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Maturation Cycles in the Herring

by

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It has been assumed that herring stocks differing in the time of spawning will differ in a similar way in the time over which they will mature and that at all times or at specific times individuals will differ in their maturation stages and the stocks in the distribution of these stages. This implies that the process of maturation and the act of spawning are part of the same continuous physiological cycle, the one following the other without a pause or break. Assumptions such as these are the basis of the separation of mixed spawning stocks, fish at lower maturation stages being assigned to later spawning stocks and those at higher maturation stages to earlier spawning stocks (Burd, 1958; Symonds, 1960), or of the identification of spawning stocks. Thus stage V fish on the Dogger in August, September and October have been taken to be Dogger autumn spawners (Polder and Zijlstra, 1959; Baxter and Hall, 1960).

There are, however, no reliable estimates for any stock of the duration of the maturation cycle or of the stages into which it is divided, and there is even some confusion as to what is meant by duration. Naumov (1956), for instance, gives as the duration of a maturation stage for the Murmansk herring the period over which it is most often or usually recorded, and a similar criterion is used by Aasen (1952). The information required is the time spent by the individual fish in each maturation stage or, for a stock, the mean time spent in each stage by individuals in the population; unless all individuals mature together in exact phase, which is never so, this will always be less than the period over which it is found in the population as a whole. To be able to describe and discuss maturation quantitatively it is necessary to know not only the duration of the stages for individuals, as defined here, but also the extent to which the population is out of phase; this communication describes a method for investigating these and discusses the results obtained by applying it to data from a number of different herring stocks. Although it is realised that the data in many instances are relatively sparse and maturation stages are not always strictly comparable, sufficient information is available to draw some general conclusions and to discuss some specific problems.

METHOD

The probability of an individual being captured while in a particular stage of maturation is proportional to the duration of that stage. Random samples taken from a mature population which breeds with equal intensity throughout the year will give numbers in each stage in proportion to the duration of each stage, and the relative durations can then be calculated.

If the total length of the reproductive cycle is known, for example if it is known that individuals breed once each year, the duration can be calculated in absolute time units. For such a population Fig. 1a shows the percentage numbers of each stage during a period equal to one reproductive cycle. The duration of each stage is calculated as the area under its curve in approximate time units. If breeding is seasonal and every individual is in exact phase, then at any one time only one stage will be recorded, i.e. at a level of 100%. Fig. 1b illustrates this; the duration of each stage is the period during which the stage is recorded or, again, the area bounded by the curve for each stage.

Naturally occurring populations resemble neither of these models; breeding is usually seasonal and individuals are not all in phase, as is shown by the occurrence over the maturation period of more than one or several stages at the same instant of time. Under these circumstances a plot of the percentage in each stage of the total number recorded over the cycle will give a series of curves as in Fig. 1c. The curves of maturation stages rise to a maximum and fall off, but in each case the mean duration is again estimated as the area under the curve.

Because percentages are used, mortality over the maturation period will not affect estimates unless it can be shown that at any one time it is higher or lower for some stages than for others. Nor is it necessary to cover the whole maturation and spawning cycle; the duration of any stage through which the population passes during the sampling period can be estimated independently.

Data are available from several herring fisheries in a form which allows estimation of the duration of maturation stages for the populations exploited by the fisheries. The curves obtained agree with the types given in Fig. 1c; for instance, they are in general symmetrical and in some cases this allows extrapolation with relatively little error, even if they are not complete.

North Shields fishery

The North Shields fishery lasts from about early May to about early September. Since 1950 two or three samples a week each of 100 fish have been examined for maturation and a large body of data is therefore available. The data for 1954 and 1957 to 1961 have been analysed for both sexes separately and from 1953 to 1961 for both sexes combined.

Three year olds only were considered (i.e. with two winter rings and a third growth zone), from samples caught in the general area centred about 30 miles north-east of Tyne. Later in the season fishing takes place also to the south-east of Tyne in the Whitby area, where an autumn spawning stock is found. Samples from this area are not included, as they would represent autumn spawners alone, whereas the North Shields fishery proper is based on a mixture of both autumn and winter spawners. Burd (1958) estimated that in July the winter stock predominates, forming 80% of the whole for the three year olds.

The data were combined in fortnightly periods designated May I, II, June I, II, etc. and for each period the percentages in each stage were calculated. The mean percentages for each period for the years examined are plotted in Fig. 2 and Fig. 3 for the males and females respectively.

The area under each curve representing a single stage is a direct estimate of the mean time spent in that stage by individuals of the population represented by the fishery. Complete curves can be drawn for stages III, III-IV and IV, and for stages I and I-III they can be completed with little error since they are the only stages present in the early part of the year. Extrapolation gives for both sexes a time in March when the maturation cycle can be said to begin.

Table 1 Estimated mean duration (days) for North Shields three year old herring

Maturation Stage	I	I-III	III	III-IV	IV	IV-V	Total I-III to IV-V
Males	56.9	44.4	16.8	4.6	15.6	4.9	86.3
Females	55.4	52.3	27.5	6.1	16.8	9.2	111.9

In particular we note that the spread is similar regardless of the estimated duration (compare the curves for III-IV and I-III) and that the maximum percentage is greater for the longer stages. The curves themselves are unimodal. If two separately maturing populations differing greatly in either the phasing or the duration of stages were present it would be expected that some of the curves, and particularly the later ones, would be bimodal.

The stages are based on Heincke's scale (see Aasen, 1952) and are here described.

I Virgin herring. Gonads very small, 2-3 mm broad; ovaries wine red, torpedo shaped; testes whitish or grey brown, knife shaped.

I-III Virgin herring. Gonads more of the form of those of adult fish, but still small, 5-6 mm; eggs not visible.

III Gonads more thick and swollen, 1-2 cm broad depending on fish size; ovaries yellowish; eggs visible; testes greyish.

III-IV Intermediate stage.

IV Gonads almost as long as the body cavity; ovaries orange or pale yellow; eggs uneven size, opaque; testes whitish.

IV-V Intermediate stage.

V Gonads fill body cavity; ovaries yellowish; eggs round and some hyaline; testes milk-white.

VI Flowing roe and milt.

VII Spent herring. Gonads slack; ovaries blood red; testes greyish red; eggs or milt still present.

II Recovering spent herring. Gonads in firmer condition, about 1 cm broad; no sign of eggs; colour, dark wine red.

The average time in stage I spent from mid March is almost the same for both sexes, indicating that maturation begins at about the same time, but the

males mature more rapidly from I-III onwards and they reach stage V about 25 days earlier. This higher maturation rate is reflected in the marked preponderance of males at stage IV and above in July - a feature of all the years studied. It is difficult to compare maturation between the sexes since the process differs markedly in respect to gametogenesis (Bowers and Holliday, 1961), but it is likely that the difference is one of increase in size of the gonads, the male gonad growing more quickly. Holliday (in press) finds that the male portion of the gonads of hermaphrodite herring is cytologically more advanced than the female and suggests that the female is less sensitive to the action of the pituitary. This independent evidence confirms the conclusion reached on the basis of estimates of duration of maturation stages, but the North Shields data show that the difference is manifested at all stages of the maturation process and is not confined to the later stages when the action of the pituitary becomes evident (Holliday, 1960).

Maturation and gonad growth

The eggs to be spawned in the current season are segregated very early in the maturation cycle at stage II (Hjort International scale) when the follicles are formed (Bowers and Holliday, 1961), and develop more or less together. It follows that egg number is fixed or at least limited very early and maturation can for the female be related directly to increase in egg size. Mrs. A. D. Woodhead has kindly made available data on egg size for North Shields herring at different stages of maturity. The mean diameter for each stage (from sectioned material) is converted to volume, in arbitrary units, and in Fig. 4 is plotted on the time scale for the North Shields female three year old fish. The volume at stage V is indicated by a horizontal line A B. This is the growth curve for the female gonad and it would appear that the absolute gonad growth rate increases markedly over the later stages of maturation, indicating that the gonad is provided with a proportionately greater share of the available food materials. Whether this involves a decrease in the available material for body growth is not known, and the possibility that seasonal growth and maturation are mutually inhibitory is worth investigation.

It is possible from the gonad growth curve to estimate roughly when stage V is reached by the North Shields population of three year olds as a whole. Extrapolation of the curve to meet A and B gives minimum and maximum estimates for the mean length of the maturation cyle from its start in mid-March. The average time for the attainment of stage V for females on this estimate lies between 180 and 200 days, which gives a time at the end of September at which 50% of the Shields females will have reached stage V.

North Minch fishery

The North Minch fishery offers perhaps the best opportunity for the study of maturation. The stock exploited appears to be largely self-contained and localised, and fishing is carried out in every month of the year except April. Both spring and autumn spawners occur in the area but in recent years and in particular during 1958 and 1959 VS counts and otolith studies indicate that

the major proportion of the catch consists of autumn spawners. Parrish et al. (1960 and 1961) give the percentages of autumn spawners as follows:

Table 2 Percentage autumn spawners - North Minch

	January-March	May-June	July-September	October-November
1958	87.5	84.1	64.9	87.2
1959	90.2	74.0	68.6	89.4

The more marked influx of spring spawners in the period July to September consists mainly of young and immature fish, and inspection of the tables in the Annales Biologiques indicates that the correlation between high VS counts and very low maturity stages is such that most of the spring spawners can be eliminated. There are, however, no data for individual age groups or for the sexes separately, and the estimates for the duration of the stages are therefore the means for all fish. The Hjort scale is used rather than the Heinke, but even so stages III, IV, V and VII can be used to give a reasonable comparison with the Shields information. Stage VII-II includes fish which have been recently spent and also recovering fish in early stages of maturation to the time when eggs are visible, so that it overlaps our stage III to some extent. Table 3 gives the estimates derived from Fig. 5.

Table 3 Duration (days) of maturity stages (North Minch autumn spawners)

	III	IV	V	VII	VII-II
1958	32.9	25.0	15.2	6.1	280 (approx.)
1959	21.4	26.2	12.2	3.0	

The herring of the north-western North Sea

The Buchan prespawning and spawning fisheries extend from about April to September, beginning at about the same time as the Shields fishery and ending rather later in the year - both significant points. In the 1950's the majority of the fish caught were typed by VS counts and otolith characters as autumn spawners, the remainder being spring spawners of the oceanic herring group. These latter were more abundant in the early part of the fishery and in the northern and eastern areas of the fishery, so that by leaving out records for April and for landings at Lerwick in the Shetlands from the tables given in the Annales Biologiques, we deal predominantly with the autumn spawning stock. For instance, Aberdeen landings give percentages of autumn stock as being 90% or above from May onwards and landings at Fraserborough and Peterhead show similar percentages (Annales Biologiques, Vol. X-XVII).

The staging is comparable with that used for the Minch fish, as sampling was carried out at the same laboratory, but there would appear to have been minor changes in the system used. Before 1957, for instance, stages VII and VII-II are combined so that estimates for stage VII are not available over the whole period (see Fig. 6). As for the Minch data, all age groups and both sexes are treated together.

Table 4 Duration (days) of maturity stages for north-western North Sea herring

	III	IV	V	VI	VII
1952-59	17.1	16.1	14.3		
1958	16.7	20.5	17.4	5.3	10.8
1959	28.5	27.0	10.2	4.2	5.9

The differences between the years 1958 and 1959 may or may not be significant since there are too many variables involved which cannot be evaluated from the tables from which these estimates are derived, but Table 5 gives the mean duration for 1958 and 1959 for the North Minch and north-western North Sea fish, together with the North Shields mean for both sexes.

Table 5 Duration (days) of maturity stages for herring of the three fisheries (mean of 1958 and 1959)

	III	IV	V	VI	VII
N.W. North Sea	22.6	23.7	13.8	4.8	8.3
N. Minch	27.1	25.6	13.7	-	4.5
N. Shields*	22.4	23.3			

*III and III-IV are combined as are IV-V and IV to give the estimate for stages III and IV.

The similarity between the estimates of the duration of the stages for the two autumn spawners is striking and the relative shortness of stage V indicates that maturation to stage V is followed fairly rapidly by spawning. The duration of stages III and IV for the North Shields fish is similar to that of the autumn spawners, indicating that they mature at a similar rate, since it is in these stages that most of the growth occurs (see Fig. 4).

The l_1 distributions of the Shields fish have been taken to indicate that the three year olds contain a high proportion of Channel spawners (Burd, 1958; Cushing and Burd, 1961). If this is so then any large difference in the maturation cycle must be the result of a difference in the phasing rather than in the rate of maturation. Because two systems are used, differing in the early stages of maturation, we cannot compare the Shields data and the Minch and Buchan data during the early period of the fisheries. We can compare the distributions for the month of July, when both show a wide range of maturation stages including III, IV and V which are similarly defined in both the Hjort and Heincke systems.

Table 6 gives the mean percentage (males and females combined) for the years 1953-59 inclusive, for July.

Table 6 Percentage maturation stages for July (1953-59 inclusive)

	I	(II) I-III	III	III-IV	IV	IV-V	V	VI	VII	VII-II
N. Shields	8.5	30.1	33.5	6.3	11.8	3.4	6.3			
N.W. North Sea	11.0	21.8	28.8		19.7		11.7	1.3	1.4	4.6
N. Minch	-	42.7	26.8		15.4		10.4			

In recent years the three year olds have been predominant in the N.W. North Sea and the N. Minch, so we are comparing, very largely, data for fish of the same age. Stage II (Hjort) is equated to I-III (Heincke) and both will include early maturation.

The figures for the North Minch need further explanation. VS counts indicate that nearly all stage I fish are spring spawners, but that stage II fish contain both autumn and spring spawners. The VS mean for stage II fish in July is 56.63 compared with 56.49, 56.51 and 56.53 for stages III, IV and V respectively. The VS for all spring spawners is about 57.0 and perhaps a little higher. Taking 56.51 as the VS of autumn spawners and 57.0 as that of spring spawners we estimate that 75% of stage II fish are autumn spawners and 25% spring spawners. The numbers in stage II given in the tables in the Annales Biologique are adjusted and the percentages in each stage calculated after this adjustment.

There are differences in the distribution of maturation stages between the Shields fish and the other two, which have a higher mean stage, but these differences are relatively small and for all three fisheries the percentage below stage IV is more than 60.

If the population exploited by the Shields fishery contains a considerable proportion of winter spawners and if these differ in the phasing of their maturation cycle by the three or four months difference in spawning time the distributions in July would differ markedly. We must conclude therefore that differences neither in the rate of maturation nor in the phasing of the maturation cycle can account wholly for the difference in spawning time. It will be shown below that winter spawners have a much longer stage V and that this accounts for a large proportion of the difference.

English inshore spring spawners

The English inshore herring has been rather neglected in herring work but its study is of interest in the light it throws on maturation. It is recorded from the southern and eastern coasts of England, particularly perhaps in the Thames estuary and the Wash, and its characteristics include a low 1_1 distribution, small length for age, low VS count, and a spring spawning period. Of the data available at Lowestoft the most interesting are those obtained from four samples from the Thames estuary in late 1958 and early 1959. Table 7 gives the percentage in each maturity stage, with other details.

Table 7 Maturation stages - English inshore herring

Date	Area	Sample No.	I-III	III	III-IV	IV	IV-V	V	VS
14 Nov. 1958	W. Mersea	G.M.1	2	9	4	28	25	32	54.67
27 Jan. 1959	Southend	H.M.1	5	6	3	20	13	51	54.76
23 Feb. 1959	W. Mersea	H.M.2	4	3	3	10	7	68	55.03
25 Feb. 1959	W. Mersea	H.M.3	0	0	0	6	15	76	54.85

The low VS for each sample serves to identify the population. These fish are expected to spawn from March to May and yet by November over 50% are in stages

IV-V or V. When the sexes are separated, another point becomes clear.

Table 8 Percentage distribution of maturation stages for Thames herring

			IV	IV-V	V
G.M.1	14 Nov. 1958	♂	22	14	50
		♀	34	38	12
H.M.1	27 Jan. 1959	♂	14	15	58
		♀	30	5	27
H.M.2	23 Feb. 1959	♂	10	8	70
		♀	6	6	70
H.M.3	25 Feb. 1959	♂	5	16	79
		♀	11	13	76

The females are predominantly IV's and IV-V's whereas the males are IV-V's and V's, illustrating again the difference in maturation between the sexes. For both sexes the percentage of stage V is only slightly increased by the end of January, some two and a half months later, but from January to February the process of maturation accelerates. Overwinter conditions slow down maturation markedly, but even so a large proportion of the population spends some three months in stage V.

The Norwegian Large spring spawners

The Norwegian Large spring spawners are fished off the Norwegian coast in December and January. Runnstrom (1941) discusses the winter fishery for Norwegian herring very fully and makes a distinction between the Large herring caught in December and January and the Spring herring caught in February and March, both however spawning in the spring. His figure 9 gives data for December and January for the Large herring. The fishery is divided into four regions, of which we consider three which are much larger than the fourth.

Table 9 Percentage maturation stages IV and V, Norwegian Large herring (data from Runnstrom, 1941)

	More Trondelag		Sogn Fjordane		S. Hordland	
	IV	V	IV	V	IV	V
December	40	47	40	47	30	47
January	40	47	40	47	30	47

Eighty to ninety per cent of all fish were in stages IV or V by December and a large percentage must overwinter in stage V. Moreover the percentages in stages IV and V (and indeed also in the lower stages) are identical for December and January, indicating that no maturation occurs over at least mid-winter. Wood (1930) discussing the herring caught in the neighbourhood of the Fladen ground in November, December and January says that a large proportion of stage V and "VI" fish, i.e. fish nearly ripe for spawning, are usually recorded. These he regards as undoubtedly spring spawners and he infers that sexual development commences some time before the onset of winter conditions and that it is far advanced long before spawning time. Watkin (1933), discussing the herring of the Smalls fishery, also recognises that spring spawners may mature over the previous autumn.

The Lusterfjord herring

Aasen (1952), in dealing with the isolated and characteristic Lusterfjord herring, includes maturity data for some 1100 individuals unequally distributed over 13 months. For stage VI the data are likely to be biassed, as spawning is localised and the fishermen from whom the samples were obtained know the position of the grounds accurately. The high percentages of stage VI fish recorded during March and April therefore imply that spawning shoals are differentially exploited. For the rest of the period the data are more representative of the whole population, and stages III and IV (Heincke's system) are of significance. Taking both stages together the percentage rises from nil in June to 84 in August and from October onwards until January it is nearly 100. No stage V's are recorded over this period, but from February onwards maturation proceeds rapidly to be followed quickly by spawning in March and April. Again there is a discontinuity in the maturation over the winter period, this time in stage IV mainly and in stage III. Despite a long period during which it might be possible for the whole population to become synchronised, stage VI fish are recorded in the three months of March to May, which implies that maturation is greatly slowed down not at a particular point of the maturation process but at a particular time of year.

The Onega herring

The herring of the White Sea has been divided into separate stocks labelled biotypes by Russian workers. Of the two types found in the Gulf of Onega the so-called White Sea herring is dealt with by Mikhailovskaya (1957), who gives maturation data for the whole year. The scale used is apparently similar to that defined by Naumov (1956) in which V is "ripe" or spawning and III about equivalent to IV of the Hjort or Heincke scales. He describes a winter period from November to March when the majority of fish are in stage III (≡ IV of Hjort stage), a prespawning period from the end of April to the beginning of May when gonad development is intensive and III-IV's and IV's (IV-V's and V's) are predominant, and a spawning period from the second half of May until the first half of July. In July and August feeding is intensive; growth zones on the scale become evident and stages II and II-III (III and III-IV) are the common stages recorded; then in September and October the gonads pass in the main to stage III (IV). Here is another instance of a spring (or perhaps early summer) spawner with an overwintering stage at a relatively high degree of maturation. Stage IV is reached six or seven months before the time of spawning.

The Murmansk herring

The Murmansk herring spawns in March, April and May, with peak spawning intensity in April (Naumov, 1956). Naumov discusses the development of the oocytes of the Murmansk herring and gives data collected on four cruises in the Barents and Greenland seas. The data are rather variable and none are given for December, but the percentage of stage III (IV) rises rapidly from September onwards and Naumov gives the period during which stage III (IV) fish

are recorded (which he calls "duration") as some six months. There are discrepancies between his Fig. 12, Table 9 and the text, in that he states, "In the autumn the maturation has proceeded further, characterised by the transition from stage III to IV" (Hjort stages IV to V), whereas his Fig. 12 gives stage III (IV) as being the most commonly recorded stage from July to the end of the year, but once again for a spring spawner a long over-winter period occurs to slow or halt maturation.

The Manx herring

The spawning of herring in eastern Manx waters takes place from the beginning of September until November, with September as the time of maximum spawning intensity (Bowers, 1952). The spawning stock can therefore be described as autumn spawners. Data on the maturation stages from the Manx fishery are given by Smith (1957) for the years 1945 to 1953 and by the same author (Smith, 1948) for the years 1923-44. Symonds (1960) suggests that the Manx fishery consists of three components, the autumn-spawning Manx fish, found on the east and west coasts of the island, another autumn-spawning stock off the Irish coast, and a late winter or early spring-spawning stock found between the Isle of Man and the Irish coast, the spawning ground of which is unknown. The pattern of fishing has changed markedly in recent years. Until 1951 the fishing area was confined largely to the south and west of the island and near the shore, the eastern side of the island being worked regularly only for a few days in September. From 1951 onwards the traditional pattern changed and fluctuated. Catches on the east coast tended to become frequent and later in the 1950's the Irish coast regions were fished as well. The data for the years 1923-51 therefore cover a smaller area than for 1951-53 which includes more fish caught nearer the spawning area. If there is an appreciable proportion of non autumn-spawning stock included in the data it is likely to be of a late winter or spring spawning type. This point is made because any bias would tend to show up as a higher proportion of lower maturation stages. A comparison of the maturation stages between the Manx fish and the Buchan fish for July now has considerable significance.

In the Buchan fishery for the period 1951-53, Stage VI herring have been recorded mainly in August and September and in almost equal proportions, indicating that peak spawning of the Buchan fish is of the order of one month earlier than that of the Manx spawners. Despite this the percentage of fish in stage V or above in the Buchan fishery for July was only 15% (Parrish et al., 1952, 1953, 1954) whereas for the Manx fishery it was 59% (Smith, 1957). For the years 1945-50 the percentage was 32 and it must be concluded that the Manx autumn spawners mature earlier or more quickly than an earlier-spawning stock. The duration of stages has been calculated for the two periods and is given in Table 10.

Table 10 Mean duration of maturation stages (days); Manx herring

	II	III	IV	V
1945-50	42	14	17	55
1951-53	21	12	10	65

The differences in the rates and phasing of maturation between the Buchan and the Manx spawners is more than balanced by the length of stage V of the Manx fish, which on the available evidence is an autumn spawner with a long stage V. It might be possible to account for the high percentages of stage V's in July and August by postulating that the fishery exploits a population spatially differentiated for maturation stage and is located in an area where the higher stages congregate, but Smith (1948) states that in August when both inshore and offshore groundsare worked both areas yield fish with, mainly, full roes.

The data presented by Smith (1948) show variation in the maturation cycle between age groups for the years 1923-44 and Table 11 gives the estimates of the duration of stages for four age groups.

Table 11 Mean duration (days) of stages by age groups (1923-44); Manx herring

	I and II*	III	IV	V
2+	54	17	18	39
3+	34	18	20	46
4+	22	16	17	61
5+	16	18	20	62

(*The mean time spent in stages I and II from the beginning of June, which gives an indication of the phasing of the cycle. A longer duration indicates that maturation begins, on average, later in the season.)

The older fish appear to begin to mature rather earlier in the year than do the younger, but the rate of maturation is similar for all age groups as is indicated by the estimates for III and IV, during which most of the gonad growth occurs. The older fish reach stage V earlier and remain in it longer, which would tend to prevent age (or length) groups from spawning as units. It is clear therefore that quite large differences in the maturation cycle may occur within a spawning population and between age or size groups, and a full treatment for any stock would have to include a study of this variation.

The Dunmore herring

The Dunmore fishery takes place from about September to about the end of January. J. Bracken has kindly made available data for the 1961-62 season extending from October to early February. It is suspected that in October a proportion of the Dunmore fish belongs to an autumn-spawning stock (Bracken - personal communication) but from November the majority will be winter spawners. The figures for November (Bracken's data) give only 2% below stage V if immature and recovering spent fish are eliminated, and the percentage in stage V remains high until the third week in December;

even in January it is 40%. The mean duration of stage V calculated from Bracken's data and extrapolating backwards in time from November is found to be about three months. This is longer than that found for the Channel spawners, which would appear to spawn rather earlier than do the Dunmore fish.

Channel spawners

The East Anglian fishery exploits predominantly fish spawning in the Channel in the winter, and while spawning can take place from about November to January, December is probably the month during which the spawning intensity is highest.

Burd concludes that the North Shields fishery exploits Channel spawners which form a high proportion of the three year olds caught in that fishery, the remainder being autumn spawners of the Banks stock (Burd, 1958). If this is so then the similarity between the maturation stages of the Shields fish and the Buchan and Minch fish could be taken to indicate that the difference in the maturation cycles is not great.

We can draw conclusions from the East Anglian data itself, for in some years sampling begins in the first week in October. Table 12 gives for this time the percentage of fish in stage IV, below stage IV (including immature fish and spents) and above IV, for seven years for which this information is available.

The mean percentage for seven years' data for the first week in October is 63.5. In 1956 the percentage was only 22.6, but only one sample was available and there is reason to believe that it is not representative, as in the same year the percentage of above IV's for the last week in October is if anything below average.

Table 12 East Anglian herring; percentage maturation stages for first and last weeks in October.

	First week			Last week	
	Below IV	IV	Above IV	IV and below	Above IV
1952	14	31.5	52.0	7.6	92.4
1954	1.8	9.7	89.0	16.7	83.3
1956	23.6	53.7	23.6	5.6	94.4
1957	3.7	24.3	71.2	7.9	92.1
1958	3.0	27.5	65.3	2.8	97.2
1959	17.6	20.9	61.6	0.4	99.6
1960	1.5	12.0	83.2	1.0	99.0

By the last week in October the mean percentage of fish at stage IV and below is only 6. During September, therefore, a large proportion of Channel fish mature past stage IV, and by the beginning of November the majority have completed their maturation to stage V. It follows therefore that during September and October stage V autumn- and winter-spawning herring can co-exist in time and that the Channel spawners, like the Dunmore herring and the spring spawners, can reach a high stage of maturity some time before

spawning. The evidence from the spring spawners indicates that winter conditions inhibit maturation. If this applies to all herring then the relatively early maturation of the Dunmore and Channel spawners and the long stage V is explained. Any stock spawning during the winter will have to reach stage V before the onset of conditions inhibiting maturation, and it would appear that these occur from about the beginning of November. I am using the term maturation here in the special sense as involving increase in gonad size. There must be changes in the physiology of the eggs during stage V, resulting in changes in transparency and in the properties of the membrane permeability and stickiness, but until the final imbibition of water on shedding these do not involve growth or change in volume, since stage V itself is defined as that stage at which the body cavity is filled.

The important conclusion is that stage V Channel spawners can co-exist in time with stage V autumn spawners in September and October, on the evidence from the East Anglian fishery. This is confirmed by data given by Gilis (1961) for the years 1956-60 and the Sandettie sector of the southern North Sea. The mean percentage of stage V's for October is given as 93.4%, higher even than the mean East Anglian percentage for the month - the area covered being more to the east. The point to be made is that the East Anglian figures are unlikely to give an overestimate of the maturation stages for the Channel spawners as a whole.

Stage V fish caught during September and October in the central North Sea could therefore be either autumn or winter spawners and there are data which support this possibility. Gilis (1954) gives maturation stages for August, September and October for fish caught in an area including the Great Silver Pit, the Easternmost Edge, Brucey's Garden, the Northwest Rough and the Middle Rough. An estimate for the duration of stage V from these data is about 40 days, which is almost three times that obtained for the Buchan and Minch spawners and indicates an admixture of fish with a longer stage V. It is possible to calculate from Gilis' data for August the expected distribution of maturation stages for September, on the assumption that all the fish are autumn spawners with similar durations of the stages to those of the Buchan fish. The expected percentage of fish above stage V for September is 75, whereas in fact 75% are stage V or below. From the September figures it is calculated that 87% would be in stage VI or above; in fact only 51% are. It could be argued that the Dogger spawners themselves have a long stage V (as do apparently the Manx autumn spawning fish) and that there is not necessarily an admixture of Channel fish, but the limited fecundity data available from Dogger fish support the view that Channel spawners in stage V do occur on the Dogger in September and October. Polder and Zijlstra (1959) examined stage V Dogger females in the years 1954-57 in the months of September and October. They assumed them to be Dogger spawners although they realised that this introduced some small

doubt as to their future spawning grounds. They found that the mean fecundity of the smaller fish approached that of the Southern Bight (Channel) fish, while that of the larger fish was similar to that of the Buchan fish, the overall fecundity being intermediate. Baxter and Hall (1960) referring to these data recognised two fecundity groups but assumed that both were Dogger spawners, and that therefore the Dogger spawners consisted of two components, one allied to the Southern Bight spawners and one to the Buchan spawners. It is suggested that the low fecundity Dogger V's are in fact Channel spawners and that the true Dogger spawners are much more homogeneous for fecundity. This can be tested in two ways. The high fecundity of the autumn spawners is associated with a small-sized egg. Baxter (1959) comparing the Buchan spawners with the Southern Bight fish found a difference in volume of 100% (on p.78 Baxter refers to a diameter difference of 25%, which is equivalent to a volume difference of 100% and not a "size" difference of 25%) for stage V. If this difference is reflected in the stage VI eggs then Dogger spawn should be much smaller in size than Channel spawn. Alternatively research vessel sampling on the Dogger should enable stage VI gonads (i.e. with translucent eggs, free within the ovary but not yet shed) to be studied for fecundity. Recent samples of Whitby fish in stage VI have included individuals with entire gonads even though eggs could be extruded by pressure.

It is important that the status of the Dogger stage V's and the Dogger spawners be determined with respect to fecundity. While it is accepted that the Dogger spawners belong to two fecundity groups it is not possible to differentiate between autumn and winter spawners, when and where they mix in the North Sea, on the basis of egg number; and this character, differing by a factor of 100%, would afford easily the best available separation on an individual basis.

Discussion

Any study of maturation is made more difficult by the variety of systems of classification in common use, and standardisation of staging techniques is a necessity. The most important stage to be accurately standardised is that at which the maturation cycle can be said to have begun for the current year, both for first time spawners and for fish maturing for a second or subsequent time. The variation of the time at which this occurs within a spawning stock, or for a length or age group within a spawning stock, is a main factor in determining the distribution of maturation stages at any subsequent time. The other factor, the duration of the stages themselves, can be evaluated from maturation data, provided of course that a good sampling programme gives representative samples of the population over the period that is being studied.

Although many of the conclusions drawn in this communication are to some extent affected by the possible differences in systems of maturity classification and the difficulties of identification of stocks, it is clear that a detailed study of the maturation cycle is needed, not only to determine the

extent to which maturation stages can be used to identify stocks and estimate proportions of stocks in mixed populations, but also for the light that can be thrown on factors influencing and controlling the interaction of the feeding, growth, maturation and spawning cycles. The differences between the phasing of the maturation cycles and the rate of maturation as between autumn and winter spawners in the North Sea are not as great as expected, and certainly not as great as the difference between the spawning times. On the other hand the rate of increase of gonad size is rapid in the later stages of maturation so that small differences in the maturation cycle can mean quite large differences in gonad size, and it may be possible, if sufficient is known of variation between for instance length and age groups, to use the distribution of maturation stages at particular times of year to derive estimates of mixing rates. This would be an advantage, as routine staging can give a much larger body of information than can say fecundity data, but a re-examination both of the staging and of the way that maturation data is presented in tables in official publications is necessary to begin with.

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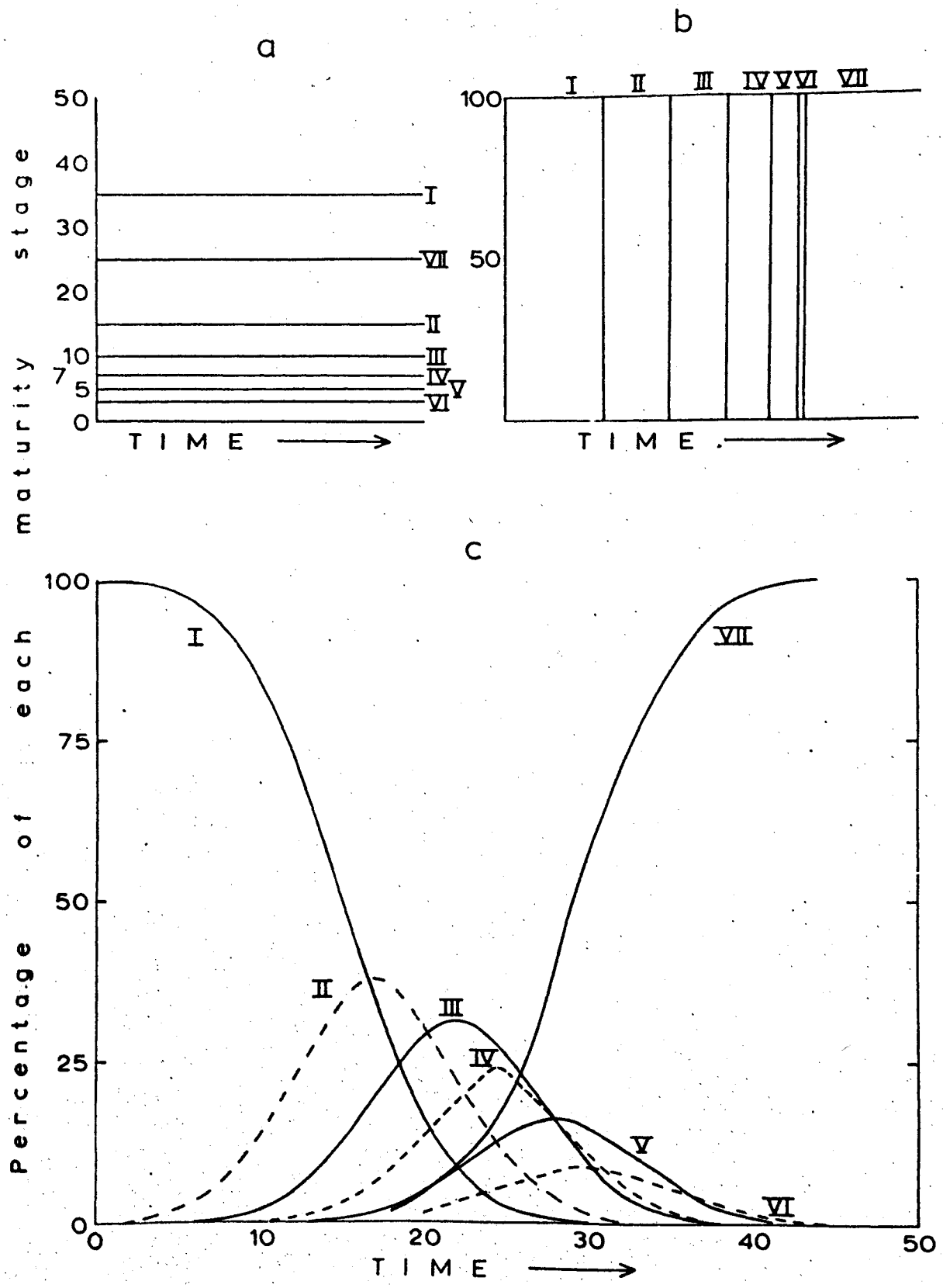

Figure 1 a b and c.
Theoretical distributions of maturation stages. (see text)

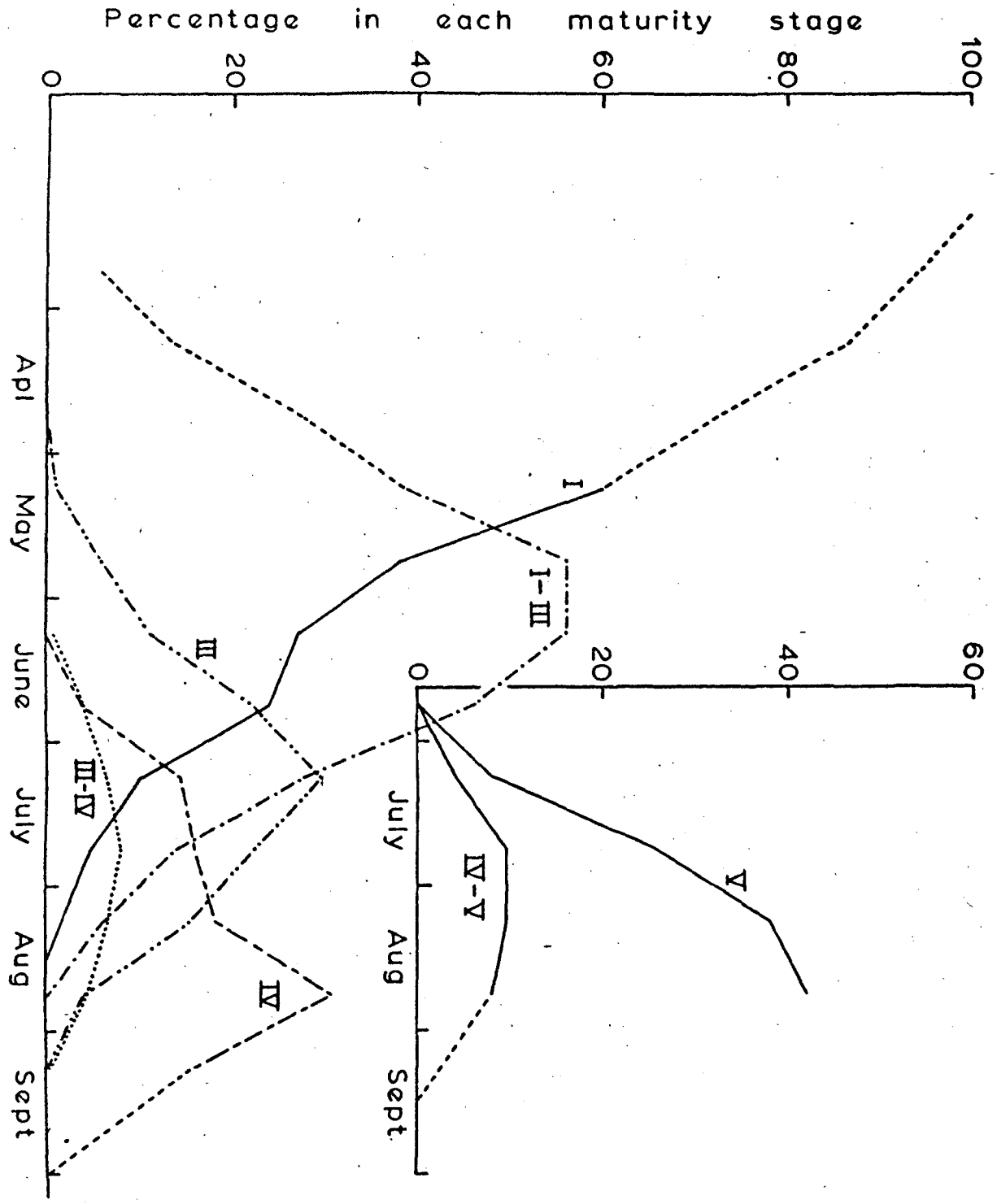

Figure 2

North Shields herring, 1954 and 1957-61. Males - percentages of maturation stages, in half-monthly periods.

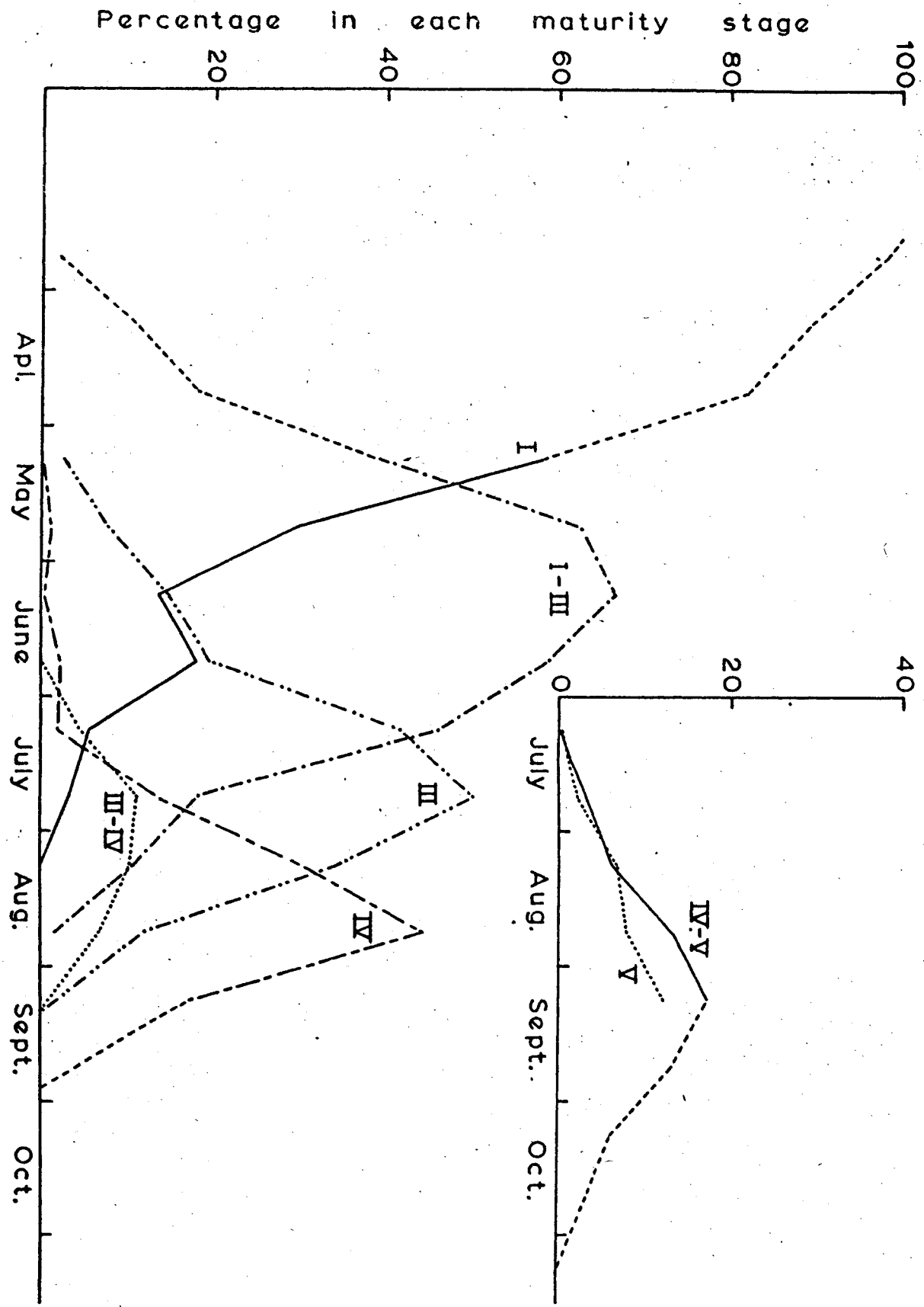

Figure 3

North Shields herring, 1954 and 1957-61. Females - percentages of maturation stages, in half-monthly periods.

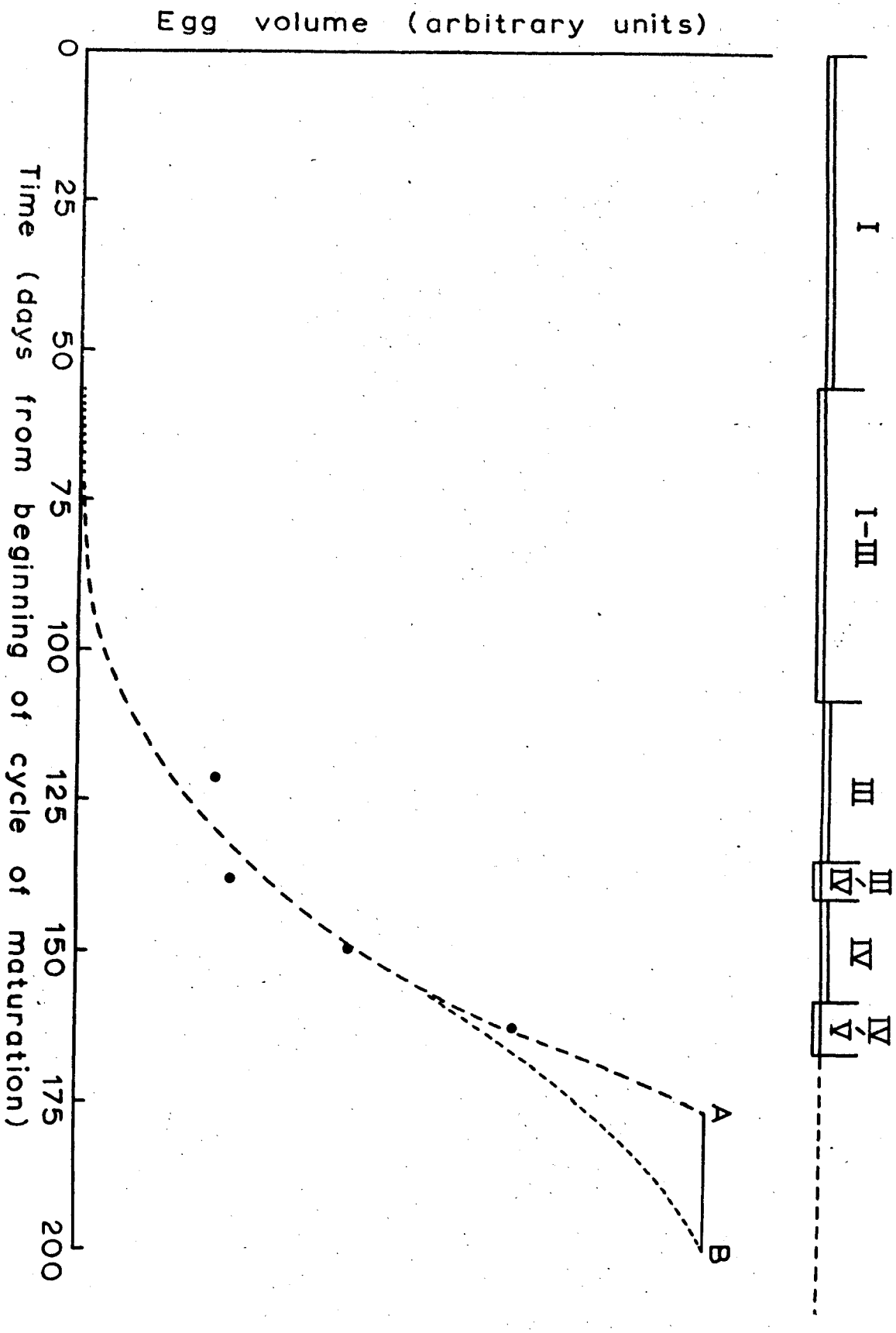

Figure 4

North Shields herring. Increase in egg volume with time (Egg data from A. D. Woodhead.)

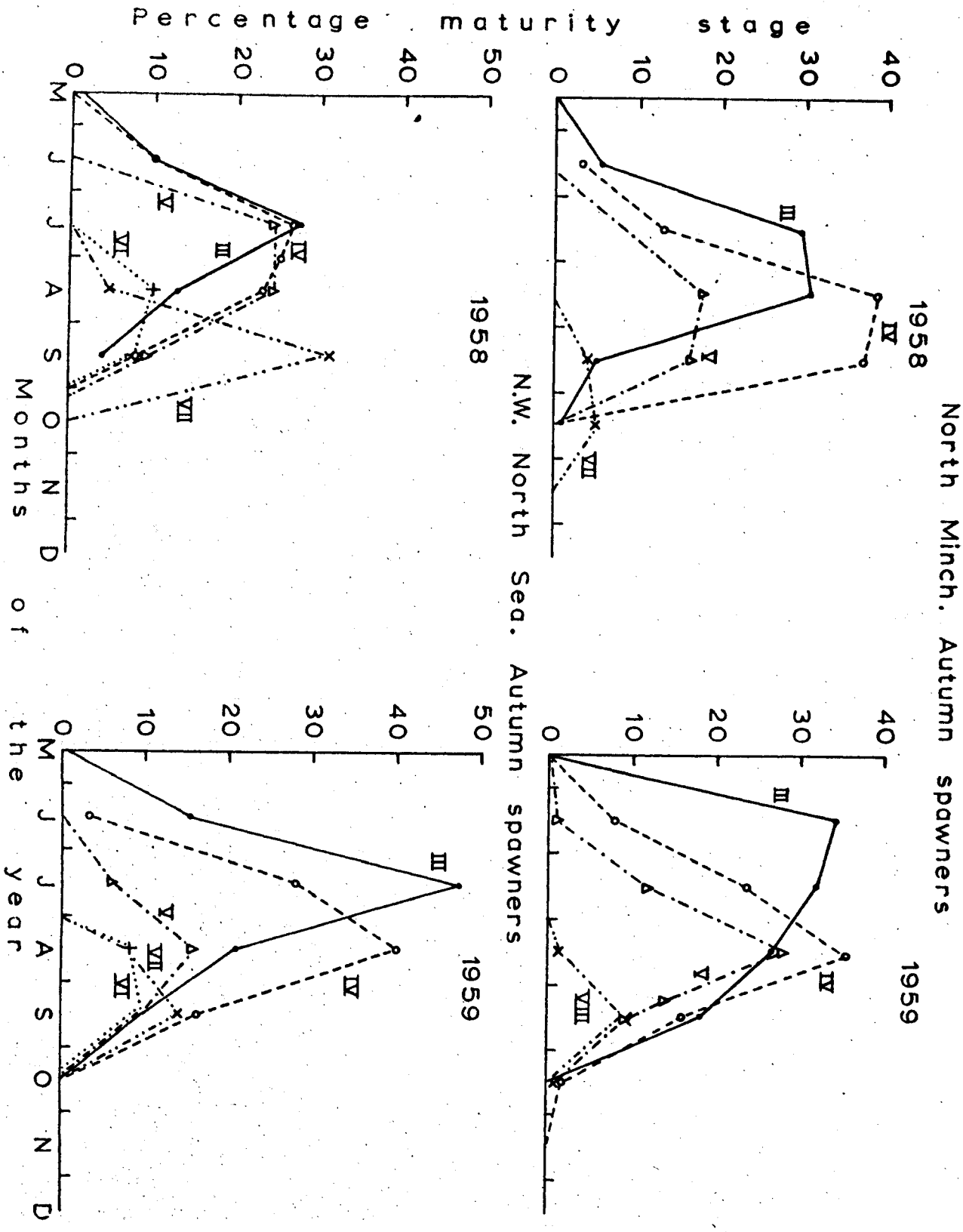

Figure 5

North-western North Sea and North Minch herring. 1958 and 1959. Percentages of maturation stages, at monthly intervals.

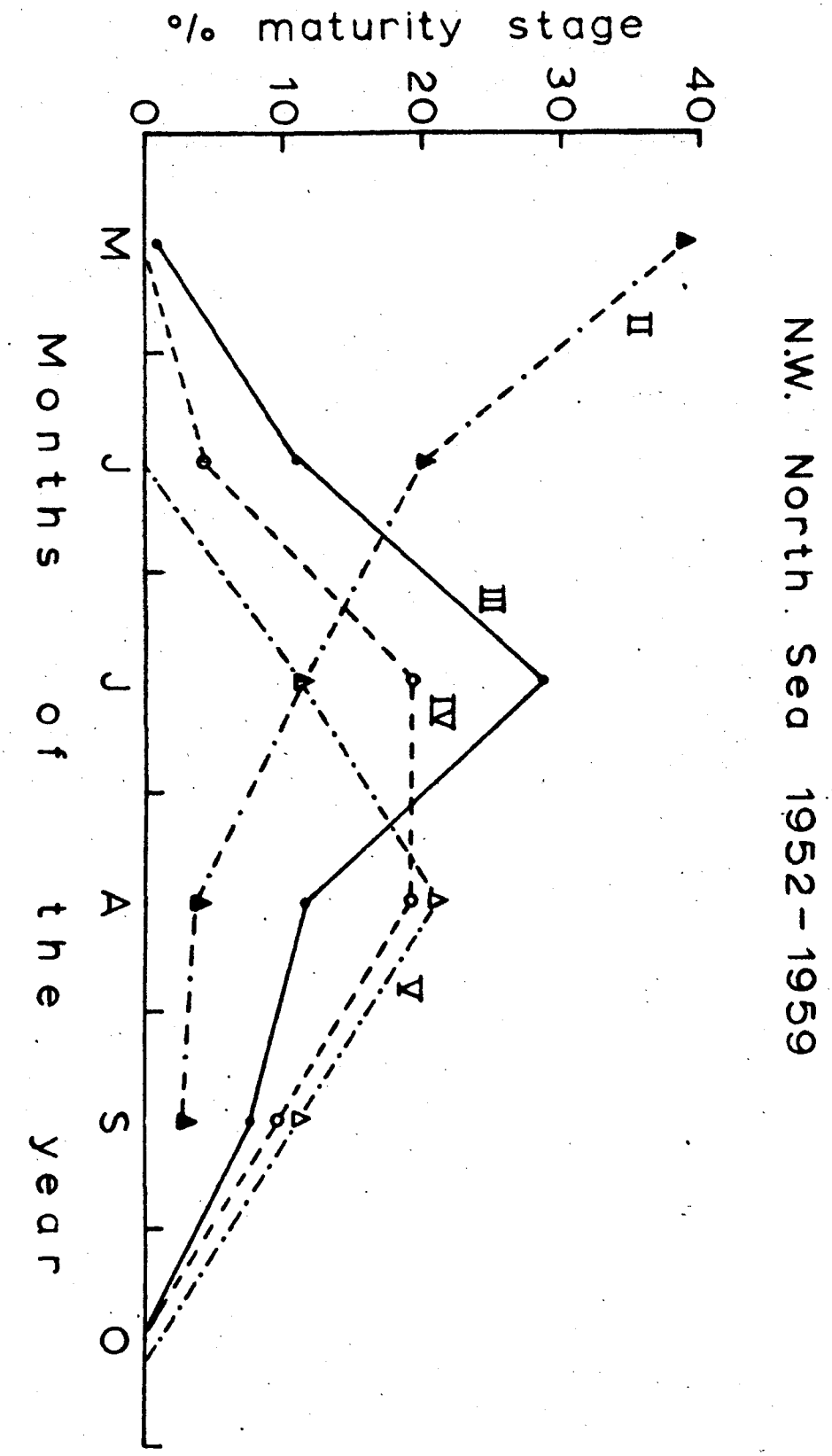

Figure 6

North-western North Sea herring, 1952-59. Percentages of maturation stages, at monthly intervals.