Flødevigen rapportser. 1, 1986. ISSN 0333-2594

A COMPARISON OF PRIMARY GROWTH RINGS IN OTOLITHS OF *SPRATTUS SPRATTUS* FROM NORWAY AND *SARDINELLA* SPP. FROM SRI LANKA

P. Dayaratne

Department of Fisheries Biology, University of Bergen, Norway

Present address:
National Aquatic Resources Agency, Crows Island, Colombo 15, Sri Lanka

ABSTRACT

Dayaratne, P. 1986. A comparison of primary growth rings in otoliths of *Sprattus sprattus* from Norway and *Sardinella* spp. from Sri Lanka. Flødevigen rapportser. 1, 1986: 23-47.

The present paper describes the otolith structure and the ring deposition pattern in 0-group sprat (*Sprattus sprattus*). This is compared with that of *Sardinella* from tropical waters. Age was estimated by using the primary growth rings in the otoliths and the estimated age was used to calculate the spawning time and to estimate growth.

Otolith structure and ring deposition were found to be similar in sprat and *Sardinella*. In sprats, the number and the thickness of the rings in the nuclear region seemed to vary with the time of spawning. This indicated a difference in the age of metamorphosis of sprat larvae. In *Sardinella*, however, the period of metamorphosis was shown to be a species-specific characteristic.

Back-calculated birth dates of sprat generally suggested a protracted spawning from February to July with a peak in April - June. Estimated spawning in Nordfjord (west Norway) is confirmed by the known spawning curves. The calculated spawning for other locations too, in genereal agrees well with the known spawning.

The resulted growth estimates of sprat with K = 0.82 corresponds to previous estimates. The results (growth and birth dates) verify the daily periodicity of rings. The similarity of the otolith structure of sprat to that of *Sardinella* and herring (*Clupea harengus*) also indirectly validates the hypothesis that the rings are formed daily.

INTRODUCTION

The presence of primary growth rings in otoliths of some tropical and temperate fishes was discovered in the early 1970's (Panella 1971, 1974). These rings seem to be formed daily and their daily periodicity has been verified for many species. A recent review showed that most of the studies aimed at verifying the daily nature of these rings have been successful (Gjøsæter et al. 1983). Since the list includes species from very different environments and geographical regions, it seems reasonable to assume that the daily incremental growth is a universal phenomenon in fish otoliths.

One of the advantages in otolith microstructural studies is the possibility to trace back the early life history of the fish. Several studies (Panella 1971, 1974; Brothers et al. 1976; Struhsaker and Uchiyama 1976, and others) suggest that in many species of teleosts, the otolith microstructure documents a detailed chronological growth history.

In temperate fishes, work has concentrated on larvae and juveniles. For short-lived tropical species, adults have been aged using daily growth rings too. Brothers et al. (1976) suggested that the method may be reliable at least up to an age of two hundred days.

As the pattern of rings seen in an otolith was basically similar in all the Clupeid species studied from Sri Lanka, this was taken as an indication that growth and ring formation in Clupeidae may follow a certain pattern characteristic of this family. The hypothesis of a fixed growth pattern in the Clupeidae has previously been advocated by Iles (1980).

To gain evidence for this hypothesis it was decided to compare the otoliths from Clupeidae from two different environments Sri Lanka with a tropical climate and Norway with temperate conditions.

The sprat *Sprattus sprattus* was selected as a Norwegian clupeid and *Sardinella* spp. from Sri Lanka, previously studied by Dayaratne and Gjøsæter (1986), was used for comparison.

Similarities between these species could be regarded as family characteristics as they were subjected to completely different environmental conditions. The present study also aims to verify the daily nature of these rings in *Sprattus sprattus*. This was attempted by comparing the calculated spawning season with the available spawning curve.

MATERIALS AND METHODS

The material for the present study was collected from the fjords and coastal waters along the west and south-east coasts of Norway. A total of about 380 specimens of sprat (*Sprattus sprattus*) from 12 different locations were studied. About 30 specimens of herring (*Clupea harengus*) from a single location were also examined. This sample was used to compare the otolith structure of a similar species from the same waters.

The material from station 2-6 (Fig. 1) was collected during a cruise with the R/V "Michael Sars" in October 1983. A pelagic trawl with a small meshed cod end was used. This material was made available to the author by Mr. Erling Bakken of the Institute of Marine Research, Bergen. The rest of the material, from station 7-12, was collected by beach-seines and was supplied by Ms. Else Torstensen of the Flødevigen Biological Station, Arendal.

More details about the material studied are given in Appendix 1. All the material was kept frozen.

In addition, the data on *Sardinella* spp. previously worked out by the author were used for comparison.

Length measurements of the fish were taken to the nearest millimetre and the otolith extraction was carried out under a binocular microscope.

The procedure used in the preparation of otoliths was the same as that described for *Sardinella* spp. (Dayaratne and Gjøsæter 1986). The otoliths from smaller fish were mounted directly on a synthetic mounting medium "Protexx" without grinding but a little grinding was found to increase the visibility in larger otoliths.

The countings of the total number of rings and the measure-

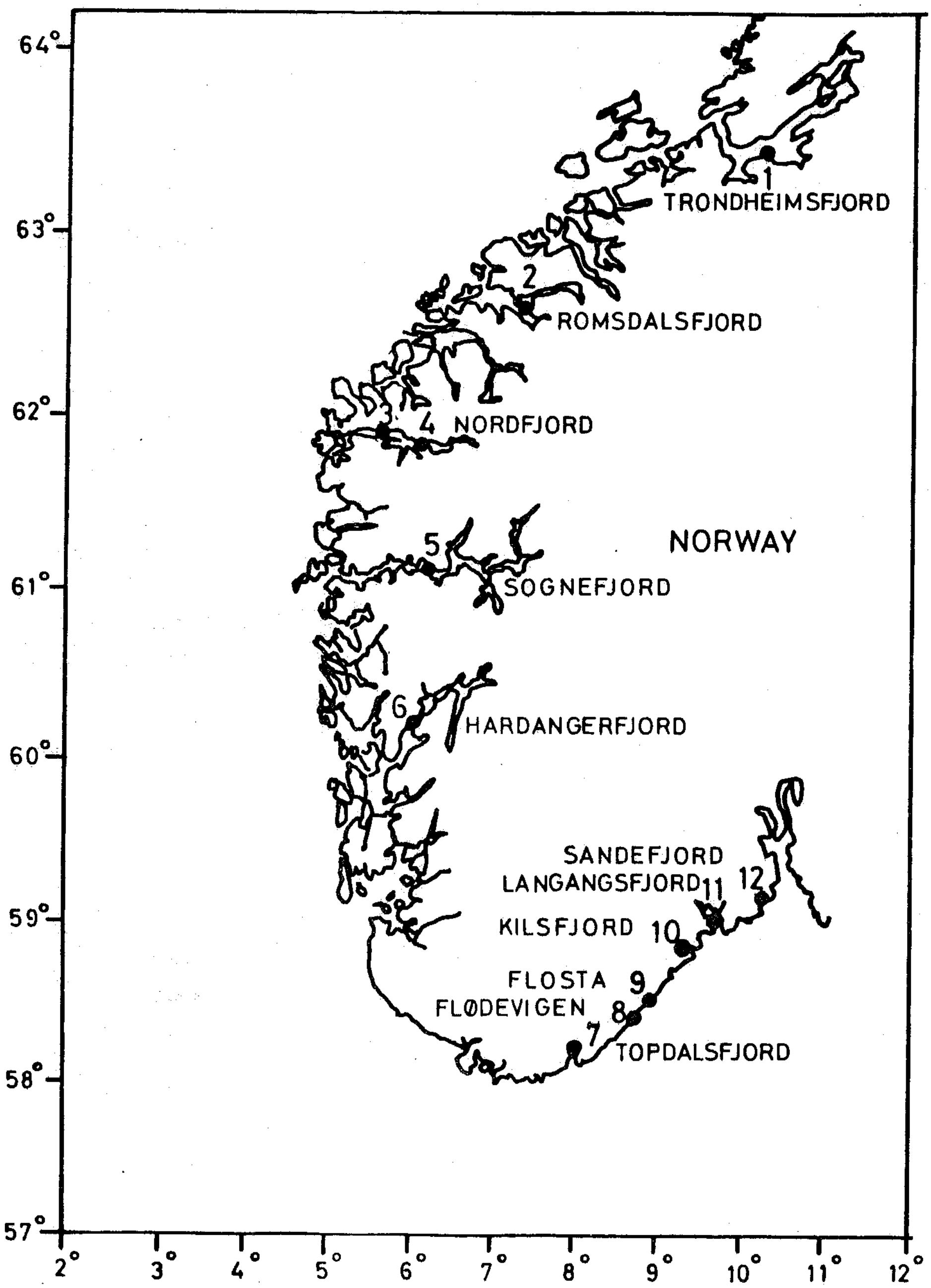

Fig. 1. Map showing the stations in southern Norway with numbers referred to in the text.

ments of the otolith radii were carried out under a light microscope at 400 magnification. In all the otoliths the measurements were taken along the longest axis, from the nucleus towards the posterior edge.

The number and radii of the rings in the nuclear region of about 10 otoliths from stations 1, 7, 10 and 12 were also recorded. These stations were selected as they showed some difference in the back-calculated spawning time. These measurements were used to compare the nuclear region within sprats and also between sprats and *Sardinella* spp. (Fig. 2).

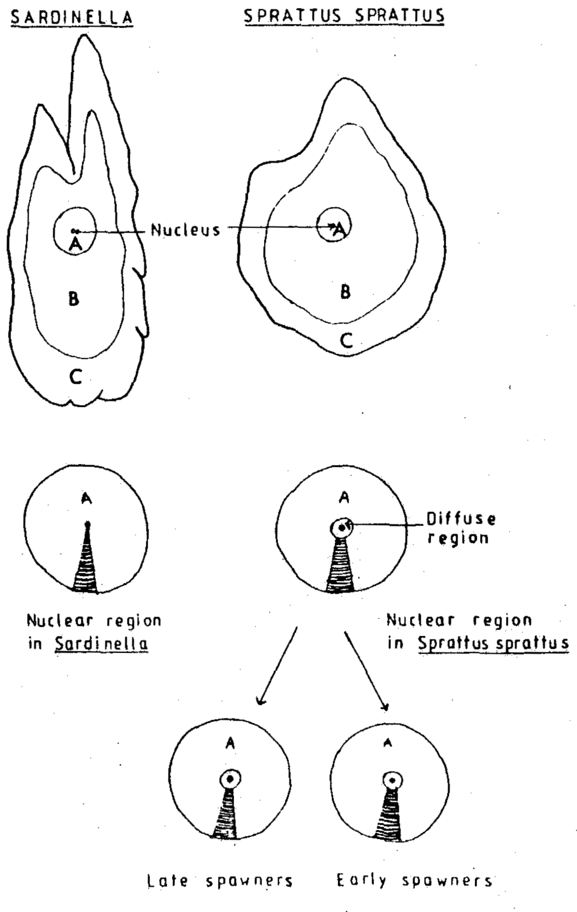

Fig. 2. Schematic drawings of *Sardinella* and sprat otoliths.

As the trial plots of the otolith radius against fish length indicated a linear relation, predictive regressions were fitted to these data. At first, separate regressions were fitted to data from different stations. No significant difference was found between the slopes, except for the one from station no. 2. As the deviation of this regression was explained by the poor fit of the data, all these stations were combined and a common regression was fitted (Fig. 3).

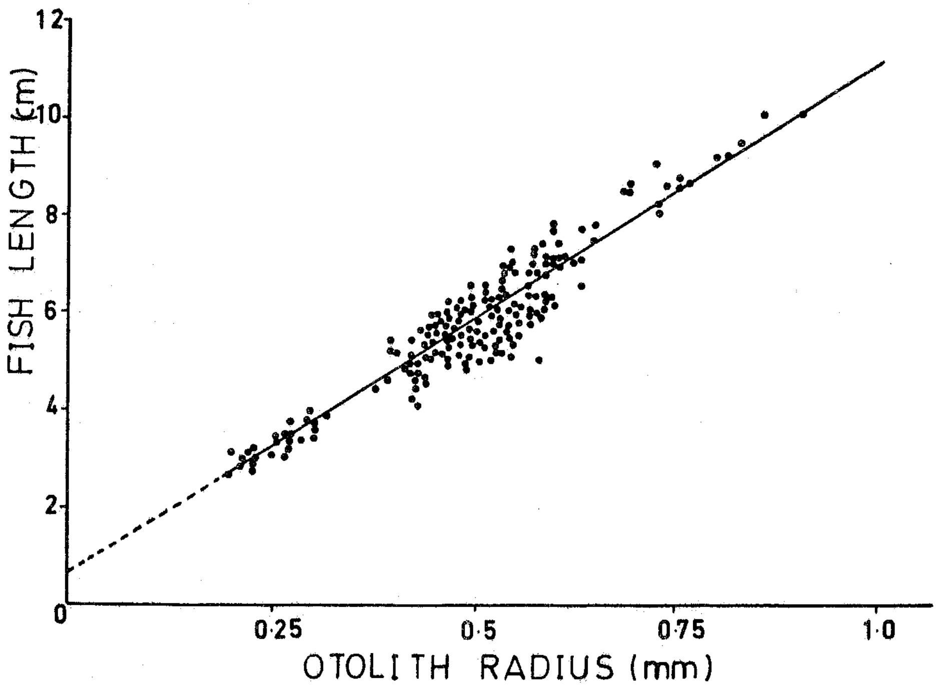

Fig. 3. Regression of fish length on otolith radius of sprat.

The growth estimates of sprat were carried out by assuming that the primary rings found in the otoliths are laid down daily. The estimated age for individual fish was plotted against the fish length. A von Bertalanffy growth equation - $L_t = L_\infty\ (1-e^{-(t-t_o)})$ was fitted to these data by using least squares method.

The estimated ages were used to calculate the birth dates, from the day on which the fish were caught. Examination of the otoliths showed that samples from station 6 contained both 0-group and I-group fishes. Only the 0-group fishes were used to estimate the age. However, the I-group samples were used to calculate the spawning season by counting rings from the nucleus up to the inner egde of the winter zone. The spawning periods of the two successive years were compared.

RESULTS AND DISCUSSION

Otolith structure of sprats and comparison with that of herring and *Sardinella*

The general otolith structure appears to be similar in sprat, herring and *Sardinella* spp. All these otoliths are antero-posteriorly elongated with two anterior rostra. The otoliths of sprats, however, are slightly widened along the dorso-ventral axis, making it more or less circular apart from the two anterior rostra. The herring otoliths are very similar to those of *Sardinella*.

The average otolith size of about 7-8 cm long fish of different species is as follows:

species	otolith size (length)
Sprattus sprattus	1.3 mm
Clupea harengus	2.2 mm
Sardinella spp.	1.3-1.6 mm (depending on the species)

A similar pattern of ring deposition was observed in the three species. Three regions, the nuclear region, the central region and the outer region could be distiguished as described for *Sardinella* spp. (Dyaratne and Gjøsæter 1986) (Fig. 2).

Interpretation of the differences observed in the otoliths of sprat and *Sardinella*

Detailed studies revealed that there are marked differences in the nuclear region of the otoliths of the two species. In *Sardinella*, distinct rings are deposited right from the centre of nucleus. In sprats, however, there is a diffuse region of about 12 µm radius around the nucleus, before any distrinct rings are deposited. There are about three faint rings within this diffuse region. This indicates a difference in the initiation of the ring deposition in the two species (Fig. 2).

According to Brothers et al. (1976) the daily increments begin to form at different ages in different species. Some species hatch with increments already formed, while others apparently to not form increments until later. In *Clupea harengus* the ring formation begins just after yolk sac absorption in about five days after hatching (Rosenberg and Lough 1977). Radtke and Dean (1982) suggested that embryos with long incubation period, form rings before hatching while those with short incubation period might not start ring formation until, or few days after hatching.

The differences seen in the nuclear region of *Sardinella* and sprat might be due to a difference in incubation period (John 1951, Thompson et al. 1981). The faint rings found within this region are probably formed during the incubation period. These interpretations, however, remain inconclusive as the time when increment formation begins is not known for any of these species.

The number of rings in the nuclear region too, differ in *Sardinella* and sprat. It was suggested by Dayaratne and Gjøsæter (1986) that for *Sardinella* this is a species-specific characteristic, with the number of rings varying from 14-28, depending on the species concerned. For sprat, however, it seems to vary from 20-55 depending on the time of the year in which they are born. Those that are born earlier seem to have a larger number of rings than those spawned later (Table 1).

It has also been suggested that the number of rings in the nuclear region of the otolith corresponds to the age at metamorphosis. If this is so, *Sardinella* spp. seem to have a distinct period of metamorphosis ranging from 14-28 days, depending on the species. For sprat, however, this period seems

Table 1

Number of rings and ring width in the nuclear region of sprat otoliths.

	Early spawners (spawn in February)			Late spawners (spawn in May-June)		
	N	Mean	S.D.	N	Mean	S.D.
Number of rings	20	55.3	6.7	20	2.17	3.0
Average ring width (μm)	10	1.36	0.01	10	3.24	0.03

to vary according to what time of the year they are born. Those born early in the spawning season seem to take a longer period (about 50-60 days) than those born later (ca 21 days) (Table 1). A probable reason for this could be the different temperatures prevailing at the beginning and the end of the rather extended spawning season of sprat. It is also possible that a difference in the availability of food during this period has some influence on the timing of metamorphosis.

At station 1 larvae of about 3-4 cm length were caught, and their external appearance suggested that they had not completed metamorposis. The otoliths of these larvae had fairly narrow rings and the central region corresponding to the fast growing period just after metamorphosis was not formed. The average otolith size of these larvae was about 0.25 mm which was larger than the usual radius of the nuclear region (0.09-0.15 mm) observed in other juveniles. This sample of larvae was collected on 30 October and it is unlikely that they would have metamorphosed later in the year when the winter begins. These larvae probably over-winter as larvae without metamorphosing. This evidence supports the suggestion of Iles and Johnson (1962) that not all sprat metamorphose before their first winter. Those spawned later seem to over-winter as larvae. Newly metamorphosed sprat of 3-4 cm have been recorded in the northwestern North Sea at the beginning of the spawning season. It seems more likely that they were derived from wintering larvae (Bailey 1980).

The ring width in the nuclear region also differs considerably according to the time of birth. Table 2 gives the ring width measurements of samples from a few stations where the samples were of fish with different spawning times.

Table 2

Ring width measurements in the nuclear region of sprat with the corresponding spawning time.

Station number	Back-calculated spawning time	Ring width (µm) N	Mean	S.D.
10	18 February	10	1.36	0.08
12	21 April	10	3.24	0.27
7	17 May	10	2.93	0.33
1	27 July	10	2.49	0.13

The highest mean ring width (station 12) was compared with the lowest (station 10). The resulting t value was 1.61, indicating that there is no significant difference between these values. Despite this, there is a trend for the early spawners (station 10) to have the lowest ring width and those born in the middle of the spring (station 7 and 12) to have the highest (Table 2). The late spawners in July (station 2) seem to have an intermediate value.

If the thickness of these primary rings are used as an indication of growth, those born in the middle of the spring (Table 2) seem to grow faster, at least during the first month of their life. Whether it is the time of spawning or any other environmental factor that causes this difference in growth is not clear, as these samples were taken from different locations.

In sprat the thickness of the rings in this region (mean 8 µm) is less than in *Sardinella* spp. (16-20 µm). The difference in L/R ratio alone does not explain this difference. This could be taken as an indication of a faster growth of

Sardinella when compared with sprat.

The outer region of the otolith of 0-group sprat is very similar to that of *Sardinella*. A gradual reduction in the width of the rings was observed with narrower rings near the outer edge. The otoliths from sprat longer than about 8.0 cm were found to contain the distinct winter zone. The primary rings could be seen up to the formation of the first winter zone. Although similar rings were seen in the second fast-growing period they were rather narrow and some were barely visible under x 400 magnification.

The above description shows that in general the otolith structure and ring deposition pattern are similar in sprat, herring and *Sardinella* spp. This seems to indicate a similarity in the growth pattern. As these species are from completely different environments this common feature could probably be an inherited characteristic of clupeiodes.

Fish length versus otolith radius

Sprattus sprattus

Table 3 shows the results of the regression analysis of fish length/otolith radius for different stations. The results of the analysis of covariance to compare the slopes and the intercepts of these regressions for different stations are as follows:

F (slope) = 3.06 N = 352

F (elevation) = 57.49 K = 12

F value (3.06) indicated a significant difference between the slopes. A Newman Keuls test showed that only the slopes of station 2 and 6 were different from one another. This difference, however, was not taken into consideration as the regression of station 2 was not very satisfactory as indicated by the low correlation coefficient and a high value for the intercept.

Therefore, in spite of this difference of slope for station 2, the data from all the stations were combined and a common regression was fitted:

$$L = 10.13 R + 0.92$$

where L = fish length in cm, and R = otolith radius in mm (Fig. 3). The coefficient of determination was $r^2 = 0.78$.

Table 3

Fish length - otolith radius relation in *Sprattus sprattus*. Parameters of the predictive regression L = bR + a, where L = fish length in cm, R = otolith radius in mm, a = elevation, b = slope.

Station number	Number of individuals	Slope	Elevation	Coefficient of determination
1	28	8.67	1.10	0.86
2	36	4.99	3.50	0.49
3	34	10.30	1.47	0.93
4	34	9.63	1.67	0.89
5	26	9.99	1.47	0.74
6	36	10.99	0.50	0.98
7	26	8.19	1.61	0.71
8	36	8.67	1.40	0.66
9	24	10.56	0.66	0.72
10	24	5.99	3.38	0.49
11	40	7.56	1.69	0.64
12	32	10.29	0.02	0.79

Clupea harengus

The data available for herring were rather scarce, but still a linear regression was fitted to compare the results with that of sprat. The values obtained for the regression are as follows:

$$L = 5.59\ R + 1.66 \qquad N = 31$$
$$r^2 = 0.78$$

Comparison of fish length - otolith radius relation of sprat, herring and *Sardinella*

Table 4 gives the results of regressions of fish length versus otolith radius for the different species. Comparison of the slopes of the regressions of sprat and herring showed that there is a highly significant difference between these two species ($t = 27.07$, $DF = 403$). The slopes of the regressions of the three *Sardinella* spp. were shown to be different from one another (Dayaratne and Gjøsæter 1986). Therefore, the regres-

Table 4

Results of the regressions of fish length (cm) versus otolith radius (mm) of different species.

Species	Value of the slope	Coefficient of determination	Number of samples
Sprattus sprattus	10.1	0.78	374
Clupea harengus	5.6	0.58	31
Sardinella sirm	11.5	0.84	57
Sardinella albella	10.7	0.92	59
Sardinella gibbosa	14.9	0.92	60

sion of *Sardinella albella* which had a value of slope closest to that of sprat was used for comparison. The resulted t value ($t = 20.9$, $DF = 424$) indicates that even these two slopes are significantly different. Therefore, it can be concluded that all the species studied had different slopes for the fish length otolith radius relationship. This means that the increase in otolith size for a unit increase in fish length is different. This could probably be a species-specific characteristic.

These results should, however, be considered tentative as the regressions were based mostly on large size groups. Even for sprat, larvae smaller than 2.7 cm were not available. Therefore, the extrapolation of the observed linear relation to larvae may not be accurate.

Length at age data

The age of the fish was tentatively estimated by counting primary growth rings, and assuming that they are formed daily (Fig. 4). At most stations the variation in age was small (Table 5). Although stations 2, 3 and 4 gave similar mean lengths, there was a remarkable difference in age. (Fig. 5). Fish from station 2 were older than those from station 3 and 4 and therefore had a lower growth rate. Fish from station 9 and 11 also had the same mean length, but different age.

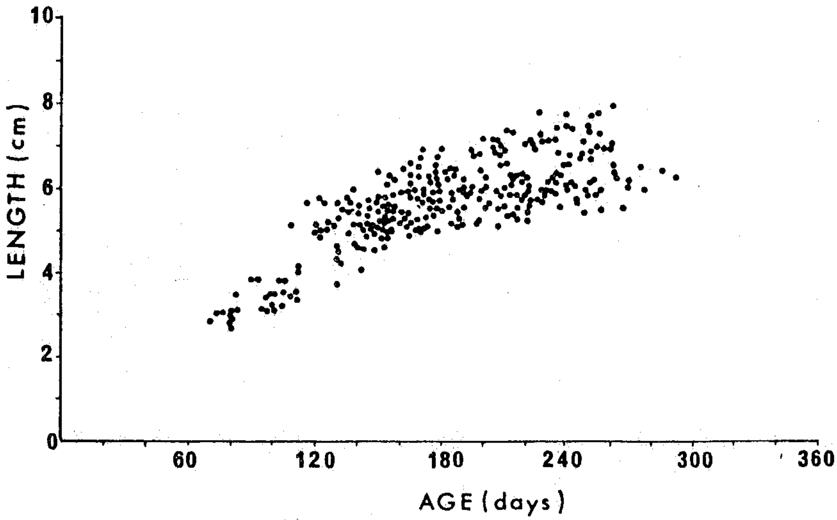

Fig. 4. A plot of the estimated age versus fish length of sprat.

Table 5

The mean lengths and the estimated ages of different samples.

Station number	Number of individual	Length (cm) Mean	S.D.	Estimated age (days) Mean	S.D.
1	30	3.3	0.4	96	14.3
2	36	6.0	0.3	237	25.3
3	34	6.4	0.9	183	41.6
4	34	6.2	0.8	184	39.0
5	27	6.7	0.7	204	38.8
6	21	5.9	0.6	194	22.1
	18	8.8	0.7	203	12.8*
7	22	5.3	0.4	133	15.6
8	41	5.3	0.4	157	13.0
9	23	5.7	0.4	167	16.1
10	25	6.9	0.4	217	22.1
11	40	5.7	0.3	214	43.4
12	29	5.4	0.5	159	16.5

* age estimated up to the winter zone

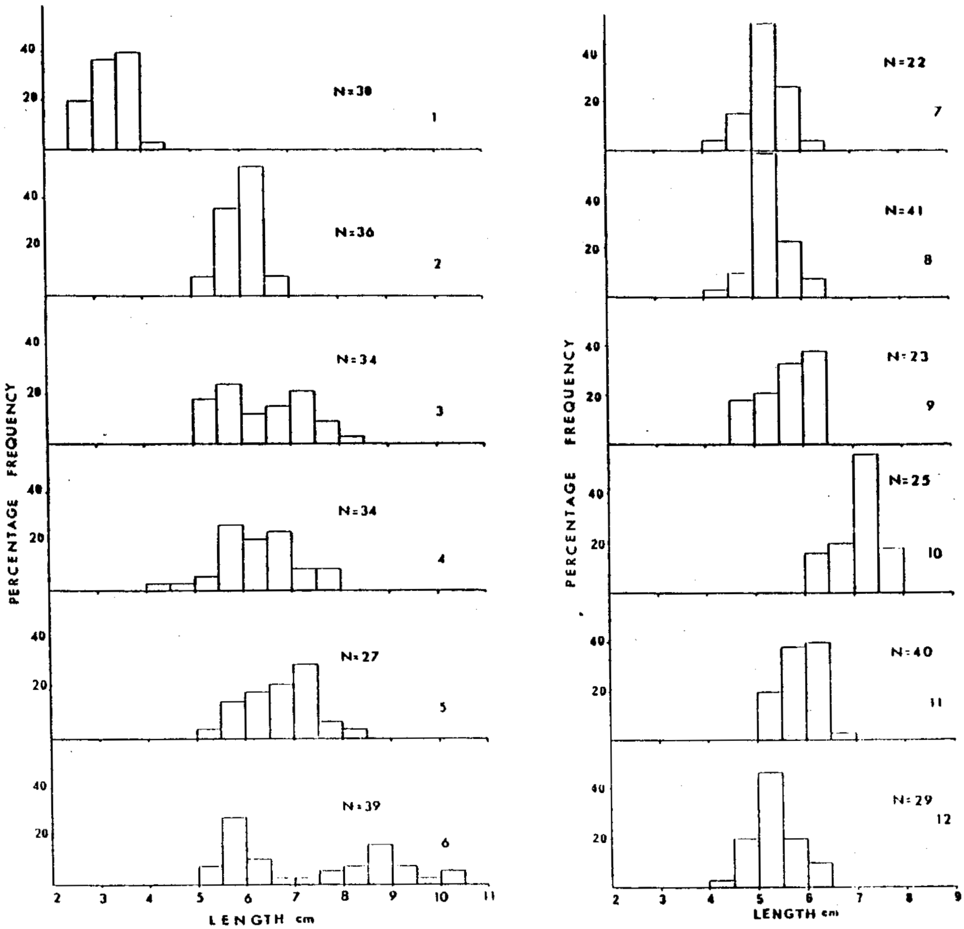

Fig. 5. Length frequency distribution of sprat.

These differences could partly be due to bias in ageing. Some of the differences could also be explained as geographical variations. Finally, the protracted spawning period for sprat (Johnson 1970, Grainger and Woodlock 1981) combined with a tendency to school by size (Freon 1983) could be expected to give effects like those observed with samples with a narrow size range giving highly viariable age.

Comparison of growth estimates of sprat with that of *Sardinella* spp.

A plot of the estimated age versus length of all the sprat samples is shown in Fig. 4. As only a fraction of the size and age range was available, attempts to fit a von Bertalanffy growth curve directly to the data were not satisfactory. A more reasonable fit was obtained by assuming L_∞ to be 14.0 cm (Grygiel 1978, Johnson 1970, Wilson 1979). When a fixed L_∞ value was used it resulted in a K value of 0.82. This seems to be a rather reasonable estimate and could be compared with the available estimates which could be summarized as follows:

Source	von Bertalanffy growth parameters	
	K	L_∞ (cm)
Johnson (1979)	0.53	13.2
Grygiel (1978)	0.61 - 0.88	13.9 - 15.4
Wilson (1979)	0.62 - 1.07	13.7 - 15.2

The main purpose of estimating these growth parameters was to compare them with those of *Sardinella* and these estimates are accurate enough for this purpose.

Table 6 shows the growth parameters for the three *Sardinella* spp. (Dayaratne and Gjøsæter 1986) and the current estimates for *Sprattus sprattus* which were all estimated by counting the primary growth rings in the otolith. *S. albella* and *S. gibbosa* seem to attain a maximum length of about 13-14

Table 6

von Bertalanffy's growth parameters of *Sardinella* spp. and *Sprattus sprattus*.

Species	L_∞ (cm)	K (year)
Sardinella sirm	22.0	3.7
Sardinella albella	13.8	2.03
Sardinella gibbosa	14.1	3.49
Sprattus sprattus	13.0	0.82

cm which is not different from that of sprat. Yet they seem to have quite different growth rates. According to the current estimates sprat seem to attain a length of about 7-8 cm (largest size observed) in about 8 months. These fishes were born early in the year, and those born later in the year probably over-winter as larvae as they are too late to metamorphose before the winter (Iles and Jonhson 1962). Therefore, for sprat, the growth within the first few months of life depends strongly on the time at which they are hatched. This shows the effect of the changing environmental conditions on the growth of clupeoids in temperate waters.

Sardinella albella and *S. gibbosa* attain the same length in about 3-4 months. Even though the spawning of these species too is affected by the changes in the environmental conditions (such as monsoonal changes), it seems unlikely that their growth is so much affected and delayed by these changes.

Spawning season

The age estimated by counting the primary growth rings in otoliths was used to back-calculate the birth-date of the individual fish. Fig. 6 shows the frequency distribution (weekly) of the birth-date for each station. It seems that sprat have a protracted spawning period extending from February to July. The majority of samples, however, showed spawning during March-May. Those from st. 1 had a rather late spawning with a peak in July-August. They were probably from a local spawning within the fjord. Calculated spawning for st. 3 and 4 is somewhat similar, showing a bimodal distribution (Fig. 6). They seem to have one mode in March and another in May-June. The other stations on the west coast (st. 2 and 6) seem to have more extended spawning. Those from the south and southeast coast (st. 7-10) are not particularly protracted. However, samples from st. 11 have shown an extended spawning from the beginning of February to the beginning of May.

The specimens from st. 6 were found to contain individuals from two year-classes. They were separated as 0-group and I-group sprat after examining the otoliths. The spawning time

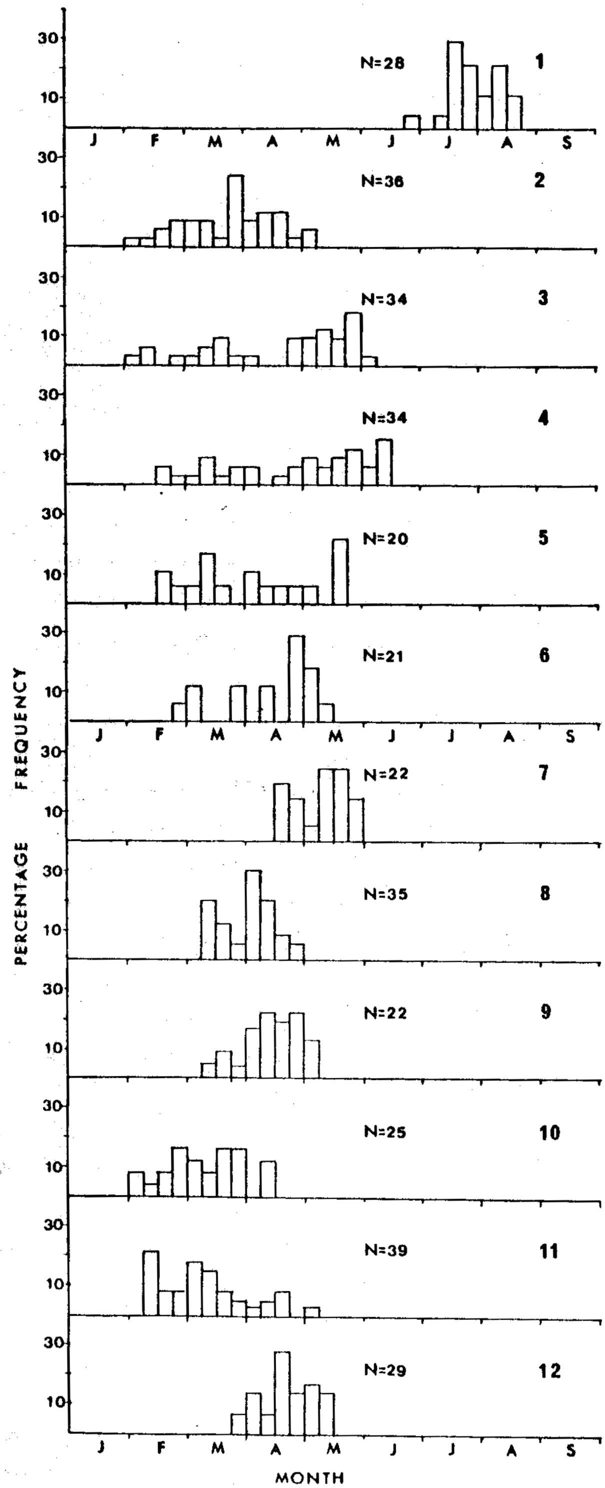

Fig. 6. Percentage frequency distribution of the back-calculated birthdates, grouped in weekly intervals.

of I-group individuals was calculated by counting the primary growth rings up to the formation of the winter rings (Fig. 7) which are assumed to appear around the first of November (Wilson 1979).

No particular trend in the timing of spawning was observed from north to south. Nevertheless, the northernmost station (st. 1) had a later spawning than those from the south (st. 7-9). This could probably be related to the water temperature at the time of spawning. There is evidence that sprat in the North Sea spawn earlier in the south than in the north (Bailey and Braes 1976).

It is not clear whether all the individuals from a single

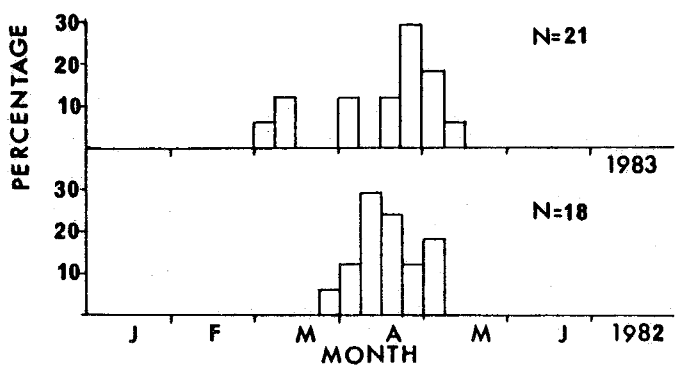

Fig. 7. Calculated spawning for 0-group and I.group fish from st. 6.

station are from the same spawning population. According to Lindquist (1978), the sprat in the Norwegian fjords stem mainly from the Skagerrak spawning area. These larvae have drifted along with the prevailing currents and there is probably an influx of larvae into the fjords. Also, there is evidence of local spawnings within the fjords (E. Bakken, pers. comm.). Therefore, the samples collected could be a mixture of influx larvae and those spawned within the fjord itself.

Spawning of sprat in Skagerrak and the Kattegat (northeastern North Sea)area seems to have a peak in April-June (Lindquist 1978). The peak spawning at st. 7-9 is almost the same as in Skagerrak and Kattegat. Therefore, the origin of the sprat at st. 7-9 could probably be the Skagerrak area. This is reasonable as these stations are nearer to the spawning area and there are prevailing currents in this direction. However, the reason for the extended spawning season for st. 10 which is not far from st. 7-9 (Fig. 1) remains unclear. Estimated spawning for st. 11 (Fig. 6) is supported by the available evidence. According to Dahl et al. (1983), sprat eggs are found in the Langesund area from February to June with a peak during April-June.

Bimodal distribution in spawning frequency for st. 3 and 4 is supported by the otolith microstructure. These otoliths had two types of rings in the nuclear region, suggesting a difference in time of spawning. Egg and larval surveys in Nordfjord in 1983 had shown an extended spawning with a higher peak at the beginning and another lesser peak during the later part of June (Torstensen 1984). Spawning was also observed in March (Torstensen pers. comm.). The present estimates also showed an extended spawning with a higher peak at the beginning of June and another lesser one in March. Spawning in late June was not observed in the present analysis. It could be that those who spawned later were too small to be caught by the sampling gear.

Spawning season estimated by using 0-group and I-group fish from st. 6 showed that there was not much difference in the spawning time in two successive years (Fig. 7). The age estimates of I-group samples are, however, not very reliable as the exact time at which the winter ring formed was not known.

Evidence for daily periodicity of the primary rings in sprat otolith

In general, the estimated spawning season of sprat seems to fit well with the known spawning (Johnson 1970, Baily 1979, Grainger and Woodlock 1981, Lindquist 1978, Hill and Dickson 1978). The early spawning observed at st. 11 is well supported by the results of egg and larval surveys which had been carried out over a period of time (Dahl et al. 1983). The bimodal distribution of the spawning time in Nordfjord (st. 3 and 4) is confirmed by the abundance of eggs and larvae during the same spawning season (Torstensen 1984 and pers. comm.). The calculations of the spawning season were based on the age estimates. As the age estimates were carried out by using the primary growth rings in the otoliths, the above results support the daily periodicity of the rings in sprat.

As the material used for the present study were all juveniles, it was not possible to get reliable growth estimates for sprat. However, the resulted values are not contrary to the available growth estimates.

The structure and pattern of ring deposition in sprat is very similar to that of herring and *Sardinella*. Previous studies on herring (*Clupea harengus*) have validated the daily nature of the primary rings (Rosenberg and Lough 1977, Gjøsæter 1981) although some results are contradictory (Geffen 1981). The daily periodicity of these rings has also been verified for *Sardinella* spp. (Dayaratne and Gjøsæter 1986). The similar otolith microstructure of all these species therefore gives more confidence in the hypothesis that the primary rings in sprat otoliths are formed daily.

CONCLUSION

The otolith structure and the pattern of primary growth ring deposition of the clupeids from tropical and temperate waters seem to be similar. This indicates that all these species studied follow the same pattern of growth. As these species are from extremely different environments, the observed similarities probably reflect characteristics typical of clupeids. The differences observed in the nuclear region in sprat otoliths suggests that the onset of metamorphosis is determined by environmental factors.

The early life history of sprat seems to be affected by the changing environmental conditions. As most of the larvae born later in the year seem to over-winter as larvae, the study of otolith microstructure would be useful to get an accurate estimate of age, especially when annual rings are used. However, more detailed studies on this aspect are needed befor firm conclusions can be drawn.

ACKNOWLEDGEMENTS

I wish to place on record my gratitude to Dr. Jakob Gjøsæter, Flødevigen Biological Station, for his valuable guidance throughout the preparation of this paper.

Discussions with Mr. Erling Bakken of the Institute of Marine Research, Bergen, were invaluable. I owe him a particular debt for providing some of the material used for this study.

Ms. Else Torstensen of Flødevigen Biological Station deserves special thanks for collecting sprat samples and providing useful information. She also gave valuable comments to the manuscript.

Thanks are also due to NORAD for giving me a fellowship making my studies in Norway possible.

REFERENCES

Bailey, R.S. 1980. Problems in the management of short lived pelagic fish as exemplified by North Sea sprat. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 177: 477-488.

Bailey, R.S. and Braes, A. 1976. Preliminary observations on the maturation cycle and fecundity of sprats in the northwestern North Sea. Coun. Meet. int. Coun. Explor. Sea 1977 (H:32):

Brothers, E.B., Mathews, C.P. and Lasker, R. 1976. Daily growth increments on otoliths from larval and adult fishes. Fish. Bull. U.S., 74: 1.8.

Dahl, E., Torstensen, E. and Tveite, S. 1983. Fiskeribiologiske undersøkelser i Langesundsområdet 1974-1978. Flødevigen rapportserie 1, 1983:

Dayaratne, P. and Gjøsæter, J. 1986. Age and growth of four *Saridnella* spp. from Sri Lanka. Fisheries Research, 4: 1-33.

Freon, P. 1983. Body length variability in fish schools and cohorts, application to fisheries biology in tropical waters. In: Sharp, G.D. and Csirke, J. (Editors), Proceedings of the Expert Consultation to examine changes in abundance and species of neritic fish resources. San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep., (291)3: 557-1224.

Geffen, A.J. 1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Mar. Biol., 71: 317-326.

Gjøsæter, H. 1981. Dagsonelesing som metode i aldersstudier på fisk, med anvendelse på tropiske og boreale arter. Thesis, University of Bergen, Norway,

Gjøsæter, J., Dayaratne, P., Bergstad, O.A., Gjøsæter, H., Sousa, M.I. and Beck, I.M. 1983. Ageing tropical fish by growth rings in the otoliths. FAO Fish. Circ., 776: 1-54.

Grainger, R.J.R. and Woodlock, J. 1981. Sprat egg surveys off the south coast of Ireland in 1980. Coun. Meet. int. Coun. Explor. Sea, (H:43):

Grygiel, W.J. 1978. Growth pattern of the sprat caught in the southern Baltic in 1974-1977. Coun. Meet. int. Coun. Explor. Sea, (J.12):

Hill, H.W. and Dickson, R.R. 1978. Long term changes in North Sea hydrography. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 310-334.

Iles, T.D. and Johnson, P.O. 1962. The correlation table analysis of sprat (*Clupea sprattus* L.) year-class to separate two groupes differing in growth characteristics. J. Cons. Perm. int. Explor. Mer, 27: 287-303.

John, M.A. 1951. Pelagic fish eggs and larvae of the Madras coast. J. Zool. Soc. India, 3: 41-69.

Johnson, P.O. 1970. The wash sprat fishery. Fishery Invest. Lond., Ser. 2, 26(4): 77 pp.

Lindquist, A. 1978. A century of observations on sprat in the Skagerrak and the Kattegat. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 187-196.

Nævdal, G. 1981. Further studies on blood protein polymorphism in sprat. Coun. Meet. int. Coun. Explor. Sea, (H:65): 160-182.

Pannella, G. 1971. The otoliths: Daily growth layers and periodical patterns. Science, 173: 1124-1127.

Pannella, G. 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In: Bagenal, T.B. (Editor), The ageing of Fish. Unwin Brothers Ltd. Old Woking, England: 28-39.

Radtke, R.L. and Dean, J.M. 1982. Increment formation in the otoliths of embryos, larvae and juveniles of the mummichog, *Fundulus heteroclitus*. Fish. Bull. U.S., 80(2): 201-215.

Robertson, J.A. 1938. The sprat and the sprat fishery of England. Fish. Invest. Lond. Ser. 2, 16(2): 103 pp.

Rosenberg, A.A. and Lough, G.R. 1977. A preliminary report on the age and growth of larval herring (*Clupea harengus*) from daily growth increments in otoliths. Coun. Meet. int. Coun. Explor. Sea, (L:20): 1-16.

Struhsaker, P. and Uchiyama, J.H. 1976. Age and growth of the Nehu, *Stolephorus purpureus* (Pisces: Engraulidae) from the Hawaiian islands as indicated by daily growth increments of sagittae. Fish. Bull. U.S., 74: 9-16.

Torstensen, E. 1984. Sprat spawning in two fjord areas of western Norway in 1982 and 1983. Coun. Meet. int. Coun. Explor. Sea, (H:41):

Townsend, D.W. and Graham, J.J. 1981. Growth and age structure of larval Atlantic herring, *Clupea harengus harengus*, in the Sheepscot river estuary as determined by daily growth increments in otoliths. Fish. Bull. U.S. 79: 123-130.
Wilson, J.P.F. 1979. Length and age composition and back-calculated growth rates of sprats in Scottish waters. Coun. Meet. int. Coun. Explor. Sea, (H:39):
Zar, J.H. 1974. Biostatistical analysis. Prentice Hall Inc. Englewood Cliffs, N.J., 620 pp.

Appendix I

Details of the studied material

Station number	Location	Date of collection	Number of fish	Length range (cm)
1	Trondheimsfjord	31.10.83	30	2.7-4.0
2	Romsdalsfjord	27.10.83	36	5.2-6.6
3	Nordfjord (Hyen)	24.10.83	34	5.2-8.1
4	Nordfjord (Føryset)	24.10.83	34	4.8-7.8
5	Sognefjord	23.10.83	27	5.4-8.0
6	Hardangerfjord	21.10.83	39	5.3-10.2
7	Topdalsfjord	15.09.83	22	4.2-6.1
8	Flødevigen	02.09.83	41	4.5-6.1
9	Flosta	08.09.83	23	4.7-6.2
10	Kilsfjord	22.09.83	25	6.2-7.8
11	Langangsfjord	23.09.83	40	5.2-6.7
12	Sandefjord	25.09.83	29	4.1-6.2
	Eidangerfjord*	23.09.83	31	4.9-6.4

St. 1-12 sprat samples
* herring samples