

How may feeding data be integrated into a model for a Norwegian fjord population of cod (*Gadus morhua* L.)?*

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SUMMARY: We investigate how cod feeding data may be included into a recently developed age-structured model for a coastal cod population in a small fjord in northern Norway. The model integrates data from mark-recapture experiments, trawl-surveys and commercial catches. The fjord population has high biomass density (2-3 tonnes km⁻²) and low fishing mortality rates ($F < 0.30 \text{ year}^{-1}$). The model output parameters (cannibalism mortality rate, other natural mortality rate, fishing mortality rate, recruitment numbers, gear selection functions for commercial and research trawls and trawl catchability coefficient) are estimated using a weighted least-square minimisation routine. We evaluate different strategies for, and effects of, inclusion of feeding data in the model, and evaluate the effects of uncertainty in the different data sets. Representation of the feeding data as an Ursin lognormal distributed size (predator weight/prey weight) food preference function yielded realistic cannibalism mortalities. The sensitivity of the results to data input are discussed.

Key words: cannibalism, mathematical population model, cod, feeding, mortality

INTRODUCTION

Coastal cod is a dominant predator and an important commercial species in the fjords and coastal waters in northern Norway (Bax and Eliassen, 1990). The Norwegian coastal cod substocks are relatively stationary and inhabit the fjords and coastal areas in contrast to the Northeast Arctic cod group that are long range migrators inhabiting the Barents Sea and using the Norwegian coast as their spawning area (Jakobsen 1987). Sør fjord, the inner part of the Ullsfjord-system in Troms County, northern Norway, has been studied as a site for a cod enhancement programme (Berg and Pedersen, 2001; Pedersen and Pope, subm.). In the course of this, the

area has also intensively been sampled by trawl and extensive tagging experiments of wild and released cod have also been performed (Nøstvik and Pedersen, 1999a, b). A recently developed model for the coastal cod population in Sør fjord (Pedersen and Pope, subm.) uses data from mark-recapture experiments together with data on the numbers at age caught in trawl surveys and by the commercial fishery for a seven-year period (1989-1996). The existing model utilises the data sets to produce estimates of abundance and mortality of fish older than two years of age, but in this paper we use data on cod feeding to expand the model to estimate abundance and mortality rates also for the 0-1 age groups.

Tagging results indicate that there is a minor migratory exchange of cod between Sør fjord and other areas, and there are no indications of seasonal

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migrations of cod out of the fjord (Nøstvik and Pedersen, 1999b). Growth, maturity and recruitment patterns all indicate that the cod inhabiting Sør fjord form a discrete fish stock with dynamics that differ both from the northeast arctic cod stock in the Barents Sea, and from coastal cod in adjacent areas (Berg and Pedersen, 2001).

Cod is the dominant piscivore fish species in Sør fjord and bottom trawl catches typically consist of c. 70% cod by weight (Nøstvik and Pedersen, 1999a). Feeding data from the fjord indicate that cannibalism may be an important source of mortality of young cod (Kanapathippillai *et al.*, 1994). Cannibalism may be an important population regulator mechanism in fish stocks (Bogstad *et al.*, 1994; Nilssen *et al.*, 1994; Punt and Hilborn, 1994), and improved understanding of factors that determine cod juvenile mortality patterns may be helpful for both enhancement and management actions (Ulltang, 1984).

Several previous attempts to include cannibalism in models have been based on expanded virtual population models (VPA) (Leonart *et al.*, 1984; Sparre, 1991). Traditional VPA-type models assume that the catch-data are sampled without statistical errors (Quinn and Deriso, 1999). In contrast to the VPA-type models approach, we attempt in this paper to integrate data on cannibalism with data from tagging, surveys and commercial catch at age using a least-square model. We further attempt to indicate major sources of uncertainty in the data and the estimates. The fitted model was also used in simulation mode to estimate the impact of increased fishing mortality on cannibalism mortality.

MATERIALS AND METHODS

Investigation area and sampling

The investigation area Sør fjord is situated in Troms county, northern Norway, and is the inner part of the Ullsfjord-Sør fjord system. A 300 m wide and 8 m deep sill separates Sør fjord and Ullsfjord. The maximum depth in Sør fjord is 130 m and the area is 55.2 km². For a more detailed description of the topography of the investigation area and sampling of fish, see Kanapathippillai *et al.*, (1994), Berg and Pedersen (2001) and Pedersen and Pope (subm.).

Cod stomachs (n=3543) were taken for estimation of the consumption of cod from quarter 4 in 1989 to quarter 4 in 1996 using trawl caught cod.

The sampling of stomachs was length stratified in 5 cm groups in order to adequately sample all sizes of fish. Stomachs were removed by cutting the pylorus and the oesophagus at the pharynx. Individual stomachs were then either preserved in 4% formaldehyde (1989-1991) or kept frozen (1992-1996).

Gill nets were used for sampling during 1989-91 and 1994-95 in order to sample the fjord slopes where the bottom is steep, rough and hence inaccessible to the bottom trawl. Gill-net fleets sets composed of sets of different mesh-sizes (16, 22, 46 and 70 mm) were set for c. 20 hours before hauling. A similar sampling scheme for fish and for stomachs was applied to the gill-net catches as was used for the trawl catches.

Temperature was measured at each trawl location using a Neil Brown CTD, and the average temperature for the water column was calculated. The fjord was divided into four strata, each having one trawl location stratum, and it was assumed that the average water temperature in the water column was representative for the local cod habitat. Average habitat temperature for the whole fjord for each quarter was calculated by weighting the temperatures by strata areas.

Feeding data

Stomach data were available from 22 quarters. In the laboratory, food items in cod stomachs were identified to the lowest possible taxa, and total wet weights were recorded for each prey category. The total lengths for cod found in the stomachs were recorded.

Daily food consumption of cod was estimated using the food consumption model described by Santos and Jobling (1992, 1995). The model estimates the consumption of cod per hour (C), and takes into consideration effects of temperature, weight of the predator, weight of cod in the stomach, weight of total prey (meal-size), as well as prey-specific digestion rate coefficients.

$$C = \frac{\ln 2 \exp^{a1 \cdot T} B^{a2} S_c}{a3 (\sum S_i)^{a4}}$$

T is temperature, B is the total weight of the predator in gram, and S_c is the weight of cod in the stomach. a₁, a₂ and a₄ are coefficients accounting for the effect of temperature, predator body weight and weight of other prey on the stomach evacuation

rate and hence the consumption rate. a_3 is the assumed half-time of cod using the value (84 hours) from haddock (*Melanogrammus aeglefinus*) given in Santos and Jobling (1995). S_i is the weight of different prey groups in the stomach of the cod. To avoid bias in the calculation of consumption we applied the model to the individual stomach samples and then estimated the mean consumption by size class.

The average consumption of cod prey in $g\ day^{-1}$ for each 5-cm predator length group was estimated for each quarter. The average number of cod eaten in each quarter and age group by each 5-cm predator length group was then calculated by dividing the consumption in $g\ cod\ quarter^{-1}$ by the estimated fresh weight of the ingested cod. The fresh weight was calculated from the total length of the cod eaten using a cubic length-weight relation.

The fisheries model describes fishing mortality as an annual rate modified by size selection factors fitted separately to research trawl and commercial gears (Appendix 1, Table 1). The selection curves are based upon a simple three parameter model (Appendix 1).

Cannibalism model

Cod cannibalism mortality rate $M_2(y,q,a)$ was modelled using the approach of Pope and Macer (1991), which adopts a Ursin size selection function (Ursin, 1973), weighted by a constant um_2 predation cannibalism mortality per unit predator weight. This is then multiplied by the average predator biomass $Ps(y,q,a')$ for the year, quarter and age. Hence,

$$M_2(y,q,a) = \sum Ps(y,q,a') * um_2 * \exp\left(-0.5 \cdot \left(\frac{(LWR(y,q,a,a') - \mu)}{\sigma}\right)^2\right)$$

where um_2 , μ and σ are model parameters and where,

- a age of prey
- a' age of predator
- y year
- q quarter

$$LWR = \ln\{Wt(y,q,a')/Wt(y,q,a)\}$$

and $Wt(y,q,a')$, $Wt(y,q,a)$ are the respective weights of predator and prey.

Model fitting

The model structural equations (Appendix 1) are used together with initial values of the model parameters to provide estimates as follows.

- Commercial catch at age data from 1994 q1 to 1996 q4.
- Survey catch at age data from 1989 q4 to 1996 q4.
- Commercial recaptures at age for each year-quarter from each of the 5 tagging experiments initiated in 1990, 1991, etc.
- Survey recaptures at age for each year-quarter from each of the 5 tagging experiments
- Numbers of cod prey in each 5 cm length group to be eaten per quarter for each 5 cm predator length group. The number of predator cod in each 5 cm length group was calculated from the numbers at age and age-length keys.

The model estimates of items 1 to 5 together with the sampling based estimates of the same factors are used to construct a least squares function which is summed for all available ages and year-quarters to provide a total sum of squares for the factor. The form of sum of squares function used for each factor was as follows. For convenience in tables and equations these are given short names.

- Catch = $SSq(Com.Catch) = w_1 * (\text{observed} - \text{expected})^2$
- Survey = $SSq(Surv.Catch) = w_2 * (\text{observed} - \text{expected})^2$
- TagCatch = $SSq(Com.Tag.Catch) = w_3 * (\text{observed} - \text{expected})^2 / \text{expected}$
- TagSurvey = $SSq(Surv.Tag.Catch) = w_4 * (\text{observed} - \text{expected})^2 / \text{expected}$
- Feeding = $SSq(Stomach\ Contents) = w_5 * (\text{observed} - \text{expected})^2 / \text{expected}$

The weights (w_1 - w_5) are introduced in order to weight the different data sets and to be able to investigate the effects of different weighting of the different sets. These weighted factor sum of squares are combined into an objective function:

$$\text{Total sum of squares} = \text{Catch} + \text{Survey} + \text{TagCatch} + \text{TagSurvey} + \text{Feeding}$$

EXCEL solver is used to adjust model parameters (Appendix 1) to minimise this objective function taking care by repeated minimisation attempts to ensure that it reached a true minimum. Resulting model parameters and the consequential estimates of population numbers, fishing mortality rate and predation mortality rate then form the output of the

TABLE 1. – Overview of key model parameters

Parameter	Explanation	Unit
α	shape commercial selectivity funct. (right hand slope)	cm ⁻¹
β	shape commercial selectivity funct. (left hand slope steepness)	cm ⁻¹
δ	shape commercial selectivity funct. (length at 50 % sel. when $\beta=0$)	cm
k	catchability term	hour ⁻¹
ϕ	shape survey selectivity funct. (steepness)	cm ⁻¹
γ	shape survey selectivity funct. (length at 50 % sel.)	cm
um2	consumption parameter cannibalism	
μ	preferred ln(predator weight/prey weight)	
σ	standard deviation of lognormal predator weight/prey weight preference function	
M1	non-cannibalism natural mortality rate	year ⁻¹

model. The spawning stock biomass was calculated using the maturity ogive given by Berg and Pedersen (2001).

A key model run was estimated using $c1=0.5$, $c2=80\%$, $c3=10\%$ and $c4=10\%$ year⁻¹, and the right hand slope of the gear selection curve (α) of the commercial fishery was held fixed at a small value (0.015 cm⁻¹) during this run. In a key run, the sums of squares of the four sets of data were weighted so that their contributions to the total sum of squares were about equal. The model residuals of all sets of data were inspected visually.

Sensitivity analysis

We investigated the effects on parameter estimates of double weighting of the sum of squares of each data set in turn. In the case of the feeding data, which is the key concern of this paper, we also investigated the effects of giving very low weight (1/8 of the key run weight) to the feeding data. For some key parameters (Table 1) we further investigated the sensitivity of the objective function to their values by fixing them to specific values. The model was run either with a fixed value of the right hand slope (α) of the commercial gear selection function, or with α estimated by the model.

Simulation

The model could also be run forward in time to provide simulations of the effects on future stock structure of different levels of fishing mortality, etc. Thus, we simulated the stock abundance, biomass of total and spawning stock and the yield for a period of 30 years from 1997 to 2027. In the simulations, we used the average size at age for the period 1989-1996 and the estimates of output parameters from

the estimation model. The abundance at age in quarter four in 1996 were used as starting values. Since there are uncertainty with regard to whether the stock in Sør fjord is fully self-recruited or mainly recruited by 0-group drifting into the fjord from outside, we made all the simulations with two modes 0-group recruitment, either as constant recruitment from the outside or as fully self-recruitment (internal recruitment). Self-recruitment was simulated using a constant production of 15 0-group settled recruits per kg spawner biomass.

RESULTS

Feeding

Invertebrate prey dominated the diet for small and medium sized cod less than c. 50 cm in length in all years (Fig. 1). Fish prey other than cod (mainly herring (*Clupea harengus*), other gadoids and long rough dab (*Hippoglossoides platessoides*)) were most important for medium sized cod (30-50 cm in length), while cod was most important in the diet of cod longer than c. 50 cm in the period 1990-91. A total of 86 cod were identified in 3543 cod stomachs. Cod were observed in cod stomachs from all years except for in 1989. We also observed cannibalism in stomachs sampled by gill nets during the period 1990-91 and in 1994 (Table 2). Cod of lengths 4-40 cm were eaten by cod 30-100 cm long (Fig. 2). Cod longer than 50 cm had the highest consumption of 5-35 cm cod in terms of number of prey eaten per quarter per predator. These largest cod fed cannibalistically on a broader length range than did smaller cannibals (Fig. 2). However, the main predation pressure on 0-10 cm cod came from the more numerous cod of 30-60 cm of length (Fig. 2).

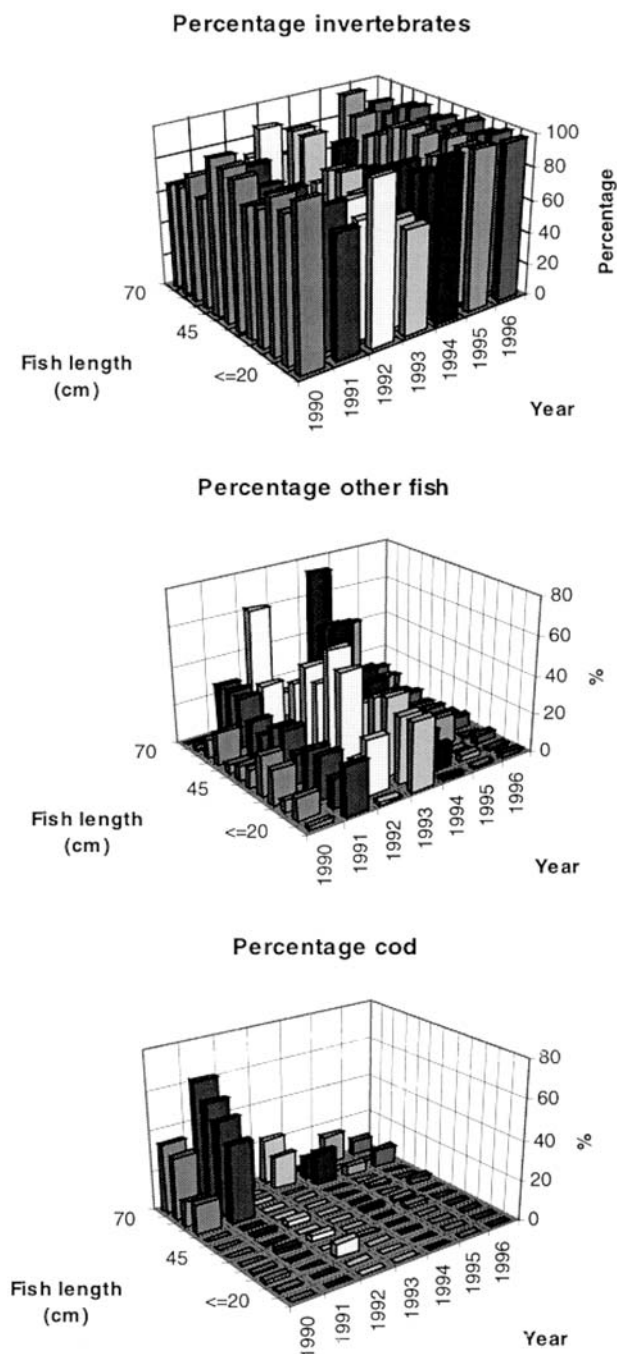


FIG. 1. – Overview of yearly average percentage consumption of different prey groups related to cod predator length for the period 1990-1996 in Sjørdfjord.

Key model run

A key model run was made with the standard weighting of the various sum of squares function found to provide satisfactory fits to all datasets. Key run results are shown in Figure 3. The total and spawning stock biomass increased from 1990 to

TABLE 2. – Overview of the numbers of cod stomachs sampled by trawl and by gill nets and the number of cod recorded in the stomachs each year

Year	Number of stomachs		Number of cod recorded in stomachs	
	Trawl	Gill nets	Trawl	Gill nets
1989	69	9	0	0
1990	218	224	7	4
1991	295	93	6	7
1992	440		5	
1993	466		14	
1994	598	105	18	2
1995	482	49	14	0
1996	495		9	
Sum	3063	480	73	13

1993 and the annual commercial fishing mortality rate rose from low levels during 1990-92 to about 0.20 year⁻¹ in 1995-96 (Fig. 3A and B). The non-cannibalism natural mortality (M1) was estimated by the model to be 0.26 year⁻¹. The observed and modelled number of cod eaten per predator and the total number of cod cannibalised seem to correspond reasonable well (Fig. 2). An exception to this is the model-predicted cannibalism from predator cod smaller than 30 in length on cod prey smaller than 10 cm that has not been observed in the stomach data (Fig. 2). The cannibalism mortality (M2) was larger than M1 for age 0 to 2 for the whole period. M2 was largest in age-1 cod, and ranged from *c.* 0.5 to 2.0 year⁻¹ (Fig. 3C). The yearly M2 of age group 1 to 4 increased by a factor of about three from 1990 to 1995 as the large 1987 year-class grew to sizes which could take these prey, and then decreased in 1996 (Fig. 3C, 4).

Effects of up-weighting sum of squares of data sets

Table 3 shows the sum of squares from the key-run and the modified values when sums of squares of each data set were double weighted. It is apparent from the table that the main data tensions exist between the survey and catch results and the feeding results. Increased weighting of either one of these sets causes the sum of squares of the other two sets to increase. Sums of squares of the other two tagging data sets were more tolerant of double weighting of the sum of squares of the other sets. The tension between fitting the survey and catch data and the feeding data results because both make somewhat different statements about the abundance of the smallest fish that are not found in the other data sets.

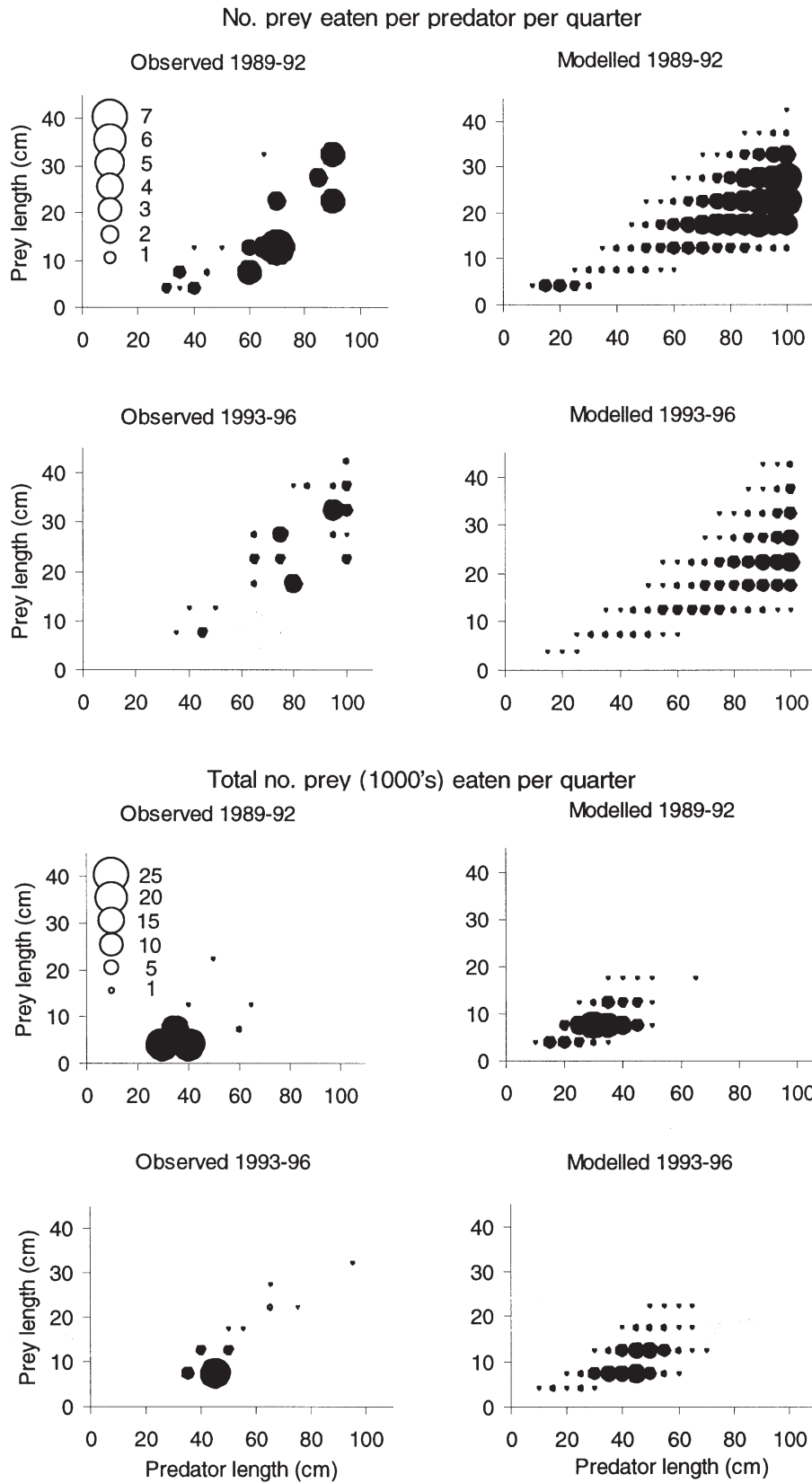


FIG. 2. – Overview of number of cod eaten per quarter per predator for the periods 1989-92 and 1993-96 (upper four figures), and total number of cod in 1000's eaten for the periods 1989-92 and 1993-96 (lower four figures). Left figures show observed values and right figures show modelled values. Circle areas are proportional to numbers and are indicated by open circles.

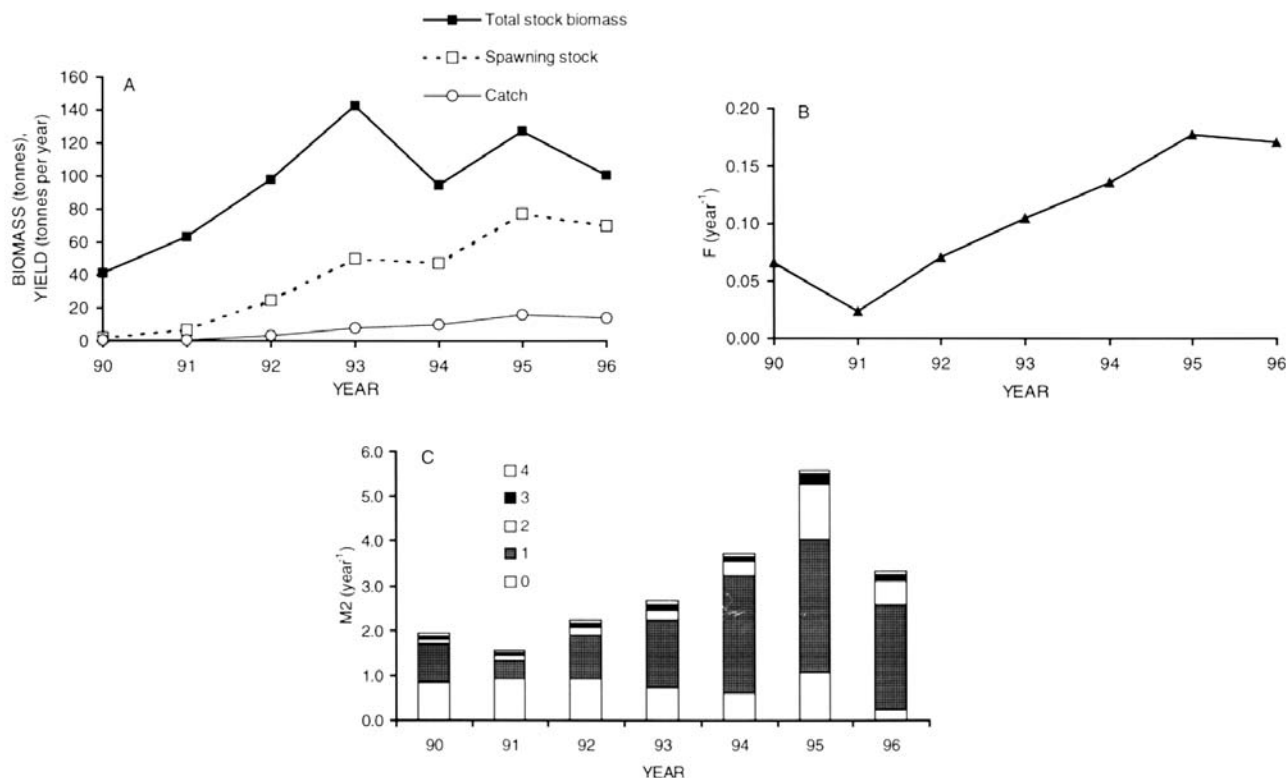


FIG. 3. – A: Model estimates (key run) of total and spawning stock biomass, and yield for the period 1990-1996. B: Estimates of commercial fishing mortality rate. C: Model estimates (key run) of the cannibalism mortalities (M2) for each age group and year. For 0-group the summed values for quarter 3 and 4 are given.

TABLE 3. – Overview of the results of the sensitivity analysis. Each table row represents a separate model run. The results from model runs in which either datasets were given double weight (Catch, Survey, TagCatch, TagSurv, Feeding), or where key parameters were kept fixed and changed by +10% relative to key run is given. In the run “ α estimated by model” the α parameter were also estimated by the model, whereas this parameter was fixed during the other runs. The run with feeding weight 1/8 of key run simulates very low weight to the feeding data. Total sum of squares for the total model (Total), commercial (Catch), survey data (Survey), commercial tagging (TagCatch), survey tagging (TagSurv), and feeding data (Feeding).

Data-set weighted/parameter fixed	Total	Catch	Survey	Sum of squares TagCatch	TagSurv	Feeding
Key run	2357	708	578	445	294	331
Double weighting						
Catch	2990	1155	692	466	317	360
Survey	2911	783	1052	443	290	342
TagCatch	2786	731	594	837	296	328
TagSurv	2649	720	591	444	577	317
Feeding	2649	765	627	446	288	523
Sensitivity fixing parameters						
um2	2358	713	577	444	293	331
μ	2366	713	569	448	296	341
σ	2358	709	578	446	295	330
M1	2371	716	572	455	298	330
k	2366	725	576	453	292	321
γ	2378	688	604	450	302	333
ϕ	2358	711	577	445	294	331
δ	2366	731	573	437	294	330
β	2359	705	579	449	294	331
α estimated by model						
α	2294	714	577	384	292	327
Feeding weight is 1/8 of key run	2004	661	519	442	313	70

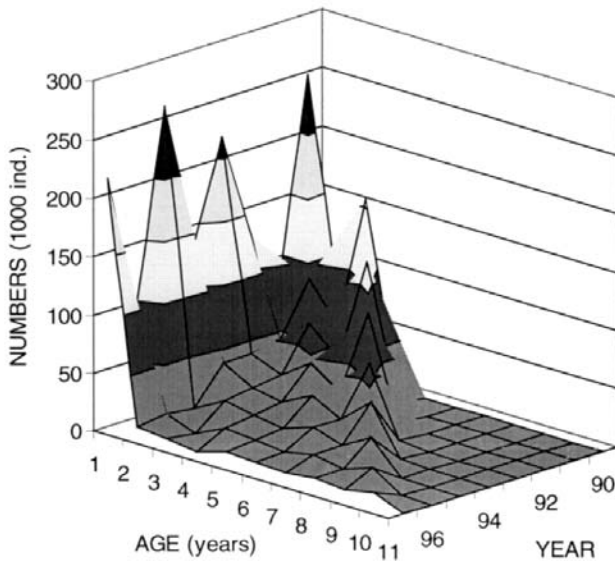


FIG. 4. – Overview of the numbers at age estimates from the model during the period 1990-1996. Youngest age group shown is one year old.

The effects of sum of squares weighting of the feeding data is of particular concern for the predation estimates which form the focus of this paper. When the weight applied to this sum of squares was reduced eight times, this resulted in increased initial numbers, slightly decreased F for 1993-96, and increased spawning biomass and catch by about 30% (Table 4). Furthermore, there was a shift in M2 from 1 and 2-group to 0-group cod, probably caused by a smaller preferred prey size, i.e. larger μ and lower σ in the feeding relation (Table 4). When the feeding weight was decreased 8-fold relative to the key run, the feeding data sum of squares decreased only by about five-fold (331/70) (Table 3), indicating a poorer fit of the feeding data at low feeding data weight. The lower Table 3 also indicates how the other sums of squares affect the fitted parameters.

The effects of changing important parameters from the key-run

Table 3 shows the effects of change in certain parameters by 10% from their key-run values. Only changes to δ and γ (commercial and survey selection length) and k (catchability) had much effect on the sum of squares of the commercial catch at age data. The survey and commercial tag returns sums of squares are little affected by any of the changes, except the survey catchability (k). The sum of

TABLE 4. – Overview of sensitivity analysis results. See table legend for Table 3 for explanation of table. The output statistics in addition to key parameter estimates are: initial numbers in q4 1989 (N_2), average numbers at age 0 in q3 for 1990-92 and 1993-96, average annual commercial fishing mortalities (F), spawning biomass and catch yield for 1992 and 1993-96, average cannibalism mortality for age 0, 1 and 2 for the whole period. Nominal values are given for the key run and for the other runs, the percentage deviations relative to the key run are given.

Data-set weighted/parameter fixed	um2	μ	σ	MI	k	γ	ϕ	δ	β	α	Init. N_2	Recruits		F	Sp. biom.		Yield		M2 at age			
												90-92	93-96		90-92	93-96	90-92	93-96	0	1	2	
Key run	1.21·10 ⁻²	4.26	0.79	0.26	1.4·10 ⁻⁴	29.6	0.26	48.0	0.14	0.02	168	386	374	0.06	0.17	38	101	2	12	0.73	1.54	0.31
Double weighting	-17	-1	1	1	-5	4	-14	-3	12	0	8	8	10	0	-2	8	16	6	17	-5	-2	-3
Catch	14	0	2	3	2	-2	6	1	0	0	4	-1	-5	2	0	-6	-12	-8	-10	4	4	3
Survey	4	-1	-1	0	-2	-1	2	3	-6	0	1	-2	1	2	0	-4	-1	-3	-3	4	4	0
TagCatch	4	-1	2	-1	2	-1	4	0	0	0	-2	-2	-1	-1	0	-7	-5	-7	-5	-1	4	5
TagSurv	7	-1	3	1	6	0	3	1	0	0	-12	-20	-3	1	0	-17	-13	-16	-13	-6	-2	0
Sensitivity fixing parameters																						
um2	10	0	-5	1	0	0	0	0	0	0	-1	1	1	0	0	-2	-1	-2	-1	3	4	-4
μ	-9	10	27	-2	0	0	1	1	-3	0	1	18	-10	-1	1	4	1	6	2	33	-15	-2
σ	-8	2	10	-1	0	0	1	0	-1	0	0	4	-4	-1	0	1	0	1	0	4	-4	6
MI	5	0	-8	10	5	2	-8	5	3	0	5	-3	5	28	17	0	-4	-4	-2	-4	-7	-20
k	1	0	0	3	10	4	-15	2	0	0	-1	-3	-1	11	7	-1	-4	-2	-3	-1	-4	-5
γ	-8	0	1	4	10	10	-21	3	1	0	4	2	4	13	8	4	2	3	3	-3	-5	-3
ϕ	0	0	0	0	2	1	10	10	0	0	0	0	0	-1	-1	0	0	0	0	0	0	1
δ	2	1	0	3	2	1	-3	10	-15	0	2	0	-4	21	23	0	-2	2	-2	3	-4	-8
β	-1	0	-1	0	0	0	0	-2	10	0	0	-2	3	4	-2	0	0	-2	0	-2	0	0
α estimated by model																						
α	4	1	0	-1	1	0	-1	24	262	2681	-2	2	-5	32	22	-1	-1	4	4	6	-2	-6
Feeding weight is 1/8 of key run																						
α	-4	9	-8	1	-8	-1	0	-1	4	0	17	5	-4	-1	-4	36	24	32	23	29	-24	-34

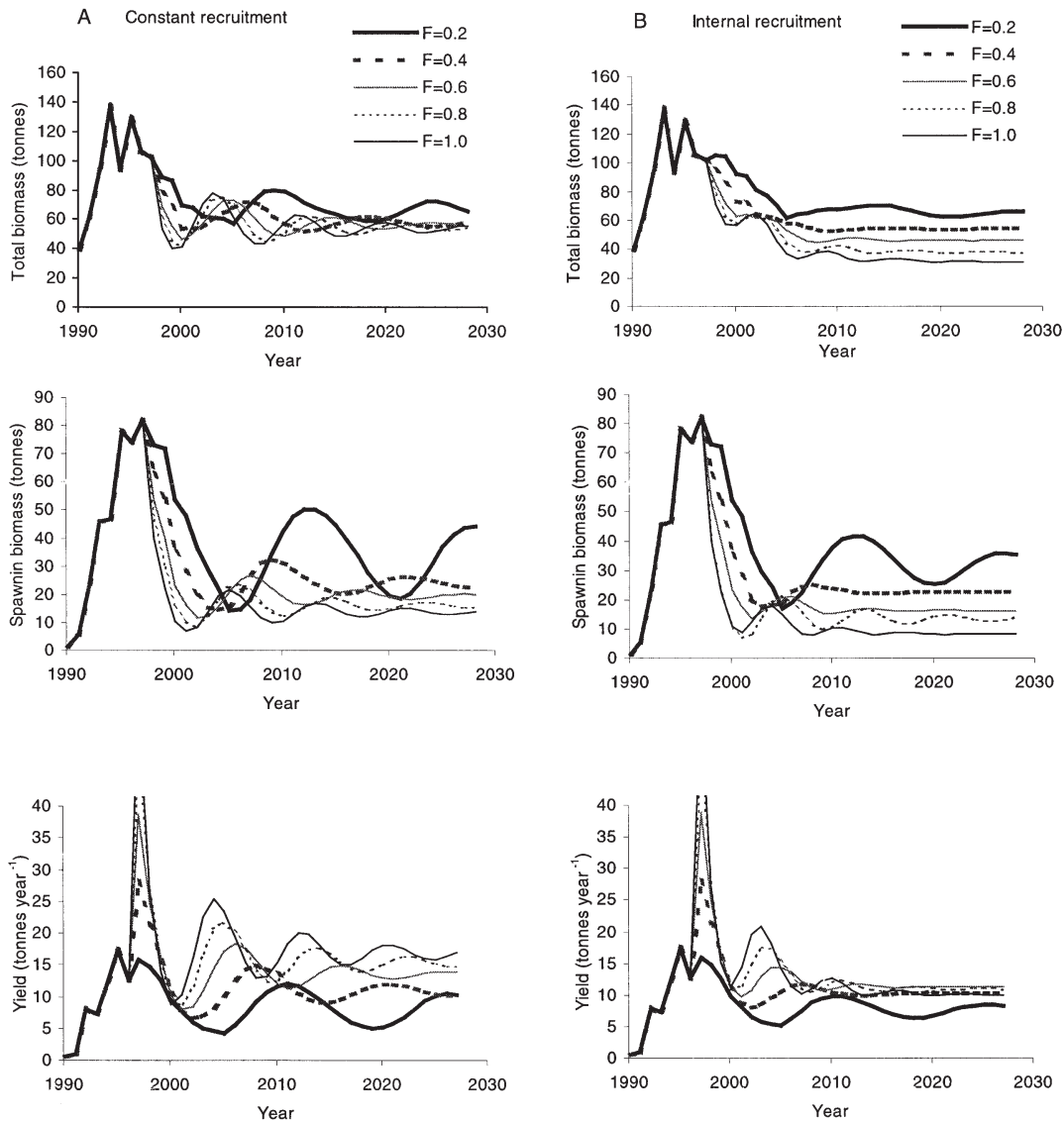


FIG. 5. – Simulated total biomass (upper), spawning stock biomass (mid) and yield (lower) for the period 1997–2027 for different fishing mortality rates for passive gears. A: constant 0-group recruitment; B: 0-group recruitment produced by the spawning stock in the fjord (internal recruitment).

squares of the survey catch rate is only affected by the change to the 50% selection value (γ) and by change to the natural mortality rate $M1$. The fit to the feeding data is little affected by any of these changes, except for a 10% change in k and μ . When $M1$ was increased by 10%, the $M2$'s decreased by 4–20%. When the right-hand slope (α) of the commercial gear selectivity function was estimated within the model, this did not greatly affect the estimates of feeding parameters, 0-group recruitment or predation mortality (Table 3 and 4).

Effects on other parameters

Table 4 shows the effect on other results of changing the value of certain parameters by 10% from their

key-run value. The largest impacts result from changes in μ which affect σ , the recruitment estimates and $M2$ at age. A 10% increase in μ caused a 33% increase in $M2$ for 0-group and a decrease in $M2$ for 1 and 2 group. Changing $M1$ by 10% produces widespread changes in other parameters.

Simulation studies

Simulations of total and spawning stock biomass, yield and cannibalism mortality with low F ($= 0.2$ year⁻¹) typically resulted in dampened cycles (Fig. 5). When fishing mortality was increased to values larger than 0.2 year⁻¹ from 1997 onwards, the cycles became shorter and the perturbations in biomass dampened out faster, particularly when recruitment

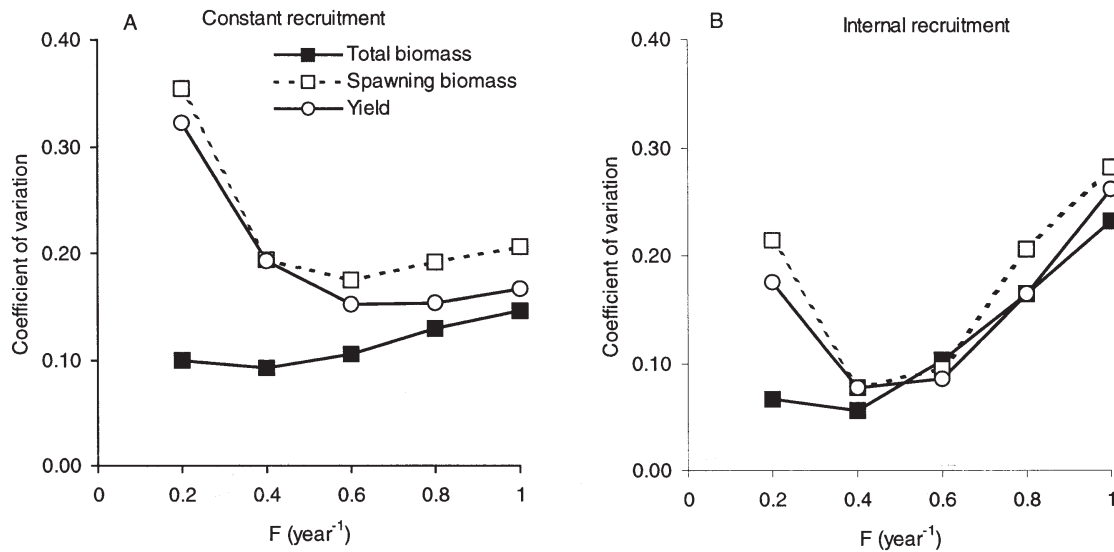


FIG. 6. – Coefficient of variation (CV) for simulated total biomass, spawning biomass and yield for different values of fishing mortalities from the stock simulation. CV was calculated for the period 2002-2027. A: constant 0-group recruitment; B: 0-group recruitment produced by the spawning stock in the fjord (internal recruitment).

was assumed to be self-generated (Fig. 5). The coefficient of variation for biomasses and yield was lower at levels of fishing mortality rate < 0.8 when the stock was considered to be self-recruited than when it was considered to have constant recruitment (Fig. 6). For the case of internal recruitment, the self-dampening appeared to be most effective at medium fishing mortality rates ($F = 0.4-0.6$ year⁻¹) resulting in lower coefficients of variation for the total stock biomass, the spawning stock biomass and the yield than at lower and higher F 's (Fig. 6B). This trend was less pronounced when constant recruitment was assumed.

For the period 1997-2027, chosen to approximate to a steady state, the simulated average total stock biomass and spawning stock biomass was reduced with increased fishing mortality and the reduction was largest when self-recruitment was assumed (Fig. 7). The yield increased with increasing fishing mortality, but the increase was slight above fishing mortality of 0.4 year⁻¹ (Fig. 7). At low fishing mortality rates the simulated average cannibalism mortality for the period 1997-2027 was high in groups 0, 1, 2 and 3 (Fig. 8). When the F was increased, the cannibalism mortality of age 1 to 3 decreased, but M_2 on age 0 was not greatly affected by changes in

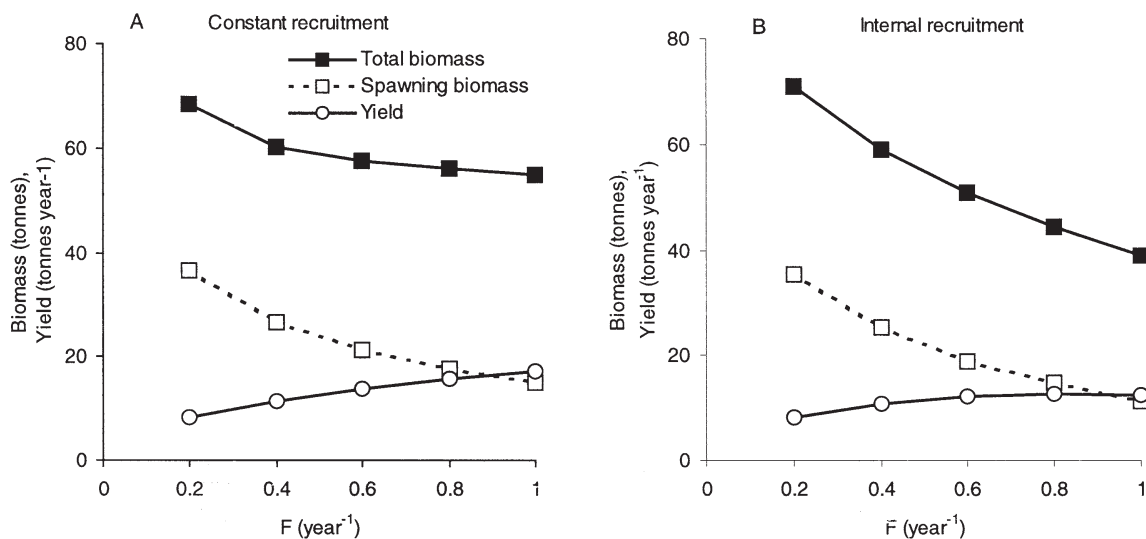


FIG. 7. – Simulated average total biomass, spawning biomass and yield simulated for the period 1997-2027 at different fishing mortality rates. A: constant 0-group recruitment; B: 0-group recruitment produced by the spawning stock in the fjord (internal recruitment).

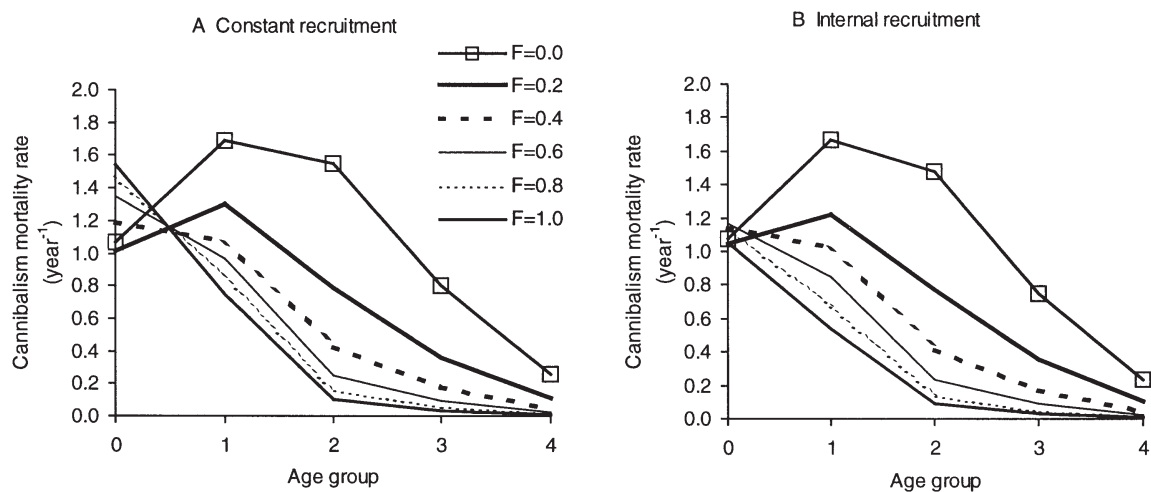


FIG. 8. – Average cannibalism mortality rate for different age groups simulated for the period 1997-2027 at different fishing mortality rates for commercial fishing gears. A: constant 0-group recruitment; B: 0-group recruitment produced by the spawning stock in the fjord (internal recruitment).

fishing mortality (Fig. 8). There was a similar effect of F on cannibalism mortality for both constant and internal recruitment.

DISCUSSION

Model structure, sensitivity and uncertainty

The inclusion of feeding data into the population model for 2+ cod (Pedersen and Pope, *subm.*), did not change the major trends in estimates of abundance, biomass, gear selection patterns, other natural mortality rate and fishing mortality rates of 2+ cod. The reason for this may be that the major cannibalism mortality is concentrated on year classes younger than two years of age. The only other data set that appeared to make slightly different statements about the abundance of young fish is the survey and catch data, which also include some 0-2 year old cod. The results from the sensitivity analysis indicate that the integration of the feeding data into the model did not cause any loss in robustness of the model (Tables 3 and 4) since most changes in estimates were relatively small. Thus, the least-square model produced fits to the data that integrated different sources of data and gave reasonable estimates despite the relatively short time-series used.

Our model does not take into account possible effects of variability in alternative prey biomass, since in the model cannibalism mortality rate is proportional to predator biomass. The apparent discrepancy between observed and modelled cannibalism mortality from predatory cod shorter than 30 cm in

length (Fig. 2) may possibly be due to a large biomass of invertebrates with sizes overlapping with cod shorter than 10 cm, and hence reduced cannibalism by cod smaller than 35 cm, or it might result from these very vulnerable sizes adopting predator avoidance behaviours.

The possible role of alternative prey in modifying cannibalism mortality rates in coastal cod needs further investigation. In the Barents Sea, capelin abundance does affect cannibalism mortality in juvenile cod (ICES 2000). It is known that the importance of krill in the diet of cod in Sørøfjord increased in the period 1993-96 (*unpubl. results*) while small herring was food for both cod and other predators in the period 1990-1991 (Kanapathippillai *et al.*, 1994). There are also indications of increased individual growth rates during the period 1990-96, possibly being a response to improved feeding conditions at least for large cod (*unpubl. results*). Our model predicts that the decrease in percentage weight and in number eaten per predator in the period 1993-96 (Figs. 1 and 2), is due to relatively low numbers of cod juveniles settling at age 0 in these years, and many large predatory cod sharing these prey. Alternatively, increased abundance of alternative prey in 1993-96 could hypothetically have reduced the cannibalism mortality and hence the total number eaten. If this was the case, the 1993-96 year classes should be relatively strong at older ages. So far, these year classes appear not to be strong at age 3-7 year (*unpubl. results*). The model calculation that cod in the length range of 35-55 cm have larger predatory and population regulatory impact than larger cod (Fig. 2), even though the larger cod

TABLE 5. – Overview of published cannibalism (C), predation mortality rates (P), and total natural mortality rates (M) for cod based on feeding data and tagging experiments. Mortality rates are given as annual rates, and are averaged for the given time periods. Estimates are based on either feeding data (F) or tagging data (T)

Stock/area	Mort. rate type	Time period	0	Age group 1	2	Mort. rate	Length range (cm)	Reference
Sørfjord	C, F	1989-96	0.7	1.5	0.3			This study
Barents Sea	C, F	1984-98	-	1.0	0.5			ICES (2000)
Eastern Baltic Sea	C, F	1977-94	0.3-0.5	0.1-0.2	-			Neuenfeldt and Köster (2000)
Western Baltic	C, F	1977-94	0.2	0.1	-			"
North Sea	P, F	1974-80	0.8	0.5	0.1			Pope and Macer (1991)
"	P, F	1981-86	0.5	0.4	0.1			"
Malangen, Northern Norway	M, T	1987-95				1.1	14-30	Larsen and Pedersen, (2002)
Heimarkspollen, western Norway	M, T*	1983-88	1.1-1.8					Svåsand and Kristiansen (1990)
Øygarden, western Norway	M, T*	1991-96		1.9-2.8				Otterå <i>et al.</i> , (1999)
Flatanger, mid- Norway	M, T*	1991-94				1.6	25-40	Kristiansen (1999)

*released hatchery-reared cod

have higher per predator consumption rates than smaller cod (Figs. 1 and 2), results from the much lower numbers and biomass of the older, larger cod (Fig. 4).

Effects of cannibalism on stock dynamics

The relation between the sizes of cod prey and cannibals indicated in Figure 2 resemble very much the patterns observed for other cod stocks at Newfoundland, Iceland and the Barents Sea (Bogstad *et al.*, 1994). Our estimates of preferred prey size ($\mu=4.26$, predator weight/prey weight =1:71) are lower than that estimated for cod in the North Sea ($\mu=3.26$, predator weight/prey weight =1:26) by Anon. (1988) and used by Nilssen *et al.* (1994) for the Barents Sea. This difference may, however, have been influenced by a different estimation procedures in our study than for the North Sea Stock where μ is fitted only to nonzero values of M2 from the Multi-species Virtual Population Analysis. The Sørfjord results are similar to those found for combined cod prey in the North Sea using the 1981 and 1991 North Sea stomach data sets ($\mu=4.30$ or 4.14, predator weight/prey weight=1:74 or 1:63) (Anon, 1994). It is also important to recognise that the latter estimates of μ , based on much larger data sets than those available from Sørfjord, had coefficients of variation of about 9%, which might lead to 95% confidence intervals of preferred prey size of between about 1:30 to 1:130 although neither of these extremes seems very plausible.

The apparent similarity of preferred prey size in several cod stocks indicates that some basic physiological and behavioural constraints determine this preference. In Sørfjord, the spatial overlap between small and large cod are probably large although the

small cod seem to prefer shallow areas while the large cod is distributed at all depths (Nøstvik and Pedersen, 1999b; Berg and Pedersen, 2001). In other cod stocks, stock-specific spatial size-distribution patterns may influence how cannibalism mortality depends on prey size and age (Anderson and Gregory, 2000; Uzars and Plikshs, 2000).

The level of cannibalism mortality in 0 and 1 year old cod in our study of about 1-1.5 year⁻¹ is similar to tagging based estimates of total mortality rates of small and young (age 0 and 1) coastal cod from western, mid and northern Norway (Table 5). This indicates that cannibalism may be a major source of mortality for young Norwegian coastal cod. In Sørfjord, cod make up about 70% of the trawl haul catches (Nøstvik and Pedersen, 1999a), and this emphasises the role of cod as a major source of mortality in this system. Estimates of cannibalism mortality rates in Sørfjord are similar to average estimates from the Barents Sea cod for the period 1984-98, but higher than cannibalism mortality rates from the Baltic and total predation mortality rates estimated by MSVPA for cod in the North Sea (Table 5). In our study, the large increase in cannibalism mortality (about two-fold) predicted as the strong 1987-year class grew and increased its cannibalism impact (Fig. 4) may have the potential to cause changes in recruitment by a factor ($\exp(2)$) of about 7. Thus, cannibalism mortality may significantly modify recruitment after the 0-group has settled to the bottom and cannibalism is thus a very important mechanism for coastal cod stock regulation.

The estimates of fishing mortality in Sørfjord (about 0.2 year⁻¹) are much lower than in most other exploited cod stocks (Garrod and Schumacher, 1994), but similar to a coastal cod stock in Malangen, northern Norway (Larsen and Pedersen,

in press). Correspondingly, the total biomass of cod of about 2-3 tonnes km⁻² in Sør fjord is higher than levels in the 1990s in most other stocks (Svåsand *et al.*, 2000). Thus, the Sør fjord cod stock may be in an “antique” state similar to that of the past early stages of exploitation of other stocks. This raises the question of whether the results from this stock may be used to infer how high cannibalism mortality might have been in the lightly exploited periods of other cod stocks, for example the Barents Sea cod during WWII.

The effect that changes in fishing mortality rates had on simulated cannibalism rates in Sør fjord (Fig. 8) indicate that exploitation level interacts tightly with cannibalism mortality. Increasing fishing mortality caused a decrease in spawning stock (Fig. 7) and the number of large cannibalistic cod, and hence in turn a decrease in cannibalism (Fig. 8). Similar to predictions from conventional single-species models, the simulated average biomass decreased with increasing fishing mortality rate (Fig. 7). The cod in Sør fjord has 50% maturation at about 5.5 years and 42 cm in length (Berg and Pedersen, 2001). The selection function of the passive gears (gill nets, long line and hand line) is dome shaped and the age of 50% of maximum selection is about 5.5 years of age (Pedersen and Pope, *subm.*). Thus, in Sør fjord, much of the fish has spawned once or twice before they are caught, and this explains the relative slight decrease in spawning stock when the fisheries mortality rate increases (Fig. 7). The lowest legal length limit in northern Norway is 47 cm. In southern Norway, much higher levels of fishing mortality and individual growth in coastal cod have been observed (Svåsand *et al.*, 2000). Cannibalism mortality has been proposed to be a possible density-dependent mortality factor that may affect cycling and periodicity in cod stocks (Bjørnstad *et al.*, 1999). Our results suggest that it is important to take into account both predator-prey size-preference relationships, age and size at maturity, growth patterns and fishing mortality when analysing the role of cannibalism as a density-dependent population regulator in cod stocks.

In the simulations of the Sør fjord stock, the interaction between fishing mortality and cannibalism mortality did appear to affect the potential for population stability as the self-dampening was largest when self-recruitment was assumed and at intermediate fishing mortalities of about 0.4 to 0.6 year⁻¹ (Figs. 5 and 6). This great potential for self-dampening at moderate fishing may be a result of a co-

variation between 0-group recruitment and removal of fish by cannibalism. Thus, in a time period with a large spawning stock producing high numbers of settled 0-group in quarter three, there may also at the same time be a large cannibalism mortality, and the two processes may cancel each other out. These simulation results suggest that the interaction between cannibalism mortality and fishing mortality may have consequences for how the stock may react under environmental perturbations. The age structure in 1990 with very few old fish (Fig. 4) suggests that a recent major perturbation of the cod stock had occurred, possibly due to predation from harp seals during the seal invasion in 1987 and 1988 (Nilssen *et al.*, 1992). Further studies on the long-term changes in mortality and population dynamics are needed to test whether the predictions from the simulation model holds true.

CONCLUSION

We conclude that inclusion of feeding data into the model for coastal cod indicates that cannibalism mortality is high among 0-2 year old cod and that the level of harvesting affect the age and size structure of the potential cannibals and in turn the cannibalism mortality and population stability.

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APPENDIX 1

Model structure

The fjord population $P(y,q,a)$ in numbers and the populations of the separate batches of tagged fish $P_{tag}(y,q,a,\#)$ (for year y , quarter q , age a and tag batch no $\#$) are modelled in year-classes by quarter year. The reporting rate (c_2) was integrated in the model. Recruitment estimated as numbers at age 0 in q_3 all years and numbers at age 0 to 17 in q_4 in 1989 are model parameters for the wild population. For the various batches of tagged fish initial populations are estimated as numbers at age at the beginning of the year, quarter in which they were tagged, from age length keys applied to the length distribution of tagged fish at the time of their tagging. These estimates are modified by a parameter describing neo-tagging mortality (c_3). The populations of each year class in subsequent year, quarters is then developed using modelled estimates of fishing and natural mortality rate in a standard exponential survival model. The natural mortality rate $M(y,q,a)$ is modelled as the sum of a non-predation mortality rate (M_1) constant for all ages and years and a cannibalism mortality rate estimated for each year, quarter and age group:

$$M(y,q,a) = M_1 + M_2(y,q,a).$$

In the case of tagged fish the non-predation natural mortality rates were augmented by a modelled yearly tag loss rate (c_4).

Commercial fishing mortality rate

Commercial fishing is predominantly by gill net and by hooks and reliable effort data were not available. Consequently commercial fishing mortality rate $F_{com}(y,q,a)$, for each year y , quarter q and age a was modelled as,

$$F_{com}(y,q,a) = F_c(y) * I(q) * Sel\{L(y,q,a)\}.$$

Where the model parameter, $F_c(y)$ is the annual fishing mortality rate, the model parameter $I(q)$ is a quarterly intensity rate and $Sel\{L(y,q,a)\}$ is a length-based selection pattern. In the above formulation $L(y,q,a)$ is the average length at age in each year and quarter, which is available from age length distributions of the research catch and consequently was not modelled. Given the nature of the commercial fishing gears $Sel\{L(y,q,a)\}$ was chosen to have a dome shaped selection form and scaled so its maximum value at age was 1,

$$[\exp\{-\alpha * L(y,q,a)\} / \{1 + \exp(\beta * (\delta - L(y,q,a)))\}].$$

where α , β and δ are model parameters describing the shape of the selection curve.

Research fishing mortality rate

Research fishing mortality rate $F_s(y,q,a)$ was believed to be significant in Sør fjord. It was modelled in the form,

$$F_s(y,q,a) = f_s(y,q) * (1/c_1) * k * Sels\{L(y,q,a)\}.$$

Where $f_s(y,q)$ was the measured survey trawling time (or effort), the model parameter k is a catchability term and $Sels\{L(y,q,a)\}$ is the selectivity at length $L(y,q,a)$ of the survey gear available. c_1 is an efficiency factor between the two different trawls used in the study ($c_1 = 1.0$ for the large trawl and 0.5 for the small trawl). The small trawl was used during the time period 1989-1991 and the larger trawl was used during 1992-1996. Since the survey gear was a trawl, an asymptotic form of selection curve was chosen,

$$Sels\{L(y,q,a)\} = 1 / \{1 + \exp(\phi * (\gamma - L(y,q,a)))\},$$

where the model parameters ϕ and γ describe the shape of the curve.