The effect of including length structure in yield-per-recruit estimates for northeast Arctic cod

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Kvamme, C., and Bogstad, B. 2007. The effect of including length structure in yield-per-recruit estimates for northeast Arctic cod. – ICES Journal of Marine Science, 64: 357–368.

For northeast Arctic cod (*Gadus morhua*), traditional age-based estimates of yield per recruit (YPR) are compared with alternative, though comparable, YPR estimates calculated using an age–length-structured model. In the age–length-structured model, growth, fishing mortality, and natural mortality depend only on length, not on age. This model considers possible changes in size-at-age caused by, for example, a length-selective fishery, and therefore, by comparing the different YPR estimates, the importance of considering the stock's length structure can be evaluated. Length- and weight-at-age of stock and catches were influenced by exploitation pattern and pressure. Such changes are not considered in traditional estimates of YPR, for which weight-at-age is fixed and strictly speaking only representative for the current fishery. Consequently, traditional YPR estimates were somewhat higher than the age–length-based estimates for exploiting smaller fish than at present, and the other way round for exploiting larger fish. Both models indicated a gain in YPR for reducing just exploitation pressure (traditional YPR, 13%; alternative model, 20%) or both reducing exploitation pressure and postponing exploitation (traditional YPR, 23–31%; alternative model, 33–48%), compared with the current fishery.

Keywords: age–length-structured population model, age-structured population model, Gadget, *Gadus morhua*, yield per recruit.

Received 1 November 2005; accepted 6 November 2006; advance access publication 16 January 2007.

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Introduction

Estimates of yield per recruit (YPR) give information about the yield in weight from a single recruit under different rates and patterns of exploitation for a specific stock. The results depend upon the growth in weight and the mortality experienced by a year class. YPR estimates may advise managers about which exploitation rate and pattern to select to utilize optimally the growth potential of year classes and to avoid growth-overfishing (Jennings *et al.*, 2001: too high a fishing mortality, resulting in the catch of too many fish before they have had a chance to utilize their growth potential).

In the traditional way of estimating YPR, the stock is described by numbers-at-age and mean weight-at-age. Length- and weight-at-age usually vary within a year class. Additionally, the fishing activity usually is length-selective, often with the relative probability for a fish to be captured rising with increasing fish length (e.g. logistic selection). A fishery may therefore alter the mean length- and weight-at-age of a stock (Sund, 1911; Lee, 1912; Ricker, 1969; Kristiansen and Svåsand, 1998) by selectively removing the largest fish from each year class, and it is therefore important also to model the length structure of a population when estimating YPR.

An early study of the effect of size-selective mortality was that of Ricker (1969). He constructed an age–length-structured model and calculated the yield and the mean size-at-age for each age group in a hypothetical population, assuming a fishing mortality that increased linearly with length. The main difference from our modelling approach is that Ricker assumed all fish of a given age to grow through the same number of length classes in each year (a time-step). Therefore, he did not incorporate stochastic variations in growth. The difference in mean size-at-age between an unexploited population and a population subject to a specific fishing mortality and length-specific selectivity can be derived from Ricker's work. He did not, however, calculate YPR.

The ICES Study Group on Age–Length Structured Assessment Models (ICES, 2005) mentions three reasons for adding length structure to population models:

(i) when it is thought that such models better represent biological and fishery-related processes;
(ii) when problems with age determination do not permit the use of age-structured models or make such models less reliable;
(iii) when age is not considered to be a good proxy for length.

A review of existing length- and age–length-structured models is given in the report of the first meeting of that Study Group (ICES, 2003b).

The Fleksibest model (Frøysa *et al.*, 2002) incorporated into the Gadget modelling framework (Begley and Howell, 2004; Begley, 2005; www.hafro.is/gadget) for age–length-structured population models (which may be multi-area, multispecies, and/or multi-fleet) was used for the simulations made here.

Björnsson and Sigurdsson (2003) describe an age–length-structured model for golden redfish (*Sebastes marinus*) in Icelandic waters, using the BORMICON model (the predecessor of Gadget). They calculated YPR in the same way as we do, by simulating one year class with a given initial number for 40 y and calculating the total yield. They also showed how fishing mortality and fishing pattern influence mean length-at-age. Their study did not, however, consider in detail how size-at-age depends on fishing mortality and fishing pattern. Another study using an age–length-structured model for estimating YPR (for a given exploitation level) is Leigh and O'Neill's (2005) work on the Queensland/New South Wales tailor (*Pomatomus saltatrix*) fishery.

Age–length-structured models may also be used to study the effect of growth variability on YPR: Parma and Deriso (1990) estimated YPR and $F_{\max}$ of Pacific halibut (*Hippoglossus stenolepis*) for a given, fixed size selectivity with a YPR model, allowing for intrinsic and environmental variability in growth and therefore a weight-at-age depending upon the size-selective fishing mortality. They found that YPR increased with intrinsic variability at moderate fishing levels, whereas the trend reversed at higher levels. Another example of a population model that can be structured both by size and age is the Stock Synthesis Model of Methot (1990, 2000). This model exists in both an age-structured version and an age-and-size-structured version that allows for size-specific survival, and therefore considers the possible reduction in mean size-at-age caused by size-specific fishing mortality.

Here, we investigate the effect of including length structure in YPR calculations for northeast Arctic (NEA) cod (*Gadus morhua*). Cod is well suited for studies of fishery-induced size-selective mortality, because its maximum age is relatively high (Nakken, 1994), and it continues to grow in length throughout life. Also, the fishery is carried out with several gears with different size selectivity, resulting in gradual recruitment to the fishery and hence a strongly size-selective fishery. YPR considerations are especially relevant, because the stock is exploited by several fleets targeting different size classes (ICES, 2003a). The exploitation pattern has varied historically: from 1932 to 1945, the mean age in catches was >8 y, whereas during the last 50 y, it has been <6 y (Hylen, 2002; ICES, 2004).

For the NEA cod stock, an age–length-structured model (Fleksibest) has been used as an auxiliary assessment model in addition to a conventional virtual population analysis (VPA)-type model (XSA) (ICES, 2004). The age readings are considered to be reliable, and the reasons for adding length structure relates to points (i) and (iii) above, because most of the processes controlling stock dynamics are related to size rather than age (e.g. cannibalism and fishing mortality) and because mean size-at-age varies considerably between years (ICES, 2005). NEA cod recruit to the fishery at an age of 3–4 y, and the minimum allowable catchable sizes in the Norwegian and Russian economic zones are 47 and 43 cm, respectively (Nakken, 1994). They attain first maturity at an age of 6–12 y and a length of 65–100 cm (Jørgensen, 1990), and the spawning season is in March and April (Bergstad *et al.*, 1987).

Material and methods

We here compare three methods of estimating the YPR of NEA cod: use of an age-structured population model (Beverton and Holt, 1957) with either an annual (model 1a) or a quarterly time-step (model 1b), and an age–length-structured population model (Fleksibest: Frøysa *et al.*, 2002) with a quarterly time-step (model 2). In all cases, mortality is applied at the beginning of the time-step (before growth). The choice of models was based on those currently used to assess NEA cod. Recently, an age-structured (VPA) model with an annual time-step has been used as the main assessment model for NEA cod, whereas model 2 (Fleksibest), which has an age–length structure and a quarterly time-step, has been used as an auxiliary model (ICES, 2003a, 2004). In order to separate the effect of the time-step from the effect of length structure, we include both models 1a and 1b.

The input data for all simulations, irrespective of model, originate from the 2003 ICES AFWG (Arctic Fisheries Working Group) Fleksibest assessment (ICES, 2003a), either as mean values over the time range of the assessment (1985–2003) or as models fitted to the estimates of the assessment. This ensured comparable results for models 1 and 2 for the historical exploitation rate and pattern. Only the fishing pressure (F_r) and the exploitation pattern [$S(l)$] were changed between simulations (Table 1 gives the notation) [for more details on the model/data comparisons and estimation method used in Fleksibest/Gadget, see Frøysa *et al.* (2002), Begley and Howell (2004), Bogstad *et al.* (2004), and Begley (2005)]. The estimated and fixed parameters of the ICES AFWG 2003 assessment with Fleksibest are described in ICES (2003a), and details of the data used for fitting the model are provided by Bogstad *et al.* (2004). In all models, cod was assumed to recruit at 3 y of age. The maximum age was set to 30 y (increasing the maximum age did not change the results), and the maximum length and weight were 149.5 cm and 31.83 kg, respectively. In ICES (2003a), 135 cm was used as the upper limit, but in our runs, this was extended to avoid significant aggregation of fish in the highest length group at low fishing mortality. All values of model parameters used in the simulations are provided in Table 1.

We used the run closest to the current fishery in terms of exploitation pressure ($F_r = 0.9\ \mathrm{y}^{-1}$) and exploitation pattern ($a_{50} = 6$ y) as a base case for comparisons of YPR.

Age-structured population model

For the age-structured model with annual time-steps, the YPR (Beverton and Holt, 1957) estimates were calculated from:

$$\frac{Y}{R} = \sum_{a=3}^{30} \frac{F_a \bar{w}_a}{M + F_a} e^{-\sum_{j=3}^{a-1}(M+F_j)} \left(1 - \mathrm{e}^{-(M+F_a)}\right), \qquad (1)$$

where Y is the yield (kg), R the number of recruits, F_a and M the fishing (per year, i.e. y^{-1}) and natural mortalities (y^{-1}), respectively, a the age (y), and $\bar{w}_a$ the mean weight-at-age in both catch and stock (kg) (Table 2). The ICES AFWG uses mean weights-at-age estimated from catch samples in YPR calculations.

The YPR estimates for the age-structured model with quarterly time-steps were calculated in a similar manner. Instead of summing over ages (in years), the summation was carried out over quarter-years.

Age–length-structured population model

YPR estimates were calculated by simulating one year class (of 580 million recruits) for 28 y, i.e. from age 3 to 30. Recruits were therefore only supplied for the initial year of the simulations, so just a single year class was followed. A quarterly time-step was used, and the year class was split into an immature and a mature sub-stock. All recruits were assumed to be immature. The age and length ranges were 3–30 y (immature, 3–12 y; mature, 4–30 y) and 15–150 cm (immature, 15–105 cm; mature, 55–150 cm), respectively. The width of each length group was set to 1 cm. In

Table 1. Notations and model equations. FB = Fleksibest (the age–length-structured population model of model 2).

Notation	Explanation	Value or range	Source
Y	Yield (kg)	–	–
R	Number of recruits	–	–
N	Number of individuals at age/length	–	–
w	Weight (kg)	–	–
F	Fishing mortality (y^{-1})	–	–
M	Natural mortality (y^{-1})	–	–
l	Length (cm)	–	–
Indices			
a	Age (y)	3–30	1
u	Time-step (quarter) number	13–124	1
j	Length group (1 cm) number	15–149	2
m	Sub-stock (1, immature; 2, mature)	1–2	3
l_{max}	Maximum length, the upper limit of FB (cm)	149.5	4
w_{max}	Maximum weight, the upper limit of FB (kg)	31.83	4
Exploitation pattern			
Model 1a:	$F_a = F_r \times S(\bar{l}_a)$		
Model 1b:	$F_u = q_u \times F_r \times S(\bar{l}_u)$		
Model 2:	$F_{u,j} = q_u \times F_r \times S(l_j)$		
	$S(l) = (1 + \exp(-4\alpha(l - l_{50})))^{-1}$		
$F_a/F_u/F_{u,j}$	Fishing mortality for a given age/time-step/length	–	–
$\bar{l}_a/\bar{l}_u$	Mean length of year class at age a/time-step u (cm)	–	–
l_j	Mean length of length group j, i.e. $l_j = (j + 0.5)$ cm	–	–
F_r	Annual exploitation rate of fully exploited fish (y^{-1})	Varied	–
q_u	Distribution of F_r on quarters (1, 0.345; 2, 0.282; 3, 0.187; 4, 0.186)	–	–
$S(l)$	Relative probability of capture, exploitation pattern, by length	–	–
l_{50}	Length with 50% relative probability of capture (cm)	Varied	–
α	Parameter deciding steepness of $S(l)$ (cm^{-1})	0.055	5
SR	Selection range, $l_{75}-l_{25} = \ln 3/2\alpha$ (cm)	10	5
a_{50}	$a_{50} = x$ used to describe selection curve with $l_{50} = l_x$	Varied	–
Age-structured population model (models 1a and 1b)			
von Bertalanffy growth function: $\bar{l}_a = l_\infty (1-e^{-K(a - a_0)})$			
$\bar{l}_a$	Mean length of year class at age a (cm)	–	–
l_∞	Length of fish of infinite age (cm)	196.6	6
K	Measure of the speed at which the length approaches l_∞ (y^{-1})	0.065	6
a_0	Scaling factor (y)	0.355	6
Length/weight relationship: $w(l) = cl^b$			
$w(l)$	Weight (kg) at length l (cm)	–	–
c	Condition (kg cm^{-b})	7.904×10^{-6}	6
b	See condition, c, above	3.03	6
Age–length-structured population model (model 2)			
Growth: $\Delta l_{imm}/\Delta t = k_1$; $\Delta l_{mat}/\Delta t = k_1 k_2$			
$\Delta l/\Delta t$	Annual mean growth (cm y^{-1}) of sub-stock	–	–

Continued

Table 1. *Continued*

Notation	Explanation	Value or range	Source
k_1	Growth rate (cm y^{-1}) of immature sub-stock	9.54	7
k_2	The ratio between the growth rates of mature and immature fish	0.74	3
Maturation: $P(l_j) = (1 + \exp(-4\alpha(l_j - m_{50})))^{-1}$			
$P(l_j)$	Probability of maturation for length group j	–	–
α	Parameter deciding steepness of $P(l_j)$ (cm^{-1})	0.03	3
m_{50}	Length with a 50% probability of maturation (cm)	76	3

1. Lower limit as in the 2003 assessment run with Fleksibest (ICES, 2003a). Upper limit was chosen to include all ages contributing to the YPR. Other age spans (3–20 and 3–60 y) were also explored.
2. Lower limit as in the 2003 assessment run with Fleksibest (ICES, 2003a). Upper limit was chosen to include all length groups important for the stock even when lightly exploited.
3. 2003 assessment run with Fleksibest (ICES, 2003a).
4. Mean length of the largest length group of Fleksibest, and the weight belonging to this maximum length.
5. Kvamme (2005). Also see text.
6. Fitted to the mean lengths-at-age for the period 1985–2002 (2003 first quarter) in the 2003 assessment run with Fleksibest (ICES, 2003a). Von Bertalanffy growth model: Chapman's method: $(\bar{l}_{a+1} - \bar{l}_a) \sim \bar{l}_a$ (Chapman, 1961) $\rightarrow K$ and l_∞, $r^2 = 0.968$; Beverton's plot: $\ln(l_\infty - \bar{l}_a) \sim a$ (Beverton, 1954) $\rightarrow t_0$, $r^2 = 0.998$. Length/weight relationship: $\ln(w) \sim \ln(c) + b^*\ln(l)$, $r^2 = 0.996$. Also see text.
7. Mean for the period 1985–2002 (2003 first quarter) in the 2003 assessment run with Fleksibest (ICES, 2003a).

Gadget, the order of processes within a time-step is as follows: fishing mortality–natural mortality–growth (Begley, 2005).

The probability of maturation for fish in length group j was modelled as a logistic function of length (Table 1). Maturation takes place at the end of the fourth quarter.

The length distribution was updated in each time-step, based on the average length growth (Table 1) and using the beta-binomial distribution to model the variability in individual growth (for a description, see Taylor *et al.*, 2004). Sensitivity studies indicated that the model results were insensitive to the value of β over a wide range of values for this parameter. One reason for this is probably that the average number of length groups a fish grows during one time-step is small (9.54 cm/4 ≈ 2.4 cm for immature fish). The maximum number of length groups a cod can grow during a time-step was set at five (ICES, 2003a).

For the age–length-structured population model with quarterly time-steps, the YPR estimates were calculated from

$$\frac{Y}{R} = \frac{\sum_{u=13}^{124}\sum_{m=1}^{2}\sum_{j=15}^{149}\frac{N_{u,m,j}F_{u,j}w_u(l_j)}{M+F_{u,j}}(1-e^{-(M+F_{u,j})})}{\sum_{j=15}^{149}N_{13,1,j}}. \quad (2)$$

Equation (2) is similar to Equation (1), but the catches are summed over the 1 cm length groups j and the immature ($m = 1$) and mature ($m = 2$) sub-stocks before they are summed over the quarterly time-steps u. $N_{u,m,j}$ is the number of fish in length group j and sub-stock m at the beginning of time-step u. The weight-at-length $w_u(l_j)$ depends on quarter, whereas fishing mortality $F_{u,j}$ depends on length and quarter, as for model 1b. The number of recruits R, i.e. the number of immature fish at the beginning of the first time-step, is given by

$$R = \sum_{j=15}^{149} N_{13,1,j}. \quad (3)$$

Modelling growth, fishing mortality, and natural mortality

As mean length- and weight-at-age in the age–length-structured model are dependent on fishing mortality, the mean length-at-age for the different models cannot match exactly because the mean weight-at-age in the age-structured models is assumed to be constant. We have tried to make the process models as similar as possible, but the choice of an existing set-up for the age–length-structured model led to the use of different equations in the two cases. As shown below, however, the differences in the

Table 2. Input to the age-based estimates of YPR calculated on an annual basis.

Age (y)	Mean l (cm)	Mean w (kg)
3	31.13	0.26
4	42.94	0.74
5	52.53	1.32
6	61.56	2.08
7	70.36	3.08
8	78.56	4.30
9	85.79	5.65
10	92.30	7.12
11	98.97	8.87
12	105.82	10.97
13	110.35	12.23
14	115.79	14.15
15	120.89	16.12
16	125.66	18.12
17	130.14	20.15
18	134.33	22.18
19	138.25	24.20
20	141.93	26.20
21	145.38	28.18
22	148.61	30.12
23–30	149.50	31.83

The length (l) and weight (w) are from the beginning of the year (1 January).

actual growth and mortality patterns were rather small for the base case run ($F_r = 0.9\ y^{-1}$, $a_{50} = 6$ y).

Growth

In model 1a, $\bar{w}_a$ for ages 4–12 were the means of the estimated weights-at-age (1 January) for the period 1985–2003 in the 2003 assessment run with Fleksibest (ICES, 2003a). Therefore, $\bar{w}_a$ should be representative for the growth conditions and exploitation level/pattern in recent years. The average F_{5-10} in the period 1985–2002 was 0.69 y^{-1} (estimated in the Fleksibest assessment; ICES, 2003a).

For ages 3 and 13+, the mean weight-at-age was estimated by first estimating mean length-at-age, then the mean weight-at-age was calculated from a length/weight relationship (see Table 1 for parameter values). The lengths-at-age were calculated by a von Bertalanffy growth model (von Bertalanffy, 1938; Pitcher and Hart, 1982) fitted to the estimated mean lengths-at-age for ages 3.25–12.00 (from the 2003 Fleksibest assessment in ICES, 2003a) in order to extrapolate to ages above 12.00 as well as age 3. A length/weight relationship fitted to the data for fish aged 3.25–12.00 was subsequently used to calculate the weight-at-length for ages 3 and 12+ fish (Table 1).

In model 1b, $\bar{w}_u$ (Table 1) and $\bar{l}_u$ for ages 3.25–12.00 were the means of the estimated weight- and length-at-age per quarter for the period 1985–2002 (and 2003 first quarter) in the 2003 assessment run with Fleksibest (ICES, 2003a). For ages 3.00 and 12.25+, the lengths-at-age and weights-at-length were calculated in the same manner as for the model with an annual time-step.

In model 2, the annual mean growth was linear, but different for immature and mature fish (Table 1). The growth rate was the same for all quarters. The growth rate is lower for mature than for immature fish, and because immature fish gradually recruit to the mature sub-stock by a logistic maturation function of length (Table 1), this results in a curvilinear growth pattern by age for the whole stock (immature + mature). The growth pattern for the whole stock is similar to the von Bertalanffy growth pattern of the age-structured population model.

The initial length distribution for age 3 cod in the first time-step ($u = 13$) was set to a normal distribution with mean length 31.13 cm and standard deviation 4.15 cm (the mean standard deviation for the years with a length close to 31.13 cm). A length–weight relationship, constant between years but differing between quarters, was used to calculate the weight for each length group. This length/weight relationship is a mean for the period 1985–2002 (2003 first quarter) in the 2003 assessment run with Fleksibest (ICES, 2003a).

To summarize, the growth models differ between models 1a and 1b (von Bertalanffy) and 2 (linear growth within each sub-stock). The estimates of mean length- and weight-at-age from the two models for the common base case ($F_r = 0.9\ y^{-1}$, $a_{50} = 6$ y), however, do not differ much (Figure 1).

Fishing mortality

The fishing mortality for each age/length group was modelled as a product of an exploitation rate, F_r, and an exploitation pattern, $S(l)$ (Table 1). In models 1b and 2, the annual fishing pressure is distributed in quarters by q_u (Table 1), and the quarterly distribution is based upon the average quarterly distribution of the catch of NEA cod by weight (Frøysa *et al.*, 2002).

For all models, a range of fishing pressures (F_r between 0 and 1.4) and selection patterns were explored. A selection range of 10 cm was used for all runs. The effect of changing the selection range has been investigated by Kvamme (2005) and found to be much smaller than the effect of changing l_{50}. The selection patterns used had values of l_{50} corresponding to $\bar{l}_x$ for a range of ages x. The notation $a_{50} = x$ is used to describe the selection curve with $l_{50} = \bar{l}_x$. The parameter $\bar{l}_x$ is the mean length-at-age in the age-structured population model (Table 2).

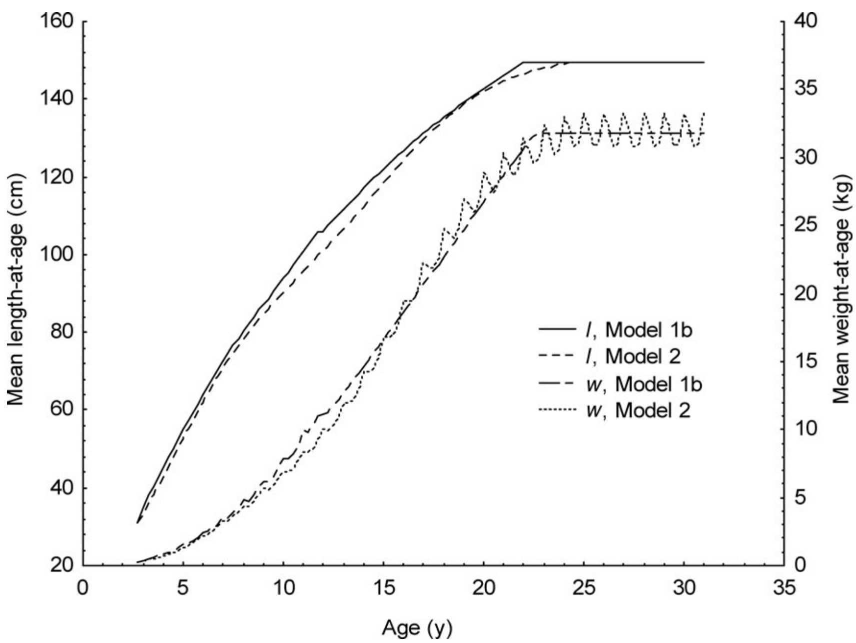

Figure 1. Mean length- (l) and weight-at-age (w) used in models 1a and 1b, and the values derived from a specific run (base case: $F_r = 0.9\ y^{-1}$, $a_{50} = 6$ y) with model 2.

Natural mortality

In ICES assessments for NEA cod (ICES, 2003a), cannibalism is included and natural mortality M is set to $0.20\ \mathrm{y}^{-1}$ plus the natural mortality induced by cannibalism (mainly on cod aged 3 and 4 y). In all models here, M was set to $0.20\ \mathrm{y}^{-1}$ for all ages. This was done to avoid problems of comparing age–length- and age-structured models, because it is impossible to obtain exactly the same M in both cases if M in the age–length-structured model is length-dependent, whereas M in the age-structured model is age-dependent. The natural mortality was equally distributed on quarters.

Results

When length structure was considered, the largest fish were removed first in the fishery and consequently mean weight- (Table 3) and length-at-age in the stock (Figure 2) as well as mean weight, age, and mean weight-at-age in catches (Figure 3) changed according to exploitation pattern (a_{50}) and intensity (F_r). The influence of the fishery increased with decreasing a_{50}. As such changes were not considered in traditional estimates of YPR, these estimates were somewhat higher than the age–length-based YPR estimates for exploiting smaller fish than at present, and the converse when exploiting larger fish (Figure 4). Both models indicated a gain in YPR when reducing just exploitation pressure (traditional YPR, 13%; alternative model, 20%) or when reducing exploitation pressure and postponing exploitation (traditional YPR, 23–31%; alternative model, 33–48%), compared with the current fishery (Figure 5).

Differences between age–length- and age-structured models

YPR estimates from the three models are compared in Figure 4 and Table 4. For comparison, the latest YPR estimates presented in detail by ICES (2001, 2002) are also given in Table 4. Models 1b and 2 had similar estimates of YPR because the catches were taken throughout the year, but the F_{5-10} giving maximum YPR was lower for model 2. The estimates from the Fleksibest simulations (model 2) were mostly lower for $a_{50} = 5$ y, then for $a_{50} = 9$ y they shifted to being higher at F_r values $<0.6\ \mathrm{y}^{-1}$, and were consistently higher for $a_{50} = 13$ y. This may be explained by the potential changes in population size-at-age imposed by the fishery (Table 3). In model 2, fishing mortality is related to size, so fishing may change size-at-age. With a logistic exploitation pattern, the largest fish in each age class are removed first, so fishing may lower size-at-age. Postponing fishing to older ages (e.g. $a_{50} = 13$ y) therefore seems more profitable when length structure is included in the model. This is not taken account of in the age-structured models (1a and 1b), where size-at-age is constant. Model 2 therefore gave higher estimates of YPR than model 1b for large a_{50}s, and vice versa, lower estimates of YPR for smaller a_{50}s.

The estimates of $F_{\max}$ and maximum YPR were quite similar for all three models for $a_{50} = 6$ y, but were somewhat higher than the estimates made by the ICES AFWG (ICES, 2001, 2002). The difference may be explained by the lower natural mortality, because simulations with model 2 using $M > 0.2\ \mathrm{y}^{-1}$ (including cannibalism mortality) for the youngest age groups gave an estimate of YPR about 0.2 kg lower. Our estimates were in the range $F_{\max} = 0.18–0.23\ \mathrm{y}^{-1}$, and maximum YPR = 1.35–1.44 kg (Table 4, Figure 5). Using $a_{50} = 6$ y provides an exploitation pattern close to the present exploitation pattern estimated by the AFWG.

Effects of changing selectivity

A fishery with an exploitation pattern by length described by a logistic curve will influence length-at-age. In the simulations with model 2, any change in length-at-age (Figure 2) was mirrored in the proportion mature-at-age as well as the mean weight-at-age in the catch (Table 5) and the stock (Table 3), because both are functions of length. The proportions mature-at-age were little influenced by the fishery for $a_{50} = 9$ and 13 y, whereas for $a_{50} = 5$ and 7 y there was some influence. By increasing a_{50} from 5 to 13 y, the proportion of mature 8-year-olds rose from 63 to 71% ($F_r = 0.6\ \mathrm{y}^{-1}$) and from 50 to 71% ($F_r = 1.4\ \mathrm{y}^{-1}$). For low a_{50} (e.g. 5 y), fishing pressure was important for the proportion of

Table 3. Estimated mean weight-at-age (kg) in the stock (at 1 January) under different exploitation rates ($F_r = 0.025$, 0.3, 0.6, and 1.4 y^{-1}) and patterns ($a_{50} = 5$, 7, 9, and 13 y) obtained from the simulations with the age–length-structured population model (model 2).

Age (y)	Model 1b	Model 2																
		No fishery	$a_{50} = 5$ y				$a_{50} = 7$ y				$a_{50} = 9$ y				$a_{50} = 13$ y			
			0.025	0.3	0.6	1.4	0.025	0.3	0.6	1.4	0.025	0.3	0.6	1.4	0.025	0.3	0.6	1.4
3	0.26	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27	0.27
4	0.74	0.63	0.63	0.62	0.62	0.62	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63
5	1.32	1.15	1.15	1.13	1.11	1.07	1.15	1.15	1.15	1.15	1.15	1.15	1.15	1.15	1.15	1.15	1.15	1.15
6	2.08	1.90	1.90	1.83	1.76	**1.61**	1.90	1.89	1.87	1.84	1.90	1.90	1.90	1.90	1.90	1.90	1.90	1.90
7	3.08	2.89	2.88	2.76	2.62	**2.30**	2.89	2.82	2.75	**2.60**	2.89	2.88	2.87	2.84	2.89	2.89	2.89	2.89
8	4.30	4.12	4.11	3.94	3.74	**3.22**	4.11	3.93	3.76	**3.40**	4.12	4.05	3.99	3.86	4.12	4.12	4.12	4.11
9	5.65	5.56	5.54	5.33	5.10	**4.41**	5.53	**5.24**	**4.93**	**4.25**	5.54	5.34	5.16	**4.80**	5.56	5.54	5.52	5.48
10	7.12	7.21	7.19	6.95	6.67	**5.84**	7.18	**6.75**	**6.30**	**5.19**	7.17	6.76	**6.37**	**5.63**	7.20	7.12	7.04	6.88
11	8.87	9.12	9.10	8.81	8.49	**7.50**	9.07	**8.53**	**7.92**	**6.26**	9.06	8.36	**7.69**	**6.39**	9.09	8.83	8.60	**8.18**
12	10.97	11.32	11.30	10.97	10.59	**9.42**	11.27	**10.61**	**9.83**	**7.50**	11.23	10.22	**9.19**	**7.11**	11.26	10.66	**10.17**	**9.34**
13	12.23	13.81	13.78	13.41	12.99	**11.48**	13.75	**12.98**	**12.05**	**8.95**	13.70	**12.39**	**10.95**	**7.85**	13.70	12.62	**11.74**	**10.35**
14	14.15	16.53	16.50	16.10	15.64	**13.50**	16.46	**15.62**	**14.55**	**10.67**	16.40	**14.84**	**12.98**	**8.62**	16.36	**14.71**	**13.34**	**11.25**
15	16.12	19.35	19.32	18.91	18.43	–	19.28	18.39	**17.25**	**12.67**	19.21	17.48	**15.27**	**9.46**	19.14	**16.94**	**15.01**	**12.07**

The emboldened mean weights-at-age differ by more than −10% from the values in the no-fishing situation. The weights-at-age of the age-structured population model (model 1b) are included for comparison.

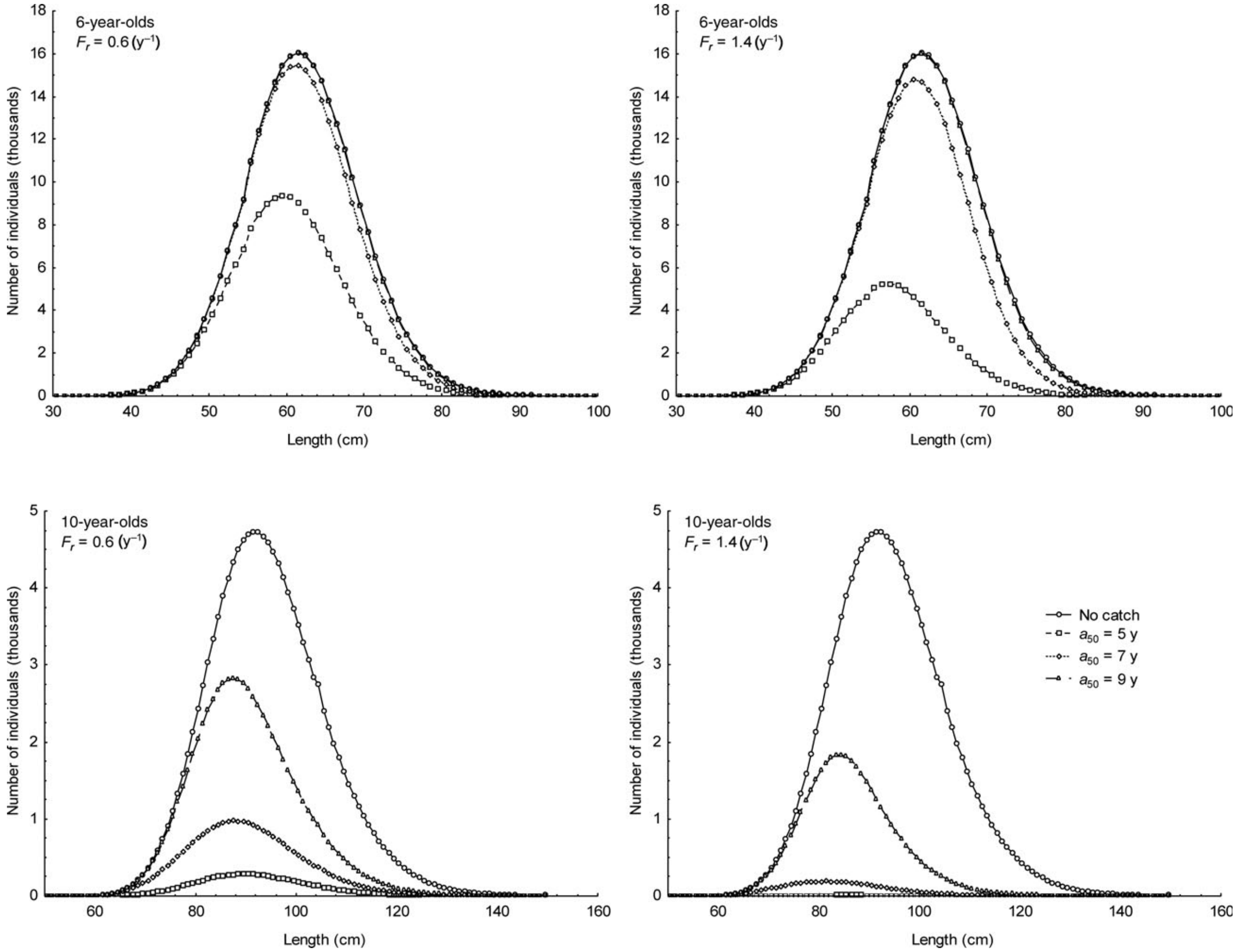

Figure 2. Numbers at length for cod aged 6 and 10 y (on 31 March) under different exploitation levels ($F_r = 0.0$, 0.6, and 1.4 y^{-1}) and patterns in the age–length-structured population model (model 2). For technical reasons, data from 31 March are presented instead of data from 1 January.

mature-at-age, because, for example, the mature proportion of 8-year-olds was reduced from 63 to 50% when increasing F_r from 0.6 to 1.4 y^{-1}.

Mean weight-at-age in the catches is shown in Table 5. The high mean weights of the youngest fish are caused by the logistic selection curve for the fishery, because for a large a_{50} few, but consistently the largest, of the youngest fish were removed. Later, when the fish approached full exploitation [$S(l) = 1.0$], the mean weights-at-age in catches were reduced as a consequence of the earlier removal of the fastest-growing fish of the year class. The mean weights and ages of fish in the catches as a function of fishing pressure, compared between different a_{50} values, are shown in Figure 3. For a fishing pressure of $F_r = 0.6$ y^{-1}, the difference in mean weight and age in the catches between $a_{50} = 5$ and 9 y was about 5 kg and 3.6 y, whereas it was nearly 8 kg and 3.0 y between 9 and 13 y. The lower the a_{50}, the faster the mean weight and age in the catches were reduced as fishing pressure increased.

The highest estimates of YPR were achieved for $a_{50} = 11$ y (1.72 kg, model 1b) and $a_{50} = 13$ y (1.81 kg, model 2) under maximum fishing pressure ($F_r = 1.4$ y^{-1}). Reducing fishing pressure to more moderate levels ($F_r = 0.6$ y^{-1}), however, only slightly lowered the maximum estimates of YPR (3–5%). The runs with $a_{50} = 13$ y are difficult to evaluate, because such an exploitation pattern is far from the current one. The population dynamics for old/large fish, which will have a large impact on the results, is not well known.

When YPR estimates are plotted against fishing pressure (F_r) and compared between different a_{50}s, there is a similar pattern for models 1b and 2 (Figure 5). However, when comparing in detail models 1b and 2, the maximum estimates of YPR were slightly lower (Figure 5: nearly 0.1 kg when comparing maximum YPR within each model), the a_{50} giving maximum YPR was 2 y lower, and within each a_{50} run, estimated $F_{r,\max}$ was higher (Figure 5, Table 4) for model 1b. A lower $F_{r,\max}$ for model 2 meant an even lower $F_{5-10,\max}$ (Figure 6).

The estimated F_{5-10} is affected by fishing pressure (F_r), exploitation pattern (a_{50}), and the population model, as shown in Figure 6. Model 2 generally provided lower estimates of F_{5-10} than model 1b for a_{50}s up to 10–11 y, whereas the estimates of model 2 were slightly higher for a_{50}s above 11 y. This can be explained by the differences in length-at-age between the models.

The curves for a_{50}s above 8–9 y (models 1b–2) were flat-topped, so the difference in YPR between F_rs of 0.6 and 1.4 y^{-1} was small (Figure 5). The most reasonable fishing strategy seemed

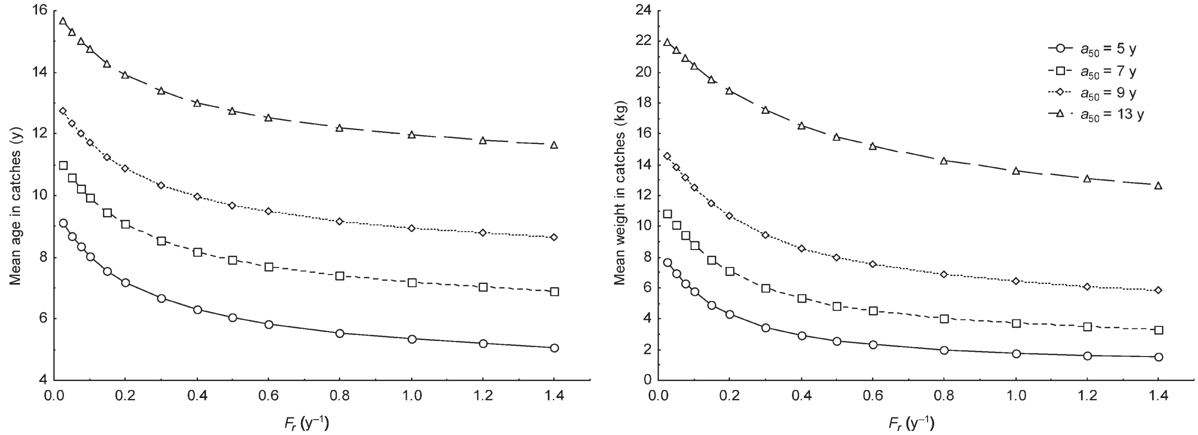

Figure 3. Mean age (y) and weight (kg) in the catch (weighted by catch numbers) for a year class as a function of F_r for four different exploitation patterns ($a_{50} = 5$, 7, 9, and 13 y). The results are from the simulations with the age–length-structured population model (model 2).

to be an a_{50} of 8–11 y (model 1b and 2) and a fishing pressure, F_r of 0.4–0.6 y^{-1}, which would give a YPR of 1.6–1.7 kg (Figure 5), with estimates slightly higher (up to 0.1 kg) for model 2 than for model 1b. This is 15–20% higher than the maximum YPR obtained with the current exploitation pattern (YPR ~1.4 kg). By including length, the optimal estimates of YPR were achieved for a higher a_{50} and a lower F_r than when not considering the variability in length-at-age. This is because relaxing fishing pressure and postponing exploitation is rewarded with a higher size-at-age in model 2.

Discussion

Here, we quantified the effect on YPR and size-at-age estimates using an age–length-structured population model vs. an

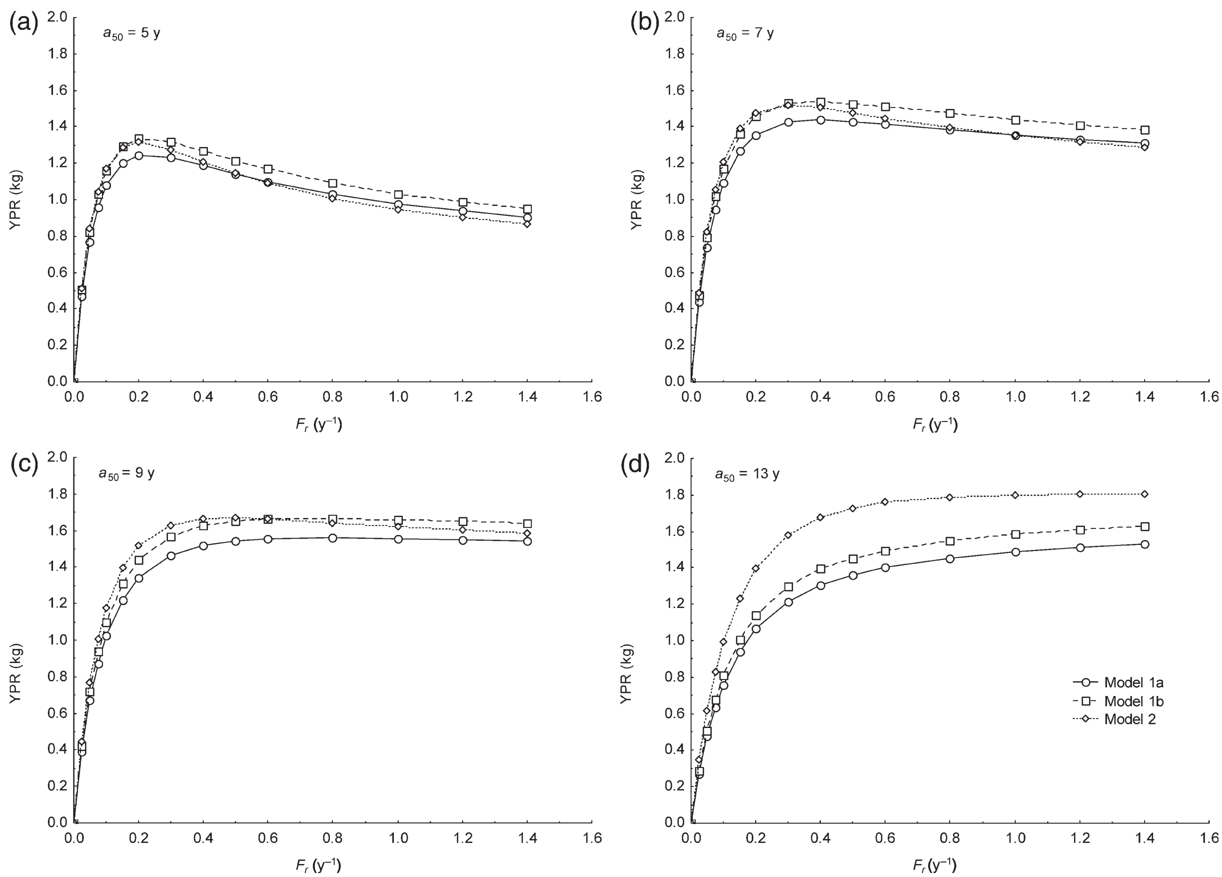

Figure 4. Comparison of estimates of YPR of NEA cod as a function of F_r for three different models. The models are: (1a) age-structured, with an annual time-step (circles); (1b) age-structured with a quarterly time-step (squares); (2) age–length-structured with a quarterly time-step (diamonds). (a) $a_{50} = 5$ y, (b) $a_{50} = 7$ y, (c) $a_{50} = 9$ y, and (d) $a_{50} = 13$ y.

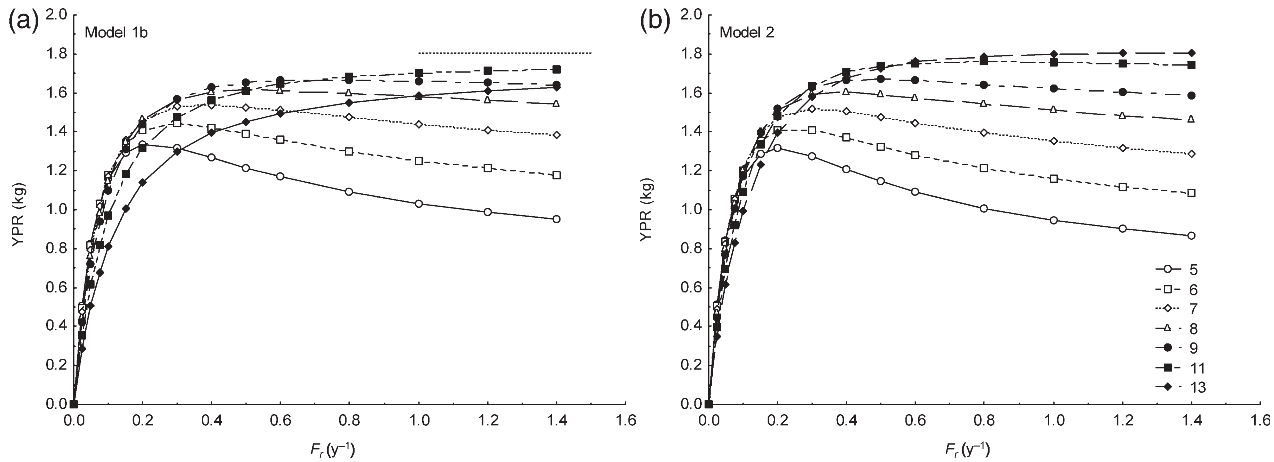

Figure 5. YPR estimates as a function of F_r from the two models with quarterly time-steps (models 1b and 2). The legend shows a_{50}, the age experiencing a fishing mortality of $0.5F_r$. (a) Age-structured population (model 1b). The horizontal line shows the maximum YPR achieved with model 2. (b) Age–length-structured population (model 2).

age-structured model for the NEA cod stock. The optimal selection pattern differed between the two models. The age–length-structured model suggested reduced exploitation on smaller fish and increased exploitation on larger fish, as well as reduced fishing pressure compared with the age-structured model. The loss of yield when F was increased above $F_{\max}$ was slightly higher when an age–length-structured model was used.

This study only considers the difference between point estimates obtained from different models. We did not investigate the uncertainty in model parameters and model results. All three models suggested that the YPR could increase by exploiting larger cod than at present. This is in accordance with the YPR estimates of Ulltang (1987), calculated using an age-structured population model. Depending on exploitation pattern, Ulltang found an $F_{\max}$ in the range 0.2–0.3 y^{-1} and an estimate of YPR in the range 1.2–1.4 kg. These values for $F_{\max}$ and YPR agree reasonably well with our results. The highest estimates of YPR were generated by lowering fishing pressure on juvenile cod. Ulltang (1987) concluded, for the NEA cod stock, that considerable gains would have been achieved in terms of a higher and more stable yield in the period 1970–1983 by introducing a 150 mm (as opposed to a 120 mm) minimum trawl mesh size in addition to the total allowable catch regulations in the 1970s. Currently, the bottom trawlers fishing for NEA cod in the Norwegian economic zone use codends with 135 mm meshes (Nakken, 1994) combined with a sorting grid with a minimum bar distance of 55 mm (Kvamme, 2005).

Table 4. Estimates of $F_{r,\ \max}$, corresponding $F_{5-10,\ \max}$, and YPR (kg) for $a_{50} = 6$ y, using different models.

Model	a_{50}	$F_{r,\ \max}$	$F_{5-10,\ \max}$	YPR
1a	6	0.295	0.22	1.35
1b	6	0.290	0.23	1.44
2	6	0.245	0.18	1.42
ICES (2001)	–	0.22	0.21	1.24
ICES (2002)	–	0.30	0.25	1.26

$F_{5-10,\ \max}$ is the F_{5-10} (the arithmetic mean of F for ages 5–10) giving the maximum YPR for a given a_{50}, and $F_{r,\ \max}$ is the corresponding F_r. ICES estimates are included for comparison.

The effect of fishery on mean size- and maturity-at-age, as estimated by the age–length-structured population model, is significant. This study shows that taking account of length can be important even when individual growth is constant over time, because changes in fishing pressure and gear selectivity are likely to lead to changes in size-at-age that cannot be reflected properly in age-based models that assume fixed weight-at-age. For example, with a fishing pattern close to the present ($a_{50} = 7$ y), mean weight- and length-at-age for ages 6–9 is reduced by 2–14% (Table 3) and 1–5%, respectively, when F_r increases from 0.6 to 1.4 y^{-1}. This range of F_r corresponds approximately to the range of F values experienced in the past 50 y. However, these weight changes are smaller than the variation range in weight-at-age in the stock for these age groups in the period 1946–2003 (1.5–2.8 kg for age 6, 3.7–8.9 kg for age 9). Including length structure in a population model for this stock may help in separating the effect of length-selective mortality from other factors (temperature, food availability, population size, genetic changes, etc.) that affect cod growth.

Our study assumes that the growth process is Markovian, i.e. the growth of fish in a length class during a time-step does not depend on how much the fish has grown in previous time-steps. However, a stock will generally be composed of fish with different genetic properties as far as growth is concerned, so length-selective mortality will tend to remove the fastest-growing fish in the cohort (Silliman, 1975; Pitcher and Hart, 1982; Law, 2000). This would give a stronger effect on size-at-age than our results show and could also result in a permanent change in the population's growth characteristics.

Here we used a fixed natural mortality of 0.2 y^{-1}. Our analysis could be extended by modelling cannibalism too, using the size selectivity for cod cannibalism described by Bogstad (2002). The age range of the analysis should then be extended to include also ages 1 and 2, because cannibalism mortality on ages 1 and 2 cod may be high (more than 2.0 y^{-1} for age 1 in some years (ICES, 2003a). The results of the YPR analysis may change significantly if cannibalism is included. In such an extended analysis, one should also consider that the level of cannibalism seems to depend upon

Table 5. Estimated mean weight-at-age in the catch (throughout the year) under different exploitation rates (F_r = 0.025, 0.6, and 1.4) and patterns (a_{50}= 5, 7, 9, and 13 y) obtained from the simulations with the age–length-structured population model (model 2).

Age (y)	Model 1b	Model 2								
		a_{50} = 5 y			a_{50} = 7 y		a_{50} = 9 y		a_{50} = 13 y	
		0.025	0.6	1.4	0.6	1.4	0.6	1.4	0.6	1.4
3	0.26	0.59	0.59	0.58	0.63	0.63	0.64	0.64	–	–
4	0.74	1.07	1.04	1.00	1.31	1.30	1.36	1.37	1.33	1.43
5	1.32	1.60	1.52	**1.42**	2.10	2.05	2.49	2.47	2.68	2.71
6	2.08	2.31	2.12	**1.91**	2.83	2.70	3.71	3.63	4.97	4.94
7	3.08	3.27	2.96	**2.57**	3.59	3.33	4.78	4.60	7.42	7.28
8	4.30	4.53	4.10	**3.50**	4.48	**4.01**	5.75	5.42	9.34	9.06
9	5.65	6.04	5.51	**4.73**	5.59	**4.81**	6.74	6.17	10.83	10.38
10	7.12	7.79	7.18	**6.24**	**6.96**	**5.76**	7.83	**6.90**	12.11	11.42
11	8.87	9.84	9.12	**8.01**	**8.63**	**6.87**	9.07	**7.61**	13.29	12.30
12	10.97	12.19	11.38	**10.09**	**10.64**	**8.17**	**10.54**	**8.34**	14.45	13.07
13	12.23	14.83	13.93	**12.22**	**12.98**	**9.71**	**12.28**	**9.08**	15.65	13.77
14	14.15	17.65	16.71	16.67	**15.59**	**11.47**	**14.30**	**9.86**	16.92	**14.43**
15	16.12	20.49	19.56	–	**18.36**	**13.72**	**16.58**	**10.71**	**18.26**	**15.05**

The underlined and emboldened weights-at-age differ by more than +10% and −10%, respectively, from values with a_{50} = 5 y and F_r = 0.025 y^{-1}.
The weights-at-age of the age-structured population model (model 1b) are included for comparison.

capelin (*Mallotus villosus*) abundance (ICES, 2003a). Also, the difference between an age-structured and an age–length-structured model in terms of the effect of cannibalism could be studied, because cannibalism is length-selective and depends on predator as well as prey length.

The results of Beverton *et al.* (1994) indicate that spawning mortality might be the main component of natural mortality among mature cod. Jakobsen and Ajiad (1999) found that the data on sex ratio in survey and commercial catch data indicate a higher natural mortality in mature males than in mature females. The difference is close to 0.05 y^{-1}. The difference in maturation between male and female NEA cod is described by Ajiad *et al.* (1999); the length at 50% maturity (not the proportion maturing) was ~65 cm for males and ~75 cm for females, i.e. a difference of about 10 cm. The growth rate of immature fish is approximately the same for both sexes, but males mature smaller. Owing to differences in mortality as well as in growth and maturation, it could be of interest to model male and female fish separately. The Gadget framework is well suited to such studies.

Observed changes in size-at-age can result from density-dependent or environmental factors influencing growth rate, as

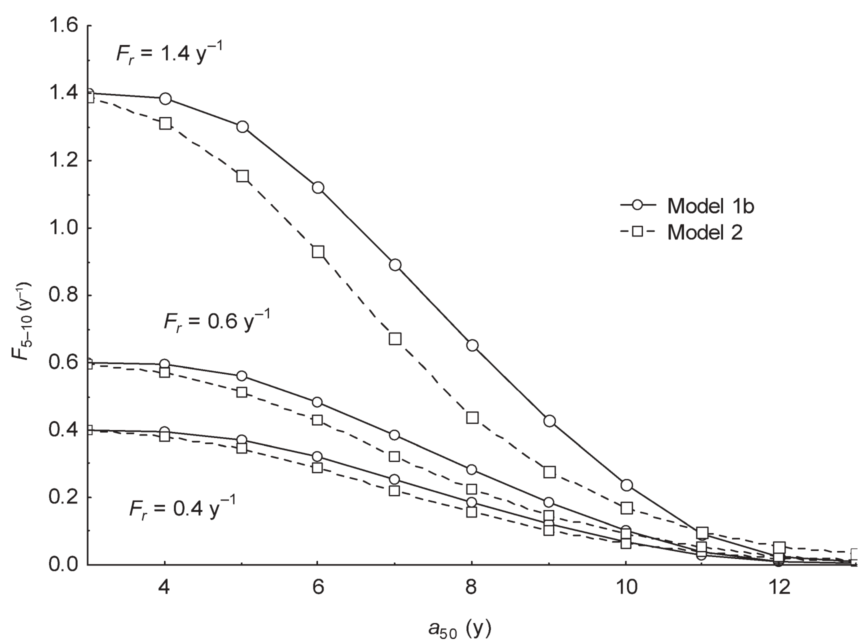

Figure 6. The annual arithmetic mean fishing mortality for ages 5–10, F_{5-10}, plotted against a_{50}, for F_r = 0.4, 0.6, and 1.4 y^{-1} and models 1b and 2.

well as size-selective mortality. Here we used a fixed annual growth rate throughout the simulation period. The study could, however, be extended by introducing density-dependent growth. This phenomenon would tend to give higher size-at-age at high fishing mortalities because the stock size would then be lower. ICES (2004) found weight-at-age for cod aged 6–9 to be density-dependent. Marshall *et al.* (2004) investigated the development in length- and weight-at-age in NEA cod from 1947 on and found an increase in mean length-at-age for the oldest cod; for example, the length of age 12 cod increased from about 95 cm in 1947 to 110 cm (1980-present). This could be the result of long-term increases in fishing mortality, either favouring survival of large cod that swim faster and have a higher probability of escapement or resulting in reduced intra-specific competition for food (density-dependence).

Sinclair *et al.* (2002a) studied the relative importance of size-selective mortality, density-dependence, and temperature on growth of Atlantic cod in the southern Gulf of St Lawrence, Canada. They found that the strongest effect was variation in size-selective mortality, followed by a negative effect of population density and a weak positive effect of ambient temperature. Size-selective mortality may change between periods. For instance, for cod in the Gulf of St Lawrence, size selection changed from favouring fast growth in the 1970s to favouring slow growth in the late 1980s and 1990s (Hanson and Chouinard, 1992; Sinclair *et al.*, 2002b). Changes in length-at-age for female Pacific hake (*Merluccius productus*) from Georgia Strait, British Columbia, were studied by Welch and McFarlane (1990). They found a decline in the maximum size attained and argued that it most likely resulted from selective removal of the largest fish from the population rather than environmental or density-dependent factors.

All models given here can be extended by including a stock-recruitment relationship as well as density-dependence, and studies of the maximum sustainable yield (MSY) for different fishing mortalities and selection patterns could then be made. The effect of including density-dependence in YPR studies has been investigated, e.g. by Shin and Rochet (1998), who found a more optimistic estimate of YPR for North Sea Downs herring (*Clupea harengus*) when the observed negative relation between herring abundance and growth was incorporated, compared with the classic YPR estimates with constant weight-at-age; the use of constant growth would overestimate the positive effects of reducing fishing effort. An age-structured model of that type for NEA cod already exists (ICES, 2004), and studies of MSY with such a model are in progress (Kovalev and Bogstad, 2005). The age–length-structured cod model described by Bogstad *et al.* (2004) could be extended to be compatible with the age-structured model, so a comparison of MSY between age and age–length models could be made, similar to the comparison of YPR given here.

Using a length-structured model and length-dependent selectivity ensures consistency between size-at-age in the stock, in the catch, and in the maturity ogive. The inability to match these may be a problem in age-structured models, so age–length-structured models may be required. The importance of including length structure will depend on the shape of the function describing mean growth, the method used for modelling individual variability in growth (Parma and Deriso, 1990), and the exploitation pattern. A general study comparing the importance of considering length structure between stocks with different life histories, e.g. concerning growth pattern, could therefore be valuable.

Acknowledgements

This work was funded by the Research Council of Norway (Project No. 134850/140). We thank Daniel Howell, Dankert W. Skagen, Øyvind Ulltang, Helen Dobby, Kristin G. Frøysa, editor Verena Trenkel, and three anonymous referees for comments and grammatical corrections. We also thank Morten N. Åsnes for practical help with the simulation runs and Arvid Hylen and Kjell H. Nedreaas for making the VPA runs from Hylen (2002) available to us.

References

Ajiad, A. M., Jakobsen, T., and Nakken, O. 1999. Sexual difference in maturation of Northeast Arctic cod. Journal of Northwest Atlantic Fishery Science, 25: 1–15.

Begley, J. 2005. Gadget User Guide. Marine Research Institute Report 120. Marine Research Institute, Reykjavík, Iceland. 90 pp.

Begley, J., and Howell, D. 2004. An overview of Gadget, the Globally applicable Area-Disaggregated General Ecosystem Toolbox. ICES Document CM 2004/FF: 13. 15 pp.

Bergstad, O. A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fisheries Research, 5: 119–161.

Beverton, R. J. H. 1954. Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. United States Fishery Laboratory, Beaufort, North Carolina. Miscellaneous Contributions 2. 181 pp.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fishery Investigations, Series 2, 19. HMSO, London. 533 pp.

Beverton, R. J. H., Hylen, A., and Østvedt, O. J. 1994. Growth, maturation, and longevity of maturation cohorts of Northeast Arctic cod. ICES Marine Science Symposia, 198: 482–501.

Björnsson, H., and Sigurdsson, T. 2003. Assessment of golden redfish (*Sebastes marinus* L.) in Icelandic waters. Scientia Marina, 67 (Suppl. 1): 301–314.

Bogstad, B. 2002. A model for size preferences in cannibalism in Northeast Arctic cod (*Gadus morhua* L.). Annex C.6 in: dst2. Development of Structurally Detailed Statistically Testable Models of Marine Populations. QLK5-CT1999-01609. Progress Report for 1 January to 31 December 2001. Marine Research Institute Technical Report 87. Marine Research Institute, Reykjavík, Iceland. 320 pp.

Bogstad, B., Howell, D., and Åsnes, M. N. 2004. A Closed Life-Cycle Model for Northeast Arctic Cod. ICES Document CM 2004/K: 26. 26 pp.

Chapman, D. G. 1961. Statistical problems in dynamics of exploited fisheries populations. Proceedings of the 4th Berkeley Symposium on Mathematical Statistics and Probability. Contributions to Biology and Problems of Medicine, 4: 153–168.

Frøysa, K. G., Bogstad, B., and Skagen, D. W. 2002. Fleksibest – an age-length structured fish stock assessment model. Fisheries Research, 55: 87–101.

Hanson, J. M., and Chouinard, G. A. 1992. Evidence that size-selective mortality affects growth of Atlantic cod (*Gadus morhua* L.) in the southern Gulf of St Lawrence. Journal of Fish Biology, 41: 31–41.

Hylen, A. 2002. Fluctuations in abundance of Northeast Arctic cod during the 20^{th} century. ICES Marine Science Symposia, 215: 543–550.

ICES. 2001. Report of the Arctic Fisheries Working Group, Bergen, Norway, 24 April–3 May 2001. ICES Document CM 2001/ACFM: 19. 380 pp.

ICES. 2002. Report of the Arctic Fisheries Working Group, ICES, Copenhagen, Denmark, 16–25 April 2002. ICES Document CM 2002/ACFM: 18. 451 pp.

ICES. 2003a. Report of the Arctic Fisheries Working Group, San Sebastian, Spain, 23 April–2 May 2003. ICES Document CM 2003/ACFM: 22. 448 pp.

ICES. 2003b. Report of the Study Group on Age-Length Structured Assessment Models, Bergen, Norway, 3–6 June 2003. ICES Document CM 2003/D: 07. 88 pp.

ICES. 2004. Report of the Arctic Fisheries Working Group, ICES, Copenhagen, Denmark, 4–13 May 2004. ICES Document CM 2004/ACFM: 28. 475 pp.

ICES. 2005. Report of the Study Group on Age-length Structured Assessment Models (SGASAM), ICES, Copenhagen, Denmark, 14–18 March 2005. ICES Document CM 2005/D: 01. 63 pp.

Jakobsen, T., and Ajiad, A. M. 1999. Management implications of sexual differences in maturation and spawning mortality of Northeast Arctic cod. Journal of Northwest Atlantic Fishery Science, 25: 125–131.

Jennings, S., Kaiser, M. J., and Reynolds, J. D. 2001. Marine Fisheries Ecology. Blackwell Science, Malden, USA. 417 pp.

Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). Journal du Conseil International pour l'Exploration de la Mer, 46: 235–248.

Kovalev, Y. A., and Bogstad, B. 2005. Evaluation of maximum long-term yield for Northeast Arctic cod. *In* Ecosystem Dynamics and Optimal Long-Term Harvest in the Barents Sea Fisheries. Proceedings of the 11th Russian–Norwegian Symposium, Murmansk, Russia, 15–17 August 2005, pp. 138–157. Ed. by V. Shibanov. IMR/PINRO Joint Report Series, 2/2005. 331 pp.

Kristiansen, T., and Svåsand, T. 1998. Effect of size-selective mortality on growth of coastal cod illustrated by tagging data and individual-based growth and mortality model. Journal of Fish Biology, 52: 688–705.

Kvamme, C. 2005. A simulation study of the effects of changes in fishing pressure and exploitation pattern on the northeast Arctic cod (*Gadus morhua* L.) stock. *In* The Northeast Arctic Cod (*Gadus morhua* L.) Stock: Gear Selectivity and the Effects on Yield and Stock Size of Changes in Exploitation Pattern and Level. DSc thesis, Department of Biology, University of Bergen, Norway.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659–668.

Lee, R. M. 1912. An investigation into the methods of growth determination in fishes. Conseil Permanent International pour l'Exploration de la Mer. Publications de Circonstance, 63. 35 pp.

Leigh, G. M., and O'Neill, M. F. 2005. Stock assessment of the Queensland – New South Wales tailor fishery (*Pomatomus saltatrix*). Southern Fisheries Centre, Deception Bay. Department of Primary Industries and Fisheries, Queensland Government, Australia. 98 pp.

Marshall, C. T., Needle, C. L., Yaragina, N. A., Ajiad, A. M., and Gusev, E. 2004. Deriving condition indices from standard fisheries databases and evaluating their sensitivity to variation in stored energy reserves. Canadian Journal of Fisheries and Aquatic Sciences, 61: 1900–1917.

Methot, R. D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. Bulletin of the International North Pacific Fisheries Commission, 50: 259–277.

Methot, R. D. 2000. Technical description of the stock synthesis assessment program. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS–NWFSC–43. 46 pp.

Nakken, O. 1994. Causes of trends and fluctuations in the Arcto-Norwegian cod stock. ICES Marine Science Symposia, 198: 212–228.

Parma, A. M., 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. Canadian Journal of Fisheries and Aquatic Sciences, 47: 274–289.

Pitcher, T. J., and Hart, P. B. 1982. Fisheries Ecology, 1st edn. Chapman and Hall, London. 414 pp.

Ricker, W. E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. Journal of the Fisheries Research Board of Canada, 26: 479–541.

Shin, Y-J., and Rochet, M-J. 1998. A model for the phenotypic plasticity of North Sea herring growth in relation to trophic conditions. Aquatic Living Resources, 11: 315–324.

Silliman, R. P. 1975. Selective and unselective exploitation of experimental populations of *Tilapia mossambica*. Fishery Bulletin US, 73: 495–507.

Sinclair, A. F., Swain, D. P., and Hanson, J. M. 2002a. Disentangling the effects of size-selective mortality, density and temperature. Canadian Journal of Fisheries and Aquatic Sciences, 59: 372–382.

Sinclair, A. F., Swain, D. P., and Hanson, J. M. 2002b. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Canadian Journal of Fisheries and Aquatic Sciences, 59: 361–371.

Sund, O. 1911. Undersøkelser over brislingen i norske farvand væsentlig paa grundlag av "Michael Sars"s togt 1908. Aarsberetning Vedkommende Norges Fiskerier for 1910. 1910 (3dje hefte): 357–473 (in Norwegian).

Taylor, L., Begley, J., Kupca, V., and Stefánsson, G. 2004. A simple implementation of Gadget for cod in Icelandic waters. ICES Document CM 2004/FF: 23. 41 pp.

Ulltang, Ø. 1987. Potential gains from improved management of the Northeast Arctic cod stock. Fisheries Research, 5: 319–330.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws, 2). Human Biology, 10 (2): 181–213.

Welch, D. W., and McFarlane, G. A. 1990. Quantifying the growth of female Pacific hake (*Merluccius productus*): an example of measuring uncertainty and bias in non-linear parameter estimation. Canadian Journal of Fisheries and Aquatic Sciences, 47: 672–681.

doi:10.1093/icesjms/fsl027