sund, O. 1911. Undersøkelser over brislingen i norske farvand vaesentlig paa grundlag av "Michael Sars's" togt 1908. Årsberetning Vedkommende Norges Fiskerier (1910), 3: 357-410.

Sutherland, W.J. 1990. Evolution and fisheries. Nature. Vol 344: 814-815.

Svåsand, T. 1990. Comparison of migration patterns of wild and recaptured reared coastal cod, *Gadus morhua* L., releases in a small fjord in western Norway. Aquac. Fish. Manag., 21: 491-495.

Svåsand, T. 1994. Cod enhancement studies - A review. Contribution to ICES workshop to evaluate the potential for stock enhacement, May 19-24, 1994, Charlottenlund Castle, Denmark.

Svåsand, T., and Kristiansen, T.S. 1990a. Enhancement studies on coastal cod in western Norway II. Migration of reared coastal cod. J. Cons. int. Explor. Mer., 47:13-22.

Svåsand, T., and Kristiansen, T.S. 1990b. Enhancement studies on coastal cod in western Norway IV. Mortality of reared cod after release. J. Cons. int. Explor. Mer., 47:30-39

Øiestad, V., Kvenseth, P.G., and Folkvord, A., 1985. Mass production of Atlantic cod juveniles (*Gadus morhua*) in a Norwegian saltwater pond. Trans. Am. Fish. Soc., 114: 590-595.