

INTERNATIONAL COUNCIL FOR THE
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Demersal Fish (Northern) Committee.

RESULTS OF A STUDY OF CONSUMPTION AND PRODUCTION
OF NORTH SEA COD

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This paper not to be cited without prior reference to the author.

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Introduction.

Since 1967 a study has been devoted to the production biology of the North Sea cod with the main emphasis on food intake, growth and fecundity and the efficiencies involved in the energetic transformations. In view of the recent development with relation to the regulation of the North Sea fisheries a short account of the main findings of this research is presented in this paper, because information has become available on the interrelationship between cod and other commercial fish stocks. In addition several ecological effects of a change in fishery parameters have been quantified, which might be of interest for assessment purposes. Full details cannot be given here, but more extensive reports are in preparation.

Food intake of cod in relation to size.

A quantitative analysis of the food of cod in the North Sea has been carried out by means of stomach sampling from 1968 until 1971 (DAAN, in press). The southern North Sea was the main object of study and from this area (fig. 1) a total number of 5705 stomachs over the years of sampling have been analysed. The northern area was sampled less intensively (1725 stomachs), but these data served as a check on the more general validity of the findings. The sampling has been carried out during routine trawling surveys at random throughout the seasons and throughout the area, in order to be sure that the material would be representative for the total population. The geographical distribution of the samples is shown in fig. 1. The stomachs were grouped according to 10 cm length classes of cod and in the laboratory wet weights were determined and numbers of organisms counted for all different components separately.

Table I presents the overall percentages of the important commercial fish species in the food as related to size of cod. The main conclusion to be drawn from these data is that the adult North Sea cod depends for its food in the southern area to a great extent and in the northern predominantly on the same resources as the fisheries. Additional information on the length of the fishes found in the stomachs (fig. 3) reveals that cod over 50 cm feeds mainly on fish in the range of 5-20 cm, which roughly corresponds with 0- and I-group. For flatfish there are apparently also II-group fish eaten by the largest size group. Thus it is mainly during the pre-exploited phase of life that commercial fish species are fed upon by the cod stock.

In fig. 2 a double logarithmic plot is given of the mean weight of the stomach contents against length of cod for different seasons in the southern North Sea and for the total year in the northern. Apparently an exponential function is involved. Statistical analysis showed the seasonal and geographical differences not to be significantly different. The estimated value of the exponent deviated not significantly from 3 and therefore the equation:

$$(1) \quad w_c = \phi L^3$$

can be used as the functional relationship between stomach content weight (w_c) and length (L), where ϕ represents a feeding coefficient. Applying this relation in addition to experimental evidence on the rate of digestion a model has been developed (DAAN, in press) to describe the absolute amount of food consumed per day in relation to length of cod:

$$(2) \quad \phi_L = \frac{2 \phi}{\delta} L^2,$$

where ϕ_L represents the daily ration by a fish of length L and δ a digestion coefficient. Values of the feeding coefficient and the digestion coefficient were estimated at $\phi = .00016$ and $\delta = .06$ respectively. Using these values the daily rations of cod of different sizes have been calculated (table II). In the absence of seasonal and geographical differences in the value of ϕ these values relate to the mean feeding rate of the total North Sea cod.

Growth.

Mean length at age data, derived from five years of market sampling from 1968 until 1972, were used to calculate Bertalanffy growth curve parameters, following the least squares method described by TOMLINSON and ABRAMSON (1961). The estimated values with their variances and 95% confidence intervals are presented in table III. For the estimation of the intervals the assumption has been made that the estimators are normally distributed. However, as has been pointed out by TOMLINSON and ABRAMSON, the distribution of the estimators is virtually unknown and cannot be readily determined. Therefore not too much value should be attached to the intervals. Yet, the suggestion is given that the difference in L_∞ between the two areas is probably not significant, whereas the intervals of the K -values appear to be wide enough apart to attach some meaning to the difference observed. The t_0 -intervals are just in touch, so that we can be less sure about the significance here.

Comparison of the estimated curves with the actual data (fig. 4) shows that there is good agreement and obviously the Bertalanffy curve presents a fair description of growth of North Sea cod. In this analysis northern has a different meaning from northern as used in the stomach analysis. In fig. 1 the areas distinguished in the market sampling program have been indicated.

Deepfrozen samples of cod (477 fish in the length range of 5-133 cm) from all seasons were used for the estimation of the mean condition coefficient in order to be able to convert lengths to weights. An average value of $k = .0104$ appears to be appropriate for cod over 20 cm in length. For smaller cod a value of $k = .0083$ has been obtained.

Fecundity.

Miss E. Oosthuizen, temporarily working at the Institute, determined the egg fecundity of 91 female ripe cod, sampled during the spawning seasons of 1970 until 1972. For this purpose a dry egg counting system (DECCA Master Count) has been used. Several fecundity-length and -weight relations as reviewed by SCHOPKA (1971) were calculated, the highest correlation coefficient (.87) being given by the equation:

$$(3) \quad E_w = \epsilon (W - W_0)$$

where E_w is the fecundity of a fish of weight W , c is the fecundity coefficient and W_0 is the theoretical weight at which the fecundity equals zero. In fig. 5 the individual fecundity estimates are presented and the calculated function is drawn. The parameters have been estimated at $c=495$ and $W_0=238$. Applying the same equation SCHOPKA found values of $c=526$ and $W_0=1042$ respectively and for comparison this function is also presented in fig. 5. Obviously there is very good agreement between the two sets of data. In addition egg samples were taken from 29 running cod in order to determine egg weights. The average dry weight was found to be 7.25 mg/100 eggs with a 95% confidence interval of 4.95-9.50 mg/100 eggs.

Caloric values.

In order to express food intake, growth and fecundity in the same energetic units measurements of caloric values of cod, cod eggs and some important food species (fresh) were carried out in a PARR bomb calorimeter at the Department of Experimental Ecology (University of Amsterdam) in cooperation with Dr. K. Kersting. Table IV summarises the available information.

Production efficiency.

From the information in the foregoing sections the yearly food intake, the growth and the egg production in calories can be calculated for each year of life, following the scheme outlined by STEELE (1965). To this end the daily amount of food consumed by a fish of a certain size has to be integrated between a time interval to allow of growth of the fish during this period. Combining the Bertalanffy growth equation and equation (2) gives upon integration between ages t and t' (in years) the following solution:

$$(4) \quad \Phi_{t'-t} = 365 \frac{2\phi}{\delta} L_{\infty}^2 \left\{ (t'-t) + \frac{2}{K} e^{-K(t'-t_0)} - \frac{2}{K} e^{-K(t-t_0)} + \frac{1}{2K} e^{-2K(t'-t_0)} - \frac{1}{2K} e^{-2K(t-t_0)} \right\}$$

Yearly growth in weight can be directly estimated from the Bertalanffy curve after conversion of lengths to weights by subtracting W_t from $W_{t'}$:

$$(5) \quad G_{t'-t} = W_{t'} - W_t$$

Spawning takes place in the first two or three months of the year. The development of these eggs relates obviously to the year of life before. Therefore the egg production during a certain year of life is related to the weight reached at the end of that year:

$$(5) \quad E_{t'-t} = c(W_{t'} - W_0)$$

Table V provides the results of the calculations outlined above and after conversion to calories growth production, reproduction and total production efficiencies have been calculated for both areas (fig. 6). With increasing age the growth efficiency decreases exponentially and ultimately approaches to zero, as could be expected from the nature of the Bertalanffy model. Reproduction efficiency rises during the first years of maturity and levels off to a value of 10%. The results for the two areas of investigation are not essentially different. The change in total production efficiency and the shift from a higher growth to a higher reproduction efficiency with increasing age suggests that variations in the age structure of the cod population due to changes in fishing effort will have important effects on the energetical

balance and in order to quantify these effects it appears useful to incorporate these features in the dynamical fishing model, developed by BEVERTON and HOLT (1957).

Production and consumption model.

The total growth production of a population equals the weights of the fish, which leave the population both by natural causes and by fishing. Thus following the lines developed by BEVERTON and HOLT to arrive at the yield equation and substituting Z for F and adding an analog amount, representing the growth production in the pre-exploited phase, when only a natural mortality is acting upon the population, a model for the total growth production of the population can be easily arrived at. The egg production model as developed by these authors is based on different assumptions regarding the fecundity-size relationship than have been made plausible for cod above. However, as BEVERTON and HOLT have pointed out their model can be easily adapted to other approximations of the fecundity-size relationship. The model used here for further calculations is thus basically the same, including two alternatives of the age at maturity being reached before or after the age at which the fish recruit to the fishery. The food consumption model described by BEVERTON and HOLT cannot be readily used for the present purposes and some revision is needed. The amount of food consumed by the population can be considered to consist of four portions: the amount eaten during the pre-exploited phase of life by the fish, which leave the population by natural causes during this phase; the amount consumed during this phase by fish, which survive to the age of entering the fishery; the amount consumed during the exploited phase by fish, which leave the population both by natural causes and by fishing during this period; and finally the amount of food consumed by fish during the exploited phase by fish, which reach the maximum age (t_x) without being killed. Application of equation (4) to these four fractions^λ gives upon integration the equation presented in the appendix, where the different parts are easily recognized.

Application of the model to southern North Sea cod.

The equations for growth production, egg production, food intake and yield to the fishery have been programmed on a Hewlett-Packard 9810A computer and assuming a natural mortality coefficient of .15, an age of entering the population $t_p = 1$ and using the parameter values presented in this paper (listed in the appendix), calculations have been carried out for different values of the age at which the fish recruit to the fishery ($t_p = 2, 3, 4$) and of the fishery mortality ($F=0 - 2.0$). In fig. 7 a,b,c the results are given as the percentage of the value, when there is no fishery ($F=0$). The yield per recruit curves are in absolute weights (fig 7 f). The effect of fishing on these different ecological parameters appears to vary considerably. Egg production is the most vulnerable to fishing and growth production is much less reduced than food consumption. These effects are more clearly illustrated in fig. 7 d,e, which present the calculated efficiencies after conversion of the data to calories. Apparently the different population efficiencies are no constant parameters, but are subject to the dynamics of the population, higher mortalities resulting in higher growth production efficiency. In other words the population reacts to fishing with a higher utilisation of the available food for growth at the expense of reproduction.

Weights and numbers of commercial species consumed per recruit.

The consumption model developed above can be used to calculate the amount of food consumed per recruit during subsequent years of life as depending on the fishery parameters. HOLDEN and FLATMAN (1972) have estimated the fishery mortality in the northern North Sea (region IV a) at $F = .4$ and in the southern (region IV b,c) at $F = .5$. From their data an approximate age of recruitment to the fishery of $t_p = 2$ appears to be appropriate for both areas. These figures have been applied in the model and the results are presented in table VI. For the present purposes some further grouping of these data and also of the relative food composition (table I) has been made. By combination the mean amount of the different commercial species consumed per recruit of cod can be calculated. In addition the relative length distributions (fig. 3) have been used for the calculation of the mean weights of the different organisms consumed (by application of $W = k L^3$, the k -values for the different species being derived from material available at the laboratory). Division of the total weight per species consumed by the mean weight of the organisms gives the actual numbers eaten per recruit. The calculations are set out in table VII.

Quantitative predator-prey relations of North Sea cod.

HOLDEN and FLATMAN (1972) presented estimates of the yearclass strengths of North Sea cod as numbers of 2-year old fish for the years 1961-1968. From their table 5 average recruitment figures for those years can be estimated at 46 million fish in area IVa and 76 million in area IV b,c. From our fig. 1 it appears that our subdivision of the North Sea for stomach sampling purposes is merely a subdivision of area IV b,c. It seems reasonable to appoint half of the total recruitment figure for the southern and central North Sea (67 million) to each of the subdivisions used in our study. Thus multiplying the average recruitment of 38 million cod by the weights and numbers of the commercial species consumed per recruit in both areas gives an estimate of the total weights and numbers of these species consumed by the average cod population in the North Sea area IV b,c (table VIII). These figures can be compared with available recruitment figures of the different species, which have been brought together in the table.

The most striking fact is the considerable amount of cannibalism, the mean number eaten during the pre-exploited phase being 50 times the amount, which survives up to the age of recruitment. However, this figure is biased to some extent, because closer inspection of the basic data revealed that practically all cannibalism had taken place during the years 1970 and 1971, when the very rich yearclass 1970 appeared in sea. Thus the amount consumed should be compared with the recruitment figure of the 1970 yearclass, which will be much higher than the mean value. Yet, even allowing of this deficiency, a direct inverse stock-recruitment relationship in North Sea cod appears to be a feasible feature according to these data, which throws new light upon the causes of the raised level of recruitment of the southern stocks of cod during the sixties.

For herring the numbers eaten are 17% of the average amount of 0-group. However, this appears to be an underestimate, because the herring recruitment figure applies to the total North Sea, including IVa, where an additional amount might be consumed.

For plaice and sole the amounts consumed and the recruitment to the fishery are in the same order of magnitude (67% and 115% respectively), suggesting a considerable natural mortality during the pre-exploited phase merely by the cod.

The figures presented here can only be of a preliminary nature, because as yet too little information is available about the actual recruitment of the different species during the four years of observation, which they should obviously^b be compared with. Also a more refined assessment of the North Sea cod and the other species would give the possibility to present much more accurate figures. Yet, in spite of all inaccuracies the conclusion seems to be justified that in general the consumption of commercial species, including cod itself, by the North Sea cod is of a magnitude, which might be expected to have measurable effects on their recruitment. This stresses the importance of more research on the interrelationship of North Sea fish species.

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TABLE I - Weight percentages of commercial fish species in the food of cod of different size classes.

Size class cod	SOUTHERN NORTH SEA								NORTHERN NORTH SEA									
	Number of samples	Mackerel	Cod	Whiting	Haddock	Herring	Plaice	Sole	Total	Number of samples	Mackerel	Cod	Whiting	Haddock	Herring	Plaice	Sole	Total
cm																		
5-9	597	-	-	-	-	-	-	-	-	58	-	-	-	-	-	-	-	-
10-19	922	-	1.4	-	-	-	-	-	1.5	420	-	-	-	-	-	-	-	-
20-29	1297	-	2.2	0.1	-	-	-	+	2.4	457	3.0	24.7	0.8	+	-	-	-	28.6
30-39	962	-	2.0	+	-	1.1	-	0.9	4.0	260	6.6	14.0	1.9	4.4	2.0	-	-	28.9
40-49	627	-	1.4	2.0	-	1.6	0.2	0.8	5.9	111	5.0	6.7	0.4	20.8	2.9	-	-	35.8
50-59	393	-	0.2	3.2	1.7	4.5	-	+	9.6	77	12.8	5.8	3.9	23.2	8.2	-	-	54.0
60-69	298	-	0.5	5.8	3.3	4.1	0.9	2.3	16.9	55	7.8	10.9	10.6	34.8	4.4	-	-	68.4
70-79	187	3.1	2.2	7.6	0.2	5.1	4.2	1.2	23.6	50	4.1	8.8	6.2	42.0	16.5	-	-	77.5
80-89	202	0.5	1.0	8.3	1.6	5.0	5.9	2.2	24.5	75	11.9	16.4	0.2	24.3	9.3	-	-	62.1
Σ 90	220	0.7	1.6	7.0	0.4	14.3	18.2	4.0	46.2	152	10.1	10.4	5.2	38.8	2.4	3.3	-	70.1

TABLE II - Estimated daily rations (grams) of North Sea cod of selected lengths.

Cod length:	10	20	30	40	50	60	70	80	90	100 cm
Daily ration:	0.53	2.1	4.8	8.5	13	19	26	34	43	53 gr.

TABLE III - Estimated Bertalanffy growth curve parameters of southern North Sea cod with variances and 95% confidence intervals (least squares method according to TOMLINSON and ABRAMSON, 1961).

	SOUTHERN NORTH SEA				NORTHERN NORTH SEA			
	L_{∞}	K	t_0	$W_{\infty} = .0104L^3$	L_{∞}	K	t_0	W_{∞}
Estimate	110.8 cm	.333	.77	14.150 gr	118.7	.269	.87	17 390
Variance	784	.00103	.0199		3138	.00128	.0261	gr.
95% conf. interval	102.1-119.5	.323-.343	.73-.81		101.3-136.1	.258-.280	.82-.89	

TABLE IV - Caloric values of cod, eggs and food organisms of cod (measured in a PARR bomb calorimeter, in cooperation with Dr. K. Kersting, Department of Experimental Ecology, University of Amsterdam)

Species	Number of samples	Dry weight *)	Kcal/gr Dry	Remarks
COD	2	20.0%	4.60	Samples include 5 whole cod in the range of 10-15 cm.
COD-EGGS	1	0.0725mg/egg	5.70	Mixed samples of ripe eggs from 8 running females.
FOOD FISH	10	23.0%	5.06	Including 37 specimens of cod, whiting, herring, sprat, dab.
CRUSTACEANS	4	32.6%	3.27	Including 17 specimens of <u>Portunus</u> , <u>Pagurus</u> , <u>Crangon</u> , <u>Nephrops</u> .
APHRODITE	1	15.2%	3.56	Including 2 specimens.

*) in percentage of wet weight, except the information on eggs.

TABLE V - Growth, Egg production and Food intake of cod during subsequent years of life and calculated efficiencies after conversion to calories.

Year of life	Growth in grams	Eggs * produced	Food consumed in grams	Growth ** efficiency	Reproduction** efficiency	Production** efficiency
SOUTHERN NORTH SEA						
2nd	531	-	1215	36.6	-	36.6
3rd	1500	89.10 ³	4610	27.2	0.7	27.9
4th	2010	943.10 ³	8520	19.7	4.2	23.9
5th	2054	2612.10 ³	12100	14.2	8.1	22.3
6th	1836	3811.10 ³	15000	10.2	9.5	19.7
7th	1521	4564.10 ³	17400	7.3	9.9	17.2
8th	1202	5159.10 ³	19100	5.3	10.1	15.4
9th	921	5615.10 ³	20400	3.8	10.3	14.1
10th	692	5957.10 ³	21400	2.7	10.5	13.2
NORTHERN NORTH SEA						
2nd	313	-	765	34.2	-	34.2
3rd	1130	60.10 ³	3500	27.0	0.7	27.7
4th	1763	735.10 ³	7070	20.9	3.9	24.8
5th	2043	2232.10 ³	10700	16.0	7.9	23.9
6th	2042	3491.10 ³	13900	12.3	9.4	21.7
7th	1875	4420.10 ³	16700	9.4	9.9	19.3
8th	1632	5228.10 ³	19000	7.2	10.3	17.5
9th	1370	5906.10 ³	20900	5.5	10.6	16.1
10th	1122	6461.10 ³	22300	4.2	10.9	15.1

* A maturity rate of 0; 0.1; 0.5; 0.9; 1.0; 1.0; etc. has been applied for the 2nd and subsequent years of life respectively.

** Growth, Eggs and Food intake have been converted to Kcal by applying raising factors of respectively .92 (920 cal/gram wet for cod); .41 (0.0000725 x 5700 cal/egg); 1.1 mean value for fish + crustacea 1120 cal/gram wet). Cf table IV.

TABLE VI - Food intake per recruit during different years of life in the southern and northern North Sea ($t_R = 1$; southern $F = 0.5$; northern $F = 0.4$; $t_p = 2$; $t_\lambda = 25$)

FOOD INTAKE PER RECRUIT		
year of life	southern	northern
2 nd	1098	689
3 rd	3285	2492
4 th	3009	2797
5 th	2191	2408
6 th	1118	1807
7 th	1043	1248
8 th up to 25th	1175	2134
Regrouped		
2 nd	1098	689
3 rd + 4 th	6294	5289
5 th up to 25th	5527	7597 grams

TABLE VII - Calculation of the mean numbers consumed per recruit in the southern and the northern North Sea.

a. SOUTHERN NORTH SEA

	Mackerel	Cod	Whiting	Haddock	Herring	Plaice	Sole
year of life	Relative food composition (cf table I)						
2nd	-	1.9	-	-	0.4	-	0.3
3rd+4th	-	0.7	1.7	1.7	3.4	0.4	1.0
5th up to 25th	1.3	1.6	7.6	0.7	8.1	9.4	2.8
	Absolute amounts (grams) consumed per recruit						
2nd	-	21	-	-	4	-	3
3rd+4th	-	44	107	107	214	25	63
5th up to 25th	72	88	420	39	448	520	155
	Mean weight/organism *)						
2nd	-	7	-	-	19	-	2
3rd+4th	16	11	62	78	36	12	9
5th up to 25th	28	30	62	78	33	142	52
	Absolute number consumed per recruit						
2nd	-	3.0	-	-	0.2	-	1.5
3rd+4th	-	3.9	1.7	1.4	6.0	2.2	7.0
5th up to 25th	2.6	2.9	6.8	0.5	13.7	3.7	3.0
Tot.	2.6	9.8	8.5	1.9	19.9	5.9	11.5

*) Based on the length distributions in fig. 3 (southern and northern area combined) by converting to weight by means of $W = k \cdot L^3$; k-values applied: Mackerel $k = 0.0073$; Cod $k = 0.0104$; Whiting $k = 0.0090$; Haddock $k = 0.012$; Herring $k = 0.0083$; Plaice $k = 0.0085$; Sole $k = 0.0085$)

TABLE VII - b NORTHERN NORTH SEA.

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Mackerel Cod Whiting Haddock Herring Plaice Sole							
year of life	Relative food composition (cf table I)						
2nd	1.5	12.0	0.4	-	-	-	-
3rd+4th	8.1	9.4	4.2	20.8	4.4	-	-
5th up to 25th	8.7	11.9	3.9	35.0	9.4	1.1	-
Absolute amounts (grams) consumed per recruit							
2nd	10	83	3	-	-	-	-
3rd+4th	428	497	222	1100	23	-	-
5th up to 25th	661	904	296	2659	714	84	-
Mean weight/organism *)							
2nd	-	7	-	-	19	-	2
3rd+4th	16	11	62	78	36	12	9
5th up to 25th	28	30	62	78	33	142	52
Absolute number consumed per recruit.							
2nd	0.6	12.8	0.3	-	-	-	-
3rd+4th	26.8	44.0	3.6	14.0	0.6	-	-
5th up to 25th	23.6	30.1	4.8	34.0	21.6	0.6	-
Tot.	51.0	86.9	8.7	48.0	22.2	0.6	-

TABLE VIII - Weights and numbers of commercial species consumed by the average North Sea cod stock in comparison with available recruitment figures of these species.

	SOUTHERN AREA		NORTHERN AREA		TOTAL		IV b,c	Available	recruitment figures
	Weight	Number	Weight	Number	Weight	Number		Number	AREA
	(10 ³ tons)	(10 ⁶)	(10 ³ tons)	(10 ⁶)	(10 ³ tons)	(10 ⁶)		(10 ⁶)	
mackerel	5	94	40	1836	43	1930			
cod	6	360	53	3128	59	3488		67	Area IV b,c ¹⁾
whiting	19	306	19	313	38	619			
haddock	5	68	135	1728	140	1796			
herring	24	716	27	799	51	1515		8727	Total North Sea ²⁾
plaice	20	212	3	22	23	234		350	Total North Sea ³⁾
sole	8	403	-	-	8	403		350	Total North Sea ⁴⁾

Notes 1) numbers as II-year-old fish, average yearclass 1961-1968 (HOLDEN AND FLATMAN, 1972)

2) numbers of 0-group fish, average yearclass 1960-1969 (ANON., 1972).

3) numbers of II 3/4-year-old fish (ANON, 1973) Recruitment IV b,c only will be approximately identical to total North Sea.

4) numbers of II-year-old fish (ANON, 1972) Recruitment IV b,c only is identical to total North Sea.

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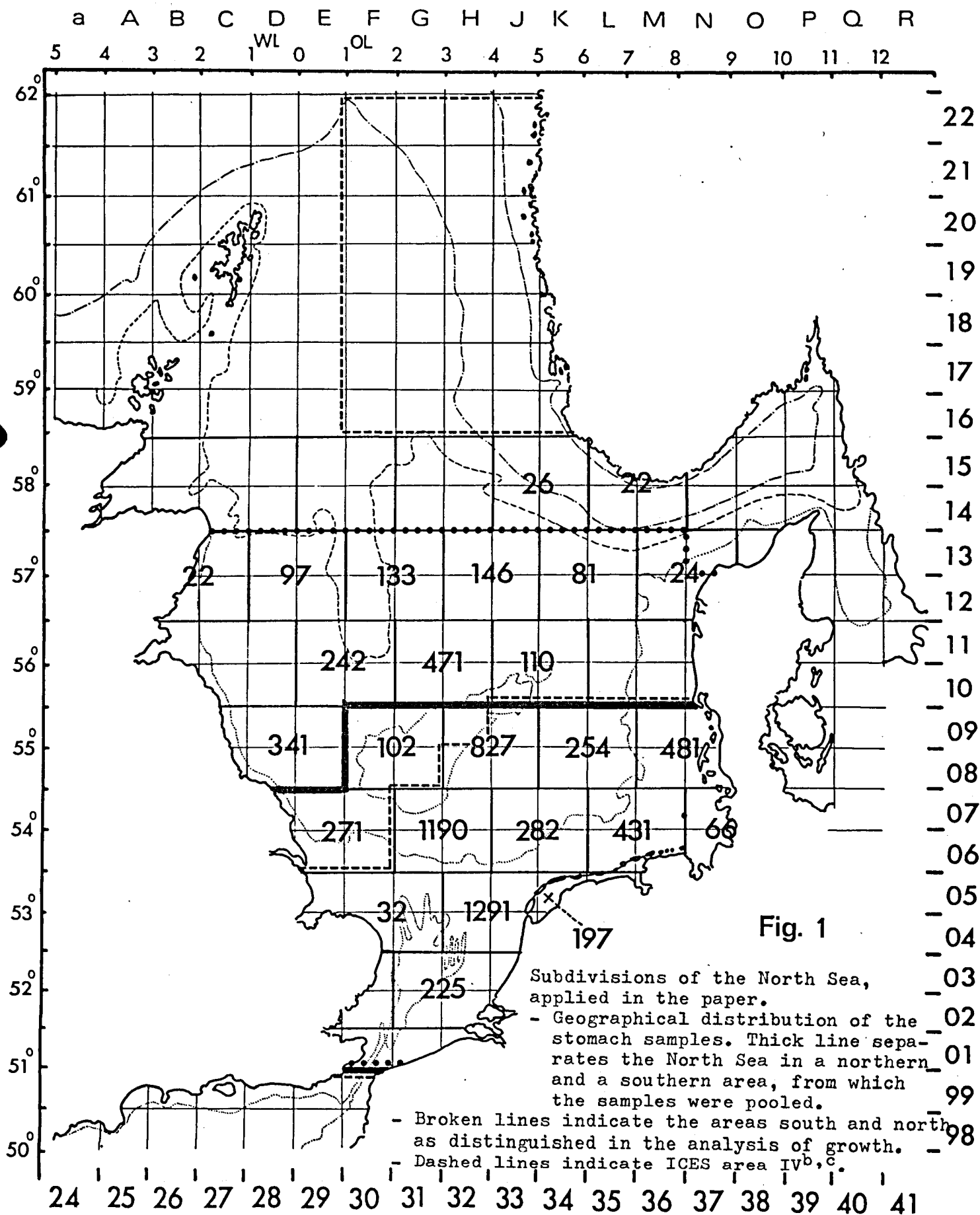
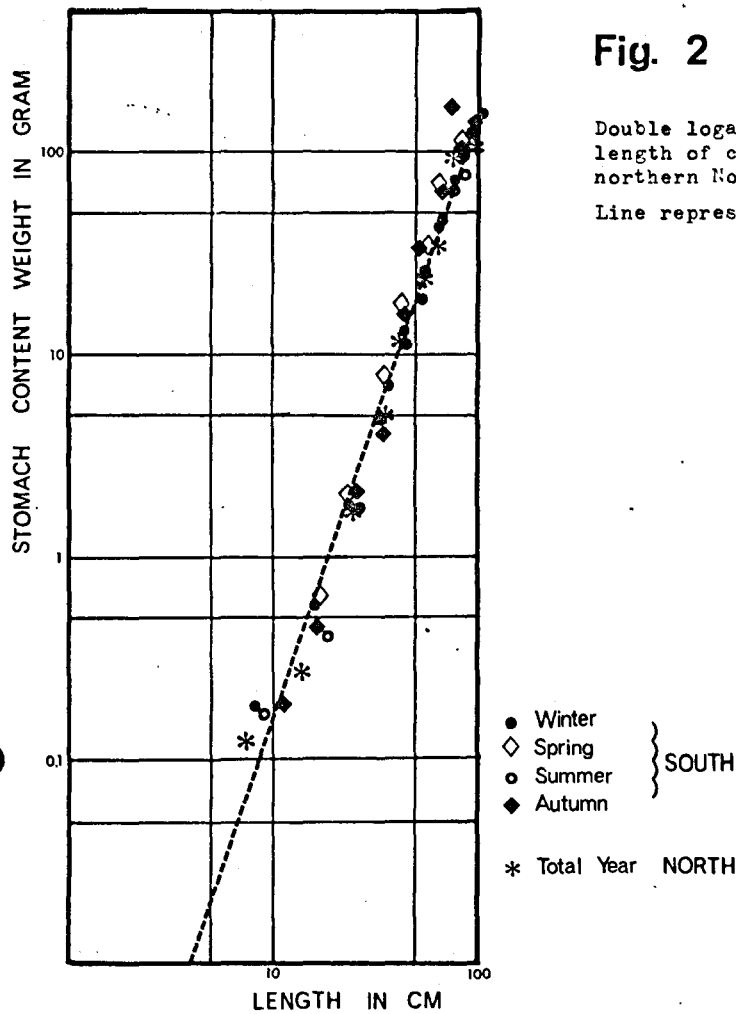


Fig. 2



Relative length frequencies of commercial fish species in the stomachs of different size groups of cod. (N = the number of measurements; lines represent the minimum landing size of the protected species.)

Fig. 3

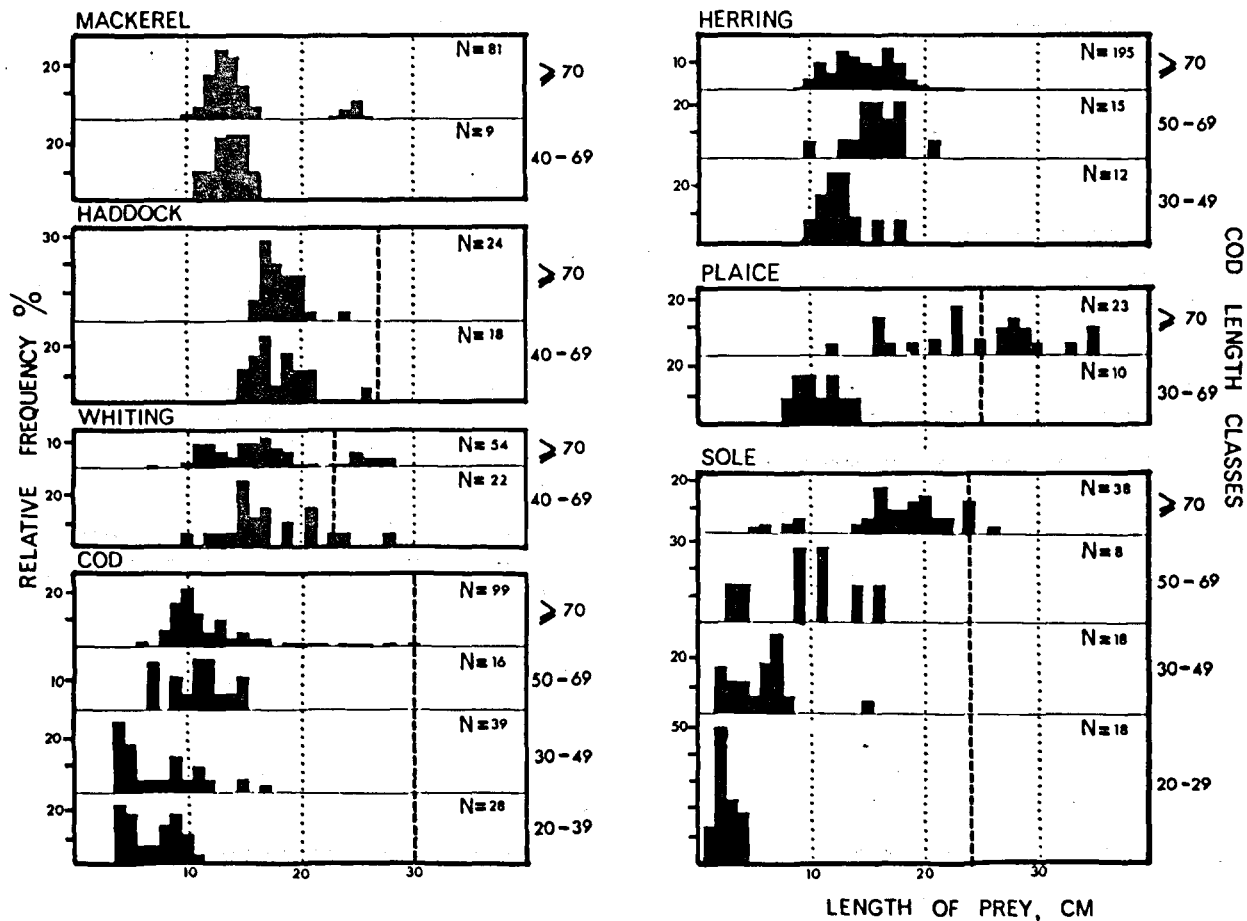


Fig. 4

Estimated Bertalanffy curves for growth in length and weight of cod.

A: SOUTHERN NORTH SEA

B: NORTHERN NORTH SEA

Actually observed values of length at age are plotted.

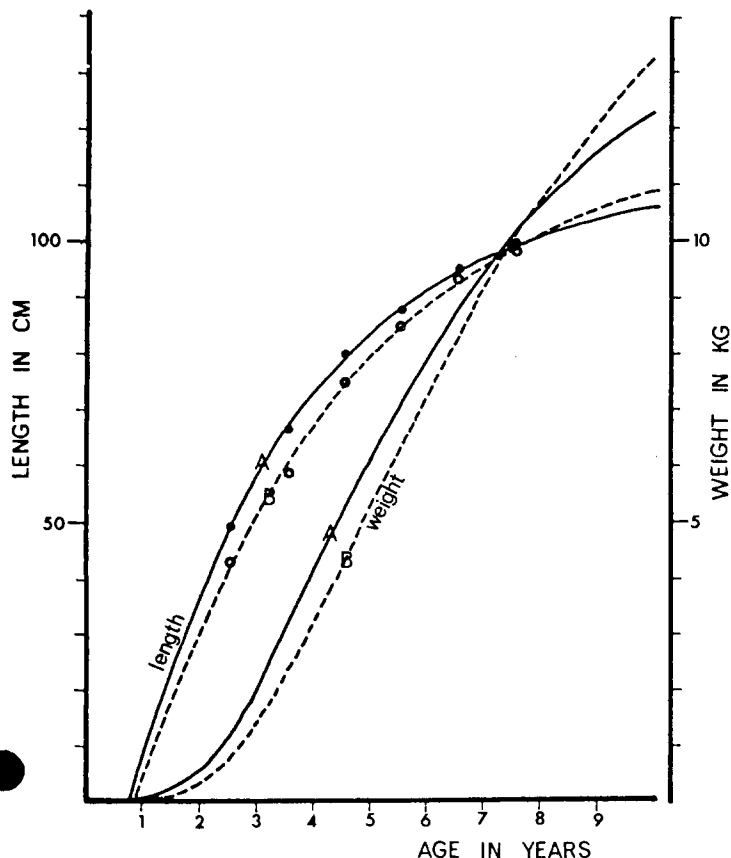


Fig. 5

Estimated fecundities of North Sea cod in relation to the weight of the fish. The drawn line represents the estimated function and for comparison the function found by SCHOPKA (1971) is also plotted.

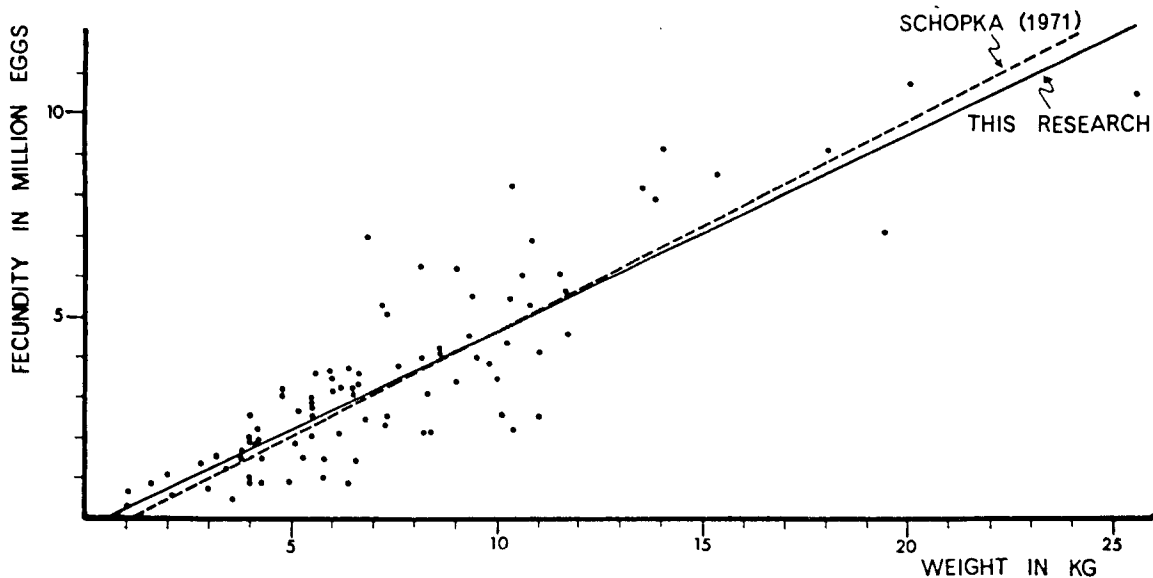
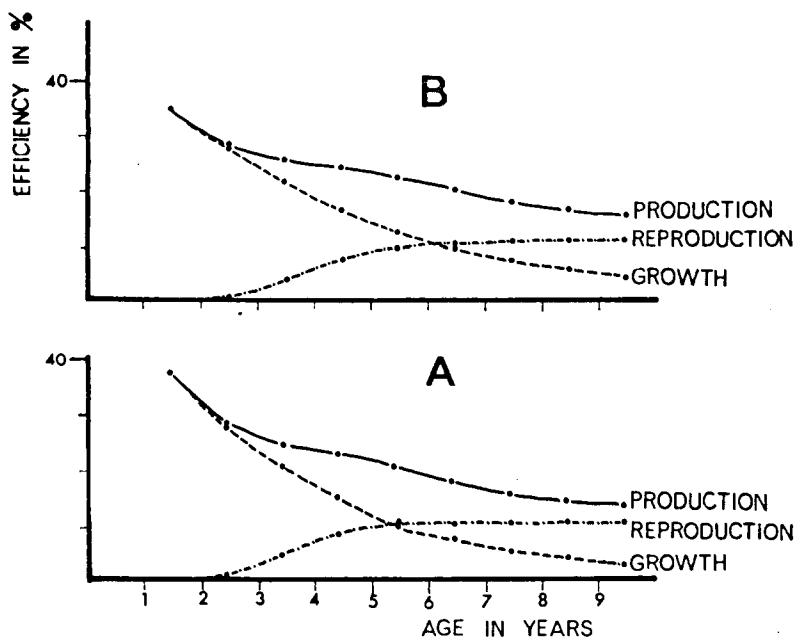


Fig. 6

Estimated GROWTH-, REPRODUCTION- and PRODUCTION- (= growth + reproduction) EFFICIENCY in cod in relation to age.

A : SOUTHERN NORTH SEA

B : NORTHERN NORTH SEA



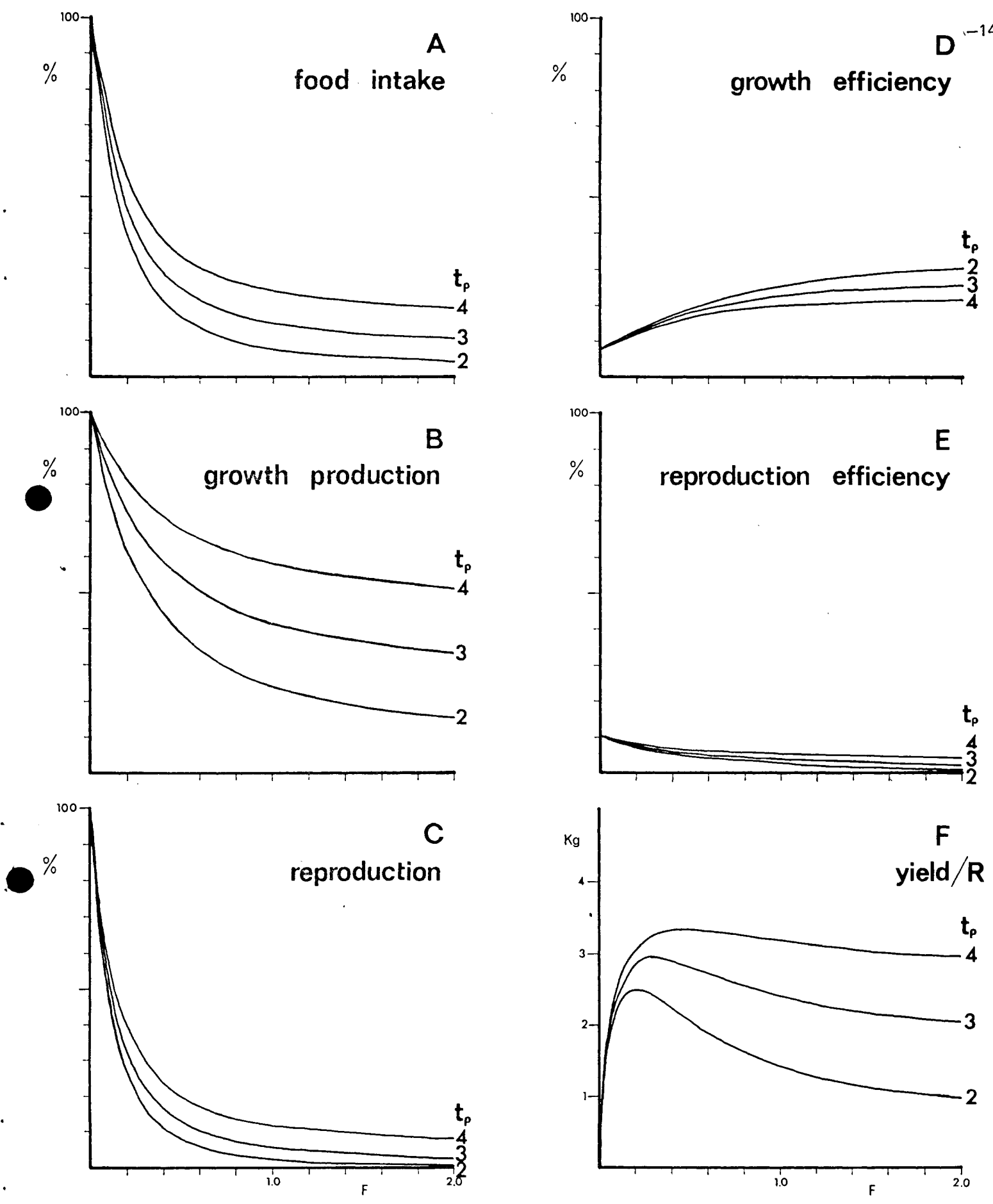


Fig 7

Graphs of food intake, growth production and reproduction in North Sea cod populations in relation to fishery mortality (F) and age of recruitment (t_p) as percentage of the value in the unfished situation (F=0); Population growth-production and reproduction efficiency as calculated from these figures after conversion to cal.; Yield per recruit curves in absolute weights.

APPENDIX.

Dynamical model for the yearly food consumption (Φ) by a population as depending on fishery parameters.

$$\begin{aligned} \Phi = 365 \cdot \frac{2\phi}{\delta} \cdot L_{\infty}^2 & \left(R \left(t_R - t_p \cdot e^{-M_p} + \frac{2K - 2KM t_R - 4M e^{-K(t_R - t_o)} + M e^{-2K(t_R - t_o)}}{2KM^2} \cdot (1 - e^{-M_p}) + \frac{2M e^{-K(t_R - t_o)}}{K(K+M)} \cdot (1 - e^{-(K+M)p}) - \right. \right. \\ & \left. \left. - \frac{M e^{-2K(t_R - t_o)}}{2K(2K+M)} \cdot (1 - e^{-(2K+M)p}) \right) + \right. \\ & + N_{t_p} \left(p + \frac{2}{K} \cdot e^{-K(t_p - t_o)} - \frac{2}{K} \cdot e^{-K(t_R - t_o)} + \frac{1}{2K} \cdot e^{-2K(t_p - t_o)} - \frac{1}{2K} \cdot e^{-2K(t_R - t_o)} \right) + \\ & + N_{t_p} \left(t_p - t_{\lambda} e^{-Z\lambda} + \frac{2K - 2KZ t_p - 4Z e^{-K(t_p - t_o)} + Z e^{-2K(t_p - t_o)}}{2KZ^2} \cdot (1 - e^{-Z\lambda}) + \frac{2Z e^{-K(t_p - t_o)}}{K(K+Z)} \cdot (1 - e^{-(K+Z)\lambda}) - \right. \\ & \left. - \frac{Z e^{-2K(t_p - t_o)}}{2K(2K+Z)} \cdot (1 - e^{-(2K+Z)\lambda}) \right) + \\ & \left. + N_{t_{\lambda}} \left(\lambda + \frac{2}{K} \cdot e^{-K(t_{\lambda} - t_o)} - \frac{2}{K} \cdot e^{-K(t_p - t_o)} + \frac{1}{2K} \cdot e^{-2K(t_{\lambda} - t_o)} - \frac{1}{2K} \cdot e^{-2K(t_p - t_o)} \right) \right) \end{aligned}$$

where

- Φ is the yearly food consumption by the population,
- t_o is the hypothetical age at which fish would have been of zero length,
- t_R is the age at which the fish recruit to the population,
- t_p is the age at which the fish enter the fishery,
- t_{λ} is an arbitrary maximum attainable age,
- M is the natural mortality coefficient,
- Z is the total mortality coefficient ($M+F$),
- R is the number of recruits to the population,
- N_{t_p} is the number of fish reaching t_p ($N_{t_p} = R \cdot e^{-M_p}$),
- $N_{t_{\lambda}}$ is the number of fish reaching t_{λ} ($N_{t_{\lambda}} = R \cdot e^{-M_p - Z\lambda}$),
- p is the pre-exploited lifespan ($p = t_p - t_R$),
- λ is the exploited lifespan ($\lambda = t_{\lambda} - t_R$),
- L_{∞} is the maximum length,
- K is the growth constant,
- ϕ is the feeding coefficient,
- δ is the digestion coefficient.

The following parameter values were applied in the calculations:

$t_R = 1$
 $t_p = 2 \text{ (3,4)}$
 $t_\lambda = 25$
 $M = .15$
 $F = .5 \text{ (southern area); } .4 \text{ (northern); range } 0 - 2.0$
 $t_o = .77 \text{ (southern); } .87 \text{ (northern)}$
 $L_\infty = 110.8 \text{ (southern); } 118.7 \text{ (northern)}$
 $K = .333 \text{ (southern); } .269 \text{ (northern)}$
 $\phi = .00016$
 $\delta = .06$
 $R = 1 \text{ (giving food consumption on a recruit basis)}$

In addition have been used for the calculation of population efficiencies as depending on fishery parameters:

$t_p = 2; 3; 4$
 $F = 0 - 2.0$
 $t_\eta = 3 \text{ (age at maturity)}$
 $k = .0104 \text{ (condition coefficient)}$
 $W_\infty = 14 \text{ 150gr (southern); } 17 \text{ 390gr (northern), (maximum weight)}$
 $c = 495 \text{ (fecundity coefficient)}$
 $W_o = 238 \text{ (theoretical weight at which fecundity equals zero)}$