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SPAWNING AND LIFE HISTORY INFORMATION FOR NORTH ATLANTIC COD STOCKS

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TABLE OF CONTENTS

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1. INTRODUCTION

This synthesis of information on spawning and life history of North Atlantic cod stocks originated from two separate initiatives, which were subsequently merged. The ICES Larval Ecology Working (which became the Recruitment Processes Working Group) began to bring together the existing data on early life stages of cod and haddock in 1987, using a checklist which was circulated to Working Group members and participants at the ICES Early Life History Symposium in 1988. The ICES Study Group on Cod Stock Fluctuations (which became the ICES/GLOBEC Working Group on Cod and Climate Change) produced syntheses of Atlantic cod stocks as appendices III and IV of its report in 1990 (ICES CM 1990/G:50). The resultant information and a large amount of additional material, produced by over thirty contributors, whose names are given in Table 1, has been edited and some of the information has been extracted into Tables as a summary. A single reference list has been prepared, but the task of indexing this list by key words is not complete.

The main purpose of this report is to provide information for comparative studies of cod biology and population dynamics. The rationale for this approach is given by Bakun (1985) and Brander (1993 and in press). Inevitably the process of bringing together information in this way has no convenient end point and the present report must therefore be regarded as "work in progress". The spawning checklist initiative, whose outcome was only intended for circulation among contributors, recognised this at the outset and stated:

> "Depending on the level and quality of the response, it may be worthwhile to put all the contributions together in some form of ICES publication, but if it does no more than generate some collective thinking about comparative aspects of recruitment studies, it will have served a useful purpose."

The spawning checklist tried to elicit limited information on early life history in a systematic and clearly defined way by means of series of detailed questions (these are given below). The results highlighted the difficulty of defining terms unambiguously (e.g. what is meant by "duration of the pelagic stage"), the gaps in our knowledge for many areas and the need to relate information to the context or model in which it is to be used. For example the information on duration of the pelagic stage could be included in a model of survival or in a model of transport and the latter might require additional details on vertical behaviour. An iterative process of formulating questions and defining and obtaining information develops and it may be more useful to have an address list of experts who are familiar with the information available for their area and are able to point out further relevant details than to have a necessarily incomplete synthesis.

In spite of these reservations and the fact that new data and analyses are constantly appearing in this fast-moving subject area, it is hoped that this report will provide useful background material as well as a valuable source of information on earlier studies and a starting point for those trying to access the grey literature.

As will quickly be apparent from looking through this report, the amount and quality of information presented for the different stocks is uneven. This partly reflects real differences in the amount of research which has been carried out on different stocks, but also the volume of materials supplied by contributors, which has not been edited for length and uniformity of presentation. In some cases (notably Arcto-Norwegian cod) the material includes information on the history of the fishery and of research, the structure of the stock, the fishing pattern etc whereas in others only brief answers to the checklist questions and references are given.

Very little stock assessment material has been included apart from Tables and readers are referred to Myers, Blanchard and Thompson (1990) for a recent synthesis of VPA derived stock data. The reasons for excluding such stock assessment data are that these are updated annually, they appear regularly in ICES and CAFSAC reports already and they require careful interpretation based on more background detail than could easily be included in a report such as this. This report is more concerned with biological background information, particularly concerning events in the early life history.

The arrangement of the report into separate sections for each stock is a natural one given that most research on cod is divided up in this way, to correspond with units of assessment and management, but the main purpose of the report is to encourage comparisons between stocks and perhaps to help to overcome the fragmentation which such stock divisions bring about. Underlying this is a belief (which needs to be tested) that the processes, which govern cod population dynamics (growth, reproductive strategy, behaviour patterns), have shared properties at the species level, rather than being different for each stock.

Given the quantity of assessment related and biological research on the cod stocks of the North Atlantic, this species probably has a great body of population and biological data than any other marine species and any exploited non-farmed species. For this reason it has been recognised as a key species in studying the effects of physical factors on biological production in the sea and in particular for examining the effects of climatic change. This report is intended as a contribution to that study and to cooperative research among the ICES countries.

Table 1 Contributors to checklists for cod

Code	Stock	Area	Contribution
W1	W Greenland	1	Hovgaard, Buch
W2	Labrador/Grand Bank	2J3KL	Anderson
W3	Flemish Cap	3M	Anderson
W4	S Grand Bank	3NO	Anderson
W5	N Gulf of St Lawrence	3Pn4RS	Gagne, Frechet
W6	St Pierre Bank	3Ps	Anderson
W7	S Gulf of St Lawrence	4TVn	Gagne, Chouinard, Hanson, Delafontaine
W8	Banquereau & Sable	4VsW	Campana, Fanning
W9	W Scotian Shelf	4X	Campana, Lambert
W10	Gulf of Maine	5Y	Laurence, Lough, Serchuk, Berrien
W11	Georges Bank	5Z+6	Laurence, Lough, Serchuk, Berrien, Cohen
E1	E Greenland	14	Hovgaard, Buch
E2	White Sea	1E	Serebryakov
E3	NE Arctic	1&2	Ellertsen, Sundby, Sunnana, Solemdal, Skreslet, Godø
E4	Iceland	11	Asthorsson
E5	Faroe Plateau	5A	Hansen, Kristiansen
E6	Faroe Bank	5B	Hansen, Kristiansen
E7	W Scotland	6	
E8	North Sea	4	Munk, Heesen, Nichols
E9	Celtic Sea	7F&G	Brander
E10	Irish Sea	7A	Brander
E11	English Channel	7D&E	Brander
E12	Skagerrak	3A	Moksness
E13	W Baltic (22&24)	3D	Modin, Schnack, Larson, Pliksh
E14	Baltic (25-32)	3D	Modin, Schnack, Larson, Pliksh

INTRODUCTION

Checklist of Biological and Environmental Data for Comparing Reproductive Strategies

This is the checklist originally circulated by the ICES Larval Ecology Working Group in order to bring together existing data on early life stages of cod and haddock. When reading some of the individual stock sections it may be helpful to refer back to this list of questions, because the numbering and form of the answers follows from this list.

1 Species, Stock and Area of Distribution:

1.1 Evidence of stock discreteness, e.g. genetic distance, tagging.

1.2 Units for which assessment of spawning stock biomass and recruitment are available.

1.3 Time series of spawning stock biomass and recruitment data e.g. from commercial catch and effort data, fishing surveys or VPA.

2 Time of Spawning:

2.1 Date of spawning and interannual variability or trend.

2.2 Time of day when spawning occurs.

2.3 Timing of spawning season in relation to planktonic production cycle.

2.4 Timing of spawning season in relation to hydrographic events.

2.5 Timing of spawning season in relation to other fish species which spawn in the same location.

3 Location of Spawning:

3.1 Geographic location and extent of spawning area and evidence of its variability from year to year.

3.2 Does spawning regularly begin in one part of the spawning area and then move to other parts?

3.3 Can the location be described in relation to hydrographic features, e.g. "at the boundary between two water masses"; "in the upper, mixed layer"?

3.4 Can location be described in relation to other species, including food organisms and predators?

3.5 Can location be described in relation to water mass circulation, e.g. "in the north flowing coastal current"; "in the Taylor column circulation over a bank"? How might this affect transport of eggs and larvae?

4 Biological Details:

4.1 Fecundity, i.e. number of eggs produced per female per year (as a function of age). Specific fecundity, i.e. number of eggs produced per unit weight.

4.2 Evidence of changes in fecundity with time.

4.3 Percentage mature at age (including the population not on the spawning grounds). Length at 50% maturity.

4.4 Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae.

4.5 Typical densities, i.e. number per m^3 of eggs and larvae.

4.6 Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva.

4.7 Larval development rate as a function of temperature.

4.8 Condition factor and nutritional status.

4.9 Egg and larval mortality rates.

4.10 Time of first feeding of larvae and food at first feeding.

4.11 Food of larvae during development.

4.12 Evidence of predation during the egg and larval stage?

5 Recruitment

5.1 Are there several spawning sites which contribute to the same stock unit (e.g. there are several spawning areas which contribute to the North Sea stock and their relative contribution may vary from year to year).

5.2 Earliest time in the life history when year class strength can be predicted.

5.3 Hypotheses which have been put forward to account for year-to-year variability in year class strength.

5.4 Evidence of long term trends in recruitment.

5.5 Evidence that variability in recruitment is linked to variability of other species in the same area; the same species in other areas or other species in other areas?

5.6 Evidence of inter- or intraspecific competition.

2 SUMMARY TABLES

The six Tables presented in this section provide summaries of stock size and early life history information for fourteen cod stocks in the NE Atlantic and eleven in the NW Atlantic. There are a number of difficulties in presenting comparative information in this way. One is that the information rapidly becomes out of date, particularly when it derives from annual stock assessments which not only add new information each year, but often revise and recalculate figures for earlier years. The reader is advised to consult the most recent assessment reports and to seek advice from those carrying out the assessments on how to interpret them.

A second difficulty is in using standard definitions and estimates. For example the numbers of recruits given in Tables 2.1 and 2.2 can be estimates for age 1,2 or 3, depending on the growth rate and age of entry to the fishery. Other examples occur in all the Tables.

The purpose of the Tables is to allow simple comparisons of early life history characteristics across all North Atlantic cod stocks in order to identify common features and patterns (e.g relationship between temperature and duration of the pelagic stage). These may help in studying the causes of variability population dynamics for the species.

Tables 2.1 and 2.2 - Stock summaries

These are based on a standard stock summary used by ACFM and give basic information on the size of all stocks and the range in landings, stock biomass and recruitment.

Table 2.3 - Spawning and egg stage data summary

These summaries are necessarily crude and the individual sections should be consulted for further detail. Most stocks contain more than one spawning area, often with different spawning periods and duration, and a mean date of spawning for the stock may be rather misleading.

Depths are in meters.

Temperature are in degrees. In many cases the temperature at which spawn occurs is not known precisely, because there may be a vertical thermal structure and the depth of spawning is not known.

Egg size is in mm.

Density of eggs means specific gravity and is given as (Specific gravity - 1)*10^3

Concentration is Number*m^{-3}.

Mortality is daily instantaneous rate.

Table 2.4 - Larval stage data summary

Sizes at hatch, metamorphosis and settlement are all lengths in mm.

Growth is in mm*d^{-1}.

Mortality is daily instantaneous rate.

Dates at hatch, metamorphosis and settlement are either callendar dates or days form spawning.

Distances from spawning to settlement are in km. They are linear rather than following the actual track. For example in a retention area eggs and larvae may travel a long distance but end up where they started, in which case the distance from spawning to settlement would be nil.

Table 2.5 - Adult stage and biological data summary

Recruits is $\log_{10}$ of number of 3 year old recruits. Where a different age was given in the original source the numbers have been adjusted using a value of natural mortality (instantaneous annual rate) of 0.2.

Spawning biomass is in thousand tonnes. The NE Atlantic spawning biomasses are given in Table 2.1.

Age of maturity is estimated in different ways for different stocks (e.g. age in catch or age in population) and has varied considerably with time in some stocks, therefore the individual stock sections should be consulted carefully when using these data.

Fecundity is average number of eggs produced by a mature fish or specific fecundity (i.e. eggs per gm).

Table 2.6 - Factors affecting survival

This is to give an overview of the possible causes of variability in survival which are being investigated in different areas.

2.1 Stock summaries for N.E. Atlantic stocks

Code	Stock	ICES area	Landings (000 t)				Spawning stock biomass (000s t)				Recruitment (No. in millions)				References
			Max	*Min*	*Mean*	*1991*	*Max*	*Min*	*Mean*	*1991*	*Max*	*Min*	*Mean*	*1991*	
E1	E. Greenland*	14	33 (1990)	2 (1985)	14 (81-91)	22	No data			45p	No data				North Western WG C.M. 1992/Assess:14
E2	White Sea														
E3	NE Arctic*	1 & 2	1343	187 (1990)	691 (50-91)	258	1526	149 (1987)	513	680	1818	112	604	227 (Age 3)	Arctic Fisheries WG C.M. 1993/Assess:1
E4	Iceland	11	538	265	384 (55-92)	313	1383	188	490	221	428	73	197	135 (Age 3)	North Western WG C.M. 1993/Assess:18
E5	Faroe Plateau*	5A	39 (1985)	8 (1991)	28 (82-91)	8	75 (1986)	39 (1990)	56	39	50 (1984)	11 (1986)	23	13 (Age 2)	North Western WG C.M. 1992/Assess:14
E6	Faroe Bank*	5B	3.5	1.9	(82-88)		No data				No data				North Western WG C.M. 1992/Assess:14
E7	W. Scotland*	6	24 (1981)	11	17 (66-91)	12	50	17 (1991)	30	17	29 (1987)	4 (1988)	11	12 (Age 1)	N. Shelf Demersal Stocks WG C.M. 1993/Assess:2
E8	North Sea*	4	341	86 (1991)	207 (63-91)	86	263	56 (1991)	160	56	847 (1980)	109 (1985)	373	155 (Age 1)	Demersal Stocks WG C.M. 1993/Assess:5
E9	Celtic Sea*	7F & G	15.3 (1989)	2.1	5.9 (71-91)	6	13.2 (1989)	3	5.8	5	12.9	0.4	2.9	5.9 (Age 1)	S. Shelf Demersal Stocks WG C.M. 1993/Assess:3
E10	Irish Sea*	7A	14.9 (1981)	6.3	9.9 (68-91)	6.7	10.2 (1986)	2.5 (1991)	7	2.5	15.1 (1987)	2.7	6.7	11.9 (Age 1)	N. Shelf Demersal Stocks C.M. 1993/Assess:2
E11	English Channel	7D & E	No data				No data				No data				Irish Sea & Bristol Channel WG C.M. 1992/Assess:1
E12	Skagerrak*	3A	28.9 (1981)	12.1 (1991)	20.2 (78-91)	12.1	32.5 (1982)	14.2	22.7	17.5	33	10.2 (1987)	18.6	10.2 (Age 1)	Demersal Stocks WG C.M. 1993/Assess:5
E13	W. Baltic (22 & 24)*	3D	54	15 (1991)	40 (65-91)	15	49	14 (1991)	35	14	145	14 (1990)	70	24 (Age 1)	WG Demersal Stock in the Baltic C.M. 1992/Assess:12
E14	Baltic (25 & 32)*	3D	391 (1984)	122 (1991)	218	122	811	178 (1991)	461	178	773	54 (1991)	347	54 (Age 2)	WG Demersal Stock in the Baltic C.M. 1992/Assess:12

Notes

p Predicted or assumed

* Updated from 1992 ACFM

2.2. Stock summaries for N.W. Atlantic stocks.

Code	Stock	NAFO area	Landings (000s t)				Stock biomass (000s t)				Recruitment (No. in millions)				References
			Max	*Min*	*Mean*	*1991*	*Max*	*Min*	*Mean*	*1991*	*Max*	*Min*	*Mean*	*1991*	
W1	W. Greenland	1	112 (1989)	7 (1986)	45 (81-91)	20	639 (1987)	5 (1991)	198 (81-91)	5 (1+)**	-	-	-	-	ICES C.M. 1992/Assess:14 ICES May 1992 ACFM Rept
W2	No. Labrador	2GH	94 (1966)	0 (1991)	14 (53-91)	0	-	-	-	-	-	-	-	-	CAFSAC Res. Doc. 89/43 CAFSAC Adv. Doc. 92/7
W2	So. Labrador/ No. Grand Banks	2J3KL	810 (1968)	139 (1978)	363 (59-91)	171	1611 (1962)	94 (1977)	541 (62-91)	109*** (7+)	1196 (1966)	138 (1974)	456 (62-91)	176*** (Age 3)	NAFO SCR Doc. 92/18 NAFO SC Rep. 1992 (Pt B)
W3	Flemish Cap	3M	60 (1965)	2 (1988)	26 (60-91)	11	41 (1979)	4 (1990)	21 (78-91)	7 (1+)**	-	-	-	-	NAFO SCR Doc. 92/13 NAFO SCR Doc. 92/27 NAFO SC Rep. 1992 (Pt C)
W4	So. Grand Bank	3NO	227 (1967)	15 (1978)	68 (53-91)	29	193 (1967)	21 (1976)	114 (59-91)	80 (SSB)	210 (1966)	6 (1990)	62 (59-91)	8 (Age 3)	NAFO SCR Doc. 92/75 NAFO SC Rep. 1992 (Pt C)
W5	N. & E. Gulf of St. Lawrence	3Pn4Rs	106 (1970)	32 (1991)	77 (61-91)	32	187 (1984)	53 (1991)	112 (74-91)	53 (7+)	196 (1980)	49 (1987)	118 (74-91)	57 (Age 3)	CAFSAC Res. Doc. 92/77 CAFSAC Adv. Doc. 92/7
W6	St Pierre Bank	3Ps	84 (1961)	27 (1978)	50 (59-91)	43	151 (1961)	34 (1976)	96 (59-91)	120 (6+)	100 (1967)	27 (1979)	62 (59-91)	61 (Age 3)	CAFSAC Res. Doc. 92/7 (in prep by Bishop *et al.*) CAFSAC Adv. Doc. 92/7
W7	W. Gulf of St. Lawrence	4TVn (Jan-Apr)	105 (1956)	22 (1977)	57 (50-91)	44	284 (1985)	69 (1977)	179 (71-91)	190 (5+)	230 (1983)	34 (1972)	107 (71-91)	67 (Age 3)	CAFSAC Res. Doc. 92/55 CAFSAC Adv. Doc. 92/7
W7	Sydney Bight	4Vn (May-Dec)	13 (1981)	4 (1975)	9 (70-91)	5	-	-	-	-	-	-	-	-	CAFSAC Res. Doc. 92/8? CAFSAC Adv. Doc. 92/7
W8	Banquereau & Sable Island	4VsW	80 (1968)	10 (1977)	50 (58-91)	33	231 (1983)	63 (1976)	153 (70-91)	137 (3+)	169 (1988)	28 (1984)	75 (70-89)	69* (Age 1)	CAFSAC Res. Doc. 92/54 CAFSAC Adv. Doc. 92/7
W9	W. Scotian Shelf	4X	36 (1968)	12 (1958)	22 (48-91)	27	95 (1966)	45 (1987)	66 (48-91)	84 (3+)	43 (1964)	9 (1952)	21 (48-91)	20 (Age 1)	CAFSAC Res. Doc. 92/46 CAFSAC Adv. Doc. 92/7
W10	Gulf of Maine	5Y	18 (1991)	3 (1963)	9 (60-91)	18	28 (1990)	14 (1987)	20 (82-91)	21 (SSB)	16 (1989)	2 (1991)	6 (82-91)	2 (Age 2)	NEFSC Ref. Doc. 93-04 NEFSC Ref. Doc. 93-06
W11	Georges Bank	5Z + 6	57 (1982)	11 (1960)	34 (60-91)	38	93 (1980)	55 (1991)	73 (78-91)	55 (SSB)	42 (1986)	8 (1990)	22 (78-91)	18 (Age 1)	NEFSC Ref. Doc. 93-05 NEFSC Ref. Doc. 93-06

*Predicted or assumed; **Trawlable stock biomass from RV survey data; ***From ADAPT tuning

2.3 Spawning and egg data stage summary

Code	Stock	Area	Dates		Depth	Temperature		Egg				
			Mean	Duration		Adults	Eggs	Size	Density	Conc'tn	Mortality	Total prod
W1	W Greenland	1	April	Feb-July	20-1000	.5-4	.5-4			21000		
W2	Labrador/Grand Bank	2J3KL	April	March-June	300-600	3-5	<1	1.2-1.6				
W3	Flemish Cap	3M	March	Feb-May	200-400	3-6	3-5	1.2-1.6				
W4	S Grand Bank	3NO	May	April	200-400	3-5	2-5	1.2-1.6				
W5	N Gulf of St Lawrence	3Pn4RS		April-June								
W6	St Pierre Bank	3Ps	May	April-June	200-400							
W7	S Gulf of St Lawrence	4TVn	June									
W8	Banquereau & Sable	4VsW	Apr-May	Mar-June	40-60	4	4-6			1		
W9	W Scotian Shelf	4X	Apr (a)	Feb-May (a)	100	4	4-6	1.5		2	0.2	1E+13
W10	Gulf of Maine	5Y										X*1E12
W11	Georges Bank	5Z+6	Feb-Mar	Nov-May	60-90	3-5	3-7	1.5	25-26	100-300	.025-.041	40-110E12
E1	E Greenland	14	April	March-July	170-400		3.2-5.2					
E2	White Sea	1E	April	March-May	15-100		1.4-1.6					
E3	NE Arctic	1&2	01-Apr	60-70 days	60-150	4-6	1.3-3.6	1.2-1.6	23.5-26	400	0.1	4E+13
E4	Iceland	11	April	March-May	30-100	5-7	5-7	1.3-1.5		10		
E5	Faroe Plateau	5A	March	Feb-May	80-180	6-7	6-7					
E6	Faroe Bank	5B	March	Feb-May								
E7	W Scotland	6										
E8	North Sea	4	Feb-Mar *	Jan-April *	30	5-7	5-7	1.4		1-10	.027-.404	
E9	Celtic Sea	7F&G	March	Feb-April	70	8-9	8-9			1-10		
E10	Irish Sea	7A	March	Feb-April	20-50	6-7	6-7			1-10		
E11	English Channel	7D&E	Feb	Jan-March	20-50	7-8	7-8			1		
E12	Skagerrak	3A	March	Feb-April		4-6	4-6	1.1-1.7	23.8-27.1			
E13	W Baltic (22&24)**	3D	March	Feb-April								
E14	Baltic (25-32)**	3D	May	March-Aug	60-80		3-7	1.4-2.0		100		

Note
* Also Autumn spawning
** For additional information see Baltic cod section 3.9

SUMMARY TABLES

2.4 Larval stage data summary

Code	Stock	Area	Size			Growth	Mortality	Date			Distance from spawn to settle
			at hatch	at metamorph	at settle			at hatch	at metamorph	at settle	
W1	W Greenland	1									
W2	Labrador/Grand Bank	2J3KL	3-4	20-25							300-600
W3	Flemish Cap	3M	3-4	20-25		0.2-0.42	.023-.079	April			Retention
W4	S Grand Bank	3NO	3-4	20-25							Retention
W5	N Gulf of St Lawrence	3Pn4RS									
W6	St Pierre Bank	3Ps	3-4	20-25							Retention
W7	S Gulf of St Lawrence	4TVn									
W8	Banquereau & Sable	4VsW		17				May			Retention
W9	W Scotian Shelf	4X	2.9	17	50-70	0.500	0.2	Apr20-May1		July	100
W10	Gulf of Maine	5Y									
W11	Georges Bank	5Z+6	3-5	15	40-70		.025-.033	14	40-55	100-120	10-150
E1	E Greenland										
E2	White Sea	1E									
E3	NE Arctic	1&2	4	12-15	60-100	0.2-0.4	0.1 *	late April	June	Oct	600-1600
E4	Iceland	11									
E5	Faroe Plateau	5A									
E6	Faroe Bank	5B									
E7	W Scotland	6									
E8	North Sea	4									
E9	Celtic Sea	7F&G									
E10	Irish Sea	7A									
E11	English Channel	7D&E									
E12	Skagerrak	3A	4.5	~12	~30***			April	May	July	
E13	W Baltic (22&24) **	3D									
E14	Baltic (25-32)**	3D									

Note
* Hatching 2(3) months=0.12
2(3)-4(5) months=.02
4(5)-3 years=.0016
** See Baltic cod section 3.9
*** In coastal area

2.5 Adult stage - stock and biological data summary

Code	Stock	Area	Mean Latitude	Recruits (Age 3)	Spawning Biomass	Landings	Maturity 50% Age	Maturity 50%Length	Fecundity
W1	W Greenland	1	62	4.841	182	197	5-6		
W2	Labrador/Grand Bank	2J3KL	51	5.611	431	377	6	49-56	14
W3	Flemish Cap	3M	47	4.643	72	25	5	55-60	
W4	S Grand Bank	3NO	44	4.731	78	71	6	59-62	
W5	N Gulf of St Lawrence	3Pn4RS	49	5.289	185	81	5.5	48	
W6	St Pierre Bank	3Ps	46	4.740	83	52	6	60	
W7	S Gulf of St Lawrence	4TVn	48	4.952	231	57			
W8	Banquereau & Sable	4VsW	45	4.569	168	52	3	40-45	
W9	W Scotian Shelf	4X	43	3.875	61	22	2.5	40-45	
W10	Gulf of Maine	5Y	45	0.499	10	9	2.2	32-36	
W11	Georges Bank	5Z+6	42	.962 *	31	33	1.8	39-41	
E1	E Greenland	14	65	4.841	182	197	(Jonsson 1957,73)		
E2	White Sea	1E	65						
E3	NE Arctic	1&2	73	5.652	7-800	354	7	75	1.40E+06
E4	Iceland	11	65	5.310			7		
E5	Faroe Plateau	5A	62	3.927					
E6	Faroe Bank	5B	61	3.569					
E7	W Scotland	6	58	5.128					
E8	North Sea	4	57	2.867	90	100	4	65	600egg/gm
E9	Celtic Sea	7F&G	51	3.380					
E10	Irish Sea	7A	53	3.420					
E11	English Channel	7D&E	50	3.868					
E12	Skagerrak	3A	58	4.438					
E13	W Baltic (22&24) **	3D	55	4.438			2		
E14	Baltic (25-32)**	3D	55	5.249			2		3.70E+06

Note
* Age 1
** See Baltic cod section 3.9

SUMMARY TABLES

2.6 Factors affecting survival (Hypothesis being tested)

Code	Stock	Area	Starvation	Predation	Advection	Other
W1	W Greenland	1			X	Climate
W2	Labrador/Grand Bank	2J3KL			X	Salinity, FW Outflow, C.I.L,temperature
W3	Flemish Cap	3M				Temperature
W4	S Grand Bank	3NO			X	as W2
W5	N Gulf of St Lawrence	3Pn4RS	X	Seals		Low oxygen,shrimp by catch, temperature
W6	St Pierre Bank	3Ps				as W2
W7	S Gulf of St Lawrence	4TVn	?			
W8	Banquereau & Sable	4VsW				
W9	W Scotian Shelf	4X				
W10	Gulf of Maine	5Y				
W11	Georges Bank	5Z+6	X		X	Climate,Stratification
E1	E Greenland	14			X	Climate
E2	White Sea	1E				
E3	NE Arctic	1&2	X	X	X	Microturbulence maternal effects
E4	Iceland	11				
E5	Faroe Plateau	5A				
E6	Faroe Bank	5B				
E7	W Scotland	6				
E8	North Sea	4				
E9	Celtic Sea	7F&G				
E10	Irish Sea	7A	X			
E11	English Channel	7D&E				
E12	Skagerrak	3A				Direction of Wind and stability of Water masses
E13	W Baltic (22&24)	3D		X*		Oxygen **,salinity **
E14	Baltic (25-32)	3D		X**		Oxygen, salinity ***

Note
* ICES paper Ohldag et al 1991
** Phd thesis : Koster 1994; Koster & Schumach 1994: Sarsia
*** Wieland et al 1992; Wieland et al 1994: Sarsia

3. SPAWNING CHECKLISTS AND STOCK SUMMARIES

3.1 WHITE SEA COD

White Sea cod is a subspecies (*Gadus morhua maris albi Dorjugin*) of Atlantic cod (*Gadus morhua morhua* L.). This subspecies inhabits mainly shallow waters of the White Sea, it is distributed in the Kandalaksha Bay and around the Solovetsky Islands. The White Sea cod does not migrate for a long distance.

Spawning of this cod occurs in the coastal zone, in bays and sounds above 15-100 meter depth. The spawning starts (in the Verkhnyaya Salma sound) in the middle of March under ice cover with surface water temperature -1.6 to -1.40°C and salinity as high as 30 promille. Spawning peak time is the first half of April when surface water temperature is still low, -1.2 to -1.0°C. The spawning ends in the second half of May. The water temperature has risen to 4.0°C by this time; there is no ice cover, and surface salinity has dropped.

Batch spawning was observed in the White Sea cod. Usually the eggs are spawned in 5-6 batches by a female. Eggs are pelagic and with 1.45-1.70 mm diameter. Eggs of the same batch could be of different buoyancy. Eggs spawned in March develop under almost constant temperature -1.6 to -1.4°C, but the development of eggs spawned in April occurs under gradually increasing temperature from 0 to 1.0°C. Also desalinisation of surface water was observed during this time, which resulted in eggs sinking to subsurface and deeper layers, where the egg development continued successfully. Normal White Sea cod development as it was revealed in the laboratory experiments could go on in a wide temperature range - from -1.5°C to +8.0°C with duration of the embryonic development from 45-50 days to 12-14 days depending on temperature.

Newly hatched larvae of 4.2-4.9 mm TL occurs in plankton in the second half of May. Complete yolk absorption occurs by larval length of 5.5 TL, nearly ten days after emerging from the egg capsule. Larvae and postlarvae are distributed in the coastal zone while cod eggs could be obtained in the open sea.

0-group and young cod are also distributed in the shallow water coastal zone. 0-group cod attaining TL of 20-35 mm transfer from pelagic to demersal way of life usually in the second half of June. Adult cod feed on stickleback, sand lance, capelin, herring and other fish as well as on crustaceans. Growth rate of this cod is faster than that of the Barents Sea cod during first two years of life, then it becomes slower. The White Sea cod attains maturity at age 3-5 years and length of 25-35 cm TL. This cod lives for 10-11 years reaching 2.5 kg of weight and 60 cm TL.

This cod stock is not very abundant and commercial exploitation is not high. Total registered catches are from some tons to some hundreds of tons. Last decade it was not higher than 650 tons.

3.2 LIFE HISTORY OF THE ARCTO-NORWEGIAN COD STOCK

3.2.1 The cod fishery history

The skrei (mature Arcto-Norwegian cod) fishery in Lofoten has been important at least since the 9th century. The first written Norwegian history (Egils saga) refers to Torolv Kveldulvson who had fishermen at the fishing village Vågan in Lofoten catching skrei in the year 875. The importance of the fishery is indicated by what Egils saga tells about the trading with the cod: Torolvs man Torgils Gjalande sailed to England with stockfish and skins, and returned with wheat, honey, wine and clothes. Gultorers saga also indicates that the Lofoten spawning fishery must have been widely known: He tells that Icelanders who stayed in Norway during the last half of the 9th century and the beginning of the 10th century went to Lofoten to make money on the skrei fishery. The first history gives the impression that the fishery was quite an ordinary business, so it is reason to believe that it is much older.

Throughout the centuries there are many descriptions of the variability of the fishery. Helland (1908) gives some indications of it from different historical sources: It was most probable good through the 14th, 15th and the first half of the 16th century according to the Hanseatic office in Bergen. During the last part of the 16th and the first years of the 17th century there seemed to be several years of poor fishery. Around 1650 the catches seemed to be back to normal, but it was less good during the last years of the 17th century. Around 1750 the fishery was again back to the level of a hundred years before. A new decline occurred in the late 1780s, and this was probably influenced by large scale cool climate (Wyatt, 1987).

Arcto-Norwegian cod has traditionally been exploited at spawning grounds. For many hundred years (until around 1650) the gear type they used was line and hook. Then the technical improvements started, first by introducing long line. In the 18th century the nets came, and in the 19th century purse seines were introduced. This must have had a substantial influence on the fishing mortality.

During the 19th century there was a steady increase of the catches, only interrupted by two minor declines in the beginning of the 1840s and the late 1850s/early 1860s (Solhaug 1976). The Norwegian export of stockfish and salted fish increased from around 15 million fish in 1815 to 90 million fish in 1880 (Figure 3.2.1). This increase was most probable due to several factors such as technical improvements of the gear, the rise in consumption from a rapidly increasing European population, and an increasing fishing effort. It is interesting to note that the exploitation at that time was at the level of present days values.

3.2.2 The history of cod research

The scientific history of the Arcto-Norwegian cod started in 1864 when Georg Ossian Sars did the first field investigations at the spawning grounds in Lofoten (Sars, 1879). He observed that eggs and larvae from cod were floating in the surface layers after being spawned at depth. The relation between cod and climate came also immediately in focus: already that same year Sars emphasized that the temperature influenced the distribution of the spawning cod, and he suggested that routine deep water temperature measurements should be started to advise the fishermen of the location of the cod. However, the government did not start such measurements before 1878. In 1887 the measurements organized by the government ceased, but several fishermen had found the information useful and continued on their own (Sundby, 1980). They were all of the opinion that the fish was located in the deep layers at temperatures of 4-5°C, In 1891 the Norwegian Parliament funded an investigation aimed at revealing the relation between the distribution of cod and temperature. This resulted in the first systematic investigation of the temperature conditions in the Vest Fjord (Gade, 1894). He concluded that the spawning cod preferred temperatures 4-6°C, and these temperatures were found in the thermocline at varying depths between 50 and 200 m.

From the turn of the century Johan Hjort exerted a large influence on the research on biology of the cod, and particularly he put the recruitment problem in focus (Hjort, 1914). However, at the same time a schism developed between the physical oceanographers and the biologists, which would become an impediment to the development of the many important physical aspects of the recruitment research.

3.2.3 General structure of the stock

The Arcto-Norwegian cod stock has historically been the largest cod stock in the North Atlantic. However, the stock size has been decreasing during the last 45 years from 6.7 million tons in 1946 to 0.9 million tons in 1989. There is a periodic variability in stock size of 6-9 years superimposed on the decrease. The amplitude of the variability is large compared to other cod stocks. Stock size as estimated by virtual population analysis is available from 1946 (Figure 3.2.2).

The Arcto-Norwegian cod is a relatively long-living type of cod. Typically, it matures at about 7-8 years of age. It recruits to fisheries at an age of 3-4 years and is seldom caught above age 15. The recruitment varies, and the influence of large year classes on the stock structure is quite strong. Figure 3.2.3 shows the variation of recruiting year classes since 1946.

Age material is available since 1904 in a limited form and since 1946 in an extensive form. This gives us time series of catch at age for the total stock, and divided by country and gear back to 1946. Catch at age based on otolith readings from the Norwegian catch goes back to about 1930. Further, when using information from age readings from scales and the extensive length measurements done before 1930, it is possible to establish an estimate of variation in year class strength back to the beginning of the century. Using this material it may be possible to run a VPA back to this point.

The stock is widely distributed along the Norwegian coast and in the oceanic regions of the Barents Sea - Svalbard area. The southernmost distribution is found during spawning, which normally occur in Norwegian coastal areas south towards 62°N. Minor spawning has occasionally been recorded even as far south as Bergen. The northernmost and easternmost distribution is found during the summer-autumn feeding season, when cod feed close to the polar front, mainly on capelin and shrimp. As an effect of short term climatic changes, considerable variations are found between years in horizontal distribution of fish due to changes in the front position. In the Spitsbergen area cod may be found in considerable concentrations as far north as 80°N. The distribution in the east, which reaches to Novaya Zemlya, is more southerly than in the Spitsbergen area (Figure 3.2.4). In the winter major concentrations of cod may occur in ice covered areas. The western distribution is limited by the continental shelf, although tagged vagrants have been recaptured in very small numbers in Greenland and Iceland fishing areas (Godø, 1986).

The Arcto-Norwegian cod is managed as one stock unit. There is a distinction between the Barents Sea and the Svalbard components, which are geographically separated when immature (Trout, 1957; Maslov, 1972). During spawning the fish from the two components mix at the same spawning areas. Further, a considerable portion of the Svalbard component mixes with the Barents Sea cod during the post spawning feeding season in the eastern Barents Sea (Trout, 1957; Garrod, 1967).

Although not strictly proved, several studies of migration and general biology, indicate a partial separation between spawning individuals from the two components. While the eastern Barents Sea component mainly spawns in coastal areas from Lofoten and northwards, the western component spawns generally more off-shore and also in areas south of Lofoten (Trout, 1957; Hylen *et al.*, 1961; Godø, 1984, 1986).

The Norwegian coastal cod overlap the distribution of the Arcto-Norwegian cod in Norwegian coastal areas. It is considered as a separate management unit based on its unique biological characteristics and geographically limited distribution (Rollefsen, 1993; Godø, 1986; Jakobsen, 1987). These characteristics seem to be strongly related to environment (Møller, 1968; Godø, 1984; Godø and Moksness, 1987). The genetic separation of the two units has been a question of scientific disagreement (compare Møller, 1968; Mork *et al.*, 1985; Jøorstad, 1984; Dale, 1991).

3.2.4 Fishing pattern

The Arcto-Norwegian cod has historically been the most productive cod stock in terms of commercial landings. At times the catch has reached 50% of northeast Atlantic cod landings (Garrod, 1988). Stock assessments are available from 1946, at which time the stock abundance was high due to the limited exploitation during the Second World War. During the 1950s and 1960s a modern trawler fleet from several countries increased exploitation dramatically, and the catch reached its maximum in this period. The periodic variation in catches is strongly related to recruitment. Since the beginning of the 1970s there has been a decreasing trend in the landings, and the 1990 catches were the lowest recorded since the start of modern fisheries (Figure 3.2.5).

The small mesh sizes used in the codend during the expansion period implied also a considerable hidden mortality due to discarding of small fish. Garrod (1967) reported discard rates up to 40% of catches in numbers in the British trawl fishery in the Bear Island area. Mesh regulations and area closures have reduced the problem in the direct cod fishery. The development of the oceanic shrimp fishery in the 1980s has, however, again increased the problem with discard of prerecruits. Area closure and a ban on discard were introduced in the Norwegian EEZ to minimize the problem. Nevertheless, hidden exploitation of small fish is still a problem in periods when rich year classes recruit to the fishery.

Before World War II, exploitation was concentrated on large mature fish (the skrei fishery) and secondly on migratory prespawning cod following the capelin to the northern Norwegian coast (the Finnmark fishery). The increasing trawler effort led to a gradually lower mean age in the catch (Figure 3.2.6). Simultaneously, the level of exploitation increased gradually to its maximum in the 1980s. At this stage strict regulations were enforced, which reduced the fishing mortality to the same level as that just after World War II (Figure 3.2.7, Anon., 1992).

Detailed information on fishing pattern and exploitation level is available from 1946. Systematic collection of age data from that time supplies catch at age information by gear and country, and hence stock abundance estimates from VPA are available from 1946 (Figure 3.2.2). In the late 1970s and during the 1980s a severe stock reduction followed, which seem to be connected to both the high exploitation level (Figure 3.2.7) and reduced recruitment at age 3 (Figure 3.2.3).

3.2.5 Environment.

The feeding habitat of the juvenile and adult cod comprises mainly the ice free parts of the Barents Sea and the narrow shelf region to the west of Svalbard, which is an area of about 0.6 - 0.7 mill. km^2, or about 40 - 50 % of the entire area of the Barents Sea. Spawning occurs mainly outside the feeding habitat, at distinct and separate locations along the Norwegian coast from Sørøya to Møre (Figure 3.2.14). The drift of eggs, larvae and early juveniles takes place in the upper 50 m of the sea, mainly in the Norwegian Coastal Current, where they are passively advected from 600 - 1600 km and dispersed back into the habitat of juveniles and adults.

Loeng (1989) has reviewed the ecological features of the Barents Sea with emphasize on the physical conditions and the primary and secondary production. The mean depth of the Barents Sea is 230 m. The Bear Island Channel, which intrudes eastwards from the western shelf edge, is the deepest part of the sea with depths between 400 and 500 m. Large areas of shallow depths, less than 100 m, are found between Spitsbergen, Bear Island and Hopen (Figure 3.2.8).

There are two sources of warm water supply to the Barents Sea, the large and salty Norwegian Atlantic Current, which carries about 3 Sverdrups, and the fresher Norwegian Coastal Current, which carries about 1 Sverdrup, (Figure 3.2.9). Both these currents run parallel towards northeast along the coast of North Norway and turn east into the Barents Sea in the region of the Tromsøflaket bank. The coastal current spreads out in a clock-wise circulation above Tromsøflaket, while the Norwegian Atlantic Current splits into two branches northwest of Tromsøflaket. One branch flows around the bank and into the Barents Sea, the other continues north towards Spitsbergen along the shelf edge. The scalar speed of the Coastal Current is 10 - 30 cms^{-1}, while the maximum speed is 80 - 100 cms^{-1}. The speed of the Atlantic Current is about 50 cms^{-1} along the shelf break off the Norwegian coast, but decreases when it turns into the Barents Sea and gets wider.

Cool water enters the Barents from the Arctic Basin through the straits between Svalbard and Franz Josefs Land (The East Spitsbergen Current) and Franz Josefs Land and Novaya Zemlya (The Persey Current) (Dickson *et al.,* 1970). Recent current measurements in the strait between Novaya Semlya and Franz Josef Land indicate that 3 Sverdrups of Atlantic Water flows through the strait from the Barents Sea into the Arctic Basin (Loeng et al., 1993).

Even though the Norwegian Atlantic current is much larger than the Norwegian Coastal Current, the latter is the most important conveyor of eggs and larvae from the coast of Norway to the Barents Sea. The Coastal Current extends above the continental shelf of Norway, and its circulation is strongly influenced by the bottom topography, creating numerous stationary and quasi-stationary eddies and bends. The influence of bank topography on the circulation has been studied (Eide, 1979), and it has been demonstrated that the bank topography influences the distribution of eggs and larvae (Sundby, 1984; Bjørke and Sundby, 1984). The Tromsøflaket in the southwestern Barents Sea (Figure 3.2.10) is a key region for early juveniles. The clock-wise circulation above this bank creates an interim retention of early juveniles in July on the drift route from the spawning fields at the Norwegian coast to the central parts of Barents Sea. During the early juveniles survey in July 40-90% of the year class is found within this bank (Bjørke and Sundby, 1987). The area of Tromsøflaket is no more than 25.000 km^2, while the total area of early juvenile distribution ranges from 100.000 to 200.000 km^2.

The habitat of the Arcto-Norwegian cod is influenced by four masses, Atlantic Water, Coastal Water, Arctic Water and Norwegian Sea Deep Water. The first three of these water masses are present in the habitat, while the fourth, the Norwegian Sea Deep Water is only present as a mixing product with the Atlantic Water. Figure 3.2.11 shows the positions of all four water masses in a temperature-salinity plot.

1. The Atlantic water occupies the deep layers of the Norwegian continental shelf, the entire water column above 500 m depth off the shelf break and the central parts of the Barents Sea. The salinity in the core is 35.0-35.2 and the temperature ranges from 6-8°C. The temperature and salinity decrease as the water mass flows northwards along the shelf edge and eastwards into the Barents Sea. At the entrance of the Barents Sea the mean salinity and temperature in the core in the autumn was 35.13 and 6.2°C respectively (Blindheim and Loeng, 1981). This

water mass is the main habitat of the juvenile and adult Arcto-Norwegian cod.

2. A wedge of coastal water flows parallel to the Atlantic water close to the coast. The temperature-salinity characteristics have a large yearly amplitude, being fresh and warm in summer, cool and more saline in winter. The extreme values are typically 10-12°C and 33.2-33.6 in August and 2-4°C and 33.7-34.4 in March/April. As the water mass flows north and eastwards the temperature decreases due to heat loss from the surface, and the salinity increases due to mixing with the saline Atlantic Water. During the egg, larva and early juvenile stages the coastal water is the habitat of the Arcto-Norwegian cod.

3. Arctic Water originates from the inflow of water through the straits between Svalbard and Franz Josefs Land and Franz Josefs Land and Novaya Zemlya. It flows southwest through the Barents Sea along the northern slope of the Bear Island Channel. In this region ice is formed during winter and melts again during summer. Its average temperature and salinity is -1.8°C and 34.5 respectively. The position of the Arctic Water limits the northern extension of the Arcto-Norwegian cod. Increased mortality due to low winter temperatures has been reported for 0-group and 1-group cod. However, there are also examples of adult cod that intrude into water of -1°C in summer when chasing capelin.

4. The Norwegian Sea Deep Water occurs only as a mixing product with the Atlantic Water in the habitat of the cod. This mixing product is found in the deepest troughs of the Norwegian continental shelf and in the Bear Island Channel. It has a very constant salinity of 34.92 and a temperature ranging from 0.5 to -1.0°C.

There are considerable variations in sea ice conditions from year to year in the Barents Sea. Figure 3.2.12 shows the variation in the position of the ice edge, based on satellite images from a period of 10 years, 1971-1980, for 6 months of the year. The seasonal extremes are found in March-May and August-September (Loeng, 1979). Figure 3.2.13 show the distribution of ice during April-August for three periods 1898-1922, 1929-1939 and 1971-1980. There was a distinct decrease of the ice in the Barents Sea from the first to the second period. This decrease was a result of alterations in the atmospheric and oceanic circulation (Hesselberg and Johannessen, 1958; Zubov, 1943).

3.2.6 Spawning

Mature cod aggregate off the coast of Finnmark during late autumn, start their spawning migration along the Norwegian coast in December and arrive at the Lofoten spawning grounds from late January (Bergstad, Jørgensen and Dragesund, 1987). The spawning migration is counter-current along the coast and takes place mainly in the thermocline between the upper cool Coastal water (2-4°C) and the warmer Atlantic water (7°C) below. This implies that the cod have the opportunity to select the ambient temperature within the range of 2-7°C at most of the spawning sites. Sætersdal and Hylen (1959) described the migration: The spawning route along the coast seems to be the same each year, southwards along the shelf break and along specific troughs from the shelf break into the near shore spawning grounds. The average migration speed of the schools is 8-10 n.m. per day, or 17-20 cm s^{-1}. The highest concentrations are recorded within eddies along the route. In regions of strong current the concentrations are low. The largest and oldest specimens arrive at the spawning grounds first (Rollefsen and Hylen, 1981).

The spawning areas of Arcto-Norwegian cod are patchy, located in the Norwegian coastal current off Mid and North Norway, along a 1200 km coastline (Figure 3.2.14). The spawning areas are at the same sites every year, although the magnitude of the spawning at the sites may vary. Most of the eggs are spawned along a limited part of the coastline, in Lofoten and Vesterålen, between 67°30'N and 69°N. From 1983 to 1985, 60-70 per cent of the total egg number were spawned here, when the production varied between 3.1×10^{13} and 4.7×10^{13} eggs (Sundby and Bratland, 1987). Especially in Lofoten the spawning schools are very dense, the peak egg concentration may exceed 10.000 eggs per m^2 surface (Wiborg, 1950; Sundby, 1980). Such high concentrations are not only caused by dense spawning, but are also due to higher retention at the Lofoten spawning grounds than at the other spawning sites (Sundby and Bratland, 1987). A characteristic feature of all the larger and most of the medium size spawning fields is that they are found either in bays close to the coast, or on offshore banks where the bottom topography induces a clock-wise circulation (Sundby, 1984). Both in the bays and on the banks where spawning takes place, the residence time of the water masses is prolonged. However, not all of the major spawning grounds are found in areas of high residence time of the water masses. Especially at some of the Vesterålen offshore spawning grounds, cod eggs are subjected to rapid transport and dispersion (Sundby and Bratland, 1987). Altogether, about 20-30 percent of the eggs are spawned at sites where there is short residence time of the water masses. Most of these eggs are spawned close to the offshore front between the coastal water and the Atlantic water. In this region both water masses move rapidly northwards along the shelf edge.

The influence of changing winds on the spawning behaviour and distribution and spreading of eggs in

Lofoten has been described (Ellertsen *et al.*, 1981a; Ellertsen *et al.*, 1981b; Furnes and Sundby, 1981; Sundby, 1980). Northeasterly winds in Vestfjorden increase the egg transport out of the fjord, while southwesterly winds increase the spreading within the fjord. Calm wind conditions give a low rate of both transport and spreading.

Spawning occurs in March and April. In Lofoten, where the largest spawning sites are found, the spawning intensity has been monitored each year since 1975 (Solemdal, 1982; Ellertsen *et al.*, 1984). Spawning proceeds in a remarkably constant way between years, starting during the first days of March, reaching maximum intensity during the first week of April and petering out within the first half of May (Figure 3.2.15). The spawning intensity has also been monitored at several other major spawning fields (Anon., 1983), revealing a tendency towards later spawning at the grounds farther north. The spawning period is delayed by about 2 weeks at the northernmost spawning field relative to the Lofoten area (Sundby and Bratland, 1987).

Pedersen (1984) examined the long term changes of the maximum spawning intensity in Lofoten based on cod roe investigations from fish catch statistics since 1929. He found a tendency towards later spawning, by approximately 7-15 days, during the period from 1930 to 1960.

The Arcto-Norwegian cod spawn in the thermocline between the cold Coastal water and the warmer Atlantic water, at temperatures between 4 and 6°C, both pelagically and where this layer intersects the bottom (e.g. Gade, 1894; Sund, 1925). The depth of the thermocline may vary considerably from year to year (Eggvin, 1932), but short term variations caused by wind effects may also be of great importance for the depth of the thermocline causing upwelling or downwelling at the spawning fields (Furnes and Sundby, 1981; Ellertsen *et al.*, 1981a).

3.2.7 Egg and larval stages

Ellertsen *et al.* (1989) summarized recent research on the early life stages of the Arcto-Norwegian cod.

The eggs are buoyant compared to the natural environment, and hence tend to rise towards the surface layers (Solemdal, 1970; Solemdal and Sundby, 1981). The neutral buoyancy and egg diameter for the entire egg population are Gaussian distributed, and range from 29,5 to 33,0 p.s.u., and from 1,2 to 1,6 mm, respectively. From these values the ascending speed of the eggs was calculated to range from 0,2 to 1,8 mms^{-1} (Solemdal and Sundby, 1981; Sundby, 1983). Solemdal and Sundby (1981) showed that neutral buoyancy is correlated to the weight of the eggshell, whose thickness may vary between 5 and 9 mm (Davenport *et al.*, 1981). The specific weight of the eggs increases through the development (Sundnes *et al.*, 1965). The chorionic material, which is the heavy fraction of the egg, has a specific gravity of 1.2 g cm^{-3}, while the internal material has an average specific gravity of 1.017 g cm^{-3}; variation in egg size is the most important factor for buoyancy variations in the egg (Kjesbu *et al.*, 1992).

The eggs are found in the entire upper mixed layer, but the concentration increases towards the surface. High concentrations are found at the surface during calm conditions, and most of the eggs are found above 20 m depth. During rough weather the eggs are mixed downward due to the influence wave action and turbulence, Figure 3.2.16. When the wind speed exceeds 15 ms^{-1} the vertical concentration profile of cod eggs shows only a very slight increase towards the surface, and may be found in relatively large concentrations down to the bottom of the mixed layer. Models for how the vertical distribution of pelagic and bathypelagic eggs in general are influenced by buoyancy and turbulence are described by Sundby (1983), Sundby (1990) and Westgård (1989). The vertical spreading of the pelagic Arcto-Norwegian cod eggs is mainly determined by wind induced turbulence, and only to a very small extent by the buoyancy distribution.

The years 1981 to 1983 represent two extreme years with respect to temperature during incubation; the mean March/April temperatures in the upper 30 m in the Vestfjord were 1.3 and 3.6°C, respectively. Peak hatching varied by approximately 2 weeks between 1981 and 1983 (Solemdal, 1984; Ellertsen *et al.*, 1987), hatching time for the earliest spawned eggs in 1981 was ca. 35 days.

Egg mortality estimates for the years 1983 and 1984 have been made in Lofoten (Ellertsen *et al.*, 1987; Fossum, 1988), based on population fecundity estimates by egg surveys (Sundby and Solemdal, 1984; Sundby and Bratland, 1987) and subsequent measurements of late egg stages. In both years the mortality from spawning to hatching was 90 per cent (Fossum, 1988). The causes of the mortality are not well known, but there is evidence that predation by herring may be considerable (Melle and Ellertsen, 1984; Melle, 1985). Stock fecundity estimates by egg surveys were in good agreement with acoustic measurements of the biomass of spawning fish (Godø, Nakken and Raknes, 1984; Godø, Raknes and Sunnanå, 1985).

The cod larvae, like the eggs, in the Lofoten area are trapped in the upper mixed layer of the cod Coastal current. The maximum recorded concentration of larvae before 1992 was approximately 200 per m^2 surface, which is about 5% of the maximum recorded concentration of newly spawned eggs. The number of larvae estimated during one survey varied between years from 2 x 10^9 to 1,2 x 10^{11} (Ellertsen *et al.*, 1987). The horizontal distribution of larvae has been recorded since 1979. The horizontal distributions of larvae for the two years 1981 and 1983 are shown in Figure 3.2.17. During a larval survey in spring 1992 anomalous high concentrations of larvae were recorded. There were larvae in the entire area of Vestfjorden and in the larger part of the shelf region off Lofoten. The highest concentration was 2700 larvae per m^2 surface. The larval survey results are presently not published. The year class turned out to become the strongest 0-group ever recorded (Anon., 1992).

Investigations on the vertical distribution of cod larvae have been carried out with large pumps (Solemdal and Ellertsen, 1984). The majority of first feeding larvae in Lofoten waters are distributed in the upper 30 m of the water column (Ellertsen *et al.*, 1979; Wiborg, 1948). The peak concentration occurs between 10 and 20 m, and the concentration above the 5 m depth is very low. Diurnal vertical migration depends on the ability of the larvae to move and vertical turbulence. During extremely calm conditions larvae seem to "control" their vertical position in the water column, and show diurnal migration (Ellertsen *et al.*, 1984).

Like most marine fish larvae, cod larvae are visual feeders (Ellertsen *et al.*, 1980), and select their prey on the basis of size (Ellertsen *et al.*, 1979). Larval gut content analysis from the Lofoten area shows that nauplii of *Calanus finmarchicus* are the dominant prey item (Ellertsen *et al.*, 1984; Wiborg, 1948). A larval bioassay technique (Lasker, 1975) tested in Lofoten showed that cod larvae were able to capture nauplii at rather low concentrations (Ellertsen *et al.*, 1979), and that larvae were feeding on copepod fecal pellets. Fish larvae have been frequently reported with green food remains in the gut (Lebour, 1919). Wiborg (1948) reports the same findings in cod larvae from the Lofoten area. Nordeng and Bratland (1971) have identified the phytoplankters *Peridinium pellucidum* and *Coscinodiscus* sp. in the gut of cod larvae from the same area. Analysis of polyunsaturated fatty acids in the cod larvae from Lofoten shows influence of specific fatty acids from phytoplankton (Tilseth *et al.*, 1987). The significance of this observation from a nutritional point of view is not yet fully understood. The first feeding larvae were active feeders on larger plankters like *Peridinium* sp. (50-80 mm).

Active feeding in fish larvae usually occurs only above a certain light intensity (Blaxter, 1966). Cod larvae fed *Artemia salina* were able to capture *Artemia* nauplii at 0.4 lux, but not at 0.1 lux, and highest feeding incidence was observed at 1.4 lux (Ellertsen *et al.*, 1976, 1980). Providing that the light intensity threshold for visual feeding of cod larvae on nauplii is close to 0.1 lux (Blaxter, 1966), there are 22-24 hours available for feeding per diurnal period in May in the Lofoten area.

Ellertsen *et al.*, (1987) examined the prey density and larval distribution in different regions of the Lofoten area and found higher prey densities, higher larval feeding incidence and higher number of larvae with full gut in the areas of Vestfjorden where retention is high. On a smaller spatial scale Skreslet (1989) also found a correlation between larval concentration and prey concentration. In the surrounding areas these parameters were much more variable. Comparison of the gut fullness of stage 7 larvae caught in the upper 40 m during daytime, and the integrated nauplii concentration in the water column showed that maximum gut fullness was reached when the nauplii concentration exceeded 10 per litre. The empirical data indicate a critical prey density of 5-10 nauplii per litre. However, wind generated turbulence was demonstrated by Sundby and Fossum (1990) to have a substantial impact on the contact rate between the cod larvae and their prey, as outlined in the theory by Rothschild and Osborn (1988). When the average wind velocity increased from 2 m s^{-1} to 6 m s^{-1}, the contact rate increased by 2.8, which corresponds fairly well with the theory. In Figure 3.2.18 the relation between the number of nauplii in the larval gut and the nauplii concentration in the sea are drawn for three different wind situations.

Ellertsen *et al.*, (1987) and Fossum (1988) examined survival of cod eggs and larvae within the Lofoten spawning area in 1983 and 1984, when strong year classes were produced. Only 2-3 per cent of the eggs spawned in 1983 and 1984 reached the stage of first feeding larvae. Larval length/dry weight results for the first feeding periods in 1982-1985, indicate that the first feeding larval condition is correlated to the year class strength.

Various plankton pumps and particle rate meters have been used to investigate the vertical distribution of copepod nauplii (Ellertsen *et al.*, 1976, 1979; Mohus, 1981; Tilseth and Ellertsen, 1984a). The highest concentrations of nauplii usually occur at 5-15 m depth, occasionally at the very surface (Ellertsen *et al.*, 1979; Tilseth and Ellertsen, 1984a), and the general impression is that very high concentrations of nauplii at the surface usually occur in the evening during calm weather (Ellertsen *et al.*, 1979).

Almost all *C. finmarchicus* nauplii in the Lofoten occur within the upper 50 meters due to spawning close to the surface, the sinking velocity of eggs and the incubation time. However, the vertical distribution of copepod nauplii is not constant throughout a 24-hour period. Numerous 24-hour stations in 1975-87 have revealed an increasing concentration in the upper 0-5 m in the evening versus a daytime maximum at 5-15 m (Ellertsen *et al.*, 1979; Tilseth and Ellertsen, 1984a; and unpublished data). it can be concluded that the medium and larger size nauplii show a diurnal vertical migration, while the smallest ones, (< 120 mm carapace length) do not seem to migrate.

First feeding cod larvae are seldom observed to make vertical migration, and such migration has only been observed during very calm weather conditions. Usually, they have their maximum concentration at 0-20 m depth throughout the 24 hour period (Ellertsen *et al.*, 1979; Tilseth and Ellertsen, 1984a), or undertake a vertical migration over a few meters. Cod larvae show a reduced feeding intensity at night (Ellertsen *et al.*, 1979; Tilseth and Ellertsen, 1984b), coinciding in general with a period of reduced nauplii concentrations at 10-20 m. The smallest nauplii which are prevailing at cod larval depths at night time are in general too small to be eaten by the cod larvae, which seem to select food organisms over a certain size (Ellertsen *et al.*, 1979).

The horizontal distributions of copepod nauplii in the Lofoten area in the years 1980-1985 are shown in Figure 3.2.19. These maps, together with series of previously published (Ellertsen *et al.*, 1984; Tilseth and Ellertsen, 1984a) data give an impression of Lofoten as a variable area with regard to naupliar distribution. In general there are higher concentrations of nauplii within the smaller fjords like Austnesfjord, while the lowest densities are usually found outside the Lofoten archipelago. Ellertsen *et al.* (1989) showed that the production of nauplii is highly dependent on the temperature of the upper layer where the mature *C. finmarchicus* spawn. Figure 3.2.20 shows the date of maximum occurrence of *C. finmarchicus* copepodite stage 1 as a function of the average temperature of the upper layer during March-April. The time of maximum occurrence varies by more than 1½ month, being late in cold years and early in warm years.

Temperature seems to be an important parameter related to recruitment. Only small year classes are produced when the temperatures in the early larval distribution areas are low (Figure 3.2.21), while year classes of all strengths are produced under higher temperatures. The most prominent environmental feature of the year 1983 was the high temperature of the coastal water masses during spawning, of 3.6°C, the highest recorded since 1961. Only two years earlier, in 1981, eggs and early larvae experienced the lowest environmental temperature (1.3°C) ever recorded since the temperature measurements started in 1936, and became a very poor year class. The relationship between year class strength at age 3 years and the temperature during the egg/early larval stages indicates that temperature is a necessary condition for the formation of strong year classes, it also implies that other processes are important, since far from all years with high temperatures produced a strong year class.

Temperature dependent recruitment is found in other cod stocks living on the border of their distribution area, for example the cod stock at West Greenland (Hansen and Buch, 1984). They suggested that it could be caused by variable advection of juveniles from warmer Icelandic waters. Obviously, many processes related to recruitment are temperature dependent. For the Arcto-Norwegian cod the temperature-dependent spawning of *C. finmarchicus* in Lofoten, causing a delay in spawning of 1½ month in the coldest year compared to the warmest, may be a very important process to cause variable larval survival (Ellertsen *et al.*, 1989).

The significance of temperature is supported by the work of Sætersdal and Loeng (1987), who found that strong and medium year classes occurred most frequently in years with high temperatures along the Kola section. Since most of the temperature variations in the Norwegian Sea/Barents Sea are of a geographically large scale (Dickson and Blindheim, 1984; Blindheim, Loeng and Sætre, 1981) the same variations also appear in the Lofoten spawning area.

3.2.8 Juveniles

There is a gap of information and research on stages around metamorphosis, when the fish is about 8-15 mm long. This is due to lack of adequate sampling gear. During these periods the concentrations are too low and the mobility of the creatures is too high to get good samples by low speed plankton nets or large pumps. However, a Norwegian survey of early juveniles has been carried out each July since 1977, when the juveniles have reached a size of 20-50 mm. From these surveys, maps of distribution and an abundance index are made. The sampling gear is a mid water trawl with an opening 29 x 29 m, the same gear as is used during the subsequent International 0-group survey of the Barents Sea in August-September when the juveniles have reached a size of 50-80 mm and obtained their terminal pelagic distribution before they settle to the bottom. Figure 3.2.22 shows two examples of the distributions during early larval stage in July and the 0-group stage in August-September (Sundby *et al.*, 1989).

The spatial distribution of early juveniles (20-50 mm) is described by Bjørke and Sundby (1984; 1987). Like the larval stage, they are mainly found above 30 m depth, but the peak concentration is different from the larvae. While the larvae have their maximum concentration between 10 and 20 m depth and seem to avoid the upper 5 m of the sea, the early juveniles are often found in high concentrations in the upper 5 m. The horizontal distribution is strongly influenced by the mesoscale circulation and particularly by bottom topography steering. This results in high concentrations above the two banks Tromsøflaket and Nordkappbanken in the southwestern Barents Sea (Figure 3.2.10).

Like the early larval stages, the main prey organism of the early juveniles is *C. finmarchicus*, but now older stages. The larger fraction also feeds on young krill stages (Sysoeva and Degtereva, 1965). Model simulations by Sundby (1993) indicate that the influence of turbulence induced contact rate between cod and their prey is important up to the stage of 2 months old juveniles. Bjørke and Sundby (1987) found that early juveniles in the southern and western parts of the area are considerably larger than in the eastern part, even though it is to be expected from consideration of the circulation that larvae in the eastern part are older. It is assumed that this apparent paradox is due to the combined effect of higher temperature and food supply in the southwestern region (Suthers and Sundby, 1993).

International 0-group surveys in the Barents Sea have been conducted each year since 1965. They give maps of distribution and an abundance index. The survey is carried out during three weeks in August-September which is prior to juveniles settling to the bottom.

Randa (1984) studied the relation between the 0-group abundance index and the abundance at age three based on virtual population analysis for a period in the 1970s. He found that there was a good correlation indicating that the year class strength is mainly determined at the 0-group stage. Sundby *et al.* (1989) studied the early juvenile data and found that the year class strength is largely determined already at this stage. However, it was concluded that during periods of large ecological changes, the year class strength may change considerably after the stages of early juveniles and 0-group. This happened for the 1983-1986 year classes which were recorded to be strong at the pelagic stages (Figure 3.2.3). Except for the fairly high recruitment at age 3 of the 1983 year class, these year classes were strongly reduced before exploitation. Several factors have been suggested to have influenced the lack of correlation between indices of the pelagic stages and abundance at recruitment to the fishery in this period:

1) *The survey method explanation*

Recruitment indices of cod, both from the pelagic stages and the bottom stages are known to be subject to errors caused by selectivity and efficiency of the sampling gears (Godø, 1990; Engås, 1991; Godø *et al.*, 1992). Not only the precision is affected, but also serious effects on accuracy might be expected.

2) *The cannibalism explanation*

Due to severe reduction of the capelin stock in the mid 1980s, the rapidly increasing cod stock suffer from food shortage. This led to a reduction in growth and increasing predation on juvenile cod (Bogstad and Mehl, 1991; Mehl and Sunnanå, 1991). It is thus hypothesised that the lower than expected recruitment to the fishery was caused by cannibalism (Hamre, 1990).

3) *The ecological explanation and*
4) *The exploitation explanation*

The ecological and exploitation explanations go further and stress impact of man on the harvestable production. The lack of ecological considerations taken in the exploitation of the different fish and sea mammal stocks of the Barents Sea, reduce the total yield of the ecosystem (Hamre, 1990). In addition, the extremely strict catch regulation on cod, where the Fs have been reduced towards the level of the natural mortality used in the assessment (Figure 3.2.7), add more uncertainties in the stock abundance calculations.

5) *The environmental explanation*

The environmental explanation is based on fact that survival in the northern areas is largely dominated by variation in environment, in contrast to the higher influence of competition in temperate and tropical areas. As the primary and secondary production of the Barents Sea is dependent on influx of nutrition and recruitment of zooplankton from the Norwegian Sea, the ecosystem will necessarily be sensitive to variation in physical oceanography. Normally this will affect survival of the larval stages, but survival during the first winter can also be affected (Godø and Skjoldal, 1992).

The explanation why the rich recruitment at the pelagic stages in the period 1984-1986 was not reflected in later surveys and in commercial catches, is certainly not dependent on only one single factor. It is basically a question of understanding the interaction between the above five different factors.

The population mortality during three periods from hatching to the 3-group stage was studied by Sundby *et al.* (1989). The instantaneous mortality declined from an average value of 42 y^{-1} during the period from hatching to early juveniles (2-3 months old), to a value of 8 y^{-1} during the preceding period from 2-3 months old to 4-5 months old (0-group survey). During the third period from 4-5 months old to 3-group fish the instantaneous mortality was on the average 0.6 y^{-1}. The range of variation in the accumulated mortality was largest during the first period (from hatching to 2-3 months old fish) : 67. During the subsequent period (from 2-3 months to 4-5 months) the range of variation was reduced to 3. Besides, most of the variation during this second period could be ascribed to density dependent mortality, and hence it is predictable. Even though the instantaneous mortality is as low as 0.6 y^{-1} during the third and long period from 4-5 months to 3 years, the range of variation of the total mortality is relatively high, 2.8, due to the much longer duration. There is no indication of density dependent mortality during this period. The results of Sundby *et al.* (1989) demonstrates that the first three months is the most important period in the formation of year class strength, and they conclude that mortality during this period is most probably caused by a combination of predation and starvation.

3.2.9 Adults

Maturation and growth

The Arcto-Norwegian cod mature mainly between ages 6 to 9. The median age at maturity is at present about 7 years, however, there has been a gradual decrease from 9-11 years before 1950 to about 7 years in the late 1970s and 1980s (Jørgensen, 1990). He proposed that increased growth rates of juvenile cod was responsible for the reduced age at maturity, however, later studies of growth do not support this hypothesis (Jørgensen, 1992). Changes in growth and age at first spawning are found for other species in the same area (Godø and Haug, 1989; Haug, 1990), and such changes seem to be linked to high exploitation pressure. Borisov (1978) and Law and Grey (1989) express concern for reproduction and productivity of the cod stock under the current exploitation because, according to them, genetic impoverishment may occur. Individuals which are genetically determined to mature late will not reach maturation and hence not reproduce the ability for late maturation. Short term changes in age at maturation (Godø and Moksness, 1987) demonstrate the plasticity of these parameters, probably as a response to the changing environment. Therefore, there is still uncertainty about the extent to which high exploitation leads to damage to the gene pool.

Age and length of Arcto-Norwegian cod is close to linearly related. The reduction in growth rate with increasing age found for many populations, is not prominent. It has been suggested that the shift to a fat prey like capelin, gives sufficient extra energy to maintain the growth rate.

Migration

Migration of the Arcto-Norwegian cod is size dependent. The east and north boundaries of the distribution are limited by the polar front. The immature stages perform seasonal migrations as a response to the changing environment, i.e. they follow the winter-summer movements of the polar front. With increasing age more extensive seasonal migration are performed. The fish make "dummy runs" in the year before maturation, i.e. the large immatures follow the schools of mature fish towards the spawning grounds before returning to feed on capelin along the northern Norway coast (Trout, 1957). The spring migration of immatures towards the coast for feeding on spawning schools of capelin is the basis for the traditional seasonal "Finnmark fishery". Nakken and Raknes (1987) found that the older individuals are more distributed to the west, in warmer water, in the Barents Sea than the younger year classes.

Arcto-Norwegian cod also show great variation in vertical distribution (Godø and Wespestad, 1992). In some areas and during periods extensive vertical migration is observed (Engås and Soldal, 1991). These behavioural aspects may affect catchability in the commercial fisheries as well as year to year comparability and reliability of abundance estimates from surveys (Godø, 1990).

Feeding

The spectrum of prey categories found in cod stomachs is broad. Mehl (1991) gave a list of 140 categories. In the same paper he pointed out that on the average only 9 species or categories contribute more than 1% by weight to the food. These are amphipods (*Hypaeridae*), deep sea shrimp (*Pandalus borealis*), herring (*Clupea harengus*), capelin (*Malotus villosus*), polar cod (*Boreogadus saida*), cod, haddock (*Melanogramus aeglefinus*) and redfish (*Sebastes* spp.). Individual, spatial, seasonal, and year to year variation in the diet has been recorded (Mehl, 1986). In the 1980s capelin was the main prey item for medium sized cod, but shrimp and amphipods are also frequently found in the stomachs. Large cod seem to predate on available fish such as haddock, redfish, blue whiting, flatfish, and cod (Mehl, 1991).

Long term changes in stomach content of many of the most important prey species are found, and these variations are linked to variation in abundance of both the prey and the predator (Ponomarenko and Yaragina, 1978, 1979, 1984).

The dependence of sustainable high production of the Arcto-Norwegian cod stock on abundant capelin and particularly herring stocks is emphasized by Hamre (1990). The relative importance of capelin and herring in the food of cod is determined by the herring stock. This is because the prospects of survival for capelin is governed by the abundance of herring (Hamre, 1990). Small cod predate mainly on copepods, euphausiids and amphipods (Mehl, 1991). The importance of euphausiids on the growth and survival of pre-recruits is emphasized by Ponomarenko (1984). Cannibalism is considered as a stock regulation mechanism, and small cod may be a relatively important food item when rich year classes of cod and low abundance of other prey species occur simultaneously (Korzhev and Tretyak, 1989; Mehl, 1991).

Fecundity

The fecundity of Arcto-Norwegian cod is substantially lower than the fecundity of Coastal cod from North Norway. The fecundity (F)-length (L) relations according to Kjesbu (1988) are:

$F = 1.25 \times 10^{-2} \times L^{4.27}$; for the Arco-Norwegian cod, compared to
$F = 1.38 \times 10^{-5} \times L^{6.01}$; for the Coastal cod. The relatively high fecundity of Coastal cod from North Norway corresponds well with the fecundity of West Norway Coastal cod (Botros, 1962).

Kjesbu *et al.* (1991) found experimentally that the number of eggs actually spawned compared to the number of oocytes produced in the gonad depends on the condition of the mother fish: While starved fish spawned only 20 per cent of the oocytes, well fed fish spawned 80 per cent. Second time spawners produce larger and better eggs than first time spawners (Kjesbu *et al.*, 1992).

Acknowledgement

Thanks are extended to Nigel Markham for correcting this section of the manuscript.

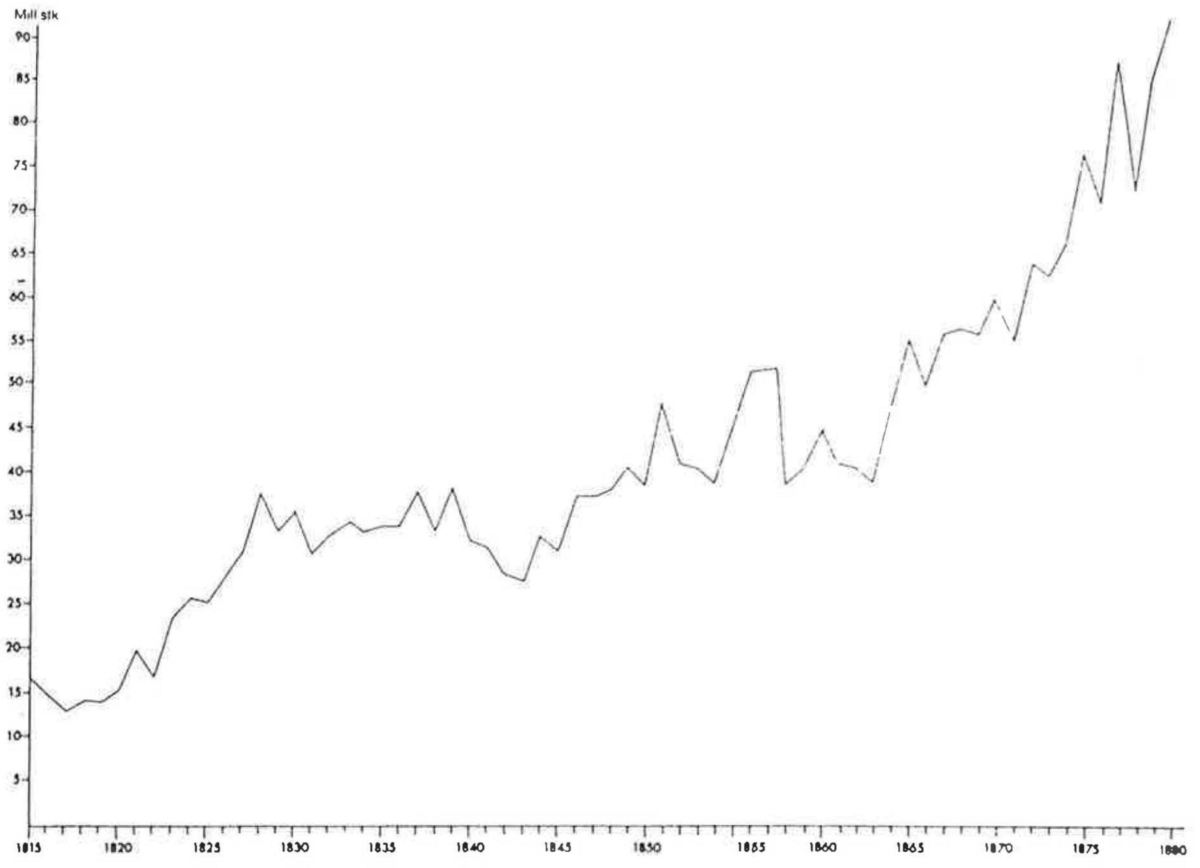


Figure 3.2.1. The export of cod in numbers x 10^6 from Norway during the period 1815-1880. (Solhaug, 1976).

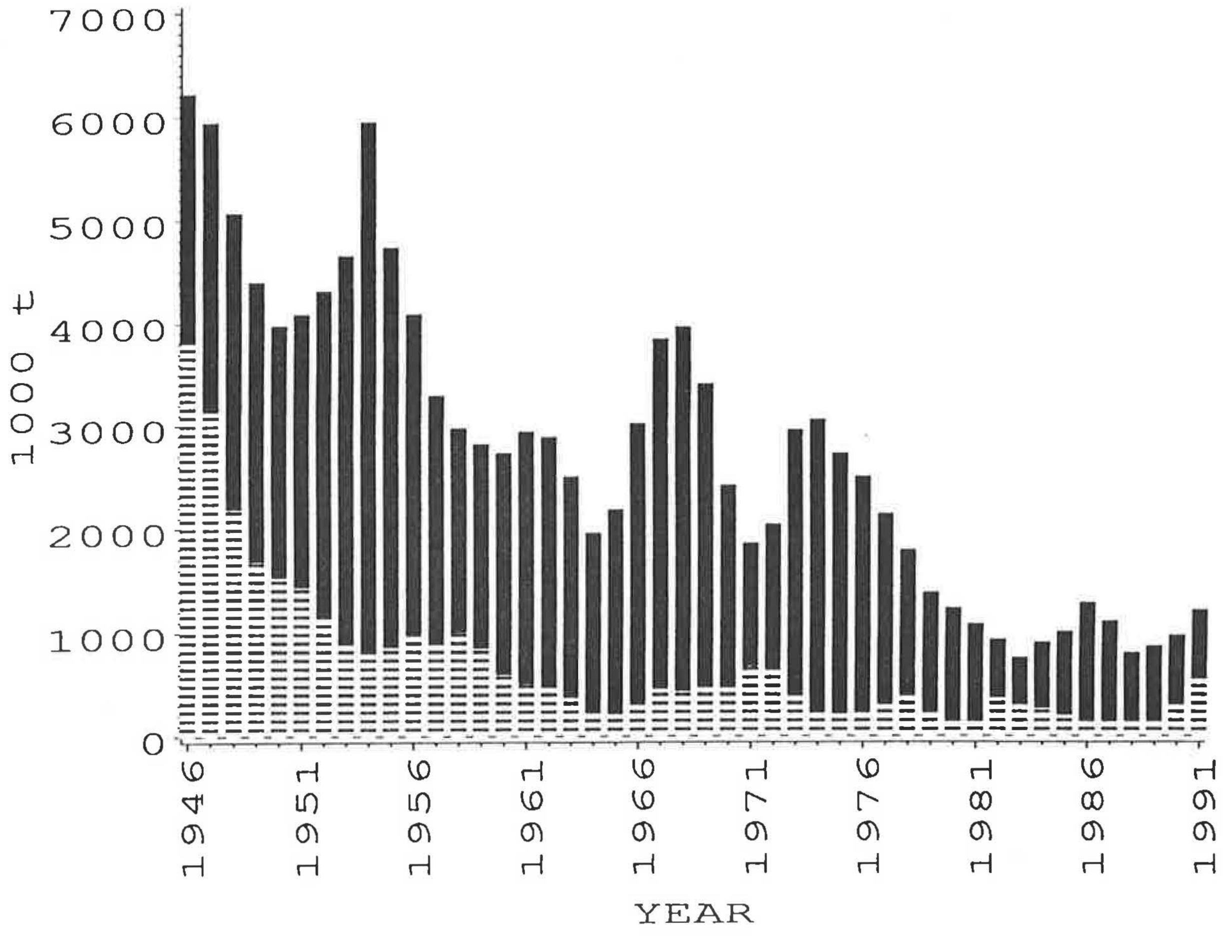


Figure 3.2.2. Total biomass of Arcto-Norwegian cod stock since 1946. Spawning stock is hatched.

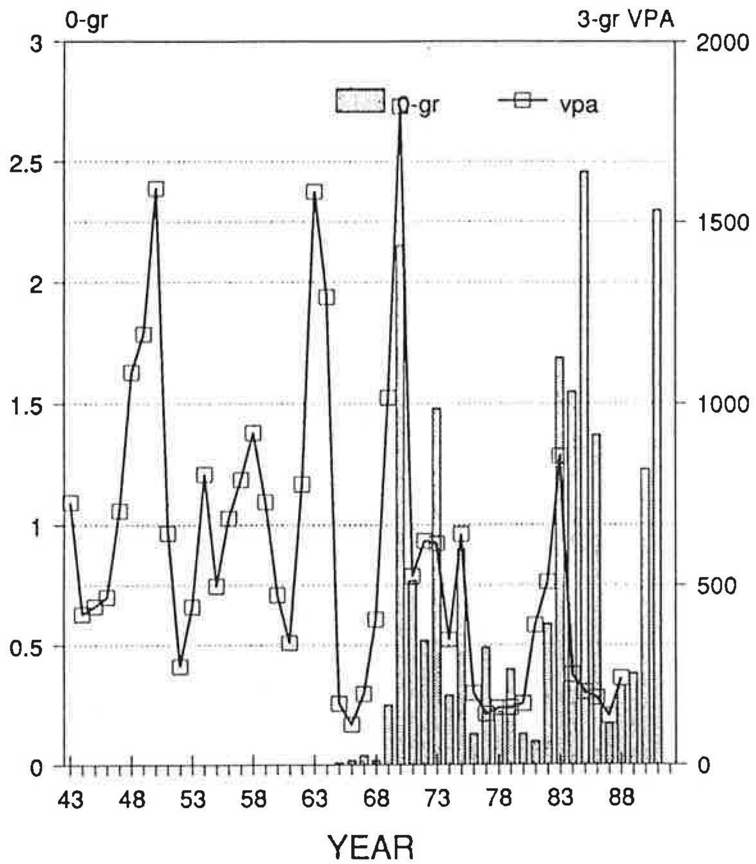


Figure 3.2.3. Year class strength from VPA (age 3 fish in millions) since 1946, and recruitment as estimated from the 0-group surveys since 1965.

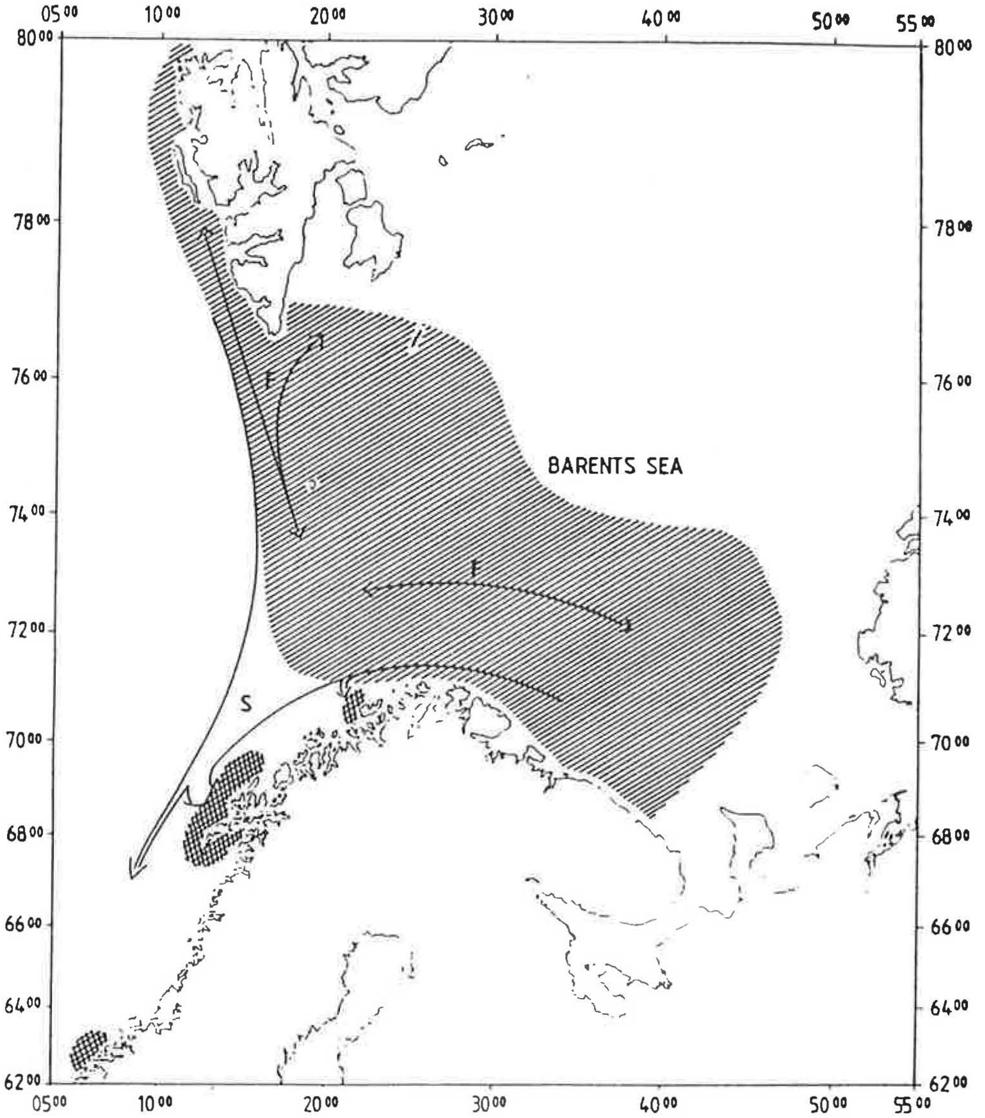


Figure 3.2.4. The general distribution of cod at the feeding areas in the Barents Sea - Svalbard area (hatched) and the main spawning areas (double hatched). Feeding (F) and spawning (S) migrations are indicated.

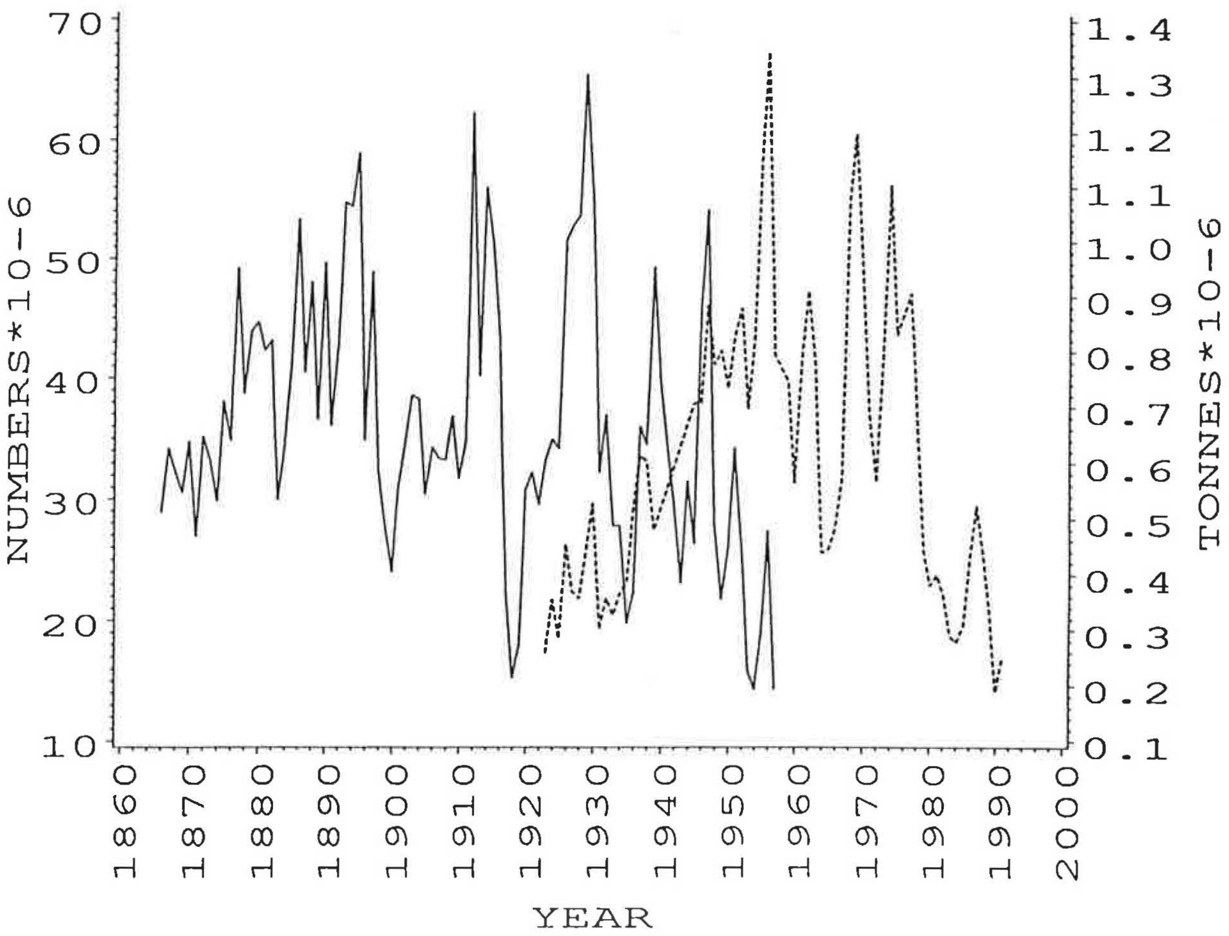


Figure 3.2.5. Catches of skrei (spawning cod) since 1866, continuous line shows catch in numbers and dotted line gives catch in tonnes (A). Catches of skrei in Lofoten (continuous line) and off Møre (dotted line) 1866-19 (B). Total catch since 1923 ©.

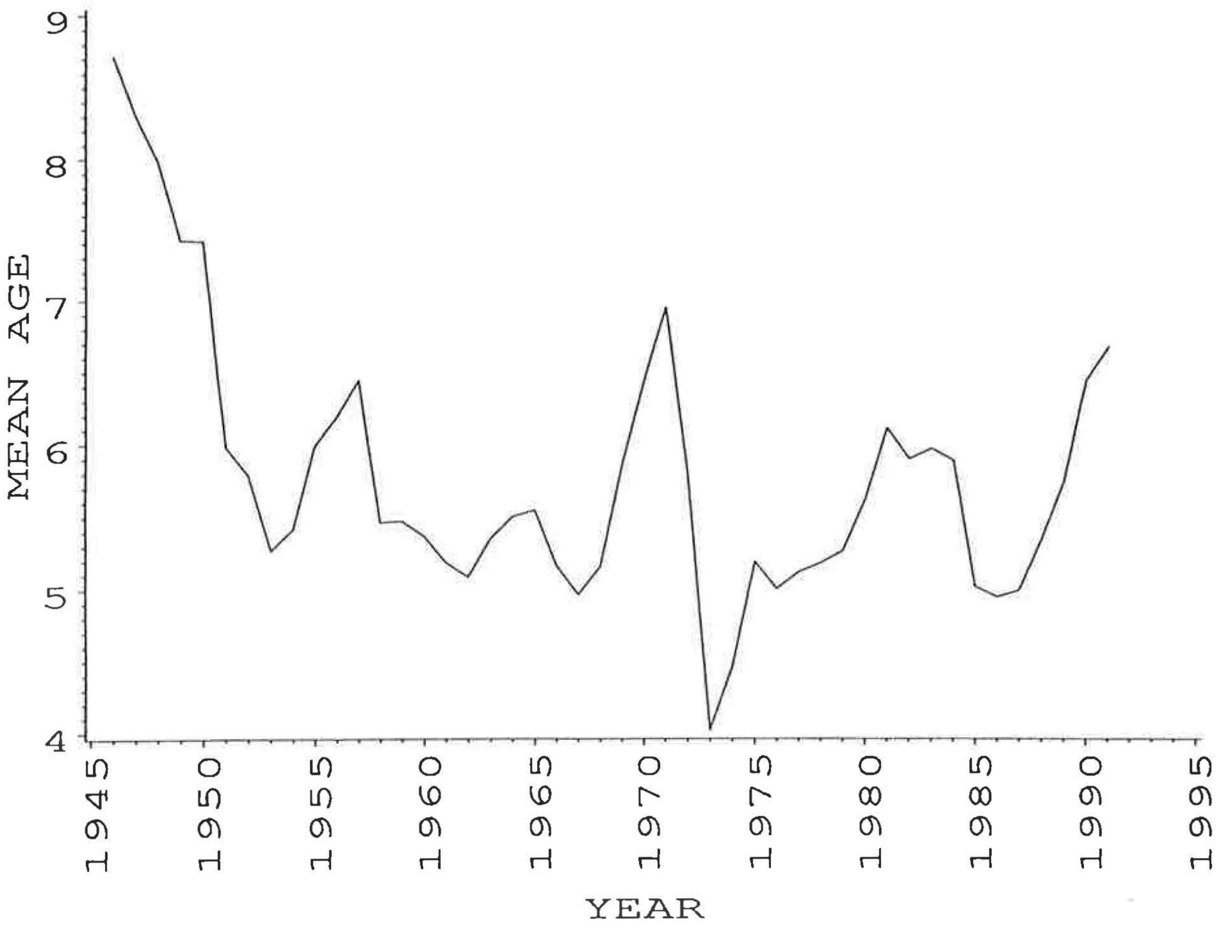


Figure 3.2.6. Mean age in catch.

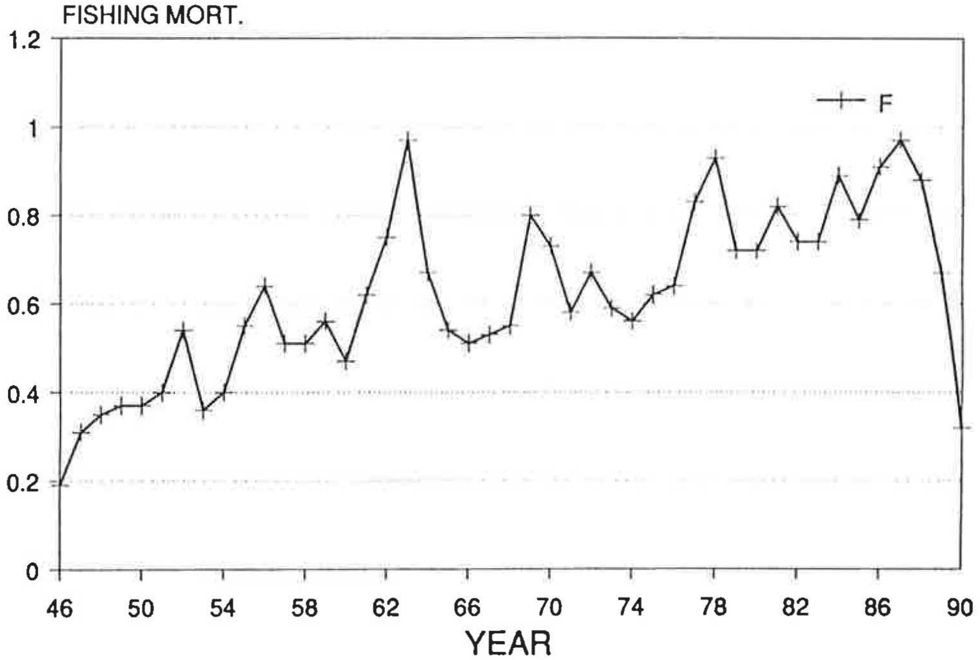


Figure 3.2.7. Fishing mortality (A), changes in fishing pattern given as average relative mortality, (F5-10=1, adopted from Jakobsen (1991) (B).

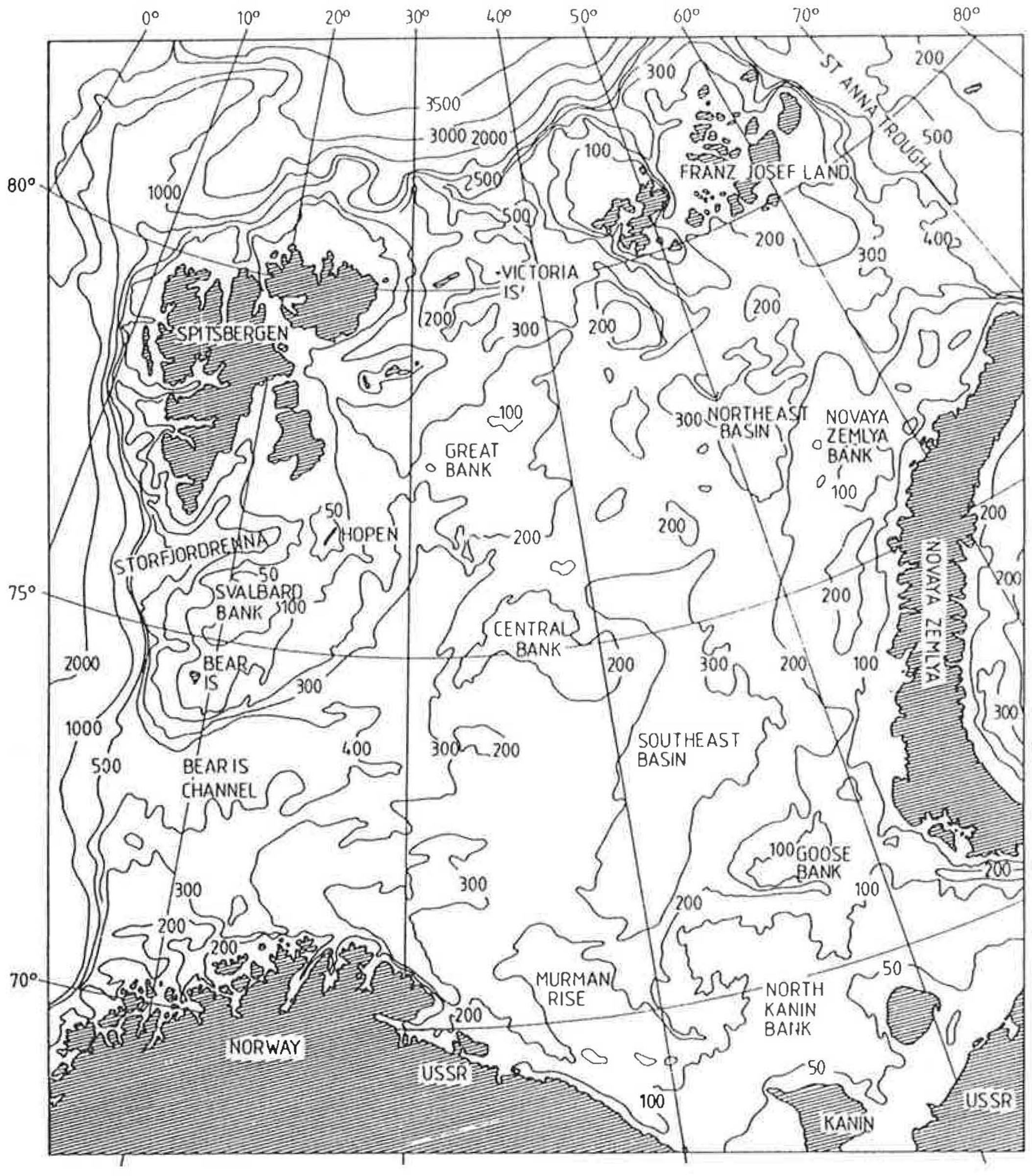


Figure 3.2.8. Bathymetry of the Barents Sea (Loeng, 1989).

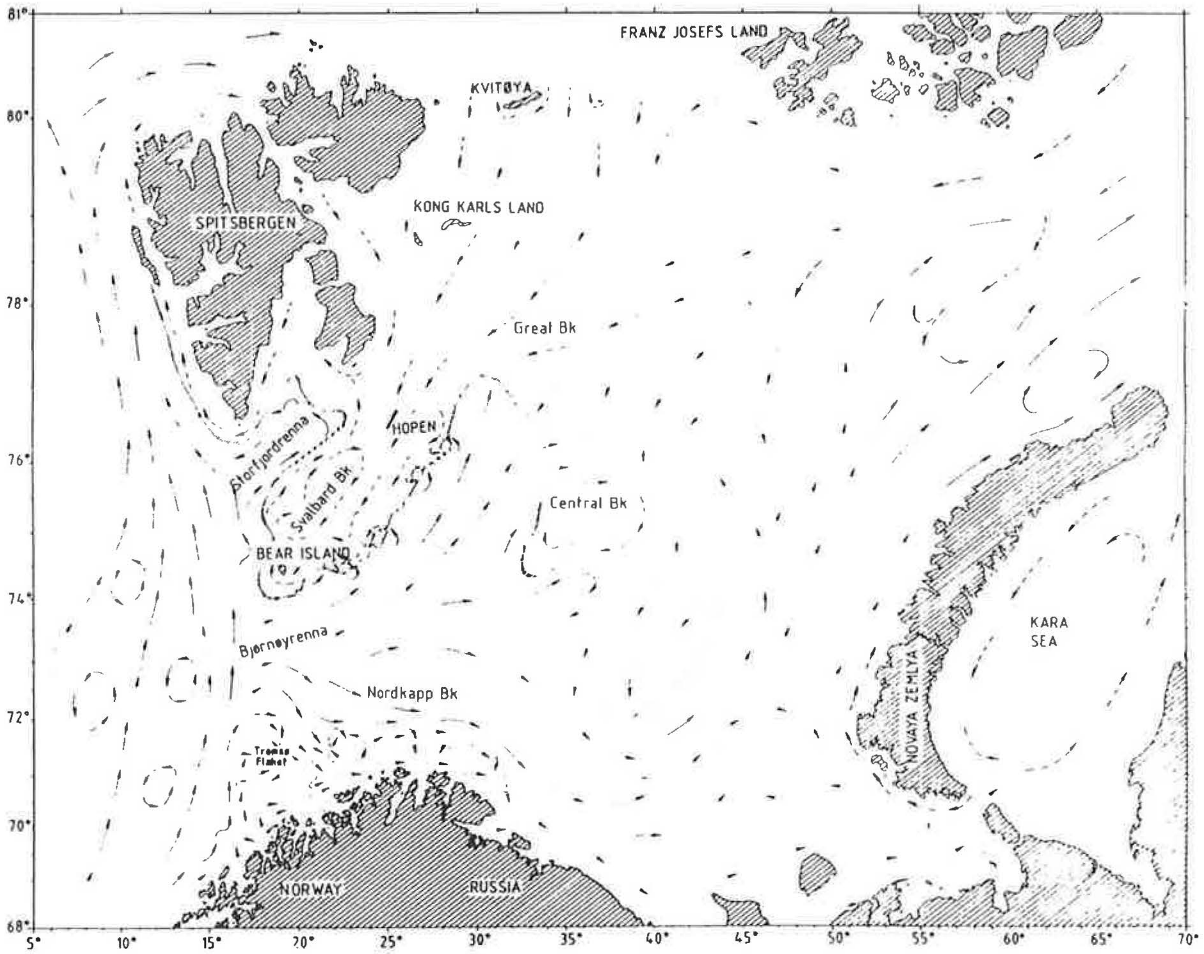


Figure 3.2.9. General circulation of the Barents Sea (Loeng, 1989).

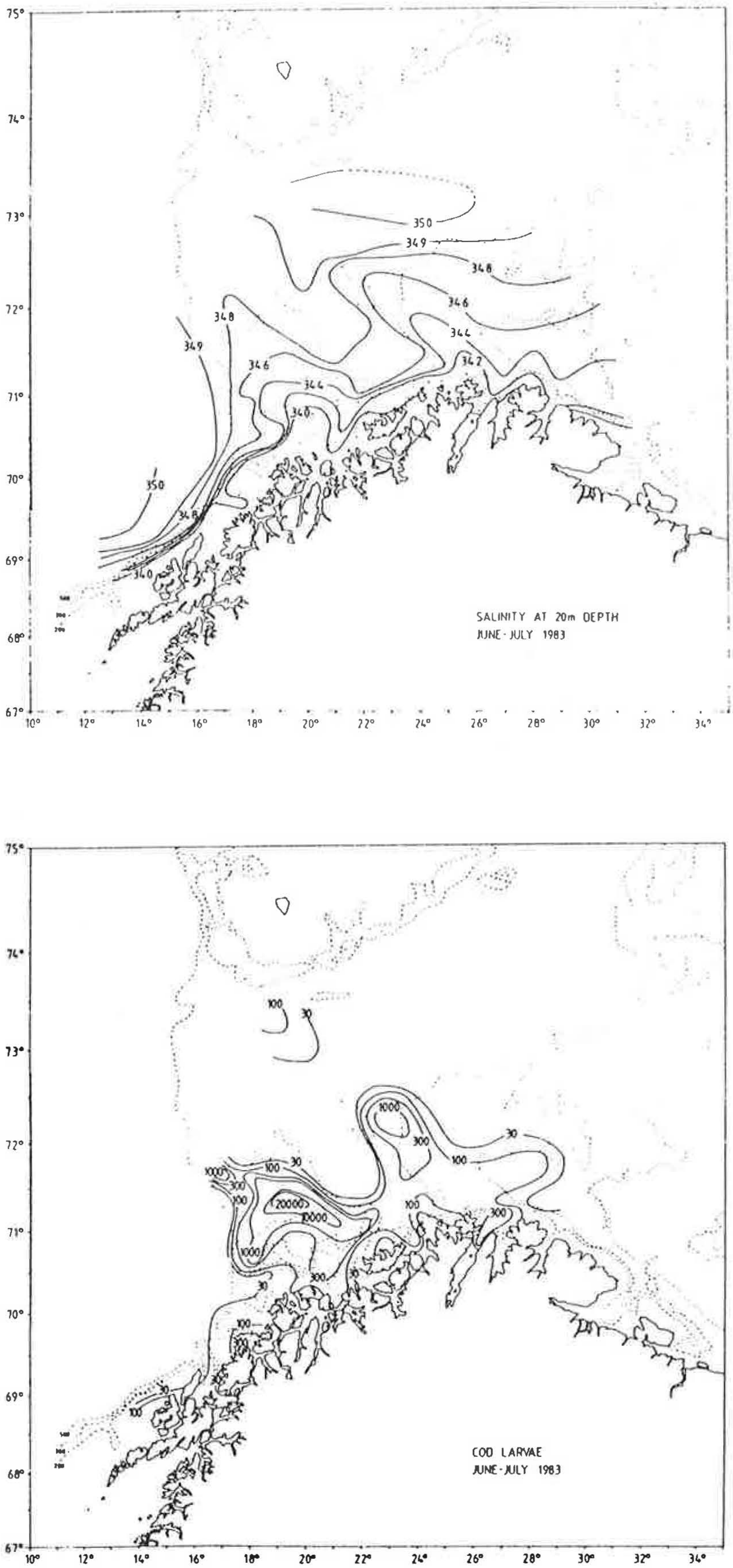


Figure 3.2.10. Distribution of salinity and concentration of early juveniles cod at the banks Tromsøflaket and Nordkappbanken in 1983. (Bjørke and Sundby, 1986).

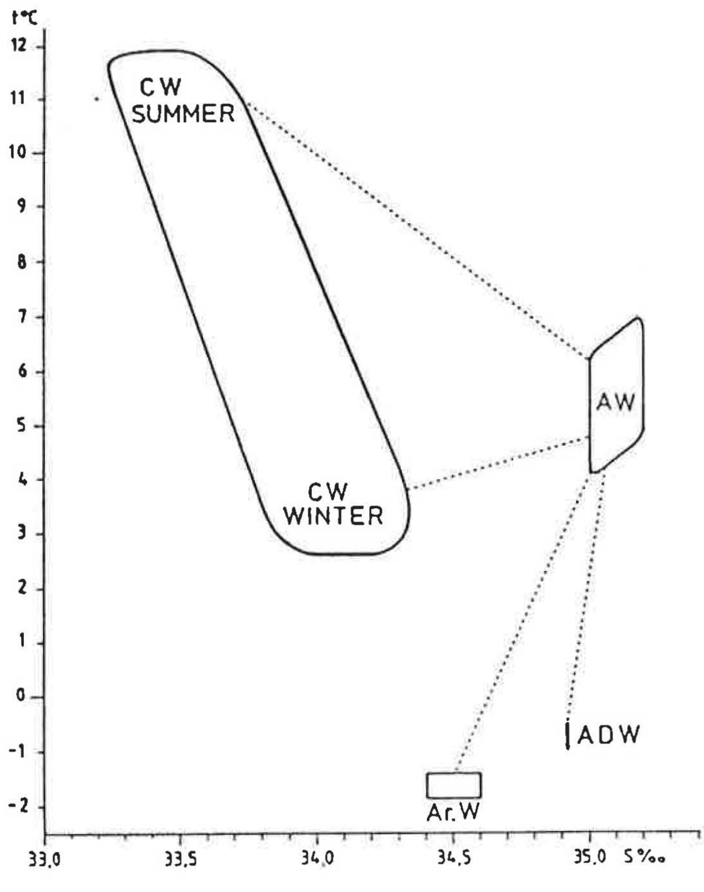


Figure 3.2.11. Temperature-salinity characteristics of the ambient water masses of the Arcto-Norwegian cod. (Loeng and Sundby, 1986).

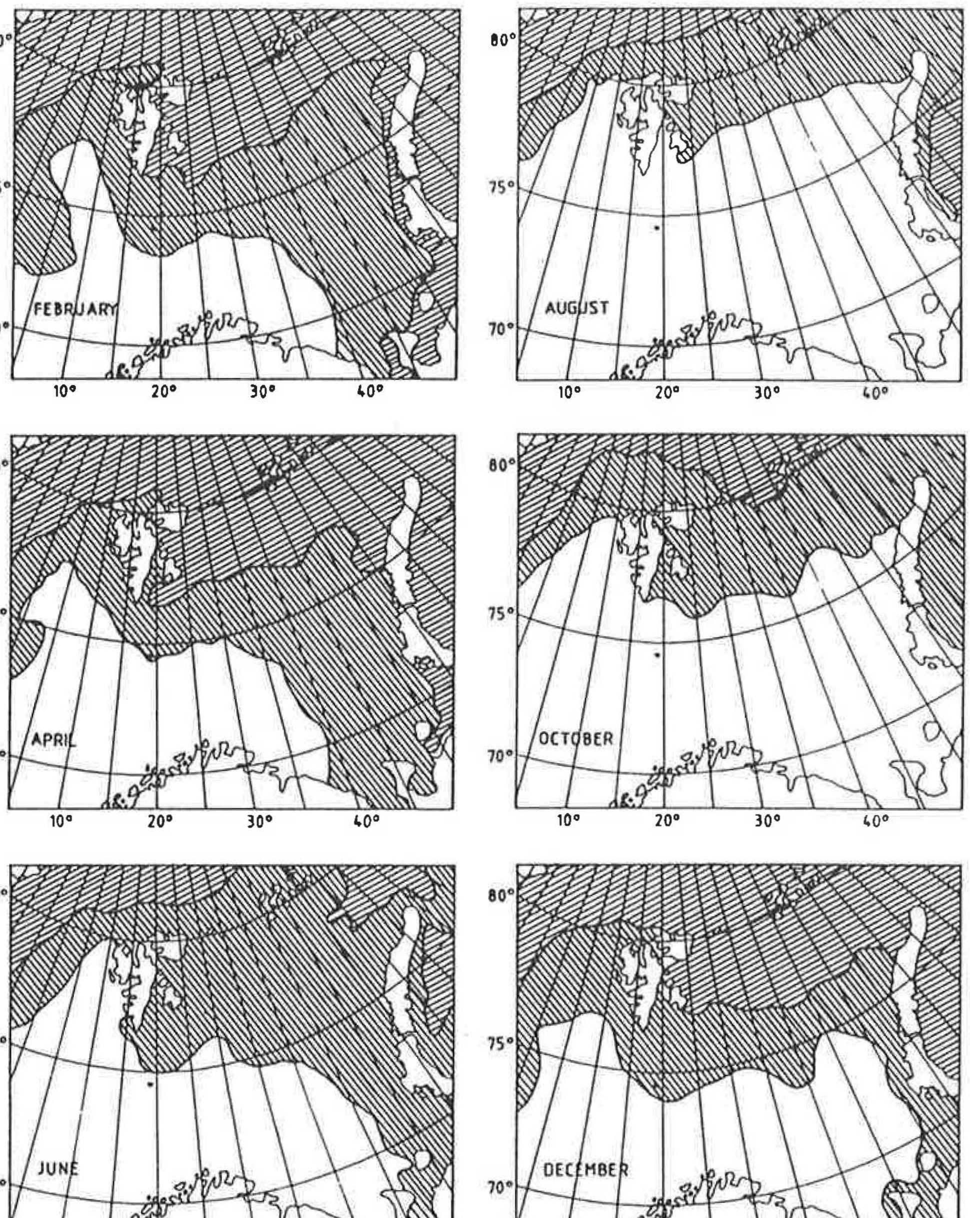


Figure 3.2.12. Southern limits of sea ice at the end of the months February, April, June, August, October and December for the period 1971-1980. (Vinje, 1983).

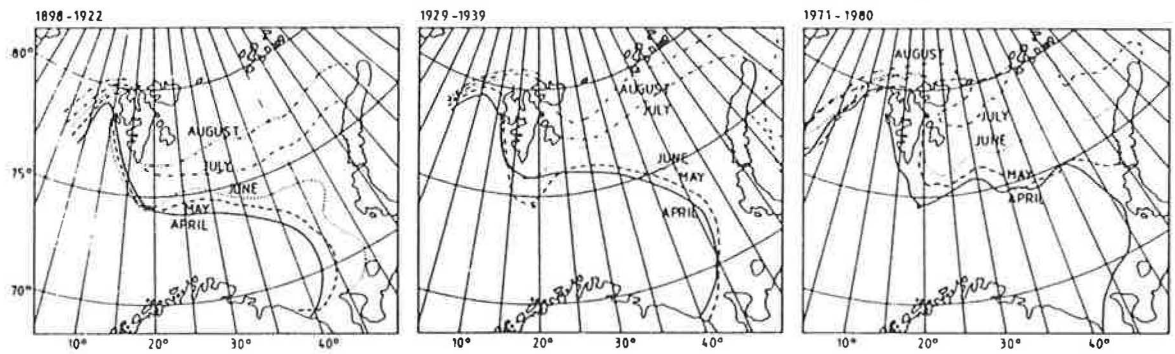


Figure 3.2.13. Mean position of the ice border at the end of the months April, May, June, July and August for three different periods. (After Loeng, 1989).

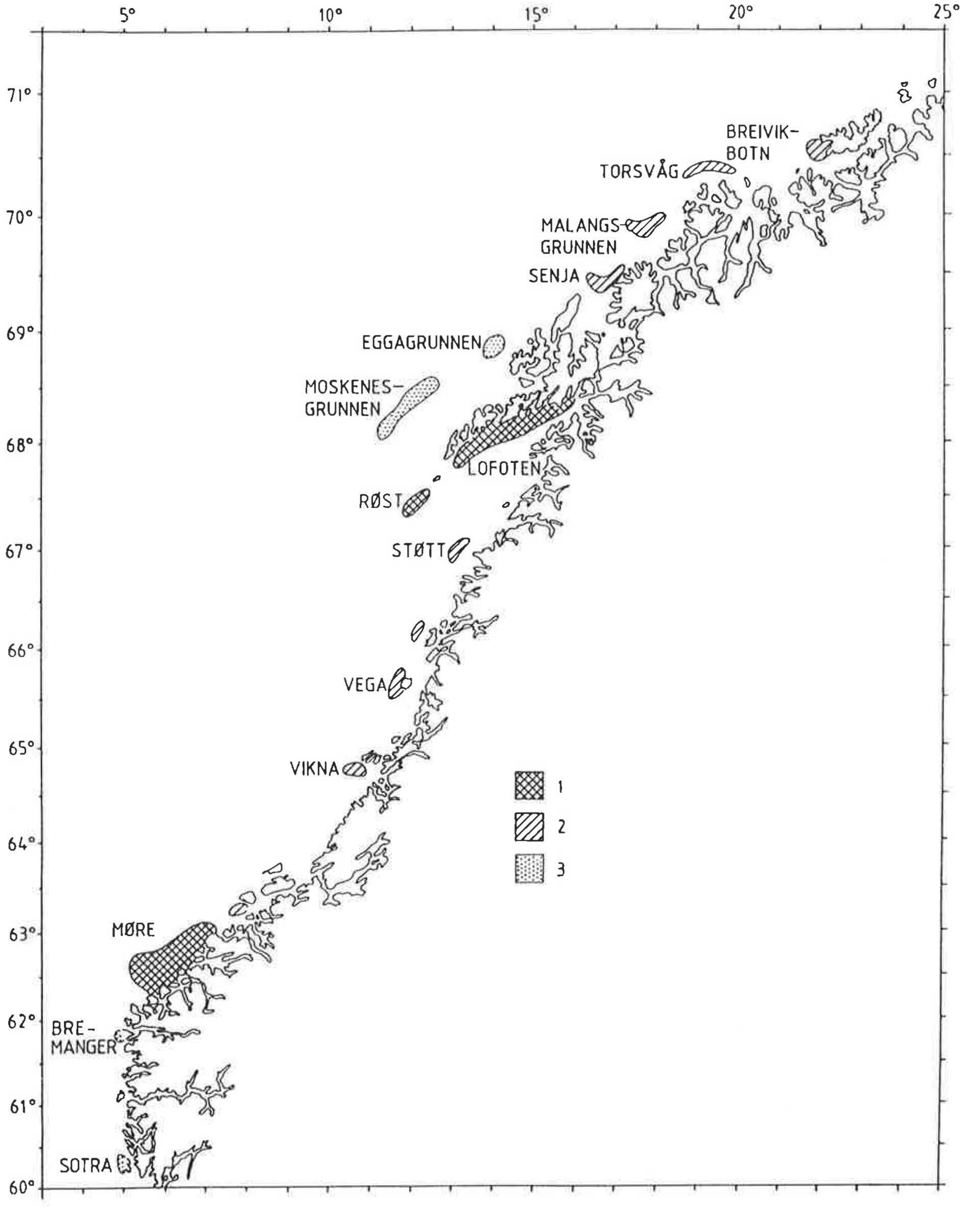


Figure 3.2.14. 1. major spawning areas, 2. minor spawning areas and 3. areas of occasional spawning of the Arcto-Norwegian cod.

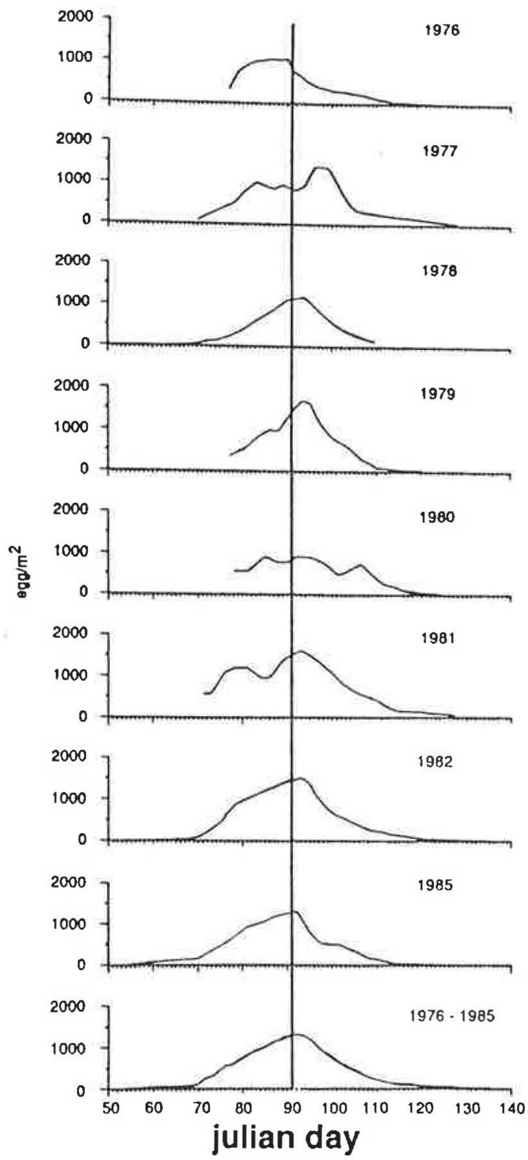


Figure 3.2.15. Spawning period of cod in Lofoten represented as the average concentration (numbers m2) of newly spawned eggs for the years 1976-1983. (Ellertsen *et al.*, 1989).

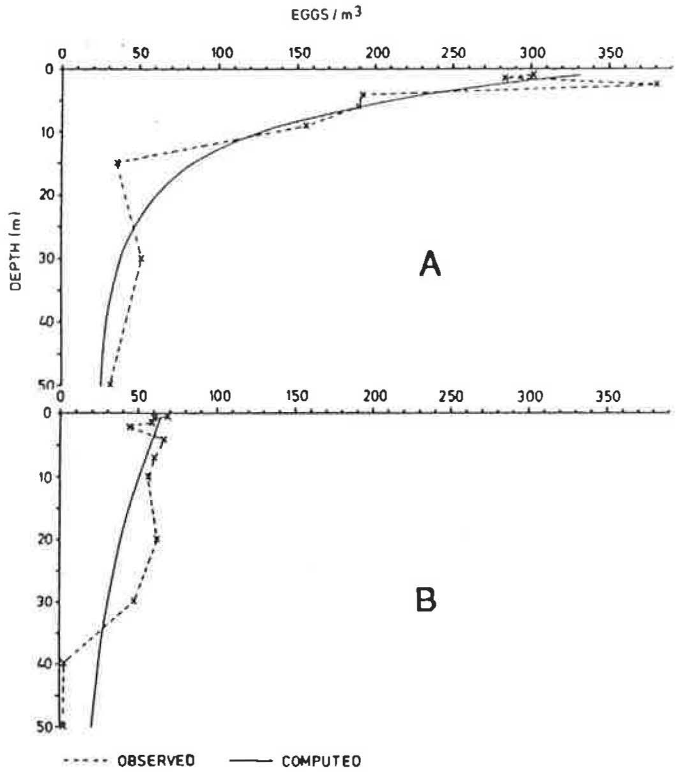


Figure 3.2.16. Observed and computed vertical distribution of cod eggs during A) low wind speed and B)Higher wind speed. (Sundby, 1983).

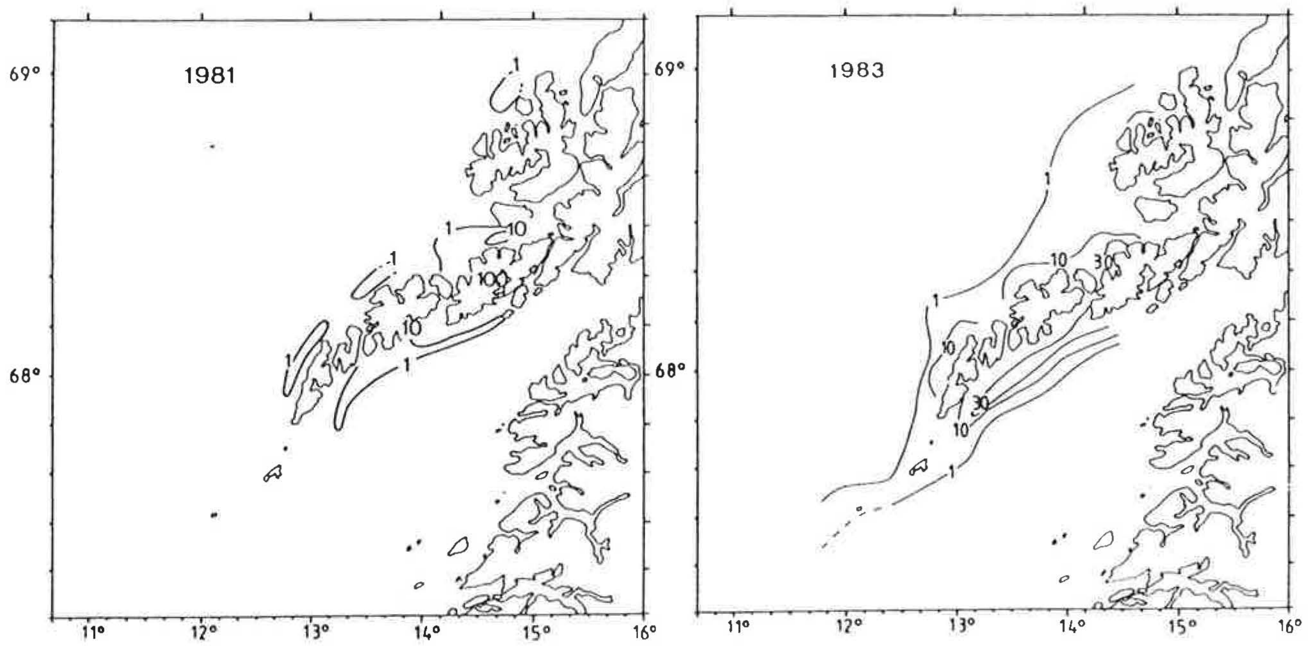


Figure 3.2.17. Distribution of cod larvae in early May (number m^2) in 1981 and 1983. (Ellertsen *et al.*, 1989).

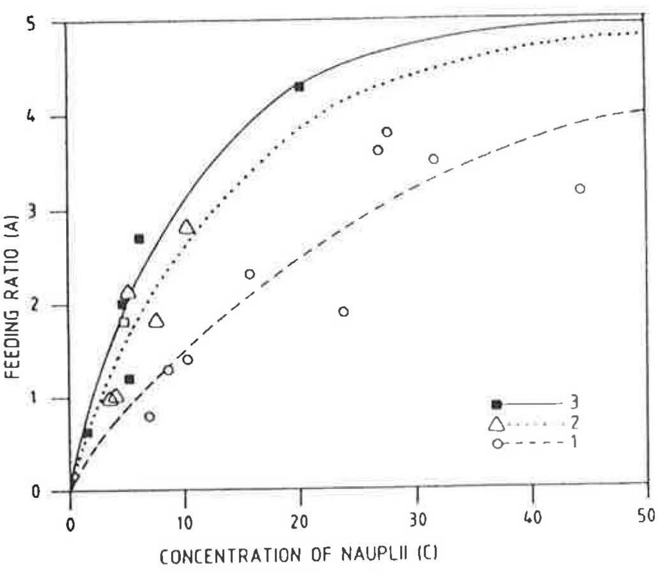


Figure 3.2.18. The feeding ratio (number of nauplii per larval gut) of about 7 days old larvae from Lofoten as a function of the nauplii concentration in the sea for 3 different wind speeds. 1) 2 ms^{-1}, 2) 4ms^{-1} and 3) 6ms^{-1}. (Sundby and Fossum, 1990).

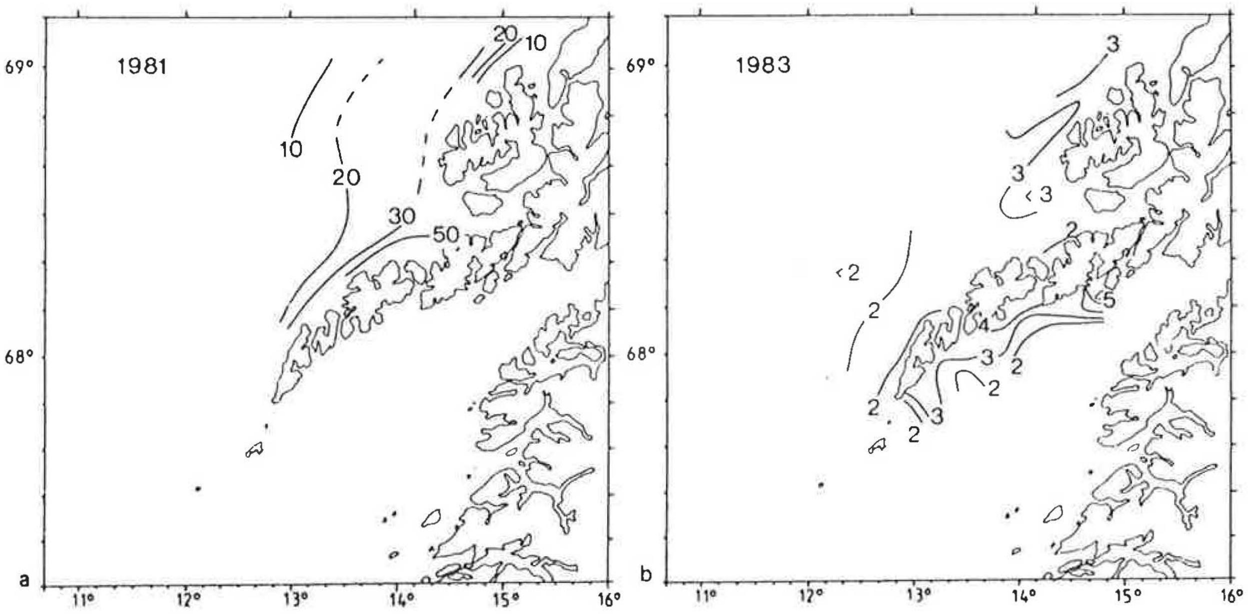


Figure 3.2.19. Horizontal distribution of copepod nauplii (number l^{-1}) in Lofoten 1981 and 1983. (Ellertsen *et al.*, 1989).

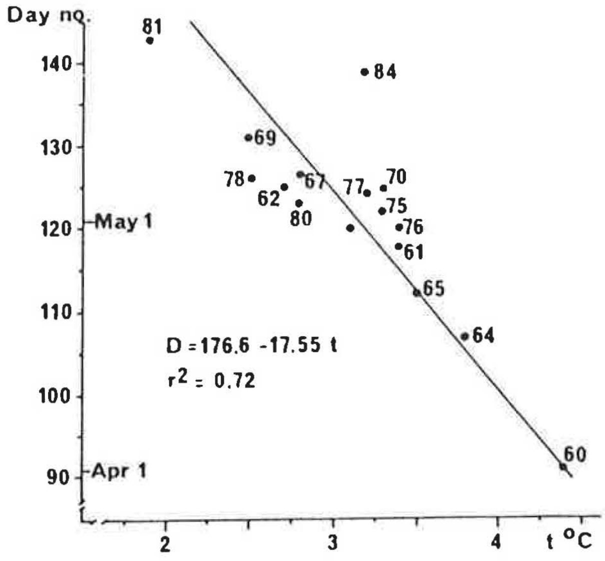


Figure 3.2 20. Time of maximum occurrence of *C.finmarchicus* copepodite stage I versus the average temperature of the upper layer in April. (Ellertsen *et al.*, 1989).

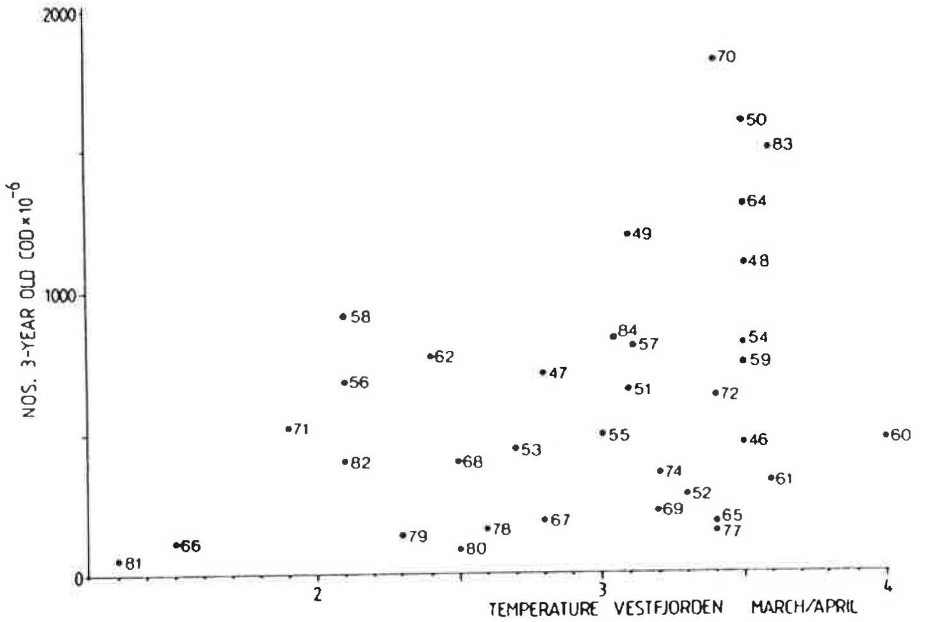


Figure 3.2.21. Relation between the year-class strength at 3 years and the mean temperature of the upper layer in March-April in Lofoten. (Ellertsen *et al.*, 1989).

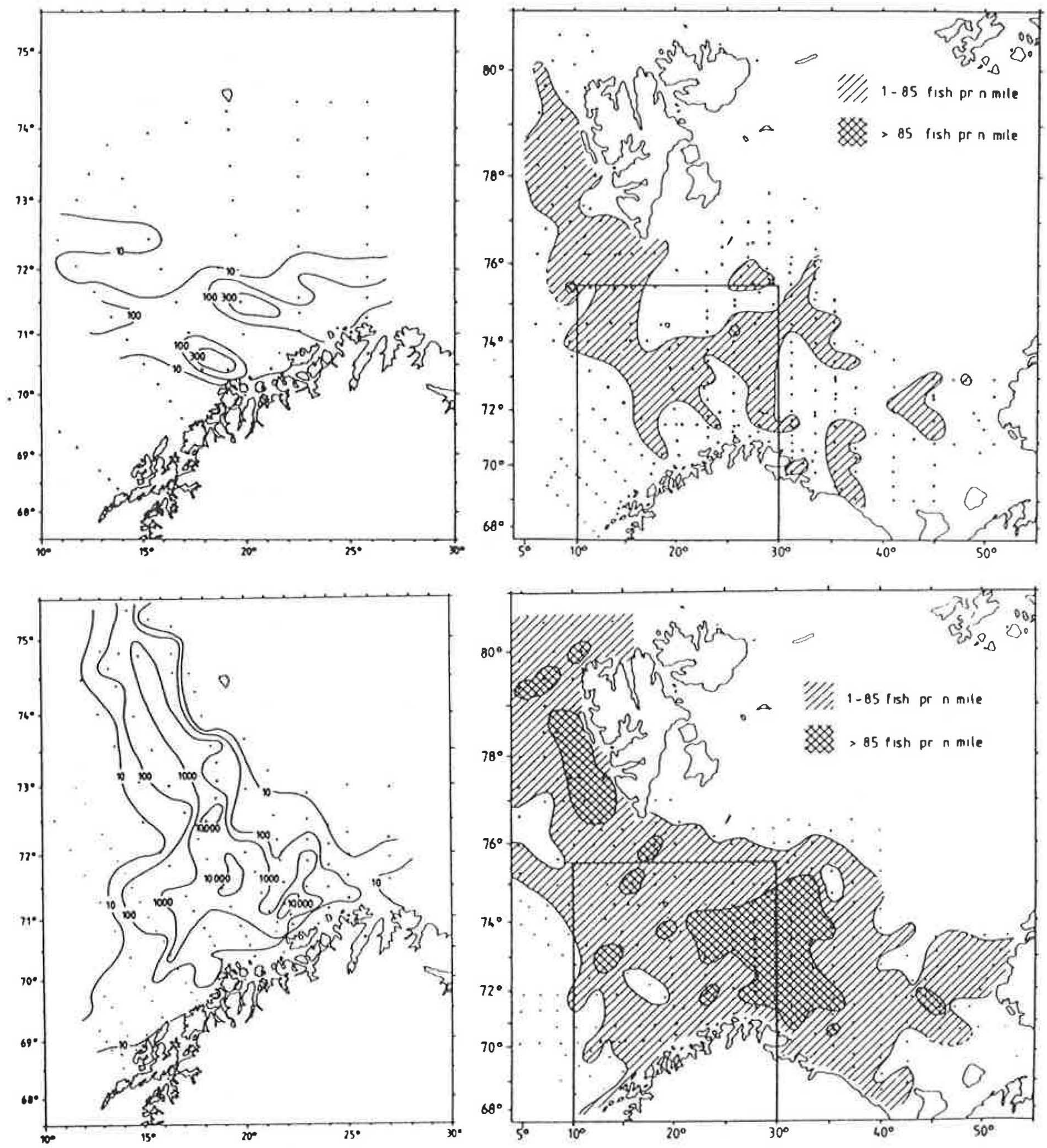


Figure 3.2.22. Distribution of early juveniles (2-3 months old), left, and 0-group (4-5 months old), right, for a typically weak year class, 1979 above, and for a typically strong year-class, 1985 below. (Sundby *et al.*, 1989).

3.3 N.E. ARCTIC COD

This summary was prepared according to the checklist format. It complements and overlaps with the life history information on Arcto-Norwegian cod given in section 3.2.

3.3.1 Species, stock and area of distribution:

Arcto-Norwegian cod (Northeast-Arctic cod). The feeding habitat of the juvenile and adult cod comprises the ice free parts of the Barents Sea and the narrow shelf region to the west of Svalbard, which is an area of about $0.6\text{-}0.7 \times 10^6$ km^2, which is about 40-50% of the entire area of the Barents Sea.

Evidence of stock discreteness, e.g. genetic distance, tagging

The genetic experts do not agree whether the genetic distance is significant or not. Analysis of blood proteins show different results from different regions, but it has been claimed that this may be due to environmental effects.

However, tagging experiments show that there is a relatively distinct western component confined to the West Spitsbergen region. This component mainly spawn in the offshore regions and at the southernmost spawning field (Møre in mid-Norway). Tagging and genetic studies do not indicate reproductive isolation.

There are definitely several components of coastal cod all along the coast of Norway. In mid and northern Norway they spawn partly at the same spawning grounds as the Arcto-Norwegian cod, but different properties of the eggs and larvae of coastal cod have not been observed. This implies that they are subjected to the same processes of transport and spreading as the Arcto-Norwegian cod. Nevertheless, trained fishermen and fisheries biologists can see differences in body shape of the adults of coastal cod and the Arcto-Norwegian.

For further information see Mork *et al.*, (1985), Godø, O. R. (1986) and Jakobsen, T. (1987).

Units for which assessment of spawning stock biomass and recruitment are available.

Assessment is available from the ICES Arctic Fisheries Working Group.

Time series of spawning stock biomass and recruitment data, e.g. from commercial catch and effort data, fishing surveys or VPA.

Spawning stock biomass and VPA for 3 years and older cod are available since 1946, and in a limited form since 1904 for the Arcto-Norwegian cod. Up to 1980 only data from the commercial fisheries were available for the VPA. 0-group indices are available since 1985 from a systematic pelagic trawl survey carried out annually in August. The indices have proved valuable as a first indication of year class strength (Randa, 1984). However, an abnormal situation in the mid-1980s with cannibalism and starvation of young cod disrupted the statistical relationship between 0-group index and recruits at age 3. Indices of early juveniles (2-3 months) are available for the period 1978-1991.

In the last decade estimates of recruitment and indices of abundance by age from Norwegian and USSR scientific surveys have become increasingly important both for the VPA and for the predictions (Hylen *et al.*, 1986, Anon. 1990c). The surveys are carried out from September to March using a combination of bottom trawl survey and acoustic survey techniques (Hylen *et al.*, op. cit.). In addition the spawning stock is acoustically surveyed in March-April. Year class strength at recruitment (age 3) varies by a factor of about 20. Additional complexity to the assessments and predictions is due the striking inter-annual variation in growth and age at maturation (Jørgensen, 1989).

3.3.2 Timing of spawning

Date of spawning and interannual variability or trend

Spawning starts in middle of February, lasts until end of April/early May. Date of 50% spawning during the period 1976-86 varies between 29 March and 5 April (Ellertsen *et al.*, 1989). Peak spawning has been delayed 10-14 days since 1930, mainly caused by the reduction in age (Pedersen, 1984) or the genetic composition (Kjesbu, pers. comm.) of the spawning population due to fisheries.

Time of day when spawning occurs

The spawning occurs mainly in the evening and during the night, demonstrated both in field (Solemdal, pers. comm.) and experimentally (Kjesbu, 1989).

Timing of spawning season in relation to planktonic production cycle

While cod spawning show small interannual variations with respect to time, the production of the main prey, nauplii of *Calanus finmarchicus* is very temperature dependent, and therefore more variable in time.

In years with mean temperatures during the egg and early larval stages, the peak of the production curve of copepod nauplii is some days ahead of the peak of first feeding cod larvae (Ellertsen *et al.*, 1989). By increasing the age of the spawning population a better overlap between peak of nauplii and first feeding larvae would occur. Interannual variations in temperature in the coastal water have great impact on the degree of overlap between the production cycles of nauplii and first feeding cod larvae. Taken into account the critical nauplii density of 5-10 per liter for high larval survival, it can be demonstrated that large year classes resulted from years with coastal water temperatures above average (Ellertsen *et al.*, op. cit.). However, not all such years have resulted in large year classes, showing that other factors also control recruitment.

Timing of spawning in relation to hydrographic events

Since the time of cod spawning is very constant between years, variations in hydrography do not influence time of spawning.

Timing of spawning in relation to other fish species which spawn in the same location

Haddock (*Melanogrammus aeglefinus*) has a peak spawning in the last days of April, i.e. 3-4 weeks later than the cod (Solemdal *et al.*, 1989). At some of the cod spawning grounds spawning of haddock occurs to a limited extent. The main spawning grounds of haddock are located more off-shore than the cod's.

In some years when the capelin spawning is westerly, there may be an overlap in the distribution of first feeding larvae at the spawning grounds to the north of Lofoten (the banks between Andøya and Sørøya).

3.3.3 Location of spawning

Geographic location and extent of spawning area and evidence of its variability from year to year

The spawning areas of Arcto-Norwegian cod are patchy, located in the Norwegian coastal current off mid and north Norway between Møre and Sørøya, along a 1200 km coastline. The spawning areas are the same sites every year, although the magnitude of the spawning at the sites may vary. Most of the eggs (2/3-3/4) are spawned along a limited part of the coastline, in Lofoten and Vesterålen, between 67°30'N and 68°30'N. The intensity of spawning at Møre and at the offshore grounds off Vesterålen is rather variable (for further information see Sundby and Bratland 1987).

Does spawning regularly begin in one part of the spawning area and then move to other parts?

Peak spawning in Lofoten occurs during the first days of April and show very little variation between years. The peak spawning is delayed by about 14 days at the northernmost spawning field, Sørøya (Sundby and Bratland, 1987), while the spawning at the southernmost ground (Møre) occurs at about the same time as in Lofoten (Godø and Sunnanå, 1984).

Can the location be described in relation to hydrographic features, e.g. "at the boundary between two water masses; in the mixed, upper layer"?

The spawning occurs mainly in the transition layer between the upper cool coastal water (2-4°C 33-34 S) and the warmer Atlantic water (6-8°C, 34.8-34.9 S) below. The preferred spawning temperature is 4-6°C. The spawning may occur pelagically in this layer, but most often near the bottom, where this layer intersects the bottom. The depth and position of the layer may vary both between years (due to variations in the fresh water content and convection processes in the coastal water during winter), and between days (due to upwellings, internal waves and other motions generated by atmospheric processes). This means that the positions of spawning within a certain spawning ground may vary due to motions of the transition layer.

Can location be described in relation to other species, including food organisms and predators?

Production of *Calanus* finmarchicus nauplii takes place at the same locations as the spawning of cod. Highest densities of food organisms are found to occur at the same time as the highest densities of first feeding cod larvae (Ellertsen *et al.*, 1987).

Can location be described in relation to water mass circulation? How might this affect transport of eggs and larvae?

About 70-80% of the spawning occurs in near-shore regions where the advection is relatively low. At the spawning grounds between Andøya and Sørøya the eggs and larvae are trapped in the clockwise circulation above the banks, and the advection out of this region is reduced (but not stopped!). In Lofoten (the Vest fjord) the eggs and larvae are not trapped by Taylor columns, but the advection out of the Vest Fjord is relatively low.

The remaining stock spawns at off-shore banks off Vesterålen and close to the shelf edge where there is a rapid transport of eggs and larvae.

(For further information see Furnes and Sundby (1981), Sundby and Bratland (1987), and Ellertsen *et al.*, (1989).

3.3.4 Biological details

Fecundity, i.e. number of eggs produced per female per year (as a function of age). Specific fecundity, i.e. number of eggs produced per unit weight.

Mean individual fecundity varies from 0.5 x 10^6 to 15 x 10^6 (age 4-15) (Kjesbu, 1988). Specific fecundity, i.e. number of eggs produced per unit weight.

Evidence of changes in fecundity with age

Fecundity is rather a function of body weight than age, r2 = 0.93 and 0.84, respectively. F = 6.84 x 10^3 x $A^{2.83}$ (A = age) (Kjesbu, *1988*).

Egg size and evidence of changes with age and with time during the spawning season. Specify gravity of eggs and larvae.

Egg diameter varies between 1.20 and 1.60 mm with an average of 1.40 mm (Solemdal and Sundby, 1981). A significant reduction in egg size during the spawning period was demonstrated in field material (Solemdal and Sundby, *op. cit.*). This is caused by the reduction in egg size from successive egg batches of an individual female (Kjesbu, 1989) and the probably delayed spawning of smaller first time spawners (Sund, 1983) spawning smaller eggs.

The specific gravity of the eggs ranges from 1.0235 g cm^{-3} to 1.026 g cm^{-3}. This implies that the surplus buoyancy of the eggs in their natural habitat ranges from 0.001 g cm^{-3} to 0.0035 g cm^{-3}.

Typical densities, i.e. number per m3 of eggs and larvae

During maximum spawning at the spawning sites in Lofoten up to 13 000 eggs m^{-2} have been recorded (Wiborg, 1950; Sundby, 1980). The eggs are confined to the upper 50 m of the sea with increasing concentrations towards the surface. The highest concentration of eggs per unit volume is found at the surface during calm weather conditions when the turbulent mixing is at a minimum (Sundby, 1983). Peak concentrations in normal years are about 300 eggs m^{-3} or 7 000 eggs m^{-2}.

The larvae are confined to the upper 40 m of the sea. The highest concentrations are normally found between 10 and 20 m depth. The larvae seem to stay out of the upper 5 m. Maximum concentrations recorded are about 2 700 larvae m-2, and about 600 larvae m^{-3} (1992). More typical concentrations are about 100 larvae m^{-2} or 10 m^{-3}.

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larvae

At the prevailing temperature in the Lofoten the incubation time is about 3 weeks. The larvae hatch at a length of about 4 mm, depending on temperature (Solemdal, 1970). The larvae grow to about 5 mm on their own yolk reserves (Ellertsen *et al.*, 1980). Incubation rates are given in Strømme (1977).

There is a positive correlation between egg size and larval length at hatching (Solemdal, 1970; Knutsen and Tilseth, 1985). A special staging system for early cod larvae based on the size of the yolk sac is developed by Fossum (1986).

Condition factor and status

Larval condition has been measured as feeding incidence, feeding ratio or dry weight in relation to length (Ellertsen *et al.*, 1987). The dry weight/length relation was significantly higher in the strong year class of 1983 compared to other years.

Egg and larval mortality rates

Egg mortality has been estimated for the years 1983 and 1984, about 90%. Mortality from hatching (in April) to juveniles (June-July) is 10.9% per day (Sundby *et al.*, 1989). About 2-3% of the larvae that hatched survived day 20 (Sundby *et al.*, *op. cit.*).

Time of first feeding of larvae and food at first feeding

At 5°C the cod larvae starts feeding on day 5 post-hatching. The prey organisms consist almost exclusively of the nauplii of *Calanus finmarchicus*.

Evidence of predation during the egg and larval stages

In some instances medusae, especially ephyra of *Aurelia aurita*, have been observed with cod eggs in their stomachs, in a few cases also with cod larvae (Melle and Ellertsen, 1984; Melle, 1985). Herring are found with large numbers of cod eggs in their gut (Melle, *op. cit.*).

3.3.5 Recruitment

Are there several spawning sites which contribute to the same stock unit?

The spawning both in the Vestfjord, off Lofoten, and further north to the Tromsøflaket area contribute to the same stock unit.

Earliest time in the life history when year class can be predicted

Evidence of year class variability on the 0-group level (age 5 months) is given by Hylen (1984). Data on 3-year old cod from the VPA was correlated to the temperature at the spawning sites during egg and early larval development (Ellertsen *et al.*, 1988) indicating that temperature alone in extreme cases can be used to predict the year class strength. The year class strength is mainly determined before the post-larval (juvenile) state, and, therefore, reliable assessments of juveniles (2-3 months) might have a prognostic value.

Hypotheses which have been put forward to account for year-to-year variability in year class strength

Investigations have been carried out on the following recruitment mechanisms hypotheses:

1. Match/mismatch (Ellertsen *et al.*, 1987, 1989)

2. Microturbulence (Sundby and Fossum, 1990)

3. Predation (Oiestad, 1985; Melle, 1985)

4. Condition and age of spawning cod female (Kjesbu, 1988; Kjesbu *et al.*, 1991, 1992).

Evidence of long-term trends in recruitment

There is a trend towards delayed spawning since 1930, due to the reduced age of the spawning stock and/or a genetic change in the spawning population (see above).

3.4 THE ICELANDIC COD STOCK

3.4.1 Species, stock and area of distribution

Evidence of stock discreteness, e.g. genetic distance, tagging

Tagging experiments have demonstrated that the Icelandic cod stock is virtually discrete from the other North Atlantic stocks. Both mature fish tagged on the spawning grounds and immature fish tagged on the nursery grounds have only been caught in the Icelandic shelf area during later years. During some years, however, there have been migrations of cod from Greenland to the spawning grounds at Iceland, but these are mainly believed to be made up of individuals which originally drifted as larvae to Greenland from the Icelandic spawning grounds (Jamieson and Jónsson, 1982).

Units for which assessment of spawning stock biomass and recruitment area available

For stock assessment and recruitment studies the Icelandic cod stock is considered as one unit. Information on stock size and recruitment is available from ca. 1950 (VPA estimates) and these have been reported in ICES assessment working group papers (e.g. Anon., 1987b) and in Icelandic stock status reports (e.g. Anon., 1989a).

Time series of spawning stock biomass and recruitment data, e.g. from commercial catch and effort data, fishing surveys or VPA

For the past 5 years indices of biomass and recruitment have also been obtained during stratified groundfish surveys in Icelandic waters (Pálsson *et al.*, 1987).

3.4.2 Timing of spawning

Date of spawning and interannual variability or trend

Maximum spawning usually occurs from the fourth week of March to the first week of May on the main spawning grounds off the south-west coast. The beginning of the season may be two weeks earlier or later than the long-term mean. There are some indications of more prolonged spawning seasons during years of low environmental temperatures (Jónsson, 1982).

Time of day when spawning occurs

No information available.

Timing of spawning season in relation to planktonic production cycle and
Timing of spawning season in relation to hydrographic events

Spawning appears closely related to the onset of the phytoplankton spring bloom and the spawning of the zooplankton in the areas. Further, in the coastal area the onset of the spring phytoplankton bloom occurs earlier than in the waters farther offshore, and appears mainly to depend on stratification due to the outflow of fresh water from several large rivers dissipating there (Fridgeirsson *et al.*, 1979; Thordadottir, 1985; Ólafsson, 1985). The extension of the low salinity water, from the coast and on to the shelf, is highly variable and depends very much on the direction and strength of winds.

Timing of spawning season in relation to other fish species which spawn in the same location

Other commercially important fish stocks (haddock, saithe, capelin, herring) also spawn off the south-west coast of Iceland. The information on these species is rather limited but one can state that during the period from February to May the spawning sequence is the following: saithe, capelin, cod and haddock. Later in the summer Icelandic summer spawning herring also spawn on these same or nearby grounds.

3.4.3 Location of spawning

Geographic location and extent of spawning area and evidence of its variability from year to year. Does spawning regularly begin in one part of the spawning area and move to other parts?

The main spawning grounds are close to the shore on Selvogsbanki and in the nearshore area off Reykjanes on the south-west coast. However, the spawning area extends along most of the south and south-west coasts of Iceland. The extension and exact location of the main spawning area appears to vary somewhat between years but detailed information is limited (Fridgeirsson, 1982; Jónsson, 1982). Limited spawning occurs off the west coast of Iceland and there it appears generally to begin somewhat later than on the main grounds (Figure 3.4.1).

In some years some spawning may also take place in the fjords along the north coast of Iceland. This spawning occurs in late May and early June depending on the water temperature. During the years 1977, 1979 and 1980 eggs were found in the coastal water north of

Iceland made up approximately 3-4% of the eggs collected during larval studies in those years (Jónsson, 1982).

Can location be described in relation to hydrographic features, e.g. "at the boundary between two water masses"; "in the upper, mixed layer"?

The main spawning areas are located close to the shore within or at the boundary of the low salinity Coastal Current and the more saline Atlantic Water farther ashore (Fridgeirsson, 1983). Detailed studies on the exact location of spawning in relation to hydrographic features are lacking (Figure 3.4.2).

Can location be described in relation to other species, including food organisms and predators?

Limited information is available on the location of the main spawning grounds with respect to other species and possible predators. However, it can be stated that in the coastal area where the spawning is usually most intensive the largest densities of zooplankton are usually also encountered (Astthorsson and Gislason, unpublished data).

Can location be described in relation to water mass circulation, e.g. "in the north flowing coastal current"; "in the Taylor column circulation over a bank"? How might this affect transport of eggs and larvae?

From the main spawning grounds off the south-west coast of Iceland (within the Coastal Current or at the boundary between the Atlantic Water and the Coastal Current) the majority of the eggs and larvae are transported clockwise around the island to nursery grounds off the north-west, north and north-east coasts of Iceland. Southerly winds will tend to favour this transport and confine the drifting larvae close to the west coast and within the shelf area. On the other hand, northerly winds will distribute the low salinity water on to the western shelf (Stefánsson and Gudmundsson, 1978) and probably lead to more extensive distribution of larvae at lower densities.

3.4.4 Biological details

Fecundity, i.e. number of eggs produced per female per year (as a function of age). Specific fecundity, i.e. number of eggs produced per unit weight

Fecundity ~ 1-10 x 10^6 eggs per female. Specific ~ 3.5-4.5 x 10^5 per kg cod wet weight. See also Figure 3.4.3 based on Schopka (1971).

Evidence of changes in fecundity with time

No information available.

Percentage mature at age (including the population not on the spawning grounds). Length at 50% maturity

The percentage of cod mature at a certain age in Icelandic waters depends largely upon the area where the fish has been living. Thus, cod living all its life in the Atlantic water off the south-west coast of Iceland grows faster and matures at a younger age than those which inhabit the subarctic waters off the north coast. The figures in the table below show the percentage of cod mature off the north and south coasts as observed during a groundfish survey in 1989 (Anon., 1989a).

Age	South	North
2	0	0
3	(28)	0
4	15	2
5	47	9
6	62	29
7	87	46
8	87	47
9	100	51
10	100	100

For cod living off the north coasts of Iceland, the length at 50% maturity is ca. 71-73 cm or 8 years of age. For cod living off the south coast of Iceland, comparable figures are ca. 65-73 cm (an age of 5-6 years) (Steinarsson, personal communication).

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

The eggs of Icelandic cod, when measured 2-3 days after fertilisation, range from 1.3-1.5 mm (Fridgeirsson, 1978). No information is available on changes with age, time during spawning season or on the specific gravity of eggs and larvae.

Typical densities, i.e. number per m^3 of eggs and larvae

Numbers of 100-500 (newly spawned) and 10-50 (at hatching) eggs per m^2 in the uppermost 50 m are commonly observed on main spawning grounds. Numbers of larvae are highly variable both between stations and in relation to depth; 20-200 larvae per 100 m^3 are commonly observed in the uppermost 40 m of the water column. Much larger densities have been observed at certain depth intervals (Fridgeirsson, 1984; Jónsson and Fridgeirsson, 1986).

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

At a temperaturenof 7.2°C the embryos start hatching when 9 days of age but the majority will hatch when 9.5 to 10 days old. Information is not available on the size of larvae at hatching but at the time of first active eating (4 days after hatching) they are 5.5-5.8 mm. Six days after hatching the yolk sac is almost finished and then the larvae are 5.9 mm (Fridgeirsson, 1978). No information is available on the size of yolk sac in relation to size of larvae.

Larval development rate as a function of temperature

No information available.

Condition factor and nutritional status

No information available.

Egg and larval mortality rates

No information available.

Time of first feeding of larvae and food at first feeding

First feeding of larvae takes place ~ 6 days after hatching. The smallest larvae eat mainly copepod eggs and copepod nauplii (Bainbridge and McKay, 1968; Fridgeirsson, 1984, Jónsson and Fridgeirsson, 1986; Thorisson, 1989).

Food of larvae during development

The following summary is based on a study made by Pálsson (1974, 1976, 1980) and Thorisson (1989) during the summere of 1985. For further details consult that paper. In May copepod eggs and nauplii are the most important food for the smallest larvae while larger larvae (8-10 mm) eat euphausiids, nauplii and small copepods (*Acartia, Temora*) and the copepod stages of *C. finmarchicus*. In June the diet of 10-24 mm larvae is dominated by *C. finmarchicus* and other copepods. In July larvae between 10-20 mm were mainly eating copepods while larger larvae (30-40 mm) also had euphausiids and capelin larvae as components of the diet. In August the pelagic juvenile cod (ca. 40-80 mm) feed mainly on euphausiids, capelin larvae and *C. finmarchicus*.

Evidence of predation during the egg and larval stage?

No information available.

3.4.5 Recruitment

Are there several spawning sites which contribute to the same stock unit

No. The majority of the stock spawns off the south and south-west coasts of Iceland (Jónsson, 1982). Limited information is available about the importance or relative contribution of the spawning occurring in areas outside the south or south-west coasts. This contribution is, however, always small and, for example, in 1979, when it was considered to be relatively high, it was estimated to be about 10% (Schopka, personal communication).

Earliest time in the life history when year class strength can be predicted

An estimate of year class strength can be obtained at the age of two years from data collected in a stratified groundfish survey incorporating about 600 trawling stations and which cover the whole shelf area all around Iceland (Pálsson *et al.*, 1987; Steinarsson, personal information). Information from 0-group surveys in August has also been used to get an initial idea of year class strength. Helgason and Sveinbjörnsson (1987) have obtained significant relationships between VPA estimates of cod at three years of age and 0-group abundance, condition and environmental conditions. Further, high abundance and extensive geographical distribution are alone considered to be important indications for a possible strong year class; however, actual size of a year class on the basis of the 0-group surveys alone cannot be forecast.

Hypotheses which have been put forward to account for year-to-year variability in the year class

No detailed theories have been put forward but some initial attempts have been made to relate 0-group cod abundance and environmental parameters (Malmberg, 1988) and to relate 3 year recruitment to 0-group indices, condition and environment (temperature, salinity) (Helgason and Sveinbjörnsson, 1987).

Evidence of long term trends in recruitment

This has not been studied in detail but, since 1970, 3 year recruitment has ranged from 139-429 x 10^6 fish with no apparent long-term trend. The average recruitment is ~ 200-210 x 10^6. See Figure 3.4.4, based on data from Anon. (1989a)

Evidence that variability in recruitment is linked to variability of other species in the same area; the same spaces in other areas or other species in other areas?

Pálsson (1984) has reported covariance in the recruitment of cod and haddock in Icelandic waters, otherwise this issue has not been looked at in detail.

Evidence of inter- or intraspecific competition

No information available.

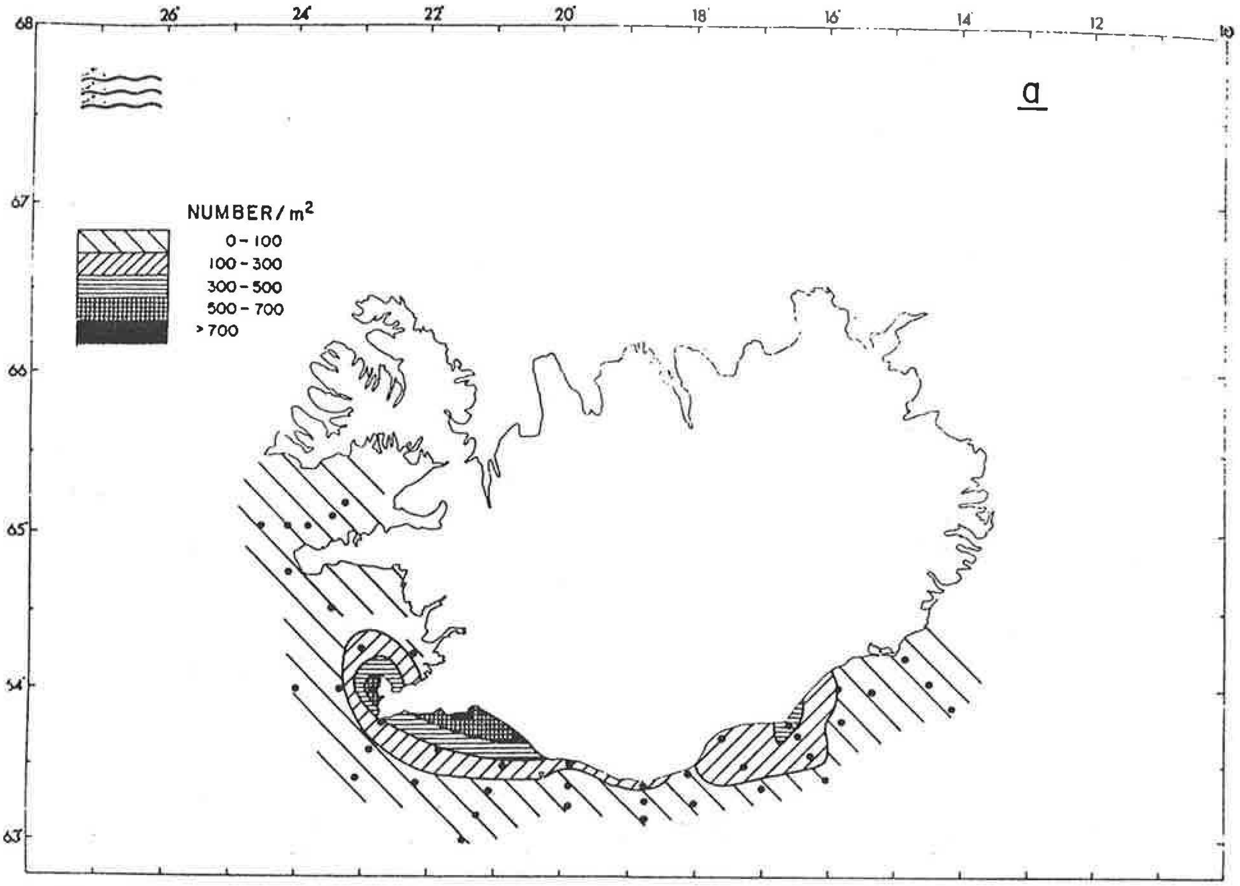


Figure 3.4.1 The mean distribution of cod and haddock eggs at stage I observed in cruises 1976-1981. (From Friðgeirsson 1982).

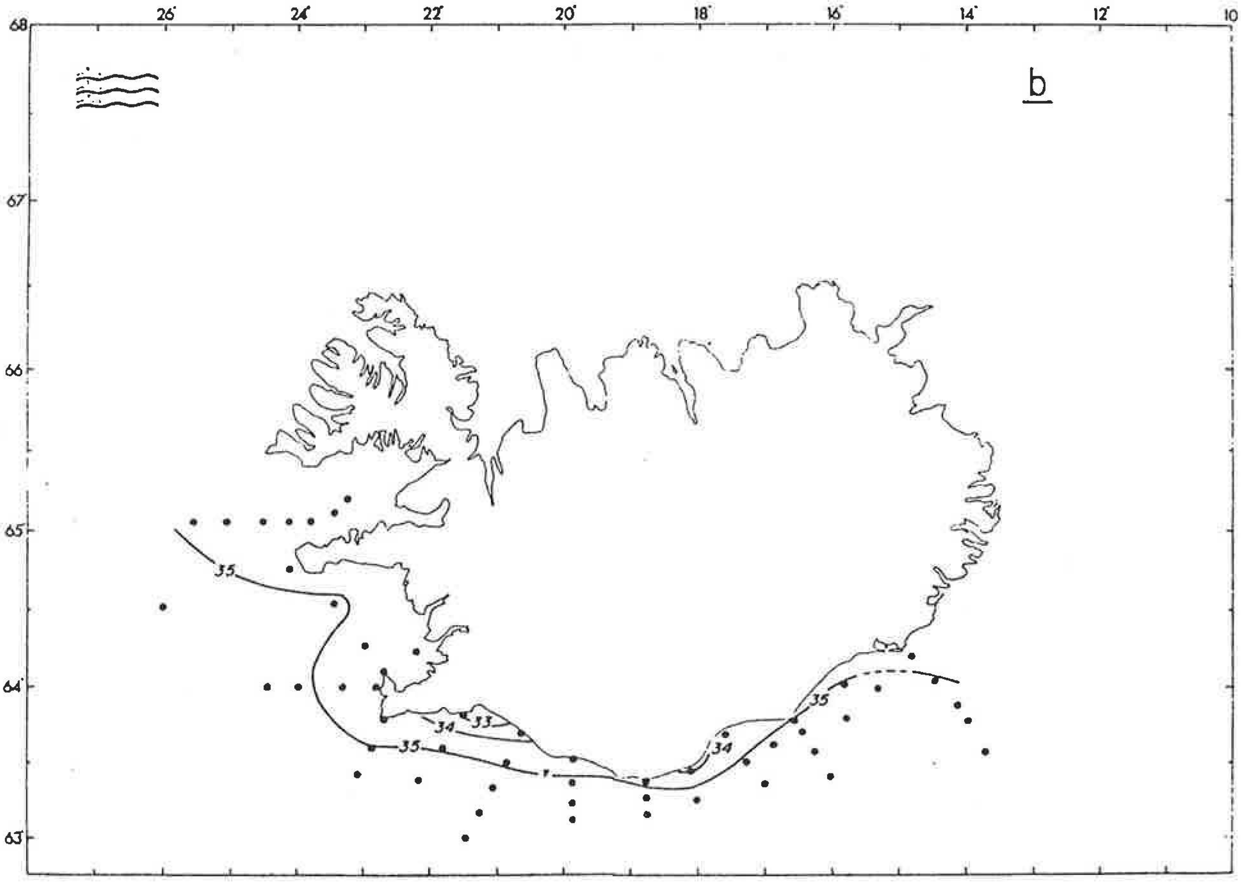


Figure 3.4.2. Mean surface salinity observed in same cruises as above. (From Olafsson, 1985).

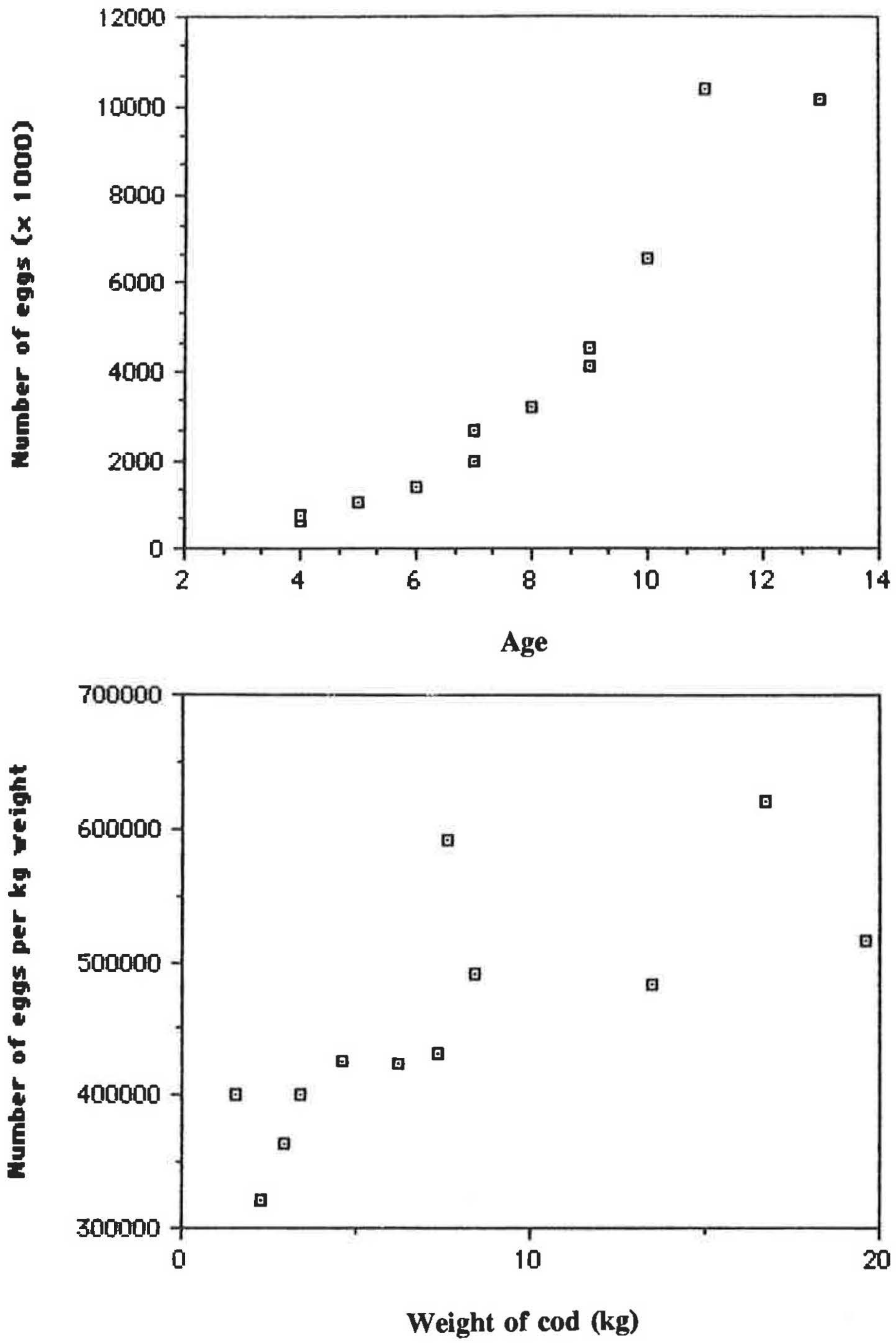


Figure 3.4.3. Fecundity data for Icelandic cod, based on Schopka 1971).

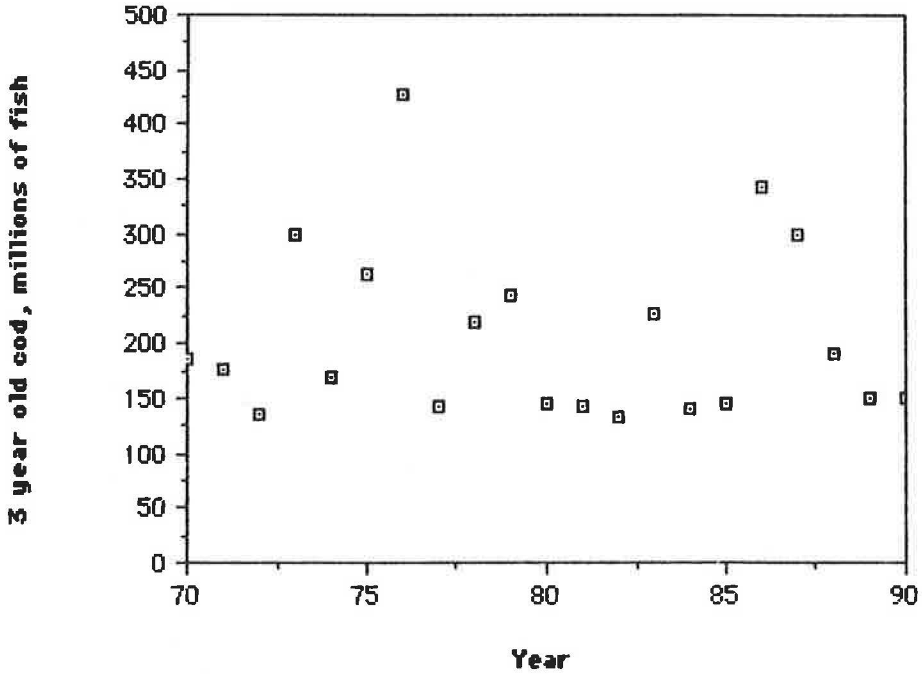


Figure 3.4.4. Recruitment data for Icelandic cod, based on Anon. 1989.

3.5 COD IN FAROESE WATERS

Cod is the commercially most important demersal species in the catches from the Faroe area. Catches back to 1903 are shown in Figure 3.5.1. Total catches have fluctuated between 20,000 and 40,000 tonnes. With the exception of the World War periods the proportion caught by the Faroese was rather low until 1970 but then increased. During the last 10 years Faroese vessels have taken more than 98% of the total catch.

The habitat of cod as well as the whole ecology of Faroese waters is dominated by the location of the islands on the submarine ridge system between Scotland and Greenland separating the warm Atlantic waters from the cold waters north of the ridge. In the northern part of the area the Iceland-Faroe Ridge (IFR) has sill depths around 500 meters while the southern part of the ridge system, the Wyville-Thomson Ridge (WTR), has sill depths around 600 meters (Figure 3.5.2). These two ridges are separated by the Faroe-Shetland Channel (FSC) and the Faroe Bank Channel (FBC) with sill depth around 850 meters. This channel separates the Faroe Plateau from the banks in the northeastern corner of the Rockall-Hatton Plateau of which the most important one is the Faroe Bank (FB).

3.5.1 Stock structure and assessment

Extensive tagging experiments have demonstrated the existence of two cod stocks in the Faroe area, one on the Faroe Plateau and one on Faroe Bank (Strubberg, 1916, 1930; Tåning, 1940; Joensen, 1956; Jones, 1966). Schmidt (1930) has shown that cod on the Faroe Bank has a lower number of vertebrae than cod on the Plateau and concluded that the stock on Faroe Bank and that on the Plateau are two different stocks. Analysis of serum protein Jamieson (1967) supports this thesis. In the assessment of cod in the Faroe area the cod on the Faroe Bank and that on the Plateau are therefore treated as two different stocks.

The catch figures shown in Figure 3.5.1 are for the total Faroe area. The catches on Faroe Bank back to 1965 are shown in Figure 3.5.3. They reached a maximum of 5,000 tonnes in 1973. Since 1985 the catches have decreased and in 1989 only 460 tonnes were caught.

Data to assess the cod stock on the Faroe Plateau are available back to 1962 while no attempts have been made to assess the Faroe Bank cod stock. Mean fishing mortalities for the age groups 3 to 7 estimated by virtual population analysis are shown in Fig. 3.5.4. From 1962 to 1974 the fishing mortality decreased from 0.8 to 0.4 and has since then fluctuated within the range: 0.4-0.7. With the present exploitation pattern F_{max} is estimated to 0.39 and $F_{0.1}$ to 0.17. The estimated recruitment as one year old and the estimated spawning stock biomass are shown in Figure 3.5.5. With the exception of the 1972, 1973 and 1982 yearclasses the recruitment has fluctuated between 10 and 30 x 10^6. The longterm recruitment is estimated to 22 10^6. The spawning stock biomass increased from 1962 up to 1977 and then decreased again due to increased fishing mortalities (Fig. 3.5.5). Due to high fishing mortality the very good 1982-yearclass did not contribute so much to the spawning stock as it would have with a more moderate fishing mortality. The low recruitment in the three following years 1984 to 1986 has caused a drop in the spawning stock biomass. It is estimated to be at a very low level at present.

3.5.2 Environment

The upper layers of the waters surrounding the Faroes are dominated by the "Modified North Atlantic Water" (MNAW) deriving from the North Atlantic Current (Becker & Hansen, 1988). This water has typical temperatures around 8°C and salinities around 35.25. The general circulation pattern of the area (Figure 3.5.6) transports this water past the Faroes on all sides; but in the Norwegian Sea north of the Faroes the "Subarctic Front" separates it from the "North-Icelandic/Arctic-Intermediate" (NI/AI) water of the East Icelandic Current. The NI/AI water is much colder (temperature around 4°C) and fresher (Salinity below 34.8) and in the upper layers it is only found north of the Subarctic Front; but at deeper levels this water may be found mixed into the MNAW in increasing amounts down to depths of 300 to 500 meters to the north and east of the Faroes. Below 500-600 meters the "Deep Norwegian Sea Water" (DNSW) takes over, and this water mass ($T < 0°C$, $S = 34.92$) dominates the deeper regions north, east and south of the Faroes, that is east of the ridge system defined by the Iceland-Faroe Ridge (IFR) and the Wyville-Thomson Ridge (WTR). Thus only the region north of the Faroe Bank and west of the IFR is in the deeper parts dominated by Atlantic water, and even in that region one finds colder water deriving from overflow of DNSW through the Faroe Bank Channel and of NI/AI water over the IFR.

There is some evidence that during the "Little Ice Age" in previous centuries the Subarctic Front was displaced fairly much to the south; but during this century it seems to have been so far north of the Faroes, that the waters on the Plateau and on the banks have had comparatively small variations in temperature and salinity although cold intrusions from the frontal region may occasionally reach the shelf region (Hansen & Meincke, 1979). Contributing to this stability are the almost closed anticyclonic circulation systems which are known to dominate the shallower regions at least on the Faroe Bank (Hansen & al., 1986) and on the Faroe Plateau (Hansen, 1979). The persistence of these flows results in long retention times for the water and planktonic organisms over the shallower regions and the fact that the circulation over Faroe Bank is separate from the circulation over the Plateau may explain how the two cod stocks can remain distinct. On the Faroe Plateau there are indications that there may be more than one gyre; but detailed knowledge on this is lacking as is knowledge on the vulnerability of the gyre systems towards storms or abnormal weather conditions.

In the shallow regions there are strong tidal currents which mix these waters very efficiently. This results in a difference between the vertically almost homogeneous shelf water and the offshore waters which in the warmer seasons become stratified. The border between these two regimes is seen as a distinct front on infrared satellite pictures both on Faroe Bank and on the Plateau. During summer the temperature difference is of the order of one degree for the front on the Plateau and somewhat less on Faroe Bank. These three regimes (well-mixed, frontal and stratified) have different conditions for primary production; but little is known about production cycles in Faroese waters and much more work is required to establish an understanding of these cycles and their dependence on the very variable weather conditions in the region.

From the beginning of the century hydrographic investigations have been made in Faroese waters, but irregularly. In the late eighties three standard sections have been established and are occupied at least four times a year. These sections were designed to coincide as well as possible to sections often occupied in the historical data set. A much more regular timeseries is the shorebased series of daily temperature measurements initiated in 1875 in Tórshavn and moved in 1914 to Mykines where it continued until 1969. A critical analysis (Hansen & Meincke, 1984) has shown that the measurements in Tórshavn have probably been influenced by local effects during summer; but the later part of the series seems to give a fairly representative picture of the seasonal variation (Fig. 3.5.7) of sea surface temperature of the Plateau waters and for the winter season the whole series gives a climatic signal (Figure 3.5.8). In 1989 an automatic temperature recording station was established close to the Mykines site abandoned in 1969 to continue the series.

3.5.3 Spawning

Tåning (1943) and Joensen & Tåning (1970) state that spawning takes place from February to May, April being the important month. Analysis of roe-landings (Hoydal & Reinert, 1977) and length distributions of pelagic larvae and juveniles (Reinert, 1979) verified this spawning period but indicated a mean spawning in the second half of March. Data from the Faroese Groundfish Surveys 1982-89 have now been used to estimate the timing of gonadal development and spawning. The results are shown in Fig. 3.5.9. Gonadal development has been determined on a scale from 1 to 7 with 1 as immature, 2-5 as maturing, 6 as spawning and 7 as spent. According to this data spawning on the Plateau starts in February on a low level. In the second half of March most of the sampled cod have been spawning. No data is available for the first half of February for the Faroe Bank but in the second half the proportion spawning is at the same level as that on the Plateau. The lower proportion of spawning cod and higher proportion of stage 5 in March on the Faroe Bank compared to the Plateau may indicate either a larger interannual variability in timing or a prolonged spawning period on the Faroe Bank.

Spawning takes place all around the Faroe Plateau at depths about 80-180 m and temperatures of 6-7°C. By far the most important spawning grounds are to the north and west of the islands (Figure 3.5.10). It should be mentioned that there seems to be a delay of about one month between the main spawning of the three main demersal gadoids in the area, with main spawning time of saithe in second part of February, of cod in second part of March and of haddock in mid April (Joensen, 1953 and Joensen & Tåning, 1970).

3.5.4 Eggs, larvae and juveniles

After fertilization the eggs ascend towards the upper layers, where the development up to hatching occurs. The incubation period is about 16-20 days (Joensen & Tåning, 1970). No other information is available on the duration of the embryonic period, but the start of exogenous feeding seems to coincide at least in most years with the onset of primary production. The youngest larvae taken are about 4 mm, and data from 1978 seem to indicate a dispersal of embryos and larvae by the anticyclonic current systems around the islands (Reinert, 1979). Later on the larvae seem to be distributed horizontally all over the Plateau by the circulation and the strong tidal currents. In June and early July the distribution of juveniles shows a very characteristic picture on the Plateau, with heavy concentrations near the islands to the north and more scattered in other areas (Fig. 3.5.11). The Faroe Plateau seems to be a retention area for eggs and larvae, created by the anticyclonic current system, and a sub-division of this system into several minor gyres could be responsible for the characteristic distribution of the juveniles in June and early July. The current system around the Faroe Bank creates a retention area there as well (see above).

The information on growth in the pelagic phase is scarce; samples from Bongo, Gulf III and capelin trawl in the late seventies indicated a logarithmic growth in agreement with Saville (1956): $L = L_0 * 10^{0.012t}$, t = no of days (Reinert, 1979).

At lengths about 3.5-4.0 cm the juveniles leave the pelagic phase and most of them migrate into the littoral zone of the fjords; this happens usually after the first week of July. On the Faroe Bank, however, the juveniles settle on the Bank proper, i.e. in relatively deep water.

In late July the demersal stages are found in the seaweed in the littoral zone, now about 4.5 cm long. In the middle of August the mean length is about 5 cm, in mid-September about 7 cm (Joensen and Tåning, 1970). The growth of cod from 1-year and onwards is shown in Figure 3.5.12.

After 1-2 years in the littoral zone of the fjords the cod migrate towards deeper waters. Tagging experiments show, however, that the cod is rather stationary while sexually immature, i.e. up to about 3 years (Joensen and Tåning, 1979). The food in the littoral zone is mainly crustaceans and the young of other fish species, e.g. saithe and sandeel.

3.5.5 Adults

When sexually mature most of the Faroe Plateau cod migrate to the spawning grounds especially north of the islands. After spawning the fish disperse all over the Plateau (Joensen and Tåning, 1970).

Data on feeding and predation is scarce. Joensen and Tåning (1970) describe the cod as feeding on nearly everything they come across and mention fish, crustaceans, worms, mussels, echinoderms, ascidians and hydroids. Of the fish species in the food the most favoured are probably sandeel and herring but also Norway pout. The abundance of these fish species and their migrations may at times be decisive for the cod migration.

In Fig. 3.5.12 the mean lengths at age for the two cod stocks in the Faroe area are shown. The figure is based on ages determined from otoliths collected over the period 1973-1982. The Faroe Bank cod grows more rapidly than the Plateau cod. At an age of 3 years the average length of cod on the Faroe Bank is around 75 cm while on the Faroe Plateau it is around 55 cm. Cod on the Faroe Bank is one of the cod populations with the fastest growth.

Very little data has been published on the maturation of cod at the Faroes. Tåning (1943) and Joensen and Tåning (1970) state that, on average, the cod on the Faroe Plateau becomes mature at an age of 4 years while the Faroe Bank cod reaches maturation at 3 years old. Since 1982 samples have been collected during the Faroese groundfish surveys in February and March to estimate maturity ogives. The results are shown in Figure 3.5.13. According to these investigations there is no difference in the maturity ogives by ages for cod on the Plateau and the Faroe Bank cod. In both cases 50% of the cod became mature at an age of 3 years, i.e. one year younger than stated by Tåning (1943) and Joensen and Tåning (1970). The rapid growth of cod on the Faroe Bank and the similar maturity ogives by ages must imply that cod must become mature at a larger length on the Faroe Bank compared to the Plateau and this is demonstrated in Figure 3.5.14. The 50% maturation length of the Plateau cod was around 40-45 cm while it was around 65 cm for the Faroe Bank cod.

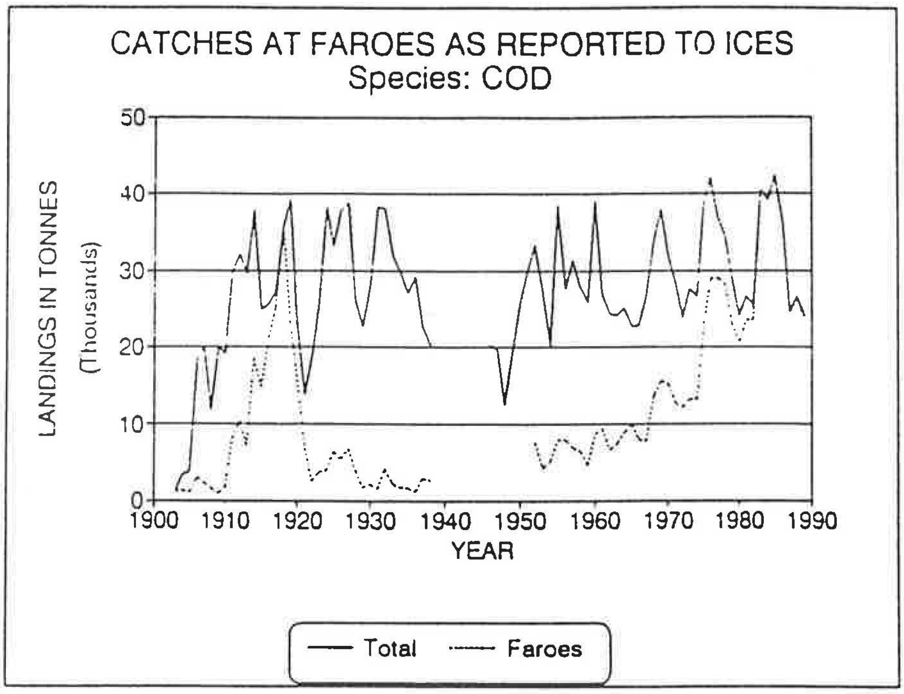


Figure 3.5.1. Total international and Faroe catches of cod for the Faroe area (ICES Div.5).

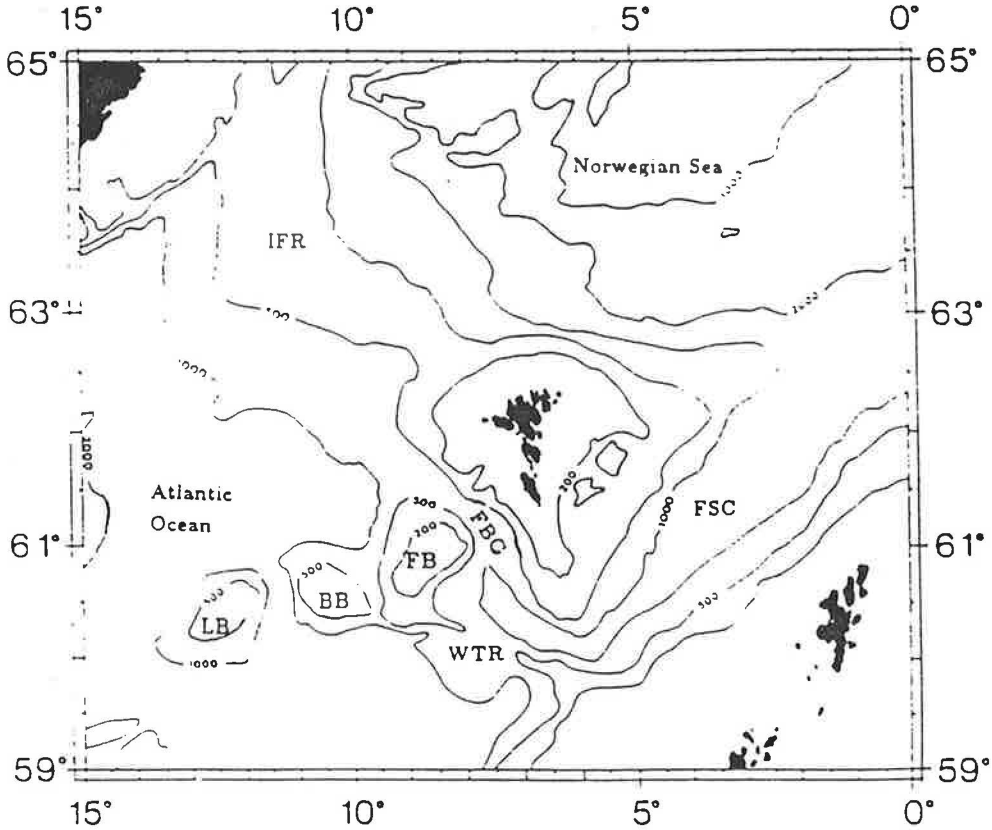


Figure 3.5.2. Topography of Faroese waters.

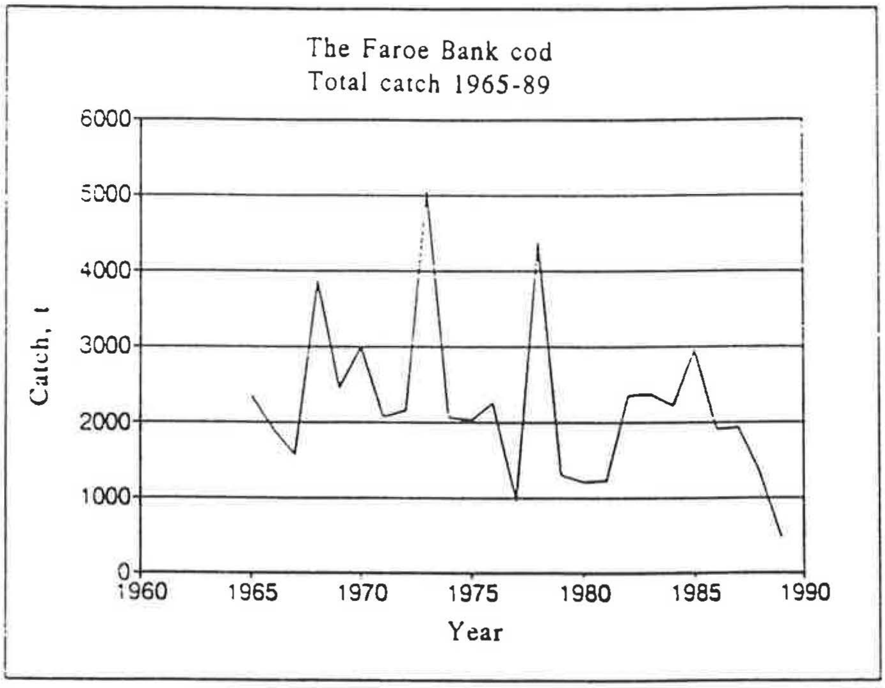


Figure 3.5.3. Catches of cod on the Faroe Bank.

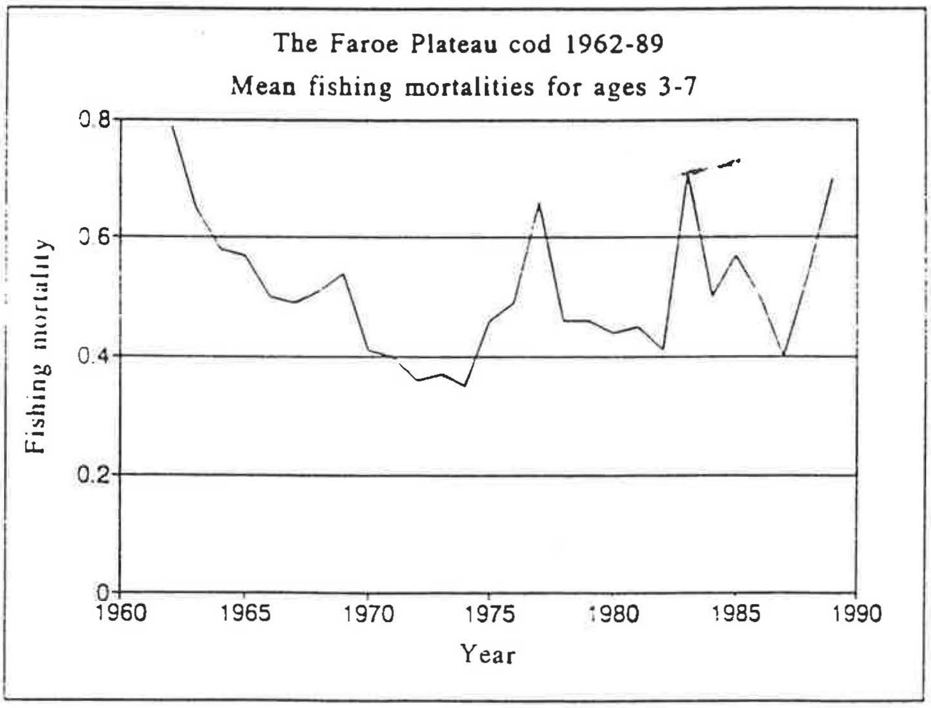


Figure 3.5.4. Mean Fishing mortalities estimated by VPA.

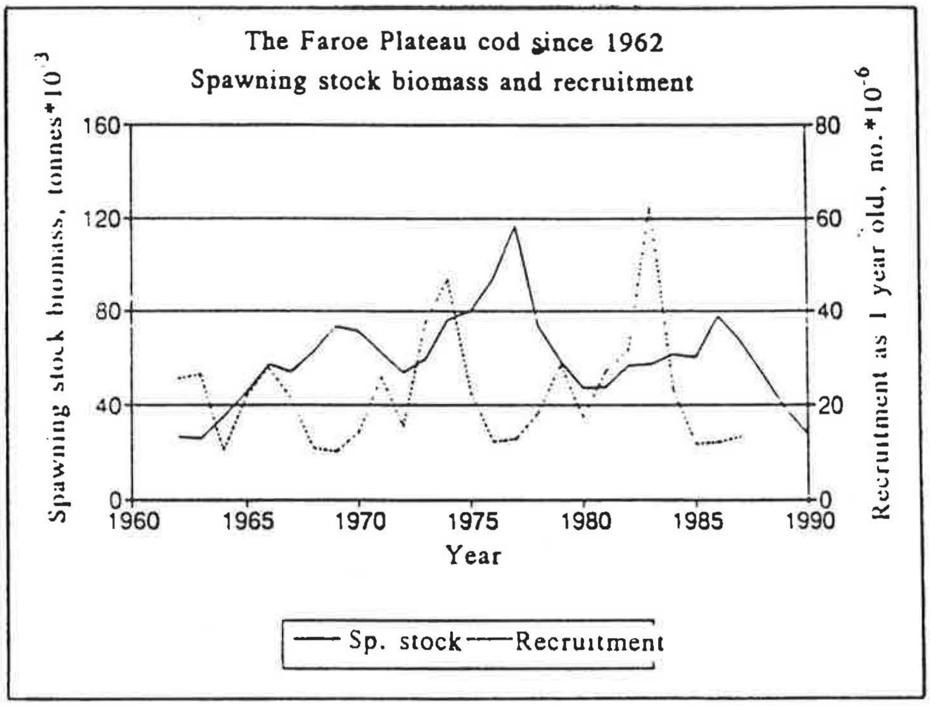


Figure 3.5.5. Spawning stock biomass and recruitment.

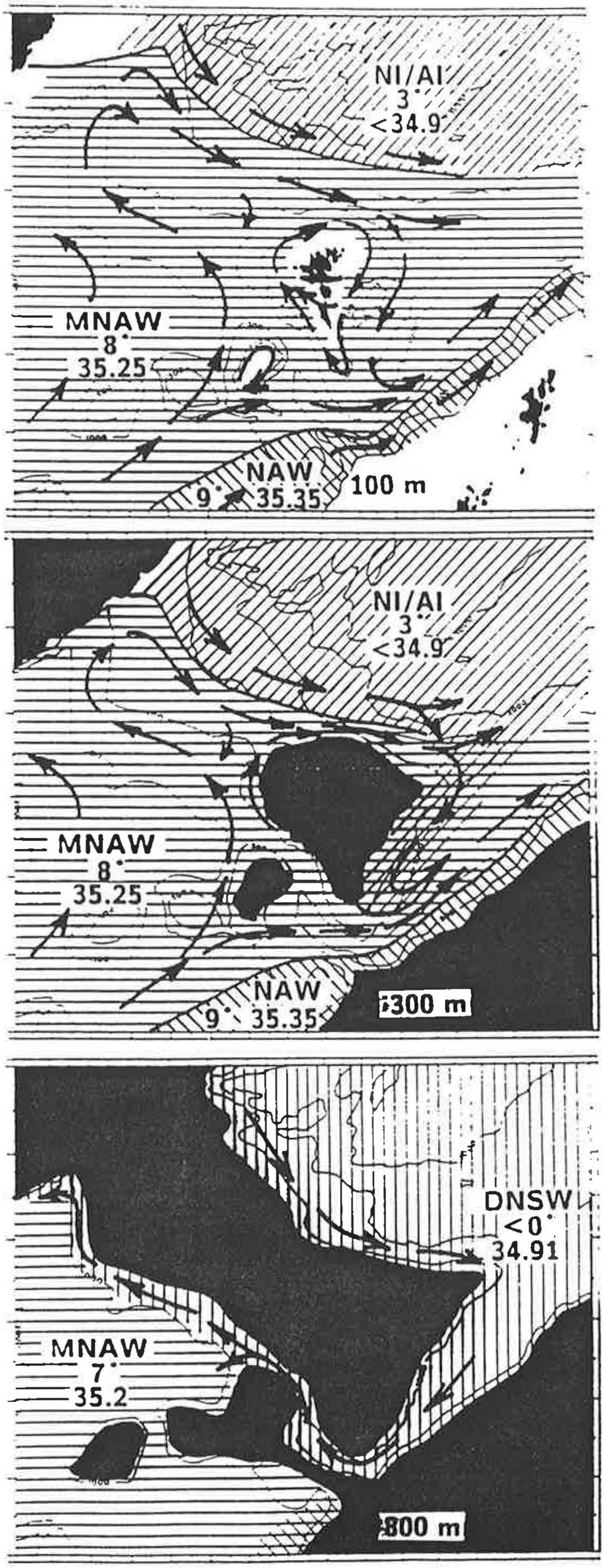


Figure 3.5.6. Distribution of main water masses and circulation patterns of Faroese waters at three different depths.

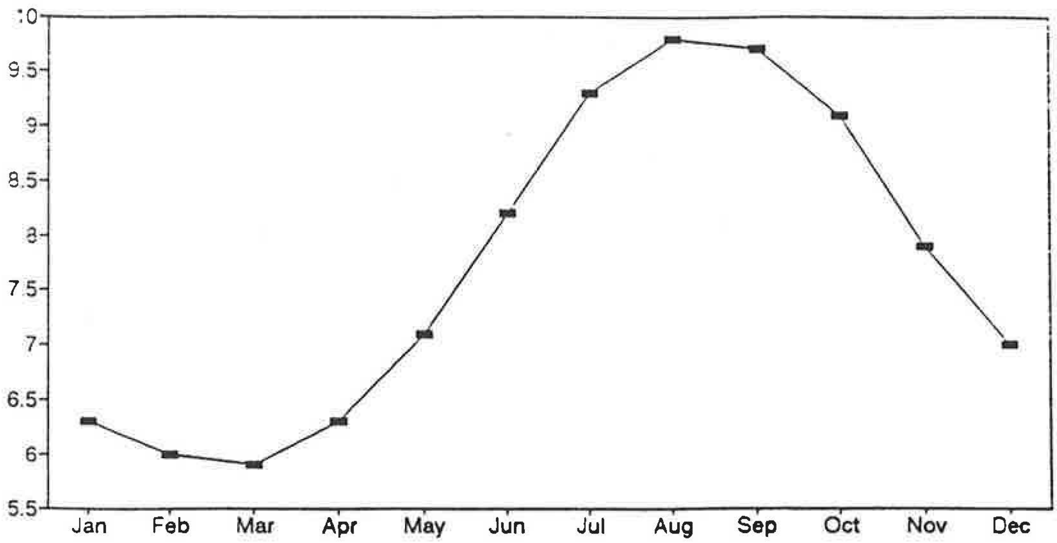


Figure 3.5.7. Seasonal variation of sea surface temperature of the Plateau waters based on monthly means for period 1914-1950, (Smed, 1952).

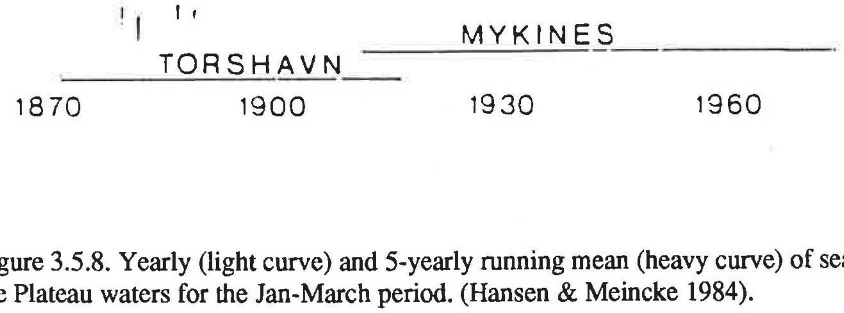
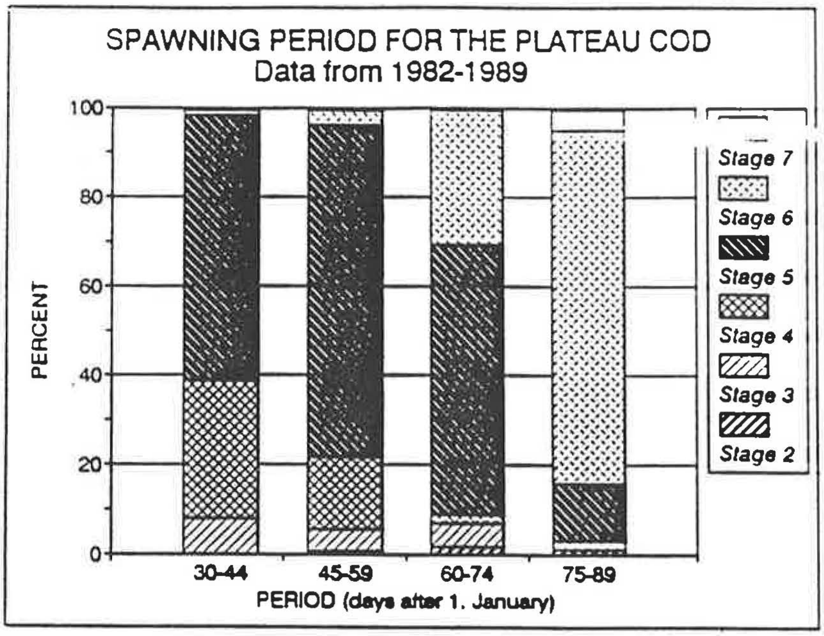
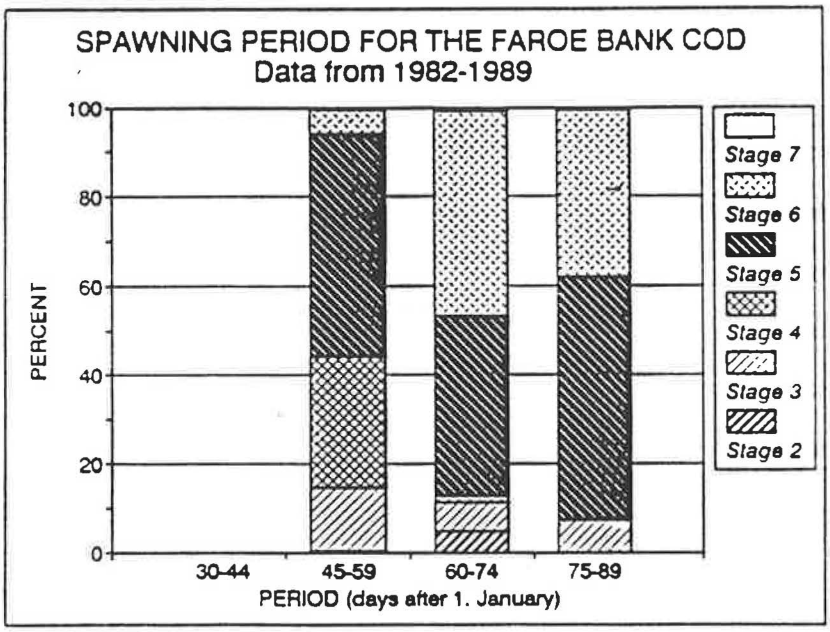


Figure 3.5.8. Yearly (light curve) and 5-yearly running mean (heavy curve) of sea surface temperature of the Plateau waters for the Jan-March period. (Hansen & Meincke 1984).



a



b

Figure 3.5.9. Estimation of gonadal development and spawning for Faroe Plateau (a) and Faroe Bank (b).

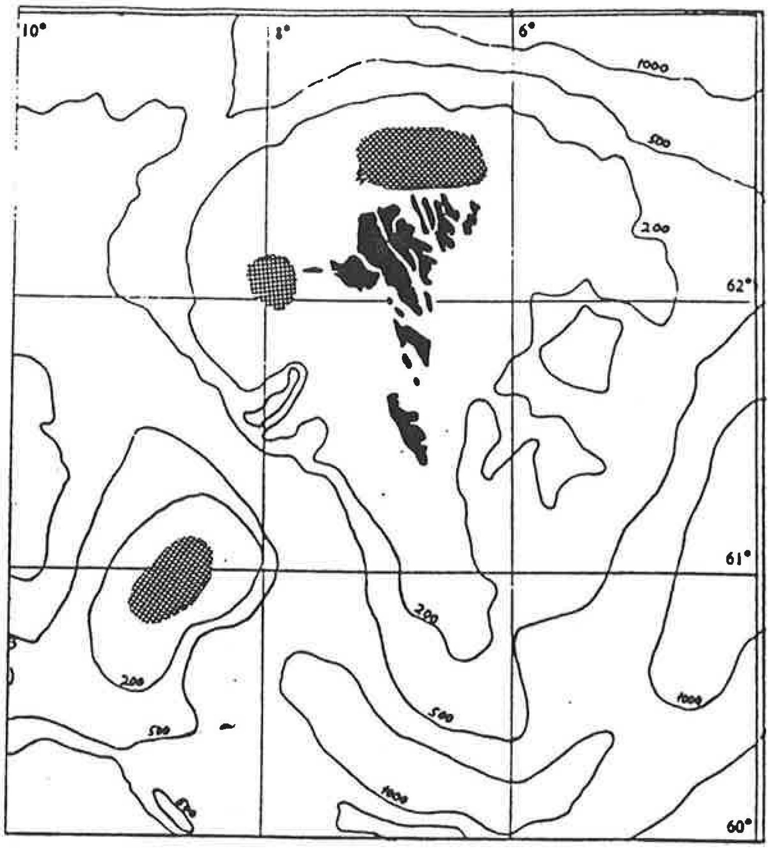


Figure 3.5.10. The main spawning areas for cod in Faroese waters (Reinert 1988).

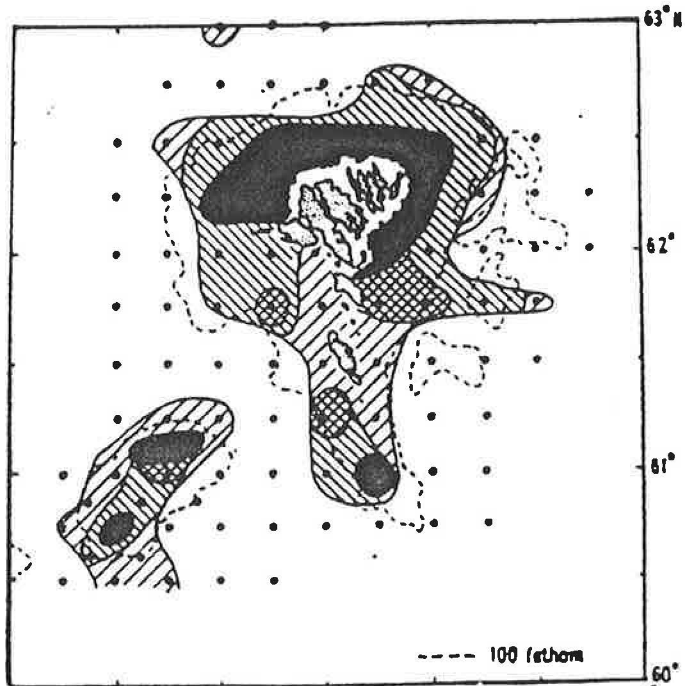


Figure 3.5.11. A typical distribution of 0-group cod in late June (Anon, 1976).

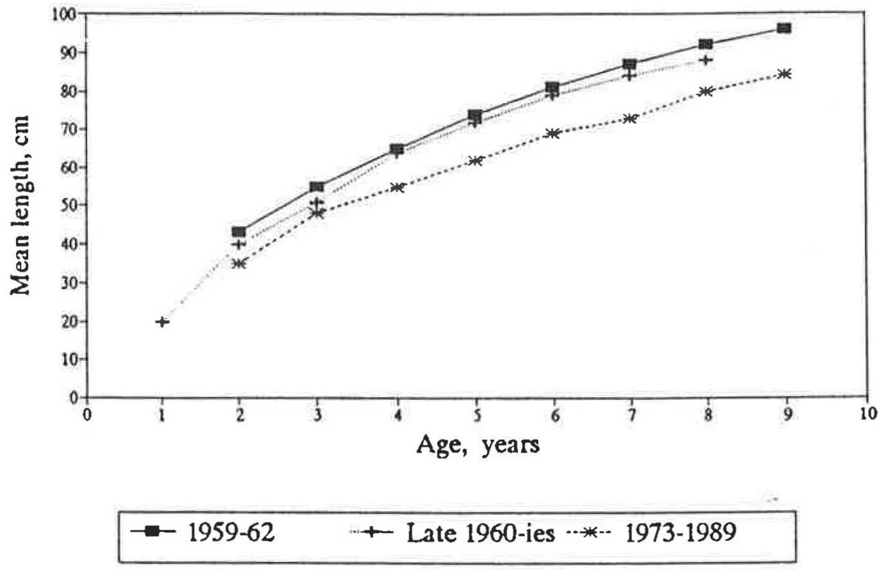


Figure 3.5.12. Mean length at age for Faroe Plateau cod in three different periods (adapted from Jones, 1966, Jones, 1978, Joensen and Tåning, 1970, and Kristiansen, 1990).

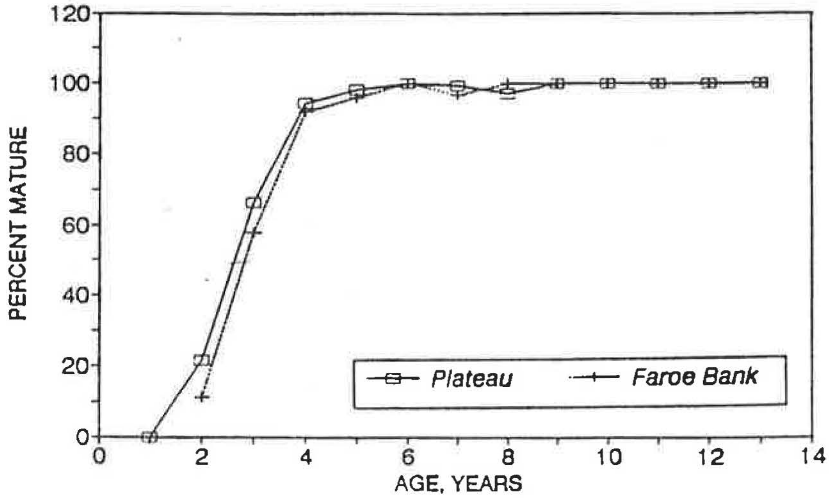


Figure 3.5.13. Average maturity ogives by age for Faroe cod. (Kristiansen 1990).

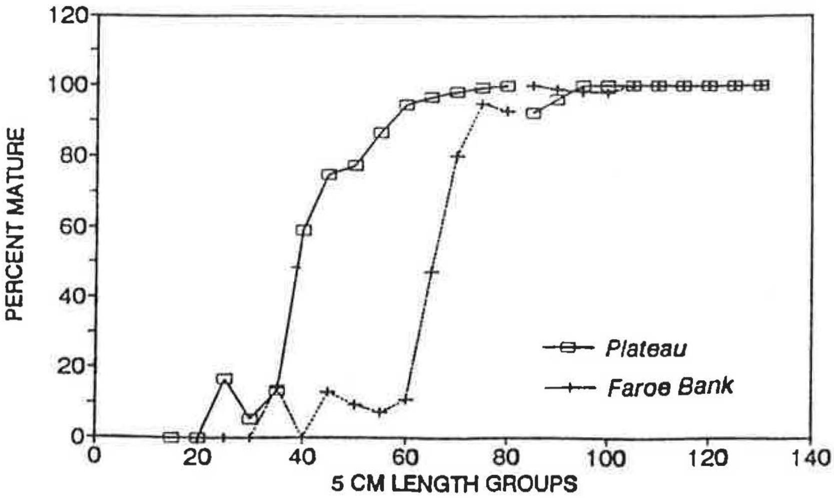


Figure 3.5.14. Average maturity ogives by length for Faroe cod. (Kristiansen 1990).

3.6 NORTH SEA COD (*Gadus morhua* L.)

3.6.1 Environment

The North Sea is a shallow basin, 30-200 m deep, with a shelving topography from southeast to northwest. Its northeastern margin is formed by a trough, the Norwegian Deeps, with a depth up to 600 m. The surface area of the North Sea is 575,300 km^2, its volume 42,294 km^3 (Anon., 1983). The North Sea is influenced by the Atlantic, mainly by input via the northern North Sea and to a lesser extent via the Channel. To the northwest of the British Isles a strong Atlantic current flows north along the edge of the continental shelf. Via different currents Atlantic water enters the northern North Sea (see e.g. Svendsen and Saetre, 1988). One of these currents enters the Norwegian Deeps (Booth and Meldrum, 1987).

The North Sea can be divided in seven geographical boxes (Figure 3.6.1), which take account of hydrographic and biological conditions (Anon., 1983). There are strong seasonal differences in the vertical structure of the water column. Most areas are vertically mixed or only slightly stratified throughout the winter. From spring to autumn, however, the North Sea is divided into areas which remain mixed and others which become stratified. In large parts of the central and northern North Sea a strong seasonal thermocline develops by May-June which deepens throughout the summer, breaking down by November. The boundaries between these different regimes may be characterised by large gradients in temperature and/or salinity (Reid *et al.*, 1988). Salinity ranges from approximately 29°/oo in the Southeast to 35.3°/oo in the Northwest.

3.6.2 General structure of the stock

Cod has a widespread distribution throughout the North Sea (Figure 3.6.2). For the last 20 years data on distribution are available from the International Young Fish Survey in February, a synoptic survey covering the whole North Sea. Age group 1 is most abundant in the German Bight, along the Dutch coast and off the coast of northeast England. The distribution of the 2-group is more or less similar but in addition areas of high abundance are found in the northern North Sea. The 3-group is most abundant in the northern North Sea. Cod of 4 years and older occur in a low abundance throughout the North Sea but are absent in the shallow parts of the German Bight, highest numbers are found in the northern North Sea. The importance of the German Bight as a nursery for young cod (age groups 1 and 2) seems to be decreasing in recent years.

On the basis of extensive tagging data, reviewed by the ICES North Sea Roundfish Working Group (Anon., 1970 and 1971), it was concluded that cod do not disperse uniformly throughout the North Sea but remain more or less within one region. As an approximation the following regional grouping was suggested:

a) the Norwegian side of the Skagerrak,

b) the Danish side of the Skagerrak,

c) one or possibly several coastal regions, from Flamborough to the Scottish east and north coasts,

d) the central North Sea,

e) the Southern Bight, from the Straits of Dover to latitude 54°N,

f) the English Channel, south and west of the Straits of Dover.

Although North Sea cod is certainly not one homogeneous stock (Jamieson and Birley, 1989), sub-stocks with clear boundaries cannot be discriminated on the basis of genetical studies.

The region off the north and north-west coasts of Scotland is an important spawning area for cod and it is likely that part of the eggs and larvae are transported into the North Sea. It might be expected that this one-way drift of eggs and larvae into the North Sea would be counterbalanced by a return migration of adolescent or mature fish to the westerly spawning grounds (Daan *et al.*, 1990). Also at the other end of the North Sea there is an interchange of spawning fish and spawning products: cod leave the North Sea to spawn in the Channel (Daan *et al.*, 1990).

From the end of the 16th until the end of the 19th century Dutch fishermen sailed to Iceland to fish for cod (Beaujon, 1885), so cod was certainly not an abundant species in the North Sea in those days. In 1903 ICES started to collect detailed information on total international landings (Figure 3.6.3), earlier data series are not available. Prior to the early 1960s, landings fluctuated between about 60,000 and 160,000 tonnes, with a marked fall during the two war periods. Landings peaked immediately after each war. In the 1960s there was a remarkable increase and a peak of about 340,000 tonnes was reached in 1972. There have been wide fluctuations subsequently, but since 1981 landings have steadily decreased and have almost reached the same level as before 1960.

Estimates from Virtual Population Analysis (VPA) of the size of the spawning stock are available since 1963 (Figure 3.6.4). Spawning stock biomass increased steadily up to 1970 when a maximum of 270,000 tones was reached. The cause of the rapid increase in biomass and in catch in the 1960s must be found in the sequence of a large number of strong year classes. English c.p.u.e data indicate that year class 1963 is the first of a series of four unequalled rich year classes. Year classes 1969 and 1970 were even more abundant (Daan, 1978). Apparently, the carrying capacity of the system for the juvenile life stages changed, but how and why this happened remains unsolved (Daan, 1986; Cushing, 1984; Brander, 1992). Since 1970 the spawning stock size has declined and is estimated to be around 90,000 tonnes at present, which is well below what is considered a safe biological limit of approximately 150,000 tonnes (Anon., 1988a).

Since 1963 recruitment of North Sea cod has varied by a factor of 10 according to VPA, but abundance indices from survey data, available for 1- and 2-group since 1970, varied by a factor of approximately 100 (Table 3.6.1). Rijnsdorp *et al.*, (1991) calculated a new index giving equal weight to VPA, 1- and 2-group index (Figure 3.6.5). Possible explanations for the discrepancy between the different data series are that discards are not included in the VPA, whereas discard rate is a function of year class strength. Also, errors in age readings will tend to re-assign, wrongly, fish from good to poor year classes. Both factors will reduce the apparent variation in recruitment estimates from the VPA. On the other hand, survey data suffer from inherent variability in catch rates (Rijnsdorp *et al.*, 1991). Recruitment shows a general alternation of good and bad year classes, but since 1970 overall a negative trend can be observed.

Cod is caught by a great variety of gears, often as the target species in a mixed demersal fishery. Fishing mortality estimated from VPA has steadily increased since 1963 but seems to remain at a stable high level of approximately 0.85 since 1980 (Figure 3.6.6). Data from Daan (1969) on the composition in market-categories of the Dutch landings show a clear increase in the proportion of small cod in the landings since 1949.

3.6.3 Spawning

Spawning occurs from the beginning of January to April, but depends to some extent on latitude. In the Southern Bight peak spawning is in February, whereas in the more northerly regions, maximum spawning activity shifts to March. On a very limited scale autumn spawning occurs in the northern North Sea, but this was more regularly observed between 1900 and 1930 than in the most recent period (Hislop, pers. comm.). Peak spawning in the southern North Sea varies from the last week of January to mid-February (Daan, 1980; Heessen and Rijnsdorp, 1989). Spawning is rather early in relation to the production cycle (Harding *et al.*, 1978; Brander, 1994).

Spawning areas are widely distributed over the North Sea (Figure 3.6.7). The importance of certain grounds may shift to some extent from year to year but the available data do not indicate that since the beginning of this century major changes have taken place in the spatial distributions of spawning (Daan, 1978). In the northern North Sea spawning occurs close to banks, but whether cod actually spawn on or just close to these banks is unknown. A difficulty in locating spawning areas in the northern North Sea is that cod and haddock spawn in the same areas at the same time, therefore only late stage eggs can be used to provide information about the location of spawning areas. The spawning area off the Dutch coast was studied in several egg surveys since 1970. The number of cod eggs produced in the Southern Bight appears to be rather variable, which is probably related to the relatively small size of the Southern Bight in relation to the total area where North Sea cod spawn (Daan, 1980 and 1981; Heessen and Rijnsdorp, 1989). Spawning areas are to be found throughout the North Sea, therefore spawning migration is only over relatively short distances.

3.6.4 Egg stage

Embryonic development is described for the temperature range of 1.7 to 11.6°C (Table 3.6.2). Abnormal development was observed at temperatures above 12°C and below 1.5°C death occurred in the early stages of cleavage (Thompson and Riley, 1981).

Several species are known to predate on cod eggs. For the southern North Sea Daan *et al.* (1985) estimated that 0.04 to 0.19% of the initial numbers of eggs produced were consumed by herring (*Clupea harengus*).

For the southern North Sea mortality data are available for 7 years (1970-1974 and 1978-1988). The observed instantaneous daily mortality rates varied between 0.027 and 0.404 (Daan, 1980; Heessen and Rijnsdorp, 1989). For the west central North Sea a value of Z of 0.14 was observed in 1976 (Harding *et al.*, 1978).

3.6.5 Larval Stage

Very little is known about the larval stage of North Sea cod. Usually, very few larvae are caught during egg surveys. The development rate was described at 6.5°C. In 6 days old larvae the yolk sac is completely resorbed and after 27 days the swimbladder is noticeable (Thompson and Riley, 1981).

Yolk-sac stage larvae in the eastern English Channel and the southern North Sea begin to feed on diatoms, dinoflagellates and tintinnids, but the principal food items of larvae are the nauplii and copepodites of calanoid copepods, particularly of *Pseudocalanus minutes* (Last, 1978).

3.6.6 Juveniles

Data on the distribution of the pelagic 0-group phase are available from the International 0-group Gadoid Surveys carried out in June-July from 1974-1983. Pelagic 0-groups are most abundant off the coast of Jutland and in the central northern North Sea (Figure 3.6.8). In the shallow parts of the southern North Sea only a few observations were made. They indicate that pelagic 0-group cod is nearly absent in the German and the Southern Bight. In some years, however, a high abundance of demersal 0-group cod are observed September/October in the Wadden Sea (Daan, 1978). Probably the duration of the pelagic phase in the shallow southern part of the North Sea is extremely short or completely absent.

Some observations on the vertical distribution of pelagic 0-group cod were made in 1974 and 1975, both in the northern North Sea. In 1974 the catch rates of pelagic 0-groups of cod and five other gadoid species were considerably higher in the surface hauls (10-30 m) than in the mid-water (30-50 m) or bottom (100-130 m) hauls. In none of these species diurnal vertical migration between the surface layers and the bottom was observed (Robb, 1981). Data collected in 1975 during the International 0-group Gadoid Survey also showed that pelagic 0-group cod was mainly confined to the upper 0-40 m stratum (Holden, 1981).

Robb and Hislop (1980) analysed the diet of pelagic 0-group cod in material collected in July 1973 in the northern North Sea. The food was dominated by copepods: *Para/Pseudocalanus* spp. and the most common fish species in the diet was Norway pout (*Trisopterus esmarki*). The food composition for different size classes of predators is shown in Table 3.6.3. In weight percentage the diet of juveniles of 20-29 mm consisted almost exclusively of copepods. From 30-39 mm onwards juveniles start to feed on fish. For the length classes of 30-39 and 40-49 mm Euphausids are important prey species but already in these size classes the diet was dominated by fish. From 50 mm onwards more than 80% in weight consisted of fish. From differences in the diet of five gadoid species it was concluded that the degree of competition between pelagic 0-group gadoids was not great.

Significant diurnal changes are found in the amount of food in the stomach as well as in food composition. Robb (1981) observed a steady increase in stomach content weight commencing late afternoon or early evening and a maximum was found at midnight, the lowest values around midday. The diet did not vary significantly with depth but changes were found in the course of the feeding period. Around 1800 hours BST and again at 0600 hours, copepods were found to be the main prey group but at midnight the stomach samples contained an abundance of euphausids.

Data on growth during the pelagic phase are given in Table 3.6.4 and in Figure 3.6.9. No cod bigger than 7 cm are caught in pelagic catches. At this size juveniles start their demersal stage of life, somewhere between June and autumn.

In the southeastern North Sea clear seasonal changes in the distribution of 0-, 1- and 2-group cod are found (Heessen, 1983). The first demersal 0-group cod are caught in bottom trawl catches in the third quarter, in particular along the coast of Denmark and Schleswig-Holstein. In the first quarter high concentrations of 1- and 2-group cod are found particularly in the inshore area (see also Figure 3.6.2). The 1- and 2-group fish leave this area in the second quarter and by the third quarter have moved to the central part of the North Sea. The changes in distribution pattern of 1- and 2-group are very similar: they aggregate in the coastal zone during the winter period and disperse in a north-westerly direction over deeper parts of the central North Sea in summer. This is in good agreement with the results of English tagging experiments off the Dutch coast and in the German Bight (Riley and Parnell, 1983).

In demersal juvenile cod the food is dominated by crustaceans (Daan, 1973 and 1989). Important predators of juvenile cod are cod themselves, whiting (*Merlangius merlangus*) and saithe (*Pollachius virens*) (Daan, 1989). In a recent study (Daan and Heessen, unpublished) predation on 0-group cod was also observed in grey gurnard (*Eutrigla gurnardus*) and greater sandeel (*Hyperoplus lanceolatus*).

3.6.7 Adults

The most comprehensive data on feeding of North Sea cod were collected during the ICES Stomach Sampling Project 1981 (Daan, 1989). In juvenile cod crustaceans are the dominant prey items but in older cod, fish comprise an increasingly important part of the diet. Most of the fish species consumed are of commercial importance. Cannibalism is frequently observed. The results for 1981, pooled for the total North Sea, are presented on a quarterly basis in Figure 3.6.10. There are large individual, regional and seasonal variations in food composition which will be partly caused by changes in the availability of the different food items. The total amount of food eaten in 1981 is estimated to be 507,000 tonnes, of which 331,000 tonnes (65.3%) consisted of commercial fish species (Table 3.6.5).

Migration of adult cod is restricted to limited areas, they do not disperse throughout the North Sea (Anon., 1970 and 1971). The distance between summer feeding grounds and winter spawning grounds varies between 20 and 120 miles. In general the spawning grounds lie to the south of the feeding areas.

Growth parameters of North Sea cod are given in Table 3.6.6. Cod in the southern North Sea grow faster than those in the North but reach a smaller maximum length (Daan, 1974). As shown in Figure 3.6.11 considerable spatial differences in size at age exist (van Alphen and Heessen, 1984). Mean length per age and by sex is given in Table 3.6.7. Within an age group the mature individuals of each sex are on average larger than the immatures (Hislop, 1984). No change in growth nor in condition factor was found between the prewar years and the 1970s (Daan, 1974).

Houghton and Flatman (1981), Macer (1983) and van Alphen and Heessen (1984) found evidence for density dependent growth, although, as concluded by Daan (1986), they point to rather different and incongruous mechanisms. The results obtained by Macer (1983) would imply that juvenile cod compete strongly with adult cod, whereas the data of van Alphen and Heessen (1984) suggest strong within year class competition during the first three years of life.

Data on fishing mortality (Figure 3.6.6) can be derived from VPA (Anon., 1991a), predation mortality at age can be estimated from Multispecies VPA (Anon., 1989c). In the Multispecies VPA, 11 commercial fish species are taken into account. The estimates rely heavily on data collected in one single year, 1981. Therefore, a large scale stomach sampling programme was repeated in 1991. The natural mortality due to causes such as diseases, spawning stress, physiological characteristics and so on are estimated to be 0.2 for all age groups. To this value the predation mortality is added to obtain the total natural mortality at age (Table 3.6.8).

Some North Sea cod become mature in their second year of life (Figure 3.6.12), but it is not before they are 6 years old that they are all mature (Oosthuizen and Daan, 1974; Rijnsdorp *et al.*, 1991). There is a tendency that cod in the southern North Sea become mature at a slightly younger age than in the northern North Sea.

Length at 50% maturity is given in Table 3.6.9 and Figure 3.6.13. Males mature at a slightly younger age and at a smaller size than females. Oosthuizen and Daan (1974) suggested that the length at first maturity had decreased between the 1930s and the 1970s. Although the difference might also be explained by geographical differences in the origin of the samples (Hislop, 1984), the data in Table 3.6.9 indicate that the values of L_{50} obtained for the two earlier periods fall within the range of annual differences observed between 1980 and 1989. This indicates that there is no evidence at all of a major change in L_{50} during this century.

Fecundity estimates are available for a small number of years in the early 1970s and late 1980s (Oosthuizen and Daan, 1974; Heessen, unpublished). The relative fecundity ($RF=F/(c*L^3)$) appears to be significantly higher in recent years (in the order of 20%) than during the earlier studies (Table 3.6.10). This increase coincided with a marked decrease in spawning stock from 265,000 to about 90,000 t.

Table 3.6.1. Recruitment data: Number at age 1 from VPA (Anon.1991a1and 2 group indices from the International Young Fish Survey (Anon.1990d) and recalculated recruitment index (see text).

Year class	VPA-1	IYFS-1	IYFS-2	calc. index
1962	183	-	-	183
1963	354	-	-	354
1964	392	-	-	392
1965	479	-	-	479
1966	461	-	-	461
1967	185	-	-	185
1968	197	-	-	197
1969	729	-	25.9	707
1970	847	98.3	34.5	1308
1971	159	4.1	10.6	177
1972	289	38.0	9.5	459
1973	232	14.7	6.2	240
1974	426	40.3	19.9	613
1975	196	7.9	3.2	152
1976	726	36.7	29.3	770
1977	426	12.9	9.3	319
1978	449	9.9	14.8	353
1979	800	16.9	25.5	616
1980	271	2.9	6.7	171
1981	557	9.2	16.6	400
1982	269	3.9	8.0	189
1983	534	15.2	17.6	445
1984	108	0.9	3.6	74
1985	581	17.0	28.8	572
1986	257	8.8	6.1	204
1987	201	3.6	6.3	149
1988	324	13.1	15.2	338
1989	-	3.4	-	75

Table 3.6.2. Development of cod eggs (Thompson and Riley, 1981). Regression coefficients for equation: loge D = AT + B, where T is temperature in degrees C and D is time from fertilization to the end of each stage.

Development stage	A	B
IA	-0.10	1.56
IB	-0.11	1.96
II	-0.11	2.26
III	-0.11	2.97
IV	-0.11	3.24
V	-0.10	3.46

Table 3.6.3. The diet of pelagic 0-group cod. Numbers and percentage by numbers of each prey species per 10 stomachs, per size (mm) group (from Robb and Hislop, 1980).

Prey	20-29		30-39		40-49		50-59		60-69		70-79		80-89		100-109		110-119	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Calanus helgolandicus			3	3			8	43										
Calanus finmarchicus									1	4								
Temora longicornis									2	7								
Para/Pseudocalanus spp.	40	100	5	5	13	31												
Metridia lucens									3	11								
Centropages typicus					2	5					1	3						
Acartia clausii			11	10														
Caligus spp.					< 1	1			1	4	1	3						
Unidentified copepods											1	3						
Meganyctiphanes norvegica					7	17	< 1	2	1	4	1	3	3	18	10	33		
Thysanoessa inermis			2	2							<1	1						
Unidentifed euphausids			4	4	14	34			2	7	1	3	3	18				
Unidentified decapod larvae					1	2	2	11	1	4	<1	1						
Podon leucarti			42	39														
Evadne nordmani			38	35														
Hyperia galba									1	4	1	3						
Oikopleura spp.									8	30								
Trisopterus esmarkii							4	22	4	15	3	10	7	41	20	67	10	100
Unidentified fish			3	3	4	10	4	22	2	7	9	29	4	24				
Unidentified Polychaetes									1	4								
Crustacean eggs											13	41						

Table 3.6.4. Length of pelagic 0-group cod in different areas and different periods in June/July, data from the International 0-group Gadoid Survey (Daan *et al.*, 1980 & 1981; Heessen *et al.*, 1982).

Year	Area	Period	mean L	min	max
1980	Norwegian Deeps	12-15	4.5	2.5	5.9
		16-22	3.9	2.0	6.9
		23-30	4.2	2.0	7.4
	Scottish coast	12-15	3.4	2.0	4.4
		16-22	3.5	2.0	4.9
		23-30	3.6	2.5	4.9
	English coast	12-15	2.5	1.5	3.4
		16-22	2.6	1.0	4.9
		23-30	2.8	1.5	3.9
	Danish coast	16-22	2.1	1.0	3.4
		23-30	3.0	2.0	4.4
1981	Norwegian Deeps	05-13	3.7	1.0	7.4
		14-22	4.2	2.0	7.4
		23-30	4.6	2.5	7.9
	Scottish coast	05-13	3.4	2.0	5.4
		14-22	3.7	2.0	5.9
		23-30	3.3	2.0	4.9
	English coast	05-13	3.1	2.0	4.9
		14-22	3.4	1.5	6.4
		23-30	3.6	2.0	4.9
	Danish coast	14-22	5.1	1.5	7.9
		23-30	4.7	2.0	7.4
1982	Norwegian Deeps	14-22	4.5	2.0	7.0
		23-01	4.8	2.5	8.5
	Scottish coast	14-22	3.7	2.0	6.5
		23-01	4.2	2.0	7.0
		02-06	4.8	3.0	6.5
	English coast	14-22	3.2	1.0	4.0
		23-01	3.6	2.0	6.5
	Danish coast	14-22	3.3	2.0	4.5
		23-01	3.9	2.0	6.0

Table 3.6.5. Amounts (in '000 tonnes) of commercial fish species eaten by North Sea cod in 1981, total biomass of the prey species and the percentage eaten.

Prey	Amount eaten	Biomass prey	Percentage
cod (*Gadus morhua*)	25	313	8.0
whiting (*Merlangius merlangus*)	64	373	17.2
haddock (*Melanogrammus aeglefinus*)	61	469	13.0
herring (*Clupea harengus*)	29	465	6.2
sprat (*Sprattus sprattus*)	30	305	9.8
Norway pout (*Trisopterus esmarki*)	60	949	6.3
sandeel (*Ammodytidae*)	62	1297	4.8

Table 3.6.6. Growth parameters of North Sea cod

L(cm)	K (yr^{-1})	t_0 (yr)	Area	Author
115	0.3	0.8	total North Sea	Daan, 1974
123	0.23	-0.16	total North Sea	Macer, 1982
111	0.33	0.77	southern NS	Daan, 1974
108	0.37	0.84	southern NS	Van Alphen, 1984

Table 3.6.7. Mean length of immature and mature cod per age and per sex for the years 1981-1983. Data from the International Young Fish Survey.

		Males		Females	
Age	Year	immature	mature	immature	mature
1	1981	20.0	-	20.5	-
	1982	20.8	-	21.2	-
	1983	20.3	-	20.8	-
2	1981	32.2	41.1	32.6	35.2
	1982	37.1	44.6	37.5	40.9
	1983	39.1	40.0	39.4	47.7
3	1981	49.8	61.8	51.3	60.7
	1982	48.7	55.9	49.7	58.7
	1983	50.4	60.0	49.2	63.2
4	1981	65.8	75.6	67.7	77.1
	1982	62.4	74.1	63.5	76.2
	1983	63.7	74.0	67.2	77.3
5	1981	75.7	85.2	72.0	87.4
	1982	68.3	83.8	75.7	87.0
	1983	64.7	84.0	66.7	86.6
6+	1981	82.4	95.8	-	102.2
	1982	80.0	95.7	77.5	100.4
	1983	87.5	97.3	-	102.8

Table 3.6.8. Total natural mortality (mean for the period 1978-1982) according to the Multispecies VPA (Anon., 1987a).

Age	Natural mortality
1	0.758
2	0.361
3	0.226
4	0.200
5	0.200
6+	0.200

Table 3.6.9. Length at 50% maturity for males and females for the total North Sea and for the northern and southern North Sea separately (roundfish sampling area 1 and 6 respectively). Data from the International Young Fish Survey.

	Males			Females		
Year	Total	Area 1	Area 6	Total	Area 1	Area 6
1981	62.0	60.9	57.4	65.8	63.7	61.7
1982	63.2	64.9	55.4	70.2	74.6	64.3
1983	64.9	71.1	64.9	71.6	73.7	72.2
1984	64.3	69.7	59.5	70.0	69.2	66.5
1985	66.8	69.9	56.8	72.4	74.1	69.0
1986	64.9	69.8	48.8	76.7	80.5	47.7
1987	64.8	65.8	63.0	69.0	71.5	66.4
1988	60.7	61.7	62.1	65.4	66.6	64.1
1989	56.9	69.9	52.1	60.8	67.2	56.9

Table 3.6.10. Relative fecundity in eggs per g body weight (data 1970-1972 from Oosthuizen and Daan (1974); (data 1987-1988 from Heessen unpublished).

Year	Southern and central North Sea	Northern North Sea
1970	541	-
1971	477	-
1972	501	-
1987	634	-
1988	617	668

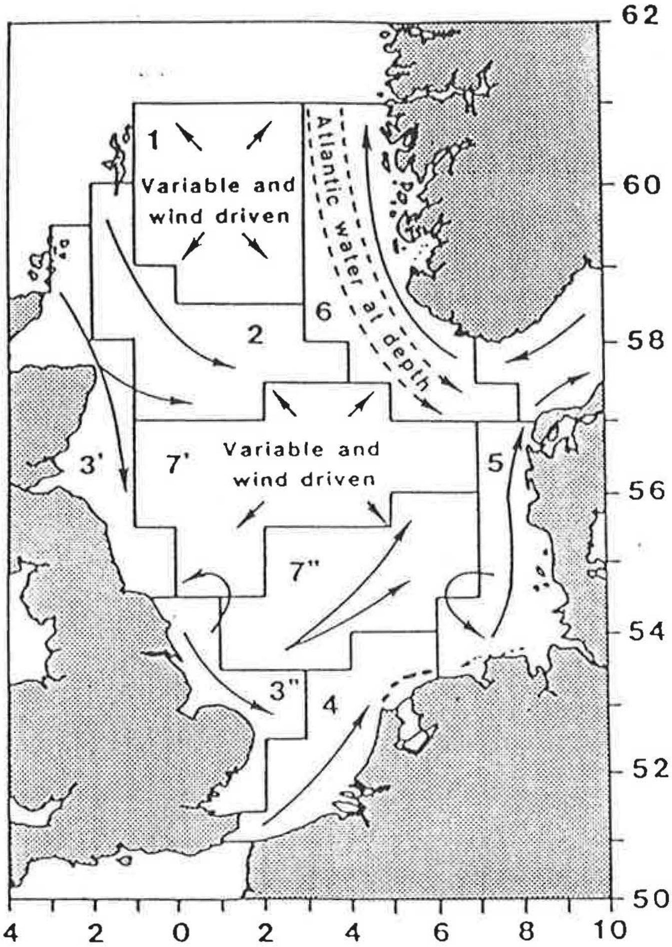


Figure 3.6.1. The North Sea can be divided into seven flushing time boxes, which take account of the hydrographic and biological conditions (Anon.,1983).

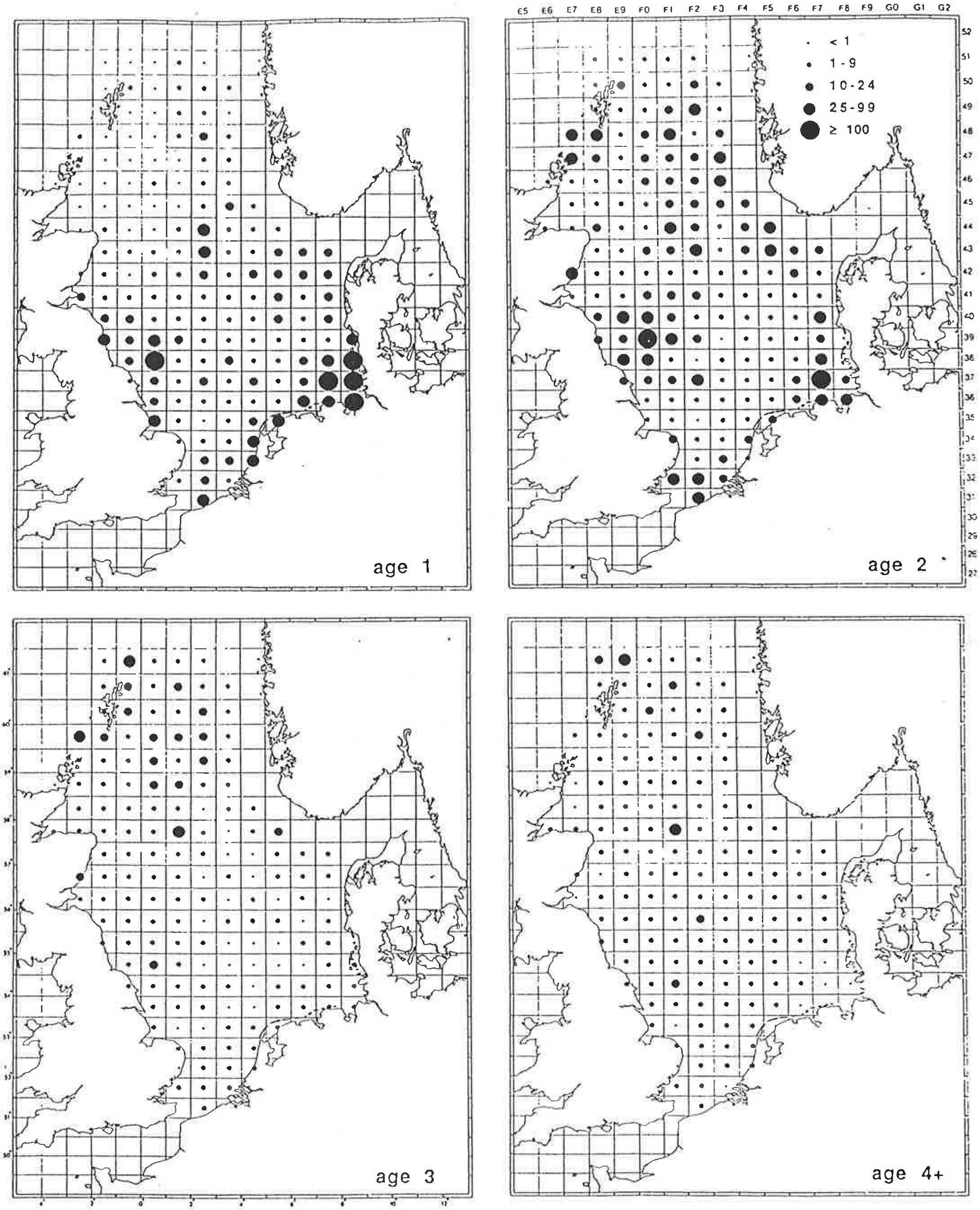


Figure 3.6.2. Distribution of cod of different ages from 20 years of February Young Fish Survey catches.

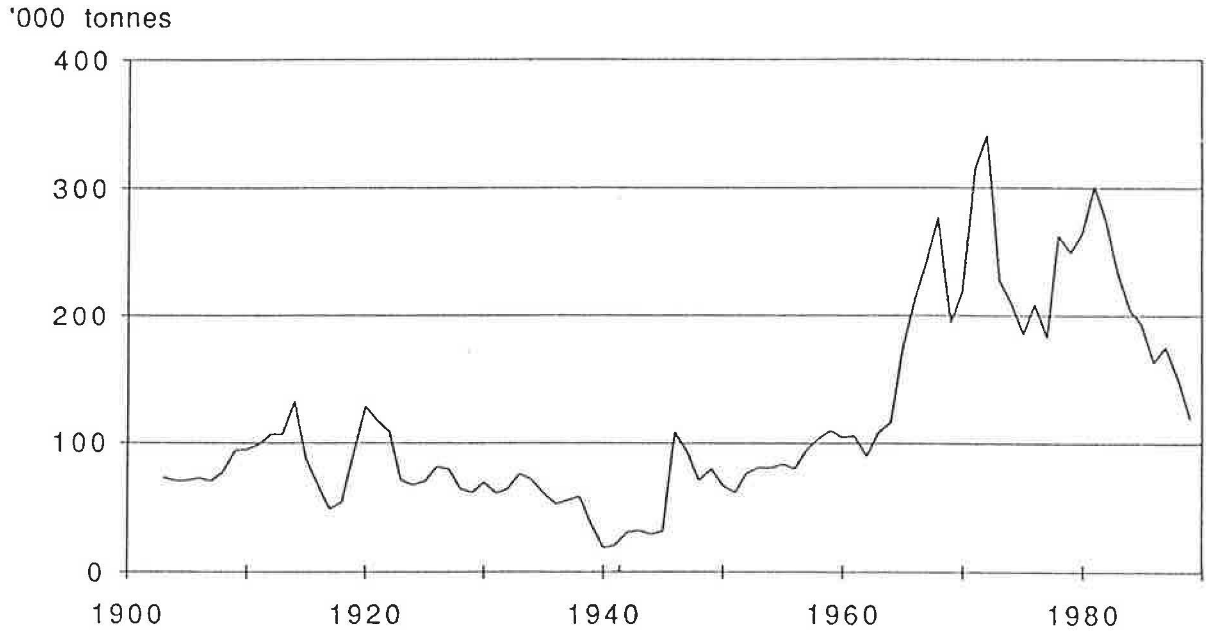


Figure 3.6.3. Total international landings of cod from the North Sea (ICES Div 4)

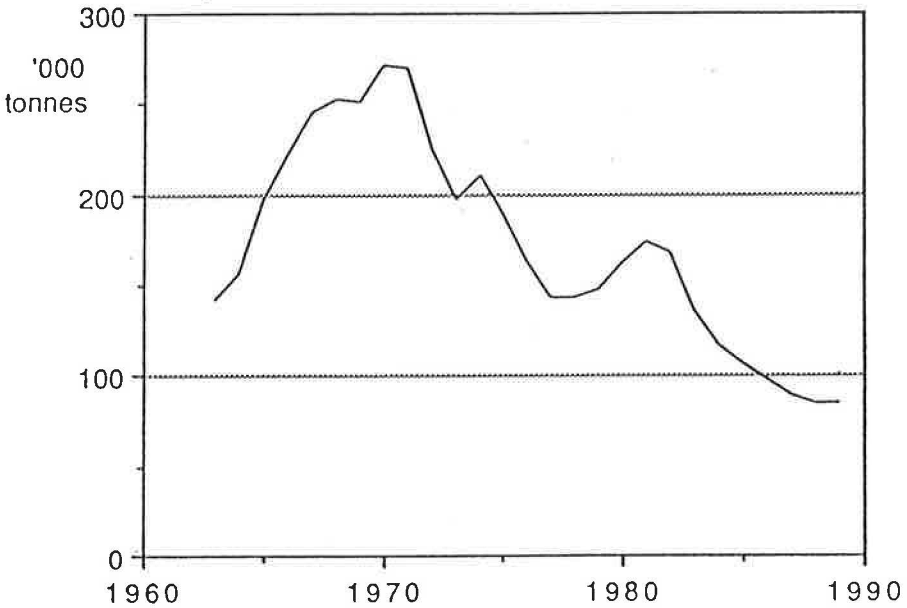


Figure 3.6.4. Estimated spawning stock biomass from VPA.

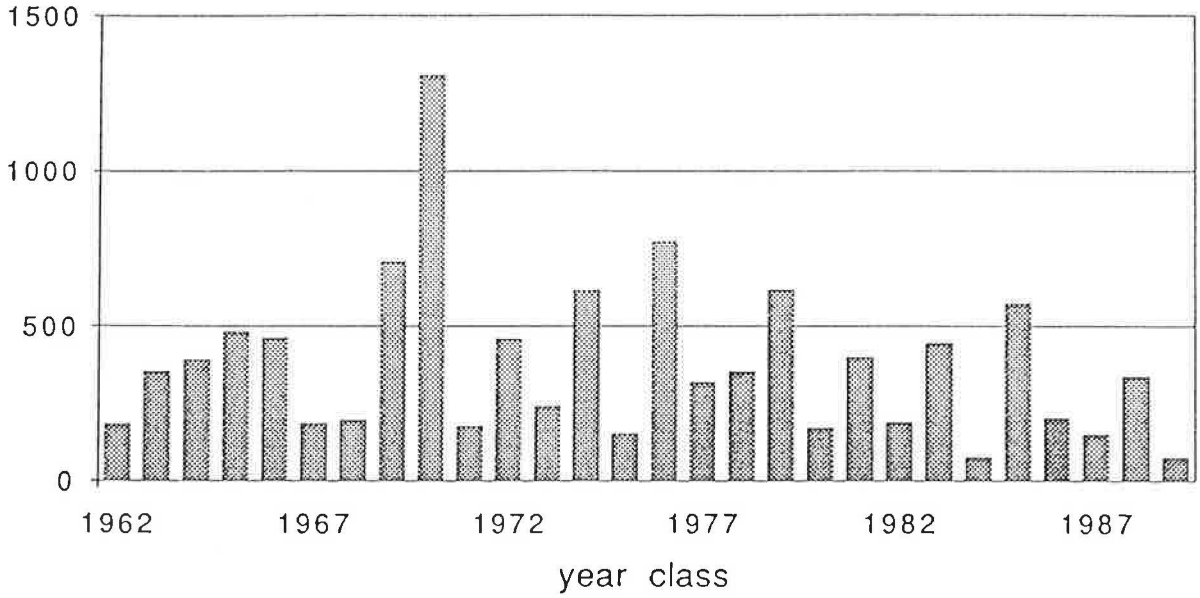


Figure 3.6.5. Recruitment index .From Rijnsdorp *et al.*, (1991).

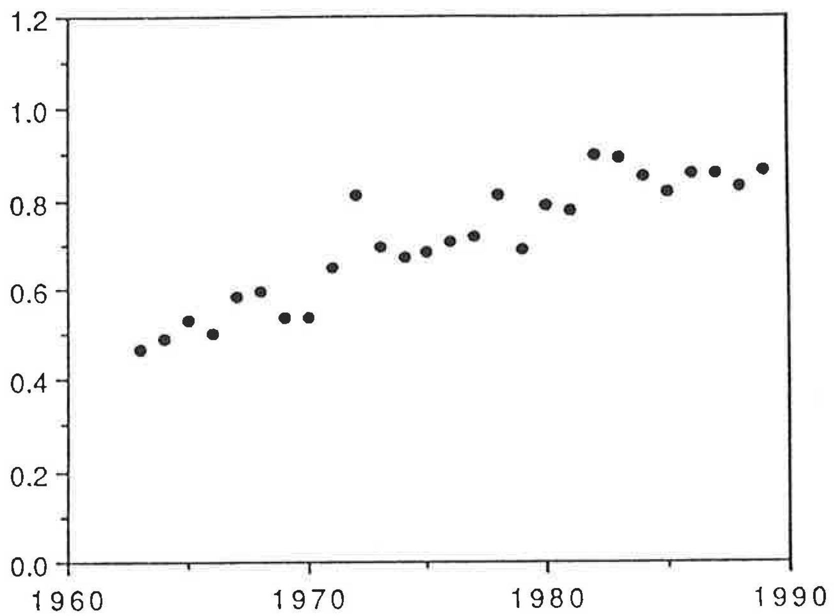


Figure 3.6.6. Fishing mortality for North Sea cod estimated from VPA.

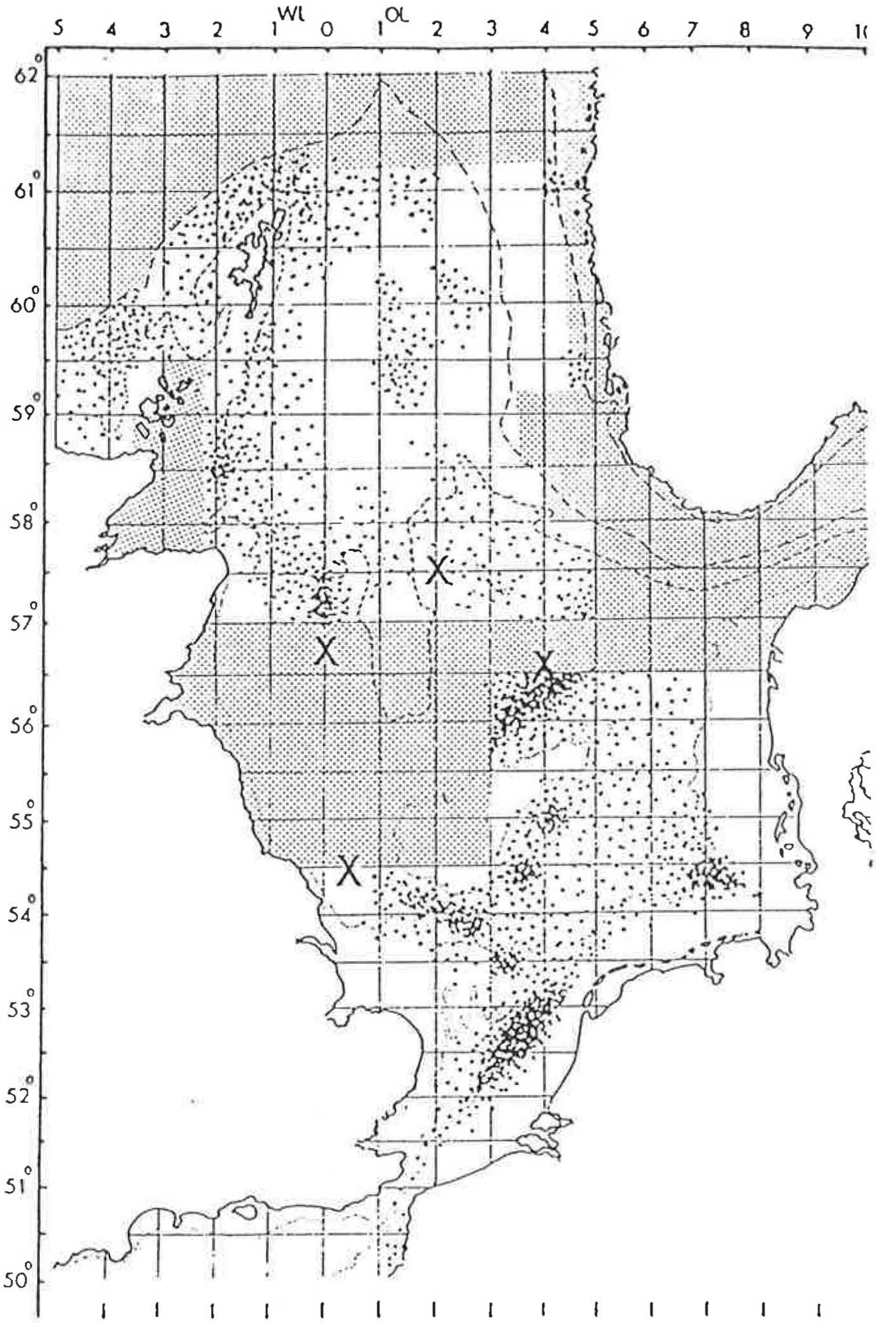


Figure 3.6.7. Distribution of cod spawning in the North Sea.

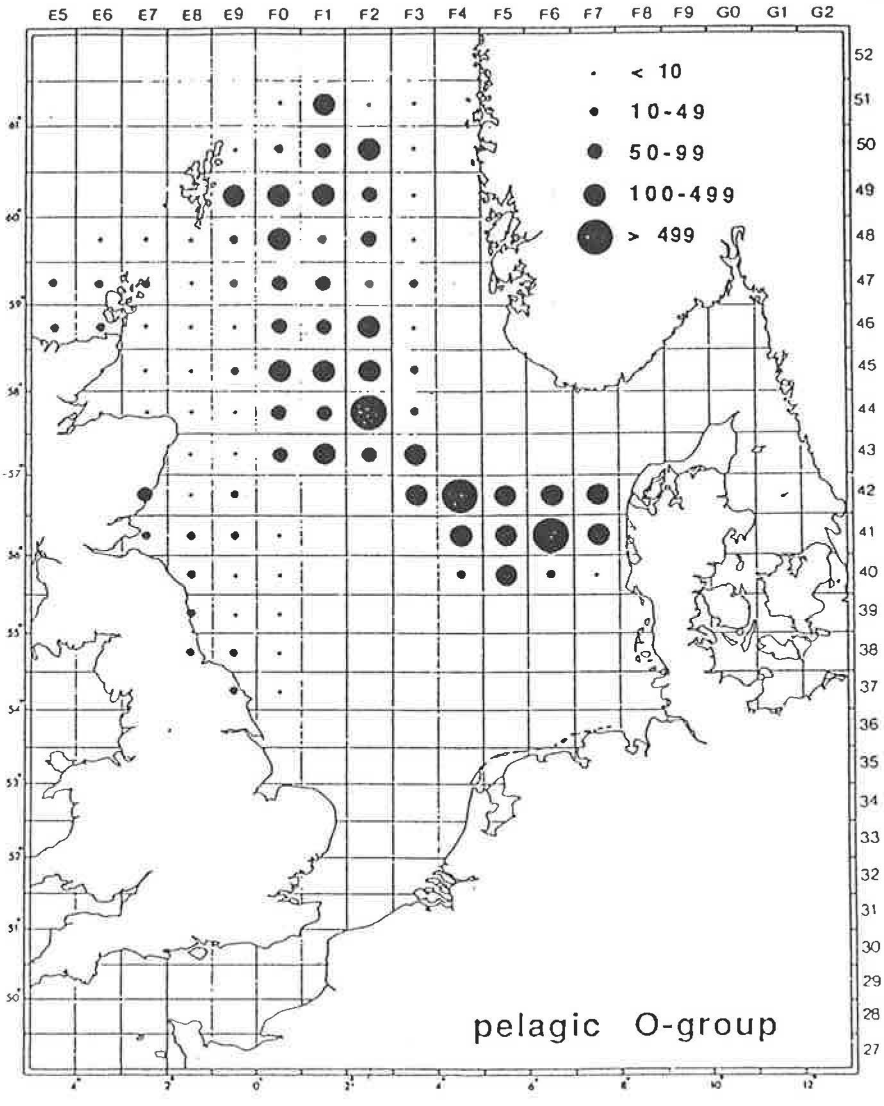


Figure 3.6.8. Distribution of pelagic 0-groups in the North Sea. Average catches in June - July 1974-83.

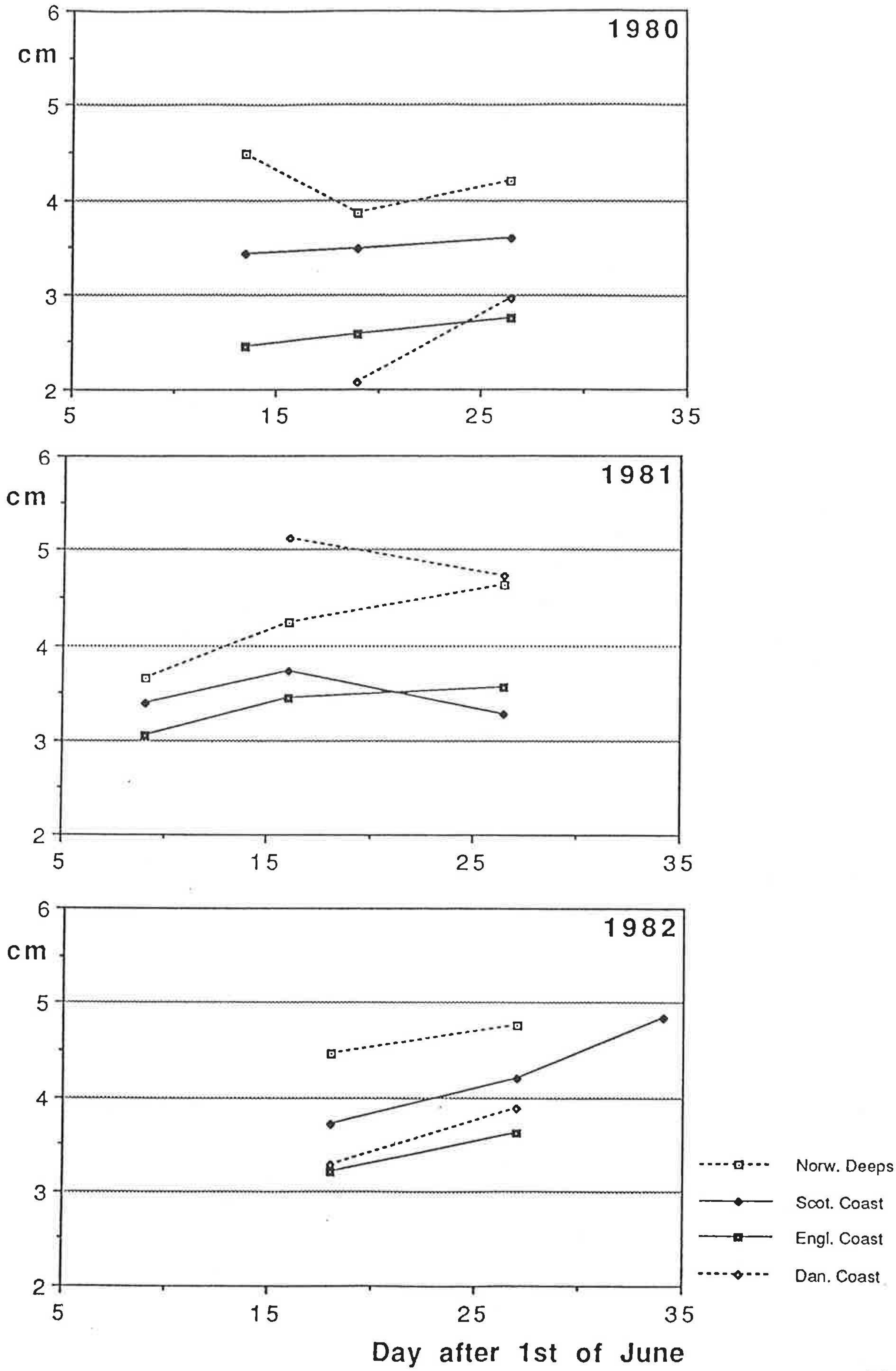


Figure 3.6.9. Mean lengths of pelagic 0-group cod.

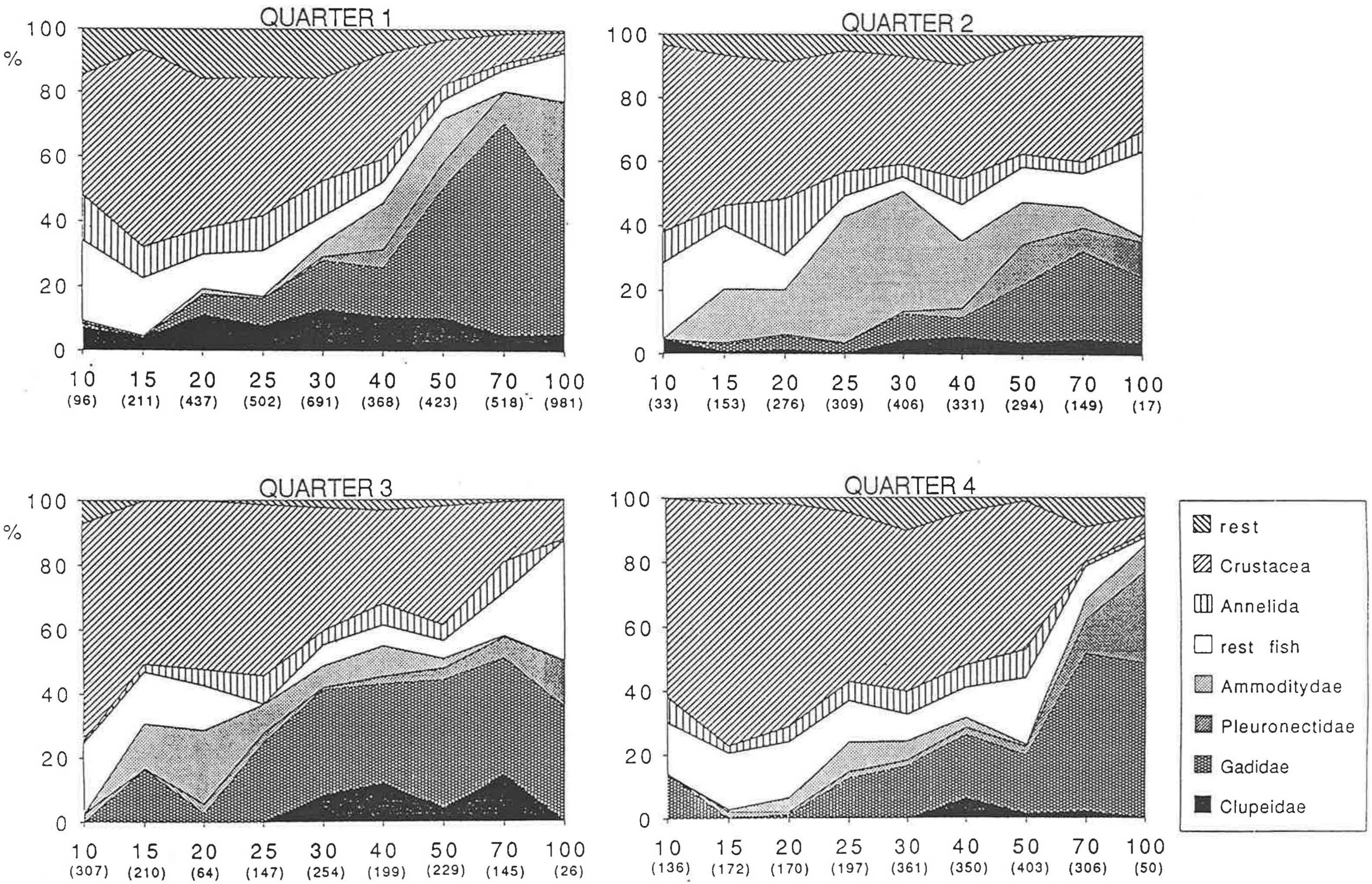


Figure 3.6.10. Feeding data for 1981, by size group for the whole of North Sea (Daan, 1989).

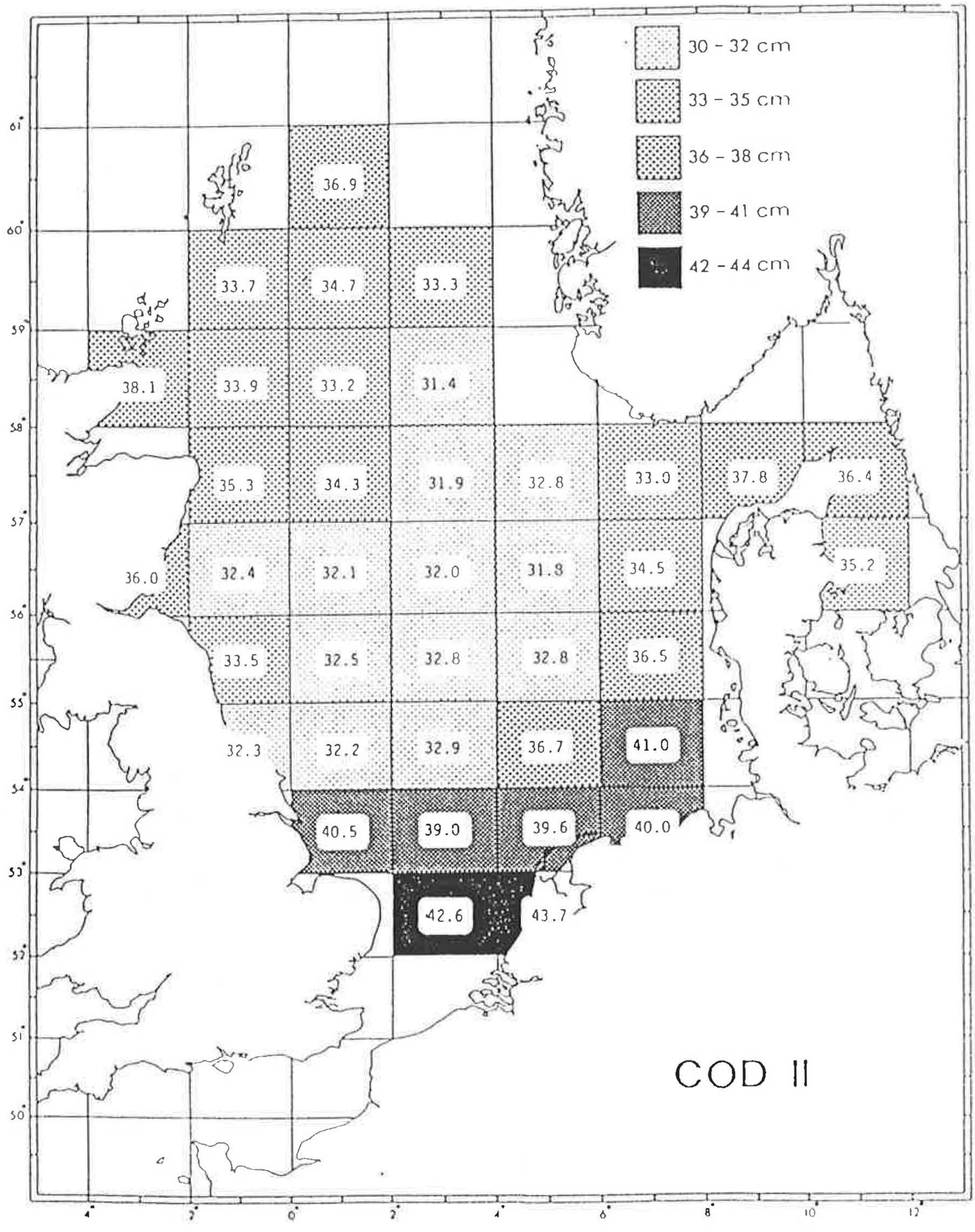


Figure 3.6.11. Spatial differences in size at age (van Alphen and Heessen, 1984).

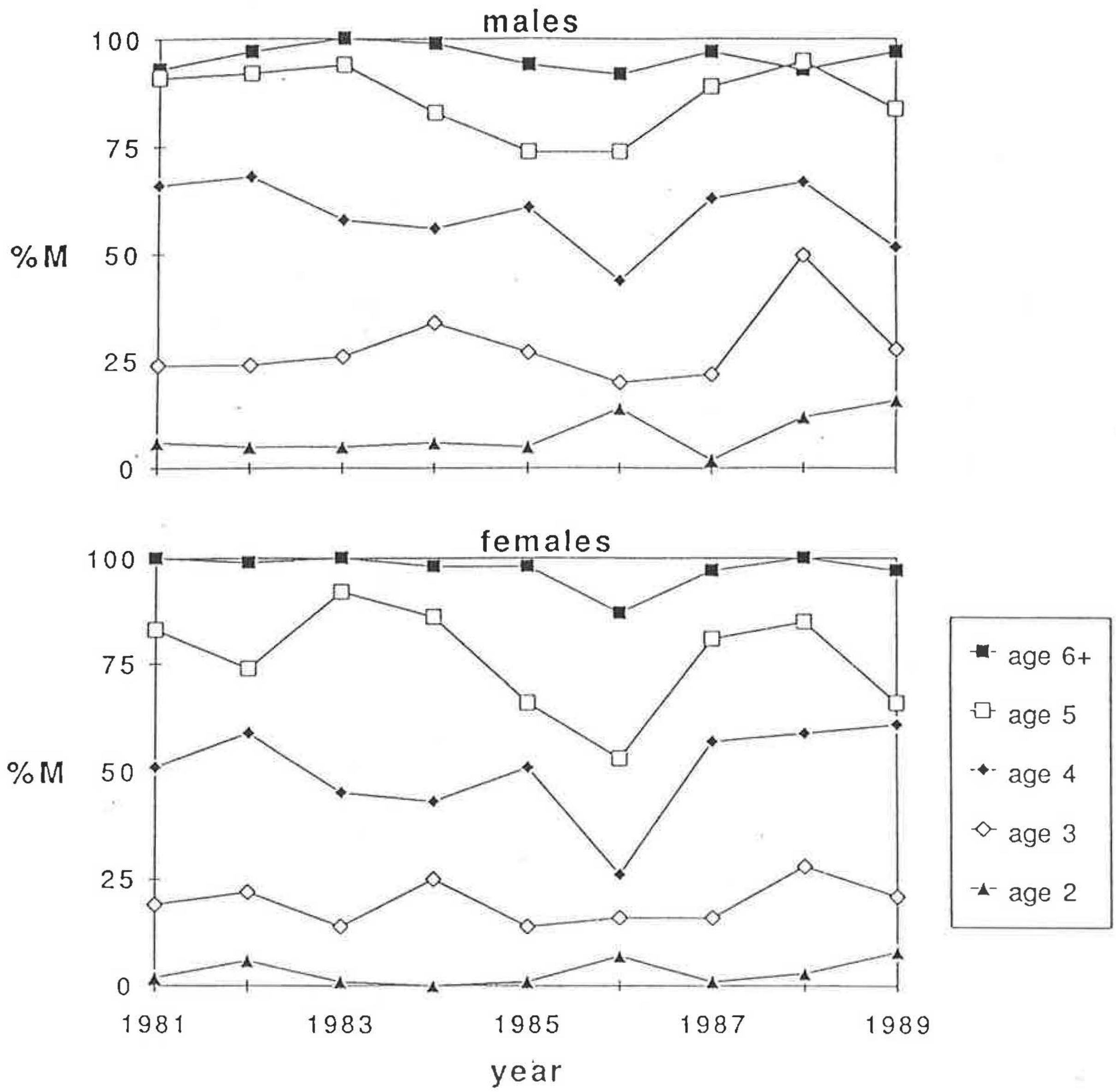


Figure 3.6.12. Proportion of fish which become mature in each age group.

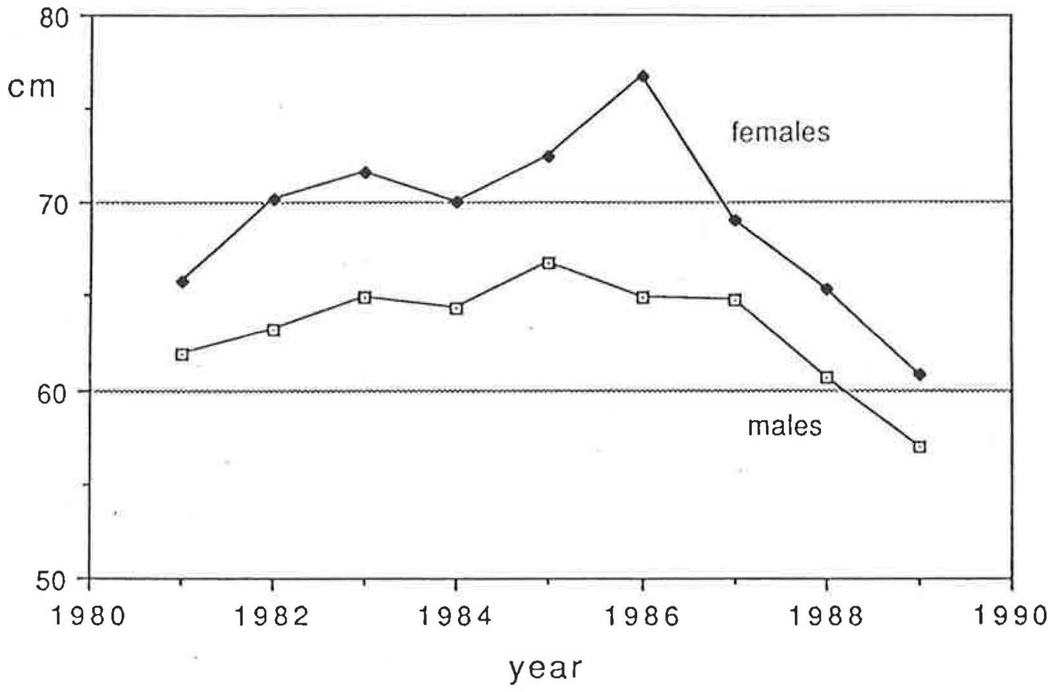


Figure 3.6.13. Length at 50% maturity.

3.7 IRISH SEA, CELTIC SEA AND ENGLISH CHANNEL COD

3.7.1 Species, stock and area of distribution

Evidence for stock discreteness

Evidence that the stocks within the Irish Sea are discrete comes mainly from the results of tagging experiments carried out during the 1970s and reported by Brander (1975). These show that mature fish tagged on spawning grounds in the northeast and northwest Irish Sea and in the Bristol Channel are recaptured from the same sites in subsequent spawning seasons. During the rest of the year there is some migration out of the Irish Sea to the south, but very few recpatures of fish which have crossed the 5 degree West longitude in either direction. Immature fish tagged in various parts of the Irish Sea (including Belfast Lough) are recaptured over a much wider area than are the mature fish and there is evidence of a substantial migration into the Celtic Sea and round the north and west of Ireland. Once these fish mature however they are recaptured mainly on the Irish Sea spawning grounds. Extensive tagging of cod West of Scotland has produced no recaptures from the Irish Sea at all.

A limited amount of tagging on the spawning areas in the Bristol Channel produced recaptures over a wide area, including the Clyde and the North Sea, but the majority came from the Celtic Sea itself.

Large numbers of 30-49 cm cod were tagged in the eastern English Channel. 40% of the recaptures were from the southern North Sea and 5% from the western Channel (Bedford 1966; Parnell unpublished data). On the other hand only 1.9% of cod tagged in the southern North Sea were returned from the eastern Channel and only 0.2% from the western Channel.

The genetic evidence is very limited and equivocal. Haemoglobin (HbI) allelle frequencies are for the most part similar all around the British Isles, but with a few unusual samples (see Table 3.7.1 from Jamieson and Birley 1989). However Glucose phosphate isomerase allelle frequencies gave evidence of separate populations in the eastern and western Irish Sea (Child 1988).

Units for which assessment of spawning stock biomass and recruitment are available

Assessments of the Irish Sea cod stock (ICES sub-division VIIA) have been carried out by an ICES Working Group since 1978 and virtual population estimates go back to 1968 (see Table 3.7.2). Some data for earlier years are also available from catch per effort analysis (Brander 1975). Young fish surveys have been carried out in September/October of each year since 1979 (Brander and Symonds 1984) and allow a prediction, which accounts for 60% of the variance, to be made of the number of one year old fish entering the VPA. Thus most of the observed variability in year class size is determined by autumn of the first year of life. The variability in year class size for this stock is quite small - the biggest and smallest year classes differ by a factor of about 5. Fluctuations in Irish Sea cod year classes do not appear to match those in the North Sea, but are similar to those in the Celtic Sea.

Assessments of the Celtic Sea cod stock (ICES sub-divisions VIIF+G) have been carried out by an ICES Working Group since 1981 and virtual population estimates go back to 1971 (see Table 3.7.3).

Stock assessments have been carried out for the English Channel in the past, but are considered to be unreliable because catch data are unreliable.

3.7.2 Location and timing of spawning

Irish Sea stocks

About half of the spawning for this stock occurs in the northwest Irish Sea, close to the mouth of Carlingford Lough, during the first two weeks in March (Brander 1975; Nichols et al. 1993, Brander 1994). Spawning seems to occur first in the cooler, less saline inshore water mass close to the Irish coast, where primary production starts early. In the northeast Irish Sea the water temperature is one or two degrees lower, primary production gets underway later and spawning is two or three weeks later than in the northwest. The precise location of spawning in relation to the fronts and the timing and nature of the production cycle are currently being investigated, as is the growth and survival of cod larvae. Some information is available on condition factors, nutritional status and feeding of cod larvae during development (Thompson and Harrop 1991).

Other species which spawn in the same general area as cod include sprat, dab, whiting and *Nephrops norvegicus* (Nichols et al. 1993). Cod begin spawning relatively early in spring. In 1993 and 1994 haddock larvae occurred more frequently than before. Cod larvae are most abundant in the coastal, stratified and frontal areas of the northwest Irish Sea and much less common in the mixed areas. In the northeast Irish Sea spawning also occurs close to the front separating coastal and offshore water. Circulation in both areas is complex and influenced by winds, but larvae do not appear to be transported very far from the spawning locations (Brander and Symonds 1984). It is not clear whether larvae from the two sides of the northern Irish Sea become mixed.

Celtic Sea

The principal spawning area in ICES sub-divisions VIIF+G seems to be in the Bristol Channel, although there is evidence that spawning also occurs off the south coast of Ireland. Perhaps the most striking feature of the Bristol Channel spawning is that it takes place relatively late in the year (mean date 24 March), considering that this is one of the most southerly spawning areas in the NE Atlantic and that the mean water temperature is 10°C during this period. The lateness of spawning may be due to the late production cycle in this area, because of strong tidal mixing (Brander 1994).

English Channel

In contrast to the Bristol Channel, spawning in the English Channel is very early (mean date 29 January). The mean temperature during spawning is around 8°C and the production cycle is early, particularly in the Bays of the Somme and the Seine, where cod spawning begins. There is also some spawning in the western English Channel, but compared with other areas around the British Isles the quantity of eggs in this most southern spawning ground (50 degrees North) is very small (Brander 1994).

3.7.3 Fecundity and maturity

No information is available on the fecundity of cod in the Irish Sea, but a study is planned.

62-83% of 2-year old cod caught on the spawning grounds in the Irish Sea during the spawning season were mature, as were all the older fish. However in order to estimate the population maturity it is necessary to know what proportion of each age group were on the spawning grounds and what the maturity stages were of fish elsewhere. Almost all 2- and 3-year old fish caught away from the spawning area were immature. A rough estimate, which takes account of differences in size-at-age, indicates that about 17% of all 2-year old cod and about 85% of all 3 year old cod were mature (Brander 1975). No information is available for the Celtic Sea or the English Channel.

3.8 SKAGERRAK COD

3.8.1 Species, stock and area of distribution

Some evidence of discreteness from tagging and genetic studies. Assessments are carried out for ICES sub-division IIIA.

3.8.2 Timing and location of spawning

Spawning occurs in coastal areas from February to April.

3.8.3 Fecundity and maturity

Egg size 1.1-1.7 mm. Unpublished data on specific gravity of eggs 1.0238 - 1.0271. Incubation of eggs takes 14 days at 6°C. Size at hatching is 4 - 5 mm.

Some data on rates of larval development - 15 days at 6°C; 5 days at 18°C.

3.9 BALTIC COD

3.9.1 History

In historical time cod has occurred in the Baltic for at most some 7500 years. Before that the Baltic had a freshwater stage, but as the land uplift was higher in the northern than in the southern part, a new connection with the ocean was established through the Danish sounds. In the initial phase of this latest sea stage the water was more saline than at present in the Baltic Sea (Voipio, 1981).

At present cod are regarded as two well separated stocks, a small stock SW of Bornholm (the western stock) and a large one inhabiting almost all the rest of the Baltic Sea (the eastern stock). As reviewed by the Working Group on Assessment of Demersal Fish in the Baltic (WGADFB) in 1990 (Anon., 1990b) these two stocks seem to be separated quite distinctly from each other and from the Division IIIa (Kattegat) stock as well.

Before the World War II the exploitation of cod in the Baltic Sea was very limited but increased rapidly during and just after the war (Table 3.9.1). The increased fishing intensity caused a reduction in the cod stock and a decrease of the mean age but also an increase in growth rate (Table 3.9.2). In Table 3.9.1 the catch for at least one country (FRG) is given as gutted weight, and discards are not included (Bagge, 1981). Table 3 is from the 1990 report of the WGADFB and shows the total catch in Subdivisions 22-32 (Figure 3.9.1) in round fresh weight including discards for at least some countries. In Figure 3.9.2 the catch is shown together with fishing moratlity for the latest 20 years. It is obvious that the present fishing mortality is much too high, by far exceeding F_{max} (ca. 0.3) (Anon., 1990b).

The peak catch in 1984, almost 450,000 tonnes, is the result of several good year-classes. For some countries the cod fishery is the most important one, e.g. for Sweden the value of the cod catches (95% in the Baltic) was 46% of the value of the total landings (Baltic and the west-coast).

In 1975 quotas for cod were introduced by the International Baltic Sea Fishery Commission together with a minimum landing size of 30 cm and a minimum mesh size of 90 mm in cod trawls. It has not been possible to agree on a TAC every year and when an agreement was reached it has always been on a higher level than the advice from ICES. The minimum landing size and mesh size were raised to 33 cm and 105 mm on 1 January 1990.

From the peak in 1984 the catches have gradually decreased to an average level, in 19I89 well below the long-term average. This is in accordance with the predictions by the WGADFB and a result of sequence of poor year-classes. Due to environmental conditions the reproduction areas have been severally reduced in the latest years, resulting in still poorer year-classes and consequently further reductions of catches to be expected in the years to come (Larsson, in press).

3.9.2 General structure of the stock

Reliable time series on stock abundance are available only from about 1970. As reflected in the catches (Figure 3.9.2) there was a peak in abundance in the early 1980s as an effect of rich year classes especially in 1976, 1977, 1979 and 1980.

The western stock has a small area of distribution and seem to be more randomly distributed over that area as adults, apart from aggregations during spawning.

The eastern stock has a limited area of reproduction (Figure 3.9.3) but from that area cod spread over almost the whole Baltic Sea. In the Bothnian Sea and Bay the density is however much lower. With average size of year-classes total catches in that area are a few hundred tonnes, but e.g. the good year-classes mentioned above (1976-80) gave rise to a stock permitting about 10,000 tonnes a year for a few years (Modin, 1987). Three such episodes are known from this century, 1915-16, 1940-42 and 1987-88. Spawning occurs in the Bothnian Sea but in that low salinity (< 7‰ in the bottom water) the eggs do not survive. Some adults migrate to the main spawning areas in the southern Main Basin (Otterlind and Norberg, 1988). The relatively small area where successful spawning is possible has prevented the development of sub-stocks.

3.9.3 Fishing pattern

The main gear used for cod fishing has been trawl, with a small and gradually decreasing proportion taken by set-nets and long-lining. At first only bottom-trawls were used but from the mid 70s pelagic trawling has become more and more important, partly because the deteriorating oxygen-situation in the bottom water has made spawning more pelagic.

As mentioned above fishing mortality has for long been far too high, F varying from 0.5 to 1.2 during the latest 20 years (Figure 3.9.3).

3.9.4 Environment

The Baltic Sea is brackish with a surface salinity increasing from almost freshwater in the north to 8-9‰ in the south. In the Main Basin there is a halocline at 60-70 m depth and below that the salinity normally is 10-16‰. The outflow from the Baltic Sea, forming the Baltic current in the Kattegat, is entirely made up of low salinity surface water. The water masses below the halocline are rather stagnant causing frequent oxygen deficiencies in the deeper basins. Periods with oxygen deficiency and formation of hydrogen sulphide have occurred more often and with longer duration in the latest decades, presumably as a result of eutrophication (Fonselius, 1977; Grasshoff and Voipio, 1981).

The salinity is maintained by frequent inflows of oceanic (deep) water from the Kattegat. In 1977 there was a major such inflow raising the salinity and the oxygen concentration in the deep basins of almost the whole Baltic Sea. Since then there has been only one average inflow in 1980 and small one in 1983. The development of the salinity since 1975 can bee seen in Figure 3.9.4 (After Juhlin, 1990).

The combined effect of low salinity from the surface and no or low oxygen concentration from the bottom creates a "reproduction volume", where both parameters have sufficient levels. In the latest two or three years there seems to have been no such volume in the two eastern of the three main spawning areas in the Baltic Sea (Anon., 1990b).

The regional climate is characterized by warm summers and cold winters creating high surface temperatures in summer and ice-cover of substantial parts of the Baltic Sea in winter, normally at least the Bothnian Sea and Bay, in some years the whole of the Baltic Sea.

The Baltic Sea has a very low species diversity. Apart from cod there are no gadoids, except occasional visitors from the Kattegat of haddock and whiting. Other visitors are e.g. mackerel, garpike (also spawning in the Baltic, but not staying there permanently as adults) and a number of species in very low numbers. The most important resident fish species in addition to cod are herring, sprat, salmon, trout, flounder, plaice, dab, turbot, sticklebacks, gobids, sandeel and eel. Also a number of freshwater species inhabit at least the coastal areas of the Baltic Sea (Voipio, 1981).

Other biota are also represented by few species but the total biomass is large, and primary production is transferred efficiently to the top predators. In a comparison with the ecosystem in Cheasapeake Bay the production of fish in relation to primary production the Baltic Sea system proved to be 3-5 times as efficient (Wulff and Ulanowicz, 1989). A large proportion of the total biomass is made up of *Mytilus edulis*, which does not grow as large as in the oceans, but covers vast areas of cliffs not inhabited by seaweeds normally doing so in the oceans. Another common invertebrate is *Mesidothea entemon*, a crustacean (Isopoda) specialized on brackish water and growing to about 12 cm in length (Voipio, 1981).

Apart from a low number of seals, cod has no natural enemies in the Baltic Sea as adults.

3.9.5 Spawning

Spawning is restricted to areas where there exist "reproduction volumes" as described above. For the western stock the main spawning area is in the Arkona Deep just north of Rügen at a depth of 40-50 m.

The eastern cod stock has three main spawning areas, the Bornholm Deep (minimum spawning depth 60 m), the southern part of the Gotland Deep and the Gdansk Deep (minimum spawning depth 80 m) and a minor area in the Slupsk Furrow (Figure 3.9.3).

To compensate for the sometimes critical abiotic conditions, the spawning season of the eastern stock in the Baltic Sea is very long. It begins in March and ends in August. In the Bornholm area it begins in February. The western stock has a more normal period, February-April. There is quite a variation from year to year and between areas, probably depending on temperature, salinity and oxygen conditions. The variation is exemplified in Table 3.9.4 (From Bagge, 1981).

From a large number of tagging experiments the migrations of cod in the Baltic Sea are rather well known. Even from long distances cod migrate to the main spawning grounds. In the Bothnian Sea spawning occurs (without result) but a number of cod (at least 10%) migrate all the way to the southern Main Basin (Bagge *et al.*, 1974; Otterlind and Norberg, 1988).

3.9.6 Egg and larval stages

Marine fish species in the Baltic Sea are slow growing but have a higher fecundity. In the North Sea a female cod 75 cm long produces an average of 1,830,000 eggs but in the Baltic Sea 3,660,000 eggs, in spite of the eggs being larger in the Baltic cod, 1.7-1.8 mm compared to 1.45 as an average for the North Sea cod (Bagge, 1981).

A part of the Baltic cod mature at an age of 2 years and all when 3 years old. In the northern parts they mature later.

The eggs of the eastern stock have a neutral buoyancy at a salinity of 11-14‰ and of the western stock at 13-16‰. That means the eggs will stay at the spawning depth or sink to the bottom or down in oxygen-free water and die. The same applies to the newly hatched larvae but when they are able to swim and regulate the swim-bladder pressure (10-15 mm) they approach the surface. At that time they are normally moved by the main surface current. That current has an anticlockwise direction and most of the larvae are transported to the Polish and Soviet coasts (Bagge, 1981).

The larvae and juveniles stay close to the coasts but not in as shallow waters as in the oceans, probably because the water has too low salinity in shallow coastal areas of the Baltic Sea (Bagge, 1981).

3.9.7 Juveniles

Very little is known about the biology of juvenile cod in the Baltic Sea. In young cod surveys juveniles (8 months-1 year) are found almost everywhere in the Baltic Sea, but predominantly at depths between 30 and 50 m.

To improve the knowledge about this stage an *ad hoc* Working Group on Young Fish Surveys in the Baltic was set up by ICES, after two meetings transformed to a Study Group, which has had another two meetings. The group has so far concentrated on young cod rather than real juveniles.

3.9.8 Adults

The von Bertalanffy growth parameters which are considered relevant for the Baltic cod are: L_∞ = 105.0 cm, k = 0.15, to = 0.5 (Bagge, 1981).

The od feed all year, except in very severe winters. The feeding of mature female cod is especially intensive under maturity stage IV. During stages V and VI feeding decreases but never ceases. For males feeding decreases during the stages IV-VI.

Food composition has in several investigations been very similar. Cod < 30 cm feed mainly on crustaceans like *Mysis* spp., *Pontoporeia* spp., *Mesidothea entomon* and the polychaete *Harmothoe sarsi*. Fish play a minor role as food except in spring when 20-30 cm cod eat 15-30% sprat by weight.

For cod > 30 cm fish are more important as food, especially sprat, which during the first 6 months of the year constitute 30-40% of the cod food, herring 9-25% and other fishes 2-10%. The corresponding figures for the second half year are 6-9%, 3-25% and 2-7% respectively. The invertebrates are still important as food. The first 6 months *Mesidothea* constitute 19-21%, *Mysidacea* 2-8%, other crustaceans 2-6% and *Harmothoe* 12-23% of the food. The corresponding figures for the second half of the year are 28-44%, 11-37%, 2-7% and 6-13% respectively (Bagge, 1981).

Cannibalism is rarely registered.

The food and feeding of cod in the Bothnian Sea is less well known but it is clear that fish are less important and *Mesidothea* totally dominate.

Several attempts have been made to calculate the annual consumption by cod. Uzars (1975) estimated it to be 2,995,000 tonnes of which 276,000 tonnes of herring and 408,000 tonnes of sprat. Danish investigations (Bagge, 1981) resulted in an estimate of 1,112,000 tonnes (315,000 tonnes of herring and 266,000 tonnes of sprat).

BALTIC COD

Table 3.9.1 Total catch of cod in the Baltic 1935, 1943, 1951 and 1965-1977.

Year	Denmark	Finland	German Dem. Rep.	Fed. Rep. Germany	Poland	Sweden	USSR	Total
1935	1,700	-		3,000	500	5,000	1,000	11,200
1943	9,900	-		53,100	-	11,900	6,100	81,000
1951	11,700	-	8,000	3,200	51,200	20,500	46,900	41,500
1965	21,450	23	8,186	5,203	41,498	19,523	22,420	118,303
1966	22,658	26	6,671	3,297	56,007	20,415	38,270	147,344
1967	25,839	27	16,839	2,520	56,003	21,367	42,980	165,575
1968	28,320	70	19,381	4,808	63,245	21,895	43,610	181,329
1969	29,371	58	21,802	7,217	60,749	20,888	41,580	181,665
1970	28,014	70	13,604	6,954	68,440	16,467	32,250	165,799
1971	30,000	53	7,375	4,562	54,151	14,251	20,910	131,302
1972	42,000	76	9,160	4,985	57,093	15,194	30,140	158,648
1973	44,650	95	10,404	15,873	49,790	16,734	20,083	157,629
1974	39,510	160	7,948	12,226	48,650	14,498	38,131	161,123
1975	46,543	298	11,271	12,465	69,318	16,033	49,289	205,217
1976	57,094	287	7,260	14,313	70,466	18,388	49,047	216,854
1977	55,749	310	9,990	19,899	47,702	16,061	23,767	173,478

Table 3.9.2 Mean age and length of Baltic cod in various periods

Period	Kiel Bay	Bornholm Deep	Gdansk Deep	Gotland Deep
Mean age				
1929-1938	4.77	4.51	4.74	5.95
1939-1944	2.77	4.22	3.48	4.48
1946-1957	2.02	3.58	3.71	4.33
1960-1967	1.59	3.60	3.68	3.78
1965-1977	2.34	3.57	3.94	4.00
Mean length of age group III				
1931-1938	38	35	35	34
1953-1956	44	42	41	41
1962-1965	44	38	38	-
1974-1977	44	41	36	-

Table 3.9.3 Total catch of Baltic cod (Subdivisions 22-32) 1965-1989. (Working Group on Assessment of Demersal Fish in the Baltic)

Year	Denmark	Finland	German Dem. Rep.	Germany Fed. Rep.	Poland	Sweden	USSR	Faroe Islands	Total
1965	35,313	23	10,680	15,713	41,498	21,705	22,420	-	147,352
1966	37,070	26	10,589	12,831	56,007	22,525	38,270	-	177,318
1967	39,105	27	21,027	12,941	56,003	23,363	42,980	-	196,446
1968	44,109	70	24,478	16,833	63,245	24,008	43,610	-	216,353
1969	44,061	58	25,979	17,432	60,749	22,301	41,580	-	212,160
1970	42,392	70	18,099	19,444	68,440	17,756	32,250	-	198,451
1971	46,831	53	10,977	16,248	54,151	15,670	20,910	-	164,840
1972	59,717	76	13,720	15,516	57,093	16,471	30,140	-	192,733
1973	66,050	95	14,408	28,706	49,790	18,389	20,083	-	197,521
1974	57,810	160	10,970	22,224	48,650	16,435	38,131	-	194,386
1975	62,524	298	14,742	24,880	69,318	17,965	49,289	-	239,016
1976	77,570	287	8,552	26,626	70,466	20,188	49,047	-	252,736
1977	73,505	310	10,967	30,806	47,702	18,127	29,680	-	211,097
1978	50,611	1,437	9,345	15,122	64.113	16,793	37,200	-	194,621
1979	59,704	2,938	8,997	19,375	79,754	23,093	75,034	3,850	272,745
1980	75,529	5,962	7,406	18,407	123,486	33,201	124,350	1,250	389,591
1981	92,648	5,681	12,936	18,281	120,901	44,330	87,746	2,765	385,288
1982	91,927	8,126	11,368	21,860	92,541	46,548	86,906	4,300	363,576
1983	107,624	8,927	10,521	25,154	76,474	53.740	92,248	6,065	380,753
1984	113,701	9,358	9,886	42,031	93,429	65,927	100,761	6,354	441,447
1985	107,627	7,224	6,593	31,798	63,260	54,723	78,127	5,890	355,242
1986	98,464	5,633	3,179	22,422	43,236	49,572	52,148	4,596	279,250
1987	83,844	3,007	5,114	18,816	32,667	47,429	39,203	5,567	235,647
1988	74,742	2,904	4,634	18,295	33,351	54,968	28,137	6,915	223,946
1989[1]	65,935	1,843	2,147	15,342	31,815	52,397	14,722	4,520	188,771

[1] Provisional data

Table 3.9.4 Variation in spawning time as reflected by number of eggs found per sq. m in 1969, 1971 and 1973

	February	March	April	May	June	July	August
Bornholm Deep:							
1969	-	29	59	71	82	87	8
1971	-	10	57	50	13	23	6
1973	2	60	129	48	37	54	-
Southern Gotland Deep:							
1969	-	0	23	18	24	20	-
1971	2	0	4.5	5	4	6	3
1973	-	4	16	10	13	0	-

Table 3.9.5 Spawning and Egg Stage Data Summary (for the eastern stock the information refers mainly to the most important spawning ground in the Bornholm Basin, whereas for the western stock most information refers to the Kiel Bight).

Dates		Depths & Temperatures		Egg				
Mean	Duration	Adults	Eggs	Size[3)]	Sp. Gravity	Concentr.	Mortality	Total Product.
May-July[2] Müller & Bagge 84 Bagge & Steffensen 91 Wieland 88 & unpubl.	March-Aug	60-100 m 3-7° Kandler 44	60-80 m 3-7° Müller & Pommeranz 84 Wieland & Zuzarte 91	1.5-2.0 mm Nissling & Westin 91a Müller & Bagge 84	1010.5 Müller & Pommeranz 84 Wieland 88 Wieland & Zuzarte 91	1-3n/m^3	91.1-99.9 Bagge & Müller 77 Graumann 74 Wieland 88	3.5-6.6*10^{12}
March Kändler 44 Müller 70	Dec-May Hilge 72 Thurow 70	20-35 m 2-6° Kändler 44 & 50 Thurow 70	10-35 m 2-8°	1.25-1.7 mm Ehrenbaum Strodtmann 1904	1016.0 Ohldag et al. 91	<0.1-0.4n/m^3 Müller 88	?	?

2) a shift in spawning time from May to July has been observed in the end of the 80s and beginning of the 90s.

Table 3.9.6 Larval stage data summary

Size			Growth	Mortality	Date		Distance from
at hatch	at metamorph.	at settle	(cm/day)		at hatch	at metamorph.	spawn to settle
3.5-4.9m[4] Wieland & Waller unpubl.	?	?	?	?	13-14 days Nissling & Westin 91b Wieland & Waller unpubl.	?	?
2.5-4.0 mm[3] Müller 70	?	?	?	?	17-21 days Ohldag et al. 91 v. Westernhagen 1970	?	?

3) without correction for shrinkage due to sampling and fixation.
4) prior to fixation

Table 3.9.7 Adult stock and biological data summary

Stock	Mean Latitude	Maturity		Fecundity[1]
		50% Age	50% Length	
Baltic East	56°00	2.7 Weber 89	38-41 cm	500-2700 eggs/cm body length Berner 60, Müller & Schulz 88, Schopka 71, Strzyzewska 62
Baltic West	55°00	2.2-2.7 Thurow 70 Weber 89	35-42 cm	360-2300 eggs/cm body length Botros 62

1) length range 35-65 cm

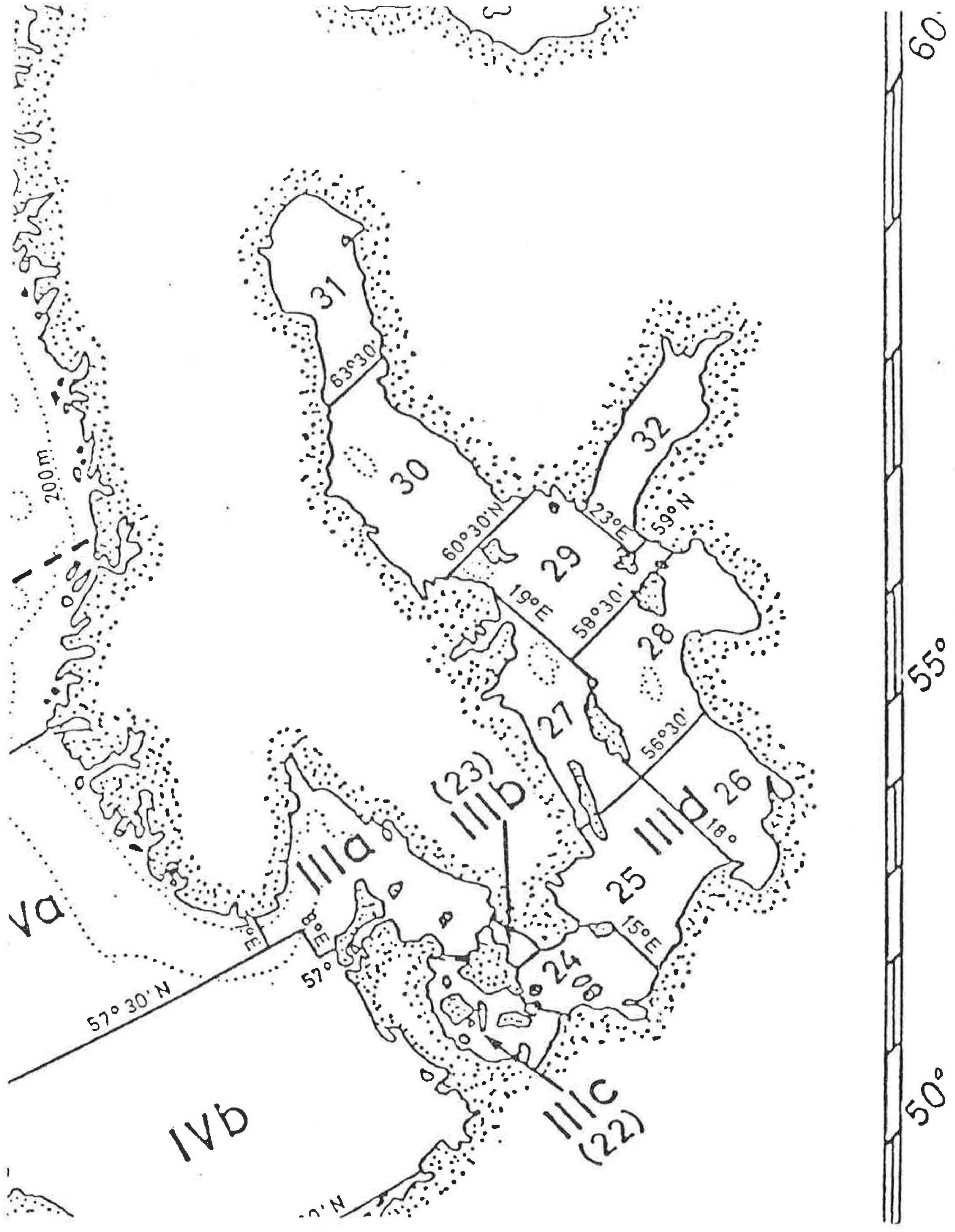


Figure 3.9.1. The Baltic Sea (IIId). Subdivision 24-29: Main Basin, SD30: Bothnian Sea, SD 31: Bothnian Bay, SD 32: Bay of Finland.

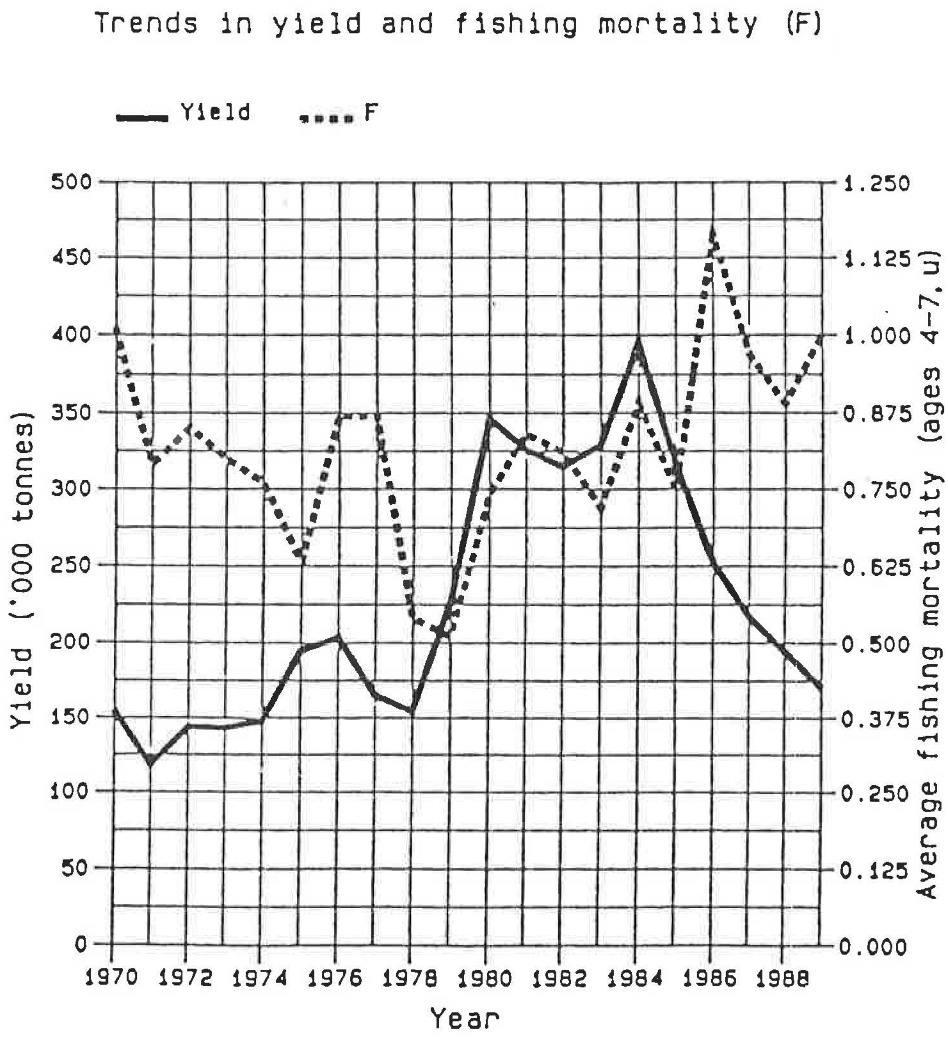


Figure 3.9.2. Trends in yield and fishing mortality of Baltic cod, eastern stock.

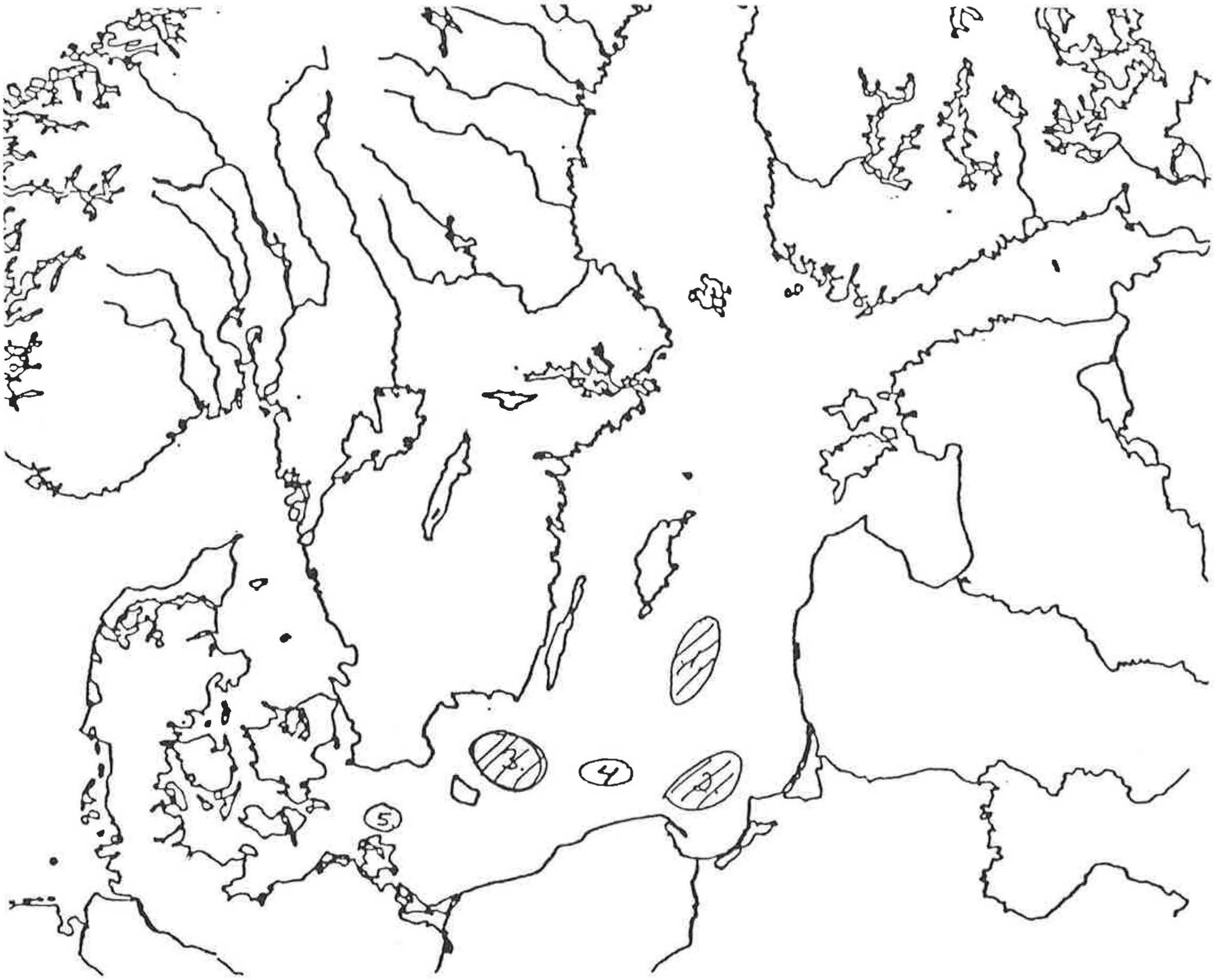


Figure 3.9.3. Spawning areas of Baltic cod. 1,2 and 3 (Gotland deep, Gdansk Deep and Bornholm Deep) main areas for the eastern stock, 4 (Slupsk Furrow, eastern stock), 5 (Arkona Deep) main area for the western stock.

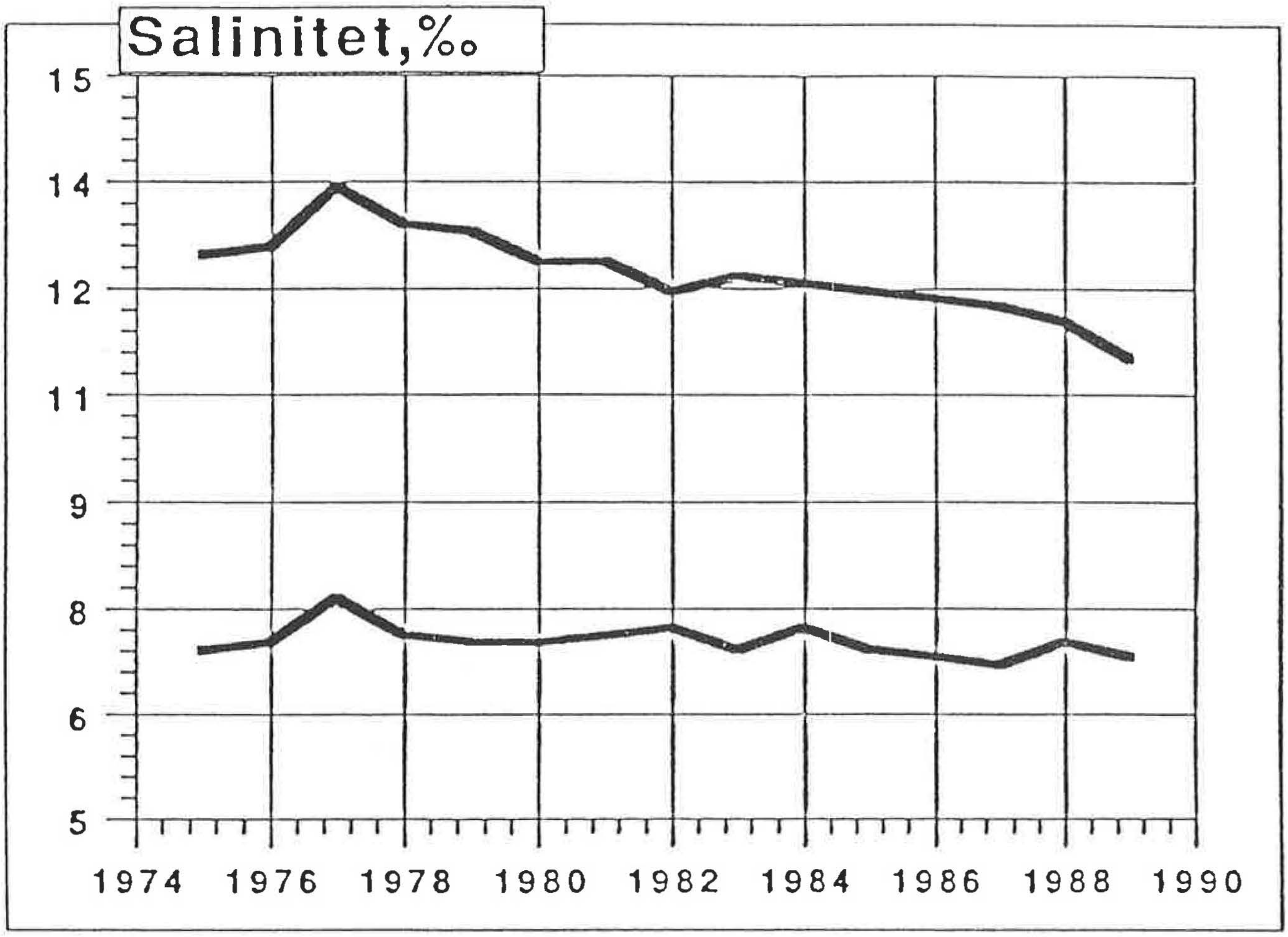


Figure 3.9.4. Salinity in the Gotland Deep 1975-1989. Surface (lower) and 225 m (upper).

3.10 GREENLAND COD STOCKS

3.10.1. Stock structure

The cod in Greenland waters is comprised of four populations with different spawning areas, larval drift and migration patterns (Anon., 1991b, Appendix 1 and 2). These are:

Icelandic cod: Spawned off Southwest Iceland. Some of the young are carried to Southeast and Southwest Greenland by the Irminger current. This flow of 0-groups and larvae takes place every year but the magnitude is very variable (Anon., 1991b Some cod tagged in Greenland waters migrate to Iceland. Returns are seen for almost all year-classes (Riget and Hovgård, 1989) but is especially pronounced for year-classes which were observed as young drifting in large quantities from Iceland to Greenland (e.g. the 1973 and 1984 year-classes, Anon., 1991b). Returns are commonest from cod tagged in Southwest Greenland or East Greenland (Hansen, 1949, Harden Jones, 1967).

East Greenland cod: Spawned offshore at East Greenland. Some of the young stages are carried to West Greenland. Some cod tagged in West Greenland are returned in East Greenland. Some of these may however be on passage to Iceland (Hovgård et al, 1989). Cod tagged in East Greenland are often returned from Iceland, only very rarely from West Greenland.

West Greenland offshore cod: Spawned off the banks of Southwest Greenland and carried northward towards Div. 1ABCD as young (see Figure 3.11.1 for location of the subdivisions). Cod tagged in these northern areas in West Greenland are normally caught in the West Greenland area (Rassmussen, 1959, Hovgård and Christensen, 1990). Only few of the northern tagged cod are returned from East Greenland or Iceland (Hansen, 1949).

West Greenland inshore cod: Spawned in fiords. The offspring probably remain within the nearby coastal areas. Cod tagged in the inshore areas are mostly retaken within the fiords where they were tagged (Hovgård and Christensen, 1990).

3.10.2. Assessment

Assessment is carried out for West Greenland by NAFO. The assessments have mostly been carried out with VPA (Horsted *et al.*, 1983; Riget 1990), but due to considerable emigration in some years, VPAs will in these cases be of little use in estimating year-class size or fishing mortality (Hovgård, 1991). Offshore groundfish trawl surveys have been carried out in autumn annually by FRG since 1982, and swept area stock abundance has been used for assessment in 1985-88 (e.g. Anon., 1987c

Assessment for East Greenland is given by ICES East Greenland Working Group. The cod stock in East Greenland is difficult to assess as it includes Icelandic cod grown in East Greenland, cod on migration from west Greenland to Iceland and 'true' East Greenland cod. The assessments have usually been based on swept area abundance (e.g. Anon., 1987c), and are in general considered as unreliable.

3.10.3 Time series

Spawning stock size and recruitment for West Greenland is available for the period 1956 to 1990 (Hovgård and Buch, 1990). Catch at age and maturity ogives are tabulated in Schumacher (1971), Horsted et al (1983) and in Riget (1990). For East Greenland, catch figures and maturity ogives are available in annual ICES working group reports since 1980. The time series for East Greenland is difficult to interpret as it is a transition area for cod moving from West Greenland to Iceland.

3.10.4. Recruitment variability

The recruitment variability observed at West Greenland is larger than observed for any other of the major cod stocks. Year-class size at age 3 varies between less than 10×10^6 to more than 500×10^6 (Hovgård and Buch, 1990). The 'true' West Greenland cod stocks were almost wiped out in the late 1960's due to a combination of overfishing and deteriorating climatic conditions. Since then the West Greenland cod fishery has depended on infrequent, but large, drifts of 0-group cod from Iceland (Anon., 1991b Drift of cod into the Greenland area is hence of major importance for recruitment. Some evidence linking temperature and later year-class size is also available (Herman *et al.*, 1965, Hansen and Buch, 1986).

It has been possible to predict important inflows from 0-group surveys carried out between Iceland and East Greenland (Anon., 1991b) Year-class size of the offshore stock components is indicated by survey abundance of age 1 and 2 cod (Anon., 1991b). Information on inshore recruitment is inferred from age 2 abundance as seen in inshore gill-net surveys (Nygård and Petersen, 1991).

3.10.5 Inshore cod at West Greenland

3.10.5.1 Spawning period

The most comprehensive information on the timing of spawning is available from the Nuuk (Godthåb) area, 64' 30"N. Smidt (1979) summarised annual plankton investigations in this area from 1946 to 1964 and found cod eggs from February to July with a distinct peak in April. However, in some years (e.g. 1949) a later spawning is inferred as large numbers of eggs were seen as late as June and this is attributed to a long lasting ice cover. The earliest observed eggs were reported from the 13 February (Hansen, 1963) and the latest from the 21 July (Jensen, 1926).

Information on the spawning period from other inshore areas indicates the same timing although data are more scarce. Jensen and Hansen (1931) observed many cod in spawning condition in March, 1928, near Manitsoq (65°30'N) and in early May, 1928, in the fiords south of Sisimiut (66°45'N). In the latter area Hansen (1949) found spawning going on in early May, 1934, and almost completed by the end of the month.

3.10.5.2 Spawning period in relation to environment

Hansen (1949) noted that inshore spawning takes place within the temperature range of 0.5 and 4.0 deg. C.

Primary production in the Nuuk area normally peaks in April-May. This is followed by an increase in zooplankton in June-July (Smidt, 1979).

Besides cod, the fiords are also spawning areas for American plaice and capelin (Smidt, 1979). Highest numbers of eggs of American place were observed in May. Capelin larvae were observed most frequently in June-July.

3.10.5.3 Locality of spawning

Inshore spawning is documented from the Ameralik Fiord (64°15N), Nuuk Fiord (64°30'N), Atangmik (64°45'N), Hamburgersund (65°40'N) and Igertoq and Amerdloq Fiords (66°45'N) (Jensen and Hansen, 1931; Hansen, 1949).

In inshore areas, plankton surveys have only shown high egg concentrations between 64 to 67 deg. N. (Hansen, 1949). It is remarkable that almost no eggs or larvae are observed in the coastal areas between 60 and 64 deg. N.

The most concentrated spawning takes place in small shallow water fiord branches. This is well documented by Smidt (1979) in the Nuuk area where three such areas are given. The same type of spawning area was observed by Hansen (1949) in the Iqertoq fiord.

3.10.5.4 Biological observations

Maturity at age.

Data from the inshore spawning population are given from the Nuuk and Sisimiut areas in the mid 30's by Hansen (1949). The 50% maturity is reached by the age of 5 to 6 year.

Vertical egg distribution

Eggs are concentrated in the uppermost water layers. Oblique hauls between 10 and 25 m showed 10 times as many eggs as similar hauls between 90 and 130 m and it was noted that the catch in the latter might have been taken while the net passed the upper layer (Smidt, 1979). Trials with vertical stramin nets revealed that the numbers of eggs did not increase when the depth exceeded 30 m.

Egg concentration.

Highest egg concentrations were found in the innermost parts of the fiords in April. Mean numbers of egg (30 min. oblique hauls with a 1 m. stramin net) in the period 1947-64 were 21000 eggs (Smidt, 1979). At the actual spawning site egg concentration could be much higher (up to 1 x 10^6), however annual variability seems to be quite high, as seen in Table 3.10.1.

Larval development.

The first larvae are observed in April or early May (Jensen and Hansen, 1931; Hansen 1949; Smidt, 1979) and the last eggs are seen in July. Hatching thus occurs between May and July. Some information on size at age as observed by stramin net catches was given by Hansen (1949). From a size of 5 mm in early May, length increased to 9.4 mm by late August. In September mean length was 20 mm. However, as pointed out by Hansen (*op. cit.*) the size might be biased due to gear avoidance. First settling, as inferred by catches in beach seines, was observed in mid-September (Jensen and Hansen, 1931). The size of these 0-groups was between 49 and 90 mm.

Larval distribution.

Most larvae were observed in the upper water layers although this is less pronounced than for the eggs (Smidt, 1979). Within the Nuuk fiord the larvae show a much more even distribution as compared to the eggs and this is attributed to a current induced dispersion.

Larval mortality.

In the Nuuk fiord the highest larval concentrations were found in June (14 larvae per 30 min. oblique haul) (Smidt, 1979). This is about 0.3% of the mean egg concentration observed in April.

3.10.6 Offshore cod at West Greenland

3.10.6.1 Spawning period

Direct observations on spawning in the West Greenland area are rare. Meyer and Lenz (1972) note that large concentrations of spawning cod in the German fishery (which was the dominant fleet) were only observed in three cases, e.g. in 1961, 1966 and 1971. In 1961 and 1966 spawning was at its peak by the end of March/beginning of April (Meyer, 1961, Meyer 1967). No dates are given for 1971. Jónsson (1957) found that 50% of the mature fish were spawning and 38% had finished spawning by the 24 April. He noted that the majority were first time spawners and hence argued that it was at the end of the spawning season. Bratberg (1963) noted that 60% of the cod caught in mid-April had finished spawning. Large spawning cod were observed in March, 1967, in Russian surveys (Konstantinov and Noskow (1968)). Maturity information from a Portuguese survey from 18 May-21 June, 1968, showed that spawning was completed, although a small fraction of the males were still in the spawning state (Dias, 1969), however, Serebryakov (1967) reported spawning cod as late as June.

In the Northwestlant surveys in April, 1963, stage I cod eggs were most abundant (Bratberg, 1963, Hansen, 1968). Stage I eggs were equivalent to Apsteins stages 1-8 (Apstein, 1909) and these eggs would have an age of up to 38 Apstein-degree-days. Raw temperature data are compiled in the Northwestlant reports. Temperatures in the Fylla Bank area, where high numbers of eggs were caught, showed a mean in the upper 30 m between 1.33 and -0.49 deg. Using Apsteins tables this means that the ages of the eggs were between 7.9 days (temp = 1.33) and 12.6 days (temp = -0.5).

In the following Northwestlant survey in May to June, 1963, the numbers of eggs were very small (approximately 100 times less than in April) (Hansen, 1968). Greenland surveys covering several months (April-July) showed the largest numbers of eggs in April and May (Smidt, 1969; Horsted 1970; Smidt, 1971).

Overall, the available data suggest a peak spawning roughly in the period March-April.

3.10.6.2 Spawning area

Direct spawning was observed west of Banana Bank (64°30'N) in deep water (350 to 550 m) in 1961 (Meyer, 1961) and in the same area down to 750 m in 1966 (Meyer 1967) and between 500 and 1000 m in 1971 (Meyer and Lenz, 1972). Serebryakov (1967) observed cod with running roe from Noname Bank (61°N) to Banana Bank (64°30'N). Konstantinov and Noskow (1968) observed spawning cod at 250 to 400 m at Fiskenaes Bank (63° N) and Danas Bank (62°30'N). Jonsson found spawning at the outer side of the Fylla Bank (64°N) at 120m (1.49 deg C). According to Meyer (1967b) the cod spawns mainly at the slopes between 600-800 m in warm Atlantic water layers off the banks. Fishing is impeded by the steep slopes except in the Banana Bank area where the slope is more gentle.

More information can be extracted from the quite frequent egg surveys carried out off West Greenland. The Northwestlant survey in April, 1963, showed a broad belt of predominantly stage I eggs off the banks at both East and West Greenland (Hansen, 1968). In West Greenland the distribution extends from 59° to 65° N. North of this, egg concentration was significantly lower. The eggs were distributed from the banks and approximately 150 km out. Norwegian surveys in April, 1961 and 1962 (presented in Hansen, 1968) and Greenland surveys in 1968 and 1970 (Smidt, 1969, 1971), showed the same pattern of egg distribution although the areas south of 61°N were not covered on these surveys. Egg surveys, carried out at Fylla bank showed that egg concentration is usually higher at the western slope than on the bank (Hansen, 1951, 1952, 1961, 1962; Horsted 1970). The egg distributions thus suggest that the spawning area is to be found on the Western slopes of the banks, south of approximately 65°N.

3.10.6.3 Biological observations

Maturity at age. Maturity ogives, 1960-83 are given by Horsted *et al.* (1983). 50% maturity is found at age 6 to 7.

Fecundity vs. Length. Egg numbers for cod between 66 and 96 cm were counted by Meyer and Lenz (1970).

Egg concentration. The egg concentrations in the offshore areas have consistently been found to be much lower than in the Nuuk fiord. Maximum numbers caught per 30 min. oblique hauls (50 to 0 m) with a 1 m stramin net are given in Table 3.10.2 (catches by a 2 m stramin net have been reduced by a factor of four).

These values should be contrasted with the high numbers of eggs observed in the innermost fiord branches in the Nuuk fiord (see above). However, it should be noted that the fiord area is very small (approximately 50 km^2) and that the offshore distribution area is vast.

Hatching Eggs are regularly observed in June although always in small quantities and in some years as late as in July (Hansen, 1959; Smidt, 1971). In the Northwestlant survey the earliest larvae were observed by RV G. O. Sars in April; 4 on the 11th, 10 on the 19th and 2 on the 21st (Anon., 1968, page 303). In the same survey more than 10000 eggs were observed. Data from the succeeding survey by RV Dana, 20 May to 14 June gave a catch of 28 eggs and 125 larvae (Anon., 1968, page 307). This indicates that hatching by and large took place in May in 1963. Information from other years are scarce. Early larvae were observed on the 30 of April, 1960 (Hansen, 1960), in May 1970 (Smidt, 1971). Larvae have regularly been observed in June (Jensen, 1926; Horsted 1970).

Egg and Larval drift. In July 1963, the Northwestlant 3 survey showed almost no larvae south of 64°N. (Hansen, 1968). As described above, the eggs were distributed in a broad belt off the banks between 59°N and 65°N in April as well as off the East Greenland coast. This suggests a northern drift of the eggs and larvae. Larval distribution in 1961, 1968 and 1970, i.e. in years where the egg distribution were estimated, showed for all years that almost no larvae were found in the bank areas south of 64°N.

For other years egg distribution in spring is not known. Larval surveys were, however, carried out in June/July 1925 and almost annually in July since 1950. Jensen (1925) caught no larvae south of 63°N. in spite of a significant effort and noted that the ratio between larvae and eggs increased in a north-western direction. He interpreted this as a drift. In the surveys since 1950 the abundance of larvae is as a general rule highest in the bank regions between 64°N and 66°N. Further south larval abundance was low and in some years, e.g. 1953 and 1955 about zero (Hansen, 1953, 1955).

In some years, e.g. 1955 (Hansen, 1955), 1956 (Hansen, 1956), 1963 (Hansen, 1968) 1964, (Hansen, 1964) and notably in 1957 (Hansen, 1958), 1958 (Hansen, 1958), 1959 (Hansen, 1959) and 1961 (Hansen, 1961) high larval abundances were observed in the middle of the Davis Strait. As the current is Westward, these larvae are lost to the Greenland stock. However, according to Serebryakov these larvae could reach the Labrador shelf by autumn (Dickson and Brander, 1993).

The drift seems therefore to be either northerly towards the banks in Division 1ABCD or more westward towards Labrador. It is notable that few larvae are ever seen at the West Greenland banks south of approximately 64°N. in July.

Larval concentration. Mean annual larval concentration (catch per 30 min. oblique hauls) in July, 1953-1979, generally varied between 1 and 10 larvae (Hansen and Buch, 1986) except for 1957 (46 larvae per tow).

Larval development. Mean larval length in July was 8.8 mm in 1925 and 12.8 mm in 1950 (Tåning, 1950). In July, 1953, mean length was 16.3 mm (Hansen, 1953). In 1963 mean size in Northwestlant 2 (May-June) was 5.6 mm and in Northwestlant 3 (19 June-31 August) 10 mm.

0-group cod were regularly taken in German ground fish trawl surveys in November although always in small quantities (poor selection of these sizes in the trawl). However, one 0-group cod was taken pelagically as late as in November (Wieland, 1991). Settling therefore seems to take place around October/November.

3.10.7 Offshore cod at East Greenland

3.10.7.1 Spawning period

Spawning takes place from March until June (Meyer, 1956, 1960, 1961; Jónsson, 1957, 1959, 1973; Serebryakov, 1967). Jónsson (1957) found cod with maturing gonads as late as 29 June and hence assumed that spawning continued into July.

In the Northwestlant survey in April high egg concentrations, dominated by newly spawned stage I eggs, were observed. In the subsequent surveys in May/June the numbers of eggs were much lower. However, even in July, 1963, eggs were still observed at ten stations off East Greenland. In one sample stage I eggs accounted for 84% of the total, indicating recent spawning (Hansen, 1968). The data therefore suggest a rather long spawning season off East Greenland.

3.10.7.1 Spawning area

The spawning area is located along the outer side of the banks at least from 62°N to 66°N, i.e. covering a distance of approximately 350 nautical miles (Jónsson, 1959). The depth where spawning occured varied from 170 m (Jónsson, 1957) to 400 m (Meyer, 1961). Bottom temperature at the spawning places are given between 3.2 and 5.2 deg. C (Jónsson, 1957, 1959). In April, 1963 (Northwestlant) eggs were found along the bank slope from the Dohrn Bank (66°N.) and down to Cape Farewell (Hansen, 1968). Serebryakov (1967) and Jónsson (1959) noted that spawning was somewhat later in the more northern area as compared to the southern area. Jónsson attributed this to a high proportion of first time spawners in the northern area.

3.10.7.2 Biological observations

Maturity ogives. Maturity ogives are given in Jónsson (1957, 1973) and in ICES Working Groups reports since 1980. For the ogives given in the latter reports it should be noted that most are from autumn samples and may refer to cod which is not in the area at the spawning time.

Egg density. Egg surveys are scarce in East Greenland. Serebryakov (1967) noted from USSR data (1962-63) that egg concentration was significantly higher than in West Greenland. This was not confirmed by the Northwestlant survey in April (Anon., 1968, pages 305-306) where the concentration differed little from that of West Greenland. The concentrations were mapped by Hansen (1968).

Larval distribution and concentration. Few larvae were observed off East Greenland in the Northwestlant 2 and 3 surveys (May-July) (Hansen, 1968). However, in July a large patch of larvae was observed between Iceland and East Greenland, signifying a drift of larvae from Iceland to Greenland.

3.10.7.3 Larval drift from Iceland to Greenland

3.10.7.4 Observations

Some information on drifting larvae is given by Tåning (1939) and Hansen (1968). The most comprehensive data come from the Icelandic 0-group surveys carried out in August since 1971 (published annually in the Anal. Biol. since 1971). A short review of the current system, the fishing method and the findings are given in Anon.(Appendix B, 1991b).

3.10.7.5 Annual variability in drift

The drift from Iceland to Greenland occurs every year, however, in very varying quantities. Only in 1973 and 1984 were very large numbers of 0-groups observed off East Greenland. Moderate numbers were seen in 1985 and 1981 (Anon., 1991b).

3.10.7.6 Distribution of 0-group

In August the 0-group cod are seen over the Dohrn Bank area (roughly 66°N, 35°W.), i.e. somewhat west of where larvae were observed in the Northwestlant 3 survey (Hansen, 1968).

3.10.7.7 Settling areas

The 1984 and 1985 year-classes completely dominated the stock, as seen in survey catches in East as well as West Greenland since 1985 (Anon., 1991b). No direct settling pattern can be deduced from the surveys, as the 0-groups of these two year-classes appeared in all parts of both areas. However, information from small haddock of the same year-classes, believed to be spawned at Iceland, indicates that the current can transport 0-groups from Iceland up to 64°N. at West Greenland (Hovgård and Messtorff, 1987).

Hansen (1949, page 30) mentioned that small cod in large quantities were observed in the coastal areas of West Greenland south of 61°N, whereas larvae are only rarely seen in these inshore areas. He therefore assumes that the small cod found here are of Icelandic origin (one may also note that the offshore larval surveys of 1925 and from 1950 onwards showed a similar scarcity of larval cod in the offshore areas in the southern part of West Greenland). Hansen later noted (1966) that the 1963 year class was only abundant in West Greenland south of 63°N and linked this to its earlier occurrence as larvae off East Greenland in the Northwestlant survey.

In inshore gill-net surveys (Nygård and Pedersen, 1991), 1 and 2 group cod were regularly caught in the Nuuk and Sisimiut fiord systems where inshore spawning is known to take place. However, in the Qaqortoq fiords (61°N) only cod of the assumed Icelandic year classes 1984 and 1985 are taken in any quantities. This suggests that the small cod seen in South Greenland is primarily of Icelandic origin.

Table 3.10.1. Maximum egg numbers caught in the Nuuk fiord, 1950-1963, as given in annual reports in Annales Biologique.

Year	Max egg number	Reference
1950	1034	Hansen, 1951
1952	75000	Hansen, 1952
1956	45000	Hansen, 1956
1957	9240	Hansen, 1958
1958	350000	Hansen, 1958
1959	1973	Hansen, 1959
1960	803	Hansen, 1960
1961	1870	Hansen, 1961
1962	1698	Hansen, 1962
1963	1300	Hansen, 1963

Table 3.10.2. Maximum egg numbers observed in offshore areas at West Greenland

Year	Max. egg nos.	Month	Reference
1951	566	4-6	Hansen, 1951
1952	85	4-5	Hansen, 1952
1956	35	4-5	Hansen, 1956
1959	93	6	Hansen, 1959
1960	3457	4	Hansen, 1960
1961	3441	4	Hansen, 1961
1961	< 1000	4-5	Hansen, 1968 N.S.
1962	52	3	Hansen, 1962
1962	< 100	4-5	Hansen, 1968 N.S.
1963	365	4	Bratberg, 1963
1968	150	4-6	Smidt, 1968
1969	70	4-5	Horsted, 1970
1970	18	5-7	Smidt, 1971

N.S. Norwegian survey reported by Hansen

3.11 LABRADOR/GRAND BANK COD

3.11.1 Species, Stock and Area of Distribution

Evidence of stock discreteness, e.g. genetic distance, tagging

The Northern Cod stock stretches over a large area spanning 9 degrees of latitude, and is more properly thought of as a stock complex. Specific spawning components have been identified on each of the offshore banks, on the north slope of the Grand Bank and recently it has been proposed there are inshore stock components in each of the major bays lying along the NE coast of Newfoundland. A review of the available data on stock structure was presented at NAFO during the 1986 annual meeting (NAFO Scientific Council Reports 1986 p.121-124).

Units for which assessment of spawning stock biomass and recruitment are available

NAFO Divisions 2J and 3KL (Figure 3.11.1).

Time series of spawning stock biomass and recruitment data, e.g. from commercial catch and effort data, fishing surveys or VPA

1962-89 - Spawning stock biomass and age 3 and age 4 recruits from VPA.

3.11.2 Timing of Spawning

Date of spawning and interannual variability or trend

New information for this area has been published recently (Myers, Mertz and Bishop, 1993). Spawning occurs primarily between March and June. The earliest spawning occurs in the northern part of the range. On Hamilton Bank spawning occurs mainly in March and April; on Belle Isle Bank from March to May but primarily in April; on Funk Island Bank spawning occurs primarily in May; on the Northern Grand Bank (NAFO Div 3L) spawning can cover the period from April to early July but occurs primarily in late May and early June.

Time of day when spawning occurs

Not known.

Timing of spawning season in relation to planktonic production cycle

It is generally believed that cod spawning peaks in April which would coincide with the onset of the spring bloom, based on recent work done in Conception Bay, Newfoundland. Peak spawning of *Calanus finmarchicus* is expected to occur in late-April to early-May. Some data from the Grand Banks collected by Mobil Oil in 1980 indicated a south-to-north trend in the onset of the spring bloom. Whether this also applies to waters off the NE coast of Newfoundland and northward to Labrador is not known.

Some information (both published and unpublished) indicates that spawning of (*Calanus finmarchicus*) occurs throughout the spring-fall period within the Labrador Current, and that this occurs in conjunction with continual nutrient renewal and primary production. We also know that cod spawning occurs over many months (at least March to July) for the 2J-3KL cod stock. Therefore, it is possible that the concept of a peak spawning in relation to a temperate water spring bloom may not be important.

Timing of spawning season in relation to hydrographic events

Spawning occurs in various places on the deep-water slopes of the offshore banks. Bottom water temperatures are usually in the range of 2-4°C. Some spawning also occurs in the deep-water bays closer to land.

Timing of spawning season in relation to other fish species which spawn in the same location

Other species present in substantial numbers are American plaice (3L), redfish and Greenland Halibut. Greenland Halibut spawn in northern areas (further north than 2J).

3.11.3 Location of Spawning

Geographic location and extent of spawning area and evidence of its variability

Some spawning areas are at Hamilton Bank, Belle Isle Bank, Northern and Southern Funk Island Bank, North Cape of Grand Bank, Woolfall Bank. Spawning depths have been reported for 110 to 182 m but are typically thought to be in 300-600 m depth. While managed as a single unit many regard the status as a "stock complex". There is no information on year-to-year variability.

Does spawning regularly begin in one part of the spawning area and then move to other parts?

This is possible, but there is no conclusive evidence. Spawning takes place over a relatively long period of time and movements of aggregations do occur.

Can location be described in relation to hydrographic features?

See section 2.4 and 3.5

Can location be described in relation to other species, including food organisms and predators?

No information.

Can location be described in relation to water mass circulation?

Spawning usually occurs outside or below the cold core of the Labrador current. This current moves from north to south and transports eggs and larvae. Historically it was felt that eggs and larvae spawned on the various banks were advected away either south or to inshore waters. Recent work demonstrates eggs spawned offshore may not be advected inshore. It has been postulated there is a south-north gradient of younger-older juvenile cod which has suggested to some that there is a southward transport of eggs and larvae followed by a gradual northward return migration during their juvenile years.

3.11.4 Biological Details

Fecundity, i.e. number of eggs produced per female per year (as a function of age) - specific fecundity, i.e. number of eggs per unit weight

A female 51 cm long will deposit about 200,000 eggs while a female 140 cm long may deposit 12,000,000 eggs (Scott and Scott 1988).

Evidence of changes in fecundity with time

No information.

Percentage mature at age (including the population not on the spawning grounds)

Length at 50% maturity

The usual rule is 50% mature at 6 years of age.

Egg size and evidence of changes with age and with time during the spawning season

Specific gravity of eggs and larvae

Eggs are 1.2-1.6 mm in diameter. Very similar to haddock and witch eggs and cannot be speciated until late stages (typically stage IV). Fertilized eggs are buoyant and rise slowly to or near the surface where they remain during incubation. Recent sampling has shown late stage eggs to be most abundant throughout the upper mixed layer depth (≤ 20 m depth).

Typical densities, i.e. number per m^3 of eggs and larvae

Not known. Sampling in 1991 indicated low egg concentrations (< 0.1 egg/m^3).

Incubation rate of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

Eggs spawned off northern Labrador in March-April take 50-60 days to hatch at surface temperatures of -1.5 to 0°C, and those spawned on Hamilton Bank in March-April take about 40 days at -1 to 1°C. At 6°C eggs hatch in about 14 days. Larvae are 3.3-5.7 mm long at hatch. No information of size of yolk in relation to larvae.

Larval development rate as a function of temperature

Not known.

Condition factor and nutritional status

Not known.

Egg and larval mortality rates

Not known.

Time of first feeding during development

Time of first feeding is expected to occur as the yolk sac is used up. The rate of yolk utilization would be temperature-dependent, and these rates are not known for Northern Cod.

Food of larvae during development

Food has not been studied for Northern Cod larvae, but it no doubt is primarily *Calanus* eggs and nauplii. Cod larvae are reported to be more facultative (efficient) feeders than either redfish (Bainbridge and McKay 1968) or haddock (Kane 1984) at the same size.

Evidence of predation during the egg and larval stage?

No information.

3.11.5 Recruitment

Are there several spawning sites which contribute to the same stock unit...?

It is felt that eggs and larvae spawned offshore drift southward and congregate: a) inshore or b) on the south NE Newfoundland Shelf. There is a renewed debate regarding stock discreteness for Labrador and Newfoundland cod. See section 3.11.1.

Earliest time in the life history when year class strength can be predicted

Age 3 estimates of abundance from RV indices are used to estimate age 3 population in SPA. Age 2 (RV) are usually good indicators of YCS but are more variable than age 3 and are not yet used for SPA calibration. Age 4 abundance have been used in recent publications (see Figure 3.11.2).

Hypotheses which have been put forward to account for year-to-year variability in year class strength

Size of the spawning stock, variability in salinity and, therefore, production, associated with the annual freshwater pulse, transport of larvae and early juveniles to inshore nursery areas.

Evidence of long term trends in recruitment

Recruitment has decreased steadily since 1962 to low levels during the early 1970's (Figure 2). Since then recruitment has fluctuated by a factor of approximately 5x, with evidence of cyclic changes on the order of 6-7 years. There is a significant correlation in the recruitment data at a lag of 2 years. Note there is reduced confidence in data collected during the 1960's (Halliday and Pinhorn, 1990).

Evidence that variability in recruitment is linked to variability of other species in the same area; the same species in other areas or other species in other areas?

There have been several studies indicating both coherence in cod recruitment among populations in the NW Atlantic, and no coherence (reviewed by Helbig *et al.*, 1992).

Evidence of inter- or intraspecific competition

No evidence.

3.11.6 Other Comments

6.1 Spawning locations are not known exactly, however, observed patterns in the geographic location of the commercial fishery, as well as results from spring RV cruises indicate that the spawning area may vary in size and location. It has been hypothesized that these variations may be the result of variability in water temperatures.

6.2 There are 3 other cod stocks in the Newfoundland-Labrador Region which may also be considered. These stocks correspond to NAFO management areas 3Ps, 3NO and 3M, which are St Pierre Bank south of Newfoundland, the southern Grand Bank, and Flemish Cap, respectively. Much of the information provided for the Northern Cod Stock is also relevant to these stocks in terms of our knowledge of cod biology and ecological factors relating to recruitment variations.

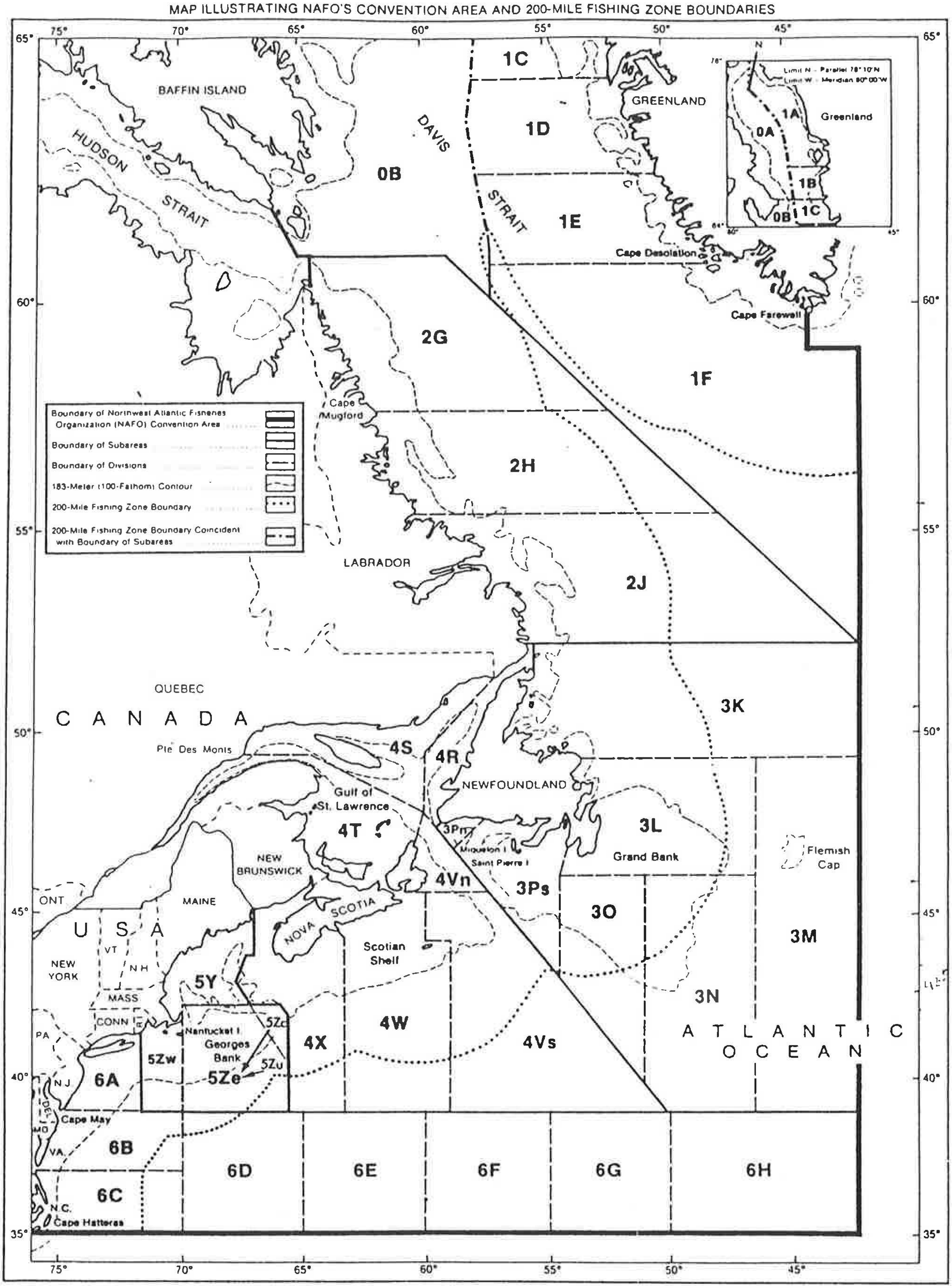


Figure 3.11.1. Map illustrating NAFO divisions.

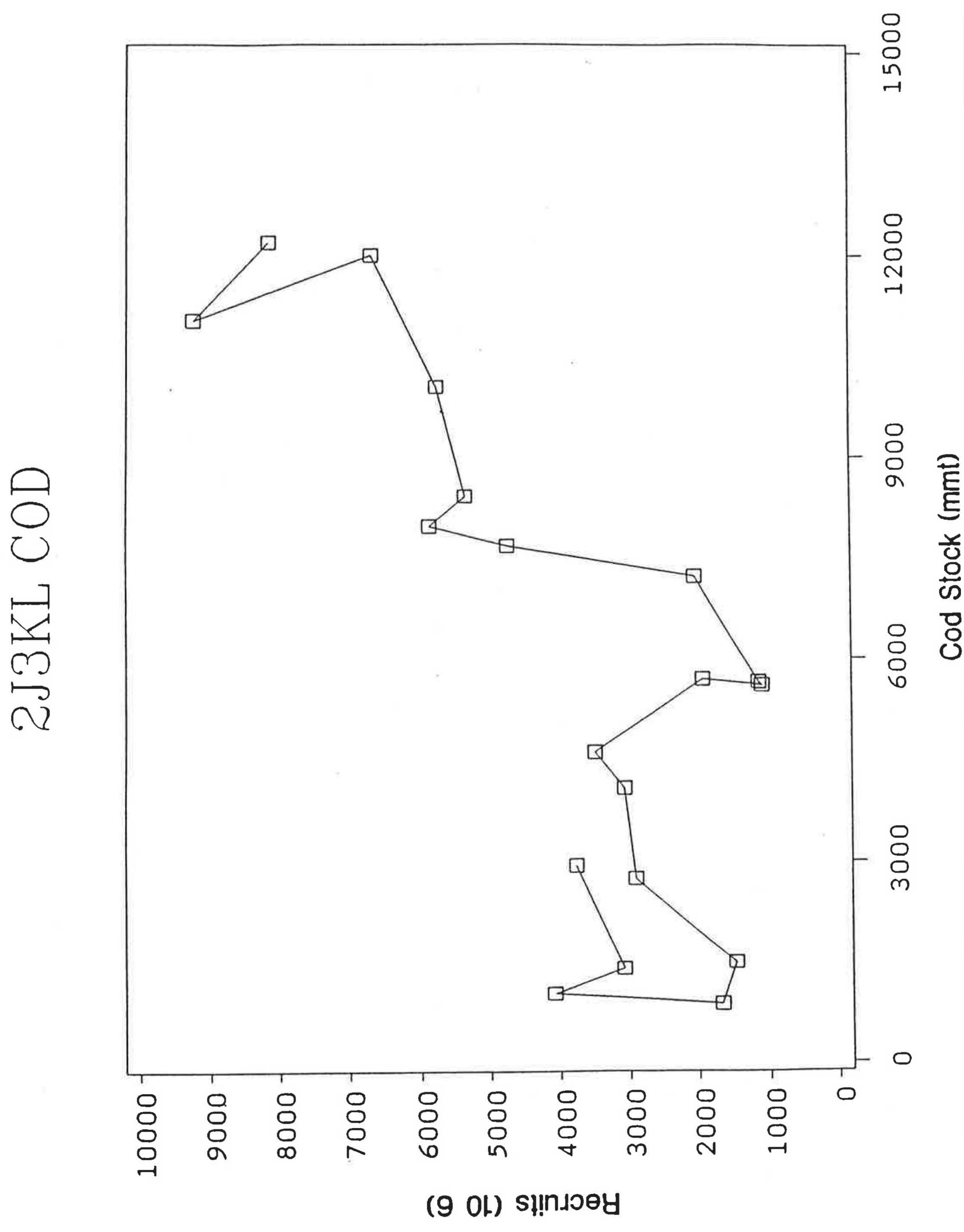


Figure 3.11.2. Estimates of year class abundance.

3.12 N GULF OF ST LAWRENCE COD

The 3Pn, 4RS cod stock inhabits the Northeastern part of the Gulf of St Lawrence in what may be considered as a semi-enclosed sea. Two straits separate the Gulf from the Atlantic Ocean, the largest being only 60 nautical miles wide. Despite this, the overwintering migration leads this stock outside the Gulf into NAFO Subdivision 3Pn, where a very important fishery takes place in the first few months of the year. As the ice cover progresses in winter, large concentrations of fish can be found at the ice edge. Strong mixing caused by upwelling at the ice edge is thought to force cod to move into deeper waters. A strong thermal gradient close to the bottom in those areas may cause an increase in catchability of cod to the otter trawls.

In April-May, as the cod are returning inside the Gulf, spawning takes place. This precedes the summer inshore migration where fixed gear catches occur. Availability of cod to these gears has been shown to be heavily dependent on upwelling of deeper waters close to shore induced by favourable winds. This particular fishery has declined substantially in recent years. Investigations are ongoing on factors contributing to this including reduced cod abundance, reduced fishing effort, slower growth of cod, unfavourable wind conditions.

Little is known about larval distribution and dynamics for this cod stock. Growth rate for this stock have declined substantially in the last decade, as is the case for the majority of cod stocks from the Canadian Atlantic. For most of these stocks, evidence supporting density dependence has been shown.

The Gulf of St Lawrence water masses are influenced by three important currents. The Gaspé current is a surface current outflow of relatively fresh waters from the St Lawrence estuary. Waters from the Labrador current can be found in the cold intermediate water mass. Finally, deep waters in the Laurentian Channel are formed by an estuarine type of circulation that brings warmer Atlantic waters into the Gulf. Temperature from this water mass (200-300 meters) have been monitored since 1955. Temperatures have risen by two degrees in 1966-1967 to reach slightly over 6 degrees in 1987. The impact of this change on distribution, migration patterns, food supply, predators and productivity of cod stocks are unknown. The impact of such a change is likely to be different for both cod stocks present in the Gulf. The 4T-Vn [Jan-Apr] cod stock inhabits the southwestern part of the Gulf, this is a relatively shallow area mostly influenced by the Gaspé current. Bottom topography for the 3Pn, 4RS cod stock is made up of deep water channels (Esquiman and Jacques Cartier) with a more typical estuarine circulation.

3.12.1 Species, Stock and Area of Distribution

Evidence of stock discreteness, e.g. genetic distance, tagging

Tagging (Gascon, 1990, Templeman, 1962) Vertebrae Count (Templeman, 1974).

Units for which assessment of spawning stock biomass and recruitment are available

CAFSAC Res. Doc. 3Pn, 4RS Cod.

Time series of spawning stock biomass and recruitment data, e.g. from commercial catch and effort data, fishing surveys or VPA

1974 - Present.

3.12.2 Timing of Spawning

Date of spawning and interannual variability or trend

April-May. Do not know. Interannual variability.

Time of day when spawning occurs

Don't know.

Timing of spawning season in relation to planktonic production cycle

Before Calanus boom.

Timing of spawning season in relation to hydrographic events

Occurs as ice cover recedes in the Gulf of St Lawrence.

Timing of spawning season in relation to other fish species which spawn in the same location

No haddock spawning in the Gulf has been reported.

3.12.3 Location of Spawning.

Geographic location and extent of spawning area and evidence of its variability from year to year

Anecdotal information: off St Georges Bay, Port au Port peninsula (NAFO Div. 4Rd, 4Rc) + Sept-Iles (4Si).

Does spawning regularly begin in one part of the spawning area and then move in other parts

Don't know.

Can the location be described in relation to hydrographic features...

Don't know.

Can location be described in relation to other spaces...

Don't know.

Can location be described in relation to water mass circulation...

Don't know.

3.12.4 Biological Details.

Fecundity, i.e. number of eggs produced per female per year....

Not stock specific. $F = (0.48W_{kg} - 0.12) \times 10^6$ (May 1967)

Evidence of changes in fecundity with time

Don't know

Percentage mature at age (including the population not on the spawning grounds)

50% mature at age M 5.1, F 6.1, combined 5.6 years old (Wiles & May)

50% mature at age M 5.5, F 6.6, combined 6.0 years old (Minet)

50% mature at length, M 45.5, F 49.7, combined 47.5 cm (Wiles & May)

50% mature at length, M 45.7, F 51.9, combined 48.8 cm (Minet)

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

Don't know.

Typical densities, i.e. number per m^3 of eggs and larvae

Don't know.

Incubation role of eggs. Size of larvae at hatching. Size of yolk sac in relation to size of larva

Don't know.

Larval development rate as a function of temperature

Don't know.

Condition factor and nutritional status

Don't know.

Egg and larval mortality rates

Don't know.

Time of first feeding of larvae and food at first feeding

Don't know.

Food of larvae during development

Don't know.

Evidence of predation during the egg and larval stage?

Don't know.

3.12.5 Recruitment.

Are there several spawning sites which contribute to the same stock unit...

Maybe Sept-Iles & St Georges Bay.

Earliest time in the life history when year class strength can be predicted

Age 4 from VPA.

Hypotheses which have been put forward to account for year-to-year variability in year class strength

None.

Evidence of long term trends in recruitment

None.

Evidence that variability in recruitment is linked to variability at other species in the same area...

None.

Evidence of inter- or intraspecific competition

None.

3.13 SOUTHERN GULF OF ST LAWRENCE COD

3.13.1 Species stock and area of distribution

Evidence of stock discreteness, e.g. genetic distance, tagging

The stock is considered to be discrete with some mixing with the Northern Gulf cod stock (3Pn, 4RS) in summer and the resident Sydney Bight (4Vn) stock in winter. McKenzie (1941, 1948), Powles (1959), Martin (1962), Jean (1963, 1964), Halliday (1974), Templeman (1974).

Units for which assessment of spawning stock biomass and recruitment are available

The assessment of this stock is for NAFO 4T and 4Vn (Jan-Apr). Assessments for this stock have been conducted since the early 1970's, mostly using calibrated VPA's. The stock was originally assessed under the auspices of ICNAF but is done by CAFSAC since 1978. G.A. Chouinard, G.A.Nielsen, L. Currie and J.P.Murphy. 1990.

Time series of spawning stock biomass and recruitment data, e.g. from commercial catch and effort data, fishing surveys or VPA

Although catch-at-age has been calculated back to 1950, uncertainties in nominal catches and poor sampling intensity prior to 1970 have restricted the use of that data to illustrative purposes to indicate general trends in recruitment and biomass Table 3.13.1. G.A Chouinard and A.F.Sinclair 1989. The years 1971 to the present are used in calibration. The otter trawl CPUE series starts in 1966. Stratified random surveys have been conducted on this stock since 1971. Year-class estimates from surveys are highly correlated with VPA results. G.A.Chouinard and A.F.Sinclair. 1989.

3.13.2 Timing of spawning

Date of spawning and interannual variability or trend

Spawning occurs generally from May to September with peak spawning from late-May to mid-June. Powles (1978), Lett (1980), de Lafontaine *et al.,* (1990).

Time of day when spawning occurs

Not known.

Timing of spawning season in relation to planktonic production cycle

Spawning occurs (mid-May to early July) at the end of the spring bloom (mid to end of April). Production is very high in this area in the period May to September. Pocklington (1988), de Lafontaine *et al.*, (1990).

Timing of spawning season in relation to hydrographic events

The whole area where cod spawn is heavily influenced by the St Lawrence river discharge which affects sea surface circulation.

Timing of spawning season in relation to other fish species which spawn in the same location

Although the exact spawning sites are not known, American plaice has a similar distribution to cod and also spawns in May-June. W.B.Scott and M.G.Scott. 1988. Mackerel also spawn in this time period. O.E.Sette. 1943. See ichthyoplankton calendar provided in de Lafontaine *et al.*, 1984, 1990.

3.13.3 Location of spawning.

Geographic location and extent of spawning area and evidence of its variability

The principal spawning areas are considered to be the area between the mouth of Miramichi Bay and the northern tip of P.E.I., the area east of the Magdalen Islands and the Baie des Chaleurs. P.M.Powles, 1958, P.F.Lett, 1980, M.J.Tremblay and M.Sinclair, 1985, de Lafontaine, in prep.

Does spawning regularly begin on one part of the spawning area and then move to other parts

Not known - although cod spawn later along the Gaspé coast and in the estuary.

Can the location be described in relation to hydrographic features.

Spawning over shallow water depths (35-100m). No spawning nearshore and above deep Laurentian Channel. Eggs and larvae found mostly at thermocline (12-20m). de Lafontaine, in prep.

Can location be described in relation to other species, including food organisms and predators?

Not known.

Can location be described in relation to water mass circulation.

The main area of spawning is influenced by the strong Gaspé current - surface water only (0-15m) - P.M.Strain. 1988, which likely transports eggs and larvae in a southeasterly direction. The presence of a gyre at the mouth of Miramichi Bay causes retention in this area. de Lafontaine, in prep.

3.13.4 Biological details.

Fecundity, i.e. number of eggs produced per female per year (as a function of age). Specific fecundity, i.e. number of eggs produced per unit weight

There is a strong relationship between fecundity and fork length. 200 thousand eggs for a 51 cm cod to 12 million eggs for a 140 cm. P.M.Powles, 1958. Specific fecundity is 379 egg g^{-1}. M.-I.Buzeta and K.G.Waiwood, 1982. Cod older than 8 years generally produce more than one million eggs. P.M.Powles, 1958.

Evidence of changes in fecundity with time

No evidence. M.-I.Buzeta and K.G.Waiwood, 1982.

Percentage mature at age (including the population not on the spawning grounds). Length at 50% maturity

Age at maturity is variable. Powles (1958), Beacham (1983) and Lett (1978). Length at maturity declined from 50 to 36 cm for males and from 60 to 36 cm for females in the period 1959-1979. Beacham (1983). Age at 50% mature was 4.96 and 6.08 for males and females in the period 1959-1964. In the period 1975-1979, the age at 50% maturity was 3.58 and 3.6 years respectively. Beacham (1983). Recent data (1990) also show that the age of 50% maturity is between 3 and 4 years (Table 3.13.2).

Egg size and evidence of changes with age and with time during the spawning season. Specific gravity of eggs and larvae

Mature eggs are greater than 250 microns. M.-I.Buzeta and K.G.Waiwood, 1982. Egg size (measured on 10% formalin preserved samples collected in Baie des Chaleurs in 1978 - de Lafontaine's data). 1.30m→1.15mm, decreased from May to July.

Typical densities, i.e. number per m^3 of eggs and larvae

In the areas of concentration, 2.5 eggs m^{-3}. P.F.Lett *et al.*, 1975.

Incubation rate of eggs

Not known for this stock in particular.

Larval development rate as a function of temperature

Not known.

Condition factor and nutritional status

Condition can be calculated from RV data. Growth takes place mostly from July to November, a decrease in condition is observed from March to June. K.G.Waiwood, 1978.

Egg and larval mortality rates

Eggs stage I→hatching larvae: 17.1%/day - based on weekly samples over spawning season. de Lafontaine, in prep.

Time of first feeding of larvae and food at first feeding

Not known.

Food of larvae during development

Not known.

Evidence of predation during the egg and larval stage?

Mackerel, but no specific study has been conducted. P.F.Lett *et al.*, 1975.

3.13.5 Recruitment

Are there several spawning sites which contribute to the same stock unit...

There are about 3 centres of abundance for eggs (3 sites) but they are not completely discrete. P.F.Lett, 1980.

Earliest time in the life history when year class strength can be predicted

Large year-classes can be detected at age 1 in groundfish surveys. G.A.Chouinard and A.F.Sinclair, 1989. Year class abundance can be accurately determined from age 2 (Sinclair and Chouinard, 1992).

Hypotheses which have been put forward to account for year-to-year variability in year class strength

Mackerel predation, cannibalism by older cod and temperature. P.F.Lett, 1978, P.F.Lett, A.C.Kohler and O.N.Fitzgerald, 1975. W.R.Martin and A.C.Kohler, 1965.

Evidence of long term trends in recruitment

Recruitment appears to be highest in the 1980's. G.A.Chouinard and A.F.Sinclair, 1989.

Evidence that variability in recruitment is linked to variability of other species in the same area....

Mackerel in the same area. P.F.Lett, 1978. Recruitment of cod 4RS (Northern) is quite similar, de Lafontaine *et al.*, 1990.

5.6 Evidence of inter- or intraspecific competition

Density-dependent growth. A.C.Kohler 1964, J.E.Paloheimo and A.C.Kohler, 1968, S.J. Crabtree and D.M.Ware, 1975, T.D.Beacham, 1981, P.F.Lett, 1980.

Table 3.13.1 Spawning Biomass and Recruitment for 4T-Vn cod

Year	Spawning Biomass (5+) ('000 t)	Recruitment (millions)
1950	238	100
1951	270	109
1952	319	111
1953	347	106
1954	369	77
1955	406	68
1956	429	81
1957	365	106
1958	311	110
1959	257	142
1960	216	133
1961	237	46
1962	261	59
1963	216	41
1964	163	59
1965	135	51
1966	118	58
1967	111	97
1968	112	87
1969	133	51
1970	154	47
1971	156	87
1972	125	34
1973	103	46
1974	82	53
1975	73	41
1976	67	226
1977	67	164
1978	124	160
1979	187	113
1980	226	113
1981	225	83
1982	224	151
1983	212	205
1984	215	110
1985	260	106
1986	250	85
1987	220	76
1988	184	63
1989	161	78
1990	136	83
1991	124	71
Average (1950-1991)	204	90

Table 3.13.2 Maturity Analysis 1990 (June-July)

Age	Number Immature	Number Mature	% Mature
1	3		0.00
2	26	3	10.34
3	149	51	25.50
4	77	112	59.26
5	23	171	88.14
6	1	137	99.28
7		166	100.00
8		99	100.00
9		70	100.00
10	1	64	98.46

3.14 SOUTH-WEST NOVA SCOTIA COD

3.14.1 Species, stock and area of distribution

Cod off south-west Nova Scotia are found both on offshore banks (primarily Browns Bank) and in the inshore region. There is considerable mixing between the two regions, particularly in the summer. While managed as a unit stock (NAFO Division 4X), a stock complex, comprised of numerous small inshore spawning aggregations, and a single large offshore spawning aggregation, is more likely. There is no evidence of genetic isolation, either within the region or between adjacent regions (Cross and Payne, 1978; Mork *et al.*, 1985). However, analysis of tag returns, morphometrics, and parasite loads have provided a consistent view of an aggregation with at least partial separation from adjacent management units to the south (Georges Bank) and the north (4VsW cod) (McKenzie, 1934, 1956; Scott and Martin, 1959; Templeman, 1962; Wise, 1963; Campana and Simon, 1984).

3.14.2 Timing of spawning

There are both spring and fall spawners in this region. The spring spawning component is the largest of the two, and is largely restricted to Browns Bank during February to April (O'Boyle *et al.*, 1984; Gagné and O'Boyle, 1984; Campana, 1989; Hurley and Campana, 1989). Fall spawning is believed to be restricted to coastal waters during October and November (Gagné and O'Boyle, 1984; Campana, 1989. P. C. F. Hurley, unpublished). Interannual variability in the timing of peak spawning has been little studied, but was less than 2 weeks (days 80-90) during the spring of 1983-85 (Campana *et al.*, 1989b). The water column is unstratified during spring spawning, and stratified during fall spawning. A sympatric haddock stock spawns approximately 2-4 weeks after cod in the spring, but is not believed to spawn in the fall. Recent research suggests that both the spring and fall spawning may occur in association with plankton blooms (Brander and Hurley, 1992).

3.14.3 Location of spawning

Offshore spawning is largely restricted to Browns Bank (a bank of 30-40 km diameter), while inshore spawning appears to be more broadly distributed along the coastline (O'Boyle *et al.*, 1984; Gagné and O'Boyle, 1984; Hurley and Campana, 1989). Offshore spawning occurs in the presence of a tidally-dominated circulation which results in a permanent gyre around the bank (Sinclair and Iles, 1989; Smith, 1989). The sympatric haddock stock spawns in association with the same bank and circulation. Episodic breakdowns in the gyre circulation apparently release large numbers of eggs and larvae to the north west, where they become entrained in a coastal current and drift towards shore; the remainder are retained on the bank (Campana *et al.*, 1989a). Thus, there is a drift-retention dichotomy for individual particles on the bank. Total egg production is approximately 10^{13} eggs y^{-1} (Campana *et al.*, 1989b).

3.14.4 Biological details

Egg development times at ambient temperatures of 3-4°C are of the order of 15-20 d (Page and Frank, 1989). At the peak of the spawning season, mean late stage egg densities are approximately 10-20/m^2 on Browns Bank (mean depth = 70 m), but are an order of magnitude higher at Stage 1 (Hurley and Campana, 1989). Mean larval densities peak at approximately 1/m^2 on Browns Bank. Larval growth is largely temperature-mediated, but will result in a 15 mm larva after 50-60 d (Campana and Hurley, 1989). Browns Bank juvenile cod had more rapid recent growth (based on otolith increment widths) than those inshore (Suthers, Frank and Campana, 1989). Studies of larval condition factor have demonstrated that larvae in poorer condition often occur higher in the water column (Neilson *et al.*, 1986), as do earlier stage eggs (Frank *et al.*, 1989). Unpublished studies indicate little or no vertical migration of cod larvae on Browns Bank in the months February-June (Campana, Hurley and Hamel, unpublished). Egg and larval mortality rates are relatively high: 0.15-0.30 d^{-1} (Campana *et al.*, 1989b). Weight at age for the period 1948-89 is reported by Campana and Hamel (1990).

Log fecundity = -0.16749 + 3.29 (log length) (Campana *et al.*, 1989b).

Z has averaged 0.75 over the past 40 years and a time series of stock biomass is given by Campana and Hamel (1990).

3.14.5 Recruitment

As mentioned in section 1 above, 4X cod appear to form a stock complex, with the primary spawning area being Browns Bank. Juveniles are widely distributed between offshore and inshore areas. Interannual distributions of larval and pelagic juvenile cod have been determined with two different gear types around south-western Nova Scotia (Suthers and Frank, 1989). There is no evidence of substantial drift of ichthyoplankton from adjacent stocks (Perry and Hurley, 1986). Year-class strength variability is apparent in a 41-year time series of VPA age 1 numbers, showing a factor of 6 difference between minimum and maximum year classes (Campana and Hamel, 1989). In an intensive, 3-year field program (Fisheries Ecology Program: FEP), the abundance of either pelagic or settled juveniles proved to be the earliest reliable indicators of year-class strength (Campana *et al.*, 1989b). Mortality between the larval and juvenile stages appeared to be most influential in determining year-class strength, but the source of the mortality could not be identified. Despite previous reports of large-scale physical forcing of recruitment patterns (Koslow *et al.*, 1987), the results of the FEP analysis indicated that local spatial and/or temporal effects could be at least as important to the recruitment process (Campana *et al.*, 1989b).

3.15 GEORGES BANK COD

In USA Atlantic waters, three major groupings of cod have generally been recognized: (1) Georges Bank; (2) Gulf of Maine; and (3) Southern New England-Middle Atlantic (Wise 1962; Serchuk and Wigley 1986). Tagging studies (Smith 1902; Schroeder 1930; North American Council on Fishery Investigations 1932; 1935; Wise 1962), parasite infestation research (Sherman and Wise 1961), spawning time data (Colton *et al.*, 1979), and growth rate analyses (Penttila and Gifford 1976; Serchuk and Wood 1979) indicate that minimal interchange occurs between the Gulf of Maine and Georges Bank groups, but that extensive mixing prevails between cod on Georges Bank and in the Southern New England-Middle Atlantic region. A seasonal southwesterly movement of cod from the South Channel area of Georges Bank occurs in autumn followed by a northeasterly return in spring. Wise (1958) postulated that the autumn movement was not a migration of Georges Bank fish (as concluded by Schroeder (1930)) but rather a return of Southern New England-Middle Atlantic fish to their native grounds for winter spawning. The presence of ripe spawning individuals off the New Jersey coast (Smith 1902; Schroeder 1930; Wise 1958) and the occurrence of cod eggs and larvae as far south as North Carolina (Schroeder 1930; Berrien *et al.*, 1978) suggest the possibility that cod in the Middle Atlantic may comprise a genetically distinct subpopulation, separate from those groupings found further north. However, the origin and fate of Middle Atlantic cod eggs and larvae have yet to be delineated, and hence the existence of the Middle Atlantic subpopulation remains to be confirmed. Serchuk and Wood (1979) found strong affinities between Georges Bank and Southern New England-Middle Atlantic cod based on growth rates, research vessel survey abundance patterns and catch composition, recruitment patterns, and commercial catch size/age distributions. The relative absence of juvenile cod in inshore and offshore research vessel surveys in the Southern New England-Middle Atlantic region (Serchuk and Wood 1979) suggests that either the southerly populations are not self-sustaining or that offspring from the southern spawning move north as ichthyoplankton or larval nekton and subsequently return south several years later as adults.

The demographic similarities of Georges Bank and Southern New England-Middle Atlantic cod are so pronounced that the two groups are presently considered to comprise a single stock (i.e., Georges Bank and South; commonly referred to as the Georges Bank stock).

The Georges Bank cod stock is the most southerly cod stock in the world. Georges Bank cod are omnivorous feeders and commonly attain lengths up to 130 cm (51 in) and weights up to 25 to 35 kg (55 to 77 lbs). Maximum age is in excess of 15 years, although young fish (ages 2-5) generally comprise the bulk of the catch. Spawning occurs during winter and early spring. Commercial fisheries for cod on Georges Bank have existed since the 1700s and modern landings statistics are available since the late 1880s. Annual commercial catches since 1960 have ranged between 11,000 and 57,000 metric tons, and have averaged about 33,000 tons per year. The commercial fisheries are conducted year-round with otter-trawls and gill nets as primary gear. Recreational fishing is also important and recreational landings have averaged about 6,000 tons in recent years.

Cod in spawning condition typically are found on Georges Bank from November to May but peak spawning occurs between February and Mid-April (Colton *et al.*, 1979). Spawning location can be anywhere on Georges Bank, however the Northeast Peak seems to be a traditional area of maximum concentration. The eggs normally develop within a temperature range of 3-6°C and adapt to the specific gravity of the surrounding water. Lough (1989) observed late stage eggs to increase in density with depth on southeast Georges Bank. Maximum concentration of eggs in the centre of patch distributions are 100-300/m^3 (Lough, 1989; Lough and Potter, 1990). Egg incubation rates have been shown to vary with temperature (Laurence and Rogers, 1976). The normal duration of development at typical spring temperatures on Georges Bank is about 2 weeks. The pelagic eggs drift to the southwest within the clockwise gyre on Georges Bank at a rate of 5-10km/day.

Size at hatching is in the range of 3-5 mm. Larval growth is correlated with temperature (Laurence, 1978; Laurence *et al.*, 1981). Daily rates of growth expressed as length, weight and protein content have been reported (Bolz and Lough 1982; Laurence 1985; Buckley and Lough, 1987). Mortality rates for the first few weeks after hatching have been estimated from field studies as 6-8%/day (Lough, 1984). Larval food consists principally of copepod eggs and the nauplius and copepodite stages of *Pseudocalanus, Calanus* and *Centropages* (Kane, 1984). Concentrations of prey organisms have been measured in field research and range from 5 to 50 prey organisms per litre (Lough, 1984; Laurence *et al.*, 1984). It is believed that the persistent gyre around Georges Bank may serve as a retention mechanism for larvae (Smith and Morse, 1985; Lough and Bolz, 1989). Larval distribution is usually within the 90 m contour. Near bottom, cross isobath currents have been measured inside 90 m and also may help keep larvae on the Bank (Lough and Bolz, 1989). Larval predations have not been conclusively identified.

Development to the juvenile stage and the transition to a demersal existence has been documented in detail (Potter *et al.*, 1990; Lough and Bolz, 1989; Lough *et al.*, 1989; Lough and Potter, (in press)). Larvae morphologically transform to juveniles at about 15 mm in length. They remain pelagic but do undergo some diel vertical migrations occurring deeper in the day and shallower at night. This pattern persists until they attain a size of 40 to 60 mm at which time they take up a demersal life style in the day and come up off the bottom 5-20 meters at night. They become mostly demersal at lengths greater than 60 mm at an age of approximately 115 days.

Year-class strength appears to be set by the time cod become demersal juveniles. Growth of Georges Bank cod is rapid - age 0 fish attain an average size of 26 cm by the end of their first year of life. The age of sexual maturity has declined in recent years, with many fish maturing at age 1. 50% ages and lengths of maturity for Georges Bank and the Gulf of Maine are:

	Males	Females
Gulf of Maine	2.3 yrs 36cm	2.1 yrs 32cm
Georges Bank	1.9 yrs 41cm	1.7 yrs 39cm

Assessments of the Georges Bank cod stock have been conducted since the early 1970s but virtual population estimates (VPA) only go back to 1978 (Serchuk and Wigley 1986; Hunt 1988; NEFC, NMFS 1989). Commercial CPUE indices for the USA otter trawl fleet exist since 1964 and Canadian CPUE data are available from 1967 to the present. Stock abundance and recruitment indices derived from autumn (1963 onward) and spring (1968 onward) USA research vessel surveys have been used to monitor changes and assess trends in population size and recruitment of the Georges Bank cod stock. Abundance indices are also available from Canadian research vessel surveys of Georges Bank (since 1986), and inshore spring and autumn bottom trawl surveys conducted by the State of Massachusetts since 1978.

VPA results indicate that fishing mortality on Georges Bank cod doubled between 1978 and 1985 ($F = 0.39$ to $F = 0.84$) and reached a record-high level in 1987 ($F = 0.95$). Spawning stock biomass at the beginning of 1988 was a record-low, about half of that in 1978. Although strong year classes have been produced with regularity (1975, 1978, 1980, 1983, 1985, 1987), significant rebuilding of the spawning stock has been hampered by a strong dependence by the fishery on mostly young fish (ages 2 and 3).

VPA results for the period 1978-1987 indicate that variability in year class strength is rather modest - the smallest and largest year classes differ by a factor of 7. The range in spawning stock biomass is more limited; the highest and lowest SSBs differ by only a factor of 3. Age 1 indices from the autumn USA research vessel surveys appear to accurately reflect relative year class strengths suggesting that year class size is determined during the first year of life. Patterns in recruitment of the Georges Bank stock are generally different from those observed in the Gulf of Maine cod stock.

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