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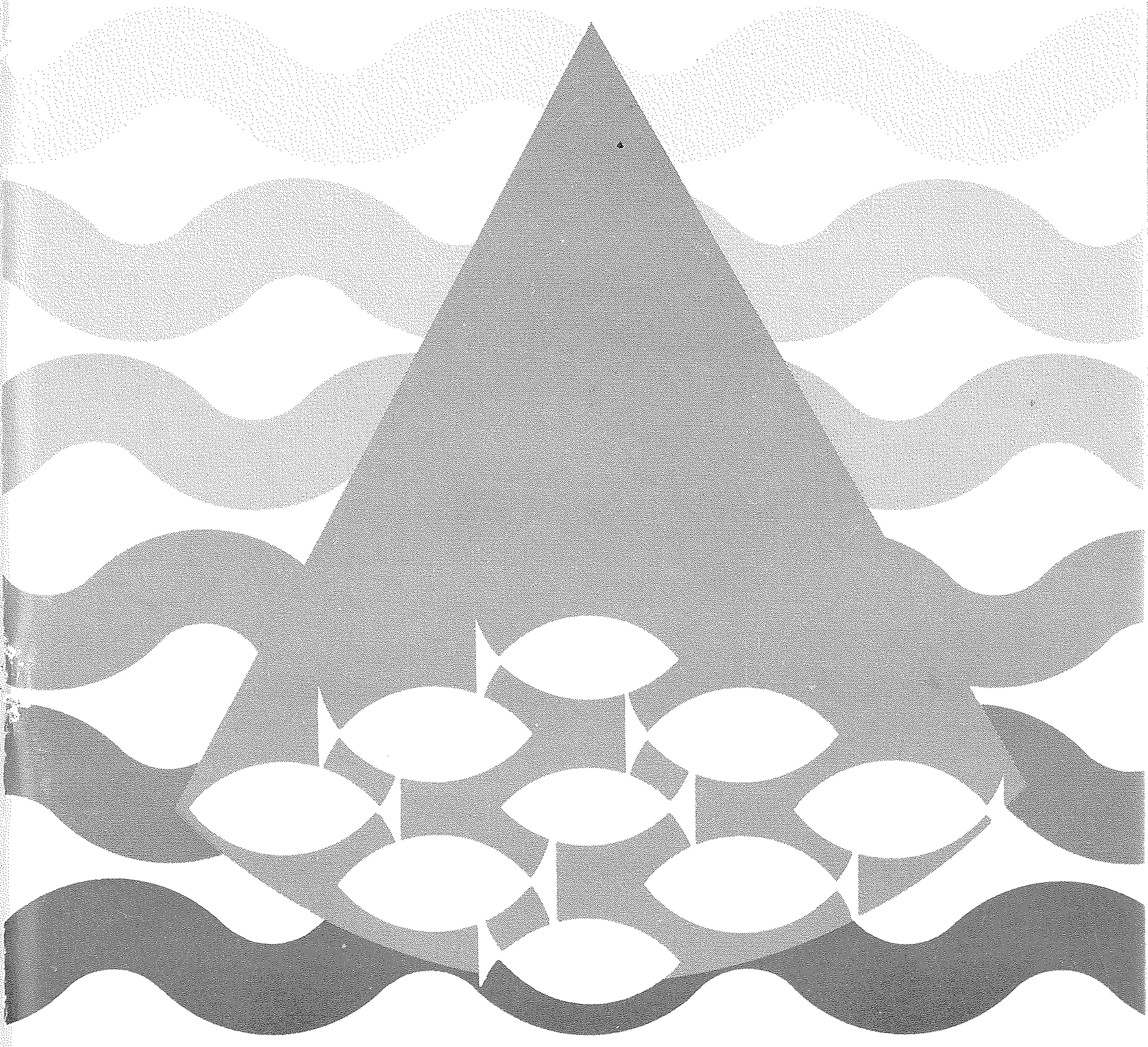

DIRECTORATE OF FISHERIES, BERGEN, NORWAY
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ASPECTS OF THE LIFE HISTORY OF THE LOCAL HERRING STOCK IN LINDÅSPOLLENE, WESTERN NORWAY

By
ULF LIE
Institute of Marine Biology, University of Bergen,
ODDVAR DAHL and OLE J. ØSTVEDT
Institute of Marine Research, Directorate of Fisheries, Bergen

ABSTRACT

LIE, U., DAHL, O. and ØSTVEDT, O. J. 1978 Aspects of the life history of the local herring stock in Lindåspollene, western Norway. *Fisk.Dir. Skr. Ser. Hav.Unders., 16*: 369–404.

Gill net and purse seine samples were obtained during 1970–1974 for studies of the biology of the local herring stock in a landlocked fjord, Lindåspollene, in western Norway. The herring stock revealed a distinct migration pattern within the system, with a well defined spawning, feeding and overwintering area. The mean number of vertebrae was 56.70. The age, as determined from scale readings, reached 15 years, but only about 2% exceeded 10 years of age. The growth of the Lindås herring was slower than that of the Atlanto-Scandian or North Sea herring stocks, reaching $L_\infty = 30.49$ cm. The raw weight of the largest individuals was about 250 g. The condition factor reached its maximum in August–October and minimum in May. The mean weight loss during spawning was about 20% of the total weight. The herring spawned in late March, usually in a small fjord arm at depths ranging from 0 to 4 m. Studies of the fecundity showed large variability in number of eggs within length groups. The strength of the year classes and the growth rate of the Lindås herring is discussed in relation to biotic and abiotic conditions of the environment.

INTRODUCTION

Along the Norwegian coast there are a number of small fjords and semi enclosed bays («poll» in Norwegian) in which there are small, more or less self contained herring populations. These local herring stocks can usually be readily distinguished from the oceanic herring by the growth characteristics, and some of the populations have been subjected to scientific studies previously (AASEN 1952, 1953, RASMUSSEN 1941, 1958).

The symposium arranged by the International Council for the Exploration of the Sea (ICES) on «Herring population studies» in Copenhagen, 1961, recommended intensive studies of small, self contained populations in order to throw light upon problems such as reproduction, larval ecology, growth and tagging techniques, which only with extreme difficulties could be studied on oceanic herring populations (ANON. 1963).

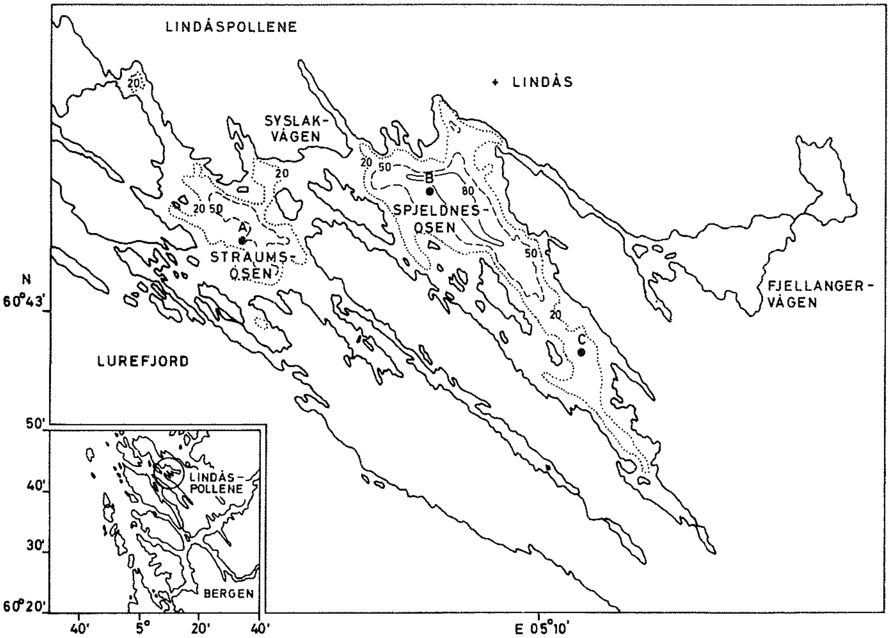

Fig. 1. Depth contour lines and hydrographical stations in Lindåspollene.

Following this recommendation, studies on a number of local herring populations in western Norway were carried out during 1962–1963 (ANON. 1969). The local stocks were as a rule rather strongly mixed with coastal herring which migrated in and out of the «polls» but the herring in Lindåspollene (Fig. 1) appeared to be less influenced by «strange» herring than the other stocks investigated. The Institute of Marine Research, Directorate of Fisheries, therfore decided to undertake intensive studies of the local herring stock in Lindåspollene. The primary emphasis should be on the description of the natural history and the population dynamics of the herring which would be a basis for studies of the relationships between stock and exploitation.

It was realized that the population parameters of the herring stock are intimately related to biotic and abiotic factors of the environment, and therefore it was decided to carry out studies of the entire ecosystem in Lindåspollene simultaneously. The Institute of Marine Biology, University of Bergen, would be responsible for the investigation on the Lindåspollene ecosystem. An outline of the research topics and the objectives of the co-operative studies between the Institute of Marine Research and the Institute of Marine Biology has been given by DAHL, ØSTVEDT and LIE (1973).

The present paper reports on the studies of the herring in Lindåspollen during the period 1970–1974, with particular emphasis on aspects of the

Table 1. Herring samples from Lindåspollene (1970–1974).

No.	Date	Number of fish	Gear	No.	Date	Number of fish	Gear
1a	23 August-70	84	Purse seine	26	4 October-72	23	Gill nets
1b	4 October-70	16	Gill nets	27	12 October-72	139	Purse seine
2	11 Nov.-70	16	»	28	9 Nov.-72	286	Gill nets
3	28 Nov.-70	100	»	29	7 Decemb.-72	4	»
4	27 January-71	76	»	30	10 January-73	24	»
5	26 Febr.-71	24	»	31	1 Febr.-73	21	»
6	18 March-71	37	»	32	23 March-73	7	»
7	28 March-71	119	»	33	28 March-73	27	»
8	22 April-71	80	»	34	29 March-73	31	»
9	5 May-71	7	»	35	11 April-73	25	»
10	10 May-71	90	»	36	25 July-73	15	»
11	8 June-71	8	»	37	15 August-73	8	»
12	10 June-71	100	»	38	23 August-73	40	»
13	29 July-71	26	»	39	12 Sept.-73	100	Purse seine
14	17 August-71	150	Purse seine	40	12 Sept.-73	124	»
15	8 Sept.-71	100	»	41	25 October-73	23	Gill nets
16	20 Sept.-71	70	Gill nets	42	16 January-74	63	»
17	19 October-71	19	»	43	20 Febr.-74	30	»
18	22 Nov.-71	150	»	44	14 March-74	83	»
19	26 January-72	275	»	45	21 March-74	147	»
20	9 March-72	57	»	46	28 March-74	8	»
21	22 March-72	37	»	47	2 April-74	100	»
22	26 April-72	14	»	48	27 July-74	9	»
23	25 May-72	7	»	49	21 August-74	36	»
24	25 May-72	15	»	50	5 Sept.-74	50	Purse seine
25	31 August-72	75	»				

life history and population dynamics of the herring. The material, which is the basis for the study, did not lend itself to estimates of stock abundance, and important topics such as recruitment, mortality, production and yield have therefore been ommitted in this report.

MATERIAL AND METHODS

The present paper is based on 44 gill net samples containing 2428 herring collected during the period October 1970–September 1974 and five purse seine samples collected during the period August–October of 1970, 1971, 1972, 1973 and 1974 (Table 1).

The gill nets (52 mm mesh size) were set on localities in Lindåspollene which are traditionally good fishing grounds (Fig. 2), and the plan was to obtain one sample per month. However, during the summer months the catches were often negative, and in February and December 1973 fishing was prevented by ice. On some occasions, particularly during the spawning

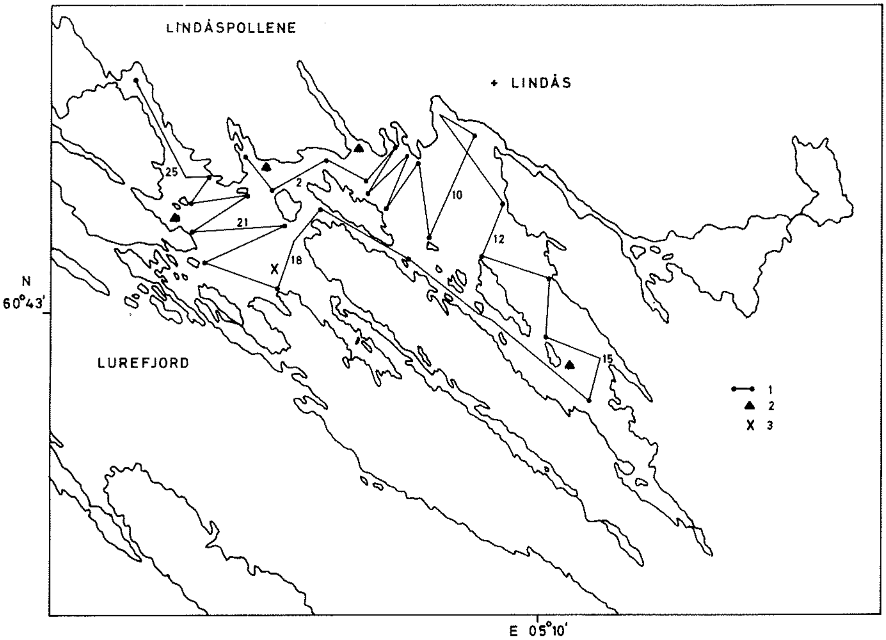

Fig. 2. Echo survey course tracks (1) gill net (2) and purse seine (3) sampling localities.

season, more than one sample was obtained in the same calender month. Data were then pooled to give monthly samples.

The purse seine catches were obtained with seines designed for commercial sprat fishing, and the sampling took place at night using artificial light. The samples contained several age groups of herring, with a preponderance of immature year classes. The purse seine catches were always made in the southern part of Straumsosen (Fig. 2).

The migrations of the herring within the Lindåspollene were determined from observations of the horizontal and vertical distribution of the herring during the investigated period. The observations were made on acoustic surveys which since March 1972 were made along fixed cruise tracks (Fig. 2). During the period August 1970–December 1973 the surveys were made with a SIMRAD EM2F (38kHz) echosounder and during 1974 with a SIMRAD EY (80kHz) echosounder.

The vertabrae were counted on 846 individuals from the gill net samples.

Length of 2421 individuals was measured from the tip of the snout to the longest caudal fin ray, with the lobes of the tail in the mid line (Anon. 1963). The lengths were measured to the nearest ½ cm below and subsequently grouped to the nearest cm below. True mean lengths have therefore been obtained by adding 0.5 cm to the calculated mean lengths.

Wet weights of 2233 herring were determined to the nearest 5 g, and grouped into 10 g intervals.

The nutritional state of the herring was expressed by the condition factor (FULTON 1911):

condition factor (K) = weight (W)/length $(L)^3$

and by the relative amount of intestinal fat classified according to AASEN (1952) into:

class 0: no fat,
class I: traces of fat,
class II: moderate fat,
class III: much fat.

The age of 2067 individuals was determined by reading the winter rings on the scales. Back calculations of lengths from measurements on the scales were performed on all the herring caught on the gill nets during 1971, using the formula of LEA (1910) and ANON. (1963)

$$l_n = \frac{s_n}{s} L$$

where s_n = radius of scale annulus at age n, s = scale radius, L = length of fish at sampling. Since length at sampling was measured to the nearest ½ cm below, 0.25 cm has been added to obtain true mean lengths.

The maturity stages of the herring were determined by the method of JOHANSEN (1919) as modified bye the ICES Working Group on Methods used in the North Sea Herring Investigations (ANON. 1963):

STAGE

I	Virgin herring. Gonads very small, threadlike, 2–3 mm broad. Ovaries wine red. Testes whitish or grey brown.
II	Virgin herring with small sexual organs. The height of ovaries and testes about 3–8 mm. Eggs not visible to naked eye but can be seen with magnifying glass. Ovaries a bright red colour; testes a reddish grey colour.
III	Gonads occupies about half of the ventral cavity. Breadth of sexual organs between 1 and 2 cm. Eggs small but can be distinguished with naked eye. Ovaries orange; testes reddish grey or greyish.
IV	Gonads almost as long as body cavity. Eggs larger, varying in size, opaque. Ovaries orange or pale yellow, testes whitish.
V	Gonads fill body cavity. Eggs large, round; some transparent. Ovaries yellowish; testes milkwhite. Eggs and sperm do not flow, but sperm can be extruded by pressure.
VI	Ripe gonads. Eggs transparent; testes white; eggs and sperm flow freely.
VII	Spent herring. Gonads baggy and bloodshot. Ovaries empty or containing only a few residual eggs. Testes may contain remains of sperm.
VIII	Recovering spents. Ovaries and testes firm and larger than virgin herring in Stage II. Eggs not visible to naked eye. Walls of gonads striated; blood vessels prominent. Gonads wine red colour. (This stage passes into Stage III).

The number of eggs per unit weight of the gonads was determined by counting parts of gonads from 73 herring under a dissecting microscope. The gonads were preserved in Gilson's fluid and treated according to BAXTER (1959) before counting. Total number of eggs per gonad was determined by multiplication with total gonad weight. The fecundity of an additional 45 herring was determined by complete counting of eggs in the ovaries by an automatic particle counter (BERGE and PETTERSEN 1974).

RESULTS

MIGRATIONS

In a preliminary report on the acoustic surveys during 1971–1972 and the first three months of 1973, ØSTVEDT, DAHL and LIE (1973) discussed the apparent migration pattern of the herring in Lindåspollene. The major conclusions were:

a) the herring spawned in Syslakvågen in late March,
b) after spawning the herring moved into Straumsosen and remained there during the summer,
c) in September–October the herring moved into Spjeldnesosen and scattered,
d) in November–December the herring concentrated in the northern part of Spjeldnesosen and remained there until spawning in March.

This migration pattern was largely confirmed by the investigations during 1973–1974, but there were also some major discrepancies between the two periods of investigation. Thus, there was no spawning migration into Syslakvågen in 1973, and no other spawning area was located. In 1974 the herring had a normal spawning migration into Syslakvågen.

The migration pattern after spawning was also somewhat different in 1973–1974 because a part of the stock moved south into Spjeldnesosen and remained there during the summer. However, the major part of the stock moved into Straumsosen as during 1971–1972.

On the basis of all the acoustic surveys performed during 1971–1974 a migration pattern, as demonstrated in Fig. 3A, B og C, is suggested. The pattern during September–March is repeated each year, but the distribution during the rest of the year is less clear. Thus, the migration to the spawning grounds must be further studied and also the distribution during May–August.

ØSTVEDT *et al.* (1973) discussed the vertical distribution of the herring and concluded that the herring during the winter was distributed at about 50–60 m depth. The distribution during the summer was higher up in the sea. They also demonstrated vertical diurnal migrations, with a distribution near the surface at night.

The acoustic surveys during 1973–1974 were carried out during daytime, and the herring was as a rule distributed at intermediate depths (Fig. 4).

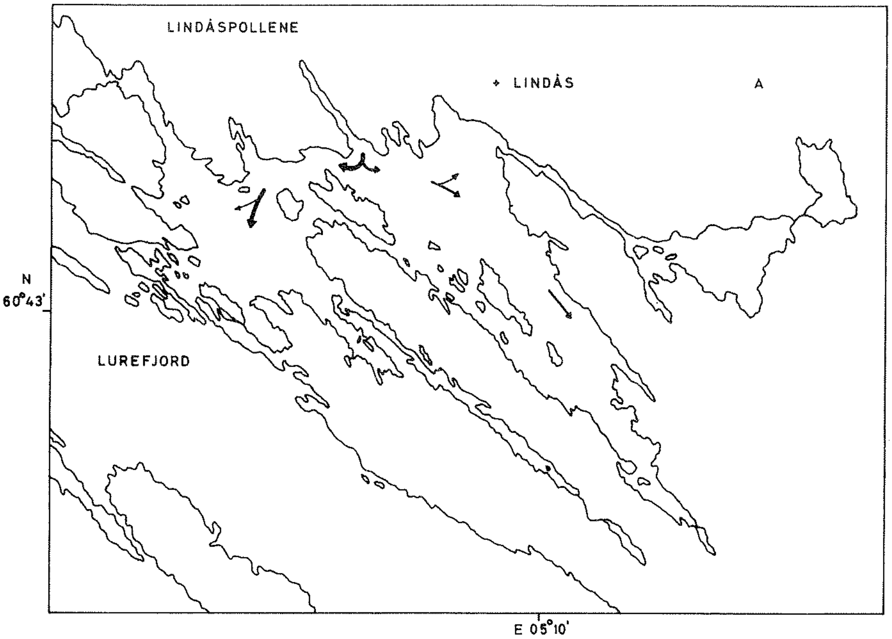

Fig. 3A. Migration pattern of the Lindås Herring during April–August.

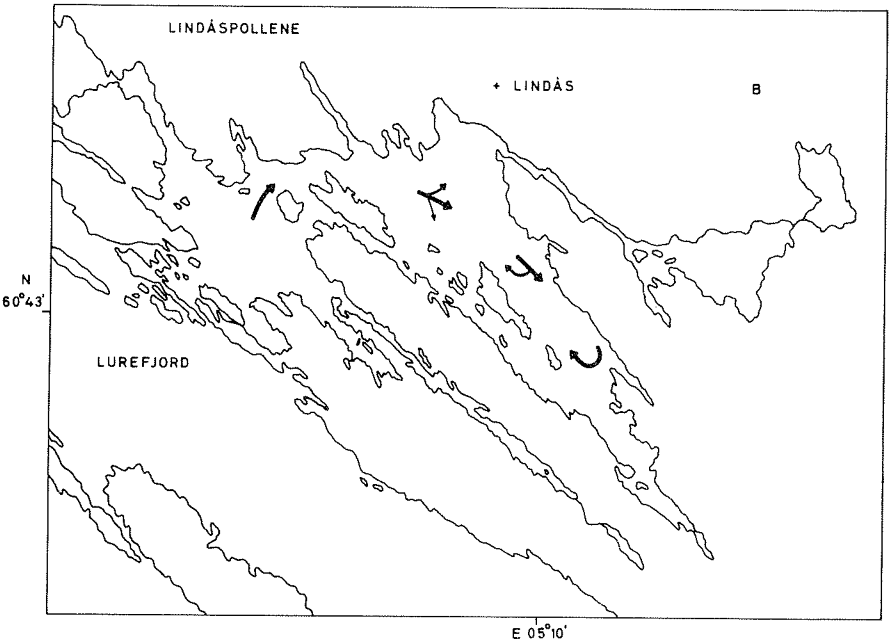

Fig. 3B. Migration pattern of the Lindås herring during September–October.

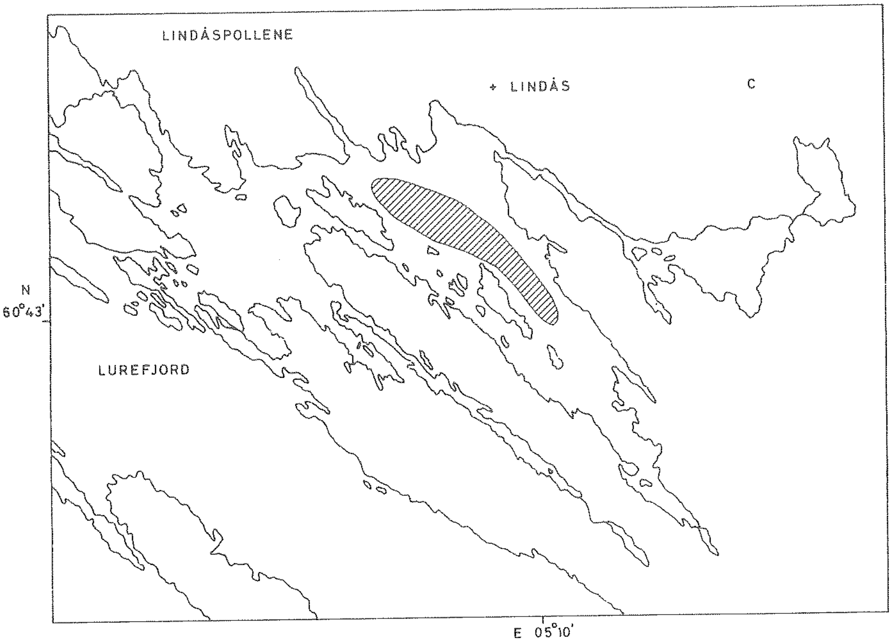

Fig. 3C. Migration pattern of the Lindås herring during November–March.

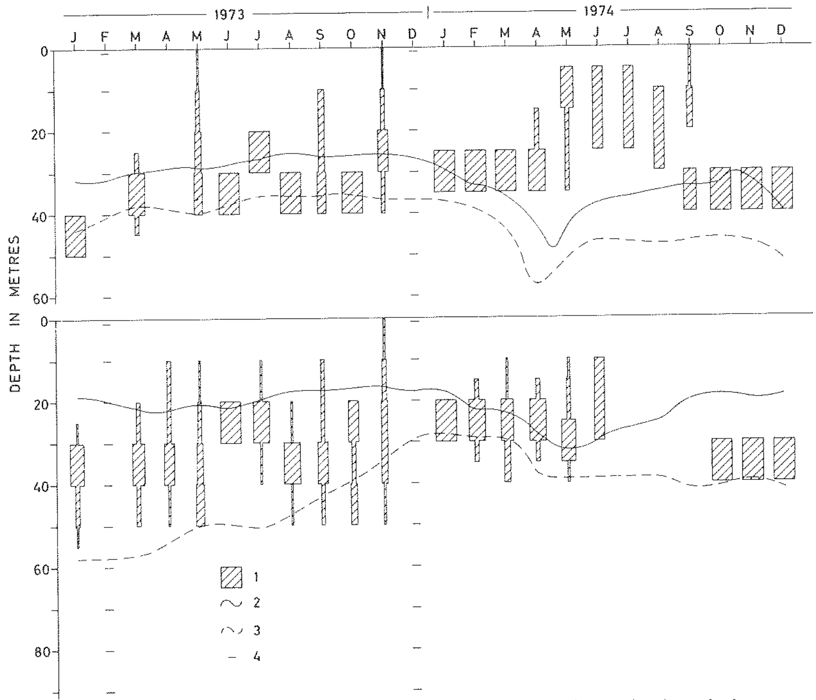

Fig. 4. Vertical distribution of the Lindås herring during 1973–1974 in relation to oxygen concentration of the water masses. 1) Herring concentration, 2) 4,0 ml O_2/l 3) *1,0 ml* O_2/l, 4) no observation.

Table 2. Frequency distribution of number of vertebrae of the herring in Lindåspollene during 1970–1973.

Data	Number of vertebrae						Mean	n	S^2	± C.I.
	54	55	56	57	58	59				
1970										
October	–	–	7	6	2		56.67	15	0.524	0.3738
November . . .	1	1	41	56	16	1	56.76	116	0.837	0.1698
1971										
January	–	1	21	45	4	–	56.73	71	0.763	0.2073
February	–	–	7	13	4	–	56.88	24	0.535	0.2986
March	–	4	41	42	10	1	56.62	98	0.527	0.1467
April	1	2	28	33	10	–	56.66	74	0.636	0.1854
May	2	5	20	52	6	–	56.65	85	0.636	0.1730
August	–	–	10	35	5	–	56.90	50	0.296	0.1539
September . . .	–	4	20	28	18	–	56.86	70	0.762	0.2087
November . . .	–	7	33	46	11	–	56.63	97	0.611	0.1587
1972										
January	3	7	27	52	7	–	56.55	96	0.734	0.1748
1973										
September . . .	–	2	20	22	6	–	56.64	50	0.561	0.2118
Total	7	33	275	430	99	2	56.70	846	0.589	0.0528

There was a tendency for the herring to be concentrated nearer the surface during the summer. It should be noticed that the data in the figure are percentages, and therefore the figure gives no information about the strength of the recordings between months. Thus, the data for Straumsosen during September–April and for Spjeldnesosen during May–August are based on very few and scattered recordings.

Fig. 4 shows that the majority of the recordings were made in the water layer limited by the isolines for 1 ml O_2 per litre and 4 ml O_2 per litre, and particularly during the winter the herring seems to remain in water masses characterized by very low oxygen tension. This is peculiar for a pelagic fish, and Kamshilov and Gerasimov (1960) demonstrated that young Murman herring kept in aquaria died in oxygen concentrations below 2 ml per litre.

IDENTIFICATION OF THE POPULATION

The preliminary investigations in Lindåspollene during 1962–1964 showed the presence of two distinct components in the herring stock: a) a slow growing component which constitute the major part of the stock, and b) a fast growing component which was considerably less important (Anon. 1964). The latter component was referred to as the «strange» herring, in accordance with Aasen (1952).

Table 3. Analyses of variance on vertebrae counts.

Source of variation	df	SS	MS	F
Among months	11	19.30	1.75	2.97 (P 0.01)
Within months	834	489.50	0.59	
Total	845	508.80		

Vertebral counts as a means of distinguishing between populations or «races» of herring from northern European waters has been used by a number of authors (viz. RUNNSTRØM 1941, AASEN 1952, CUSHING 1958 and ZIJLSTRA 1958). In order to investigate the possible relationships between the Lindås herring and neighbouring herring stocks, vertebrae were counted in 846 individuals collected during the period October 1970–September 1973.

The monthly mean number of vertebrae in the herring from the gill net samples ranged from 56.55 to 56.90, with an overall mean of 56.70 (Table 2). An analysis of variance (Table 3) showed that there was a significant added variance component among months, but this component did not amount to more than 0,95% of the total variance, and there was no distinct seasonal or annual trend in the monthly mean number of vertebrae.

It is not unexpected that herring samples collected during a timespan of about three years would reveal differences in the mean number of vertebrae. In the first part of the investigated period the samples were strongly dominated by the 1966 year class, but from about August 1972 the 1969 year class became increasingly more important. It is conceivable that variability in the sea temperatures on the spawning grounds could cause differences in the number of vertebrae of various year classes. An inverse relationship between number of vertebra and the sea temperatures on the spawning grounds has been demonstrated by a number of authors, and considerable fluctuations in the temperatures on the shallow spawning ground in Syslakvågen must be expected.

During 1962–1964 the «strange» herring had a mean verebral count of 57.0 to 57.2 whereas the slow groving component of the Lindås herring had a mean vertebral count of from 56.4 to 56.6 (ANON. 1964). The «strange» herring during the period 1970–1973 had a mean vertebral count of 56.65 and could therefore not be distinguished significantly from the slow growing component. Thus, there seems to have been a distinct change in the number of vertebrae in the «strange» herring from 1962–1964 to 1970–1973. In 1962–1964 the number of vertebrae in the «strange» herring could not be significantly distinguished from the Atlanto Scandian herring stock (ANON 1964), and during 1970–1973 the number of vertebrae did not differ from that of the North Sea spring spawning stock (Table 4). Hence,

Table 4. Mean vertebrae numbers of the year class 1969 from different groups of spring spawning herring.

Race	V. S. Mean	Number	S^2	± C.I.
Lindås herring	56.64	462	0.591	0.0715
North S. herring	56.84	107	0.380	0.1192
Atlanto Scandian herring ...	57.02	631	0.371	0.0485

the hypothesis cannot be rejected that the «strange» herring in Lindåspollene during 1962–1964 represented specimens from the Atlanto Scandian stock, and during 1970–1973 from the North Sea spring spawning stock. It is noteworthy that the change in the apparent origin of the «strange» herring component coincided with the drastic reduction of the Atlanto Scandian herring stock (Devold 1968).

The mean number of vertebrae in the slow growing component of the 1969 year class Lindås herring was quite similar to the mean number of vertebrae of the North Sea herring of the same year class (Table 4). The difference to the Atlanto Scandian stock of the same year class was more pronounced and significant beyond the 99% level of probability.

AGE

The age of the herring in Lindåspollene can easily be determined by scale readings because the winter growth rings are always well defined (Fig. 5), similar to the northern growth type of the Atlanto Scandian herring stock (Lea 1929). The age at first spawning can also often be ascertained because the growth ring during the preceding summer is distinctly reduced.

The age was determined by scale readings from 2067 individuals collected with gill nets during the period October 1970–September 1974 (Table 5). Some two year old herring were caught by the gill nets, but the population does not seem to become fully vulnerable until the fourth year.

The herring in the gill net samples ranged in age from 2 to 15 years, but only about 2% were older than 10 years. Thus, the Lindås herring is relatively short lived compared to the Atlanto Scandian herring stock where specimens reaching 24–25 years of age were frequently caught in years of high stock abundance and low fishing mortality (Devold and Dahl 1964).

The 1966 year class was strong during 1971, but from the second quarter of 1972 the 1969 year class became increasingly dominant (Table 5). Subsequently, there was a reduction in the relative strength of the 1966 year class. On the basis of the relative strengths of the year classes alone, it cannot

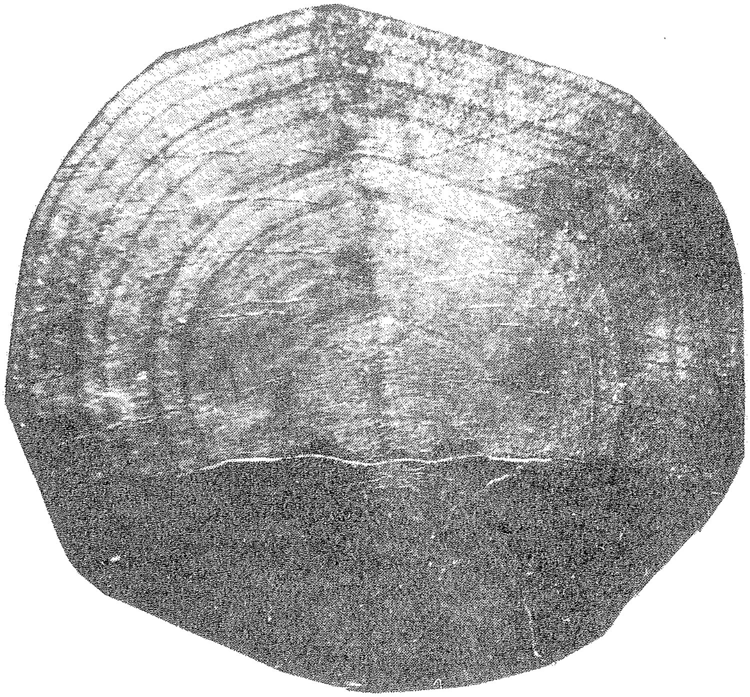

Fig. 5. Growth rings in the scale of a Lindås herring.

be determined whether the decrease in the percentages of the 1966 year class is a result of the emergence of a very strong 1969 year class, or if there was a concurrent increase in the mortality of the 1966 year class.

Table 6 shows that the 1964, 1965, 1967 and the 1968 year classes were weak whereas there is some indication that the 1962 and the 1963 year classes had been relatively strong. The preliminary investigations in Lindåspollene during 1962–1964 demonstrated that the 1959 year class was strongly dominant during that period (Dahl *et al* 1973).

LENGTH AND GROWTH

The length of the herring from the gill net samples collected during the period October 1970–September 1974 ranged from 21 to 35 cm, but about 90% of the individuals measured from 25 to 30 cm (Table 7). The majority of the individuals larger than 31 cm belonged to the «strange» herring component. The monthly mean lengths were not significantly different during 1970–1971 when the 1966 year class dominated in the samples, averaging 27.34 cm. However, there was a distinct decrease in the mean length from August 1972 when the 1969 year class became more predominant. Thus, the average of the monthly mean lengths during 1973 were only 25.57 cm.

Table 5. Seasonal composition (%) in the age structure of the Lindås herring, 1970–1974 (gill nets).

Date	Age in years														n
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
1970															
October–December	0.8	2.4	75.9	7.3	0.8	4.8	5.6	0.8	0.3	0	0.8	0	0	0	124
1971															
January–March	2.2	3.9	8.7	53.4	9.1	1.3	6.5	7.8	1.7	0.4	0	0	0	0	230
April–June	0.4	5.6	6.4	76.4	6.7	0	1.9	2.2	0	0	0	0.4	0	0	267
July–September	2.2	3.3	7.8	61.1	8.9	6.7	4.4	2.2	0	2.2	0	0	0	0	90
October–December	10.1	10.7	3.8	43.4	6.9	3.8	3.8	13.2	3.1	0	0.6	0	0	0.6	159
1972															
January–March	0	5.0	4.7	1.8	48.9	10.9	2.5	4.0	11.2	3.3	1.8	1.1	0.4	0.4	276
April–June	10.3	17.0	13.8	10.3	24.1	3.4	3.4	3.4	6.8	6.8	0	0	0	0	29
July–September	8.3	44.4	5.5	5.5	30.6	0	0	2.3	1.4	1.4	0	0	0	0	72
October–December	3.2	32.5	4.5	2.5	42.7	0.6	1.3	5.7	3.3	1.3	1.9	0	0	0	157
1973															
January–March	2.8	12.1	54.3	6.5	2.8	15.0	0	2.3	2.3	0	0.9	0	0	0	107
April–June	0	8.0	88.0	0	0	4.0	0	0	0	0	0	0	0	0	25
July–September	10.4	6.2	81.3	0	0	2.1	0	0	0	0	0	0	0	0	48
October–December	5.0	10.0	75.0	0	0	5.0	5.0	0	0	0	0	0	0	0	20
1974															
January–March	7.6	10.2	10.2	64.0	3.4	0	3.4	0.6	0.3	0	0.3	0	0	0	325
April–June	0	0	3.1	75.0	9.5	2.1	8.3	0	1.0	1.0	0	0	0	0	96
July–September	33.3	40.5	4.8	21.4	0	0	0	0	0	0	0	0	0	0	42

Table 6. Annual age composition (%) of the Lindås herring samples in the years 1970–1974 (gill nets).

Years	Age										n
	2	3	4	5	6	7	8	9	10	<10	
1970	0.8	2.4	75.9	7.3	0.8	4.8	5.6	0.8	0.8	0.8	124
1971	3.2	5.9	6.7	62.1	7.8	2.0	4.0	6.3	1.2	0.8	746
1972	2.6	19.6	5.5	3.1	45.8	6.5	2.2	4.3	7.5	5.9	534
1973	4.5	8.5	67.0	3.5	1.5	10.5	0.5	1.5	1.5	1.0	200
1974	5.9	7.8	8.6	66.4	4.8	0.5	4.5	0.5	0.5	0.5	463

Table 7 indicates that the herring in Lindåspollene did not become fully vulnerable to the gill nets before they had reached a length of about 24 cm.

The length distribution of the herring caught in the purse seine in the autumn of each of the years 1970–1974 indicates the relative strengths of the year classes that were not vulnerable to the gill nets at the time of sampling (Table 8). The samples from 1970 and 1971 were strongly dominated by the 1969 year class, and the absence of the 1970 and 1971 year classes as 0- or 1-group indicates that the latter year classes were weak. The 1972 year class, however, was very abundant in the 1972 sample as 0-group, in the 1973 sample as 1-group and in the 1974 sample as II-group which indicates that the 1972 year class is relatively strong.

The length-at-age was determined by back calculations from scale readings for 626 herring caught during 1971. Considerable and statistically significant differences among the year classes regarding growth during the first four years of life were clearly discernable (Table 9). The 1965, 1967 and 1968 year classes had significantly higher l_1, l_2, and l_3 than the year classes 1962, 1963 and 1966. The l_1 and l_2 for the 1969 year class indicate that it belongs to the latter group. In the comparison of lengths-at-age for different year classes it should be kept in mind that the results will be biased by presence of Lee's phenomenon (LEE 1920), and this would particularly apply to the 1962 and 1963 year classes in the present study. However, since the lengths-at-age are determined from the individuals caught in 1971 only, the importance of the Lee's phenomenon cannot be estimated.

It is an interesting fact that the year classes which were classified as relatively strong on the basis of the age frequencies (Table 6) were precisely the year classes characterized by low l_1 and l_2. This indicates that the growth rates during the first years of life may be density dependent. It seems also that slow growth during the first year of life is not compensated by more rapid growth during the following 2–3 years.

The length-at-age as determined for the entire 1971 material is shown in

Table 7. Length frequency distributions, true mean lengths (L), and 95% confidence intervals (C.I.) of the means, of herring from gill-net samples in Lindåspollene, 1970–1974.

	Length, cm										n	Mean L(cm)	± C.I.
	<24	24	25	26	27	28	29	30	31	>31			
1970													
October . . .			2	4	8	1		1			16	27.25	0.59
November .		1	3	28	36	17	12	13	5	1	116	28.09	0.28
1971													
January . . .			1	8	34	10	11	8	4		76	28.32	0.33
February . .		2	1	6	6	3	2	1		1	22	27.55	0.79
March.	1	1	12	25	48	26	23	9	6	5	156	28.13	0.30
April		1	9	20	31	14	3	2			80	27.31	0.26
May		1		12	50	23	5	3	2		96	27.86	0.22
June			3	18	49	24	8	4	2		108	27.83	0.27
July	1	2	1	5	9	7			1		26	27.27	0.63
September .			4	8	19	17	10	9	3		70	28.36	0.36
October . . .	1	1	1	1	3	2	2	4	4		19	28.76	1.13
November .	1	13	8	20	24	32	23	25	4		150	28.10	0.31
1972													
January . . .			12	16	71	74	60	36	5	1	275	28.54	0.16
March		2	1	8	23	29	12	12	6	1	94	28.60	0.33
April	1	3		2		2	3	1	1	1	14	27.86	1.67
May				1	5	1	9	5	1		22	29.18	0.56
August	1	12	12	11	13	16	4	3	3		75	27.10	0.45
October . . .	2	7	5	4	2	1	1	1			23	25.89	0.76
November .	2	6	26	32	25	68	66	43	14	4	286	23.53	0.22
1973													
January . . .	1	4	5	2	3	2	6	1			24	27.04	0.87
February . .	5	2	5	3	2	3	1				21	25.88	0.80
March.		8	23	8	8	4	6	6	2		65	26.95	0.46
April	1	14	4	4		1	1				25	25.30	0.55
July	9	1	4		1						15	24.03	0.80
August	4	9	19	12	2	1	1				48	25.50	0.43
October . . .			6	5	3	1	5	1	1	1	23	27.76	0.88
1974													
January . . .	1	8	16	13	13	7	2	2		1	63	26.71	0.45
February . .			5	5	4	5	3	2	1	5	30	28.53	0.88
March		9	52	80	58	22	11	5		1	238	26.89	0.17
April			9	34	22	23	7	3	1	1	100	27.55	0.26
July	1		2	5	1						9	25.94	0.47
August	24	8	3	–	–	1					36	23.25	0.26
Total	56	115	254	400	573	437	297	200	66	22	2 421		

Table 8. Length distribution of herring (in per cent) from purse seine catches in Lindåspollene, 1970–74.

Year	Length, cm																						n
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
1970						1.2	35.7	42.9	15.5	4.7													84
1971							6.4	6.8	4.3	1.7	11.5	26.7	22.2	12.4	4.3	2.1	0.4	0.4	0.4	–	–	0.4	234
1972	1.4	47.5	46.2	1.4	0.7	–	–	–	0.7	0.7	–	0.7	–	–	0.7	–							139
1973					64.0	25.0	1.0	1.0	–	–	–	1.0	–	–	–	–	1.0	4.0	2.0	1.0	–	–	100
1974									6.0	32.0	38.0	6.0	–	–	1.0	3.0	2.0	1.0	1.0	6.0	3.0	1.0	100

Table 9. Growth estimates (true mean) for the Lindås herring during the first four years of life (L_1 - L_4), with 95% confidence intervals of the means (C.I.).

Year-class	Length, cm							
	L_1	± C.I.	L_2	± C.I.	L_3	± C.I.	L_4	± C.I.
1970	9.5	0.4						
1969	9.1	0.2	16.2	0.4				
1968	11.2	0.7	19.5	0.8	24.3	0.6		
1967	10.9	0.6	19.0	0.7	23.8	0.6	25.2	0.5
1966	10.0	0.1	16.5	0.2	21.9	0.1	25.4	0.1
1965	11.0	0.3	19.3	0.5	22.5	0.4	24.8	0.3
1963	10.1	0.4	17.3	0.7	21.0	0.9	23.8	0.5
1962	10.0	0.3	16.3	0.4	20.3	0.5	23.2	0.4

Table 10. It should be noticed that the data for the 1961 and 1964 year classes were very scarce, and the estimated length-at-age for these year classes may therefore not be precise. The entries in the table along the diagonal, i.e. length at capture for the various year classes, refers to individuals caught during the last quarter of the year only, when annual growth is terminated. The table shows that the length increments for individuals older than 4 years in 1971 were small, indicating unfavourable growth conditions.

The data in Table 10 were plotted in a Walford diagram (Fig. 6) of L_{t+1} versus L_t, and the regression line:

$$L_{t+1} = 10.38 + 0.66L_t$$

Table 10. Growth estimates (true mean) for the Lindås herring from the 1971 material.

Year-class	Length, cm											n
	L_1	L_2	L_3	L_4	L_5	L_6	L_7	L_8	L_9	L_{10}	L_{11}	
1970	9.5	15.6										19
1969	9.1	16.2	20.3									96
1968	11.2	19.5	24.3	26.0								25
1967	10.9	19.0	23.8	25.2	26.8							27
1966	10.0	16.5	21.9	25.4	27.5	27.5						331
1965	11.0	19.3	22.5	24.8	27.0	28.6	28.9					55
1964	10.1	17.8	22.0	23.8	25.8	27.6	29.0	29.8				3
1963	10.1	17.3	21.0	23.8	25.5	27.2	28.9	30.0	30.4			22
1962	10.0	16.3	20.3	23.2	23.8	26.0	27.4	28.9	30.2	30.2		39
1961	9.8	15.9	20.6	24.8	25.0	26.2	27.0	28.6	29.7	30.5	30.5	9

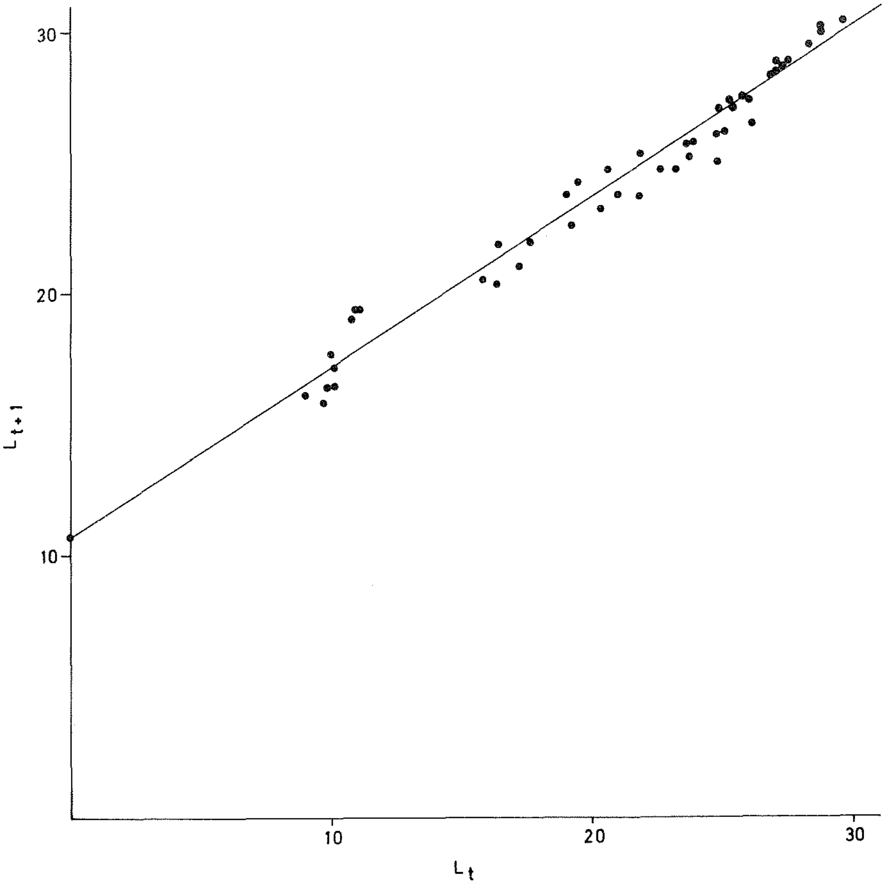

Fig. 6. Walford plot of back calculated lengths from scale readings.

could be fitted by the method of least squares. The regression line was used to determine $L_\infty = 30.49$ and $t_0 = 0.035$, and the von Bertalanffy growth equation for the Lindås herring was determined as:

$$L_t = 30{,}49\ (1 - {}_e{}^{0.416\,(t - 0.035)}).$$

The growth curve represents the mean growth of the Lindås herring well during the first four years of life (Fig. 7), but from the fifth year on the calculated growth was too high. The «strange» herring had a considerably higher growth rate during the first four years of life than the Lindås herring, whereas the Lusterfjord herring (Aasen 1952) had a slower growth (Fig. 7).

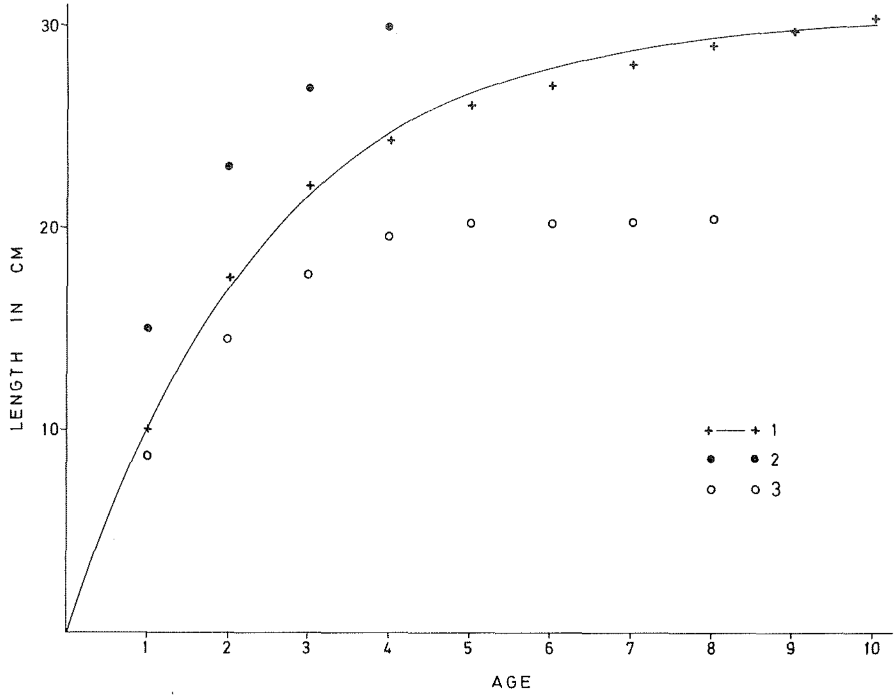

Fig. 7. Von Bertalanffy growth curve for the Lindås herring (1), and length/age plots for the «strange» herring (2) and the Lusterfjord herring (3) from Aasen (1952).

WEIGHT, CONDITION FACTOR AND INTESTINAL FAT CONTENT

The weight of the herring from the gill net samples ranged from 70 to 300 g (Table 11), and about 60% of the individuals weighed from 150 to 200 g. The monthly mean weights during 1973, when the 1969 year class dominated in the samples, were considerably lower than during the preceding years.

The 1966 year class, which dominated during 1970, 1971 and 1972, showed distinct seasonal variability in weight, with minima during the first and maxima during the last quarters of the years (Table 12).

In 1971 the herring did not attain the same weight as in 1970 whereas a pronounced increase in weight took place during 1972. This is an indication that the conditions for the herring in Lindåspollene during 1971 were poor which explains the slow growth during 1971.

The weight/age curve was typically sigmoid (Fig. 8), and the natural logarithms therefore yielded two reasonably straight lines, intersecting at the fourth year of age. This is the age of maturity for the majority of the Lindås herring, and the change in weight increase may therefore be related to the ripening of the gonads.

Table 11. Weight frequency distribution of Lindås herring, 1970–1974.

Month	Weight in g																n	Mean
	<100	100	110	120	130	140	150	160	170	180	190	200	210	220	230	>230		
1970																		
October								5	2	4	1	1	—	—	1	1	15	181
November			1	1	1	1	9	7	13	16	11	15	6	2	3	21	107	196
1971																		
January					1	8	12	12	14	4	6	3	3	3	4	1	71	173
February	2	—	—	2	—	1	3	1	5	1	2	2	1	2	2		24	170
March	1	1	3	3	11	10	23	26	18	9	11	13	3	9			141	165
April				1	6	6	12	15	22	9	3	1	1	2	—	1	79	164
May				1	3	14	22	18	23	9	1	2	1	1			95	160
June				1	5	7	24	30	10	8	10	3	6	—	—	3	107	166
July			3	—	3	1	4	5	4	3	1	1	—	1	—	1	27	160
September			2	1	1	2	6	10	12	7	2	9	8	2	5	4	71	183
October			2	—	2	2	2	—	—	3	—	1	3	—	—	4	19	185
November	1	7	7	5	10	11	16	13	17	17	10	18	7	8	—	4	151	173
1972																		
January			4	7	5	15	34	29	31	25	22	13	12	2	1		200	168
March			1	1	1	4	10	4	5	5	2	1	2	—	1		37	163
April		2	3	—	1	1	1	—	—	3	—	—	—	2	—	1	14	157
May					1	3	1	5	3	3	2	—	2	—	2		22	173
August			3	6	9	2	2	6	5	8	6	7	6	8	2	8	78	182
October			1	9	2	3	—	—	1	2	—	2	1	1	—	1	23	151
November	2	5	5	10	5	8	6	11	6	14	11	13	13	8	12	13	142	176
1973																		
January		4	3	2	2	3	1	3	1	—	1	1	1	1	—	1	24	146
February		3	2	3	—	3	3	2	1	1	—	—	1	1	—	2	22	153
March			7	12	12	2	8	2	5	3	3	1	2	1			58	144
April	2	8	9	2	1	—	2	—	—	1							25	113
July			6	3	1	1	2	1	—	—	—	—	1				15	131
August	6	1	3	5	12	9	5	3	1	1	—	1	—	—	1		48	132
September	7	7	12	23	21	17	16	6	6	3	—	1	—	2			121	132
October			1	1	3	1	3	1	3	2	2	1	1	1		3	23	176
1974																		
January	4	6	11	12	6	5	7	6	1	—	3	1	1				63	131
February		1	3	3	2	4	4	2	2	2	—	1	1	3	2		30	159
March	4	14	24	42	44	35	23	26	9	3	4	4	3	1	—		236	136
April			2	5	21	11	23	12	4	6	7	2	5	1	1		100	155
July			1				2	1	—	3	2						9	166
August	25	7	2	—	2												36	87
Total	54	66	120	161	194	190	287	262	224	175	123	118	91	62	37	69	2 233	

Table 12. Mean weight of the 1966 year class in the Lindås herring, 1970–1974.

Month	Mean weight	n
1970		
October	175	13
November	185	78
1971		
January	160	41
February	168	13
March	160	76
April	160	55
May	161	63
June	163	87
July	164	16
September	177	36
October	173	4
November	165	59
1972		
January	161	88
March	156	28
May	155	7
August	210	21
November	194	62
1973		
January	202	9
March	182	7
1974		
March	158	9
April	194	9

A regression line for weight and length data for 2233 herring (Table 13) in logarithmic transformation was determined as:

$$W = 0.011\ L^{2.9025}$$

The regression line is plotted in Fig. 9. The 95% confidence interval for the slope of the regression line (2.9025) was ± 0.1392, and the hypothesis of isometric growth, i.e. the slope was not significantly different from 3, could no be rejected.

The condition factor (FULTON 1911):

$K = W/L^3$ (W in g L in cm)

is a measure of weight per unit volume under the assumption of isometric growth, and the larger the K, the better is the «condition» of the fish.

The condition factor was determined for all the individuals collected during 1970–1974 (Fig. 10). The highest values usually occured during

Table 13. Length-weight relationship of Lindås-herring, 1970–1974.

g	Length, cm																			
	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
10	5	2																		
20	8	7	14	3																
30			1	15	9	1														
40					1	3	4	1												
50							11	8	1											
60							6	29	7		1									
70								10	16	2	1									
80									14	9	1	2								
90									3	11	3	7	5							
100										1	5	3	29	20	1					
10											3	6	33	36	10					
20											2	6	20	72	45	8				
30												2	9	76	77	21	2			
40													3	36	86	59	9	2		
50														15	72	120	22	4		
60														5	42	134	36	10	3	
70														1	25	77	78	34	4	
80														1	11	35	60	38	11	
90															3	23	38	47	19	
200															2	18	26	32	27	4
10																3	17	35	24	5
20																	10	19	16	7
30																	4	10	19	7
40																	3	8	7	11
50																		5	8	3
60																		—	3	4
70																		—	2	3
80																		1	4	4
90																			1	2

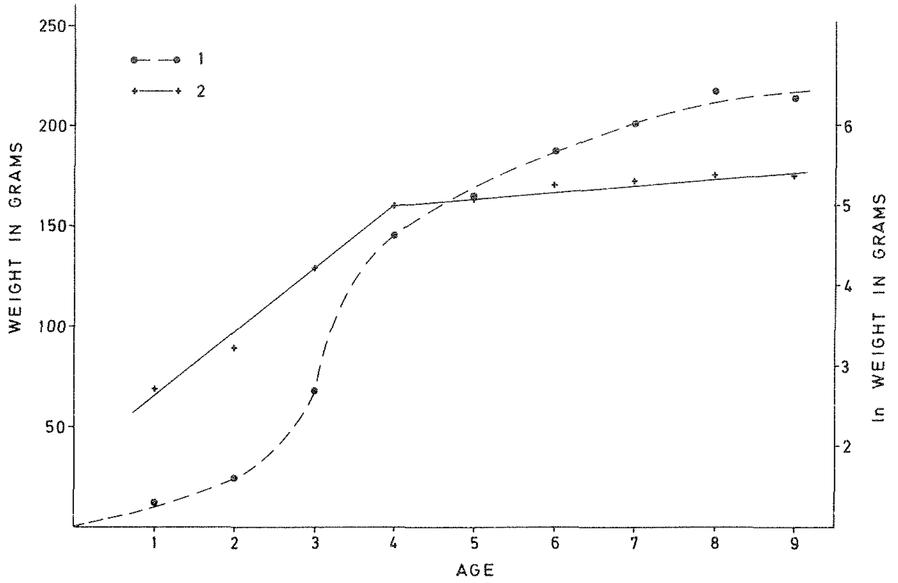

Fig. 8. Weight/age curves for the Lindås herring.

August–October, but there were distinct differences from year to year. Thus, it appears that 1970 and 1972 were particularly «good» years, whereas 1971 and 1973 had considerably lower condition factors during early autumn. A decrease in the condition factor could be observed already in October, and the minimum was usually reached in January. Then there was a rapid increase, culminating in March, and subsequently a decrease until the annual minimum was observed in May. On the average there was a decrease in the condition factor of about 15% from the autumn maximum to the May minimum, but from autumn 1970 to May 1971 the decrease was more than 20%. This decrease in weight reflects changes in body fat and sexual products, and therefore the annual variability in calorific content must be considerably higher than the variability in weight.

The rapid changes in the condition factor during the first quarter of the year coincides with the change from maturity stage IV to stage V and VI, i.e. the period of the most rapid growth of the gonads (AASEN 1952).

The amount of fat deposited on the intestines is commonly used as an indicator of quality in the marketing of herring, and the intestinal fat is thus another measure of the condition of the fish. In the present investigation the amount of intestinal fat was classified in accordance with AASEN (1952). The intestinal fat content was highest in July–August, when about 80–90% of the individuals had moderate fat content (Fig. 11). Through the autumn and winter there was a rapid decrease in the intestinal fat, and less than 10% of the individuals showed traces of fat during spawning in late March. After

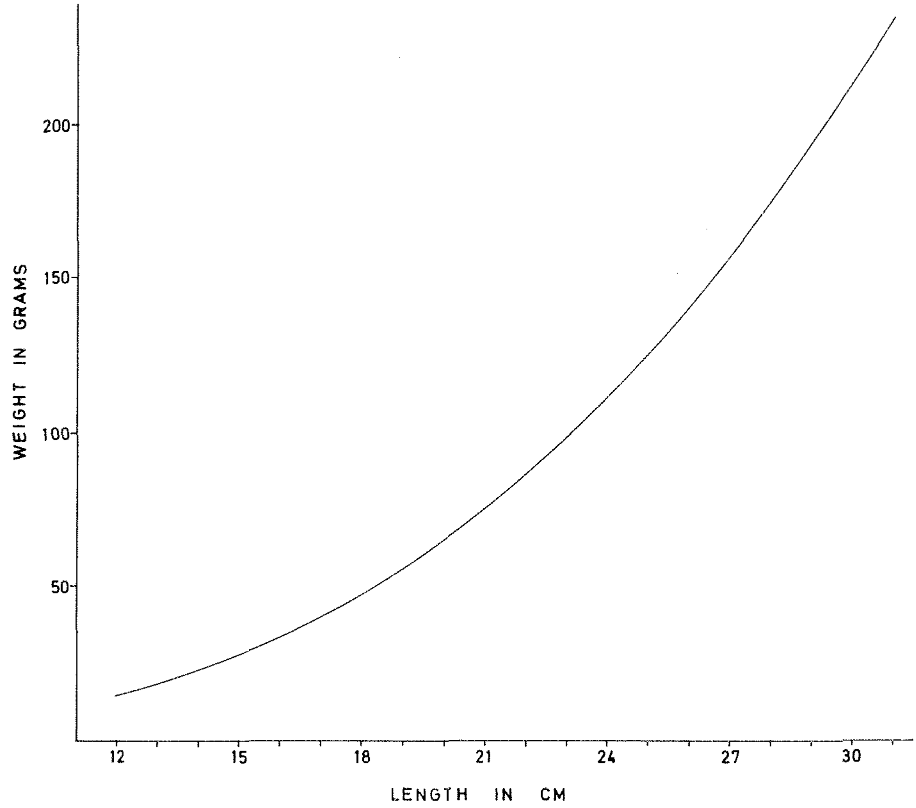

Fig. 9. Weight/length curve for the Lindås herring.

the spawning the herring very quickly startet to deposit intestinal fat again, and already in May had 45% of the individuals a moderate amount of fat.

It is interesting to note that the amount of intestinal fat started to decrease from August–September which indicates that the herring already then could not find sufficient food for maintenance metabolism, but had to utilize deposited fat as a source of energy.

There were some differences among the years in amount of intestinal fat; thus, it appeared that the decrease in autumn started one month earlier in 1971 than i 1972 and 1973. However, the inaccuracy of the classification method for intestinal fat prevents more stringent testing of annual differences.

MATURITY, FECUNDITY AND SPAWNING

The maturity stages were determined by the method of JOHANSEN (1919) which has been slightly modified and adopted for the Atlanto Scandian and

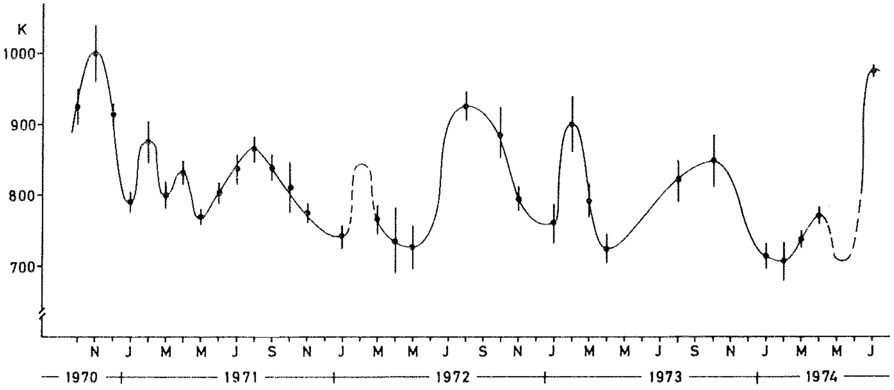

Fig. 10. Variation in the condition factor of the Lindås herring during 1970–1974. Vertical lines: 95% confidence intervals.

for the North Sea herring stocks (ANON. 1963). In a qualitative classification scheme there is always an element of subjectivity on the part of the investigator, which introduces an added variance component in the data. In the present study this component has been minimized because all the maturity stage determinations have been made by one of the authors (O.D.) who has considerable experience with the method.

The overwhelming majority of the herring caught with gill nets were mature or maturing (Table 14), only 3.6% were in stage II and none in stage I. The size selectivity of the nets is the principal reason for this, but there are also indications that the migration pattern of the immature herring may be different from that of the mature stock (ØSTVEDT *et al.* 1974). Mature and immature herring will therefore not be caught together in the nets.

Maturity stage III appears in May–June and dominates from July–August until October (Table 14), and stage IV dominates from October until February. During February–March the herring pass through stage V, and the majority of the specimens were in stage VI, i.e. with fully ripe gonads, at the end of March. High percentages of spent herring (Stage VII) were rarely encountered, but recovering spent herring (stage VIII) dominated the samples during the period May–July. The scarcity of samples during the period May–August prevents accurate determinations of maturity stage distribution during this period.

Maturity stage IV was observed for about four months, stages III and VIII about three months, whereas the stages V–VII lasted only about two to four weeks (Fig. 12 A). This maturity cycle is very similar to that of the Atlanto Scandian herring (Fig. 12 B), but each maturity stage was reached about one month later in the year.

Thus, spawning in Lindåspollene occurred in late March, which coincides with the spawning time for other local west Norwegian herring stocks,

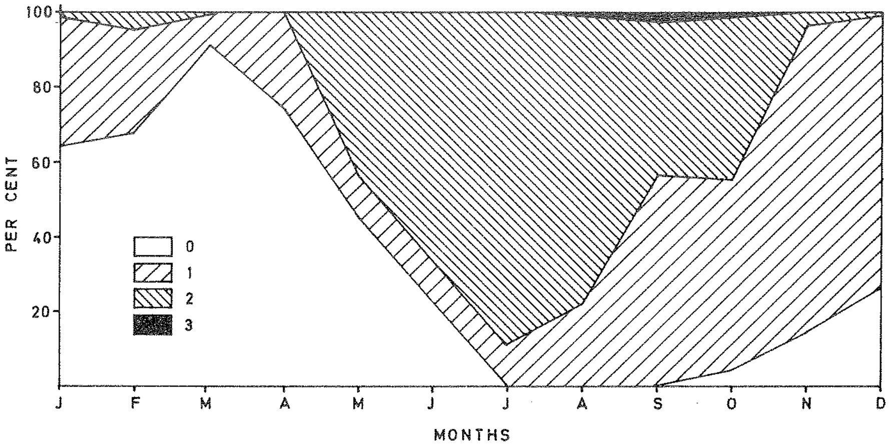

Fig. 11. Mean percent distribution in amount of intestinal fat through the year in the Lindås herring. 0: no fat, 1: traces of fat, 2: moderate fat, 3: much fat.

e.g. Heiamarkspollen and Fjellspollen (ANON. 1964) and Lusterfjorden (AASEN 1952).

Although there was a general seasonal trend in the maturity cycle of the herring in Lindåspollene as outlined above, there were also distinct differences among the years, particularly concerning maturity stages V and VII. It is noteworthy also, that a few specimens in stage VI were found in October–November 1971. Autumn spawning herring have also been observed in other polls in the Bergen area (ANON. 1964).

There were 53,2% males and 46.8% females in the total gill net catch during 1970–1974, and the males dominated in the majority of the samples. However, a t-test for the paired samples showed that the difference in sex composition was not statistically significant ($t = 1.49, 0.10 < p < 0.20$).

Fecundity was determined on 117 herring ranging in length from 24 to 31 cm. The mean number of eggs per ovary ranged from 35459 at 24 cm to 51615 at 31 cm, but there were large variabilities in fecundity within length groups. An analysis of variance on log transformed data (Table 15) showed that the variance component among length groups was significant on the 95% level of probability, and a regression line was therefore fitted. The regression equation was:

$$N = 363.33\ L^{1.42}$$

where N = fecundity, L = length in cm. The correlation coefficient was low ($r = 0.4390$) but statistically significant at the 99% level of probability.

The slope of the regression line differed quite distinctly from the results of previous investigations on the fecundity of herring. Thus, BAXTER (1959) found slope values ranging from 3.8417 to 4.3290 in three different North Sea stocks and Atlanto Scandian herring, and KÄNDLER and DUTT (1958)

Table 14. Maturity stages (%) of Lindås-herring 1970–74, per month, gill nets.

Month		Stages								n
		I	II	III	IV	V	VI	VII	VIII	
Oct.	1970			60.0	33.3	6.7				15
Nov.	»			1.8	98.2					116
Jan.	1971				95.7	4.3				71
Feb.	»			4.2	58.3	37.5				24
Mar.	»		1.3	–	5.1	17.3	75.0	1.3		156
Apr.	»						7.5	58.7	33.8	80
May	»			9.0	–	–	3.3	–	87.7	90
June	»			10.0	–	–	–	–	90.0	107
July	»		3.8	88.5	–	–	–	–	7.7	26
Sept.	»		1.5	77.1	21.4					70
Oct.	»			15.8	73.6	5.3	5.3			19
Nov.	»		1.2	4.0	92.0	0.7	0.7	0.7	0.7	150
Jan.	1972		0.5	0.5	98.0	0.5	–	0.5		200
Mar.	»				17.0	55.3	26.6	1.1		94
Apr.	»						85.7	14.3		14
May	»			13.6	–	4.5	–	4.5	77.4	22
Aug.	»		24.0	24.0	52.0					75
Oct.	»			65.2	34.8					23
Nov.	»		0.7	5.0	92.9	1.4				141
Jan.	1973		12.0	32.0	52.0	–		–	4.0	25
Feb.	»		4.8	4.8	85.6			–	4.8	21
Mar.	»					7.5	84.6	7.8		65
Apr.	»					24.0	72.0	4.0		25
July	»		40.0	13.3	–	–		–	46.7	15
Aug.	»		27.5	45.0	27.5					40
Oct.	»			87.0	13.0					23
Jan.	1974		28.6	1.6	50.8	14.2	–	1.6	3.2	63
Feb.	»		3.3	6.7	73.4	13.3	–	3.3		30
Mar.	»		5.1	3.4	7.2	65.7	16.5	1.7	0.4	236
Apr.	»					5.0	95.0			100

found slope values ranging from 3.465 to 5.063 in three Baltic and two North Sea stocks. The size of the gonads in fishes is generally an isometric function of length, i.e. the fecundity is proportional to the cube of the length (BAGENAL and BRAUM 1968), and a formula of the form:

$F = a + b L^3$

would therefore be a more realistic representation of the relationship between length and fecundity. Applying this formula to the data on the Lindås herring by the method of least squares, the regression equation:

$F = 20843 + 0.97 L^3$

was estimated.

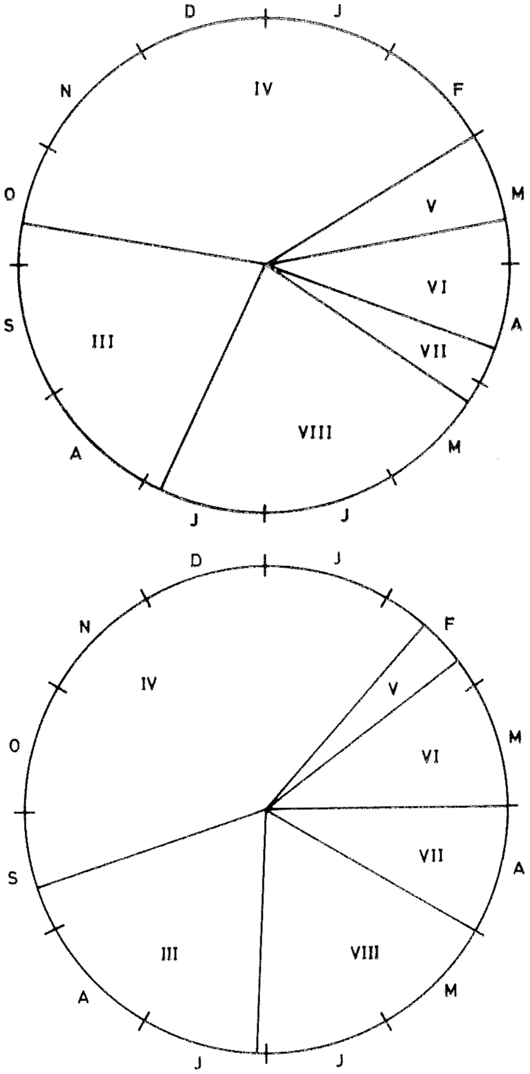

Fig. 12. Annual maturation cycle in the Lindås herring (above) and in the Atlanto-Scandian herring (belowe).

The two regression lines were not distinctly different (Fig. 13), but the line based on the cube of lengths is probably preferable.

The mean weights of the gonads collected during January, February and March of 1971 represented 12.9% ± 1.2%, 16.3% ± 1.3% and 19.3% ± 1.4% of the total body weight, respectively. A mean weight loss of about 20% during spawning must therefore be expected, and this compares favourably with other investigations on herring (Aasen 1952).

Table 15. Analysis of variance on fecundity. Herring ranging in length from 24 to 31 cm (8 length groups).
Data in log-transformation.

Source of variation	df	SS	MS	F
Among length classes	7	0.2576	0.0368	4.9066
Linear regression	1	0.1860	0.1860	15.6303
Deviations from regression	6	0.0716	0.0119	1.5866
Within length classes	99	0.7076	0.0075	

Syslakvågen (Fig. 1) has long been recognized as a spawning area for the Lindås herring (Dahl *et al.* 1973), but the investigations during 1970–1974 revealed considerable annual variability in the success of the spawning. Massive spawning was observed in Syslakvågen on 23 March 1971 and 27 March 1972 in depths from 0 to about 4m (Fig. 14). The eggs, which were clearly visible from the surface, were attached to algae, pebbles and rocks, distributed over an area of about 2 500 m^2. No eggs were observed on the spawning ground in 1973 and only a small number in 1974.

In 1971 herring larvae were collected with a Clarke-Bumpus plankton sampler in the surface waters on the spawning ground, and the maximum number of larvae, 43.5 individuals/m^3, was observed on 20 April. In 1972 larvae were observed from 16 April, reaching a maximum of 140.8 individuals/m^3 on 25 April. In 1973 no herring larvae were observed in Lindåspollene on larval surveys carried out until the month of July. Thus, there are indications that the spawning was a failure in 1973, and this hypothesis is supported by the fact that no 0-group herring were found in a purse seine catch from September 1973, nor I-group in a sample from September 1974 (Table 8).

In a detailed study of spawning and larval ecology of the Lindås herring Furevik (1976) observed spawning in Syslakvågen in 1974, but not in 1975. The highest number of larvae on the spawning ground in 1974, 151.27 individuals/m^3, was observed on 17 April, i.e. 20 days after spawning.

DISCUSSION AND CONCLUSIONS

The herring in Lindåspollene can be distinguished from neighbouring stocks by vertebral counts or growth pattern. However, both of these parameters are subject to phenotypic variation, and genetic studies must therefore be performed in order to further describe the racial identity of the stock. The component of fast growing herring occurs mainly as young

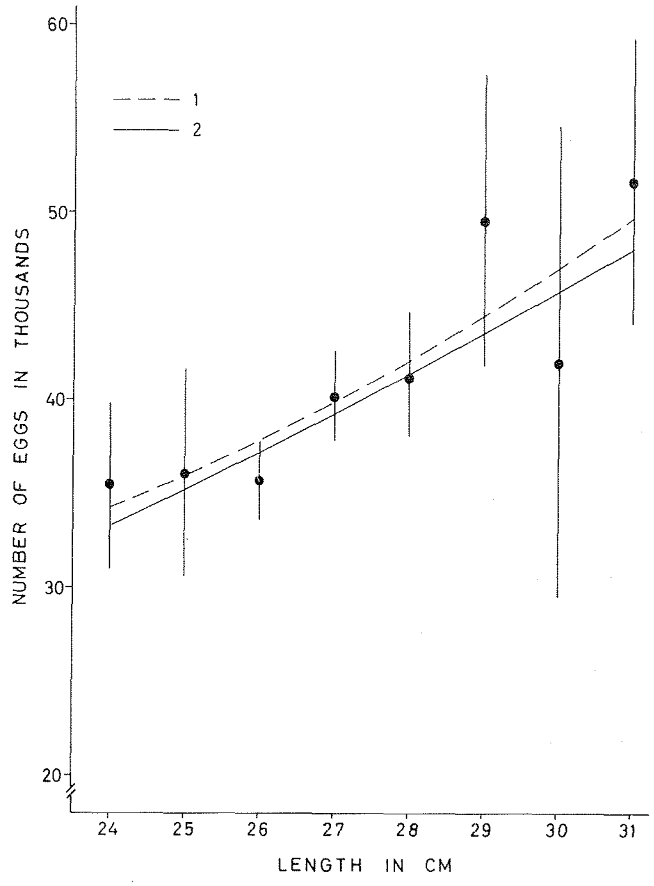

Fig. 13. Fecundity/length curves of the Lindås herring. 1:N = 20843 + 0.97 L^3, 2: N = 363.33 $L^{1.42}$

mature individuals. It seems reasonable, therefore, to conclude that the «strange» herring spends only shorter periods of their lives within Lindåspollene.

The migration of the herring stock within Lindåspollene seems to follow a standard pattern which could be compared with seasonal migration found in herring stocks in the open ocean as described by HARDEN JONES (1968). The feeding migration in spring is particularly directed towards Straumsosen, but a part of the stock moves also to the southern shallow part of Spjeldnesosen. On the basis of the hydrographical data alone it is difficult to explain this seasonal migration. A study of zooplankton during 1971–1972 revealed, however, that the spring migration coincided with a maximum of zooplankton biomass in Straumsosen and in the southern part of Spjeldnesosen in April (HAUG 1972). In the sentral parts of Spjeldnesosen a spring

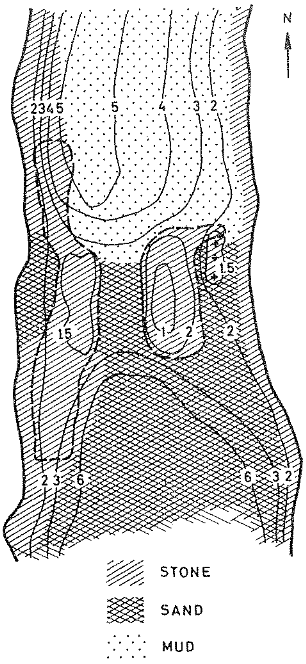

Fig. 14. Depth contour lines and bottom types at the spawning ground in Syslakvågen.

zooplankton maximum was not observed. There were also local differences in the composition of the zooplankton, *Calanus finmarchicus* being more abundant in Straumsosen (ELLINGSEN 1973). Thus, the feeding migration seems to be related to differences in quantity and composition of zooplankton within Lindåspollene.

The majority of the zooplankton during late autumn and winter was concentrated in the deeper layers of Spjeldnesosen (HAUG 1972), i.e. in the overwintering area for the herring. Attempts to catch herring at daytime during the overwintering period have not been successful, and therefore one cannot conclude whether feeding takes place or not.

Emigration of part of the Lindås herring stock to the neighbouring fjords might be expected (ANON. 1964). The differences in the environmental and feeding conditions between the outside fjord system and Lindåspollene would probable be reflected in the growth pattern as determined from scale readings, but such changes in the growth were never observed. It seems likely, therefore, that the emigrated herring do not return to Lindåspollene.

The local herring stock in Lindåspollene is characterized by large fluctuations in the relative strengths of the year classes, with a rich year class emerging every 3–4 years. The present investigation has shown that there were parallel fluctuations in the success of the spawning as determined from observations on the spawning grounds in Syslakvågen and from larval surveys (FUREVIK 1976). The prespawning aggregation of the herring in the northern part of Spjeldnesosen was observed each year, but in both 1973 and 1975 (FUREVIK 1976) the herring did not spawn in Syslakvågen. Estimates of spawning stock size are not available, but age composition data of the prespawning stock in 1973 revealed that the strong 1969 year class dominated, and one would therefore expect a relatively large spawning stock. Thus, the spawning failure in 1973 indicates that success of spawning is not directly related to the spawning stock size. Environmental conditions on the spawning grounds may, however, have a major effect on the success of spawning. In late March 1973, when the spawning failed, i.e. the mature herring did not enter the spawning grounds in Syslakvågen, the salinity at 80 cm depth was only 15.0–17.0‰. (ELLERTSEN 1975). Also RUNNSTRØM (1941) demonstrated for the Atlanto Scandian herring that environmental conditons are important during spawning, and that the herring only deposit their eggs at certain hydrographic conditions. The spawning area in Syslakvågen is shallow, and therefore it is conceivable that the environmental conditions are affected by short term variability in meteorological parameters such as temperatures and precipitation. However, there was no relationship between the strength of the year classes during the period 1959–1974 and the temperature and the precipitation during the first three months of the respective years.

The success of spawning seems to be one of the major factors determining the strength of the year classes, but there are indications that factors affecting eggs and larvae may be equally important. Thus, the number of eggs deposited on the spawning grounds in 1971 was at least as high as in 1972, but the highest density of larvae on the spawning ground at the time of hatching in 1971 was 43.5 individuals/m^3 compared to 140.8 individuals/m^3 in 1972. Observations from purse seine samples during 1971–1974 (Table 8) indicated that the strength of the 1971 year class was insignificant compared to the 1972 year class.

The spawning in 1974 was less successful than in 1971 and 1972, but the number of larvae on the spawning ground at the time of hatching was about the same as in 1972 (151.3 individuals/m^3). Thus, the effect of a successful spawning may be reduced by high egg mortality. FUREVIK (1976) observed predation on the herring eggs by cod, pollack and haddock, and he found that egg mortality was correlated with egg density.

The investigations during 1971–1974 indicate that the very considerable variability in the strength of the year classes in the Lindås herring stock is primarily related to success of spawning in Syslakvågen and to the biotic and abiotic conditions on the spawning grounds. These relationships will be the object of detailed studies in the future research programme in Lindåspollene. The time when the yolk sac has been resorbed has long been considered a critical period in the life of fish larvae (HJORT 1914, 1926) because the absence of suitable and sufficient food organisms may lead to mass starvation. SOLEIM (1942) reported on observations of large numbers of dead herring larvae in samples from the spawning grounds of the Atlanto Scandian herring.

Abundance of larvae at the egg yolk stage has often been used as an index of spawning stock size (SAVILLE 1964). The observation made in Lindåspollene both on the success of spawning and the larval abundance, shows that further studies on the relationship between spawning stock size and larval abundance are greatly needed.

The herring larvae in Lindåspollene may be subjected to considerable fluctuations in the amount of food organisms from year to year. HAUG (1972) found that the zooplankton biomass during the months of March and April was about twice as high in 1972 as in 1971, and ELLINGSEN (1973) found the same difference in the number of zooplankton organisms. Thus, the 1971 year class experienced very poor food conditions at the larval stage, which may be an additional source of reduction of the year class. The poor plankton conditions in 1971 are also reflected in slow growth of all year classes, and in that there was no increase in the mean weight during 1971. Similarly, the condition factor and the amount of intestinal fat during 1971 indicated poor feeding conditions.

The zooplankton community in Lindåspollene is strongly dominated by small copepods. The mean biomass (ashfree dry weight) during the period April–September 1971 for *Pseudocalanus elongatus, Temora longicornis,* and *Oithona similis* was 87.5, 43.7 and 43.7 mg/m^2, respectively, whereas the dominant larger zooplankton organism, *Calanus finmarchicus,* had a mean biomass of 19.7 mg/m^2 (ELLINGSEN 1973). Assuming that the composition of the zooplankton in the watermasses reflects the diet of the herring (SAVAGE 1931), the food of the Lindås herring would consist mainly of small organisms. The energy expenditure related to feeding on the small prey may reduce their relative importance as food organisms, which might explain the slow growth of the Lindås herring compared to the North Sea herring stocks and Atlanto Scandian herring. In these herring stocks *Calanus finmarchicus* constitutes the most important food organisms (RUDAKOVA 1956, CUSHING 1962).

Lindåspollene is characterized by low temperatures (5–3°C) in the water masses deeper than 25–30 m, and the hydrographic investigations during 1971–1974 revealed only small seasonal fluctuations in the temperatures at these depths (AURE 1972, WESTERGAARD 1975). During most of the year the major part of the herring stock was at day time distributed at depths exceeding 30 m, i.e. in water masses 3–4°C colder than the deep water of the

Norwegian coast and fjords (EGGVIN 1940, SÆLEN 1962). Thus, the herring are most of the year exposed to low temperatures and one might expect reduce growth rate even during good feeding conditions. The part of the Atlanto Scandian herring, which are living under the most extreme temperature conditions, e.g. the northern growth type, had reduced growth rate as compared with the more southern component of the stock (ØSTVEDT 1965).

Studies on local Norwegian herring stocks indicate, however, that food conditions play an important part in the growth of the herring. The Lusterfjord herring (AASEN 1952) lives in water masses 2–3°C warmer than the water in Lindåspollene, but it has a very slow growth rate. The zooplankton conditions in the two areas are, however, quite similar, thus *Calanus finmarchicus* comprised about 2% of the total number of organisms in Lindåspollene (ELLINGSEN 1973) and about 3% in Lusterfjorden (AASEN 1952).

The zooplankton of both areas was dominated by small copepods, e.g. *Pseudocalanus elongatus, Acartia spp., Temora longicornis, Oithona spp,* and *Paracalanus parvus.* It seems, therefore, that the slow growth of the herring in Lusterfjorden and in Lindåspollene is related to the composition of the zooplankton community rather than to the temperature of the water masses. This conclusion agrees well with CUSHING (1962) who demonstrated increased growth of the North Sea herring after 1950 as *Calanus* became more predominant in the zooplankton.

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FOOD AND FEEDING OF YOUNG HERRING LARVAE OF NORWEGIAN SPRING SPAWNERS

By
HERMAN BJØRKE
Institute of Marine Research, Directorate of Fisheries, Bergen

ABSTRACT

BJØRKE, H. 1978. *Food and feeding of young herring larvae of Norwegian spring spawners. Fisk.Dir. Skr. Ser. HavUnders., 16*: 405–421.

The gut contents of young herring larvae sampled each hour from 3 to 9 April 1967 at three depth intervals around a floating drogue were examined to study their feeding.

Copepod eggs constituted more than 90% of the food items. Feeding started shortly after sunrise within the same hour in the depth intervals 25–5 m, 30–50 m and 75–55 m. Mean length increased with diminishing yolk sac until absorption when mean length decreased. The latter could indicate lack of suitable food.

The mean gut content of feeding larvae did not increase until after absorption of the yolk sac.

Larvae from the deepest strata had less gut contents than the others, probably because a lower percentage of them had absorbed yolk sacs.

A high percentage of larvae feeding during day-time contradicted total defecation due to capture.

No correlation was found between numbers of *Calanus* eggs in the guts and in plankton. Larvae containing *Calanus* nauplii had more assorted gut contents than larvae containing *Calanus* eggs.

The critical period concept is discussed.

INTRODUCTION

Due to the widely held opinion that year-class strength of herring and other fish species is determined during early life, many investigations have dealt with larval stages.

Analyses of food and studies of feeding behaviour have drawn great interest. Several authors have compared the composition of the gut contents of herring larvae with the surrounding plankton, and attempts have been made to estimate the amount of food required for survival (for references see BLAXTER and HOLLIDAY 1963, BLAXTER 1965, SAVILLE 1971, SCHNACK 1972 and MAY 1974).

Most of these investigations, however, dealt with herring larvae from the North Sea and the Baltic and rather little is known about Atlanto-Scandian herring larvae. The plankton at the spawning grounds of this stock is dominated to a much greater degree by *Calanus finmarchicus* than the plankton at the spawning grounds of other stocks. This reduces the diversity of the available food and makes the larvae more or less dependent on one type of food organism.

DRAGESUND (1970) assumes the coincidence in time between occurrence of suitable food and hatching of herring larvae to be the most important environmental factor controlling year-class strength during early larval development of Norwegian spring spawners. The aim of the present investigation was to study a) the food composition of Norwegian spring spawners, b) factors affecting their gut contents, c) selection of food particles, and if possible d) to discover any critical periods.

MATERIALS AND METHODS

The Institute of Marine Research, Bergen, carried out extensive investigations at the spawning grounds of economically important fish as part of the International Biological Programme during the years 1967–1971. The material used in the present work was selected from an experiment to study the drift of herring larvae off the West coast of Norway (DRAGESUND and NAKKEN 1971).

Sampling was carried out 3–9 April 1967 in a larval concentration marked by a floating drogue. The sampling area around the floating drogue covered 1 nautical mile^2. Larval samples were taken almost every hour as oblique hauls with three permanently open Clarke-Bumpus plankton samplers equipped with nylon nets of 500μ mesh size. Total towing time was 20 minutes, and the samplers were raised in 5 m steps each 4 minutes. The sampling intervals were 25–5 m, 50–30 m and 75–55 m, and the towing speed was 1.5–2 knots. Plankton samples were taken at noon and midnight with Clarke-Bumpus plankton samplers equipped with nylon nets of 90 μ mesh size. The procedure was the same as for larval sampling, except for the use of the closing mechanism of the sampler and a reduction in towing time to 5 minutes.

Larvae from this material were selected for examination as follows (Table I):

a) Larvae sampled during a 45 hour period from the 25–5 m depth interval to compare feeding intensity with time of day.

b) Larvae sampled during the last 24 hours of the previous period (a) from 50–30 m and 75–55 m to compare feeding intensity in all three depth intervals. Reduction in bottom depth below the floating drogue made this sequence incomplete.

c) Larvae from the plankton samples to compare gut contents and plankton composition, and larvae from the larval hauls nearest in time to these plankton hauls to increase information when comparing gut contents and plankton composition.

The larvae were examined after six months preservation in 4% formaldehyde.

When present, 50 larvae from each sample were examined. The larvae varied in length from 6.4 to 12.4 mm with an average length of 9.8 mm.

The plankton samples were usually divided into subsamples of a hundredth with a plankton divider (WIBORG 1951), and two of these subsamples were then examined.

Reference to larvae caught at, for example, 1300 hrs., indicates that they were taken between 1230 and 1329. All times referred to are in local Norwegian time. When unspecified eggs and nauplii are mentioned, these are the eggs and nauplii of *Calanus finmarchicus.*

RESULTS AND DISCUSSION

COMPOSITION OF FOOD

Eggs of *Calanus finmarchicus* constituted in number 91.7% of the gut contents, while nauplii of the same species made up 4.6%. Eggs, nauplii and remains of copepod species other than *Calanus* constituted 2.9%.

BLAXTER (1965) reviewed work done on selection of food by herring larvae. He concluded that smaller larvae caught at sea most frequently contain copepod nauplii and eggs, mollusc larvae and some green food. However, a diet consisting of 92% copepod eggs as observed in the present work (Table 2), seems not to have been recorded from larvae of other stocks than Atlanto-Scandian herring. Other authors examining Norwegian spring spawner larvae also report a high percentage of *Calanus* eggs in the diet. SOLEIM (1942) found that *Calanus* eggs constituted the bulk of the larval diet, while RUDAKOVA (1971) found that they constituted 81.7 and 80.9% of the diet in 1966 and 1967 respectively. BJØRKE (1971) observed that *Calanus* eggs constituted in number 93% of the gut contents of young herring larvae.

SCHNACK (1972) examined the gut contents of herring larvae from the North Sea and the western Baltic. Although he found copepod eggs in the guts, no signs of digestion could be seen. This seems to be in contrast to the present investigation where the ratio of 1:2 empty shells to undigested eggs in the guts suggests that *Calanus* eggs are digested by the larvae. The finding of three empty shells and 59 undigested eggs in the foremost part of the guts shows that rather few empty shells are eaten by the larvae. Digestion of copepod eggs is also supported by a rather low percentage (3.3) of undigested eggs in the rectum. However, the findings of higher ratios of undigested to digested *Calanus* eggs as opposed to *Calanus* nauplii suggests that the digestion of eggs is slower than that of nauplii.

The largest food item, a *Balanus* sp. nauplius stage VI, was found in a larva 10.2 mm long.

Table 1. Numbers of examined larvae from the different depth strata.

	90 μ net															
Date, April	3	4		5					6	7		8		9		
Hour	24	15	16	01	02	12	14	24	13	01	12	24	14	01	13	Total
Depth, m																
25–5	7	17	12	21	30	27	35	53	9	–	1	–	5	1	2	220
50–30	–	–	–	–	11	15	–	17	30	5	6	20	5	15	4	128
75–55	–	–	–	–	53	–	7	2	–	23	5	–	–	–	–	90

	500 μ net																						500 μ net continued																				
Date, April	4	5															6						6												7				8		9		
Hour	13	06	07	08	09	10	11	14	15	16	17	18	19	20	21	22	01	02	03	04	05	07	08	10	12	13	15	16	17	18	19	20	21	22	01	02	10	11	09	12	12	16	Total
Depth, m																																											
25–5	49	50	50	49	100	50	50	50	100	50	50	98	50	49	50	100	103	–	58	50	50	127	52	37	19	32	13	29	17	16	27	49	57	8	6	–	34	24	31	3	27	49	1 913
50–30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	169	50	102	–	50	100	50	60	92	–	50	63	–	9	25	37	5	50	26	–	–	–	–	–	–	–	938
75–55	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	117	51	101	47	35	47	33	29	15	–	–	–	–	–	–	–	–	–	–	37	–	–	–	–	–	–	512

Table 2. Composition of food of 1707 herring larvae.

Undigested food			Digested food		
Types of food	Number	Percentage of total number	Types of food	Number	Percentage of total number
Calanus eggs	2 558	60.42	*Calanus* eggs	1 325	31.30
Calanus nauplii stages I—IV	58	1.37	*Calanus* nauplii stages I—IV	115	2.72
Calanus nauplii stages V—VI	7	.17	*Calanus* nauplii stages V—VI	11	.26
Microcal. nauplii	3	.07	Unidentified nauplii	11	.26
Balanus nauplii	1	.02	*Oithona* nauplii	1	.02
Unidentified nauplii	13	.31	Remains of copepods	67	1.58
Oithona eggs	17	.40	Unidentified objects	34	.81
Metridia eggs	1	.02			
Microsetella	9	.21			
Coscinodiscus	3	.07			

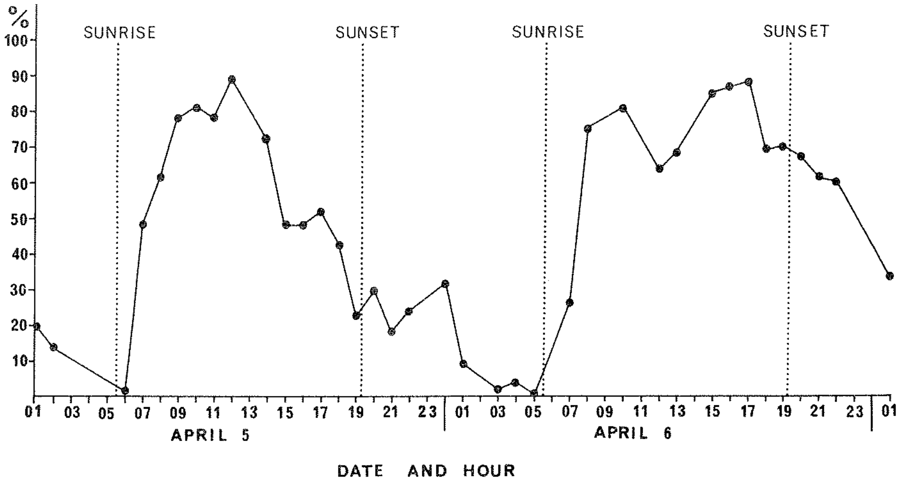

Fig. 1. Percentage of larvae from the 25 – 5 m hauls with undigested gut contents.

FEEDING ACTIVITY

Feeding started shortly after sunrise and declined at nightfall (Fig. 1).

Feeding started within the same hour in all three depth intervals. This activity correlates with observations made by BAINBRIDGE and FORSYTH (1971) on herring larvae in the Clyde. Assuming that the light threshold for feeding is the same at dusk and dawn, feeding activity should have ended at about 1830. Time available for feeding during a 24 hour period would therefore be 13 hours. This differs a little from the 16–18 hours available at 64° N as suggested by BLAXTER (1966). He points out, however, that this is a maximum period based on light measurements taken at the surface; therefore the nearly total cloud coverage of the sky during the 45 hour period of the present investigation may have altered the time available for feeding.

The percentage of larvae with undigested gut contents was rather high at 2000 hrs. in the 25–5 m layer. Therefore, references later in this report to larvae caught during daylight include larvae caught between 0630 and 2029.

YOLK SAC SIZE AND LARVAL LENGTH

The mean length of the larvae increased with decreasing yolk sac size until absorption of the yolk sac, when the mean length decreased. This could indicate insufficiency of suitable food during that period.

The yolk sacs were classified as large, medium, small, absorbed and detatched. Fig. 2 shows the mean length, observed range and 95% confidence limits of 3770 larvae with the various yolk sac sizes. The range

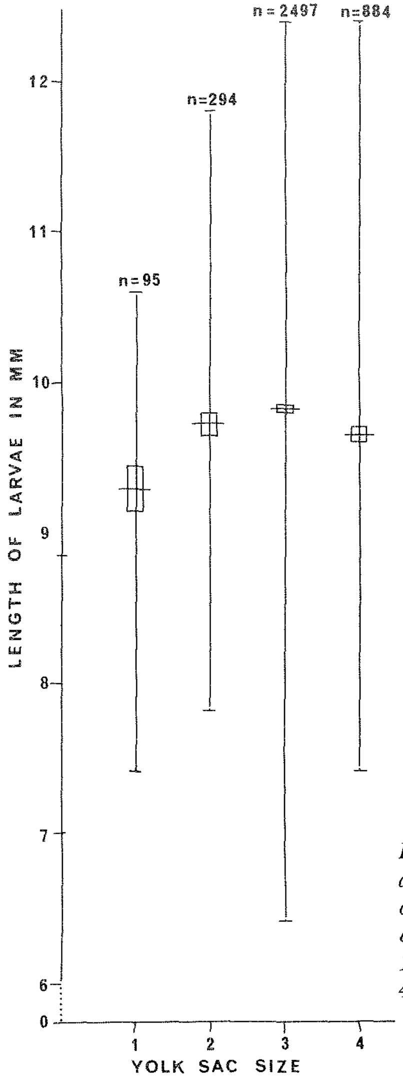

Fig. 2. Mean length, observed range and 95 % confidence limits of the herring larvae examined compared to yolk sac size.
1: large, 2: medium, 3: small, 4: absorbed.

within each stage overlaps to a considerable extent, yet t-tests show significant differences in mean length except for larvae with medium and absorbed yolk sacs. Similar overlapping was found by SOLEIM (1940) and RUDAKOVA (1971) in Norwegian spring spawners, and RUDAKOVA suggests that the overlapping shows differences in composition of the spawners. HEMPEL and BLAXTER (1963) and BLAXTER and HEMPEL (1963) found that herring females with large eggs generally produce larger and presumably stronger larvae with more yolk reserves at hatching. The overlapping in lengh of larvae with different yolk sac sizes might thus indicate differences in composition of the spawners as these authors suggest, but it might also indicate that feeding reduces absorption of the yolk sacs.

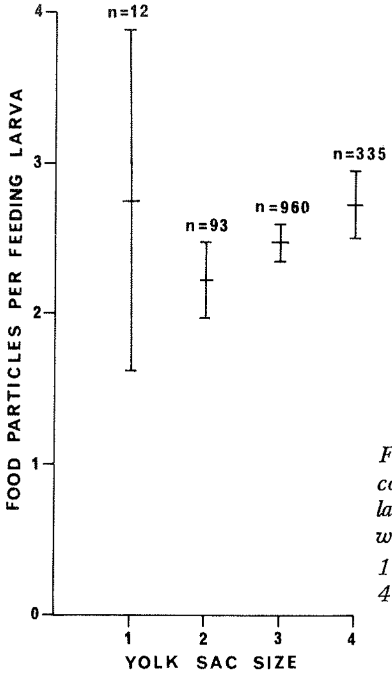

Fig. 3: Mean gut content and 95 % confidence limits of feeding larvae caught during daylight compared with yolk sac size.

1: large, 2: medium, 3: small, 4: absorbed.

Reduction in mean length with absorption of yolk sac, combined with the fact that the same larvae had the largest gut contents, (see later) could indicate insufficiency of suitable food for the larvae after absorpion of the yolk sac. BLAXTER and HEMPEL (1963) report shrinkage in body length of larvae starved under laboratory conditions.

FACTORS AFFECTING AMOUNT OF FOOD IN THE GUT

1. Yolk sac size

The percentage of larvae feeding increased with decreasing yolk sac size, but the mean gut content of feeding larvae did not increase significantly until absorption of the yolk sac.

Almost all authors who have studied feeding of herring larvae, report feeding before the yolk sac is absorbed. Of the 2150 larvae caught during daylight in the present work, 27% of those with large yolk sacs contained food, as did 61, 65 and 70% with medium, small and absorbed yolk sacs, respectively. When omitting the larvae without food, only larvae with absorbed yolk sacs had significantly greater gut contents than larvae with medium and small yolk sacs (Fig. 3).

This observation corresponds with that of ROSENTHAL and HEMPEL (1971) who found that herring larvae with yolk sacs were not successful in catching food items. The high mean gut content of the 12 larvae with large yolk sacs (Fig. 3) has to be disregarded because of few observations.

2. Depth

The highest mean gut content and the largest proportion of feeding larvae were found in the 50–30 m layer.

When studying the amount of gut contents in larvae from different depth intervals, only those caught during a short daylight period were examined to reduce the influence of changes in plankton. Therefore, only larvae caught between 0630 and 1229 on 6 April could be examined from the present material. The mean gut content per larva from the upper to the lowest depth strata was 1.1, 1.6 and 0.7 organisms, and the proportion of larvae with gut contents was 55, 56 and 39% respectively. All the differences between mean gut content were significant at the 5% level.

In the 25–5 m and 50–30 m plankton hauls taken at 1300 hrs. the numbers of *Calanus* eggs and nauplii were 4000 and 5600 organisms per m^3 respectively. Due to insufficient depth the 75–55 m plankton hauls had to be omitted that day. However, on the preceeding and following nights the densities of eggs added to nauplii were 1500 and 3200 per m^3 respectively.

It is questionable as to whether the number of food items in the different depth layers caused the differences found in mean gut content, since the variation coefficient of a single plankton sample is known to be high (CASSIE 1963). Larvae from the deepest layer had the lowest mean gut contents and the lowest percentage of feeders. It was concluded earlier that larvae without yolk sacs had higher mean gut contents than the others. The percentage of larvae at this stage was 18 in the deep layer as opposed to 53 in the two upper ones; therefore it is conceivable that the low mean gut content and low proportion of larvae feeding were due to the low percentage of larvae with absorbed yolk sacs found in this layer.

3. Defecation

Evidence for recent defecation was not found in this material. The high ratio of larvae with gut contents indicates that total defecation took place only to a lesser degree during capture and fixation.

HØGLUND (1968) observed a difference in the condition of the intestine between larvae that had apparently not contained any food for rather a long time and those that had emptied their guts shortly before capture. In the former the whole alimentary canal was transversely contracted with no hollowness visible, while in the latter the hindermost part of the gut immediately before the anus was more or less wide open. He also found a connection between time of feeding and ratio of larvae with distended guts. The condition of the intestine was recorded during the present investigation. After examination of larvae from the 25–5 m hauls no diurnal pattern could be seen in the ratio of larvae with distended guts. Eighty-eight per cent of 1371 larvae caught during daylight had distended guts, as had 90% of 625 larvae caught at night.

Some authors have observed partial or total defecation by stressed larvae (Hardy 1924, Blaxter 1965, Rosenthal and Hempel 1971). It is thus conceivable that larvae from hauls of short duration would contain more food than those from longer ones. The number of food particles from 108 larvae caught during daylight in the upper 25 m in six 5 minute hauls was compared with that of 235 larvae caught in 20 minute hauls immediately before or after the 5 minute hauls. No significant difference in number of food particles was found when applying a t-test. This does not indicate that no defecation occurred, it might just as well show that the degree of defecation at capture and fixation is the same in both types of hauls. However, the high ratio of larvae with gut contents (Fig. 1) indicates that total defecation only took place to a lesser degree during capture and fixation.

4. Selection of food particles. Food densities

The two dominant organisms in the zooplankton, *Calanus* eggs and nauplii, were also the two dominant food items. No correlation was found between the number of *Calanus* eggs in plankton and in guts.

Larvae consuming *Calanus* eggs had a less assorted diet than those eating *Calanus* nauplii.

When studying selection of food particles, only larvae caught together with the food, in this case only larvae from the daylight plankton hauls, should be examined. Unfortunately some of the plankton hauls had rather few herring larvae (Table1). When the number of larvae from these hauls was less than 15, all larvae from the previous or following larval hauls were included. If the total number thus reached was still less than 15, the data were not used. A total of eight camparisons between plankton composition and gut contents could thus be made (Table 3). The ratio of *Calanus* eggs was usually higher in the larval guts than in plankton, while that of *Calanus* nauplii was lower, except when the density of nauplii exceeded ca. 5000 per m^3. Disregarding one observation, the percentage of *Microsetella* spp. and of other copepods was always higher in plankton than in the guts. Cyclopoid nauplii were not found in the guts of these larve although they constituted up to 25% of the plankton.

Blaxter (1965) stated that herring larvae 8 mm long could take food items up to 1.3 mm in length, and this would normally include stage II copepodites of *Calanus finmarchicus* (Wiborg 1948). This implies that most of the organisms present in plankton could have been ingested by the herring larvae (Table 3), but obviously *Calanus* eggs and nauplii were preferred.

Serveral authors report discrepancies between composition of gut contents of herring larvae and surrounding plankton. Hardy (1924) found that *Pseudocalanus* was preferred to *Acartia* even when both were present in equal numbers. Bhattacharyya (1957), on examining plankton from the same hauls as larvae, found that many more planktonic organisms were available

Table 3. Composition of zooplankton and gut contens of herring larvae caught concurrently.

Sample	4 April, 15 hrs.				5 April, 12 hrs.				5 April, 14 hrs.				6 April, 13 hrs.			
Depth interval	25–5 m				25–5 m				25–5 m				25–5 m			
No. of larvae from plankton hauls	17				27				35				9			
No. of larvae from larval hauls	0				0				0				32			
Food items	In plankton		In diet		In plankton		In diet		In plankton		In diet		In plankton		In diet	
	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%
Calanus eggs	2 200	63.6	40	97.6	500	38.2	61	96.8	420	42.9	54	100	3 660	85.7	80	96.4
Calanus nauplii	300	9.5	0	0	60	4.6	0	0	110	11.2	0	0	340	8.0	2	2.4
Cyclopoid nauplii	450	13.0	0	0	330	25.0	0	0	20	2.0	0	0	90	2.1	0	0
Microsetella spp.	40	1.2	0	0	10	0.8	0	0	100	1.2	0	0	0	0	0	0
Other copepods	430	12.0	0	0	400	30,5	0	0	330	33.7	0	0	110	2.3	1	1.2
Other items	10	0.3	1	2.4	10	0.8	2	3.2	0	0	0	0	70	1.6	0	0

Continued:

Samples	4 April, 12 hrs.				6 April, 13 hrs.				7 April, 11 and 12 hrs.				9 April, 12 and 13 hrs.			
Depth interval	50–30 m				50–30 m				25–5 m				25–5 m			
No. of larvae from plankton hauls	15				30				1				2			
No. of larvae from larval hauls	0				0				24				27			
Food items	In plankton		In diet		In plankton		In diet		In plankton		In diet		In plankton		In diet	
	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%	No./m^3	%	No.	%
Calanus eggs	990	37.5	40	97.6	2 960	45.2	113	92.6	11 000	58.3	15	60.0	14 390	64.5	17	53.1
Calanus nauplii	550	20.3	0	0	2 680	40.9	6	4.9	5 320	28.2	8	32.0	5 240	23.5	11	34.4
Cyclopoid nauplii	620	23.9	0	0	150	2.3	0	0	350	1.9	0	0	260	1.2	0	0
Microsetella spp.	140	5.3	1	2.4	220	3.4	0	0	170	0.9	1	4.0	0	0	0	0
Other copepods	280	10.6	0	0	470	7.2	0	0	1 070	5.7	1	4.0	1 870	8.4	4	12.5
Other items	50	1.9	0	0	70	1.1	3	2.5	970	5.1	0	0	550	2.5	0	0

Table 4. Frequency of different kinds of gut content compared with yolk size.
A χ^2 test for *k*-independent samples.
E = Expected frequency. O = Observed frequency.

Gut Contents	Yolk sac size			Total
	Absorbed	Small	Medium and large	
Copepod eggs	E 281.8	807.5	88.6	
	O 276	820	82	1 178
Copepod eggs and other objects	E 33.5	96.0	10.5	
	O 35	89	16	140
Other objects	E 18.7	53.5	5.9	
	O 23	48	7	78
Total	334	957	105	1 396

$\chi^2 = 6.022$ df = 4 $p > 0.05$

than were eaten by the larvae. HENTSCHEL (1950) found that copepod nauplii were not eaten although they constituted up to 50% of the plankton, and that copepodites and adults were preferred instead although they constituted only 6%. WALDMANN (1961) found that copepods were by far preferred and the *Eurytemora* prevailed in the food in spite of its rare occurrence in the plankton.

A t-test for k independent samples (SIEGEL 1956) was applied to find out if a decrease in yolk sac size led to a change in the larval diet (Table 4). The test, comprising 1396 larvae containing food caught during daylight, did not show any significant change in composition of yolk sac size with different diets. Student t-tests on the same material did not reveal significant changes in mean length with different diets. This means that, within the size groups represented in this investigation, selection of food is not dependent on the age of the larva. This correlates with observations made by other authors (LEBOUR 1921, HARDY 1924, BOWERS and WILLIAMSON 1951) who found that changes in diet did not occur until after the yolk sac stage.

Table 3 shows a considerable increase in number of both *Calanus* eggs and nauplii on 7 and 9 April. In order to find any correlation between food items in the plankton and in the guts, the numbers of *Calanus* eggs and nauplii in plankton were rounded off to the nearest thousand and compared to the mean number of the same items per larva by the Spearman rank correlation coefficient (SIEGEL 1956) (Data from Table 3). Significant correlation was found with *Calanus* nauplii, but not with eggs.

To eliminate any possible influence of larvae too weak to feed, the mean numbers of eggs and nauplii per larva containing food were compared to the numbers of those items in the plankton. Again, significant correlation was found with nauplii, but not with eggs. Also the number of eggs and nauplii per larva containing food caught during daylight was correlated with the number of the same items in the plankton. The results were the same; significant correlation was found only between nauplii ingested and in plankton. A possible explanation for the above observations could be that the larvae had developed the habit of catching specific food items. After laboratory experiments ROSENTHAL (1969) suggested that herring larvae might gain preferece for certain kinds of food items during the early life stages, depending on their success in catching the first food particle. He also found that a change in diet from copepod nauplii to *Artemia* did not occur until 3-4 days after the other kind of food particle was added to the original ones. Thus the eight comparisons of diet and plankton composition in Table 3 might represent different larval populations, each population containing larvae searching for food items which they have been successful in catching previously. The increase in number of both eggs and nauplii on 7 and 9 April was obviously due to the fact that the floating drogue became surrounded by a different watermass. This increase in eggs would not lead to an increase in the number of eggs in the larval diet if the new watermass also contained larvae used to catching nauplii. This might also be the reason for the observed correlation between nauplii in plankton and diet. In the samples taken before 7 April the number of nauplii in plankton was low, and the larvae present were in the habit of catching eggs. The samples from 7 and 9 April had higher numbers of nauplii both in plankton and in the diet, and this made the correlation significant.

Of 1256 larvae containing *Calanus* eggs, 5% contained other food items; and of 40 larvae containing *Calanus* nauplii, 28% contained other food items. Larvae containing both eggs and nauplii are not included in these figures. Thus it seems that larvae eating nauplii have an increased ability to catch other food items compared to larvae eating eggs

BLAXTER (1965) refers to investigations where food concentrations required by herring larvae varied from between 300 to 22 000 organisms/m^3. In the present investigation the densities of eggs added to nauplii varied from 530 to 18 990, with an average of 6 300 food praticles per m^3, *Calanus* eggs constituting 71% of these. However, since *Calanus* eggs constituted more than 90% of the gut contents and the nutritional value of one egg is low compared to that of the usually larger organisms reported to be eaten by herring larvae, the observed densities of food in the present work were probably still too low to maintain survival and growth. Also, the decrease in mean length of larvae without yolk sacs (Fig. 2) could indicate deficiency of suitable food after absorption of the yolk sac. DRAGESUND and

NAKKEN (1971) investigated mortality among larvae from the same larval patch as was studied in the present work. They found a reduction of about 95% of the larval population at a length which corresponded to the period of completion of yolk absorption.

THE CRITICAL PERIOD

The critical period concept suggested by HJORT (1914), maintains that the strength of a year-class is determined by the availability of planktonic food shortly after the larval yolk supply has been exhausted. MAY (1974) reviewed this concept in the light of ecological and experimental data. He stated that although other factors also undoubtedly influence larval survival at sea, field and laboratory data suggest that starvation may be an important cause of larval mortality at the end of the yolk sac stage.

Attempts have been made to compare the amount of gut contents of herring larvae with the abundance of available food. LISHEV, RANNAK and LISIVNENKO (1961) report a relationship between the abundance of herring and fry and the number of food organisms in the Bay of Riga from 1955 to 1961. (Quoted from BLAXTER and HOLLIDAY 1963). BAINBRIDGE and FORSYTH (1971) found high feeding intensities associated with high biomass of available prey organisms in the Clyde. SCHNACK (1972) found correlation between biomass in guts and in plankton. Several authors, however, report discrepancies between composition of gut contents and surrounding plankton. HARDY (1924) found that *Pseudocalanus* was preferred to *Acartia* even when present in equal numbers. BHATTACHARYYA (1957), on examining plankton from the same haul as the larvae, found that more planktonic organisms were available than were eaten by the fish. HENTSCHEL (1950) found that copepod nauplii were not eaten although they constituted up to 50% of the plankton, and that copepodites and adults were preferred instead, although they constituted only 6%. WALDMANN (1961) found that copepods were by far preferred and that *Eurytemora* prevailed in the food in spite of its rare occurrence in plankton. SCHNACK(1972) found it difficult to correlate the ingestion of copepod nauplii and gastropod larvae to their quantitative presence in plankton. LEBOUR (1924) found that herring larvae contained mainly molluscs, copepods and unicellular matter (green food remains). Disregarding the latter, as it is not clear whether this is eaten by the copepods before they themselves are ingested, her data shows that only 15% of the larvae containing molluscs and 14% of those containing copepods had other gut contents. DUKA(1968) characterised clupeoid larvae as stenophagous; i.e. the qualitative food components of the larvae are restricted to two or three species of organisms. This is probably the explanation of the findings mentioned previously. The different larval populations become accustomed to catching certain food items and continue to search for these despite greater abundance of other food organisms.

Herring larvae are known to start feeding while they still have large yolk sacs, most probably in order to be able to catch food items when the yolk sac is eventually absorbed and they become dependent on external food.

As food objects *Calanus* eggs are non-motile and without spines, and should thus be easy to catch from any direction. However, they hatch within 24 hours, while development through the nauplius stages lasts for at least 20 days (JONES and HALL 1974). Even if single *Calanus* females are observed to spawn over several weeks (MARSHALL and ORR 1955) and eggs are thus to be found over a long period, nauplii are available over a much longer period. So, if a larva gains preference for *Calanus* eggs because of a temporarily high percentage in the plankton, it will still be searching for them when it becomes dependent on external food. At this stage the surrounding food items might consist mainly of nauplii hatched from the eggs. ROSENTHAL (1969) found that herring larvae needed 3–4 days to change from ingesting copepod nauplii to taking *Artemia*, in other words, from one motile organism to another. The time needed to change from non-motile *Calanus* eggs to nauplii as diet might be longer and thus exceed the time required to reach the «point of no return» as indicated by BLAXTER and EHRLICH (1974). This describes the point at which 50% of a larval population are too weak to feed if food becomes available. For herring larvae this was found to occur six days after absorption of the yolk sac. Difficulties in changing from non-motile to motile food items may also account for the rather low percentage of larvae observed containing *Calanus* eggs together with other food items in this investigation.

On the other hand, larvae starting to feed in a watermass where *Calanus* nauplii are the dominant food items have a lesser likelihood of entering watermasses containing unfamiliar food organisms, as nauplii are present in plankton for a much longer period than eggs and are thus more dispersed. It also seems from the present investigation that the ability to catch nauplii increases the ability to catch other motile food items, since the percentage of larvae containing both nauplii and other food organisms was rather high. This could increase the chance for survival due to the wider food range available to the larvae.

DRAGESUND (1970) stressed the importance of coincidence in time between hatching of herring larvae and the occurrence of suitable food when considering the survival of the larvae. It appears that this coincidence must be emphasized; not only must suitable food be present when the larvae start to feed, but if they gain preference for certain kinds of food at this stage, as suggested by ROSENTHAL (1969), it is of importance for the survival that the same kind of food is available and abundant when they become dependent on external food. This implies that larvae starting to feed when *Calanus* eggs are predominant in plankton have less chance of surviving than those starting to feed when nauplii are abundant.

CONCLUSION

The kind of food particles eaten by smaller larvae of Norwegian spring spawners was similar to that of herring larvae of other races. The proportion of copepod eggs in the diet however, was different, constituting more than 90% of the food items.

Feeding seemed to start shortly after sunrise within the same hour in the depth intervals 25–5 m, 30–50 m and 75–55 m.

The length range of larvae with different yolk sac sizes overlapped considerably, yet t-tests showed an increase in mean length with decreasing yolk sac size, except for larvae with absorbed yolk sacs which were shorter than those with small yolk sacs. This could indicate lack of suitable food after the yolk sac stage.

The percentage of larvae feeding increased with decreasing yolk sac size, but the mean gut content of feeding larvae did not increase until after absorption.

Larvae from the deepest strata, 75–55 m, had less gut contents than the others, probably because of a lower percentage of larvae with absorbed yolk sacs in this depth layer.

Some authors report larvae defecating partially or totally when stressed. Larvae from hauls of short duration did not have greater gut contents than larvae from longer ones. Total defecation was contradicted by the high ratio of feeding larvae caught during daylight.

No correlation was found between the number of *Calanus* eggs in the guts and in plankton. Larvae containing nauplii had more assorted gut contents than larvae containing eggs.

A «critical period» could arise when larvae having learned to feed on *Calanus* eggs have to change to motile objects when nauplii hatch.

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ANALYSIS OF EMPIRICAL OBSERVATIONS ON THE SCATTERING OF SOUND BY ENCAGED AGGREGATIONS OF FISH

By
KENNETH G. FOOTE
Department of Applied Mathematics, University of Bergen.

ABSTRACT

FOOTE, K. G. 1978. Analysis of empirical observations on the scattering of sound by encaged aggregations of fish. *FiskDir. Skr. Ser. HavUnders.*, *16*: 422–455.

The experimental findings of RØTTINGEN (1975 and 1976) for the scattering of ultrasonic sound by encaged aggregations of saithe and sprat are analyzed. The insensitivity of the relationship of the mean time-integrated echo intensity $\bar{\varepsilon}$ and fish number density ν to both the center frequency and pulse duration of the ensonifying signal is considered qualitatively. A general theory for the scattering of sound by a collection of randomly distributed and oriented, but otherwise identical scatterers, whose individually complicated scattering behavior is described by two parameters, the backscattering and extinction cross sections, is applied to Røttingen's experiment with saithe. The empirical ε–ν relationship is reproduced successfully with respect to a unique set of parameters of a model whose main ingredients are the following: assumption of a truncated Gaussian distribution in tilt angle for the orientation distribution; expression of the scattering cross sections in terms of the mean and variance of this distribution; assumption that the mean tilt angle is independent of ν and that the variance in tilt is the sum of two variances: the intrinsic variance, which is postulated to be an exponentially decreasing function of ν, and the perspectival variance, assumed constant, which is the mean square apparent tilt of the scatterer due solely to its azimuthal orientation relative to the generally obliquely located source/receiver. By comparing predictions of the $\bar{\varepsilon}$–ν relationship with those observed for saithe, the mean extinction cross sections at the two frequencies of Røttingen's experiment are deduced.

INTRODUCTION

In an experiment performed by Røttingen in 1973 (RØTTINGEN 1975 and 1976), which was designed to help clarify the relationship between acoustic echo energy and the number density of schooling fish when ensonified by ultrasonic pulses, the echoes from encaged aggregations of fish of uniform kind and size were observed. By elementary signal processing the information contained in each echo was reduced to a single number, the time-integrated echo intensity ε. Because of the considerable pulse-to-pulse variability in this quantity, many determinations of ε were made at each observed number density ν. A large number of independent samples were then drawn from this population of measurements and their average, $\bar{\varepsilon}$, computed with respect to this ensemble, so that the true $\bar{\varepsilon}$ at a particular number density would be known with a high degree of confidence. This determination of $\bar{\varepsilon}$ was made systematically over a wide range of ν, which probably spans that observed in nature, for each of three species of fish: *Pollachius virens* (L.) or saithe, *Sprattus sprattus* (L.) or sprat, and *Scomber scombrus* L. or mackerel.

The surprising finding of the observations on the saithe and sprat was that the relationship of $\bar{\varepsilon}$ and ν is essentially non-unique, and is distinguished primarily by fish kind and size and only secondarily by pulse duration and center frequency. The basic ν-dependence of $\bar{\varepsilon}$ is the following: linear proportionality up to a certain density; thereafter, a steady decrease in the rate of increase of $\bar{\varepsilon}$ with ν until a maximum is reached; then, a decline in $\bar{\varepsilon}$ for still higher values of ν. Thus there are values of $\bar{\varepsilon}$ which obtain at each of two distinct densities.

The observations of $\bar{\varepsilon}$ for the mackerel were quite irregular. Because these fish were observed, by mean of an underwater camera, to cluster along the netting of their cage, rather than to distribute themselves more or less uniformily throughout it as both the saithe and sprat did, their observations are not considered further in this study.

It is the aim this paper, then, to explain the basic observations of Røttingen for saithe and sprat. This will be done firstly on a qualitative level: the approximate insensitivity of the $\bar{\varepsilon}$–ν relationship to the pulse duration and center frequency of the ensonifying signal will be explained and, through a dimensional analysis of the empirical findings, the requirements for a quantitative theory will be established. A general theory for the scattering of sound by collections of scatterers, which is developed in the Appendix, will then be applied to Røttingen's experiment with saithe. A similar detailed quantitative analysis for sprat will not be carried out because of the lack of ventral aspect target strength data for sprat, which will be seen to be of crucial importance in the determination of the precise form of the $\bar{\varepsilon}$–ν relationship.

METHOD

QUALITATIVE ANALYSIS OF RØTTINGEN'S OBSERVATIONS

For convenience Røttingen's results are reproduced in a condensed format in Fig. 1 and 2. In both figures, which are distinguished by fish species and size, the empirical relationship of the mean or ensemble-averaged time – integrated echo intensity $\bar{\varepsilon}$ and fish number density ν is

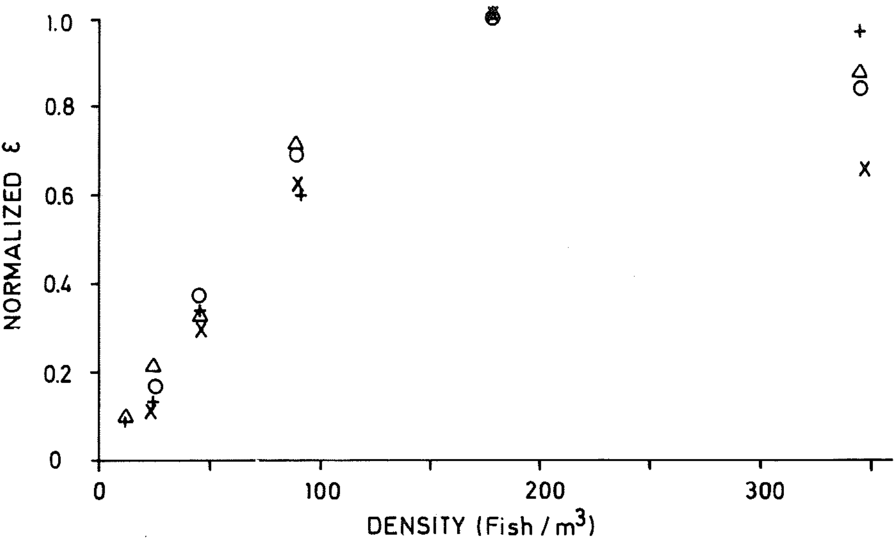

Fig. 1. Røttingen's observations of the normalized mean time-integrated echo intensity $\bar{\varepsilon}$ for saithe when ensonified by a narrowband signal for four conditions of pulse duration and center frequency: 0.3 msec at 38 kHz (o), 0.6 msec at 38 kHz (△), 0.1 msec at 120 kHz (+), and 0.6 msec at 120 kHz (x).

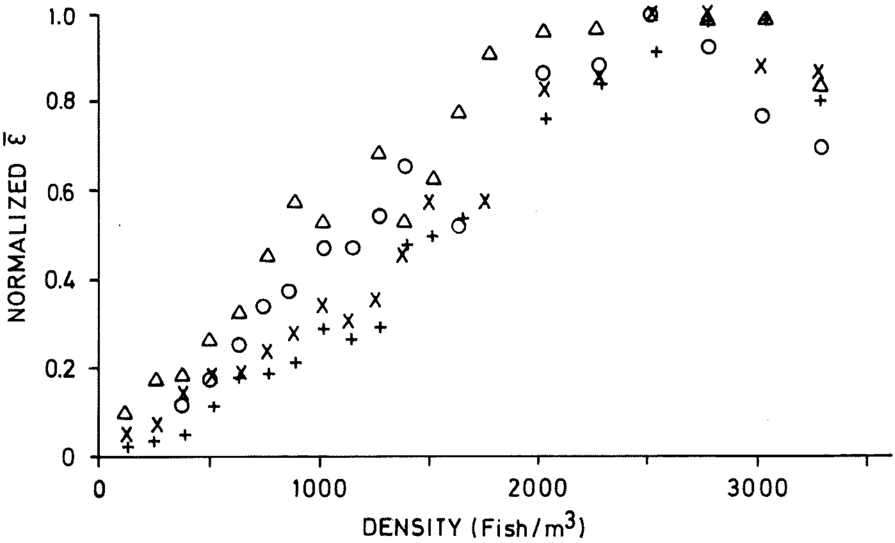

Fig. 2. Røttingen's observations of the normalized mean time-integrated echo intensity $\bar{\varepsilon}$ for sprat when ensonified by a narrowband signal for the same four conditions of pulse duration and center frequency shown in the legend of Fig. 1.

stated for the following four combinations of pulse duration T and center frequency $\omega_o/2\pi$ of the ensonifying signal: $T = 0.3$ and 0.6 msec for $\omega_o/2\pi = 38$ kHz and $T = 0.1$ and 0.6 msec for $\omega_o/2\pi = 120$ kHz; all for a pulsed sinusoid of the form $\mathrm{rect}(t/T)\cos(\omega_o t)$, as expressed in the notation of WOODWARD (1964). The four empirical $\bar{\varepsilon}$–ν relationships are stated for saithe of uniform length distribution 35.1 ± 0.6 cm and mean mass 375 g in Fig. 1 and for sprat of uniform length distribution 12.1 ± 2.3 cm and mean mass 12 g in Fig. 2.

In view of the wide ranges in center frequency and pulse duration represented by the data, it is concluded that the $\bar{\varepsilon}$–ν relationship is generally insensitive to both center frequency and pulse duration of the ensonifying signal, at least for the narrowband pulsed sinusoidal type, and is distinguished primarily by fish kind and size.

That the $\bar{\varepsilon}$-ν relationship is relatively insensitive to frequency is not difficult to explain. This is because all estimates of a characteristic scattering size a indicate that the characteristic size-to-wavelength ratio is such that the proportional quantity $ka = 2\pi a/\lambda$, where k is the wavenumber and λ is the wavelength of the signal at its center frequency, is always in excess of unity and generally is much greater than unity. Such estimates of the characteristic scattering size include those deduced from the following three sources: (1) the gross dimensions of the fish (RØTTINGEN 1976, RASMUSSEN 1960, NAKKEN pers. com.); (2) the size of the swimbladder, the chief scattering organ of these species of fish, based on the estimate that the swimbladder occupies roughly 5 per cent of the total volume (SHIBATA 1970, MCCARTNEY and STUBBS 1971); and (3) measurements of target strength, assuming approximate equality of peak ventral and dorsal aspect target strengths (NAKKEN and OLSEN 1973). In the limit that the size is much larger than the wavelength, the phenomenon of scattering is essentially geometric, and those quantities which describe the scattering behaviour of a body, for example, a fish, adopt their respective constant high frequency values. Thus, other things remaining unchanged, a change in magnitude of the center frequency of the ensonifying signal, if sufficiently high, say, above 38 kHz, should not affect the relationship of $\bar{\varepsilon}$ and ν.

The relative insentitivity of the $\bar{\varepsilon}$–ν relationship to changes in pulse duration can also be understood rather simply. The photographic evidence of Røttingen's experiment showed the spatial distribution of fish in their net cage to be generally randomly homogeneous throughout the entire volume of the cage. The pulse-to-pulse variations in the time-integrated echo intensity were large, suggesting both the importance of coherence for particular ε and the fact that the fish did not remain stationary, but moved about. That this internal movement provides a mechanism for the randomness of ε is clear, for while the ensonifying signal was narrowband, with $\omega_o T >> 1$ for all experimental conditions of ω_o and T, the fish densities were always such that the mean nearest-neighbour fish distance was much greater than the wavelength, i.e. $v^{-1/3} \gg \lambda$. Thus the phases or relative times of the constituent echoes from individual fish, which compose the whole echo, are entirely random. The effect of this is to cause the coherent contribution to ε to vanish in the mean of large numbers of independent observations of ε at particular ν, so that $\bar{\varepsilon}$ is equal to the irreducible incoherent contribution alone. This non-vanishing component of $\bar{\varepsilon}$ is linearly proportional to T as the energy contained in each constituent echo is exactly proportional to the energy contained in the ensonifying signal, which for the pulsed sinusoids of Røttingen's experiments is proportional to T. The basic form of the $\bar{\varepsilon}$–ν relationship, when normalized by or scaled to the maximum value of $\bar{\varepsilon}$ for the particular experimental conditions of ω_o and T, should, therefore, be independent of the pulse duration T.

The implication of the insensitivity of the $\bar{\varepsilon}$–ν relationship to ω_o and T for both the saithe and sprat of Røttingen's experiments is that the phenomenon of echo formation by an encaged aggregation of fish at ultrasonic frequencies is primarily geometric and incoherent. The principal evidence for this conclusion is that a variation in frequency by a factor of three and a variation in pulse duration, thence phase, by a factor of six, with corresponding changes in the scatterer size-to-wavelength ratio and mean scatterer separation-to-pulse length ratio, have only an indiscernible effect on the ν-dependence of $\bar{\varepsilon}$. If the mean echo strength were very dependent on the coherent or physical effect of interference among the constituent echoes, then there almost certainly would be considerable variations in the $\bar{\varepsilon}$–ν relationship as T and ω_o were varied; yet, what variations are present are slight and apparently even too inconsistent to justify speculation about their origin. The fact that the $\bar{\varepsilon}$–ν relationship is stable with respect to large changes in both T and ω_o for different kinds of fish of uniform size distributions, but of widely differing mean lengths and masses, strengthens the conviction that a purely geometric theory of scattering should be entirely adequate to explain the quantitative features of the $\bar{\varepsilon}$–ν relationship.

Such a theory, which is developed in the Appendix and which has some common features with the theory of acoustic scattering by wakes (WILDT 1947), is applied to the problem of Røttingen's experiment with saithe in the next section.

QUANTITATIVE ANALYSIS OF RØTTINGEN'S OBSERVATIONS

I Scattering of sound by an aggregation of fish

The theory for acoustic scattering by a collection of randomly distributed and oriented, but otherwise identical scatterers, which is presented in the Appendix, can be applied to the problem of acoustic scattering by an aggregation of fish if the following assumptions are made:

(1) the acoustic source and receiver are essentially collocated;

(2) the ensonifying signal is narrowband and of such a center frequency that the only significant multiple scattering effect is that of extinction of the incident wave;

(3) the amplitude of the signal is sufficiently weak so that all nonlinear effects can be ignored;

(4) the fish distribute themselves randomly homogenously throughout a definite volume which is fixed relative to the source/receiver and in the farfield of the source/receiver;

(5) the fish are identical in size;

(6) the scattering parameters of a single fish can be represented by exactly two parameters, the backscattering and extinction cross sections, which generally are functions of the orientation of the fish.

When these conditions are satisfied, according to the results of the Appendix, the mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ can be written

$$\bar{\varepsilon} = \frac{I_o \varrho(0)}{4\pi} \sum_n \frac{D_{S,n}^2 D_{R,n}^2}{r_n^4} \sigma_{b,n} \, exp[-4\alpha r_n - \nu\sigma_e(r_n - r_{n,o})]$$

where the overhead bar denotes the operation of ensemble-averaging, and where the several quantities have the following meanings

I_o	is the peak instantaneous intensity of the ensonifying pressure field at unit distance from the source;
$\varrho(0)$	is the maximum value of the signal autocorrelation function;
$\sigma_{b,n}$	is the backscattering cross section of the n^{th} scatterer;
$D_{S,n}$	and $D_{R,n}$ are the respective source and receiver pressure directivity factors in the direction of the n^{th} scatterer;
r_n	is the distance between source and n^{th} scatterer;
α	is the attenuation rate of the medium at the center frequency of the ensonifying signal;
ν	is the scatterer or fish number density;
$\bar{\sigma}_e$	is the ensemble-averaged extinction cross section;
$r_{n,o}$	is the distance from source to nearest surface of the volume in the direction of the n^{th} scatterer.

II. Approximation of $\bar{\varepsilon}$ for a particular geometry and its evaluation for constant scattering parameters.

In order to gain some insight into the above expression for $\bar{\varepsilon}$, which, under certain circumstances, could represent the mean acoustic energy backscattered by an aggregation or school of fish, $\bar{\varepsilon}$ is now examined for a particular geometry. For convenience this is chosen to be of the type used by Røttingen in his experiments.

Consider a cylindrical volume V boulding a collection of scatterers which are distributed randomly, but homogeneously throughout it. V is aligned with the common principal response axis of essentially collocated source and receiver. The position of the source/receiver defines the origin of a coordinate system whose z-axis is that of the common principal response axis. The transmit and receive beam patterns are broad with respect to V, which, further, is assumed to be sufficiently narrow so that the contribution to the echo from a single scatterer is, to a good approximation, independent of its location in any transverse plane of V. The general expression for $\bar{\varepsilon}$ can be reduced to the following:

$$\bar{\varepsilon} = \frac{I_o Q(0) V}{4\pi (z_2 - z_1)} \nu \bar{\sigma}_b \int_{z_1}^{z_2} \frac{\exp\left[-4\alpha z - \nu \bar{\sigma}_e (z - z_1)\right]}{z^4} dz$$

where z_1 and z_2 are the distances from source to nearer and further bounding planes of V, respectively, and where V is the measure of the cylindrical volume.

The integral in this expression for $\bar{\varepsilon}$ can be reduced to the exponential integral, so that $\bar{\varepsilon}$ can be expressed in the following alternative form:

$$\bar{\varepsilon} = \frac{I_o Q(0) V}{24 \pi l} v \bar{\sigma}_b \exp(-4\alpha z_1)\, Y(4\alpha + v \bar{\sigma}_e)$$

where $l = z_2 - z_1$ and

$$Y(a) = \int_{z_1}^{z_2} \frac{\exp\left[-a(z - z_1)\right]}{z^4} dz = 2\left[\frac{1}{z_1^3} - \frac{\exp(-al)}{z_2^3}\right] - a\left[\frac{1}{z_1^2} - \frac{\exp(-al)}{z_2^2}\right]$$

$$+ a^2\left[\frac{1}{z_1} - \frac{\exp(-al)}{z_2}\right] - a^3 \exp(az_1)\left[E_1(az_1) - E_1(az_2)\right]$$

where $E_1(x)$ is the exponential integral

$$E_1(x) = \int_x^{\infty} \frac{\exp(-t)}{t} dt$$

as defined in Abramowitz and Stegun (1964).

If the ensemble-averaged scattering cross sections $\bar{\sigma}_b$ and $\bar{\sigma}_e$ are regarded as constants, independent of the scatterer number density ν, then inspection of the integral expression of $\bar{\varepsilon}$ shows that $\overline{\varepsilon(\nu)}$ is a monotonically increasing function of ν, which increases linearly with ν for small ν and gradually becomes asymptotic to a constant for large ν. These limiting forms of $\bar{\varepsilon}$ are the following:

$$\overline{\varepsilon(\nu)} \underset{\nu \to 0}{\sim} c(c_1\nu - c_2\nu^2) + O(v^3)$$

$$\overline{\varepsilon(\nu)} \underset{\nu \to \infty}{\sim} c_3 - \frac{c_4}{\nu} + O\left(\frac{1}{\nu^2}\right)$$

where

$$c = \frac{I_o \varrho(0) V \bar{\sigma}_b}{4\pi l}$$

$$c_1 = \int_{z_1}^{z_2} \frac{\exp(-4\alpha z)}{z^4}\, dz$$

$$c_2 = \bar{\sigma}_e \left[\int_{z_1}^{z_2} \frac{\exp(-4\alpha z)}{z^3}\, dz - z_1 c_1 \right]$$

$$c_3 = \frac{c \exp(-4\alpha z_1)}{\bar{\sigma}_e z^4}$$

$$c_4 = \frac{4c_3}{\bar{\sigma}_e}\left(\alpha + \frac{1}{z_1}\right)$$

These limiting forms of $\overline{\varepsilon(\nu)}$ confirm what is expected from simple physical considerations. In the limit of very low densities the several echoes from individual scatterers are generally distinct, i.e., separated in time, since a density can be found for which the signal transmission time T is relatively short compared to the mean time difference between the echoes of nearest-neighbour scatterers, so that the total echo energy is merely the sum of the individual echo energies; thence, $\bar{\varepsilon}$ is proportional to the number of scatterers in V, and thence to ν. At high densities the effect of extinction is strong; in fact, the diminution of the incident acoustic field as it penetrates V exactly counterbalances the increased number of scatterers, whose mean

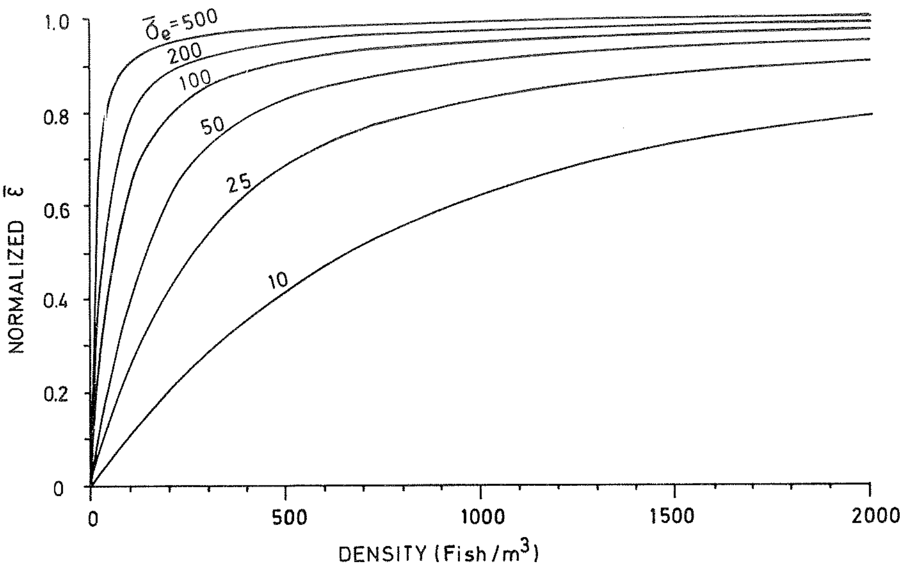

Fig. 3. Normalized mean time-integrated echo intensity $\bar{\varepsilon}$ for a collection of scatterers with constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$ when ensonified by a narrowband signal of center frequency 38 kHz. $\bar{\sigma}_e$ is expressed in units of sqvare centimeters.

contribution to the irreducible incoherent part of $\bar{\varepsilon}$ is inversely proportional to the total number νV of scatterers, and thence to ν, so that $\bar{\varepsilon}$ steadily approaches a constant as ν increases. This asymptotic behaviour is a manifestation of conservation of energy: only a finite amount of energy is contained in $s(t)$ and only a finite amount of energy – at most, that which is intercepted by V – can be backscattered. If, moreover, at all values of ν the scatterers are distributed randomly homogeneously in V, so that $\bar{\varepsilon}$ is composed only of its incoherent part, then the transition from linear growth at low densities to asymptotic constancy at high densities will be completely smooth and gradual, i.e., monotonic.

If a scatterer is of finite size and simple shape, then in the limit of the highest densities the distribution of scatterers in V may become regular, in which case the interference of the constituent echoes will make a non-negligible contribution to the total echo. The amount of acoustic energy intercepted and backscattered by V is still finite in this situation, but the dependence of $\bar{\varepsilon}$ on the now significant coherent part of the echo, in addition to the irreducible incoherent part, renders the asymptotic approach to a constant at the highest density non-monotonic, or oscillatory, in the general case. The precise approach to the high density asymptote depends on the precise narrowband signal, scatterer size, geometry of V and magnitude of $\bar{\sigma}_e$ for the case of constant, density-independent $\bar{\sigma}_b$ and $\bar{\sigma}_e$.

As an illustration of the dependence of $\bar{\varepsilon}$ on ν for constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$, the results of a calculation of $\bar{\varepsilon}$ for the case of a 38 kHz narrowband signal and cylindrical volume with $z_1 = 7.7$ m and $z_2 = 9.5$ are presented in Fig. 3. These results are shown for a range of values of the constant extinction cross section $\bar{\sigma}_e$ and are normalized to their respective high density asympotic values. Comparable results for the case of a 120 kHz narrowband signal are nearly indistinguishable from these and are, therefore, omitted.

III. *Application of theory to Røttingen's experiment with saithe.*

The particular geometry that was chosen for the approximation of the general expression for the ensemble-averaged time- integrated echo intensity in the preceding section is similar to that used by Røttingen in his experiments. For the measurements on saithe, the fish were contained in an approximately cylindrical net cage of height 180 cm and radius which varied smoothly between 70 cm and 72.5 cm. The cage was oriented vertically with its longitudinal axis nearly coincident with the common transmitting/receiving axes of acoustic transducers at 38 and 120 kHz, each of which was used in its dual transmitting/receiving capacity. The transducers were placed below the cage, which was located near the surface to facilitate the transfer of fish, so that the saithe were ensonified ventrally, instead of dorsally as is customany in such work. The distances from the transducers to the nearer and further bounding planes of the cylindriform net cage were 7.7 m and 9.5 m, respectively. The configuration of transducers and cage were such that the maximum degradation in sound source level over the cage, because of transducer directivity, in the worst case was less than 1.5 dB. All photographic observations of the saithe showed that they were distributed more or less uniformily throughout the volume and adopted no particular orientation or attitude as they might be expected to do when schooling, for example.

The circumstances of Røttingen's experiment evidently fulfill the conditions under which the general expression for $\bar{\varepsilon}$ was reduced to the simple one-dimensional integral approximation earlier, if the slight variation in sound level due to transducer directivity over the net cage is ignored, with a single difference: that the scattering properties of the saithe must be evaluated for the ventral aspect rather than the dorsal aspect. The applicability of the approximation to $\bar{\varepsilon}$ for Røttingen's experiment is thus established; evaluation of it, if satisfactory, should disclose the mechanisms underlying the observations shown in Fig. 1 and, presumably, by analogy, those for the sprat which are shown in Fig. 2.

That Røttingen's observations cannot be explained by a model in which the scattering parameters $\bar{\sigma}_b$ and $\bar{\sigma}_e$ are both independent of the fish number density ν is clear. Such a model can explain only a monotonic increase in $\bar{\varepsilon}$ with ν which becomes asymptotic to a constant at very high densities, as is illustrated in Fig. 3. The scattering parameters $\bar{\sigma}_b$ and $\bar{\sigma}_e$ must, therefore, depend on ν.

It is not surprising that $\bar{\sigma}_b$ and $\bar{\sigma}_e$ should depend on ν when it is considered that as the number, thence density, of fish in the net cage increases, an individual specimen has less space in which to move and, consequently, must curtail its orientation range to avoid interfering with its neighbours, which would be individually and socially harmful, thence prohibited. Thus, the ensemble-averages of σ_b and σ_e, which generally vary with the orientation of the scatterer, or fish, relative to the direction of ensonification, will depend on ν. In the absence of any quantitative information about the aggregating properties of the encaged saithe of Røttingen's experiment, or, in fact, of the encaged fish of any other study, a rather simple, but plausible model for the orientation distribution of the encaged saithe is proposed. A model which connects the spread of this distribution with the fish number density ν is also proposed so that $\bar{\sigma}_b$ and $\bar{\sigma}_e$, which are expressed in terms of the characteristic measures of the orientation distribution, can be computed directly in terms of ν.

In the course of determining the density-dependence of $\bar{\varepsilon}$ for the particular conditions that obtained during Røttingen's experiments with saithe, which is contained in the factor

$$\nu\bar{\sigma}_b \int_{z_1}^{z_2} \frac{exp\ [-4\alpha z - \nu\bar{\sigma}_e(z-z_1)]}{z^4}\, dz$$

where $z_1 = 7.7$ m, $z_2 = 9.5$ m and α is the medium attenuation rate at either 38 kHz or 120 kHz; an orientation distribution for the saithe is proposed; $\bar{\sigma}_b$ and $\bar{\sigma}_e$ are evaluated in terms of the variance and mean of this distribution; and the variance of this distribution is expressed as a function of the fish number density ν, so that the expressions for $\bar{\sigma}_b$ and $\bar{\sigma}_e$ can be evaluated directly in terms of ν.

IIIa. *Orientation distribution.*

The form of the orientation distribution that obtained during Røttingen's experiment with the saithe is unknown; it was not measured, and there is no formal theory which specifies the orientation distribution of encaged aggregations of saithe or of any other kind of fish. But insofar as the fish were observed to adopt a more or less random distribution in inclination about a horizontal or near-horizontal inclination, and insofar as saithe has a dorsal aspect target strength which is rater insensitive to roll over a 60 degree range (Nakken and Olsen 1973), there appears to be plausibility to the selection of a very simple form for this distribution, as is explained below.

The swimbladder, when present in fish as it is in a well-developed state in saithe, is recognized – see, for example, Shibata (1970), Harden Jones and Pearce (1958) and Cushing and Richardson (1955) – to contribute significantly to the echo, even at ultrasonic frequencies. The fact that this organ is approximately cylindriform and generally is more or less aligned with the fish center line, which is defined here as the line running from the front of the upper jaw to the root of the tail, suggests that the principal scattering properties of the fish, and not merely its echo, are rather insentitive to roll, at least over that angular range where the swimbladder presents a similar surface. This has been confirmed by measurements of the dorsal aspect target strength of saithe, cod and herring (Nakken and Olsen 1973). Inspection of the morphology of saithe (Rollefsen 1960–62 and Midttun and Hoff 1962) suggests that the ventral aspect target strength and, presumably, other similar primary scattering characteristics are insensitive to roll. It may be inferred, therefore, that the dependence of the orientation distribution of saithe on roll may be ignored since the scattering properties of interest, σ_b and σ_e, and their ensemble averages will be similarly insensitive with respect to roll.

Since the saithe of Røttingen's experiment were observed to adopt a more or less random distribution in inclination about some approximately horizontal mean inclination, the orientation distribution may plausibly be described by a truncated Gaussian distribution in inclination or tilt angle θ, which is defined as the angle that the center line of the fish makes with the horizontal plane. This distribution is described by the probability density function

$$f(\theta) = \begin{cases} \dfrac{1}{\sqrt{2\pi}\,\sigma_\theta} \; exp \left[-\dfrac{(\theta-\bar{\theta})^2}{2\sigma_\theta^2} \right] & \text{for } |\theta-\bar{\theta}| \leqq \lambda'\sigma_\theta \\ 0 & \text{for } |\theta-\bar{\theta}| > \lambda'\sigma_\theta \end{cases}$$

were λ' is a factor of the order of three if the results of Olsen (1971) for cod in the open sea are applicable. The normalizing factor $1/\sqrt{2\pi}\sigma_\theta$ is rigorously true only for infinite λ', but is underestimated by .3% for $\lambda'=3$, 1.3% for $\lambda'=2.5$ and 4.6% for $\lambda'=2$. The mean angle of inclination $\bar{\theta}$ may be assumed to be small and constant with respect to the density ν of fish, and the standard deviation σ_θ of the distribution is presumed to be a monotonically decreasing function of ν. The precise dependence of σ_θ on ν is discussed below, after the ensemble averages of σ_b and σ_e have been expressed as functions of σ_θ and $\bar{\theta}$, the characterizing parameters of the orientation distribution.

IIIb *Ensemble-averaged backscattering cross section.*

As the spatial distribution of the saithe in Røttingen's experiment was observed to be approximately randomly homogeneous throughout the net cage, the ensemble average of a scattering parameter such as σ_b or σ_e is just the average of the same quantity with respect to the orientation distribution, which, by the discussion of the previous section, is assumed to be described adequately by the probability density function $f(\theta)$. Thus, the average of the backscattering cross section σ_b with respect to the ensemble of naturally occuring configurations at a given fish number density ν, and thence at a fixed distribution spread σ_θ, is

$$\bar{\sigma}_b = \int \sigma_b(\theta) f(\theta) d\theta$$

where the range of integration is $[\bar{\theta} - \lambda'\sigma_\theta, \bar{\theta} + \lambda'\sigma_\theta]$.

The backscattering cross section is known through the more commonly measured target strength function $TS(\theta)$, which is related to $\sigma_b(\theta)$ by the usual definition (Urick 1975):

$$TS(\theta) = 10 \log_{10} \frac{\sigma_b(\theta)}{4\pi}$$

so that $\bar{\sigma}_b$ may be computed directly in terms of $TS(\theta)$ by the formula

$$\bar{\sigma}_b = 4\pi \int 10^{TS(\theta)/10} f(\theta) d\theta$$

It was this expression of $\bar{\sigma}_b$ that was evaluated for the particular conditions of Røttingen's experiment with saithe, which are expressed here through the two target strength functions shown in Fig. 4. These functions are distinguished by the center frequency of the ensonifying pulse, which was 38 kHz in one instance and 120 kHz in the other. Both curves represent averages of measurements of the ventral aspect target strength function with respect to a number of specimens of saithe actually used in the experiment. In particular, the target strength function at 38 kHz is the result of averaging the target strength functions of 16 specimens, while that at 120 kHz is the result of averaging the target strength functions of 17 specimens.

The result of evaluating $\bar{\sigma}_b$ numberically for the case that $\lambda' = 3$ is shown

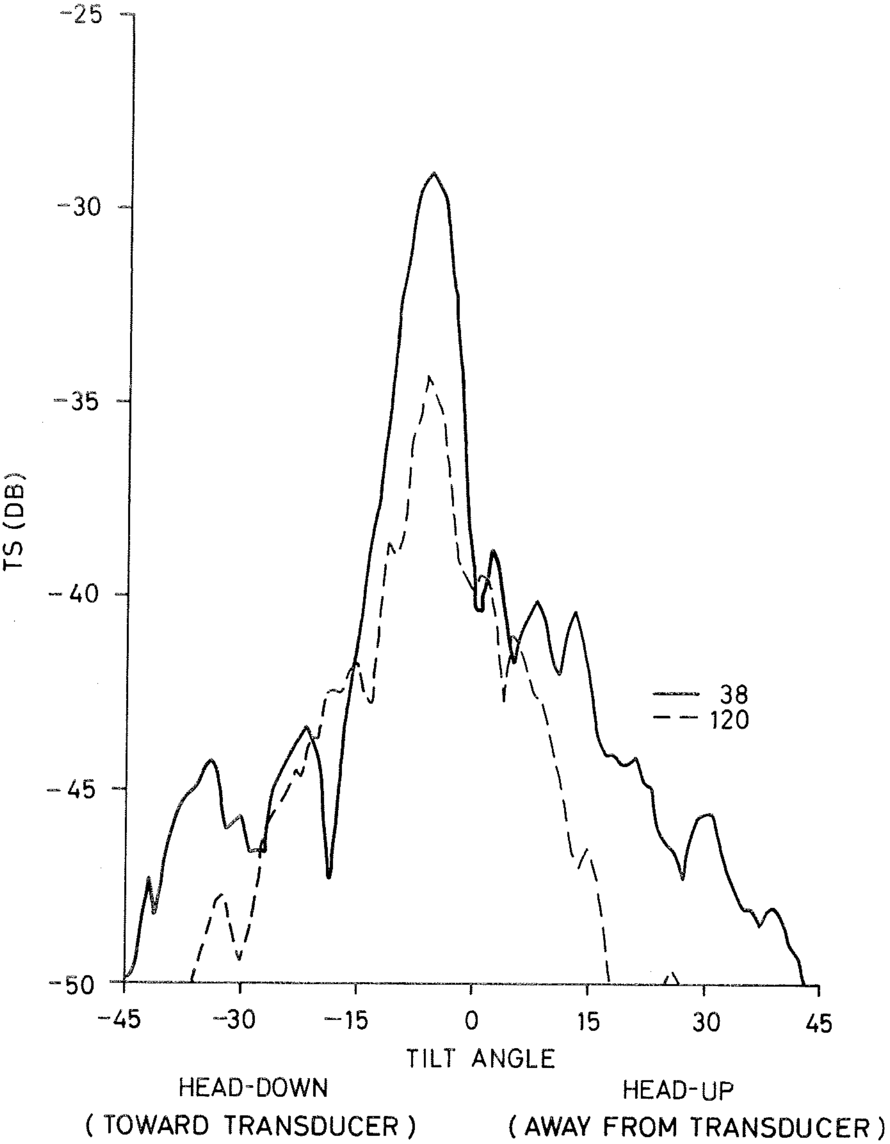

Fig. 4. Ventral aspect target strength of saithe of mean length 35.1 ± 0.6 cm at 38 kHz when averaged with respect to 16 specimens, and at 120 kHz when averaged with respect to 17 specimens.

in Fig. 5 and 6, which apply to the respective narrowband ensonifying signals with center frequencies of 38 kHz and 120 kHz. Because the mean and unknown tilt angle $\bar{\theta}$ is presumed constant with respect to the fish number density ν, while σ_θ is presumed to vary systematically with ν, $\bar{\sigma}_b$ is shown as a function of σ_θ, with $\bar{\theta}$ as a parameter which is varied over the

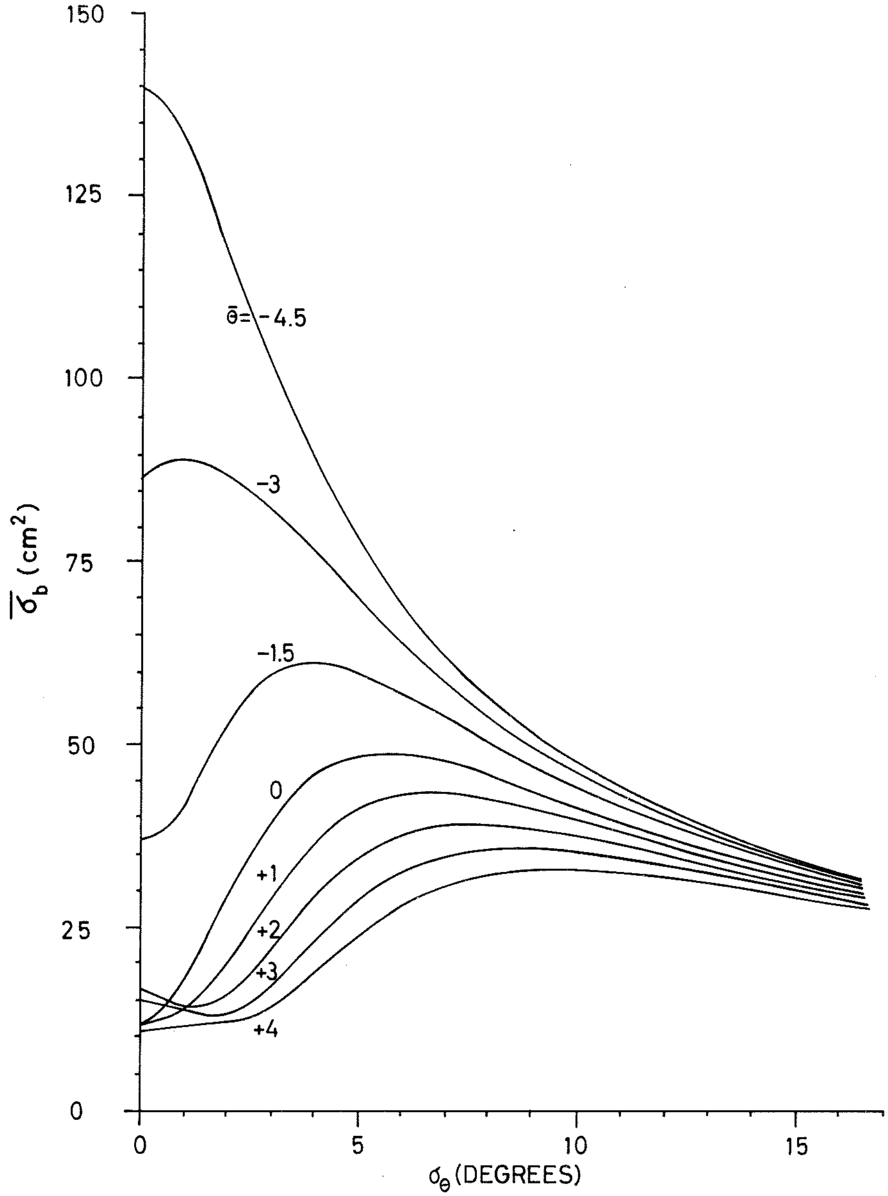

Fig. 5. Mean backscattering cross section $\bar{\sigma}_b$ of saithe in ventral aspect at 38 kHz as a function of the spread σ_θ in tilt angle distribution with mean tilt angle $\bar{\theta}$ as a parameter.

range [–4.5, 4] degrees. The sign convention used consistently throughout this paper is that negative tilt angles denote the head-down position with respect to the true horizontal, while head-up positions are denoted by positive tilt angles.

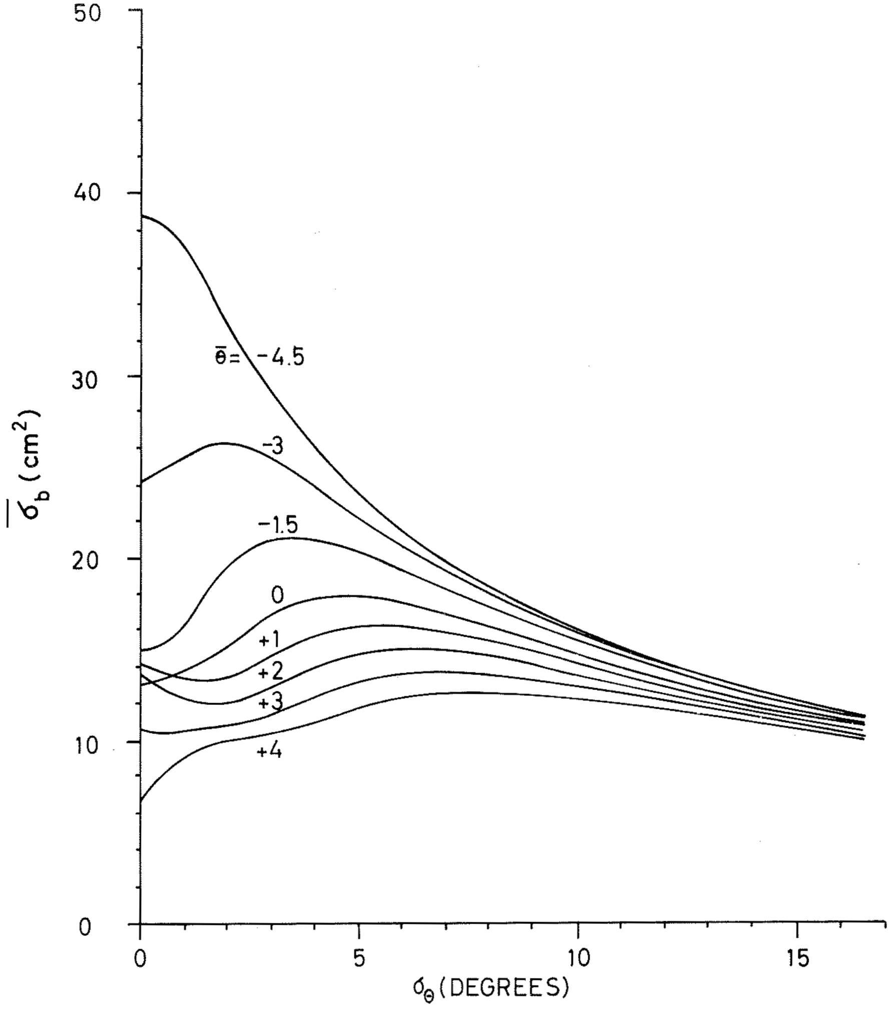

Fig. 6. Mean backscattering cross section $\bar{\sigma}_b$ of saithe in ventral aspect at 120 kHz as a function of the spread σ_θ in tilt angle distribution with mean tilt angle $\bar{\theta}$ as a parameter.

IIIc *Ensemble-averaged extinction cross section*

There is some mention of an extinction cross section for fish in the literature, but mainly in connection with the transmission of sound through fish at or near the frequency of swimbladder resonance (Davies 1973, Ching and Weston 1971, Weston *et al.* 1969). The concept of the extinction cross section is well known in other applications, as in the scattering of light by metallic spheres (Born and Wolf 1970), acoustic scattering by spherical bubbles in water (Wildt 1947), and the scattering of plane scalar fields by spheres (Morseand Feshbach 1953). According to the common definition of these references, the extinction cross section σ_e is the equivalent area normal to the direction of the incident ensonifying signal out of which energy is scattered and absorbed.

For the rather high frequencies used in Røttingen's experiment and for which the two-parameter description of fish scattering behaviour introduced in this study is probably most useful, σ_e may be assumed to be proportional to the surface area of the fish, or of its swimbladder, when projected onto the horizontal plane. If the principal scattering body is represented by an ellipsoid whose length to height to width ratio is designated by the respective dimensions a:b:c, then σ_e as a function of the inclination or tilt angle θ of the body with respect to the horizontal plane is

$$\sigma_e(\theta) = \sigma_{e,o}\sqrt{\cos^2\theta + \varrho^2\sin^2\theta}$$

where $\sigma_{e,o}$ is the value of σ_e at $\theta = 0$ and $\varrho = b/a$ is the ratio of height to length of the scatterer. The effect of roll on σ_e is ignored, which incurs no significant error for cylindriform bodies or quasi-cylindriform bodies which have no extreme roll, which is the plausible assumption for the saithe of Røttingen's experiment.

Given this model for $\sigma_e(\theta)$, the ensemble average $\bar{\sigma}_e$ may now be computed; it is simply the average of $\sigma_e(\theta)$ with respect to the orientation distribution $f(\theta)$, that is,

$$\bar{\sigma}_e = \int\sigma_e(\theta)f(\theta)d\theta$$

where the range of integration is $[\bar{\theta}-\lambda'\sigma_\theta, \bar{\bar{\theta}}+\lambda'\sigma_\theta]$.

This expression was evaluated numerically for the case $\lambda' = 3$ for saithe having the relative dimensions 17.3:3.2:2.1, which were obtained from Rasmussen (1960) and by assuming that the width is two-thirds of the height (Nakken pers. com.). It was found that $\bar{\sigma}_e$ could be represented with an accuracy better than 0.1 percent for all $\sigma_\theta \leqq 16.5$ degrees and for all $\bar{\theta}$ in [–5, +5] degrees by the simple quadratic expression

$$\bar{\sigma}_e \doteq \sigma_{e,o}\left[1-.038\left(\frac{\sigma_\theta}{16.5}\right)^2\right]$$

In the actual evaluation of $\bar{\varepsilon}$ this expression was used, but the variation of $\bar{\sigma}_e$ with σ_θ was found to be entirely negligible, so that $\bar{\sigma}_e$ could have been reduced to the constant $\sigma_{e,o}$, which, however, except in the true ray theory limit, does depend on the center frequency of the ensonifying signal.

IIId. *Connection of spread in orientation distribution and density of fish aggregation.*

It is reasonable to expect σ_θ, or the characteristic measure of spread in the tilt angle distribution of the encaged saithe, to be a monotonically decreasing function of the fish number density ν, for individual fish have less room in which to move, in the mean, as ν increases. It is also reasonable to assume that whatever preference there is for a mean inclination $\bar{\theta}$ should not be affected by the conditions of density, although this is purely speculative. Because of the extreme artificiality of the net cage environment and lack of any preferred direction, as might be established naturally by the fish when schooling (BREDER 1959), it is expected that $\bar{\theta}$ would be the neutral inclination, which would be horizontal or nearly horizontal. The entire dependence of the orientation distribution on ν is thus contained in the dependence of σ_θ on ν, which is described below.

Physically σ_θ may be separated into two independent components: that which expresses the biological expectation that σ_θ is a monotonically decreasing function of ν, i.e., that the intrinsic spread in tilt angle decreases with increasing ν, and that which expresses the perspectival effect that the intrinsic, or true, tilt angle generally appears different when viewed from the acoustic source/receiver, which generally is located obliquely, or transversely, with respect to the fish. These two components of σ_θ, which are denoted $\sigma_{\theta,1}$ and $\sigma_{\theta,2}$, respectively, are independent random variables and, as such, are summed in this manner:

$$\sigma_\theta = \sqrt{\sigma_{\theta,1}^2 + \sigma_{\theta,2}^2}$$

As the intrinsic tilt angle distribution of the encaged saithe is unknown, but is expected to be a monotonically decreasing function of ν, the connection between $\sigma_{\theta,1}$ and ν is specified very simply by the model

$$\sigma_{\theta,1} = \sigma_{\theta,1,0} \; exp \; (-\nu/\nu_{cr})$$

where $\sigma_{\theta,1,0}$ denotes the low density limit of the intrinsic spread in tilt angle and ν_{cr}, which is termed the critical density, is the density characteristic of the change in $\sigma_{\theta,1,0}$. Both $\sigma_{\theta,1,0}$ and ν_{cr} are regarded as parameters to be determined or learned by comparison of the results of evaluation of the theoretical $\bar{\varepsilon}$ with Røttingen's observations.

It is expected, however, that $\sigma_{\theta,1,0}$ will be of the order of 16 degrees, which is the figure determined by photographic measurements of cod in the open sea (OLSEN 1971), and which could be be thought of as a natural characteristic of cod, and thence of related fish such as saithe. The fact that the saithe are encaged should not lessen confidence in this rough estimate of $\sigma_{\theta,1,0}$ as it applies only in the low density limit where the net cage appears large.

The effect of perspective on altering the intrinsic spread when observed obliquely may be defined through the perspectival spread $\sigma_{\theta,2}$. This is approximately equal to the square root of the average of the mean square tilt angle due to the azimuthal variation in apparent tilt angle relative to an obliquely situated reference point, both with respect to the volume of the net cage, in which the fish are assumed to be randomly homogeneously distributed, and with respect to the transmit and receive beam patterns. In units of degrees

$$\sigma_{\theta,2} = \frac{180}{\pi}\left(\frac{1}{V}\int D_R^2\, D_S^2\, \Delta\chi^2\, dV\right)^{1/2}$$

where $D_R = D_R(\Psi)$ and $D_S = D_S(\Psi)$ are the respective receive and transmit beam patterns in relative units of pressure ratios, which are assumed to be functions only of the polar angle Ψ, and $\Delta\chi^2$ is the variance in apparent tilt angle distribution due to azimuthal variations in orientation. This latter quantity, expressed in units of square radians, is approximated for small mean inclination $\bar{\theta}$ by the expression

$$\Delta\chi^2 = \frac{1}{2\pi}\int_0^{2\pi}\left[\cos^{-1}\left(\sin\Psi\cos\varphi + \frac{\pi}{180}\,\bar{\theta}\,\cos\Psi\right) - \frac{\pi}{2}\right]^2 d\varphi$$

where $\bar{\theta}$ is expressed in degrees. This expression applies properly only in the limit of the highest density, where $\sigma_{\theta,1}$ vanishes, but is adopted here for convenience. D_R and D_S are not equated to unity here as they were earlier in justifiable approximations. They are equated to that beam pattern, expressed in units of relative pressure, which was observed by Røttingen for the transmitter at both 38 kHz and 120 kHz; namely, one which suffers an approximately uniform off-axis degradation which is −1 dB at the outer walls of the net cage. To the first and dominant term, then

$$\sigma_{\theta,2}^2 \doteq .75\left(\frac{180}{\pi}\right)^2 \frac{R^2}{(z_1 + z_2)^2} + .81\,\bar{\theta}^2$$

where R is the radius of the cage and z_1 and z_2, the respective distances from acoustic source to nearer and further surfaces of the cage. If the precise values of these parameters that applied during Røttingen's experiment with saithe are substituted,

$$\sigma_{0,2} = \sqrt{4.2 + .81\,\bar{\theta}^2}$$

where both $\bar{\theta}$ and $\sigma_{\theta,2}$ are expressed in units of degrees.

IIIe. *Evaluation of* $\bar{\varepsilon}$

The ensemble-averaged scattering cross sections, $\bar{\sigma}_b$ and $\bar{\sigma}_e$, can now be written, with respect to specific models which connect the parameters of the orientation distribution with ν, the fish number density, as explicit functions of ν. With respect to these same models the ν–dependence of the ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ can be determined directly. This was done numerically by means of a digital computer. Some characteristic results of this evaluation, in addition to the principal ones which constitute a quantitative explanation of Røttingen's observations for saithe, are presented in the next section.

RESULTS

The principal results of the quantitative analysis of Røttingen's experiments with saithe are shown in Fig. 7 and 8. In Fig. 7 the result of the evaluation of the theoretical mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ for saithe at 38 kHz, according to the approximations described above, and after normalization by the peak value, is presented for the following model parameters: a mean inclination or tilt angle $\bar{\theta} = 0$

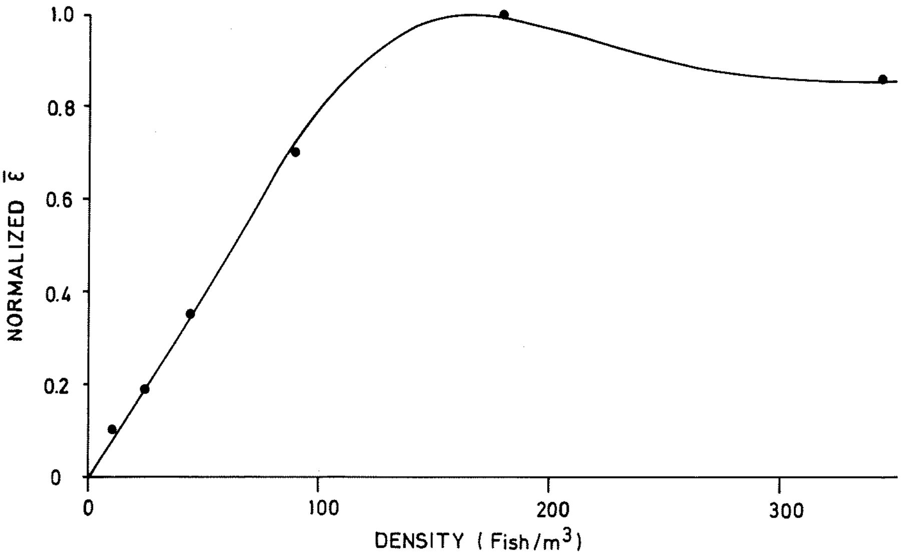

Fig. 7. Comparison of the computed normalized, mean time-integrated echo intensity $\bar{\varepsilon}$ with the mean of Røttingen's observations for saithe at 38 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 60$ cm^2; $\sigma_{\theta,1,0} = 18$ degrees; $\nu_{cr} = 100$ fish/m^3.

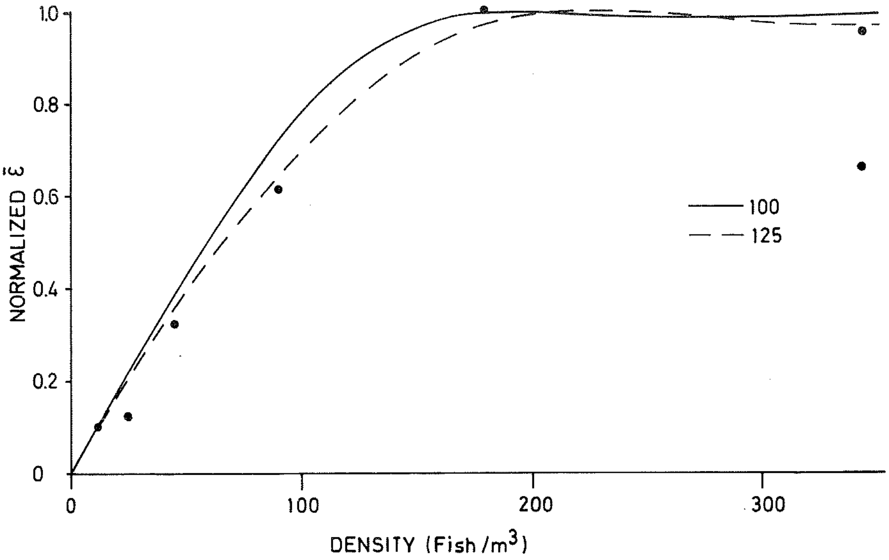

Fig. 8. Comparison of $\bar{\varepsilon}$ with the mean of Røttingen's observations for saithe at 120 kHz for the following model parameters: $\overline{\theta} = 0$ degrees; $\sigma_{e,o} = 100$ cm^2; $\sigma_{\theta,1,0} = 18$ degrees; $\nu_{cr} = 100$ and 125 fish/m^3.

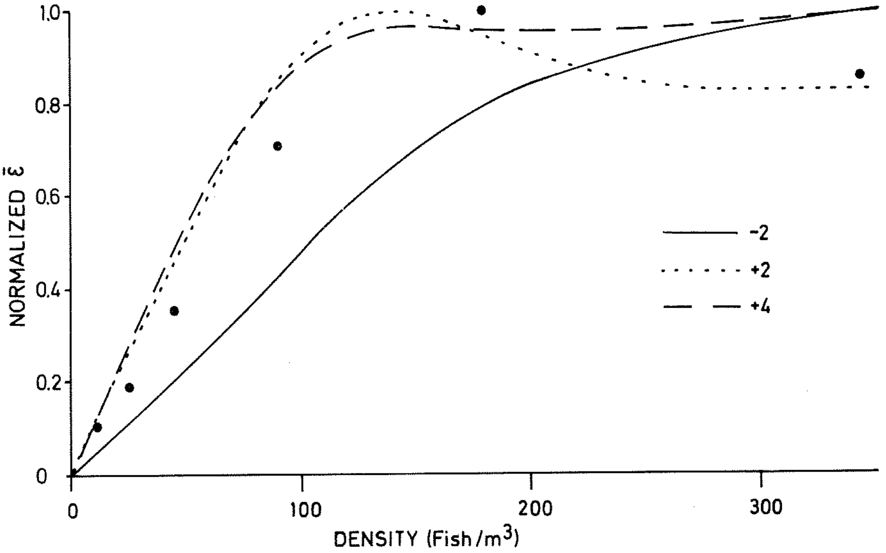

Fig. 9. Dependence of $\bar{\varepsilon}$ on $\overline{\theta}$ for 3 values of $\overline{\theta}$ for saithe at 38 kHz for the following model parameters: $\sigma_{e,o} = 60$ cm^2; $\sigma_{\theta,1,0} = 18$ degrees; $\nu_{cr} = 100$ fish/m^3.

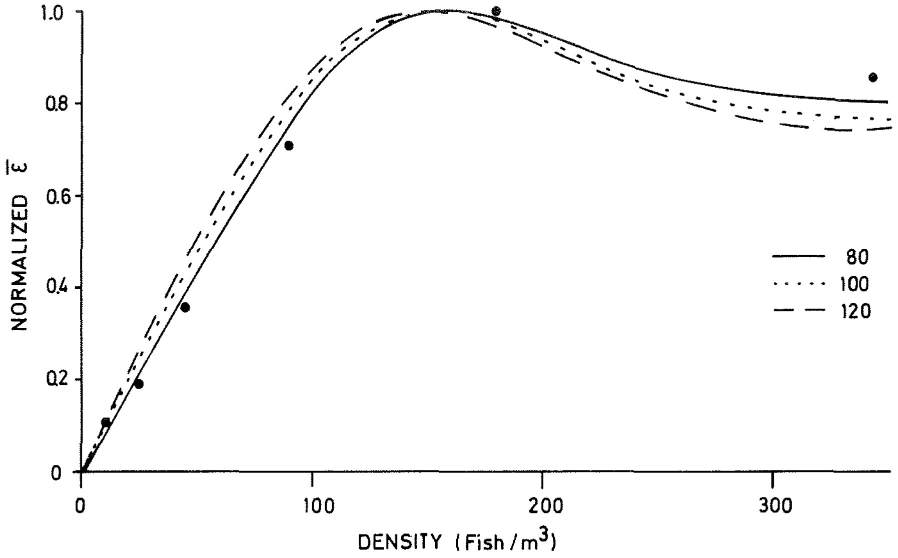

Fig. 10. Dependence of $\bar{\varepsilon}$ on $\sigma_{e,o}$ for 3 values of $\sigma_{e,o}$ for saithe at 38 kHz for the following model parameters: $\bar{\theta}$ = 0 degrees; $\sigma_{\theta,1,o}$ = 18 degrees; ν_{cr} = 100 fish/m^3.

degrees, which describes the horizontal plane; a mean extinction cross section $\sigma_{e,0}$ = 60 cm^2, which is presumed applicable in the limit of high fish number densities; an intrinsic spread in tilt angle distribution at low densities, $\sigma_{\theta,1,0}$ = 18 degrees; and a decreasing exponential ν-dependence of the intrinsic spread in tilt angle distribution which is characterized by the critical density ν_{cr} = 100 fish/m^3. The normalized theoretical $\bar{\varepsilon}$ is computed with respect to these several parameters at a density increment of 10 fish/m^3 over the density range [0,350] fish/m^3, as has been done consistently in Fig. 7 and 12 inclusive, although for different model parameters and thence different peak values and normalizing factors. For purposes of comparison Røttingen's averaged results at 38 kHz, i.e., the average of corresponding values of $\bar{\varepsilon}$ for the two conditions of ensonification at 38 kHz; namely, for pulse durations of 0.3 msec and 0.6 msec; are also presented in Fig. 7, as they are in Fig. 9 to 12 which likewise pertain to computations at 38 kHz.

In Fig. 8 the normalized theoretical estimate of $\bar{\varepsilon}$ at 120 kHz is computed for the same purely geometric model parameters described above for Fig. 7, but for a mean high density extinction cross section $\sigma_{e.o}$ = 100 cm^2. In addition to the computation at ν_{cr} = 100 fish/m^3, a computation at ν_{cr} = 125 fish/m^3 is presented here. The average of Røttingen's observations of $\bar{\varepsilon}$ at 120 kHz, for pulse durations of 0.1 msec and 0.6 msec, are shown at all observed densities except at the highest density. At this density, which is 343 fish/m^3, the respective normalized observations of $\bar{\varepsilon}$ were widely different –

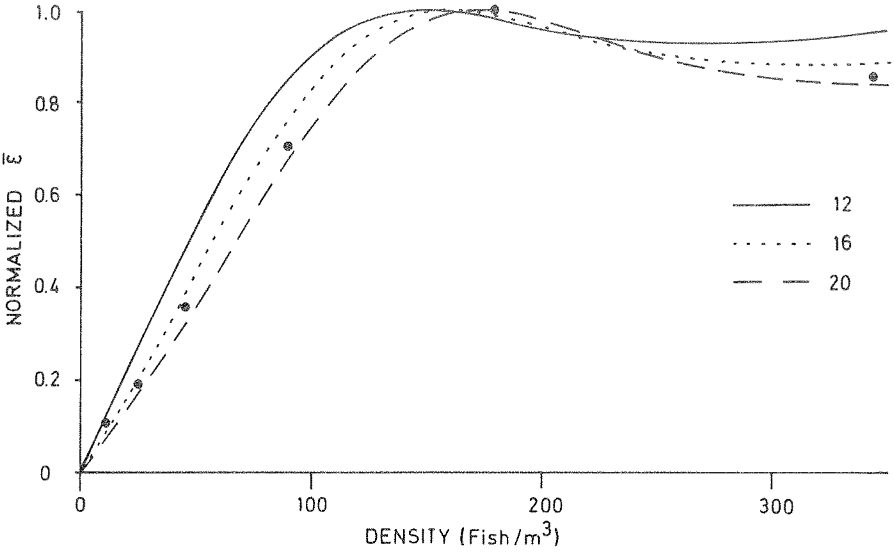

Fig. 11. Dependence of $\bar{\varepsilon}$ on $\sigma_{\theta,1,0}$ for 3 values of $\sigma_{\theta,1,0}$ for saithe at 38 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 60$ cm^2; $\nu_{cr} = 100$ fish/m^3.

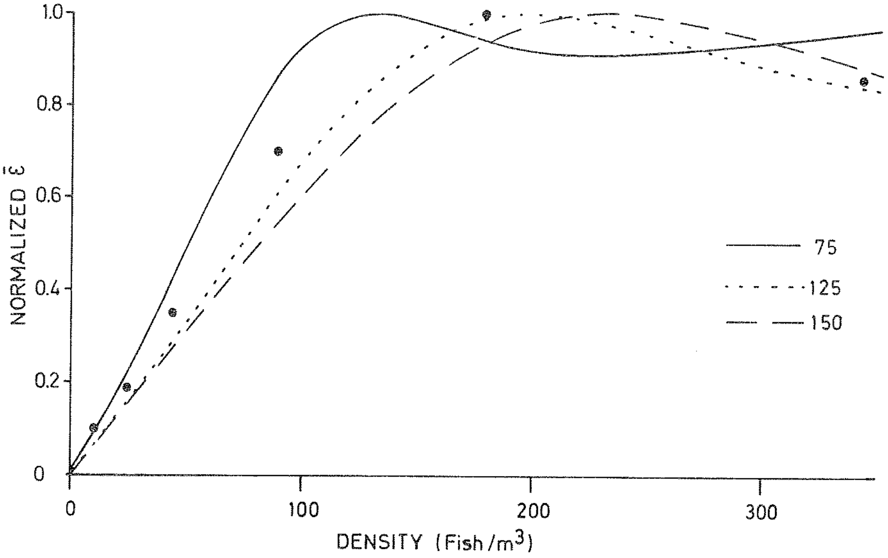

Fig. 12. Dependence of $\bar{\varepsilon}$ on ν_{cr} for 3 values of ν_{cr} for saithe at 38 kHz for the following model parameters: $\bar{\theta} = 0$ degrees; $\sigma_{e,o} = 60$ cm^2; $\sigma_{\theta,1,0} = 18$ degrees.

the only case of its kind as revealed by inspection of Fig. 1 – and are both shown in the figure.

Table 1. Values of parameters of Figures 7 to 12.

Figure number	Center Frequency (kHz)	$\bar{\theta}$ (degrees)	$\sigma_{e,o}$ (cm^2)	$\sigma_{0,1,0}$ (degrees)	ν_{cr} (fish /m^3)
7	38	0	60	18	100
8	120	0	100	18	100, 125
9	38	–2, +2, +4	60	18	100
10	38	0	80, 100, 120	18	100
11	38	0	60	12, 16, 20	100
12	38	0	60	18	75, 125, 150

The dependence of the normalized theoretical estimate of $\bar{\varepsilon}$ for saithe at 38 kHz on the several important model parameters; namely, $\bar{\theta}$, $\sigma_{e.o}$, $\sigma_{\theta,1,0}$ and ν_{cr}, are shown in Fig. 9 to 12, respectively. The respective values of each of these parameters in the computation of ε for these figures are presented systematically above in Table 1. Thus in Fig. 9, for example, the dependence of $\bar{\varepsilon}$ on $\bar{\theta}$ is shown for three values of $\bar{\theta}$; namely, –2, +2 and +4 degrees; while the other model parameters adopt the following values: $\sigma_{e,o} = 60$ cm^2, $\sigma_{\theta,1,0} = 18$ degrees and $\nu_{cr} = 100$ fish/m^3. Descriptions of Fig. 7 and 8 are included in the table for ease of reference.

DISCUSSION

The agreement of the theoretical prediction of the normalized mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ with Røttingen's averaged observations of $\bar{\varepsilon}$ for saithe at 38 kHz, as shown in Fig. 7, is better than can be expected, or can be justifiably stated without qualification, considering the inherent uncertainty in observations of $\bar{\varepsilon}$ and the uncertainty in representation of the data in a normalized format for such a sparsely sampled density range. Some estimates of $\bar{\varepsilon}$ were stated with confidence intervals in RØTTINGEN (1975), but these were not so significant as to alter the general finding of Røttingen as summarized in Fig. 1 and 2, for saithe and sprat, respectively. That only the averages of the respective observations at 38 kHz for the signals of pulse duration 0.3 msec and 0.6 msec are presented in Fig. 7, and in Fig. 9 to 12, is similarly insignificant, for examination of Fig. 1 shows the separate estimates of $\bar{\varepsilon}$ to correspond very closely. The fact that $\bar{\varepsilon}$ was observed only sparsely for fish number densities in excess of 90 fish/m^3; specifically, only at 179 fish/m^3 and 343 fish/m^3; could be a more serious source of error, but it was a fairly consistent finding of the theoretical work that the $\bar{\varepsilon}$–ν relationship is rather flat over the region of the peak, so the fact that $\bar{\varepsilon}$ was established at only a single density in this region is probably unimportant. It was also found that the relationship is entirely smooth and often is purely monotonic both above and below the peak, if present, so that a single estimate in the high density region, say about 350 fish/m^3, could be sufficient for determining the gross form of the $\bar{\varepsilon}$–ν relationship. It is assumed, therefore, that despite apparent shortcomings in Røttingen's observations and presentation of $\bar{\varepsilon}$ as a function of ν for saithe, it is a reasonably accurate statement for the true relationship.

If the agreement of theory with experiment at 38 kHz, cf. Fig. 7, is genuine, then evaluation of the postulated model for the same purely geometric, i.e., frequency-independent quantities at 120 kHz, should also produce good agreement with experiment. Observation of the curve with parameter $\nu_{cr} = 100$ fish/m^3 in Fig. 8, for which all geometric quantities have the identical values as in Fig. 7, indicates approximate agreement. Evaluation of the model for the same conditions, but with $\nu_{cr} = 125$ fish/m^3, improves this agreement. As a comparable estimate of $\bar{\varepsilon}$ at 38 kHz for this value of ν_{cr} also yields a fair agreement with experiment, cf. Fig. 12, although not so fine as the estimate obtained with $\nu_{cr} = 100$ fish/m^3, cf. Fig. 7, it may be concluded that the true value of ν_{cr} lines in or near the range 100 to 125 fish/m^3. It is admitted that the single datum at 343 fish/m^3 for a narrowband signal of center frequency 120 kHz and pulse duration 0.6 msec is completely anomalous to a wide range of evaluations of the model, which is why the empirical estimates of $\bar{\varepsilon}$ for saithe at 120 kHz are not averaged for the presentation of Fig. 8 at this particular density, the only density at which such a discrepancy exists throughout the data for saithe, at either frequency. If the two data at 120 kHz at a density of 343 fish/m^3 are both correct, then there is, evidently, a discrimination by pulse duration. This lies beyond the scope of the model, whose development at the outset assumed a certain insentitivity to the pulse duration of the ensonifying signal. That the $\bar{\varepsilon}$–ν relationship may be significantly characterized by the pulse duration of the signal, at least for some center frequencies, is a possibility, and one that might profitably be studied with respect to the larger purposes of the use of acoustic techniques in fisheries research; the present theory simply cannot explain this supposed dependence, which, it is noted, is absent for the sprat of Røttingen's experiment.

The consequence of the consistency in predictions of theory at both 38 kHz and 120 kHz with the corresponding averaged sets of empirical observations, as shown in Fig. 7 and 8, is that the general theory for the process of echo formation by an encaged aggregation of fish, with its two-parameter representation of individual scattering behaviour, is correct. In particular, it may be concluded that the purely geometric models for the orientation distribution of the encaged saithe and for the density dependences of the characterizing parameters of this distribution, on which the $\bar{\varepsilon}$–ν relationship depends crucially, are correct. Thus, the orientation distribution of the saithe is described satisfactorily by an Olsen-type distribution (OLSEN 1971), i.e., a trucated Gaussian distribution in inclination or tilt angle θ which extends over the range $[\bar{\theta}-\lambda'\sigma_\theta, \bar{\theta}-\lambda'\sigma_\theta]$, where λ' is a constant factor of the order of three and $\bar{\theta}$ and σ_θ are, respectively, the mean and spread of the distribution. For the particular conditions of Røttingen's experiment with saithe, $\bar{\theta}$ is approximately 0 degrees, a constant independent of the fish number density ν, and

$$\sigma_\theta \doteq [\sigma^2_{\theta,1,0}\ exp(-2\nu/\nu_{cr}) + 4.2]^{1/2}$$

where $\sigma_{\theta,1,0}$ is approximately 18 degrees and ν_{cr} is approximately 100 to 125 fish/m^3. The origin of the two factors in this expression has been described fully above.

It was also determined that the maximum ensemble-averaged extinction cross section $\sigma_{e,o}$ for saithe in the ventral aspect is of the order of 60 cm^2 at 38 kHz and 100 cm^2 at 120 kHz. Evidently the pure ray theory limit of acoustics is not entirely applicable to the present problem, so that frequency-dependent variations in the scattering properties of individual fish are to be expected. This is corroborated by comparison of corresponding magnitudes of the ensemble-averaged backscattering cross section at the two frequencies, cf. Fig. 5 and 6.

The ν-dependence of the ensemble-averaged extinction cross section $\bar{\sigma}_e$, through its conjectured dependence on the spread in inclination distribution, is very slight, with only a 3.8 per cent increase in magnitude as σ_θ changes from 16.5 degrees to 0 degrees; that is, presumably, as the density of encaged saithe increases from the approximately free-space value to the highest value. If the computations of $\bar{\varepsilon}$ presented in Fig. 7 to 12 were repeated for density-independent $\bar{\sigma}_e$; specifically for $\bar{\sigma}_e = \sigma_{e,o}$, then the results would be indistinguishable from the corresponding computations with density-dependent $\bar{\sigma}_e$. In view of the influence of the magnitude of $\bar{\sigma}_e$ in determining the form of the $\bar{\varepsilon}$–ν relationship – it predicts merely a monotonic and asymptotic increase to a constant for constant $\bar{\sigma}_b$, cf. Fig. 3, and determines the rate of increase of normalized $\bar{\varepsilon}$ with ν for ν less than about 100 fish/m^3, cf. Fig. 10 – it may be concluded that the ν–dependence of $\bar{\sigma}_e$ is insignificant in determining the general form of the $\bar{\varepsilon}$–ν relationship.

Thus, because the ν-dependence of $\bar{\varepsilon}$ is completely contained in the expression shown above, in section III, which predicts only a monotonic, eventually asymptotic increase in $\bar{\varepsilon}$ with ν for constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$, cf. Fig. 3, and because the ν-dependence of $\bar{\sigma}_e$ is insignificant, the ν -dependence of $\bar{\sigma}_b$ must be of crucial importance in determining the form of the $\bar{\varepsilon}$–ν relationship. This is confirmed by examination of Fig. 9, 11 and 12, which show, respectively, the sensitivities of $\bar{\varepsilon}$ to $\bar{\theta}$, $\sigma_{\theta,1,0}$ and ν_{cr}; that is, to the several purely geometric parameters of the ν -dependent orientation distribution. Variations in any one of these parameters can have a significant effect on the form of $\bar{\varepsilon}$ through $\bar{\sigma}_b$, whose dependence on $\bar{\theta}$ and σ_θ, thence $\sigma_{\theta,1,0}$ and ν_{cr}, is shown in Fig. 5 for the case of a 38 kHz signal and in Fig. 6 for the case of a 120 kHz signal.

It is noted that $\bar{\varepsilon}$, for constant $\bar{\sigma}_b$ and $\bar{\sigma}_e$, as in Fig. 3, increases linearly with ν for very small ν and begins its asymptotic approach to a constant at comparably low values of ν, which are of the order of 50 fish/m^3 for realistic values of $\bar{\sigma}_e = \sigma_{e,o}$. These latter values are of the order of 60 to 120 cm^2, which are consistent with estimates of σ_b (θ) obtained from empirical target strength data and with knowledge of the physical size of the scatterer. The fact that $\bar{\varepsilon}$ increases linearly to a rather high value of ν, of the order of 100 fish/m^3, is therefore significant. It apparently describes a σ_b which is, at least over this range of ν an increasing function of ν. This dependence of $\bar{\sigma}_b$ on ν is precisely that found at both 38 kHz and 120 kHz by computation from the measured target strength curves of saithe according to the general model in which the orientation distribution is approximately Gaussian in tilt angle and whose variance is a monotnically decreasing function of ν. The similarity in target strength curves at the two frequencies is thus seen to be responsible for the similarity in corresponding $\bar{\sigma}_b$ functions, which is also why the gross forms of the $\bar{\varepsilon}$–ν relationships are similar. If the target strength functions were very dissimilar, then the $\bar{\varepsilon}$–ν relationships also would be expected to be significantly different.

From mere inspection of the data in Fig. 1 and 2 it is difficult to assert that there are frequency-dependent differences in the $\bar{\varepsilon}$–ν relationships. In the neglect of a single datum in Røttingen's observations for saithe at 120 kHz, which was not reproduced in the observations on sprat and which remains unexplained here, what frequency-discrimination there is in the $\bar{\varepsilon}$–ν relationships is attributed to frequency-dependent differences in $\bar{\sigma}_b$ and in the conditions of ensonification of the net cage. For saithe these were found to be slight, but the uncertainty in estimates of $\bar{\sigma}_b$ at 120 kHz was considerable, so the precise form of $\bar{\sigma}_b$ is somewhat uncertain at this frequency. In the computation of the perspectival contribution to the spread in tilt angle distribution it was assumed that there was a slight, identical degradation in both transmit and receive beam patterns at the two frequencies, although this agreement was confirmed experimentally only for the two transmit beams. Admittedly the application of theory to the circumstances of Røttingen's experiment was not entirely consistent, particularly in the treatment of ensemble averages, in which the beam patterns are generally contributing factors. However, it was judged that the several ad hoc approximations used here were reasonable; at least they facilitated the computations of $\bar{\varepsilon}$ without incurring large errors and, in the case of the inferred ν-dependence of $\bar{\sigma}_b$, demonstrated the insignificant role of the beam patterns in determining the ν-dependence of $\bar{\sigma}_b$, and thence the ν-dependence of $\bar{\varepsilon}$.

In summary it is observed that the precise form of the $\bar{\varepsilon}$-ν relationship for the scattering of sound by encaged aggregations of fish, and, presumably, for the scattering of sound by schools of fish, depends on many quantities, which include the backscattering and extinction cross sections as functions of fish orientation, the spatial and orientation distributions as functions of the number density ν, the geometry of ensonification and echo reception, and the signal waveform. While little is presently known about several of these quantities, particularly the extinction cross section and the orientation distribution, much insight into their influence can be gained by the exercise of theory, by calculation of theoretical $\bar{\varepsilon}$ for different postulated models. Comparison of these predictions with observation, as in the present case with respect to Røttingen's measurements of ε for saithe at two different frequencies, can then permit selection of likely models. In particular, comparison of predicted and measured $\bar{\varepsilon}$–ν relationships for fish in a Røttingen-type experiment can permit determination of the mean extinction cross section, a quantity whose measurement is generally complicated, but whose knowledge is essential to determining the precise effect of shadowing in schools of fish.

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APPENDIX

THEORY OF ACOUSTIC SCATTERING BY A COLLECTION OF IDENTICAL SCATTERERS OF RANDOM ORIENTATION AND DISTRIBUTION

Consider a collection of randomly oriented, but otherwise identical scattering bodies which are randomly homogeneously distributed througout a definite region V of a fluid medium of homogeneous density ϱ_o, constant sound speed c_o and negligible background noise. V is ensonified by a narrowband signal $s(t)$, which is emitted by a generally directional source, or transmitting element. The corresponding echo from V is received by a generally directional receiving element, which is essentially collocated with the transmitting element with which it shares a common principal response axis is in the farfield of the source/receiver. The signal waveform $s(t)$ is sufficiently narrowband so that the pressure field modulated by it can be assumed to be attenuated by the free medium at the constant rate α, which is the attenuation constant of the medium at the center frequency of $s(t)$. The pressure due to the source, which is characterized by its value p_o at unit distance from the source, is sufficiently weak so that nonlinear effects can be strictly ignored.

Let the generally complicated scattering behavior of a single scattering body of V be represented by just two parameters: its backscattering cross section σ_b and its extinction cross section σ_e, which are defined with respect to the precise form of $s(t)$ and which generally are complicated functions of scatterer orientation $\hat{r}'$ relative to scatterer position $\underset{\sim}{r}$. The vector $\underset{\sim}{r} = \underset{\sim}{r}_n$ denoting the position of an arbitrary, or the n^{th}, scatterer, and the unit vector $\hat{r}' = \hat{r}'_n$ denoting the orientation of the same body, are defined with respect to a rectangular coordinate system whose origin is situated at the collocated source and receiver and whose z-axis is coincident with the common principal axis of source and receiver. The dependence of the two scattering cross sections on the position $\underset{\sim}{r}_n$ and orientation $\hat{r}_n$ are abbreviated thus:

$$\sigma_b(\underset{\sim}{r}_n, \hat{r}'_n) = \sigma_{b,n} \text{ and } \sigma_e(\underset{\sim}{r}_n, \hat{r}'_n) = \sigma_{e,n}.$$

The echo from V, in the form of the mean or ensemble-averaged time-integrated echo intensity ε, can now be developed directly and expressed as a function of the scatterer number density ν.

In the neglect of other scatterers the pressure field incident on the n^{th} scatterer is that of the free medium, time-retarded wave, viz.

$$\frac{p_o\, s\left(t-\frac{r_n}{c_o}\right)}{r_n} D_{D,n}\, exp\ (-\alpha r_n)$$

where $r_n = |\underset{\sim}{r}_n|$ is the distance from source to position $\underset{\sim}{r}_n$ of the n^{th} scatterer, and $D_{S,n} = D_S(\hat{r}_n)$ is a factor expressing the effect of source directivity on diminishing the transmitted pressure field in the generally oblique or non-axial direction $\hat{r}_n$ or the n^{th} scatterer. The effect of the presence of other scatterers on this field is its modification by multiple scattering, which might be treated deterministically by the inclusion of the sundry, calculable effects of absorption and refraction internal to the scatterers and reflection and diffraction external to the scatterers, inter alia, but which is treated here simply by the statistical concept of extinction. According to this mode of description, the composite or mutual influence of the scattering bodies in V on the pressure field within V is allowed to be precisely that of a further attenuation of the incident pressure field by scattering and absorption. Since the spatial distribution of the scatterers in V is randomly homogenous, the rate of this attenuation is the net oblique scattering area per unit area of beam. For the n^{th} scatterer this is the quantity $v\bar{\sigma}_e|r_n-r_{n,o}|$ where $\bar{\sigma}_e$ is the mean equivalent scattering area, or extinction cross section, which generally is a function of the location $\underset{\sim}{r}_n$ of the n^{th} scatterer, and $r_{n,o}$ is the distance from source to nearest surface of V in the direction $\hat{r}_n$ of the n^{th} scatterer. Thus $|r_n-r_{n,o}|$ is the depth of penetration into V of the incident pressure field at the n^{th} scatterer, and the effect of multiple scattering or extinction is diminution of the incident energy field by the factor

$$exp\ [-v\bar{\sigma}_e(r_n-r_{n,o})]$$

The pressure field incident on the n^{th} scatterer, in the mean, is

$$p_{inc,\ n} = \frac{p_o\, s\left(t-\frac{r_n}{c_o}\right)D_{S,n}}{r_n}\ exp\left[-\alpha r_n - \frac{v\bar{\sigma}_e}{2}\,(r_n - r_{n,o})\right]$$

which is just the free-medium, time-retarded wave as modified by multiple scattering within V.

This expression for $p_{inc,n}$ has a precise meaning only in a statistical sense: as the pressure field to be expected at the n^{th} scatterer, at fixed depth of penetration $(r_n - r_{n,o})$, in the mean with respect to the ensemble of all possible, allowed configurations of scatterers in V. It is now temporarily adopted as the description of the actual field at the n^{th} scatterer for an arbitrary particular configuration of scatterers. Later, this ad hoc use will be seen to be justified when the principal quantity of interest, the mean of the integrated echo intensity with respect to the same ensemble of configurations, is computed.

In the formation of the echo from the n^{th} scatterer the incident pressure field is generally distorted. Because this distortion depends on the precise nature of the scatterer and on the conditions of its ensonification, the wave form of the backscattered pressure field is represented by $s_n(t)$. Its strength relative to the incident field is $\sigma_{b,n}/4\pi$ in the energy domain. When the additional effects of further time retardation, medium absorption and reception by a directional element at the generally non-axial direction $\hat{r}_n$ are included, the contribution to the echo from the n^{th} scatterer may be expressed by

$$p_{sc,n} = \frac{p_o\, s_n \left(t - \dfrac{2r_n}{c_o}\right) D_{S,n}\, D_{R,n}\, \sigma_{b,n}^{1/2}}{\sqrt{4\pi}\; r_n^2} \quad exp\left[-2\alpha r_n - \frac{\nu\bar{\sigma}_e}{2}\cdot(r_n - r_{n,o})\right]$$

Here $D_{R,n} = D_R\ (\hat{r}_n)$ is the factor describing the effect of the directionality of the receiver on diminishing the received pressure field from the generally non-axial direction $\hat{r}_n$, and $\sigma_{b,n} = \sigma_b\ (\hat{r}_n)$ is the equivalent backscattering area of the n^{th} scatterer, which is a function of its orientation $\hat{r}'_n$.

The total backscattered field or echo from V after reception, in the proper weak field limit of linear acoustics, is the linear superposition of the several backscattered fields:

$$p_{sc} = \sum_n p_{sc,n}$$

where the summation extends over all νV scatterers in V. The instantaneous intensity $I = I(t)$ corresponding to p_{sc} is the product of in-phase pressure and velocity; thence, by the assumption that $s(t)$ is relatively narrowband,

$$I = \frac{1}{\varrho_o c_o}\, p_{sc}^2$$

If the signal is of sufficiently short duration T so that the echo from V is completely isolated in time from those echoes produced by extraneous scatterers in the larger medium, such as boundary surfaces, then the time-integrated echo intensity ε; namely,

$$\varepsilon = \int I dt$$

is precisely the energy contained in the echo field of V at the receiving element after effective «shaping» of the echo field by the generally directional receiving element. After appropriate substitution and integration,

$$\varepsilon = \frac{I_o}{4\pi} \sum_{n,m} \frac{D_{S,n}\ D_{S,m}\ D_{R,n}\ D_{R,m}\ \varrho_{nm}\ \sigma_{b,n}^{1/2}\ \sigma_{b,m}^{1/2}}{r_n^2\ r_m^2}$$

$$\times\ exp\left[-2\alpha(r_n + r_m) - \frac{\nu\bar{\sigma}_e}{2}\ (r_n - r_{n,o} + r_m - r_{m,o})\right]$$

where $I_o = p_o^2/\varrho_o c_o$ is a measure of source intensity, and ϱ_{nm} is the cross correlation function

$$\varrho_{nm}(\tau) = \int_{-\infty}^{\infty} s_n(t)\, s_m(t+\tau)dt$$

when evaluated at $\tau = 2(r_n - r_m)/c_o$, which is the difference in arrival times of the echoes from the n^{th} and m^{th} scatterers. Inasmuch as ϱ_{nm} expresses the degree of coherence in the echoes of the $(n.m)$ pair of scatterers, which always irreducibly yields the positive contribution $\varrho(0)$ when $n = m$, ε may be decomposed into two terms, viz.

$$\varepsilon = \frac{I_o}{4\pi}\varrho(0)\sum_n \frac{D_{S,n}^2\, D_{R,n}^2}{r_n^4}\,\sigma_{b,n}\exp\left[-4\alpha r_n - v\bar{\sigma}_e(r_n - r_{n,o})\right]$$

$$+\frac{I_o}{4\pi}\sum_{n \neq m}\frac{D_{S,n}\,D_{S,m}\,D_{R,n}\,D_{R,m}}{r_n^2\, r_m^2}\,\varrho_{nm}\,\sigma_{b,n}^{1/2}\,\sigma_{b,m}^{1/2}$$

$$\times \exp\left[-2\alpha\,(r_n + r_m) - \frac{v\bar{\sigma}_e}{2}(r_n - r_{n,o} + r_m - r_{m,o})\right]$$

which are, respectively, the incoherent and coherent parts of ε, or those terms which are independent of and dependent on the coherence of the constituent fields of p_{sc}.

Evidently, the value of the time-integrated echo intensity ε, through its origin in p_{sc}, is strongly dependent on the precise configuration of scattering bodies in V. Only for those configurations for which $|r_n - r_m| > cT/2$ for all $n \neq m$ will particular ε be independent of coherent contributions. This condition is very strong and, for the kinds of applications that are to be addressed by this calculation, uninteresting. It is assumed, therefore, that the coherent part of ε generally makes a non-negligible contribution for particular configurations of scatterers.

It has been assumed already that the signal waveform $s(t)$ is relatively narrowband and not of very long duration, although, of course, its duration must be long compared to the inverse of its center frequency in order satisfy the condition of being narrowband. In the limit that $s(t)$ is sufficiently narrowband, the power spectra of $s_n(t)$ and $s(t)$ will be very similar and, as a consequence of the Wiener-Khintchine theorem (HORTON 1969), the cross correlation function $\varrho_{nm}(\tau)$ will closely resemble the autocorrelation function $\varrho(\tau)$. If it is assumed further that $s(t)$ is unexceptional and belongs to the class of waveforms which include, for example, pulsed sinusoids and FM slides of narrow bandwidth, then $\varrho(\tau)$, and correspondingly $\varrho_{nm}(t)$, will oscillate rapidly with τ and contain nearly equal positive and negative parts, so that

$$\int_{-\infty}^{\infty} \varrho_{nm}(\tau)\, d\tau << \varrho(0)T$$

which can be shown by application of the Wiener-Khintchine theorem to the power spectrum of $s(t)$. If the collection of scatterers are randomly distributed in V, then the argument $\tau = 2(r_n - r_m)/c_o$ of ϱ_{nm} for $n \neq m$ will be a stochastic variable and the contribution of the coherent part of ε to the mean of ε with respect to the ensemble of all possible, allowed configurations of scatterers in V will be negligible. In this random-phase-type approximation, then, the mean or ensemble-averaged time-integrated echo intensity $\bar{\varepsilon}$ will be simply the ensemble-average of the incoherent contribution to ε, viz.

$$\bar{\varepsilon} = \frac{I_o \varrho(0)}{4\pi} \overline{\sum_n \frac{D_{S,n}^2 \; D_{R,n}^2}{r_n^4} \sigma_{b,n} \, exp \left[-4\alpha r_n - \nu \bar{\sigma}_e (r_n - r_{n,o}) \right]}$$

where all quantities written with an overhead bar are averaged with respect to the ensemble of all possible, allowed configurations of scatterers in V.