International Council for the Exploration of the Sea

CM 1968/Gen: 9

The regularity of the spawning season of some fishes

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I Introduction

In the open sea, the lack of structure and the variability of wind, tide and current leads to the supposition that spawning is variable in time and space. The supposition has gained support because of lack of evidence and the difficulty of obtaining it.

In contrast, the biology of the Pacific salmon has become well enough known for the regularities of its life cycle to be well revealed. The sockeye smolt puts to sea at an early age, and when the adult returns to spawn some years later in its native stream and perhaps to its native gravel redd, it has swum half-way to Japan on its travels. The fish return to their parent streams at fixed seasons. Can this regularity be observed on spawning grounds and in other fishes?

Four species of fish have been examined and their mean dates of spawning estimated. There is a distribution of spawning dates in any one year. These distributions are summed for as many years as possible and the grand mean of the summed distribution is used as the mean date of spawning.

(a) For the southern North Sea plaice the published distributions of egg production have been used.

(b) For the Norwegian herring, the dates of spawning are estimated from the age of the spawn taken in grab samples at the same position in successive years.

(c) For the Fraser sockeye salmon the mean peak date of spawning, as observed in the creeks by the bailiffs, has been used.

(d) For the Arctic cod, the peak dates of capture in the Vestfjord are available for a long period of years.

No trends were detected in the plaice and salmon data. A slight trend was found in the cod data. In the Norwegian herring a delay in maturation is noted in the catch statistics (Rasmussen, 1940; Aasen, 1962). but it is not shown decisively in the grab samples (Runnstrøm, 1941).

II The spawning seasons of four fishes

(a) Plaice (Pleuronectes platessa, L.)

In the southern North Sea there are three or four spawning groups of plaice. That in the Southern Bight has been examined by egg survey since 1911. The production of eggs starts in mid-December and reaches a peak in the second half of January, after which it declines. The distributions of egg production comprise a number of egg surveys during the season, each being a single observation (Simpson, 1959). The distributions in 1911 (5 cruises), 1921 (3 cruises), 1936 (5 cruises), 1938 (4 cruises), 1939 (5 cruises), 1947 (6 cruises), 1948 (6 cruises) and 1950 (5 cruises) have been used. The mean dates of spawning range, with no detectable trend, from 7 January to 29 January. The grand mean date is 19 January, with a standard deviation of 7 days and a standard error of 2.5 days.

(b) <u>Herring</u> (<u>Clupea harengus</u>, L.)

Runnstrøm (1941) made a series of grab samples for a number of years for spawn at fixed stations on the Norwegian coast where the spring herring spawns. The results are given in his Figure 9. I have arranged the data in the following form:-

Year	February															
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	1	1	1			1	1	1								
2				1	1	1	1	1	1	1	1	1	1	1	1	1
3					1	1	1	1	1	1	1	1	1	1	1	1
4				1	1	1	1	1	1	1	1	1	1			
Σ	1	1	1	2	3	4	4	4	3	3	3	3	3	2	2	2

Mean day of spawning 18.98 ± 0.61 (entry XIII in Table 1)

Each entry in the table above represents a day of spawning, estimated from the age of spawn in a grab sample. The distribution is then one of samples repeated at the same position in successive years (shown as 1, 2, 3, 4) on the same dates. Table 1 gives all the data for twelve spawning grounds, dated from the day of first spawning. The mean date of spawning is obtained by adding the mean day of spawning to the date of first spawning, e.g. in the first line of the table, the mean date is the 8.45 day of March. There are differences between the date of first spawning (and the mean) of up to one month, 27 January to 2 March. Also some distributions are bimodal; two sets of data published by Runnstrøm (XI and XII) have not been used because there are two distributions separated by 4-6 days. Instead of separating the components, a standard deviation and an overall mean with a standard error have been calculated. As the distribution is one of repeated positive samples, at the same positions, the low standard error estimates the regularity of spawning, even if some distributions are bimodal. The standard deviation of about 6 days means that most of the fish will spawn within a period of about 12 days.

Runnstrøm continued the work for only 7 years. Within this limit and taking into account the possibility that the bimodal distributions perhaps reflect the spawning of two groups on the same ground (for each ground comprised a number of grab stations), the data yield surprising results - a mean date with a low standard error, a distribution with a low standard deviation. It implies that the spawning grounds of the Norwegian herring comprise a number of groups, each of which spawns at the same position in successive years. Further, it implies that there are differences in spawning season of up to a month, within a fairly small area, from year to year. Since Runnstrøm's time, other restricted herring spawning grounds have been described in the southern North Sea (Bolster and Bridger, 1957) and on Ballantrae Banks (Stubbs and Lawrie, 1962).

Rasmussen (1940) and Aasen (1962) have shown that the date of the first day's catch of the Norwegian herring is correlated with the appearance of ripe and running fish. Devold (1963) demonstrated that the date of the first day's catch has shifted from September to February between 1900 and 1960. Between 1930 and 1960, the first day with 50 per cent of the sample in maturity stage VI shifted from early February to late February; indeed most of the change took place between 1941 and 1942. It is as if the spawning groups IX-XIV in Table 1 had been extinguished and had given way to groups I-IV. It is well known that the apparent spawning grounds of the Norwegian herring have shifted in recent years over great distances (Devold, 1963). There appear to be alternative explanations:-

(a) that the Norwegian spring herring changes its spawning ground with time;

(b) that the Norwegian herring is composed of groups or stocklets which spawn always on small restricted grounds, but that in time a group or stocklet may be replaced by another, spawning at a different position. Ottestad (1934) charts three main spawning areas: off Utsire, north of Stadt, and off Lofoten. The recent shift of the spawning fishery could well be considered as a shift from the Utsire stocklet to the Stadt one, and from the Stadt stocklet to the Lofoten one. The Utsire stocklet may still exist in very small and unfishable quantities.

Runnstrøm suggested that a delay in spawning could be detected in his data. There is a trend in the mean date from year to year on spawning grounds III, V and VIII. On six grounds out of twelve in Table 1, the first year is the earliest. But such trends are not found on the other nine grounds. From Runnstrøm's data it cannot be decided whether a trend took place or not. If it did, the standard deviation of the mean date of spawning is surprisingly low and the rate of change of the date was slow. If the trend did not take place, then that observed in Aasen's data is a change in the distribution of stocklets.

The Norwegian herring lives long and the stock depends upon sporadic good year-classes. So, as a stock, it is vulnerable to those changes in wind strength and direction by which production cycles are modified, starving fish larvae or letting them grow dramatically (Cushing, 1966, 1967). Devold (1963) has suggested that the alteration of Swedish and Norwegian herring periods is associated with changes in vertebral count in the Atlanto-Scandian herring. It is however possible that these changes are changes in the distribution of stocklets in time, some replacing others. An advantage of this explanation is that the changes in meristic characters do not have to be explained; they are merely differences between the existing stocklets and the changes reflect relative changes in abundance of them.

(c) The Fraser River sockeye salmon

When the sockeye return to spawn in their parent creeks in the Fraser River system, they are caught in the fishery in the Straits of Juan de Fuca and of Georgia. The stocks can be detected in the fishery quite readily by the distributions of circuli on the scales (Henry, 1961). The peak appearance of a stock in the fishery can be established; for example the Lower Adams stock peaked on 29 August 1954, on 17 August in 1955 and on 2 September in 1958. Figure 1 shows the distribution of catches in time for each of the four cycles of the Fraser sockeye. In each case the mean date of peak catch varies from year to year by as much as three weeks, but there is no systematic trend with time.

In the Annual Reports of the International Pacific Salmon Commission, the dates of peak spawning for each identified stocklet, as observed in the creeks, are given for each year. The dates are given, as for example Upper Pitt River, 8-10 September; the mid-date between the two is taken as the date of spawning. So up to 17 years of data for a given stocklet are expressed as a distribution of spawning dates with 17 observations. Not all stocklets are represented in all years and of course the four cycles are being treated as spawning at the same date in the creeks. Figure 2 gives the dates of peak spawning for 17 years for 51 creeks, rivers or lakes, sometimes incomplete, but often full. In only one case is an upward trend detectable (Tachie River); no downward trends are detectable. Nor are the differences between the 4 cycles noticeable, justifying lumping the data for this purpose. Table 2 gives the standard deviations of the mean peak date of spawning for 51 creeks, lakes or rivers. The standard deviation is usually about five days, indicating that most fish spawn within ten days of the mean peak date. Figure 3 gives the standard errors of the means, plotted on the number of observations. With less than 10 observations the standard error is high, but in general the standard error of the mean date of spawning is about 1.5 days. The data for the Sakeniche river have been excluded because there were two peaks in each year.

It is a remarkable phenomenon. Not only do the sockeye return to their parent streams, but they reach the Fraser river at a predictable season, swim up the river at a constant speed, (according to the distance they have to go), and spawn on a predictable date.

(d) The Arctic cod

The Arcto-Norwegian stock of cod spawns mainly in the Vestfjord in northern Norway. Records of catches by weeks are available from 1894 to 1967 (Arsberetning Vedkommende Norges Fiskerier, Lofotfisket), covering 13 to 15 weeks in each year. In each year a mean date of capture may be calculated. It is not a mean date of spawning, but is an index of that mean date. Figure 4 shows the distribution of the mean date of capture for the whole period. There is obviously a trend in the mean date of capture throughout the period. My colleague, Mr. H. W. Hill, has fitted a ten-year moving mean to the data. It will be seen that the range in the moving means is less than 10 days over the whole period. Treating the mean date of capture as a single observation, a distribution in deviations from the fitted curve was calculated. The standard error of that mean was 0.51 days, and the standard deviation of the distribution was 4.09 days.

So the trend detected is a small one, just over a week in the whole season of capture of 13-15 weeks. It is in itself interesting and will be investigated later, but, eliminating the trend, the standard error of the mean date of capture is low.

(e) The Californian sardine and anchovy

There are two species of fish which do not spawn as regularly as suggested above, the Californian sardine and the Californian anchovy. Ahlstrom (1966) has tabulated monthly catches of the eggs of both species for a period of 9 years, as shown in Table 3.

There appear to be spring and autumn peaks in the catches of sardine larvae in 8 years out of 9. The variability in the dates of peak catch of larvae is to be expressed in months rather than days. There is probably only one peak in the catches of anchovy larvae, but it might occur in any month between February and June. It might be objected that the catches of larvae do not really represent spawning times. However, the eggs hatch in a day or so and the samples are taken by months. Both sardine and anchovy live in an upwelling area and the fish tend to spawn at the points of upwelling (Cushing, in prep.). But the contrast between the animals living in temperate waters and those further south is not confined to the upwelling areas. Tuna larvae are found all over the northern subtropical Pacific at nearly all seasons (Matsumoto, 1966). Hence the contrast is perhaps between the subtropical anticyclone and the high-latitude cyclones.

Discussion

There are four well known stocks of fish, living in temperate waters, for which there are long-term or specialized sets of data. For the plaice, the mean date of egg production has been used as an index of spawning date. For the herring, the mean date of repeated spawnings at the same position has been used. For the salmon, the mean date of spawning, as observed on the ground, has been used. For the cod, the mean date of capture on the spawning ground was employed.

The standard error of the mean date of spawning or mean date of capture has different biological meanings in each species. There are 67 observations for the cod (with the trend excluded) and about 7 on the herring; yet the standard error of the mean is 0.51 in the former and about 1.5 in the latter. So the standard error is low whatever the form or number of observations. If the fish spawned at variable seasons or at seasons trending markedly with time, the standard error would be high. Instead, the trend observed in the Arctic cod is a low one (< 10 days), justifying the extraction of the trend before calculating the standard error.

Cushing (1966) suggested that some dramatic changes in waters around the British Isles were mediated by changes in the production cycles, themselves altered by changes in wind strength and direction. Cushing (1967) showed that the differences in spawning time of the herring populations in the north-east Atlantic were linked to differences in production cycle in different areas. The two ideas are connected; if a fish population spawns at such a time that its larvae feed at the height of a production cycle, it is vulnerable to the variation of that cycle. Production cycles change with time in spread, amplitude, and timing. Climatic change is effective through changes in wind strength and direction, advancing or delaying the production cycles. Fish can only link their times of spawning to the production cycles in an indirect manner. If they spawn at a fixed season, the population has the best chance of profiting by the variability of the production cycle. If the spawning time varied randomly the link could not be sustained. So the fixity of spawning season really follows from the variability of the production cycle and the dependence of the fish populations upon it during their larval lives.

The slow shift of time of peak capture of the Arctic cod suggests that a fish population can slowly adapt to climatic change. But on the scale of variability of the production cycle in timing it is a small-scale adaptation. The concept of the fixed spawning time linked to a variable production cycle opens the possibility of the changes in abundance with time. Stocks may increase dramatically or fail catastrophically, because the fixed spawning time keys in to the production cycle or misses it. Because populations do not easily become extinguished, a stock might survive at very low levels during a poor period, to recover later. So the cycle of the Norwegian herring is related to cycles of climatic changes (Beverton and Lee, 1965) and may include a succession of a number of stocklets.

It is possible that the regularity of spawning season is limited to high latitudes, i.e. $> 40^{\circ}$. The winds are stronger at the poleward edge of the subtropical anticyclone than nearer the equator. The seasonal variation of light intensity increases towards the pole. The ratio of compensation depth, D_c, to depth of mixing D_m, is an index of the chance of production taking place. In high latitudes, $D_c/D_m \ll 1$ during the winter and in low latitudes $D_c/D_m \geq 1$.

The seasonal differences of light intensity increase with latitude, and wind strength increases with latitude towards the boundary of the subtropical anticyclone. It is possible that on the tropical side of the boundary production continues all the year round, and that sharp seasonal cycles of production are found on the poleward side of the boundary. If so, then it is not surprising that the low-latitude fishes do not have regular spawning seasons.

The data used are not very extensive, despite their somewhat massive appearance. But it should be pointed out that the species represented comprise most of the fish caught in the North Atlantic.

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TABLE 1 Distribution of days of spawning after the date of first spawning of the Norwegian herring, estimated from the age of spawn in a grab sample (Runnstrøm, 1941)

Spawning ground	Days from 1st positive sample																																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
I	1		1	1	1	1	2	1	1	1	1																								
II	1	1				1	1	1	2	1	1	2	1	1	1	1	1									1	1								
III	1	1		1	1		1	2	1	1		1	2	2	1	1	1	1			1					1	1								
IV	1	1		1		2	3	3	2	1	1		2	3	2										1	1									
V	1	1	1							2	2	4	2	2	1	3	4	2	1	1	1	2	2	2	2	2	1	1							
VI	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	3	2	2	2	3	5	3	1	1	1	1	2	2	2	1					
VII	1	1			1				1	1	1	2	2	2	3	4	4	3	3	3	3	3	1	2	1	1			1	1	1				
VIII	1	1	1					3	3	1	1	1	1	2	1	3	4	5	5	5	2			1	1	1	1					1	2		2
IX	1	3	2	2	2	3	3	2	3	3	4	3	2	3	2	3	3	2	2	1	1	1	1	2	1		1	1	1	1					
X	1	2	1									1	1		1	1	3	4	4	5	5		2	1	1	1			1	1					
XIII	1	1	1	2	3	4	4	4	3	3	3	3	3	2	2	2																			
XIV	1		1	1	1	1					3	4	3	2	2	1				1			1	1											

TABLE 1 (Continued)

Spawning ground	Mean date of 1st spawning	Mean day of spawning	Standard deviation of the mean date of spawning	Standard error of the mean date of spawning
I	2 Mar	6.45	2.90	0.92
II	23 Feb	11.94	5.19	1.26
III	23 Feb	12.38	6.90	1.54
IV	21 Feb	10.50	5.94	1.24
V	10 Feb	16.8	6.64	1.06
VI	7 Feb	17.06	7.44	1.04
VII	4 Feb	17.50	6.31	0.94
VIII	27 Jan	17.53	7.86	1.14
IX	3 Feb	13.00	7.42	0.98
X	5 Feb	18.00	6.74	1.14
XIII	10 Feb	8.98	5.43	0.61
XIV	10 Feb	12.17	7.72	1.20

TABLE 2 Standard deviations of the mean peak date of spawning of Fraser River Sockeye Salmon

Anknil Creek	4.4	Portage Creek	6.9
Bivouac Creek	2.5	Cultus Lake	4.8
Driftwood River	3.8	Upper Pitt River	3.5
Dust Creek	4.1	Widgeon Slough	4.5
15 mile Creek	4.7	Big Silver Creek	4.5
5 mile Creek	4.7	Harrison River	3.6
Forfar Creek	3.7	Weaver Creek	7.7
Frypan Creek	4.2	Birkenhead River	4.0
Gluske Creek	4.2	Seymour River	4.7
Kazcheck Creek	7.9	Scotch Creek	5.1
Kynoch Creek	3.9	Little River	6.9
Leo Creek	3.8	S. Thompson River	7.1
Middle River	3.0	Lower Adams River	5.6
Narrows Creek	4.5	Upper Adams River	5.6
Rossette Creek	3.8	Lower Shuswap River	9.2
Shale Creek	4.0	Raft River	3.6
Tachie River	4.9	Barriere River	6.4
25 mile Creek	4.8	Chilko River	3.9
Forsythe Creek	3.4	Tasoko Lake	4.6
Felix Creek	1.6	Horsefly River	6.0
Paula Creek	1.1	Little Horsefly River	10.2
Pinchi Creek	11.5	Mitchell River	8.3
Sandpoint Creek	4.2	Endako River	3.2
Upper Bowron River	3.4	Nithi River	3.5
Gates Creek	6.1	Ormonde Creek	5.2
		Stellako River	2.2

mean SD of mean peak date of spawning 4.9

TABLE 3 Monthly catches of sardine and anchovy larvae off California (in thousands) (from Ahlstrom, 1966)

SARDINE

	Jan	Feb	Mar	Apr	May	Jun
1951	0.08	0.31	0.88	1.78	3.48	1.79
1952	0.78	1.39	2.11	7.27	3.20	2.44
1953	0.36	1.35	2.10	0.62	4.31	3.07
1954	3.94	0.97	4.53	5.94	3.88	5.31
1955	2.33	3.13	1.58	2.69	0.58	2.27
1956	1.13	2.95	1.00	0.78	0.78	1.92
1957	0.76	0.95	1.16	0.42	1.73	0.28
1958	1.26	3.87	0.81	0.60	0.35	0.20
1959	0.73	0.86	0.12	0.46	0.29	0.24
	11.37	15.78	14.29	20.56	18.60	17.52

	Jul	Aug	Sep	Oct	Nov	Dec
1951	0.09	1.28	0.10	0.14	0.73	0.42
1952	0.25	0.57	0.90	0.13	0.14	-
1953	0.13	0.40	1.32	0.56	0.0	0.18
1954	0.70	0.75	-	0.11	-	0.79
1955	1.18	-	0.0	0.13	0.0	0.24
1956	1.51	4.42	1.04	0.0	0.0	0.0
1957	1.45	1.52	1.04	0.32	0.22	0.0
1958	0.54	1.47	2.28	0.05	0.0	0.0
1959	0.53	0.63	1.04	0.44	0.0	0.04
	6.38	11.04	7.72	1.88	1.09	1.67

ANCHOVY

	Jan	Feb	Mar	Apr	May	Jun
1951	1.43	2.76	8.00	2.44	1.77	3.19
1952	1.85	5.39	11.72	8.63	3.63	14.06
1953	12.82	16.20	15.84	6.92	3.50	4.88
1954	24.86	32.71	34.31	32.84	12.50	6.50
1955	40.14	30.95	25.08	16.49	4.20	12.66
1956	8.84	29.14	16.64	22.86	11.94	18.26
1957	10.50	48.26	14.33	20.23	20.80	18.40
1958	30.00	50.17	46.88	34.89	23.08	8.08
1959	13.83	43.32	18.79	91.30	17.47	13.73
	144.27	238.90	191.59	236.60	99.38	99.76

	Jul	Aug	Sep	Oct	Nov	Dec
1951	0.69	2.14	0.66	0.79	3.90	1.78
1952	2.53	3.56	4.02	2.41	1.83	-
1953	5.64	2.86	3.01	6.10	7.47	13.93
1954	8.56	1.88	-	1.25	-	5.84
1955	7.06	-	0.72	0.65	1.16	1.08
1956	14.72	9.64	0.37	0.83	1.43	0.28
1957	8.89	1.45	0.04	0.86	2.37	0.51
1958	10.22	0.31	0.89	0.53	0.08	0.60
1959	6.42	0.54	0.31	0.17	0.16	0.71
	65.23	22.38	10.02	13.59	18.40	24.73

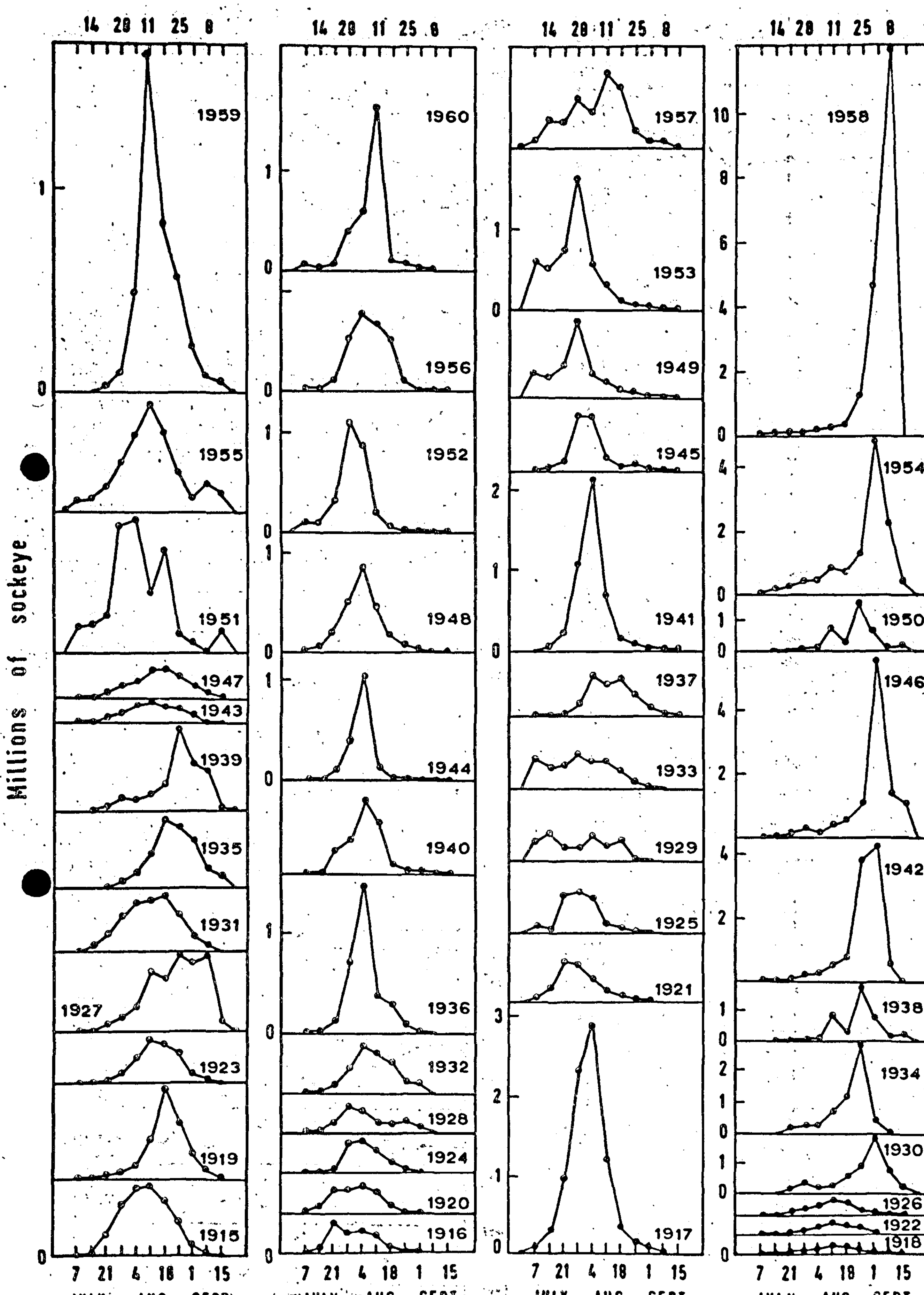

Figure 1 Weekly catches of each of the four cycles of Fraser sockeye salmon, off the Fraser River, 1915-60.

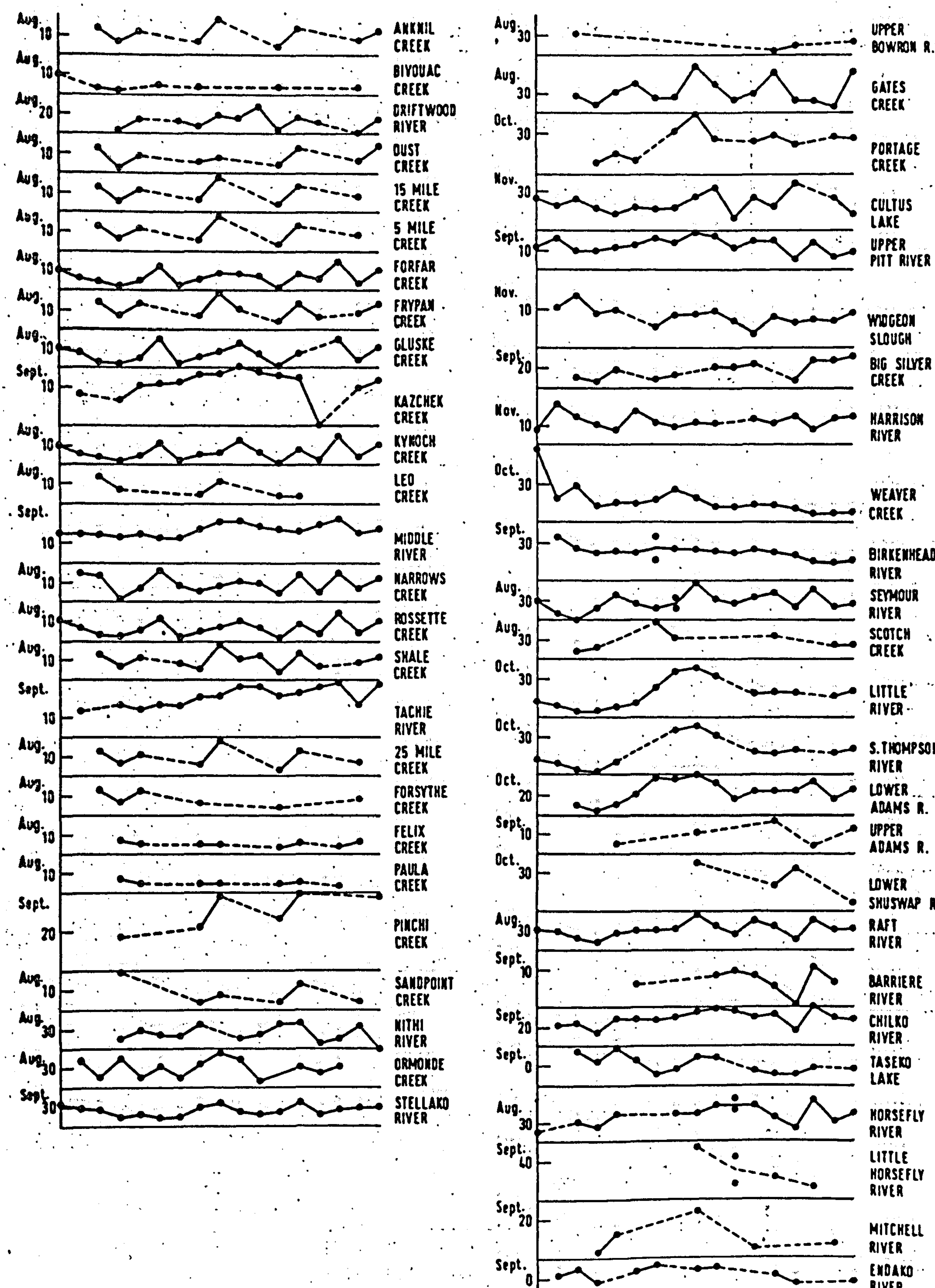

Figure 2 Time series of peak spawning dates for sockeye stocklets in the Fraser River system. (Ann. Reps, Int. Pac. Salmon Comm. 1950-66.)

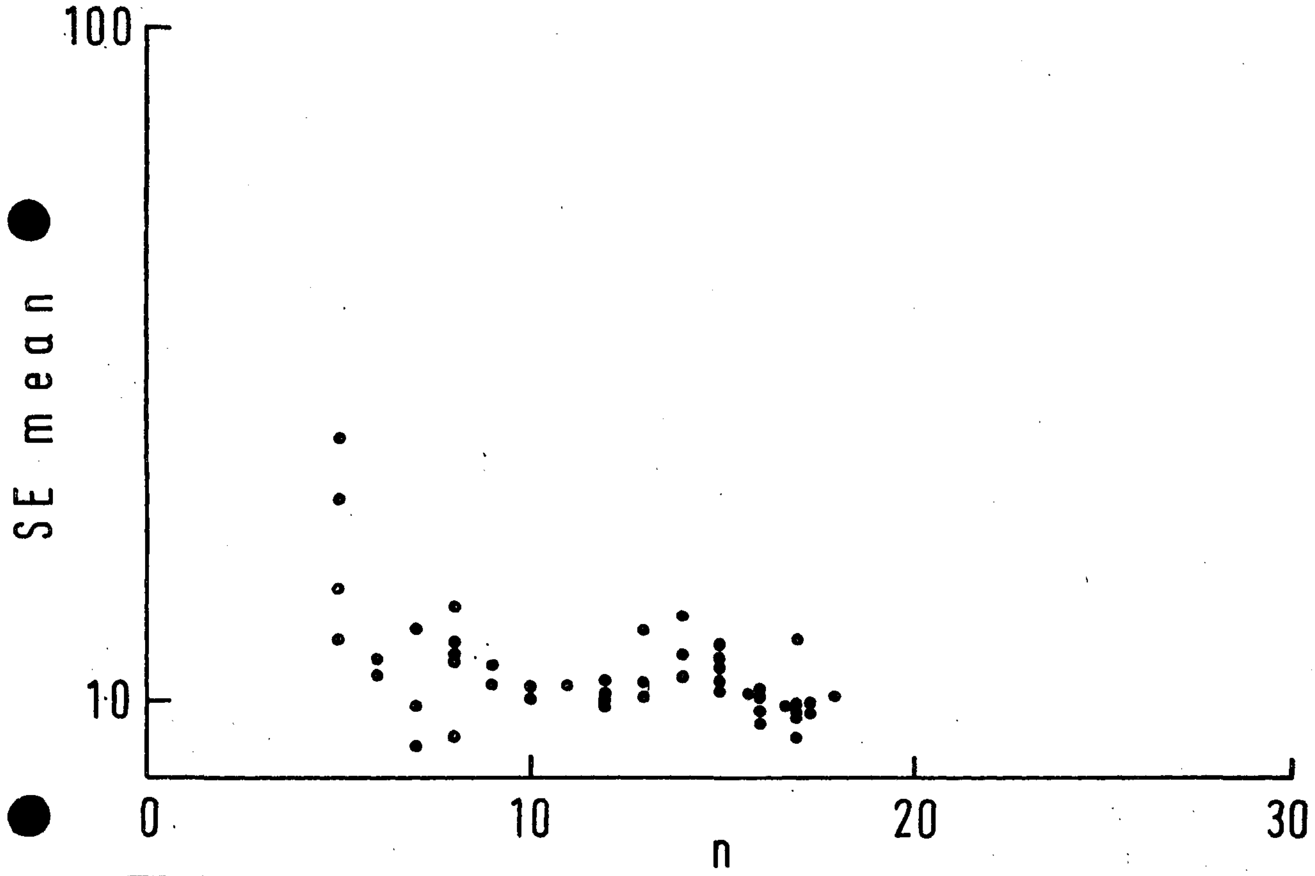

Figure 3 Standard errors of the mean peak date of spawning plotted on the number of observations for the sockeye stocklets in the Fraser River system.

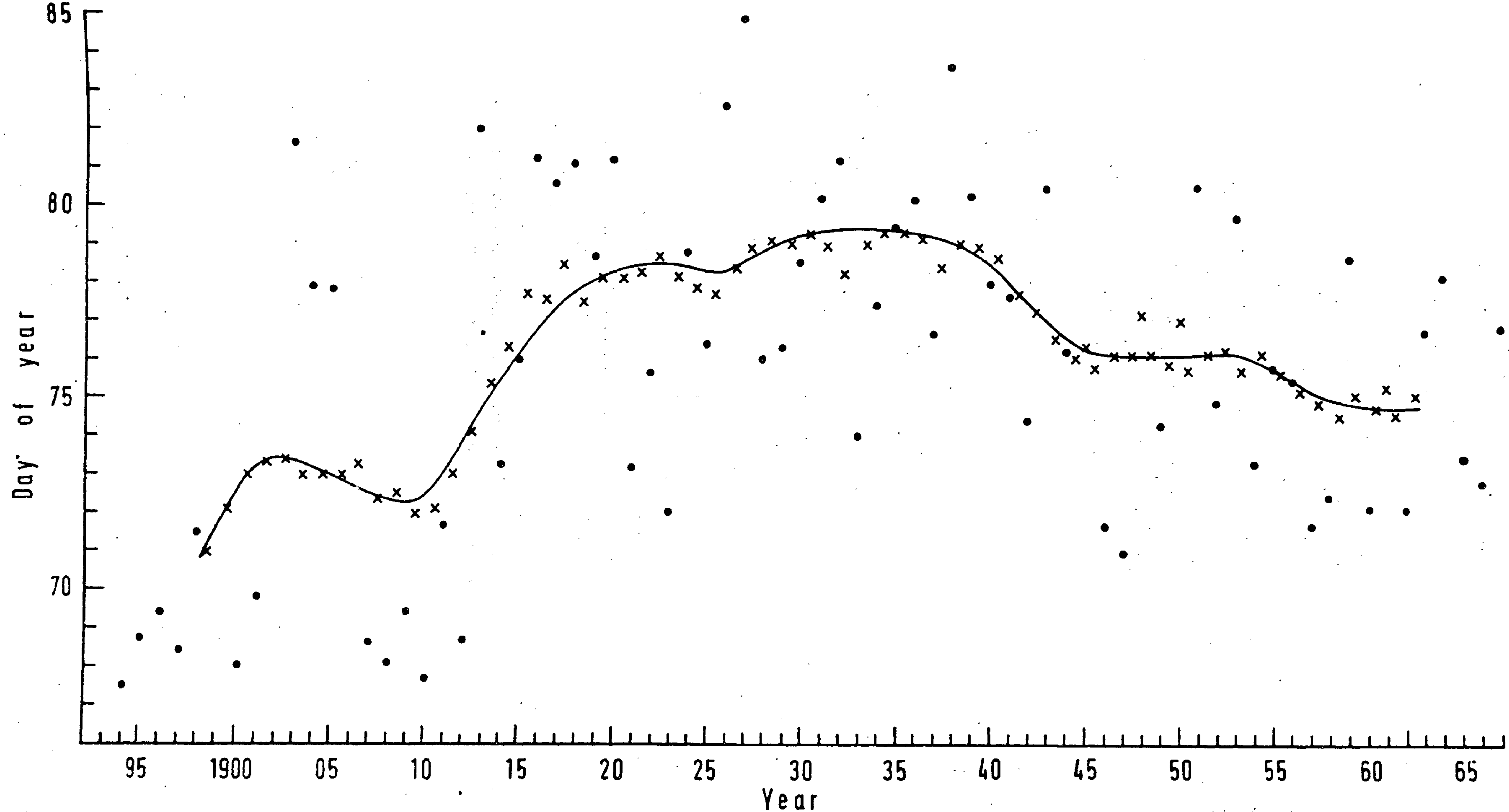

Figure 4 Mean dates of peak catches of cod in the Lofoten fishery, 1894-1967. (Arsberetning Vedkommende Norges Fiskerier, Lofotfisket.)

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