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A Survey of Spawning and Reproduction of the Icelandic Cod

by

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A Survey of Spawning and Reproduction of the Icelandic Cod

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ABSTRACT

This work deals with the spawning and reproduction of the Icelandic stock of cod based on about 1500 samples from 29 years (1953–1981). The shelf around Iceland was divided into 5 subareas and the situation analyzed within these areas in 24 two-week periods. The sources of error that might bias the calculated results are discussed. On the average the peak of the spawning season at the southwest coast of Iceland occurs during the 4th week of April. The main spawning activity takes place within 6 weeks, i. e. from the 4th week of March until the 1st week of May. The mean duration of spawning of individual cod appears to be some 3–4 weeks on the southwest grounds. Here the beginning of the season can be two weeks later or earlier than the mean. Little correlation could be found between fluctuations of the spawning season on the main grounds and deviations of near-bottom temperatures or other physical variables in these localities or in other regions around Iceland. Spawning migrations to the southwest grounds from other areas around Iceland and even from Greenland tend to obscure such a correlation. No significant differences could be found between the spawning activity of the sexes. Since 1964 the spawning season at the southwest coast has been characterized by a longer duration than previously. These prolonged spawning seasons are partly attributed to a long-term drop of sea temperature near and around Iceland, and partly to the increasing contribution of first-time spawners in the spawning stock, as these tend to spawn later in the season than veteran spawners. Spawning activity outside the main grounds at the southwest coast appears to be rather scanty. This limited activity takes place in late spring and appears to be delayed with falling temperature. The data on which the present study is based reveal no spawning activity in the areas adjacent to the main grounds, i. e. Breidafjördur and Dyrhólaey — Eystra-Horn, but egg and larvae surveys have shown that considerable spawning takes place from time to time in these areas. Limited spawning activity appears to take place every year inside fjords at the north coast and occasionally at the east coast. The breeding cycle of the Icelandic stock of cod is studied. The length of the time-span of the spawning (maturity stage III) by individual fish is believed to be roughly the same all around Iceland. Thus, when the spawning is delayed by low water temperature the time-span of the ripening period (stage II) is prolonged and the time-span of spent fish (stage IV) is accordingly shortened as cod in all areas seem to return to the ripening stage in October–December regardless of spawning time. The sex ratio of the cod stock as a whole is roughly 1:1. There is a female preponderance among large and old cod and male predominance among the smaller and the younger ones in all areas at all times. Outside the main spawning grounds the sex ratio of immature cod is relatively balanced throughout the year. The sex ratio of the mature cod is, however, always unbalanced. No systematic annual pattern of the sex ratio

could be found in the regions outside the southwest coast except that linked to size and age. A regular annual pattern of the sex ratio can be observed during the spawning season at the southwest coast. From January until the beginning of March the females are in slight majority. From then on males gain majority and retain it to the end of the season. The sex ratio is analyzed throughout the spawning season with respect to length, age and fishing gear. It appears that the main reason for unbalanced sex ratio is that males attain sexual maturity at a younger age and start spawning migrations earlier (younger) than females. This certainly explains the preponderance of males amongst smaller and younger cod and vice versa.

INTRODUCTION

Since the turn of the century, the Icelandic cod (*Gadus morhua morhua (L.)*) has been the subject of intensive studies, in particular during the last two decades. A number of questions remain unanswered, however, and many problems unsolved concerning this most valuable species of the Icelandic commercial catch. Up to now, a comprehensive long-term analysis of the extensive cod data collected over the years has not been carried out. Computer techniques have reduced the task of such studies. Computer processing was adopted at the Marine Research Institute in Reykjavík in 1965. Now all data are stored on magnetic tape. Older data, back to 1952, have also been transferred to magnetic tape.

The main objective of the present work is to analyze and present cod data covering 29 years (1953–1981) with special reference to spawning and reproduction. The Icelandic cod spawn mainly on the grounds off the southwest coast of Iceland. When does the maximum spawning normally occur on these grounds and does the timing of the season fluctuate from year to year? If so, is there any connection between water temperature and the timing of the spawning season? These questions were originally considered as the main topic of this work and are accordingly dedicated much space. However, a range of other features of the spawning stock as well as the immature cod on the main spawning grounds and elsewhere around Iceland are dealt with: The spawning stock is studied with respect to various biological parameters. The spawning activity is examined by sex. The proportion of first-time spawners in the spawning stock as well as the time of their spawning maximum is investigated. The limited spawning activity outside the main grounds, its frequency and characteristics are analyzed to the extent which the scant material from the localities outside the southwest regions allows. Other questions emerging in connection with the various topics are discussed. Finally the sex ratio of the cod stock is dealt with.

A BRIEF DESCRIPTION OF THE ICELANDIC COD STOCK

The Icelandic cod stock belongs genetically to a single stock, i. e. almost all cod originate from the same spawning stock which spawns on the grounds off the southwest coast of Iceland. In this

area where the water temperature rarely falls below 6° C, the largest part of the Icelandic cod stock is "born". The exact origin of the cod migrating in varying strength from East-Greenland to the Icelandic spawning grounds is not known. These might be individuals of Icelandic origin that have drifted to Greenland as larvae from the main spawning grounds at Iceland. The eggs and later the larvae from the main spawning grounds at the southwest coast of Iceland drift around the island in a clockwise direction. The route leads into increasingly colder waters. The larvae or O-group codlings terminate their drift at various distances from the spawning grounds and it is assumed that while immature they remain mainly at the same localities where they descend to the bottom. When reaching sexual maturity the largest part of the stock migrates to the main spawning grounds off the southwest coast for spawning.

The delaying effects of low water temperature on the growth rate of the cod and likewise on the onset of sexual maturity is well known (Jónsson 1965). Cod growing up in the warm water at the south and southwest coasts generally attain sexual maturity at the age of 4–5 years; cod growing up in the cold water at the northeast coast generally become mature at the age of 7–8 years or even older. A 3-year old cod at the southwest coast may have attained the size of 60 cm. A cod of the same age growing up in the cold fjords of the east coast is likely to measure about 40 cm.

On the spawning grounds off the southwest coast where cod from the nursing grounds all around Iceland and even from Greenland gather to spawn, a mixed heterogeneous group is formed which is referred to as the Icelandic spawning stock. When the spawning is over, most of these cod leave the grounds to feed. Individuals which have grown up in the warm waters may migrate into the cold water. Presumably their growth rate will be slowed down and vice versa for those coming from cold waters and staying in warm waters. It is obvious that after this intermixing has started the differences in the age/length ratios of cod coming from the various areas tend to be levelled out. In this respect the stock approaches homogeneity within the older age groups. However, this point is by and large not reached because the bulk of the cod growing up in colder waters does not attain maturity and start spawning migrations until around the age of 8 years, and due to exploitation, only a small part of the stock reaches the age of 10 years.

MATERIAL AND METHODS

The data used in this work include cod samples collected by the staff of the Marine Research Institute (MRI) in the region around Iceland covering a time span of 29 years, 1953–1981, and consisting of about 143,000 specimens (Table 1, for the years 1953–1974). These cod were collected in 1519 separate samples (Table 2). Thus each sample contains on the average about 94 individuals. The bulk of the samples studied

TABLE 1.

Regional distribution of the source material (1953–1974) by two-week periods for different maturity stages.

Areas	Maturity stages	MONTHS																					
		J		F		M		A		M		J		J		A		S		O		N		D	
1	1–4	2551	5773	6336	8531	7834	10996	8532	6263	5086	4630	425		164	141	161	1229	760	185	57	32	284	245	100	271
	2–4	1455	3582	4684	7031	7145	10241	8174	6122	4939	3572	192		92	18	1301	567	490	99	35	27	252	87	37	57
	1	1096	2191	1642	1500	689	755	358	141	147	1058	233		72	123	660	662	270	86	22	5	32	158	63	214
	2	1455	3568	4679	7011	7075	8935	5087	1413	108	51	1		0	0	0	1	0	0	0	2	245	63	37	57
	3	0	5	8	16	57	1056	2875	3755	2184	65	2		0	0	1	0	0	0	0	0	0	0	0	0
	4	0	9	7	4	13	250	212	954	2647	3456	189		92	18	1300	560	490	99	35	25	7	19	0	0
3	1–4	90	1789	252	71	481	142	37	152	21	100	574		708	2386	1146	208	219	31			198	311	83	
	2–4	88	725	158	61	315	66	11	54	25	0	151		343	1370	411	172	167	9			131	73	30	
	1	2	1064	94	10	166	76	26	98	6	100	423		365	1016	735	36	52	12			67	238	53	
	2	86	725	154	61	315	66	9	15	0	0	5		1	0	1	0	0	0			119	60	8	
	3	0	0	2	0	0	0	2	6	1	0	2		0	0	0	0	0	0			0	0	0	
	4	2	0	2	0	0	0	0	33	24	0	144		342	1370	410	172	167	9			12	13	22	
2	1–4		834	200	107	835	197	261	258	1232	444	242	292	1507	5499	3164	1125			99	99	298	1093	620	
	2–4		57	105	87	133	70	114	12	76	168	80	55	247	1811	1425	456			4	0	11	95	12	
	1		777	95	20	702	127	147	186	1156	276	162	237	1260	3688	1739	667			95	99	287	998	499	
	2		57	105	87	133	70	114	10	14	109	60	41	4	40	11	0			0	0	11	79	54	
	3		0	0	0	0	0	0	0	6	8	1	6	5	3	2	0			0	0	0	0	0	
	4		0	0	0	0	0	0	2	56	51	19	8	238	1768	1412	456			4	0	0	16	67	
4	1–4	528	251				99				198			490	1028	2174	177		9	264		200	231		122
	2–4	45	65				7				1			23	362	1183	63		2	69		5	4		13
	1	483	186				92				197			467	666	991	71		7	135		195	227		97
	2	44	55				7				0			0	2	5	5		0	0		5	1		10
	3	0	0				0				0			0	4	4	2		0	1		0	0		0
	4	1	0				0				1			26	356	1174	61		2	68		0	3		0
5	1–4	70	817	1897	3173	3782	4811	3631	4940	756		10		93	306	319	175	22			100				
	2–4	67	577	1638	2344	3691	4742	3619	4910	754		10		1	192	175	72	6			26				
	1	3	240	259	229	91	69	12	30	2		0		92	114	144	103	16			74				
	2	65	576	1539	2897	3355	3784	1375	786	9		0		1	0	0	0	0			14				
	3	1	1	98	47	335	944	2131	3246	384		0		0	0	0	0	0			0				
	4	1	0	1	0	1	14	113	878	361		4		0	192	175	72	16			12				

TABLE 2.

Annual number of sampling stations in the 5 areas.

Year	AREAS					
	1	*2*	*3*	*4*	*5*	*1–5*
1953	29	3	4	2	13	51
1954	25	0	1	0	14	40
1955	25	3	14	6	13	61
1956	31	1	13	5	14	64
1957	29	4	17	4	20	74
1958	29	2	4	4	19	58
1959	18	4	4	2	16	44
1960	37	9	5	2	19	72
1961	37	6	7	2	8	60
1962	40	3	3	2	13	61
1963	42	3	2	1	10	58
1964	45	0	0	0	17	62
1965	30	2	4	3	19	58
1966	37	4	5	1	8	55
1967	39	2	2	4	7	54
1968	37	8	16	12	25	98
1969	32	0	0	0	13	45
1970	35	5	0	0	12	52
1971	28	0	0	0	6	34
1972	32	25	9	1	3	70
1973	43	36	23	4	10	116
1974	39	20	9	4	13	85
1975	19				13	32
1976	12			3	10	25
1977	44				7	11
1978	8				8	16
1979	5				12	17
1980	10				16	26
1981	3				17	20
1953–1981 ..	800	140	142	62	375	1519

cover only the time period 1953–1974. The 7 additional years up to 1981 are merely analyzed with respect to the annual timing of the spawning season at the southwest coast. The fishing gear by which these samples were collected were mainly bottom trawl, long line and gill-net. Other type of gear, such as purse seine and hand-line, are of little importance. The largest part of the samples, especially from the most recent years, were collected by research vessels fitted with small-meshed trawl. The bulk of the sampling stations was concentrated on the spawning grounds in the southwest during the spawning season while there are gaps in the available material from other areas. It will not be attempted to illustrate the location of all sampling stations. To give a notion of their general distribution the locations of sampling stations for the year 1973 are shown in Fig. 1.

When working out a computer program, Icelandic waters were divided into 5 areas (Fig. 1) and the year into 24 two-week periods. Average values were then calculated for all samples within these categories. The following parameters were recorded: length, age, sex, stage of sexual maturity, spawning zones, fishing gear, date and area of collection.

The grading of the sexual maturity is based on a 4-stage method and visual grading: Stage I immature, stage II ripening (developing gonads), stage III ripe (spawning, running gonads), stage IV spent. Most of the temperature data were taken from Stefánsson and Jónsdóttir (1974), but other sources dealing with physical variables such as ice conditions, surface temperature and salinity were also consulted. The division of the Icelandic waters into sub-areas was based mainly on water temperature. As shown in Fig. 1 the 5 areas are referred to as Southwest (area 1), Northwest (area 2), North (area 3), East (area 4) and South (area 5). The water tempera-

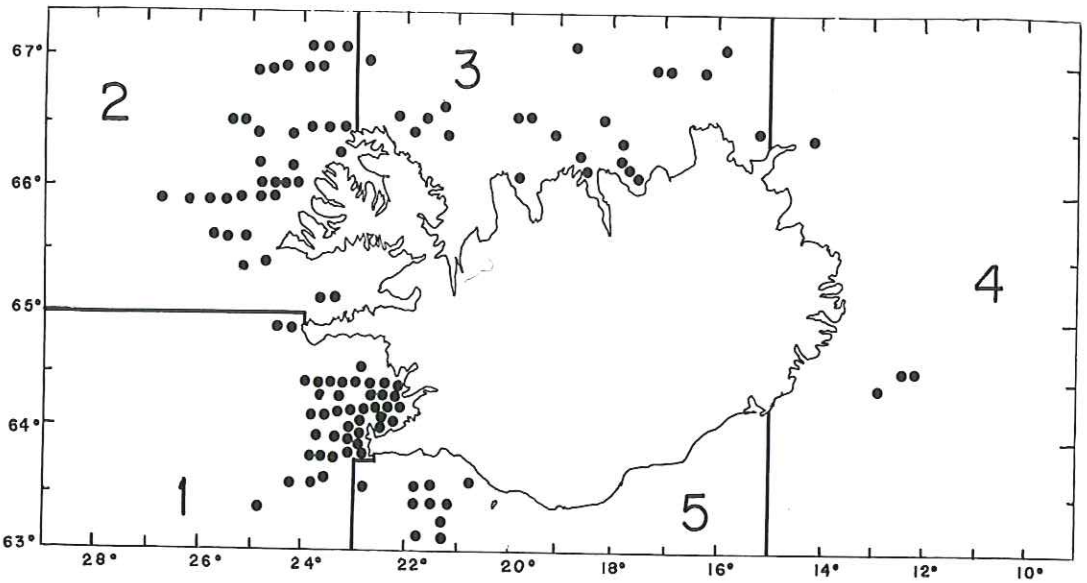

Fig. 1. Location of the sampling stations in 1973, and division of the region investigated into areas.

ture declines generally around Iceland in a clockwise direction from south to east. Normally the isotherms are roughly parallel to the coastline except off the southeast coast where they are perpendicular. This is the only place nearshore where there is a sharp boundary between Arctic water and warm Atlantic water. Elsewhere around Iceland no such sharp boundary zones are found except in the offshore region of area 2. However, on the whole the 5 sub-areas have different mean temperatures and thus different biological conditions. For determining the spawning process the following methods were used: The number of fish at a certain maturity stage (II, III, IV) was computed as a percentage of sexually mature individuals in samples collected within the area and time period in question. For deriving mean values in a certain category two methods of calculations were used. In most cases an arithmetic mean was calculated for all (n) values available within a category. Since the number of samples within some of these categories was in a few cases small and the number of values varying, a grand mean was sometimes calculated of all arithmetic means of separate samples available, giving each sample equal value regardless of size.

SOURCES OF ERROR

The main sources of error will now be discussed. At first let us consider how the stages of maturity are determined. This is done by visual grading. This classification of the sexual stages seems to be a source of errors in some cases. The development of the gonads is characterized by some morphological chan-

ges. These changes are in most cases unmistakable although an individual fish on the verge of two stages may be differently graded by different investigators, as the morphological changes are not clear-cut. A major problem is distinguishing between maturity stage IV (that of spent fish) and stage I (that of immature fish). It appears that first-time spawners at stage IV are heavily mixed with immature fish. Few investigatgors seem to have dealt with this particular problem. Sivertsen (1935) states that the ovaries and the testes of spent fish are thick, with a blue-white tint and clearly visible blood vessels. Iversen (1934) describes these same signs and some additional ones which are only visible under the microscope. Neither of these investigators nor others have mentioned a problem that at least with regard to the Icelandic cod seems to be a source of serious misinterpretation, viz. that it does not seem to become clearly visible whether spawning has taken place until the cod has spawned at least twice. Discussions with MRI staff who have investigated many thousands of cod reveal that in a visual analysis and classification of maturity stages the most reliable criterion between an immature fish and first-time spawner at stage IV is that the gonads of the spent fish tend to be slightly larger and thicker. Common with other signs this corpulence of the gonads does not become clearly visible until the cod has spawned at least twice. Signs such as different colour and visible blood vessels seldom occur prior to the thickening of the gonads and are thus not very reliable for grading when dealing with first-time spawners.

TABLE 3.

Seasonal percentages, in area 1, of mature cod in the age groups 4 and 5. Means for 1953–1974.

Age groups (years)	*January – May*	*May – December*
4	37,5 (n=4631)	63,1 (n=1286)
5	66,6 (n=6003)	91,8 (n=1750)

An attempt was made to estimate the possible extent of this misinterpretation i. e. the grading of immature fish as spent fish. The percentage of sexually mature cod within two age groups in a specific area and period was determined. From January to the middle of May 37.5% of the 4-year old cod and 66.6% of the 5-year old cod were graded as sexually mature in area 1 (Table 3). The corresponding values in the same area for the period mid-May to December were 63.1% and 91.8% respectively. The percentage of mature cod within these age groups has thus grown drastically from the first half of the year to the second half — by as much as 25.6% for the 4-year old, and 25.2% for the 5-year old. What causes this difference? In the first period the determination of sexual maturity is mainly based on maturity stages II and III. The values for this period may therefore be assumed to be reasonably reliable. On the other hand, the values for the second half of the year are mostly based on the erratic maturity stage IV. For this analysis, area 1 was chosen deliberately. Considering the young age groups in question and the high water temperature in this area,

migration of mature fish of these age groups into this area can hardly be expected in great quantities. The cod in colder areas has not attained sexual maturity at this young age. Area 5 has slightly higher temperature than area 1. Nevertheless, migrations from area 5 were disregarded, as most of the samples were collected in the adjacent sides of both areas. Hence, the marked rise in the percentage of mature fish from one season to another must have been caused by immature individuals that were incorrectly graded as spent fish during the second period. During the first period little or no spent fish were available to cause such a mistake. It is evident that this error is mostly one-sided, i. e. immature fish is graded as mature but rarely vice versa. Considering that the average proportion of first-time spawners (they seem to be mixed with immature ones more heavily than others) within the Icelandic spawning stock has been about 73% during the two decades 1953–1974 and 57% of these first-time spawners have been 8 years old or older, it is obvious that mistakes in grading the maturity stages in question must be considerable. In order to reduce these errors in the future, investigators should always grade the fish as immature when in the slightest doubt whether it is immature or spent. It must always be kept in mind that this misgrading is bound to bias all spawning curves especially late in the spawning season when the number of fish at stage IV gradually rises.

Another possible factor that might bias the results is grading by different groups of investigators in different areas. Furthermore, different timing of the spawning season in the different areas can be a source of error when analyzing the material, due to migration from one area to another. Different numbers of samples within categories studied (areas and periods) make comparison often doubtful. It will not be attempted here to evaluate these possible sources of error. They will, however, be referred to in the discussion where their effects are likely to be of significance.

THE SPAWNING SEASON AT SOUTHWEST ICELAND

a) *The peak of the spawning season*

Drawing the spawning curves (stage II, III, IV) as the mean of 22 years (1953–1974) gives the diagram shown in Fig. 2. Although spawning individuals can be found from the beginning of January until June the main season falls within a much shorter time. Thus in area 1 more than 98% of the spawning activity lies within 6 weeks, i. e. from the 3rd week of March to the 2nd week of May, the maximum spawning activity occurring between the 3rd and 4th weeks of April. At this time about 60% of the spawning stock present is spawning, i. e. has running gonads. A small remainder of the activity takes place mainly during the second half of May.

The spawning curves for area 5 show similar features. Spawning activity starts about 2 weeks earlier in this area resulting in about 20% spawning activity by

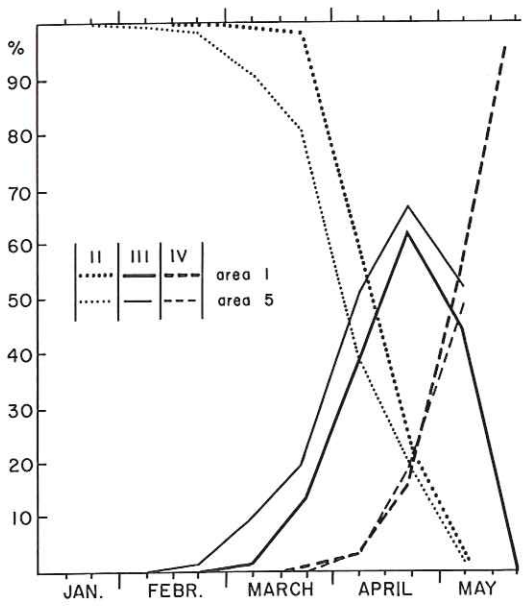

Fig. 2. Mean (1953–1974) distribution of different maturity stages during the spawning season by two-week periods for areas 1 and 5.

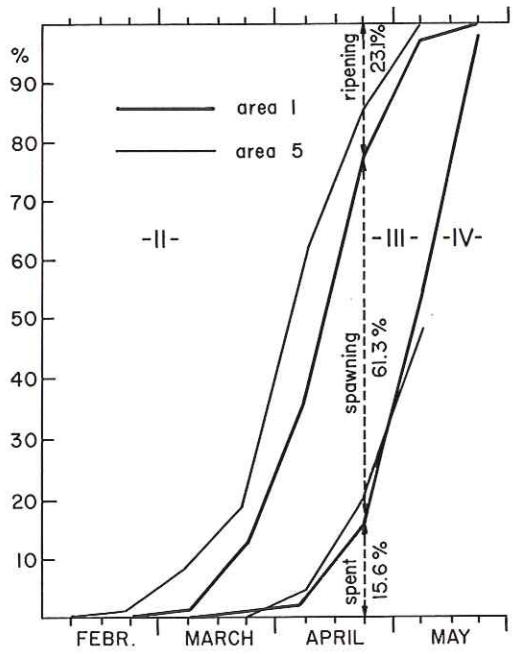

Fig. 3. Distribution, in time, of the maturity stages, i. e. percentages of ripening (II), spawning (III) and spent (IV) fish by two-week periods throughout the spawning season for areas 1 and 5. Means for 1953–1974.

the second half of March. On the whole, area 5 has slightly higher water temperature than area 1. The slightly later start of the season in area 1 is therefore in agreement with Sæmundsson's (1926) findings that the lower the water temperature, the later will be the spawning season. In spite of a somewhat earlier start it seems that the season is not finished any earlier in area 5 than in area 1 (Fig. 2). As shown in Fig. 3, stage IV curves in the two areas almost coincide. Regrettably the curves in area 5 cannot be followed to the very end of the season due to insufficient material. It seems unreasonable to assume that it takes longer time for the individuals to spawn in area 5 than in area 1. In this connection it must be kept in mind that we are not observing the same cod throughout the season. Migrating spawners are probably constantly coming from outside.

b) *The time-span of stage III for individual fish*

From the diagram in Fig. 3 the mean length of time it takes the individual cod to spawn can be read.

The duration of stage III in individual years (Figs. 4 and 5) is quite variable. It must be kept in mind that the annual curves do not represent the development of a certain number of spawners that are present throughout the season, but are those of a spawning stock gradually coming to the grounds. Spent fish

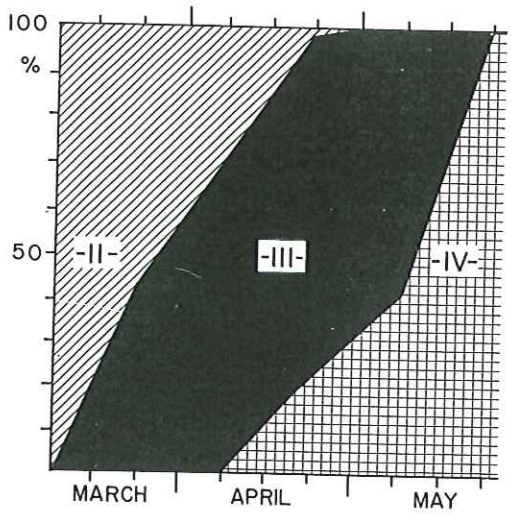

Fig. 4. Maturity stages II, III, and IV in area 1 throughout the 1965 spawning season (n=2017).

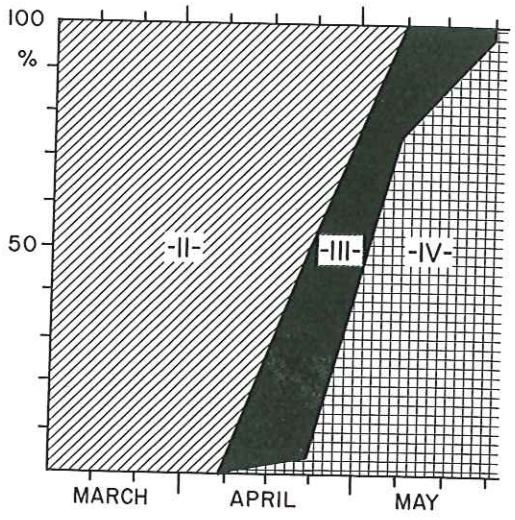

Fig. 5. Maturity stages II, III, and IV in area 1 throughout the 1954 spawning season (n=3957).

which spawn early in the season may stay longer on the grounds or they may leave them soon after spawning. One may expect that some of the fish which have already spawned in area 5 migrate into area 1 and cause a shift in the stage IV curve for that area. It is interesting to note how parallel the curves* in Fig. 6 are running. We can expect that the mean values of all 22 years tend to level out the disturbing effects. Consequently it is assumed that in the diagram shown in Fig. 6 we have a fairly true picture of the length of the mean spawning time of individual fish.

In area 1 the width of the stage III stripe (Fig. 3) corresponds to about 24 days at the 50% spawning activity level. The stage III stripe in area 5 is incomplete at the very end of the season due to lack of data, but appears to be wider than in area 1, corresponding to about 32 days. As mentioned earlier it seems unlikely that individual spawning in area 5 takes longer time than in area 1 as the water temperature in the former area is slightly higher. As so few samples were available from area 5 at the end of the season, this difference is hardly real. Considering both areas together (Fig. 6) it seems justifiable to state that the spawning of individual cod on the main spawning grounds at the southwest coast takes between 3 and 4 weeks.

Earl (1880), Ewart and Brook (1885) and Meek (1924) describe the spawning of cod at the British coast and U.S. east coast as a process lasting several weeks with pauses of several days between the separate acts. These observations were made in aquarium. Hilge (1972) states that the whole process of ovarial devel-

* The time-span between them is referred to as the stage III stripe.

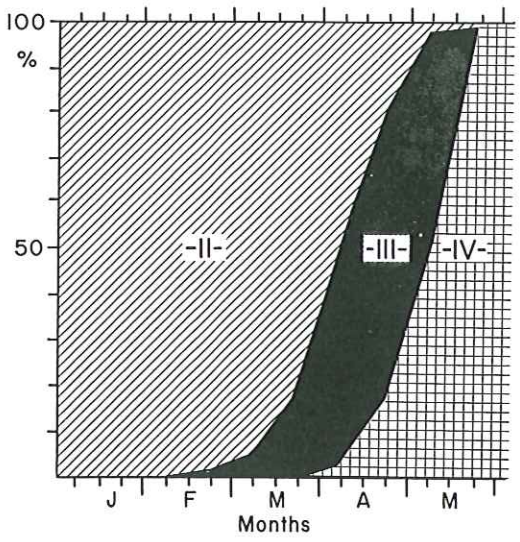

Fig. 6. Percentages of the maturity stages throughout the spawning season by two week periods at the southwest coast, i. e. areas 1 and 5 combined. Means for 1953–1974.

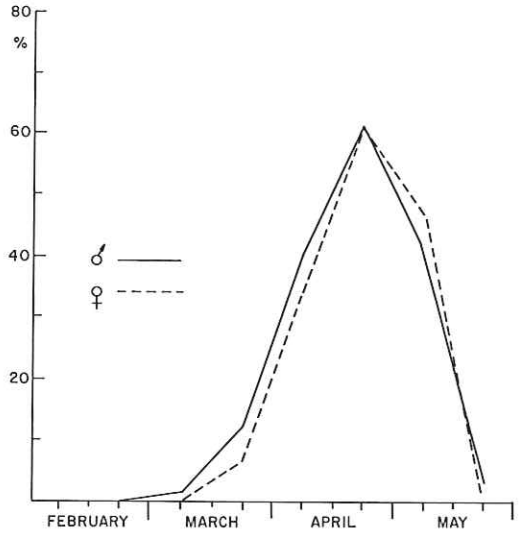

Fig. 7. Percentages of fish with running gonads (stage III), males and females, throughout the spawning season in area 1. Means for 1953–1974.

opment indicates that the cod in the Baltic Sea spawn in spurts and the laying of eggs takes considerable time. When discussing this topic most authors mention no specific time period during which spawning takes place, but speak of several weeks. However, Graham (1932) gives an example in which this took 19 days (east coast of England, presumably in an aquarium cage). These results agree reasonably well with the present findings.

c) *The sexes and the spawning activity*

The spawning curves for each sex are shown in Figs. 7, 8, 9 and 10. In area 1 it looks as if the males develop running gonads somewhat earlier in the season than the females (Figs. 7 and 9). In area 5 no such phenomenon is visible (Figs. 8

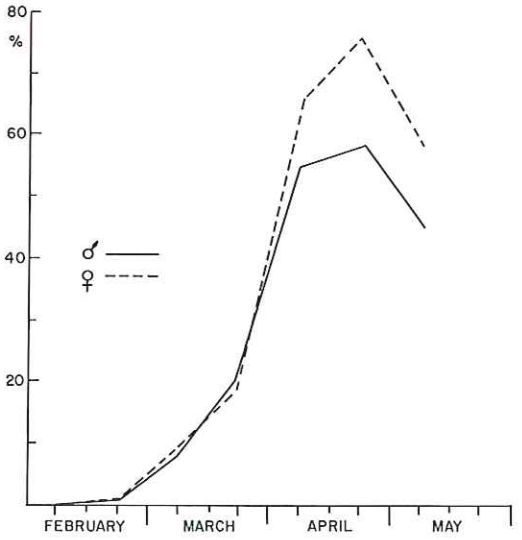

Fig. 8. Percentages of fish with running gonads (stage III), males and females, throughout the spawning season in area 5. Means for 1953–1974.

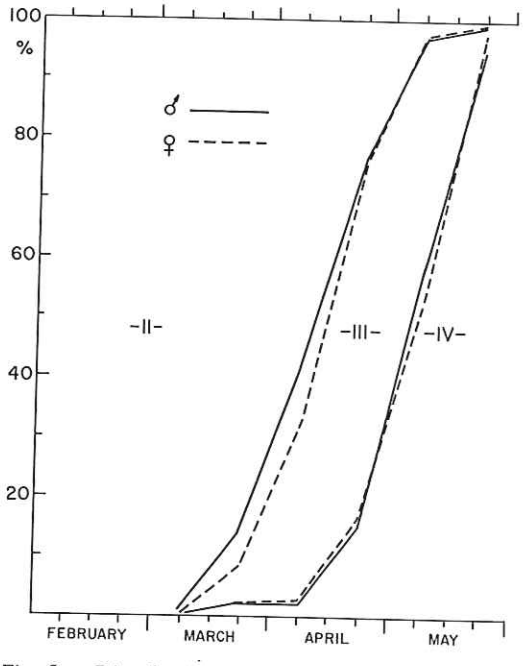

Fig. 9. Distribution of maturity stages II, III and IV in area 1 for both sexes throughout the spawning season. Means for 1953–1974.

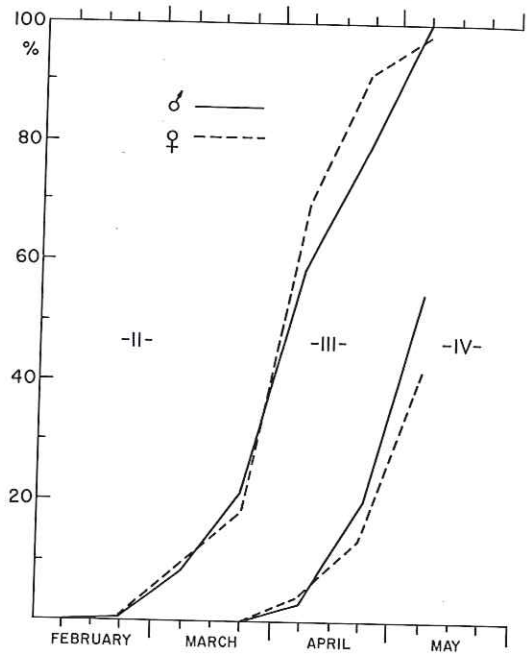

Fig. 10. Distribution of maturity stages II, III and IV in area 5 for both sexes throughout the spawning season. Means for 1953–1974.

and 10). The stage IV curves indicate that in neither area do the males finish the stage III period prior to the females. The frequently overlapping spawning curves of the sexes lead to the conclusion that there is no significant difference in the timing of the breeding cycle of the sexes. The stage IV/II turnover is not included in these illustrations. This phase of the maturation cycle occurs in the late autumn and material for that season is very limited. In analyzing the available material no difference could be found between sexes as regards the return to stage II.

Sivertsen (1935) examined the breeding cycle of cod in Norway by weighing the ovaries and the testes. He found the ripening process (stage II) in males to begin earlier than in females. He stated that the spawning covers a longer time period in males than in females. Graham (1923) investigating the gonads of North Sea cod and grading their development visually, supported the findings of Sivertsen. Ruud (1939), in a similar study of Norwegian cod found, however, that the annual development of the gonads proceeded simultaneously in both sexes. Berner (1960), discussing the Baltic Sea cod wrote that the act of spawning in females — opposite to males — starts gradually but then proceeds relatively rapidly. These findings are somewhat contradictory. Most of the authors, however, have concluded that males are

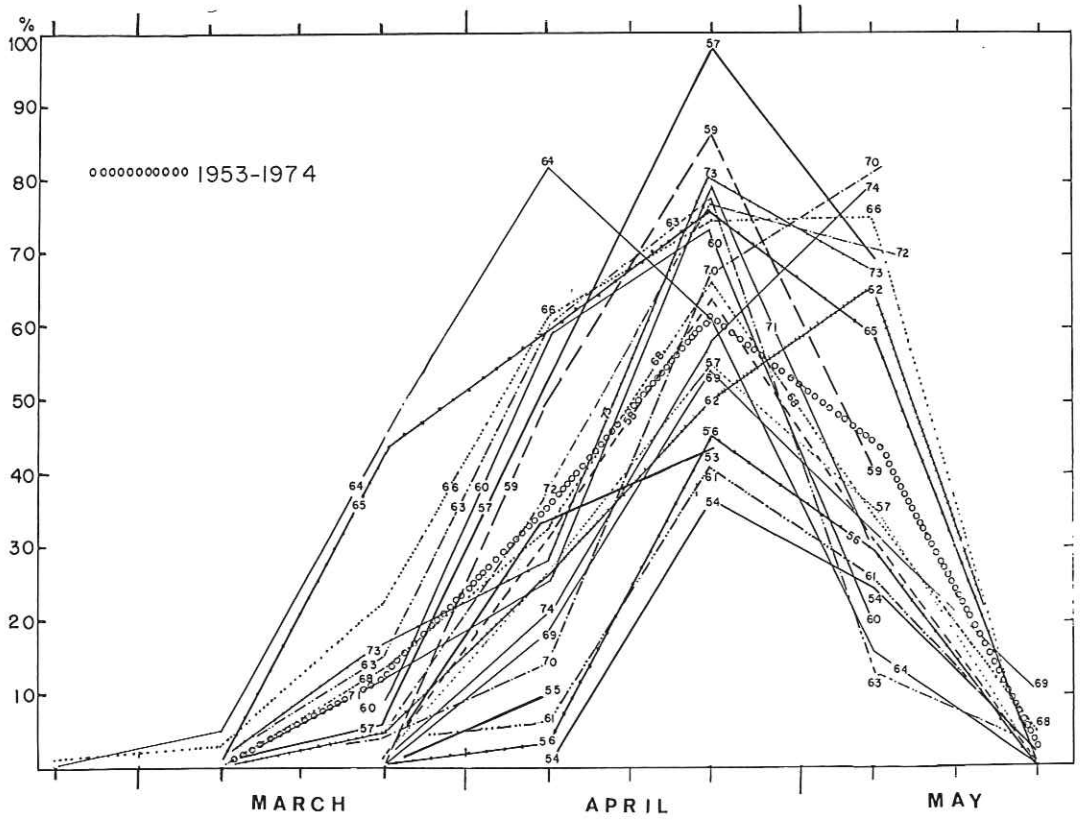

Fig. 11. Percentages of fish with running gonads (stage III) for each year from 1953–1974 in area 1.

fully ripe earlier than females. This seems to be the case in area 1.

d) *Annual fluctuations of the spawning season*

The spawning curves for fish with running gonads (stage III) for each year studied are shown in Figs. 11 and 12 for areas 1 and 5. Fluctuations of the spawning season in individual years based on spent fish (stage IV) are illustrated in Fig. 14. The spawning curves for the years 1975–1981 are shown in another diagram in Fig. 13 where areas 1 and 5 are combined, since due to their limited number of samples it was not feasible to draw a separate curve for each area. Clearly the shape of the stage III curve (Figs. 11, 12 and 13) varies markedly from year to year, i. e. the spawning season is subject to considerable fluctuations both with respect to time and percentage corresponding to the spawning peak. Here it should be recalled that the spawning grounds are entered by different spawning migrations coming from as remote areas as Greenland. Varying times of arrival of such migrations into the spawning area are bound to affect the shape of the spawning curves.

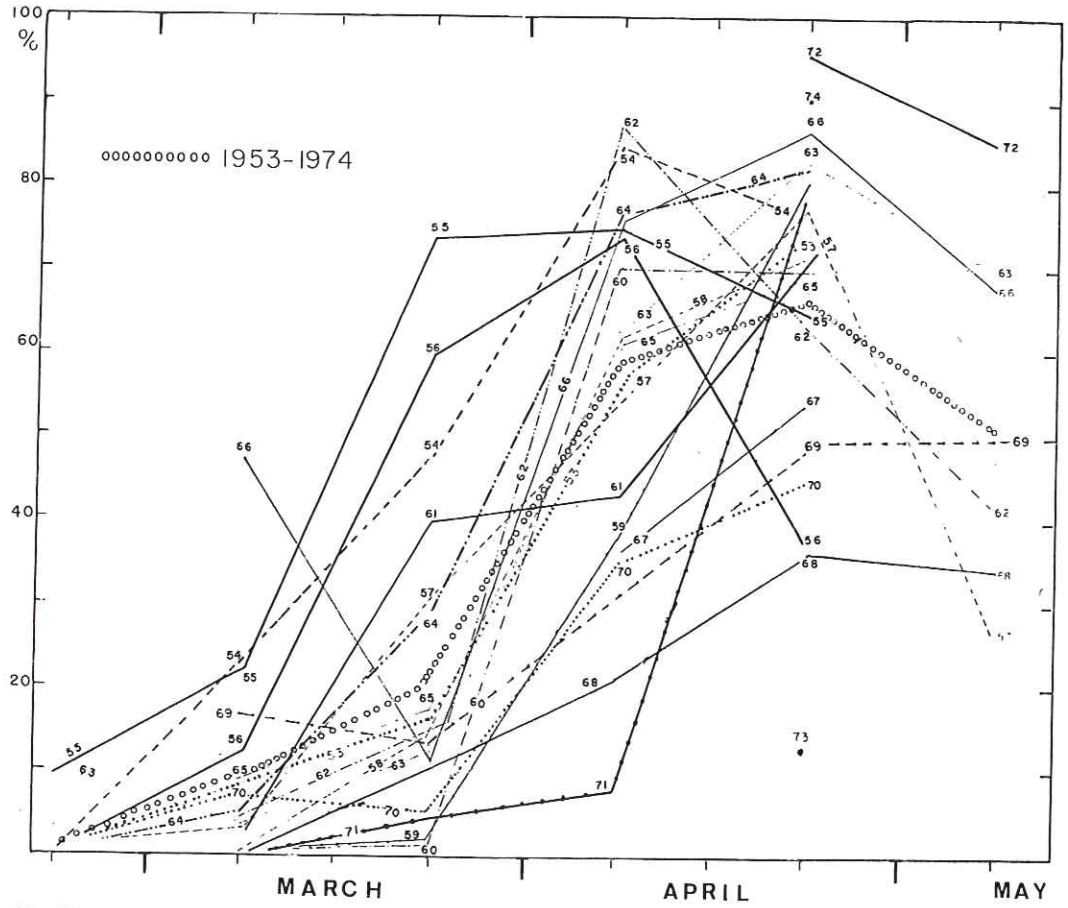

Fig. 12. Percentages of fish with running gonads (stage III) for each year from 1953–1974 in area 5.

Furthermore, the diagrams shown in Figs. 11, 12 and 13 can most certainly be subject to bias. Nevertheless, they should give a fairly true picture of the beginning of the spawning activity. Later in the season the curves may be affected by new migrations of spawners that were not present on the grounds during the first half of the main season. These factors will now be considered in more detail.

If it is assumed that it always takes individual cod the same length of time to spawn (3–4 weeks), the proportion of spent fish on the grounds should in due time grow in relation to spawning fish on the grounds. This is not always the case, however, since fish already spent may either leave the grounds immediately after the spawning or stay there for some time. Furthermore, spent or spawning fish from other areas may enter the grounds. To give an example of this, two seasons have been selected (Figs. 4 and 5). In area 1 in 1965 an unusually high percentage of cod collected during late March and early April had running gonads. Nevertheless, stage IV did not show

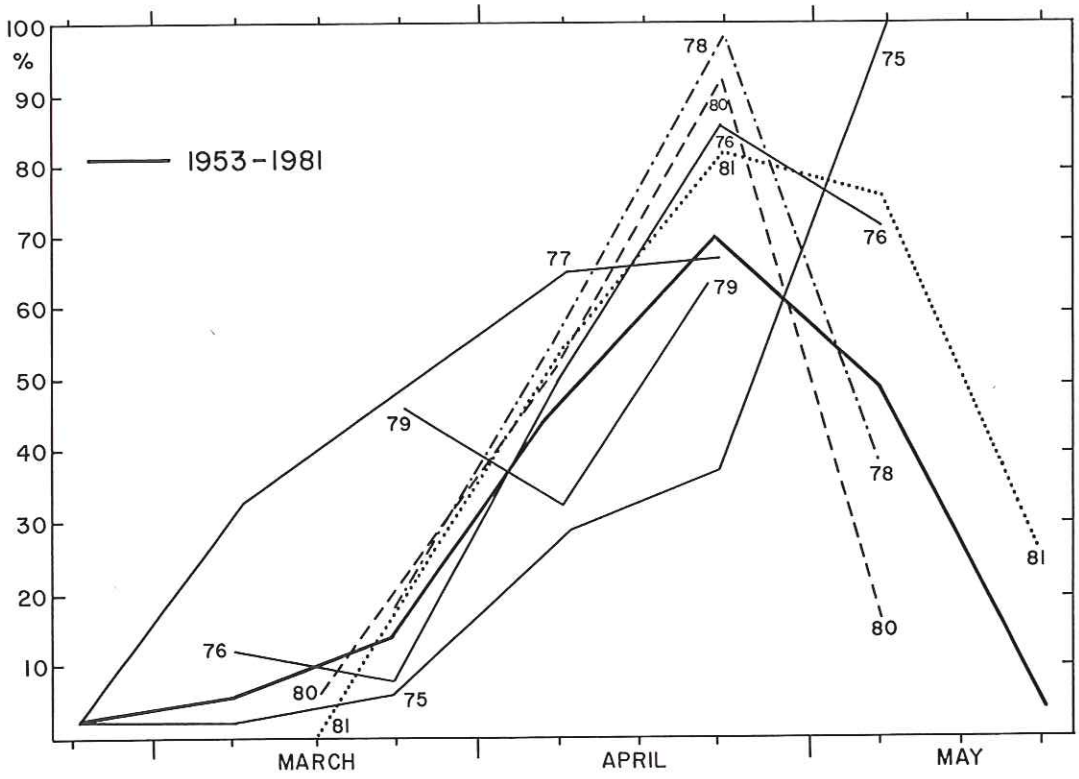

Fig. 13. Percentages of fish with running gonads (stage III) for each year from 1975–1981 and the mean of all years (1953–1981) at the southwest coast, i. e. in areas 1 and 5 combined.

up until 6 weeks later. This could be explained in such a way that spent fish were leaving the grounds quickly but large shoals of spawners already at or close to the spawning stage were entering the same grounds. This would mean that the area was dominated by spawning fish for more than 6 weeks. The opposite was found in the same area in 1954. This year the spawning activity started very late. But in the week following the onset of spawning the spent fish were showing up in numbers corresponding to the spawning activity. It seems as improbable that it took individual fish only one week to spawn in 1954 as it seems unlikely that it took them 6 weeks to do so in the 1965 season. The sudden rise of the percentage of spent fish in 1954 could have been caused by spent fish moving in from area 5. This view is supported by Fig. 12 which shows that the season began unusually early in area 5 this year. Immature fish incorrectly determined as spent ones may also have biased these data.

When comparing the annual fluctuations of the spawning season with other variables such as temperature or number of cod eggs found on the spawning grounds during the season, the fluctuations in Figs. 11, 12, 13 and 14 are diffi-

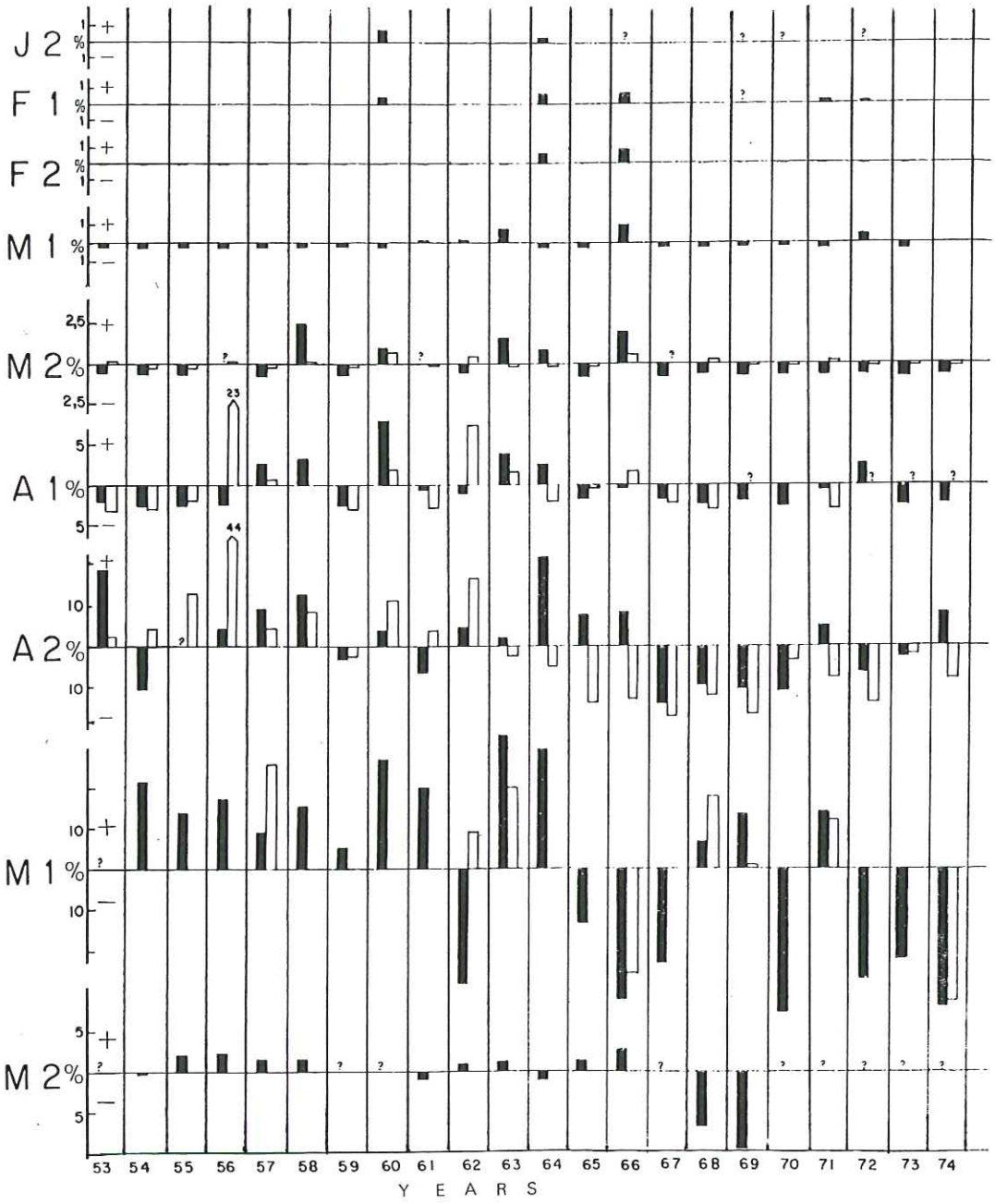

Fig. 14. Percentage deviations of spent fish (stage IV) from long term mean by two week periods. Black columns: area 5, white columns area 1. J 2: second half of January, F 1: first half of February, etc.

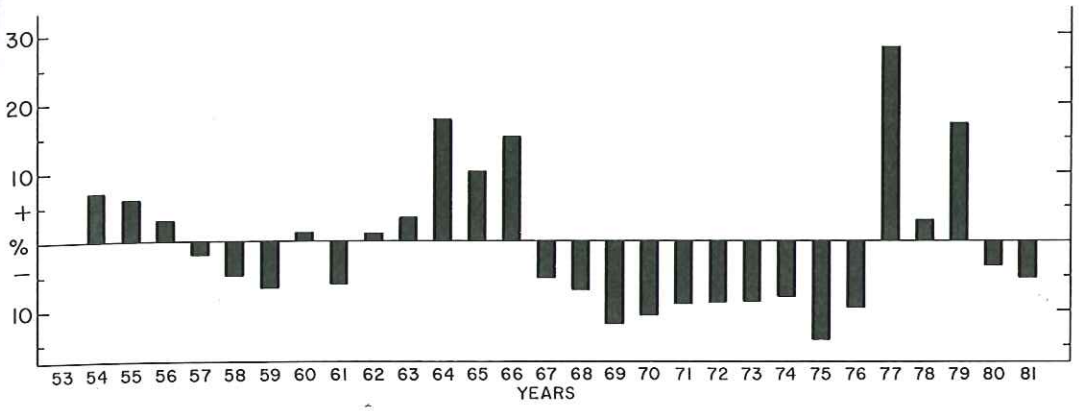

Fig. 15. Variations in the beginning of the spawning season at the southwest coast. Presented as deviations from the long-term mean of the percentage of cod with running gonads within the period from 1st of March to 15th of April. Areas 1 and 5 combined.

cult to interpret except in broad terms. To express the differences in the start of the annual spawning season more explicitly the following method was applied: The mean annual percentage of cod with running gonads (stage III) from 1st of March to 15th of April within areas 1 and 5 combined was calculated. The results are illustrated as deviations from the mean in Fig. 15. The year 1974 with the lowest intensity of spawning activity within the given period is believed to be the year with the latest start of the main spawning season. Conversely, the year 1977 with the largest spawning intensity during these 6 weeks is believed to be the year with the earliest start of the main season.

Summing up the results it is clear (Figs. 11, 12 and 13) that the onset of the main season could vary up to 4 weeks in both areas in the 29-year period studied. It is interesting to note that in years with an early start of the main season slight activities begin in some cases as early as in February or even in January.

Deviations in the spawning peak from a long-term mean based on the proportion of spent fish (stage IV) are illustrated in Fig. 14. From this diagram it becomes clear that in spite of some marked differences between areas in some years, similar fluctuations were found in other years, especially towards the end of the spawning season. This is interesting as the fluctuations during this latter part of the spawning season are likely to be subject to bias as discussed earlier. Traces of spent fish occurring occasionally as early as January are highly dubious. These must largely be immature cod wrongly graded as spent cod.

e) *What causes the annual fluctuations?*

Many investigators have described the correlation between water temperature and the general onset of sexual maturity. Less efforts have been devoted to the study of the possible connection bet-

ween fluctuations of the water temperature and the process of the annual spawning activity.

We have already seen that the start of the spawning season can fluctuate considerably. Such phenomena are also known to occur in other stocks. On the spawning grounds off the east coast of England Graham (1924) determined the annual concentration of eggs and found that the timing of the spawning season could vary up to one month. He offered no explanation of what might cause these variations. Dannevig (1930) analyzed the local hydrographical conditions of several spawning grounds in Norway and concluded that hydrographical variations can have significant effects on the spawning. He found temperature to be more effective variable than salinity. He pointed out, however, that the Norwegian fjord-cod sometimes spawned unusually late although the winter temperature was favourable.

Comparison of the near-bottom temperature deviations (Stefánsson and Jónsdóttir 1974) with the timing of the spawning season reveals some correlation, when taking only the coldest and the warmest years into account, but also some discrepancies. In area 1 January 1964 was unusually warm. The spawning season of this year was characterized by an unusually early start. The thin foretrace of spawners was exceptionally clear and the main season was in full swing by the beginning of April or two weeks earlier than the average season. The year 1966 was cold (February, March). Contradictory to the above example, unusually early spawners were much in evidence this year (1966) and the season turned out to be one of the earliest of all seasons. However, the season finished unusually late. In area 5 the 1953 season seemed quite normal in spite of a cold winter (March) and the season of the cold winter 1962 (February, March) seemed even to commence unusually early. The year 1973 had an unusually cold spell in March and April. The biological data from this season are regretfully not complete. By the second half of April spawning activity had dwindled to about 23% and the season seemed to end earlier than all others in that area. Furthermore, the years 1974 with the latest, and 1977 with the earliest onset of spawning were not abnormal with respect to temperature conditions.

Probably the correlation between the timing of the spawning seasons and anomalies in physical variables was valid, but was obscured by migrations of spawners from outside. The cause of the fluctuating time of the spawning season (its start and prolonged duration) may then relate to the water temperature on the grounds from which the migrating spawners come. The long distances between the spawning grounds and the localities from which the spawning migrations come (e. g. E-Greenland and N-Iceland) make it very difficult, however, to establish such a connection even though it exists.

Sæmundsson (1926) stated that it looks as if the migrating shoals of spawners either spawn immediately, once they have reached the grounds or they stay

for some time on the spawning grounds until spent. If this explanation applies, one could assume that the cod that spawn at once come from relatively warm waters and are almost fully ripe when they reach the spawning grounds. If true, large migrations from Greenland should delay, or more likely prolong, the spawning season on the grounds at SW-Iceland. At the same time the water temperature in both localities might be quite normal.

In the years 1953, 1964, 1966 and 1968 there were large spawning migrations from Greenland (Mayer, 1969). The spawning seasons of these years were in most cases characterized by a prolonged (late) period of intense spawning activity in both areas 1 and 5.

Other sources of data consulted, i. e. surface temperature and salinity (Stefánsson 1969, Malmberg 1969) and ice conditions (Sigtryggson 1969) did not reveal any significant correlation between these physical variables and the timing of the spawning season.

f) *Long-term fluctuations of the spawning season*

When considering long-term fluctuations of the spawning season, two aspects of the season should be looked at, i. e. its beginning and end. As already mentioned, varitations of these are not always in harmony with each other. First, consider the end of the various seasons.

It seems that the last 11 years of the period 1953–1974 have a more prolonged season than the first 11, (Fig. 14). This is not without exception, but the general tendency is quite clear. The years after 1974 are not included in the diagram in Fig. 14. The years 1975 and 1976 had a prolonged or late season but in the years thereafter no regular pattern appeared. In some cases the long-lasting seasons had an early start. In such cases the variations were presumably caused by different spawning migrations and were in little connection with the anomalies of water temperatures on the spawning grounds. This development could also have been caused partly by the contribution of first-time spawners in the spawning stock and their habit of spawning later than other spawners (Fig. 16).

However, anomalies in physical variables could be involved. Long-term changes in water temperature are well known. Sæmundsson (1934) discussed a general rise in the water temperature in Icelandic waters during the period around 1930. He stated that this caused an increase of stray fish species from southern waters. According to Stefánsson (1969) there was a marked downward trend in temperature and salinity in the North Icelandic coastal area during the period 1963–1968, whereas south of Iceland, the temperature decrease in the period 1960–1969 was only slight, although significant (Stefánsson 1970). This difference between the regions north and south of Iceland was attributed to the distribution of ice which has affected very strongly the temperature conditons north and east of Iceland during the decade 1961–1970.

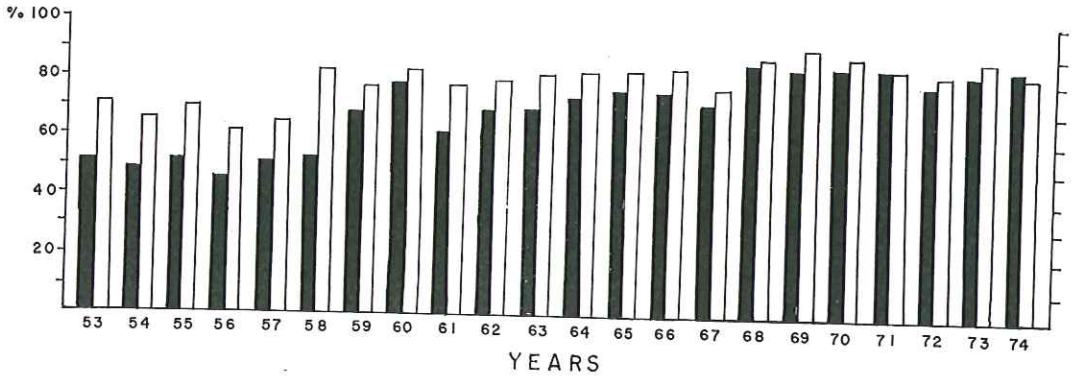

Fig. 16. Annual percentages of first-time spawners in the spawning stock at the southwest coast. White columns: area 1, black columns: area 5. Means for January – May.

Using data from various sources Smed (1976) found that the mean surface temperature in a region west, northwest and southwest off Iceland had dropped significantly since about 1960 (by about 1°C). In the adjacent region east of Iceland and in the region east of Greenland the surface temperature had dropped since about 1967. In view of the fact that the spawning stock grows up in the regions here referred to, it seems plausible that there was a connection between the drop in water temperature during the last decade and the prolonged spawning season at the southwest coast of Iceland within roughly the same period.

Long-term fluctuations in the start of the season are shown in Fig. 15. It is obvious that these variations are not following the same pattern as variations at the end of the season (Fig. 14) although we can see some similarities. Here (Fig. 15) we have rather regular phases consisting of several years with late beginning and alternating phases with early start.

g) *Long-term proportion and composition of first-time spawners in the spawning stock*

Table 4 shows the proportion of first-time spawners within the age groups from 1953–1972. It is interesting to note that even among old cod the proportion of first-time spawners is sometimes surprisingly high. This is due to the fact that the bulk of the spawning stock attains sexual maturity at relatively old age. Thus high percentage of first-time spawners at the age of 8 is quite natural. It seems that when the fish grow sexually mature and start spawning migrations they are more likely to be exploited. This is especially true for the E-Greenland cod. Fish growing up on the E-Greenland grounds do not seem to have been accessible to the fishery until they left the nursing grounds when sexually mature. During the 1950's very large "armies" of old cod spawning for the first time appeared on the Icelandic spawning grounds. In 1956, for example, 57% of the Icelandic spawning stock

TABLE 4.

Annual percentage of first-time spawners among those spawning within age groups of the spawning stock in areas 1 and 5 combined. Means for January – May.

Years	Age-groups (years)											
	3	4	5	6	7	8	9	10	11	12	13	14
1953	100	100	96,7	88,6	78,2	86,5	59,8	43,3	11,3			
1954		100	100	95,0	87,8	70,7	82,0	47,4	21,4	1,8		
1955	100	100	96,3	81,2	54,9	66,7	64,2	61,4	29,6	7,0	1,6	
1956		100	96,0	95,4	87,7	75,4	70,3	63,6	53,0	19,1	11,5	5,9
1957	100	100	100	99,2	91,3	78,2	55,1	47,3	23,6	11,0		
1958		100	93,7	97,2	89,1	90,0	75,0	47,2	25,6	3,7	1,2	
1959	100	100	98,2	94,9	84,5	86,2	76,1	55,9	21,0	7,4		
1960		100	96,0	96,7	90,0	83,4	78,1	69,5	44,5	9,3	6,7	
1961		100	99,4	99,1	81,6	82,1	67,5	63,3	48,0	19,9		
1962		100	99,6	91,0	90,1	87,3	81,8	64,3	70,8	47,8	23,3	
1963	100	100	99,1	100	97,3	87,3	77,1	66,2	47,8	38,6	13,7	1,4
1964	100	100	99,2	99,1	96,3	91,4	70,4	50,2	31,9	24,8	15,0	
1965	100	100	99,2	96,6	87,6	79,7	72,0	51,7	32,2	19,5		
1966	100	100	100	98,4	93,8	88,4	74,0	62,4	24,5	10,7		
1967	100	100	99,4	95,5	84,5	74,6	76,4	55,9	31,2			
1968	100	100	100	98,6	95,2	82,1	69,6	61,9	16,7	9,0		
1969	100	100	100	97,6	93,4	88,2	75,5	45,2	49,2			
1970	100	100	99,7	95,2	88,0	77,5	61,0	50,0	14,2			
1971	100	100	100	99,0	88,0	83,2	73,8	42,9	25,8			
1972	100	100	100	98,2	86,7	76,6	71,9	61,3	35,9			
1953–1972	100	100	98,6	95,8	87,3	81,8	71,6	55,0	32,9			

consisted of 11 year old cod, and of these, 53% were spawning for the first time (Table 4). This strong year class from 1945 did not become significant in the spawning stock until it had reached the age of 7 in 1952. A year later, 1953, this year class (then 8 year old) dominated in the spawning stock (34%) and for many years thereafter. This year class (1945) was characterized by a high proportion of first-time spawners for many years. According to Table 5 each cod in the spawning stock had, in 1955, an expectancy to spawn 1.8 times in its lifetime and in 1969 1.1 times. The proportion of the first-time spawners has thus been growing larger year by year. This development is not always evident, as strong year classes may raise the contribution of first-time spawners on the southwest grounds to an abnormally high value for a year or two. The increasing proportion of first-time spawners is of course a true sign of increasing exploitation, an exploitation which has been affecting the younger age groups more and more. From Fig. 16 it will be seen that the average contribution of the first-time spawners is 72.8% during the 22 years (for both areas). The proportion of first-time spawners is always somewhat lower in area 5 than in area 1.

TABLE 5.

Percentage division of the spawning stock based on number of spawning zones in otholiths. Means for areas 1 and 5 combined for January – May.

Calendar year	Number of spawning zones									
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*≥10*
'53	63,4	19,5	9,4	4,7	1,3	—	0,9	0,4	0,2	—
'54	60,7	22,7	6,7	2,9	3,4	—	1,1	0,8	0,5	0,5
'55	56,5	29,6	9,2	0,7	1,6	0,5	0,5	0,7	0,5	0,2
'56	60,7	22,1	10,2	4,5	0,9	1,2	0,2	—	—	—
'57	67,7	12,9	9,7	6,2	2,3	0,7	—	0,5	—	—
'58	75,0	11,1	7,7	2,6	1,3	0,7	1,3	—	—	0,2
'59	76,0	12,0	7,1	3,2	1,2	0,3	0,2	—	—	—
'60	84,3	9,7	3,1	0,6	1,2	0,4	0,1	0,3	—	—
'61	75,3	17,4	4,3	1,3	0,7	0,4	0,1	0,2	—	—
'62	82,7	8,9	6,1	2,3	0,5	0,1	0,4	—	—	—
'63	82,6	9,1	5,0	2,1	0,4	0,4	0,1	0,1	0,1	—
'64	76,2	14,1	4,5	2,0	2,4	2,3	—	0,1	—	—
'65	82,1	16,3	1,3	—	0,2	—	—	—	—	—
'66	79,1	10,0	7,4	1,3	1,0	0,1	—	—	—	0,8
'67	79,0	15,0	3,8	1,8	0,3	—	—	—	—	—
'68	89,1	7,8	2,2	0,2	0,2	0,2	—	—	—	0,1
'69	91,6	6,3	1,0	0,2	0,5	—	0,2	—	—	0,1
'70	81,6	15,7	2,7	—	—	—	—	—	—	—
'71	79,2	13,0	6,3	1,8	0,3	0,2	—	—	0,2	—
'72	74,2	17,6	5,8	1,8	0,3	0,1	—	—	—	—
,73	84,4	12,7	2,2	0,8	0,5	0,2	0,2	—	—	—
'74	69,7	21,9	3,6	2,3	0,7	1,0	0,2	0,2	—	0,2

This may be explained by the fact that the fish in the samples from area 5 are on the average older (and larger) than those collected in area 1 (Fig. 17) and the share of first-time spawners is on the average bound to decrease among older fish. However, the mean age of the first-time spawners is surprisingly high. Fig. 18 shows that fish that spawned first at the age of 8 or later constituted on the average 60.4% of the spawning stock. Of these, 70.7% were first-time spawners. From these values we can calculate that 56.5% of all first-time spawners in the spawning stock were 8 years or older during the 22-year period.

h) *The timing of the first-time spawners in the spawning stock*

The majority of first-time spawners spawn in the last two weeks of May (Fig. 19). It was not possible to trace the first-time spawners directly according to age throughout the season, their share being considerable in the beginning of the season and then slowly rising towards the end. From Tables 6 and 7 it can be inferred that the first-time spawners spawning in the beginning of the season and toward the end of it are younger than other spawners. The very young first-time spawners spawn at the end of the season. As the same length class domin-

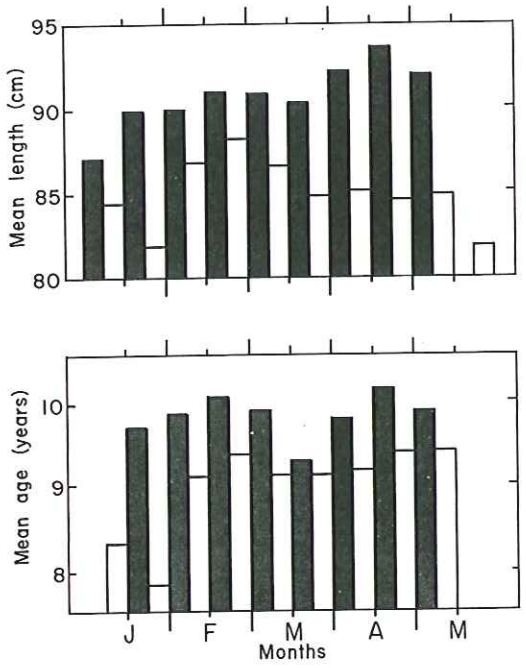

Fig. 17. The average age and length of the spawning stock at the southwest coast. White columns: area 1, black columns: area 5. Means for 1953–1974.

ated throughout the season (Table 6) we can infer a rapid growth rate of these first-time spawners which were found with running gonads at the beginning and toward the end of the season. Therefore, they presumably grew up on the southwest grounds in relatively warm water. Because spawning migrations from colder regions consist 70% of first-time spawners, it is difficult to trace the path of these first-time spawners throughout the season. However, as the percentage of first-time spawners generally rises toward the end of the season, it can be concluded that first-time spawners migrating from cold water regions tend to spawn later in the season than those spawning for the second time. This is in fair agreement with the results of Ruud (1939) who stated that it appears that young first-time spawners (cod in the Oslo fjord) always spawn later in the season than others. Jónsson (1961) found the same with respect to all first-time spawners in Icelandic waters.

SPAWNING ACTIVITY OUTSIDE THE MAIN GROUNDS

It would be somewhat misleading to talk about a spawning season around Iceland outside the spawning grounds in the southwest. The material analyzed shows that spawning activity in the colder areas northwest, north and east of Iceland is rather limited and in some years not even in evidence.

Within the large area off the southwest coast extending from Dyrhólaey at the south coast to Snæfellsnes on the west coast, the main spawning activity is known to be concentrated in the region from west of the Westman Islands (Selvogsbanki) to the southern part of Faxaflói. As shown in Fig. 1 there is practically no material available from the eastern part of area 5 which extends to the southeast corner of Iceland. The same holds more or less for the southern part of area 2 (Breidafjördur). Therefore, when discussing the spawning activity outside the main grounds at the southwest coast, the adjacent areas, i. e. Breidafjördur and the southeast coast (Dyrhólaey to Vestra-Horn) are not included. In these areas, where water temperatures are favourable, a consider-

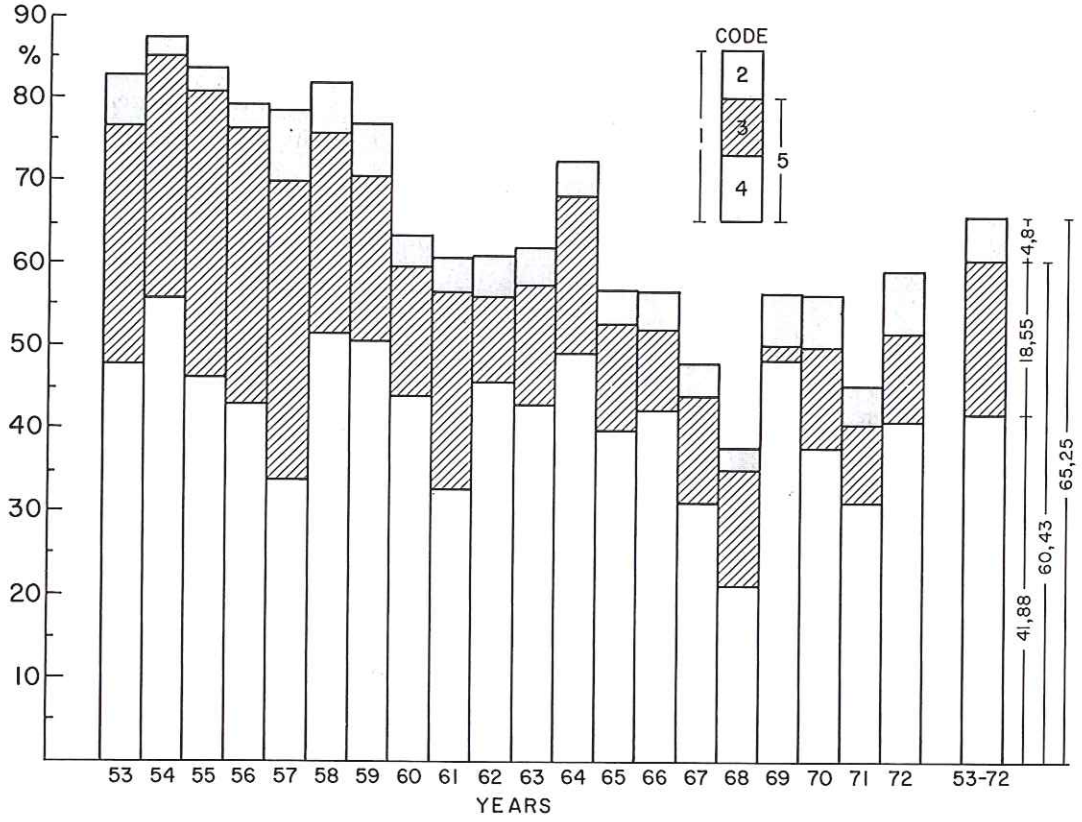

Fig. 18. The annual percentage of cod older than 7 years in the spawning stock in the period 1953–1972; the share of first-time spawners among these old spawners, and the share of those spawners which attained sexual maturity and spawned at an age of less than 8 years. Means for January – May in areas 1 and 5 combined. Explanation of code. 1: Percentage of 8 years old and older cod in the spawning stock. 2: Percentage of 8 years old or older cod in the stock that spawned for the first time younger than 8 years old. 3: Percentage of 9 years old and older cod in the stock that spawned for the first time at the age 8 years or older and are not first-time spawners. 4: Percentage of 8 years or older cod in the stock that are first-time spawners. 5: Percentage of 8 years old and older cod in the stock that spawned for the first time at the age of 8 years or older.

able spawning activity is known to have taken place (Sæmundsson 1905, Fridriksson 1932 and Fridgeirsson 1979).

It is difficult to measure or estimate the intensity of spawning occurring in areas 2, 3 and 4 but the intensity is certainly low. Individuals with running gonads (Table 1, Fig. 20) seem to have been found occasionally in these cold areas as late as July and even August during the period 1953–1974. As the samples and individuals in question are so few, such a late spawning will be regarded as a rare exception or doubtful. Northwest and north of Iceland (areas 2 and 3) a considerable amount of cod has been found spawning from April to June, however, (Fig. 20). It should be pointed out that Fig. 20 may yield misleading picture of the intensity of the spawning activity in

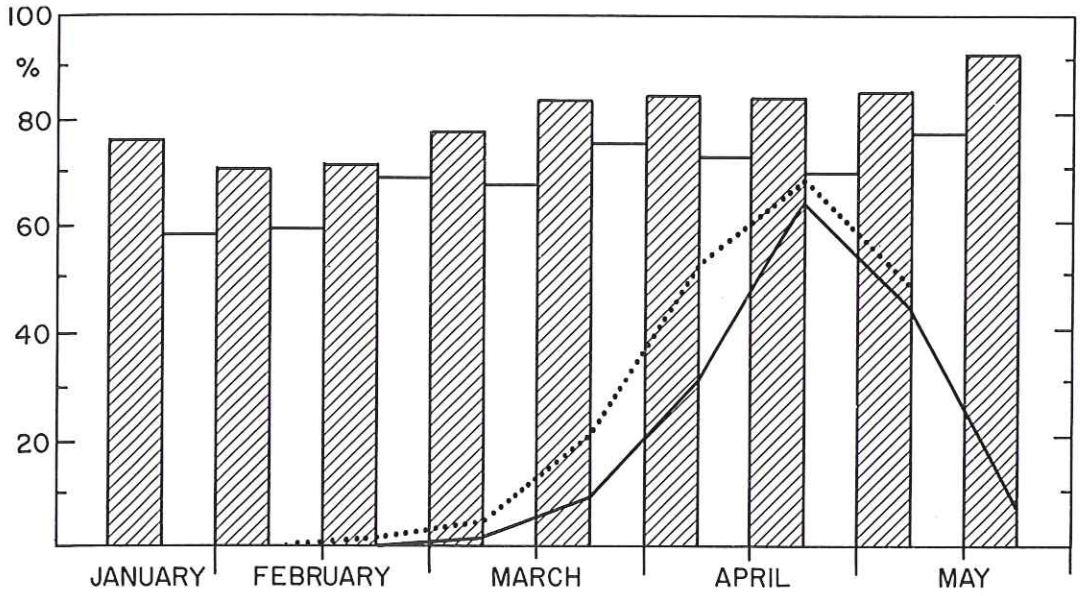

Fig. 19. Percentage of first-time spawners during the spawning season (columns) at the southwest coast and the percentage of cod (curves) with running gonads (stage III). White columns and solid line: area 1. Shaded columns and dashed line: area 5. Means for 1953–1974.

TABLE 6.

The percentage distribution of the spawning stock by length groups throughout the spawning season in area 1. Means for 1953–1974

Months	*Length-groups (cm)*							
	≤49	*50–59*	*60–69*	*70–79*	*80–89*	*90–99*	*100–109*	*≥ 110*
January	1,4	4,1	8,3	20,4	38,6	21,7	4,7	0,5
	0,2	2,6	8,3	19,8	35,9	25,3	6,7	3,0
February	0,3	1,6	4,3	14,2	37,8	32,4	7,9	1,4
	0,3	0,9	2,4	14,8	36,9	29,9	10,6	4,1
March	0,1	0,4	2,9	16,7	42,9	28,2	7,2	1,6
	0,2	0,7	3,7	23,7	42,0	22,9	5,2	1,5
April	0,1	0,4	4,2	24,1	39,2	24,6	5,0	2,3
	0,1	0,4	4,6	23,6	42,2	23,8	4,2	1,1
May	0,1	0,2	4,7	23,1	40,9	24,5	5,7	0,7
	0,2	3,0	10,5	24,1	36,9	19,4	5,1	0,6

TABLE 7.

The percentage distribution of the spawning stock by age groups throughout the spawning season in area 1. Means for 1953–1974.

Months	Age-groups (years)									
	≤4	5	6	7	8	9	10	11	12	≥13
January	12,6	15,6	18,4	16,0	15,3	10,8	6,2	2,3	2,1	0,5
	9,6	16,7	18,2	15,4	11,0	9,8	8,4	6,3	2,8	1,5
February	4,3	10,2	14,3	16,0	12,8	13,0	12,0	8,0	6,4	2,7
	3,1	7,6	12,5	13,5	15,8	14,3	14,8	9,3	4,9	4,0
March	2,3	8,2	13,7	16,3	18,3	16,2	11,8	7,4	3,7	1,9
	2,4	7,3	12,5	14,9	22,8	18,4	10,8	7,4	2,0	1,2
April	1,6	5,4	10,1	16,1	24,6	20,0	11,2	6,8	2,8	1,3
	0,9	3,1	8,3	19,1	21,1	22,5	12,4	8,7	2,7	0,9
May	1,2	4,3	7,0	19,0	20,6	20,0	15,0	8,8	2,2	1,6
	11,9	25,1	27,3	17,7	9,6	4,6	2,4	0,9	0,3	0,1

these areas. The intensity is calculated in the same way as for areas 1 and 5, i. e. the percentage of spawning fish (stage III) out of all sexually mature ones. Due to feeding migrations of spent fish from the main grounds in the southwest to the colder areas, a comparison of intensity in different regions is not meaningful since the bulk of spent fish found in areas outside the main grounds in spring (May) has nothing to do with spawning outside the main grounds. On the other hand it can be assumed that cod with ripening gonads (maturity stage II) found in these colder areas in spring and during the early summer months do not migrate for spawning to warmer water in the south. At this time of year no individuals have been found with running gonads on the southwest grounds. Cod on stage II at this time of the year can therefore be taken as evidence of spawning activity in these areas as well as those fish which are actually spawning, when collected. Taking both stages II and III into account, it is obvious, however, that spawning activity in these areas is very limited, especially at the east coast. The few cod found spawning or ripening in these areas in spring and early summer are scattered at random over the 22 years.

Among other sources for examining the intensity of the spawning in areas outside the southwest grounds are studies of eggs and larvae. Results from cod egg surveys conducted since 1977 have been published by Fridgeirsson (1979). Such surveys have revealed that cod eggs are certainly most numerous on the southwest grounds but they occur also in considerable numbers in the two adjacent areas mentioned earlier (i. e. Breidafjördur and the southeast coast). A few cod eggs were also found in May northwest and north of Iceland. According to Fridgeirsson (personal communication) the number of cod eggs found in the coastal water north of Iceland made up approximately 3–4% of the total

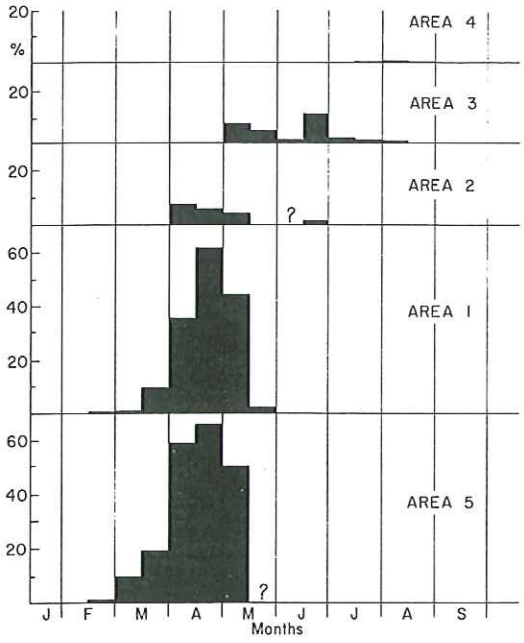

Fig. 20. Percentage of spawning cod in the collected samples by two week periods throughout the year in all areas around Iceland. Means for 1953–1974.

found during the years 1977, 1979 and 1980. (No sampling was carried out north of Iceland in 1978).

Statistics over the number of barrels of cod roes exported from the different parts of Iceland reveal that during the period 1897–1901, 99.5% of the salted cod roes came from the southwest area (Vík–Akranes), (Schmidt 1904). From the northwest part of Iceland, roughly corresponding to area 2, cod roes were exported during two of the 5 years studied, accounting for 1.4% and 0.4% respectively of the total amount exported each year. From the eastern part of area 3 "caviar" was exported only during 1 year, accounting for 0.8% of the total amount exported that year. From the western part of area 3 (Húnaflói) and from area 4 (Austfirdir), no export took place during the period in question.

Since 1971 Icelandic waters have been surveyed annually in late summer with small-meshed pelagic trawl. As discussed earlier larvae from the main spawning grounds in the southwest area drift around Iceland. The limited range of the length distribution of the O-group codlings collected all around Iceland indicate their common time and place of "birth". If we assume that spawning on the main grounds takes place on the average somewhat earlier than elsewhere, codlings from these southwest grounds can be expected to have a greater mean length than those which are offsprings of late spawning in colder areas. The length distribution of the O-group cod at the north coast in 1973 (Vilhjálmsson and Fridgeirsson 1976) is characterized by two peaks, perhaps indicating subsidiary spawning of considerable intensity outside the main grounds. In view of the fact that more than a few cod eggs have never been found at the north coast, it is unlikely that spawning there has affected the length distribution to such an extent. A subsidiary spawning is therefore more likely to have taken place west of Iceland. The scant material available (maturity grading of cod) from areas outside the southwest grounds during spring and early summer of 1973 reveal no signs of such an occurrence. The O-group survey in 1976 (Anon. 1976) revealed an unusually large amount of

codlings in the waters northeast and east of Iceland. However, the length distribution of the O-group codlings in this area is in no way unusual and they were even slightly larger than in other years. Therefore, no conclusion can be drawn from this finding about spawning outside the main grounds. Taking the O-group surveys as a whole (1971–1981) one may conclude that they indicate only very limited spawning outside the main grounds.

Other investigations of cod eggs and larvae with fine-meshed nets in these colder areas have been carried out occasionally since the turn of the century (Schmidt 1904 and 1926, Einarsson unpublished material 1950–1955). A critical review of these studies reveals that practically no cod eggs and larvae were ever found north and east of Iceland, but occasionally northwest of Iceland.

The data and material which have been considered when discussing the question of spawning outside the main grounds refer only to the continental shelf, leaving out the fjords. Fridrikson (1933), however, described some local in-fjord spawning grounds at North- and East-Iceland where limited spawning of relatively small spawners is said to take place in most years. In May 1976 a sample was obtained from such spawning in one of the cold fjords of the east coast, Nordfjardarflói, where the bottom temperature was 1.8°C and the surface temperature 1.5°C. Surprisingly, a great deal (53.7%) of the cod collected in the fjord had running gonads (Table 8). Samples taken in the same fjord revealed that 18% of the fish were ripening in February and 22% were spent in August (out of sexually mature fish present). The May spawners were very small and young (average age 5.6 years) and about the same size as the immature fish. Furthermore, their growth rate corresponded to the general slow rate of growth in this area as determined by Sæmundsson (1923) and Jónsson (1965). Two 5-year old individuals measured only 48 cm. They are among the smallest spawners ever recorded in Icelandic waters. Thus a spawning of a local population is indicated, i. e. a spawning of cod which has grown up in the area. Fridriksson found spawning cod in this very same fjord in 1931 (Table 9) of almost the same size and considered the possibility that this activity is due to a separate race which had adapted itself to the cold water. He named some conditions to be fulfilled for such a race to thrive and rejected this possibility. He offered the explanation that the small spawners were "dwarfs" that did not make it to

TABLE 8.

The mean length and percentage in age groups of cod from Nordfjardarflói, E-Iceland, May 15th 1976 (n = 67).

	Age-groups (years)				
	4	5	6	7	8
			Mature		
Mean length (cm) ..	57,0	59,8	68,5	79,3	
% in age-groups	5,5	38,5	47,2	8,5	
			Immature		
Mean length (cm) ..	53,0	59,5	69,2	68,2	61,0
% in age-groups	3,4	51,7	31,0	10,3	3,4
% in mat. stages ...	I:44,8		II:1,5		III:53,7

TABLE 9.

Percentage distribution in length groups of cod in Nordfjardarflói, E-Iceland, (N = number of speciments in samples).

Year and month	Maturity	Length-groups (cm) 30–49	50–59	60–69	70–79	≥80	Males (%)	N
February 1976	Mature (18,0%)	0,0	62,5	12,5	0,0	25,0	75,0	38
	Immature (82,0%)	28,5	32,1	39,3	0,0	0,0	53,3	
May 1976	Mature (55,2%)	5,5	33,3	33,3	16,6	2,7	89,0	67
	Immature (44,8%)	0,0	26,7	46,7	26,6	0,0	35,5	
May 1930	Mature (32,0%)	4,3	27,5	40,6	17,2	10,0	>50	216
	Immature (68,0%)	0,2	35,4	36,7	21,7	2,0	?	
August 1976	Mature (57,5%)	0,0	7,7	46,1	30,8	15,3	61,5	60
	Immature (42,5%)	10,6	21,7	60,9	6,5	0,0	42,5	

the main spawning grounds. The age determination of the small spawners in Nordfjardarflói in 1976 shows that these are not dwarfs but cod with normal growth rate for the low water temperature in question. These findings are in sharp contrast to the spawning and sexual development of the bulk of the cod stock in Icelandic waters.

As regards in-fjord spawning at the north coast, separate spawning grounds of limited size can be found scattered along the coast from Skagafjördur to Langanes (Thorsteinsson, personal communication). A sample of such spawning in Skjálfandaflói at the end of May 1975 has shown spawners which are not particularly small or young. In 1976 local fishermen described some of these spawning "patches" to the author. According to them, these grounds are very limited in size but most springs spawning can be found there. As already mentioned, Fridriksson (1932) described near-shore spawning in these areas. He stated that spawning on coastal grounds off the north coast can definitely take place by both large and small spawners and is very much in evidence in some years.

In view of the above information it is clear that a limited spawning is almost an annual occurrence on the in-fjord grounds at the north coast. Furthermore, occasional spawning of partly very young and small spawners takes place in the cold fjords of the east coast.

THE BREEDING CYCLE OF THE COD

Due to lack of data it was not possible to determine the duration of stage II for individual fish in areas other than 1 and 5. It appears that this duration is not significantly longer than at the southwest coast. As the spawning activity is occurring at different times in the different areas it is obvious that the reproduction or breeding cycle (corresponding to

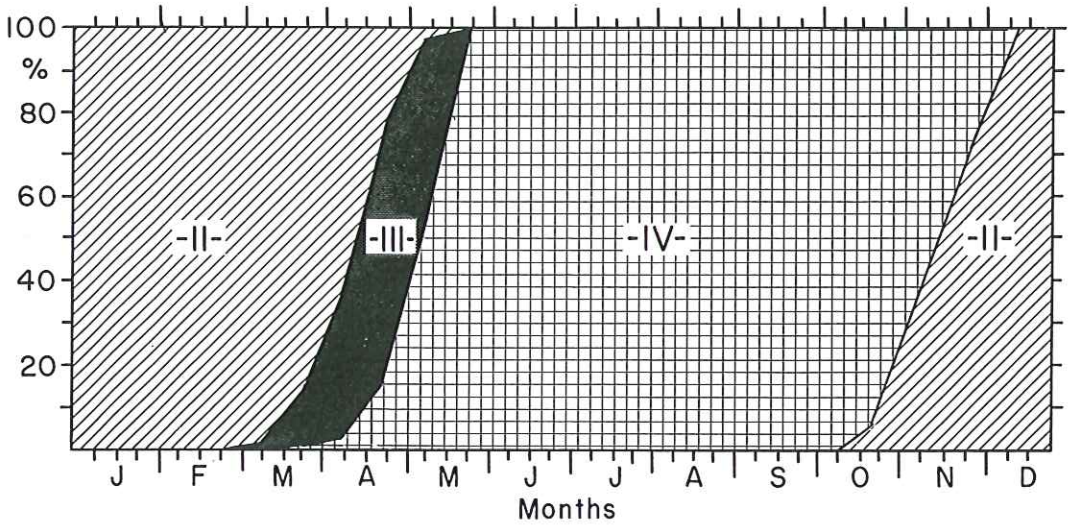

Fig. 21. Breeding cycle, i. e. the sequence of the three maturity stages (II, III and IV) in the spawning stock throughout the year in area 1. Means for 1953–1974.

the one drawn for area 1 in Fig. 21) is different for the different areas. The autumn data indicate that the stage IV to stage II transition occurs in late autumn in all areas. This transition gets into full swing in mid-October and is finished by mid-December. Thus, the later the spawning season occurs in the different areas, the longer will be the duration of stage II and the shorter the duration of stage IV. According to Sivertsen (1935) it appears that the cod at the west coast of Norway always return to stage II in the autumn (October – November), no matter how late in the year they may spawn.

SEX RATIO OF THE COD STOCK

a) *Areas 2, 3 and 4*

The available data for the years 1953–1974 were combined and a mean sex ratio for this period derived (Table 10). This method is questionable as such an approach assumes the same annual pattern of the sex ratio. However, due to the limited data a more detailed treatment was not feasible.

The sex ratio of the immature cod is relatively even throughout the year in all areas. In areas 2 and 4 male spawners predominate during the first half of the year, but they are in minority during the second half. In area 3 the situation is reversed. However, the sex ratio of the whole stock in all three areas appears to be more or less unity, looking at the whole year. When the material is divided into length groups (Table 11) the whole stock follows a common pattern. With increasing length females gain preponderance. This is true for both spawners and immature individuals, but in the immature stock the females attain majority at lower length groups than do

TABLE 10.

Total seasonal percentage (M+I) of males in the stock and of mature males (M) and immature males (I) in all 5 areas. Means for 1953–1974.

Areas	Maturity	January – June	July – December	January – December
5	M+I	55,8	55,9	55,9
	M	58,0	56,4	56,4
	I	53,8	44,9	48,2
1	M+I	54,5	48,2	48,6
	M	56,6	48,5	48,9
	I	52,6	45,8	47,2
2	M+I	50,3	52,6	51,2
	M	49,9	56,9	52,6
	I	50,7	49,3	50,1
3	M+I	51,3	49,2	50,7
	M	51,8	42,2	50,0
	I	51,1	50,9	51,0
4	M+I	50,2	50,9	50,1
	M	48,5	51,6	48,7
	I	51,2	50,8	51,1
1–5	M+I	51,7	50,2	50,9
	M	52,5	50,7	50,9
	I	51,4	47,6	49,4

the mature cod. The fact that the unbalanced sex ratio mainly occurs in the mature part of the stock suggests variables connected with the onset of sexual maturity and spawning migrations. As to how these may govern the sex ratio will be dealt with in the next section.The pattern of the sex ratio appears to vary from year to year and in separate years from month to month.

b) *Areas 1 and 5*

Taaning (1931) and Fridriksson (1932) investigated the sex ratio of the Icelandic cod. Both mentioned the balanced sex ratio of the immature fish and the unbalanced ratio of the mature ones. The former author reported that the males were in preponderance during the main spawning season on the grounds at the southwest coast of Iceland. The latter stated that it is a well known phenomenon that during the first weeks of the spawning season at the southwest coast, females are in preponderance on the grounds, but later in the season the males gain majority. He also mentioned a female preponderance amongst the larger fish. Fleming (1960), discussing the sex ratio in Newfoundland cod stock, stated that the sex ratio of the stock is relatively balanced. Furthermore, no significant imbalance was observed in the sex ratio taking length and age groups into account.

The result of the present analysis of the data from the southwest coast (areas 1 and 5) support the findings of Fridriksson and Taaning. Fig. 22 shows an unbalanced sex ratio of the stock (both mature and immature) during the spawning season. From January to mid-March the females predominate in the samples. At the end of March the males achieve majority and retain it until the end of the season. This situation can be observed every year with the same pattern in both areas amongst both immature and mature cod. After the spawning season is over and until the end of the year no systematic pattern can be found, when age and length groups are disregarded. It must, however, be kept in mind that the samples from this time of

TABLE 11.

Seasonal percentage of males by length groups in the mature (M) and immature (I) part of the cod stock in the 5 areas. Means for 1953–1974.

Area	Maturity	LENGTH-GROUPS (CM) July – December									
		≤29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	≥110
5	M				69,4	77,9	67,1	61,1	45,4	46,1	36,6
	I		50,0	47,8	44,1	50,5	45,2	47,8	50,0		
1	M			58,3	62,4	64,6	59,8	50,0	42,4	27,2	17,9
	I		53,6	48,0	47,2	46,9	42,9	34,3	39,4		
2	M			52,8	55,0	53,0	51,2	43,4	28,9	26,9	
	I		49,2	52,6	53,4	49,2	39,2	40,0			
3	M			50,8	37,6	42,5	42,5	51,2	37,9	27,0	
	I	56,0	45,8	51,5	53,2	49,5	47,1	41,4	23,8		
4	M				50,0	61,9	52,9	52,0	23,0		
	I	48,1	46,7	45,0	56,6	48,9	44,2	40,7			

Area	Maturity	LENGTH-GROUPS (CM) January – June									
		≤29	30–39	40–49	50–59	60–69	70–79	80–89	90–99	100–109	≥110
5	M				43,0	56,1	58,4	61,7	33,3		
	I	55,5	63,3	56,7	48,9	50,6					
1	M			65,2	55,2	43,8	59,7	72,0	53,0		
	I	46,0	61,2	49,2	50,5	53,8	33,3	40,0			
2	M			52,8	59,0	53,0	51,2	43,4	28,9	26,9	28,9
	I	50,0	36,1	52,1	52,1	52,5	43,1	30,0			
3	M			53,4	55,4	52,4	46,1	38,3	35,0	15,8	
	I		51,1	51,5	50,7	50,8	52,5	50,6	47,8		
4	M		50,0	49,5	51,3	48,4	46,5	34,1	26,7		
	I	52,7	55,4	49,9	44,1	46,1	56,7				

the year are extremely few compared with those of the spawning season.

As mentioned earlier, a clear female majority prevails among larger fish (Table 11) within all categories (seasons, areas and maturation groups). This female preponderance linked to size is examined further later in this section.

As was to be expected the unbalanced sex ratio is not only related to length but also to age (Tables 12 and 15). The most interesting finding is, however, that the

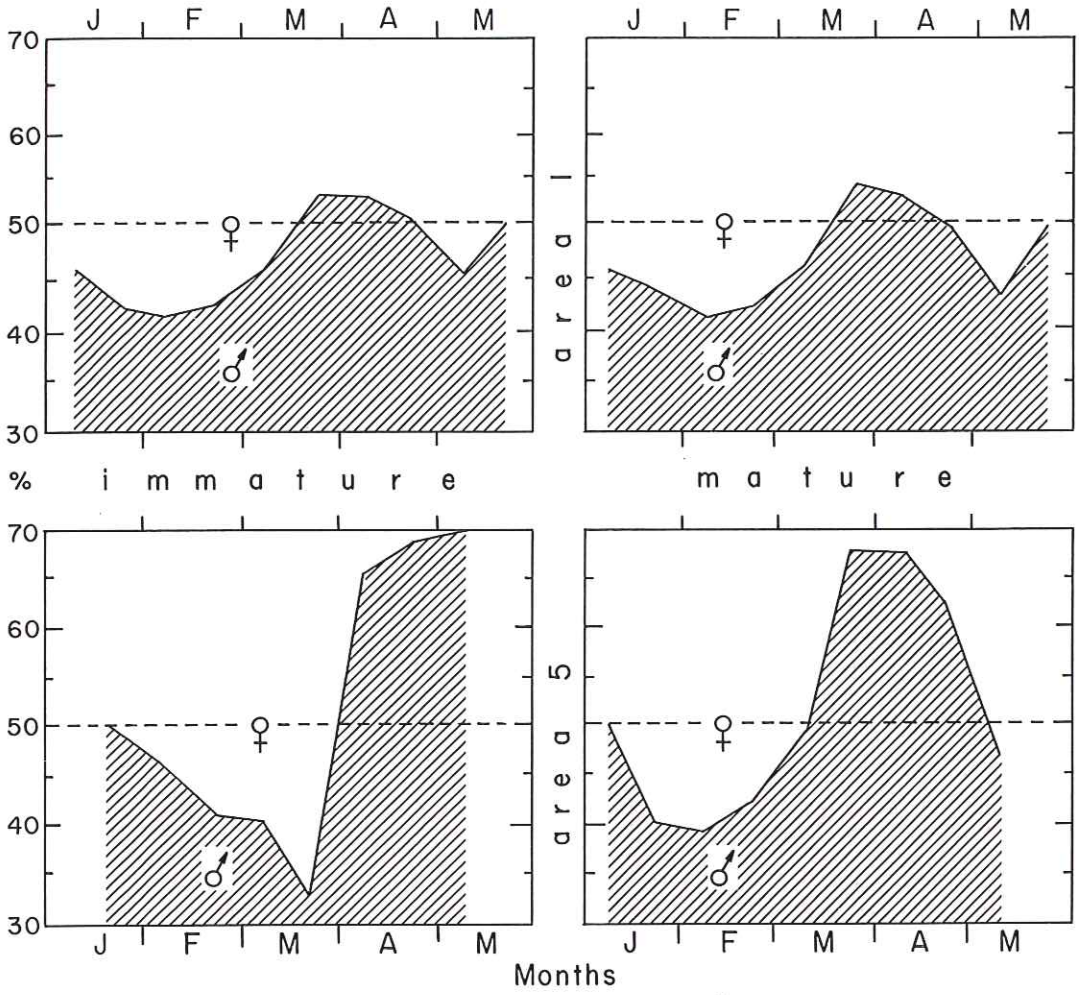

Fig. 22. The sex ratio of the cod stock at the southwest coast, throughout the spawning season, separately for area 1 and 5 and for mature and immature fish. Means for 1953–1974.

line of balanced sex ratio (1:1) climbs up into higher age and length groups as the season progresses, then falls again when spawning is over (Tables 12, 13, 14 and 15). The course of the line of balanced sex ratio follows a similar pattern in both areas 1 and 5, but it swings over greater number of groups (length and age) in area 5. The fact that the line swings up into higher age and length groups as the spawning season progresses can be explained as follows: As pointed out and discussed later in this section, males grow sexually mature at a younger age than females and females therefore dominate amongst large and old fish. Due to this difference and because of the onset of sexual maturity at a different age in the different areas around Iceland, cod growing up and maturing in

TABLE 12.

Percentage of males by length groups in the spawning stock in area 1 throughout the spawning season. The heavy line denotes balanced sex ratio (1:1). Means for 1953–1974.

Months	*Length-groups (cm)*							
	≤49	*50–59*	*60–69*	*70–79*	*80–89*	*90–99*	*100–109*	*≥110*
January	(38,1)	55,7	62,8	60,1	47,9	34,4	33,3	25,0
	(44,4)	65,9	59,2	53,2	43,4	36,7	21,3	13,9
February	66,6	67,1	67,0	58,2	46,0	31,1	22,0	18,2
	60,0	52,4	60,3	60,7	46,9	36,0	25,3	14,1
March	80,0	62,5	61,9	57,7	50,4	38,3	22,5	15,2
	55,5	80,5	72,5	63,6	55,9	44,6	35,2	22,0
April	83,3	71,9	66,7	59,2	55,4	48,3	32,7	21,8
	75,0	76,9	66,0	59,5	53,1	44,3	30,2	21,5
May		63,6	62,8	59,1	44,6	33,8	21,3	16,6
	83,3	70,6	61,7	61,7	48,5	38,7	32,6	23,8
Jan. – May	68,5	66,7	58,4	59,3	49,2	38,6	27,6	19,2

TABLE 13.

Percentage of males by age groups in the spawning stock throughout the spawning season in area 1. The heavy line denotes balanced sex ratio (1:1). Means for 1953–1974.

Months	*Age-groups (years)*									
	≤4	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*≥13*
January	53,1	55,7	50,7	44,3	47,3	43,5	40,2	50,0	34,3	50,0
	58,3	48,4	44,7	36,9	43,4	42,5	41,3	38,5	31,3	31,5
February	65,8	50,6	44,6	43,1	42,3	41,0	36,6	30,1	34,8	22,9
	59,5	49,7	49,7	45,0	42,0	40,1	37,4	34,9	29,3	26,0
March	61,3	49,8	50,6	48,0	51,2	43,8	38,5	37,8	35,0	24,1
	67,6	69,3	65,7	57,0	56,2	48,9	43,2	44,4	42,3	30,3
April	64,8	61,4	58,0	58,1	53,8	51,5	43,8	43,9	44,6	30,8
	49,1	64,1	67,0	60,0	52,4	48,7	43,2	39,8	40,0	41,0
May	52,5	54,1	68,0	51,9	42,0	41,6	39,9	38,2	38,7	21,0
	58,7	50,8	50,0	54,2	49,7	43,3	36,5	58,6	40,0	33,3
Jan. – May	59,0	55,4	54,9	49,8	48,0	44,5	40,6	41,3	37,0	27,9

TABLE 14.

Percentage of males by length groups in the spawning stock throughout the spawning season in area 5. The heavy line denotes balanced sex ratio (1:1). Means for 1953–1974.

Months	Length-groups (cm)					
	≤69	70–79	80–89	90–99	100–109	≥110
January	76,0	63,5	31,7	31,7	22,1	28,6
February	87,1	57,8	31,3	33,6	22,3	20,4
	69,2	64,1	50,2	38,7	21,9	9,5
March	73,4	69,3	58,3	47,7	31,4	18,5
	90,3	66,0	73,7	65,8	54,3	16,4
April	69,7	73,9	69,5	69,7	62,8	44,3
	85,3	71,2	64,4	59,0	57,8	50,8
May	40,0	52,0	44,0	42,0	44,8	(60,3)
Jan. – May	73,7	64,5	52,8	48,5	39,7	31,1

TABLE 15.

Percentage of males by age groups in the spawning stock throughout the spawning season in area 5. The heavy line denotes balanced sex ratio (1:1). Means for 1953–1974.

Months	Age-groups (years)									
	≤4	5	6	7	8	9	10	11	12	≥13
January	71,4	(43,9)	58,5	50,0	41,1	44,2	28,9	38,5	18,3	28,5
February	61,9	50,6	47,7	37,1	36,4	35,3	34,6	29,5	38,0	26,4
	59,3	54,3	51,1	50,1	48,3	41,8	39,3	31,0	28,3	22,0
March	63,1	70,9	66,7	57,7	54,4	47,7	46,3	41,2	30,5	29,8
	82,7	70,8	71,0	71,9	69,1	64,6	63,3	73,7	51,3	43,8
April	82,7	70,2	65,6	66,2	67,9	66,4	70,9	62,7	69,2	45,4
	72,2	75,4	59,5	64,8	57,8	58,1	60,5	62,5	61,5	57,0
May		(43,7)	55,9	47,4	45,6	40,5	42,3	43,7	(54,3)	(52,0)
Jan. – May	70,5	60,0	59,5	55,6	52,5	49,7	47,9	47,8	43,9	38,1

TABLE 16.

Seasonal percentage of males in the stock for different fishing gear and according to length groups at the southwest coast during the spawning season. Areas 1 and 5 combined. Long-line and gill-net data: means for 1965–1974; bottom trawl data: means for 1974–1976.

Period	*% Males in stock*	*% Males in ≤80 cm*	*Length Groups >80 cm*
		Gear: LONG-LINE	
Jan. – March	44,0	50,9	36,4
Apr. – May	45,1	52,5	31,3
Jan. – May	44,3	51,3	35,9
		Gear: GILL-NET	
Jan. – March	46,9	57,6	44,8
Apr. – May	54,7	69,1	51,9
Jan. – May	52,7	66,8	50,3
		Gear: BOTTOM-TRAWL	
Jan. – March	51,0	60,6	47,5
Apr. – May	59,5	63,9	49,3
Jan. – May	55,5	62,1	55,5

very cold waters are bound to push the line of balanced sex ratio up into higher age and length groups, when they finally migrate to the southwest spawning grounds.

The question arises whether we have been observing actual sex ratio or if the true ratio is biased in the samples due to some kind of selection by the collecting gear. Table 16 shows the sex ratio in samples from long-line, gill-net and bottom-trawl from the southwest coast during the whole spawning season. The ratio was examined for two length groups (≤80 cm and >80 cm) and for two time periods. For all gears and in all seasons female preponderance was evident among the larger fish and male preponderance among the smaller ones, the only exception being the gill-net samples during the latter half of the spawning season where the proportion of males (>80 cm) slightly exceeded that of females. Disregarding length groups (Table 16) the sex ratio was quite different for the three types of gear, the gill-net showing female preponderance in the first half of the season and at the same time the trawl showing a slight male majority. Nevertheless, both types of gear gave a clear male preponderance during the latter half of the season. The long-line, however, showed female predominance at all times. These results indicate that the different sampling gear are sexually selective. Such a selection could either come about through different behaviour of different size of the sexes provided the gear is size-selective. It must, however, be assumed that the

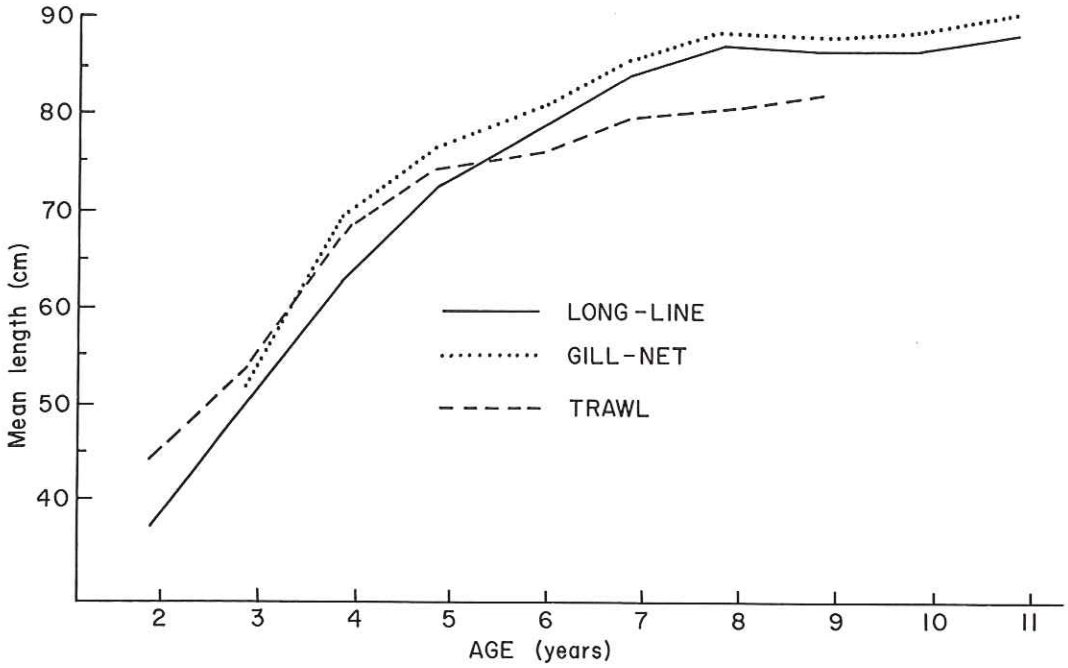

Fig. 23. The average length as function of age of sampled cod in three types of collecting gear at the southwest coast, i. e. areas 1 and 5 combined. Means for January to May 1972.

trawl catches all fish present above a certain minimal size and its samples therefore very nearly reflect the virtual sex ratio at any given time and area, i. e. a roughly balanced ratio from January to March (in areas 1 and 5) followed by a clear male preponderance during the latter half of the season.

In an attempt to account for the unbalanced sex ratio the size selection of the sampling gear was looked into (Fig. 23). Except for fish under certain minimal size the long-line and the gill-net grasp more of the larger fish on the average than the bottom trawl. Examination of growth and sexual development of the cod by sex (Fig. 24) reveals that females grow more rapidly than males when both sexes have reached a certain minimal size. It is also found (Table 17) that males grow sexually mature at a considerably younger age than females. If the cod were living in an enclosed area the faster growth of the females would not cause larger female catches (in a size-selective gear) neither for the total

TABLE 17.

Percentage of mature males and females within age groups at the southwest coast during the spawning season. Means for January — May, 1953–1974. Areas 1 and 5 combined.

	Age-groups (years)				
	4	*5*	*6*	*7*	*8*
♂	36,5	69,2	92,3	97,8	98,9
♀	23,8	57,6	87,5	96,9	98,6

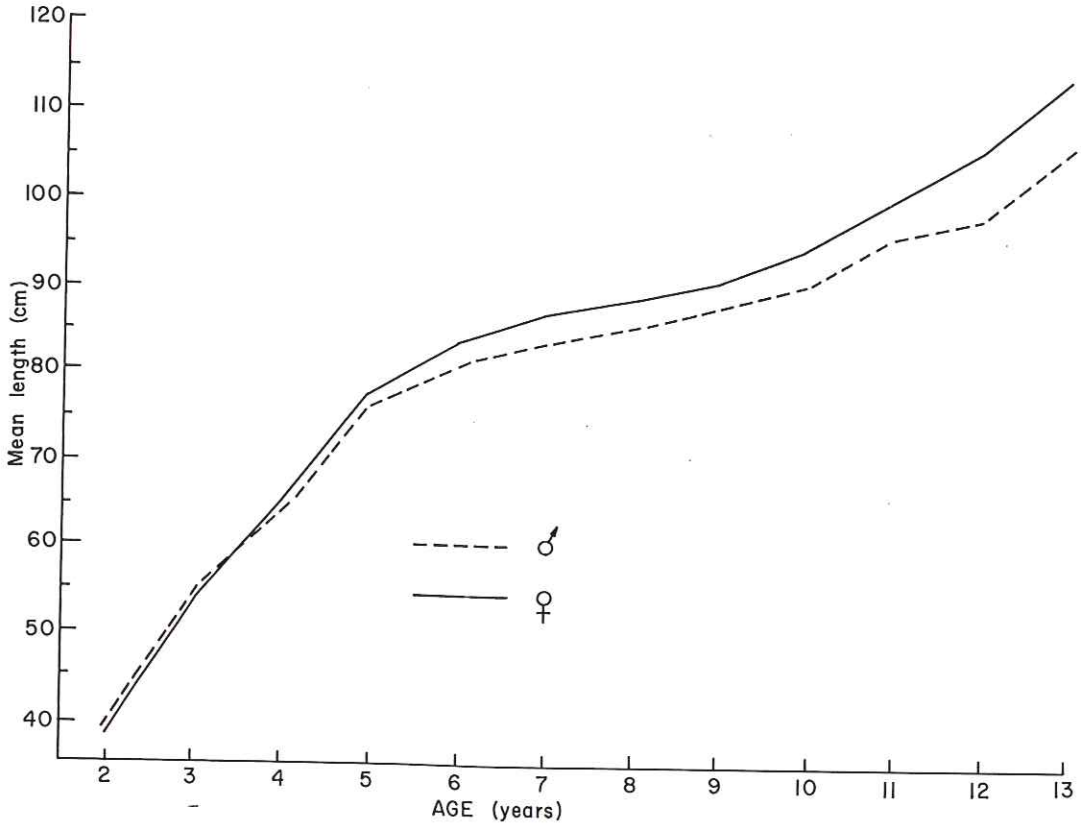

Fig. 24. The average age/length relationship for males and females at the southwest coast. Mean for January – May 1965–1973. Areas 1 and 5 combined.

nor within length groups. The reason for this is that the female preponderance within the larger length groups is levelled out due to males being less exploited while they are smaller. The true situation is, however, that the bulk of the spawners migrate from outside. Since the males attain sexual maturity at a younger age, they are bound to be more numerous than females in the younger age groups on the spawning grounds. Since the females are older, when they start spawning, they will on the average be larger than males on the spawning grounds. This female predominance among the larger fish is augmented by the fact that females grow slightly more rapidly than males. Thus female predominance amongst large fish and male predominance amongst the smaller fish is accounted for.

The discrepancy between the catches of the 3 types of gear described earlier (Table 16) can be explained by the fact that long-line and gill-net take more fish from the larger length groups in which females predominate. Therefore the two types of gear show female predominance during the first half of the season. When it comes to the latter half of the season

the males are so much more numerous on the grounds that this selection is overridden in the gill-net samples. However, long-line shows female predominance throughout the season. The author finds no logical explanation of this phenomenon except that this type of gear is selective with regard to sex, regardless of size. It is a well known fact that spawning cod have little appetite and take bait only hesitatingly during that period. It would seem that the males are even more reluctant to take bait than females while spawning.

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REFERENCES

Anon., 1976. Preliminary report on the O-group fish survey in Icelandic and Greenland waters July — August 1976. ICES C. M. 1976/H:39, 21 pp (mimeo).

Berner, M. 1960. Untersuchungen über den Dorschbestand der Bornholm- und Arkonasee in den Jahren 1953–1955. Zeitsch. f. Fisch., 9: 7–10.

Dannevig, A. 1930. The propagation of our common fishes during the cold winter 1924. Rep. Norw. Fish. Marine Invest. III, 10, 126 pp.

Earl, R.E. 1880. A report on the history and present condition of the shore cod-fisheries of Cape Ann, Massachusetts together with notes on the Natural History and artificial propagation of the species. Rep. U. S. Comm. Fish., 6: 685–740.

Ewart, J. C., and Brook, G. 1885. Observations on the spawning of cod. Rep. Fish. Bd. Scotland, 3, Appendix F, 2: 52–55.

Fleming, A. M. 1960. Age, growth and sexual maturity of cod (*G. morhua*) in the Newfoundland area 1947–1950. J. Fish. Res. Bd. Canada, 17: 775–809.

Fridgeirsson, E. 1979. Útbreiðsla hrygningar þorsks og ýsu 1976–1978. Sjómannablaðið Víkingur, 41 (3): 49–51.

Fridriksson, A. 1933. Fiskirannsóknir, Ársrit Fiskifélags Íslands 2, 1932, 77 pp.

Graham, M. 1924. The annual cycle in the life of the mature cod in the North-Sea. Fishery Investigation, Ministry of Agr. and Fish. of Great Brit. 1923 (1924) Series II 6 (6), 77 pp.

Hilge, V. 1972. Die Entwicklung des Teleosteer-ovars als Grundlage für die Reifebestimmung. Dissertation, Christian Albrechts Universität Kiel.

Iversen, T. 1934. Some observations on cod in Northern Waters. Rep. Norw. Fish. Marine Invest. 4 (8), 35 pp.

Jónsson, J. 1958. Gengur íslenski þorskstofninn til Austur-Grænlands? Ægir, 51: 20–32.

—— 1960. The spawning stock of cod (Iceland) 1958. Ann. Biol., 15: 98–99.

—— 1961. On the spawning Stocks of cod in East Greenland and Icelandic Waters in 1959. Ann. Biol., 10: 130–135.

—— 1965. Temperature and growth of Cod in Icelandic Waters. ICNAF, Spec. Publ. 6: 537–539.

—— 1969. The spawning stock of cod (Iceland) 1969. Ann. Biol., 26: 118–119.

Malmberg, S. A. 1969. Breytingar á ástandi sjávar milli Íslands og Jan Mayen. In: M. Á. Einarsson (Ed.), Hafísinn, Almenna Bókafélagid, Reykjavík: 150–164.

Meek, A. 1924. The development of the cod (*Gadus callarias*). Fish. Invest. London Series 2, 7: 1–26.

Mayer, A. 1969. German investigations of Icelandic cod 1953–1968. Ann. Biol., 25: 107–109.

Ruud, J. T. 1939. Torsken i Oslofjorden. Rep. Norw. Fish. Marine Invest., 6, 2, 83 pp.

Schmidt, J. 1904. Fiskeriundersögelser ved Island og Færöerne. Kommissionen for Havundersögelser, Skrifter 1, 148 pp.

—— 1926. The Frequency of young cod etc. at the North and the East Coast of Iceland during periods of years preceeded by a general Survey of Life History of the Icelandic Cod. Rapp. P. - v. Réun. Cons. int. Explor. Mer., 39: 139–148.

Sigtryggsson, H. 1969. Yfirlit um hafís í grennd við Ísland. In: M. Á. Einarsson (Ed.), Hafísinn, Almenna Bókafélagid, Reykjavík: 80–94.

Sivertsen, F. 1935. Torskens Gytning. Rep. Norw. Fish. Marine Invest. 4, 10, 38 pp.

Smed, J. 1976. Monthly anomalies of the sea surface temperature in areas of the North Atlantic in 1973. Ann. Biol., 31: 11–12.

Stefánsson, U. 1969a. Sjávarhitabreytingar á landgrunnssvæðinu norðan Íslands seinustu áratugi. In: M. Á. Einarsson (Ed.), Hafísinn, Almenna Bókafélagid, Reykjavík: 115–129.

—— 1969b. Sjávarhiti á siglingaleið umhverfis Ísland. In: M. Á. Einarsson (Ed.): Hafísinn, Almenna Bókafélagid, Reykjavík: 131–149.

—— 1969b. Sjávarhiti á siglingaleið umhverfis Ísland. In: M. Á. Einarsson (Ed.), Hafísinn, Almenna Bókafélagid, Reykjavík: 131–149.

—— 1970. Sjávarhiti og selta á nokkrum stöðum við strendur Íslands áratuginn 1960–1969. Hafrannsóknir 1969 (Annual report of the Marine Research Institute, Reykjavík): 9–22.

—— and Jónsdóttir, S. 1974. Near-Bottom Temperature around Iceland. Rit Fiskideildar, 5, 73 pp.

Sæmundsson, B. 1906. Fiskirannsóknir, Skýrsla til Stjórnarráðsins 1905. Andvari, 31: 105–148.

—— 1923. On the age and growth of cod (*Gadus Callarias L*) in Icelandic waters. Medd. Komm. Fiskeri, Havunders. Serie, Fiskeri, 7 (3), 35 pp.

—— 1926. Fiskarnir (Pisces Islandiae). Bókaverzlun Sigfúsar Eymundssonar, Reykjavík, 528 pp.

—— 1934. Probable influence of changes in temperature on the marine fauna of Iceland. Rapp. P. - v. Réun. Cons. int. Explor. Mer., 86: 1–6.

Taaning, A. V. 1931. Fluctuation of the stock of cod in Icelandic waters. Medd. Komm. Fiskeri. Havunders., 9 (3), 43 pp.

Vilhjálmsson, H. and Fridgeirsson, E. 1976. A review of O-group surveys in the Iceland-East-Greenland area in the years 1970–1975. ICES Cooperative Research Report 54, 34 pp (mimeo).

Ágrip

Hrygning og kynþroski íslenska þorsksins

Ritgerð þessi fjallar um íslenska þorskstofninn með sérstöku tilliti til kynþroska og hrygningar. Með aðstoð tölvu var unnið úr gögnum frá 29 árum á tímabilinu 1953–1981, aðallega á árabilinu 1953–1974. Úrvinnsla yngri gagna beindist nær eingöngu að tímasetningu hrygningar við Suðvesturland. Ritgerðin hefst á því að gerð er grein fyrir viðfangsefninu. Þá er stutt lýsing á þorskstofninum, líffræði hans, einkennum og hegðan, en síðan er gögnum og aðferðum lýst. Um er að ræða liðlega 1500 sýni frá ofangreindu tímabili, sem veita upplýsingar um rúmlega 143.000 fiska. Hafsvæðinu kringum landið var skipt í 5 svæði og ástand þeirra kannað á hálfsmánaða tímabilum. Gerð er grein fyrir hugsanlegum skekkjum í gögnum og rætt um skekkjuvalda í útreiknuðum niðurstöðum.

Helstu niðurstöður: Meðalhámark hrygningar við suðvesturströndina (þ. e. í Faxaflóa á svæði 1, og sunnan Reykjaness á svæði 5) er í 4. viku apríl. Hrygning sunnan Reykjaness byrjar almennt nokkru fyrr (7–10 dögum) en á Faxaflóasvæðinu. Meginhluti hrygningar fer fram á 6 vikum á báðum svæðum, þ. e. frá 4. viku mars til 1. viku maí. Við Suðvesturland tekur það hvern einstakan þorsk að meðaltali 3–4 vikur að hrygna. Enginn verulegur munur virðist vera á hængum og hrygnum hvað snertir byrjun og lok hrygningar. Hrygning einstakra ára getur verið allfrábrugðin meðalhrygningunni. Við Suðvesturland virðast frávik frá byrjun aðalhrygningar geta verið allt að 2 vikur. Sunnan Reykjaness eru þau stundum ólík því sem er á Faxaflóasvæðinu. Lítið samhengi finnst milli sveiflna á tíma hrygningar við Suðvesturland og frávika frá meðalbotnhita sjávar. Þar sem Suðvesturlandsmiðin eru sameiginlegur hrygningarstaður þorsks hvaðanæva að kringum landið og jafnvel frá Grænlandi, virðist lítil von til þess að beint samhengi sjáist milli sveiflna á hrygningu við Suðvesturland og hitabreytinga sjávar þar eða annars staðar. Þannig gætu hrygningargöngur sterkra árganga úr mjög köldum sjó, t. d. frá Grænlandi, seinkað eða teygt úr hrygningartímanum við Suðvesturland, án þess að til komi áhrif staðbundinna hitasveiflna eða annarra umhverfisþátta. Á árabilinu 1964–1976 virðist árleg hrygning við Suðvesturland hafa náð lengra fram á vorið en verið hafði síðustu 11–12 árin á undan. Hugsanleg skýring á þessu kann að vera sí-aukin hlutdeild þorsks, sem er að hrygna í fyrsta sinn í hrygningarstofninum, en sýnt er fram á, að slíkir nýliðar hrygna að jafnaði síðar á vertíðinni en þorskur, sem hrygnt hefur áður. En einnig er

bent á, að sjávarhiti við Ísland og á nálægum svæðum fór lækkandi á áratugnum 1960–1970. Ekki er ósennilegt, að samhengi geti verið hér á milli. Meðalhlutur þorsks, sem er að hrygna í fyrsta skipti af hrygningarfiski við Suðvesturland, var um 73% á árunum 1953–1974. Þessi hlutur hefur farið vaxandi nær árlega frá 1953. Af þessum 73% voru 58% 8 ára þorskur og eldri. Fiskur sem er að hrygna í fyrsta skipti, virðist hrygna bæði seint og snemma á vertíðinni. Þó fer hlutur hans smávaxandi, er líður á hrygningartímann, og er mestur í lok vertíðar. Þessi síðbúni fiskur er áberandi smærri og yngri en sá, sem er að hrygna í fyrsta skipti og hrygnt hefur fyrr á vertíðinni. Hrygning utan Suðvesturlandssvæðisins virðist oftast lítil og vart merkjanleg sum árin. Einkum á þetta við um svæðið fyrir Austurlandi. Slík hrygning á sér stað síðla vors eða snemma sumars og er þeim mun seinna á ferðinni sem sjór er kaldari. Vitað er að töluverð hrygning á sér oft stað á svæðum beggja vegna Suðvesturlands, þ. e. á Breiðafirði og frá Dyrhólaey að Vestra-Horni, enda skilyrði þar einna best (tiltölulega hlýr sjór) utan aðalhrygningastöðvanna við Suðvesturland. Gögn þau sem unnið var úr voru þó ófullnægjandi hvað snertir umrædd jaðarsvæði og gáfu ekkert til kynna um hrygningu þar á þessu tímabili. Klakrannsóknir sem framkvæmdar hafa verið síðustu ár, staðfesta hins vegar, að þorskur hrygni í talsverðum mæli á þessum svæðum. Sömu rannsóknir staðfesta og að hrygning fyrir Norður- og Norðausturlandi er oftast mjög lítil eða að jafnaði um 3–4% af heildarhrygningu þorsks við landið síðastliðin 4 ár. Á blettum innfjarða milli Skagafjarðar og Langaness virðist lítilsháttar hrygning eiga sér stað á ári hverju. Austanlands hefur tvívegis fundist hrygnandi þorskur í talsverðu mæli inni á fjörðum (Norðfjarðarflóa), þar sem sjávarhiti var rúmlega 1,5°C við botn og yfirborð. Þetta var að mestu ungur og smár þorskur og einstaka fiskar meðal smæstu hrygnandi þorska, sem fundist hafa hér við land. Hér virðist um mjög sérstætt fyrirbrigði að ræða, er gengur þvert á það, sem almennt gerist hjá íslenska þorskinum hvað varðar kynþroska og val á hrygningarslóð.

Rætt er um tímaskeið hinna þriggja kynþroskastiga, sem hver kynþroska fiskur gengur árlega í gegnum. Svo virðist sem hrygningarstigið, (þ. e. stig III) taki nokkuð svipaðan tíma alls staðar við landið. Eftir því sem hrygningu seinkar með lækkandi sjávarhita, teygist úr tímaskeiði endurþroskunarstigsins, (stig II) á kostnað eftirgotsstigsins (stig IV), þar sem afturhvarfið til endurþroskastigs virðist bundið við haustið og fyrri hluta vetrar (október til desember) hjá öllum þorski án tillits til þess, hversu seint hann kann að hrygna. Fjöldi hænga og hrygna er því sem næst jafn þegar litið er á þorskstofninn í heild. Í stofninum eru hrygnur ætíð fleiri hjá stórum og gömlum fiski, en hængar fleiri hjá smáum og ungum fiski. Utan hrygningarstöðvanna við Suðvesturland er hlutur kynja hjá ókynþroska fiski nokkuð jafn allt árið. Hjá kynþroska fiski er hlutur kynja aftur á móti nær

aldrei jafn. Að öðru leyti fannst ekkert reglulegt mynstur í þessum ójafna fjölda kynjanna, hvorki eftir svæðum né árstímum. Við Suðvesturland er hlutur kynja nær aldrei jafn, hvorki hjá kynþroska né ókynþroska fiski. Frá maílokum til áramóta virðist hlutfall milli kynja óreglulegt og ekki fylgja ákveðinni reglu. Hins vegar er reglulegt mynstur greinilegt ár hvert á tímabilinu frá janúar til maíloka. Framan af vertíð eru hrygnur ætíð nokkru fleiri en hængar, en í lok mars ná hængar yfirhöndinni og eru fleiri út vertíðina. Þetta virðist bæði eiga við um kynþroska sem ókynþroska fisk. Hlutfall kynja er athugað eftir lengd, aldri og veiðarfærum. Kemur þá margt athyglisvert í ljós, svo sem nokkuð mismunandi hlutfall milli kynja eftir veiðarfærum. Þá færast þau aldurs- og stærðarmörk, þegar hængar og hrygnur eru jöfn að fjölda (1:1), upp á við, er líður á vertíð og síðan niður aftur. Leiddar eru líkur að því, að ójafnt hlutfall milli kynja eigi rót sína að rekja til þess, að hængar verða kynþroska nokkru fyrr (yngri) en hrygnur og hefja þar með fyrr hrygningargöngur. Þetta atriði er örugglega orsök þess, að hrygnur eru fleiri meðal stærri og eldri fiska og öfugt meðal smærri og yngri fiska. Tilhliðrun á þessum mörkum, þar sem kynin eru jöfn að tölu, milli aldurs- og lengdarflokka, orsakast sennilega af hrygningargöngum frá köldum hafsvæðum, þar sem fiskur er stærri og eldri, þegar hann nær kynþroska og fer að ganga til hrygningar.