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CLUPEID POPULATIONS OF INSHORE WATERS
OF THE WEST COAST OF SCOTLAND

by

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ABSTRACT

Population dynamics and aspects of biology of the clupeid populations in the sea-lochs and the 'open' areas around Oban were studied from April 1970 to October 1972.

The area investigated is an important nursery ground for young clupeids. The localised distribution of O-group fish and the age structure of the sprat populations are mainly attributed to the biomass that can be supported by each locality. The composition of the commercial fishery was similar to that of the more 'open' areas.

Growth rate of O-group clupeids is not significantly different from locality to locality. A period of rapid growth in sprats after their first winter is evident. Growth curves using empirical data and back-calculated lengths were constructed.

Autumn-spawned young herring probably originate from the Minch autumn spawning stock, and the spring-spawned ones from the Clyde stock. The sprat populations appear to be homogeneous in origin.

Spawning in sprats lasts for a period of five to six months, starting in February-March. Minimum size of maturity is 88-90 mm in both sexes but males mature earlier in the season. Sprat shed their eggs in 7 to 10 batche and the significance of serial spawning is critically examined. The fecundit ranges from 8300 to 46600 in fish between 95 and 146 mm in length. It is significantly correlated to weight, length and age.

O-group clupeids tend to feed throughout the year, whereas nearly 40% of the older individuals do not feed during the winter months. The specie composition of the diet in O-group herring and sprats are identical. The

diet is mainly crustacean, the main component being copepods. Qualitative and quantitative similarity of the diet and the overlap of the daily feeding periodicities in 0-group clupeids is indicative of potential competition for food between these two species, when and if the food supply is limiting.

Two species of nematodes and one helminth were found to be parasitic in the body cavity and the gut respectively. In addition two species of the genus Lernaeenicus were parasitic on sprat.

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Section 1

GENERAL ASPECTS

1. I. Introduction

The West Highland sea-lochs and associated inshore areas have been relatively little explored in the past. Their importance as nursery grounds for commercially valuable species of fish and their potential for mariculture have come to light only in very recent years. The present study is an attempt to investigate the biology of clupeid species in sea-lochs and associated inshore areas around Oban and to evaluate the importance of these and similar areas to the commercial fisheries.

The two species of clupeids present in this area are the herring <u>Clupea harengus</u> L. and the sprat <u>Sprattus sprattus</u> (L.) (Synonym. <u>Clupea sprattus</u>). They are two closely related species and belong to the order Clupeiformes. The taxonomy, geographical distribution and specific characters are dealt with by Svetovidov (1952) and Wheeler (1969).

Herring rank among the top three species of commercial importance in European waters. In the present century the landings of herring by all European countries reached over two hundred million tons averaging 3.636 million tons a year, by the middle 50's, which represents about a third of total fish yield in the area. In recent years, however, the landings from the Atlanto-Scandian and North Sea herring fisheries have declined markedly. Some of these fisheries, for example the Icelandic and the Norwegian spring-spawning, have almost completely collapsed. On the

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Not surprisingly, as a result of its commercial importance, the herring has been the subject of intensive research by European scientists. No attempt is made at present to review the vast amount of literature that has accumulated since the end of the last century.

Parrish & Saville (1965) reviewed the biology of North East Atlantic herring populations and subsequently (1967) dealt with the changes in fisheries of North Sea and Atlanto-Scandian herring stocks and their causes. Cushing & Burd (1957) discussed the age composition, mortality, growth and effect of fishing on the herring of the Southern North Sea. Physiological and behavioural studies on clupeids were reviewed by Blaxter & Holliday (1963).

Until recently, research on herring has been concentrated mostly on commercially viable stocks, supported by regular larval surveys, but not much is known about the biology of young herring and consequently this has left a gap in understanding certain changes that have been experienced in commercial stocks. This fact has been recognised by herring biologists in recent years and a science committee of the North Atlantic Treaty Organisation, conferring on North Sea Sciences in November 1971, recommended "the factors determining year-class strength of the species, which form important parts of our fishing resources, may depend on changes in the food web, studies of which should be extended to include observations on larval and juvenile (0-gr.) fish. For example studies of the food, feeding behaviour and mortality could be of great importance to an understanding of the fluctuations in the abundance of fish stocks".

Lack of research on young fish in the early days was to a certain extent caused by the non-availability of a proper fishing gear, capable of catching young fish. The introduction of high-speed tow nets and midwater trawling has overcome this problem to a great degree. Prior to that the only available sampling gear for young fish were trap nets and beach seines, which restricted the area of sampling to shallow waters.

Though the pioneering work on young fish started as far back as 1914 by Hjort, the continuation of this type of work has been rather slow. Lebour (1924), however, studied the feeding habits of young herring off Plymouth and Marshall et al.(1939) studied the growth rates, food and feeding behaviour and seasonal chemical changes of young herring in the Clyde sea area. They recognised two stocks of herring in the Clyde, one which originated from spring spawning Clyde herring, the other to be from an autumn spawning stock. Daniel (1947) studied the growth rate of whitebait herring of the North Wales Coast.

In more recent years, Saville (1971) worked on the recruitment of young herring in the Moray Firth to their adult stock. Dragesund (1970) reviewed the studies on recruitment of Norwegian spring spawning herring. Wood (1959, 1971) discussed the origin and length frequency distribution of whitebait herring in the Southern North Sea.

The sprat, both young and adult have been almost totally neglected for which the reasons may be twofold. First it is commercially far less important in comparison to herring and is generally considered to be a 'trash' fish. Second, around the coasts of Britain, sprat fisheries are extremely seasonal and of short duration, thus making it almost impossible to study yearly cycles in feeding habits, maturation etc.

Robertson (1938) reviewed the sprat fisheries in England, but important aspects of its biology such as food, feeding and reproduction were hardly dealt with. Johnson (1970) studied the Wash sprat fishery, in which apart from commercial statistics, growth rates, size and age composition, minimum size of maturity and a few other aspects of reproductive biology were considered.

On the Scottish west coast a sprat fishery has developed since November 1968 (Langham, 1969). This fishery is of special relevance to the present work, since it is almost entirely confined to the sea-lochs. The fishery lasts for about two months, from mid-November to mid-January and it is a ring-net fishery.

The biology of 0-group sprats is almost completely unknown except for the fact that their occurrences with 0-group herring has been observed by a number of authors (Daniel, 1947; Smith, 1949; Bowers, 1952).

On the other hand the Black Sea sprat - <u>Sprattus sprattus phalericus</u> (Scheidner) and the Baltic Sea sprat - <u>Sprattus sprattus balticus</u> have been the subject of extensive study by Russian workers, notably Aslanova (1964), Kazanova (1960), and Petrova (1960). Even in these two sub-species the food habits and 0-group biology have not been dealt with in any detail.

It has been known for a long time that these two species of clupeids, in their young stages, tend to move into shallow inshore waters. Here, climatic changes could affect the availability of food and these changes may be more pronounced than in open waters. A knowledge of the biology of these species in their early phase of life and the interaction, if there is any, between the species, are possible criteria that could be used in assessing changes in the adult stocks.

The West Highland sea-lochs are comparable to the Norwegian Fjords. The fjords are the main nursery grounds for the Norwegian spring-spawned herring (Dragesund, 1970) and they also support a profitable fishery for young herring during the winter months. An attempt is made in this thesis, to assess the importance of sea-lochs and inshore waters investigated, as nursery grounds for young clupeids. The relative abundance, population structure, growth of 0-group and older clupeids have been studied. Reproductive biology of sprats was also investigated. The food and feeding habits of herring and sprats in their first year of life and in the older stages were studied, in an attempt to assess the extent to which the two species depend on a common food supply in inshore waters. Seasonal cyclical changes in condition and parasitic infection were also dealt with. Finally, an attempt was made to link these studies to the commercial fishery in case they could be made use of in future predictions of year-class strength and yield.

1. II. Sampling area

Sea-lochs and associated inshore sea areas were sampled at regular monthly intervals, as far as possible, from April 1970 to October 1972. The main sampling grounds, and the type of gear used are shown in Fig.1. In the regular sampling programme three sea-lochs on the mainland and one in the East of the Island of Mull were worked on. Loch Creran (on the mainland) was found to be unsuitable for ground trawling and as a result sampling was discontinued after September 1970. In July 1970 three sea-lochs on the West of the Island of Mull were also sampled.

Lochs Spelve and Creran are smaller than Etive, Sunart and Loch Linnhe. Loch Linnhe is by far the biggest loch but sampling in it had to be restricted close to its mouth, due to the lack of ship-time. Sampling in Loch Sunart and in the upper Sound of Mull was rather irregular, again due to lack of ship-time. Loch Etive is a long narrow loch with a small entrance compared to its size. As a result a strong tidal current of up to about 7½ knots occurs at the entrance during spring tides. It is roughly divided into an upper loch and a lower loch by a narrow neck. Two rivers, the Awe and the Etive drain into the two halves of the loch, resulting in marked changes in salinity in the surface layers during the rainy season. The volume of water, catchment area of each loch, width at the entrance the mean salinity and average depth are given in Table 1.

During the commercial sprat fishery in December 1970 to January 1971, three samples each of one hundred fish from sea-lochs on the West of Mull

Fig.1. Map showing the areas of sampling and the gear used at each station.

Stations 1, 2 - Loch Etive
Stations 3, 4 - Firth of Lorne
Station 5 - Loch Linnhe
Station 6 - Loch Spelve
Station 7 - Loch Creran
Station 8 - Bloody Bay
Station 9 - Loch Sunart
Station 10 - Loch Scridain

(BT-Bottom trawling; MT-Mid-water trawling; BS-Beach seining).

d the gear used

och Etive

irth of Lorne

och Linnhe

o h Spelve

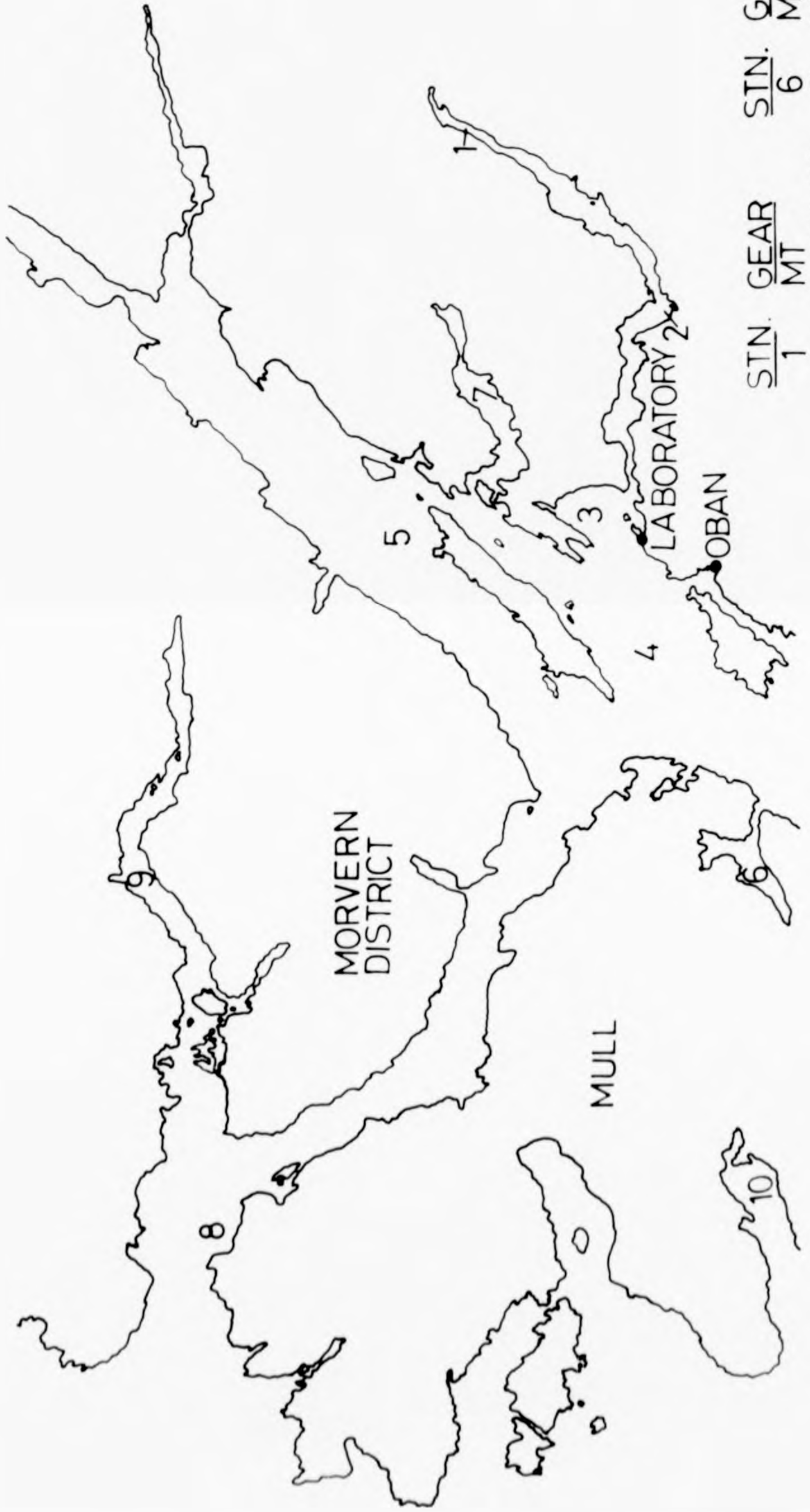
och Creran

loody Bay

och Sunart

och Scridain

awling: BS-Beach



STN.	GEAR
1	MT
2	MT,BT,BS
3	MT,BT,BS
4	MT,BT
5	MT,BT

STN.	GEAR
6	MT,BT
7	BT
8	MT,BT
9	MT,BT
10	BT

Table 1. PHYSICAL CHARACTERISTICS OF THE SEA-LOCHS SAMPLED.

	Etive	Spelve	Creran	Sunart
Surface area (km^2)	73	9	13.5	41.5
Average depth (m)	56	19	19	38
Deepest point (m)	141	50	46	97
Width of entrance (m)	280	372	465	2046
Mean salinity (‰)	22.5-29.5*	33	33	31
Catchment area (km^2)	1,383	75	167	N.A.

* Since the salinity is fairly variable in Loch Etive the range is given (Station 2).

N.A. - data not available.

were obtained. Although attempts to obtain samples from the 1971-72 fishery were unsuccessful, Dr. R. Bailey of the Marine Laboratory at Aberdeen provided the year-class composition of the West Coast fishery to be used in this thesis.

1. III. Sampling gear

Three main types of gear, 2 bottom trawls and one mid-water trawl were used from R.V. Calanus in the present investigation and on occasions a beach seine was also used. Until September 1971, a Vigneron-Dahl, manilla trawl known as the Calanus trawl was used alternately with a Gourock No.1 mid-water trawl. The Calanus trawl had a foot rope of 72 feet and head line of 54 feet. The wing netting is 18 feet long. The top of the lower wings and the square have mesh sizes of 5 inches and $5\frac{1}{2}$ inches respectively. The meshes of the belly average 4 inches and the cod-end has $3\frac{1}{2}$ inches mesh. A small mesh cover of 1 inch agassiz netting extends outside the upper half of the cod-end for its entire length of 12 feet. The last 6 feet of the cod-end is covered by chaffing material.

The Gourock No.1 mid-water trawl was first used in June 1970, and thereafter every other month until April 1972. This trawl has a foot rope of 90 feet and a head line of the same length. In August 1970 the head line was shortened to 80 feet. The 48 feet wings, of $6\frac{1}{4}$ inch mesh, lead into a square of 9 feet of the same mesh size. The belly of 31 feet has a mesh size of $4\frac{1}{2}$ inches at the beginning and tapers to a mesh size of $2\frac{1}{2}$ inches. The extension piece and the cod-end are 42 feet and

27½ feet in length respectively, with a mesh size of 1½ inches. The cod-end is further covered by 1 inch fine mesh along its entire length. This trawl was used in conjunction with a Kelvin Hughes head line transducer, fitted on to the centre of the head line. The signals emitted by the transducer was relayed through a heavy duty cable on to a Kelvin Hughes MS.39 F/M Recording Echo Sounder. From this system, the fishing depth and the gape of the net was read, and by adjusting the speed of the ship and/or the warp length, fishing at any desired depth was possible.

In August 1971, two wing trawls provided by the Marine Laboratory at Aberdeen were used for comparative fishing experiments. These were known as the Clupea and Mara trawls. The Clupea trawl was used instead of the Calanus trawl after August 1971 in the monthly bottom trawling.

The Clupea wing trawl has a head line of 58 feet, a foot rope of 76 feet and a wing rope of 36 feet. The 37½ feet wings are of 6 inch mesh and the wings lead into a square of 8½ feet of 4½ inch mesh. The mesh size in the belly tapers 4½ to 2½ inches. The 27½ feet belly leads into an extension piece of 18½ feet of 1½ inch mesh and finally to 18 feet cod-end of the same mesh size.

The Mara wing trawl has the same dimensions on the meshes of each section. It has a head line of 70 feet and a foot rope of 88 feet and wing rope of 48 feet. The wings are 38 feet and the belly is 58 feet.

1. IV. Efficiency and selectivity of gear

In fishery biology, one has to make sure that the samples obtained during a study are representative of the population present. Absolute abundance on the other hand is difficult to estimate, even using different types of gear because the more efficient the gear is, the bigger the catch would be. In general, relative abundance estimates obtained by a single fairly efficient gear would give a reliable idea of annual and seasonal fluctuations which is sufficient for most work. In this investigation, no attempts were made to determine the absolute abundance of clupeid species in this area, but the age structure of the population was determined by using three different gear over the same ground at short intervals in 2 experiments.

(1) In August 1971, two sets of trawls, one in the Firth of Lorne and the other in Loch Linnhe, were carried out. Each set consisted of three trawls each of one hour duration, carried out using the Calanus, Mara and Clupea trawls. The towing speed was between 2½ to 3 knots and the entire catch from each trawl is tabulated in Table 2.

(2) Similarly in September 1971 the Calanus and Clupea trawls were used in the Firth of Lorne and Lochs Etive and Linnhe. At each locality two hauls, each of one hour duration, were carried out using the two trawls. The composition of the catches are given in Table 3.

The data from all the hauls for any one gear were pooled together and the number of herring and sprats caught per hours fishing was calculated (Table 4). Although the number of hauls that were carried out were not sufficient to treat the data statistically, there was evidence that the Mara wing trawl of R.V. Mara was the most efficient and the Calanus trawl was the least, in catching clupeids. From the

Table 2. COMPOSITION OF THE CATCHES, OBTAINED FROM THREE DIFFERENT GEARS IN THE FIRTH OF LORNE AND LOCH LINNHE, IN AUGUST 1971.

Type	F. of LORNE			L. LINNHE		
	'Mara'	'Clupea'	'Calanus'	'Mara'	'Clupea'	'Calanus'
Dogfish	13	4	2	186	12	10
Skate	–	–	2	2	–	–
Whiting	671	448	185	1104	1177	544
Norway pout	98	13	2	1301	958	128
Poor cod	–	14	–	17	–	–
Haddock	31	33	4	102	95	13
Plaice	1	–	1	–	1	–
Long rough dab	53	179	8	2	152	4
Common dab	7	3	–	–	–	–
Mackerel	2	2	3	–	–	–
Gurnard	1	1	–	–	–	–
Dragonet	3	–	–	1	–	–
Gobies	4	–	–		–	
Herring	1270	24	8	124	403	36
Sprat	212	120	147	–	–	–

Table 3. COMPOSITION OF THE CATCHES OBTAINED FROM CLUPEA AND CALANUS TRAWLS IN THE F. OF LORNE, LOCHS ETIVE AND LINNHE IN SEPTEMBER.

	F. of LORNE		L. ETIVE		L. LINNHE	
	'Clupea'	'Calanus'	'Clupea'	'Calanus'	'Clupea'	'Calanus'
Dogfish	3	6	90	21	13	1
Skate	–	1	3	1	–	–
Whiting	5600	790	1575	136	1500	113
Norway pout	1066	14	54	2	285	33
Poor cod	–	42	–	2	285	33
Haddock	167	29	–	–	9	–
Plaice	2	1	9	1	–	–
Long rough dab	494	6	56	5	88	–
Common dab	17	–	5	1	–	–
Mackerel	2	28	–	–	4	1
Gurnard	16	–	33	1	–	–
Dragonet	–	–	–	–	–	–
Gobies	–	–	–	–	–	–
Herring	264	74	3300	680	56	6
Sprat	30	3	20	–	–	–

limited data shown Table 4 it is evident that the Clupea wing trawl is about five times as efficient as the Calanus trawl in catching herring, while its efficiency in catching sprats is no different from that of the latter.

Though the numbers of herring caught in each trawl were significantly different, the age compositions were identical. The mean lengths of each sample from the different hauls were calculated (Table 5) and the differences were found to be statistically insignificant. It is thus clear that a good estimate of the herring population could be obtained with any one gear and that there appears to be hardly any gear selectivity as regards size or age.

The amount of data available on sprats from comparative trawls is less than on herring. The only large sprat sample in a comparative fishing experiment was obtained in August in the Firth of Lorne. A complete analysis of mean size and age composition of the catches from the three hauls was carried out.

The age composition of the three samples obtained using different gears is shown in Fig.2. Itis evident that there is only a slight difference in the age-composition of the catches from the different gears. When the mean length of each age group is compared with the corresponding age group from the different samples (Table 6), it is clear that they are very close to one another and the differences are too small to be of any significance.

Thus it is evident that the differences observed in sample size are a result of efficiency of the different gears and that there is

Table 4. NUMBER OF HERRING AND SPRAT OBTAINED BY DIFFERENT GEARS PER HOUR'S FISHING (ONLY THOSE HAULS, THAT GAVE POSITIVE RESULTS WERE TAKEN INTO ACCOUNT).

	'Mara'	'Clupea'	'Calanus'
Herring	697	809.4	161
Sprat	106	56.6	50

Table 5. MEAN TOTAL LENGTH (mm) OF 0-GROUP HERRING IN THE SAMPLES OBTAINED FROM DIFFERENT GEARS.

Area	F. of Lorne			L. Linnhe			L. Etive	
Gear	'Mara'	'Clupea'	'Calanus	'Mara'	'Clupea'	'Calanus'	'Clupea'	'Calanu
August	87.9	87.0	86.8	86.9	87.0	86.9	-	-
September	-	88.3	91.8	-	-	-	92.6	98.4

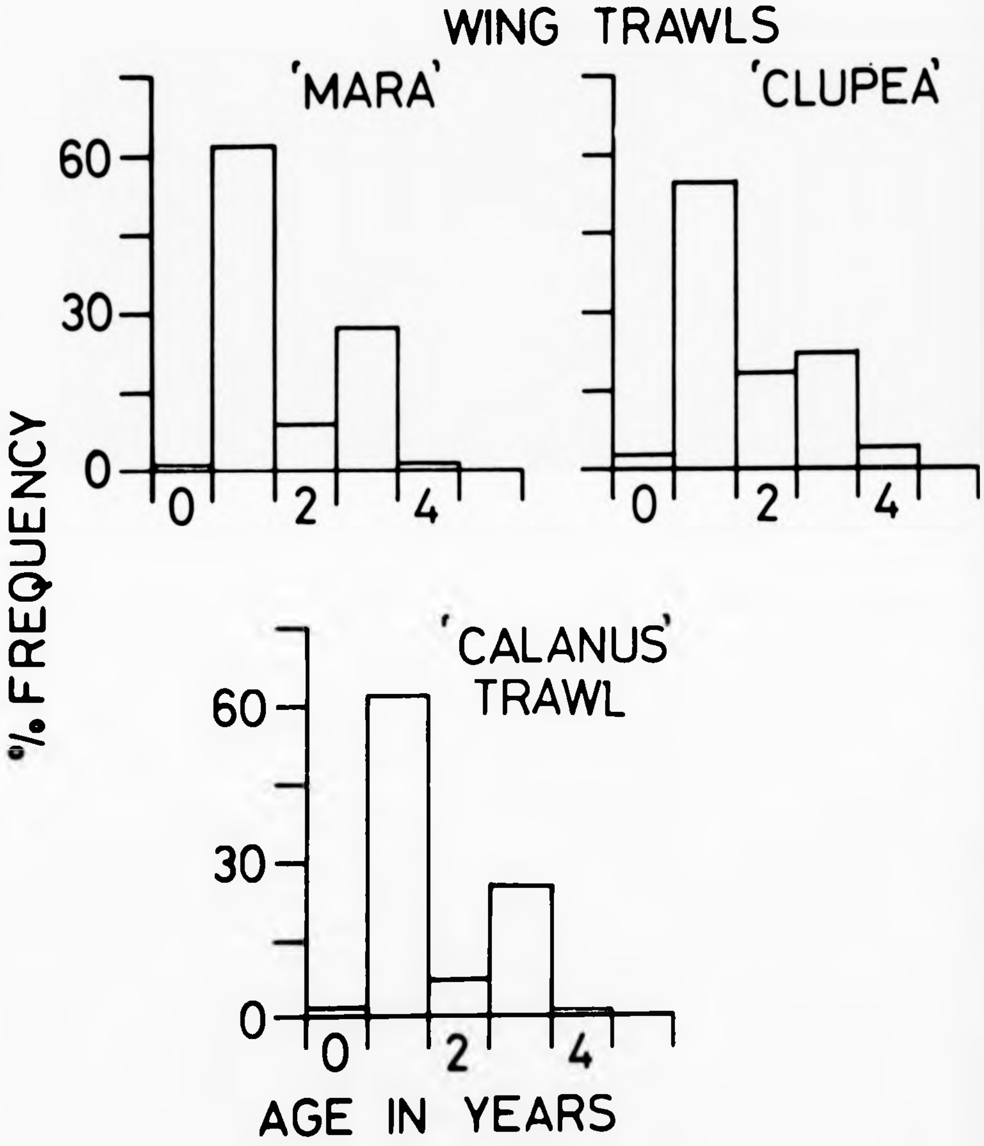
Table 6. MEAN TOTAL LENGTH OF SPRAT, OF DIFFERENT AGE GROUPS, IN THE SAMPLES FROM THE FIRTH OF [illegible], OBTAINED BY USING THREE DIFFERENT GEARS (NUMBER SAMPLED IS INDICATED IN PARENTHESIS).

	'Mara'	'Clupea'	'Calanus'
One year old	111.3 (47)	119.2 (44)	111.9 (51)
Two year old	123.0 (7)	125.9 (15)	118.5 (6)
Three year old	114.4 (13)	124.4 (18)	117.2 (20)
Four year old	132.0 (1)	127.0 (3)	136.0 (1)

Fig.2. Age composition of the sprat population in the Firth of Lorne obtained using three different gears in August 1971.

in the Firth

years in



very little selectivity as regards length and age of the catch in both species. It is reasonable to conclude that samples obtained using the Calanus trawl up to August 1971, and thereafter using the Clupea wing trawl, adequately represent the length and age of the herring and sprat populations.

1. V. Treatment of material

When the net was hauled, the clupeids were separated from the rest of the catch and the number of herring and sprats present were counted separately. When the catch was too large, the numbers were estimated by sub-sampling. A minimum of three sub-samples were counted and the total number of herring and sprats in the sample obtained.

A random sample of 80-120 fish of each species was taken and preserved in 70% alcohol. A few sprats were dissected fresh for histological studies (Section 3). From April to January, when the 0-group fish were easily distinguishable from older fish, in both species, random samples of 80-120 herring and sprats of each age group were taken. The effects of preservative on shrinkage in herring and sprat are given in Appendix 1.

Every sample was analysed after a minimum of five days but before a maximum of fourteen. Each fish was laid on a measuring board and its total length, defined as the length from the tip of the snout to the longest caudal fin-ray, was measured to one millimetre below its actual length. In the earlier samples, the standard length, defined as the length from the tip of the snout to the base of the caudal peduncle, was also measured. The gut and gonads were then removed and the fish weighed to 0.1 gm, using a Mettler, P160 balance.

Section 2. POPULATION DYNAMICS

2. I. Introduction

Population dynamics are essentially concerned with the continuous process of replacements of generations in time. Nikolskii (1965) considered it to be governed by three major factors;

(a) the birth of a generation

(b) its growth

(c) its death.

The details of the processes are in turn affected by specific adaptations and by relationships of the year-classes with the environment. Specific adaptive features that reflect these relationships are the rate and manner of replacement, the life span and the age composition of the population, while the total mass of the population is governed by the food supply.

Beverton & Holt (1957) modified this approach to suit exploited populations in a steady state. The primary factors contributing to such populations are;

(a) Recruitment of individuals to the exploited phase of the life cycle.

(b) Growth of individuals in the exploited phase.

(c) Capture of individuals in the exploited phase by fishing.

(d) Natural death of individuals in the exploited phase.

These aspects of commercially exploited fish populations have been studied either singly or together since Hjort (1914), byFord (1933), Ricker

(1948), Cushing (1959) and are considered in detail by Beverton & Holt (1957).

The present study on the clupeid populations of the West Highland sea-lochs and associated inshore waters do not conform to a steady state population, since they are characterised not by a recruitment pattern to the exploitable phase, but rather by a replacement of a year-class by a new one. Hence the theoretical models of Barnov (1918), Graham (1935), Ricker (1940, 1944), Beverton & Holt (1957) and Nikolskii (1965) are not directly applicable here.

Studies on populations similar to the one in this thesis are rare, and the importance of such studies in understanding the dynamics of commercially exploited populations have become apparent to the fishery biologists only in the recent past. The factors that govern fish population dynamics, as suggested by Nikolskii and others, have been modified to suit the present work. The main aspects dealt with in this section are abundance, age structure, growth, mortality and origin.

2. II. Material and Methods

Fish of both species were caught and treated as described in section 1. V. Total and standard length were measured in samples of 80-100 fish. The gonads were removed and fish weighed. A vertical transverse incision was made at the back of the skull to expose the largest pair of otoliths, the sagittae. They were carefully removed, using a watchmaker's forceps, washed, dried and stored in labelled envelopes for mounting.

The otoliths were mounted on black plastic cavity slides made by E. Perkins & Co., London, each of which hold ten pairs of otoliths. The mounting medium used was that recommended by Parrish & Sharman (1960)- an autoplax resin (No.102), to which was added an accelerator (No.5) and a catalyst. This medium was found to be very transparent and had an added advantage of quick drying when compared to most other media.

Otoliths were examined under a binocular microscope using reflected light at a magnification of fifty. The opaque and hyaline zones were clearly distinguishable and the number of hyaline zones in each pair of otoliths was counted. In addition, other otolith characteristics, such as the nature of the nucleus, the width of the first growth zone, the ratio of the antirostrum to the rostrum and the nature of sulci were carefully observed and noted especially in the herring. In both herring and sprat, the distance from the nucleus to the origin of each hyaline zone and the total length of the otolith were measured along the post-rostral axis, using a micrometer eye-piece.

Using these measurements and the total or standard length of a particular fish, as Lea (1910) did for herring scales, the length of the fish at each previous winter could be obtained by a simple proportion calculation.

$$\frac{\text{Length at the end of the first winter}}{\text{Total length}} = \frac{\text{Distance from the nucleus to the first hyaline zone}}{\text{Length of the otolith}}$$

Lee (1912) dealt in great detail with the errors and discrepancies which could arise in the use of direct proportion calculations and these will be discussed later.

Eighty to hundred fish from each monthly sample of herring and between two and three hundred sprats from each area were used for the determination of meristic characters. Only herring in their first year of life (0-group) were used and the reasons for this will be apparent later. In herring the characters that were counted were the number of vertebrae including the urostyle and the keeled scales between the pelvic fins and the anus; in sprats these characters and the number of rays in the pectoral and pelvic fins were also determined. When the fish were below 60 mm in total length, they were stained in Alizarin (see Raitt, 1935) and after clearing in xylene the musculature on one side was removed with forceps and the number of vertebrae counted under a binocular microscope.

2. III. Abundance

One of the greatest challenges the fishery biologists has to meet with is the estimation of abundance of a population in a given locality. Absolute abundance could be estimated by extensive use of echo traces, identifying them and computing from sample traces of known concentration the number of fish in a given area or from tagging experiments or from larval abundance studies. The vessel R.V. Calanus, used throughout this investigation, was equipped with a Kelvin Hughes MS.29F echo sounder, the performance and accuracy of which was far from satisfactory for making computations of the absolute abundance of herring or sprats. There were many instances when very good echo traces were obtained, but fishing at these points proved unsuccessful. In addition the catches in the area investigated were almost always mixed in varying proportions with other species of fish and it is doubted that even with a satisfactory echosounder estimates of absolute abundance could have been made accurately. Nevertheless, sample traces obtained in one of the rare findings of a pure shoal of herring and of sprat are shown in Fig.3.

The abundance estimates obtained from catch data are only relative estimates, since, as stated in the section on gear (1.III), a number of types of gear were used and also the area of sampling in any one loch was seriously limited by shore and bottom topography. For example in Loch Etive only one region (Airds Bay) along its entire length of 17 miles was suitable for bottom trawling. Night fishing using mid-water gear was restricted to three stations in Loch Etive, the Firth of Lorne and the Bloody Bay where space was adequate. In Lochs Spelve and Creran the area for manoeuvering was a limiting factor even in daylight while in Loch Sunart the presence of small islands made it difficult to manoeuvre the ship.

Allowance has been made, as accurately as possible, for change of gear (Section 1.III) and the estimates are indicative only of the relative abundance. As regards 0-group, more than 95% of the catches were made with one type of gear (mid-water) and the errors, if there are any, are further minimised.

The relative abundance of 0-group herring and sprat of year-classes 1970 and 1971 are given in Fig.4. Fig.5 shows the relative abundance of herring and sprat in their first year of life and thereafter for each sea-loch and open area. Year-class abundance of both species at six monthly

Fig.3. Echo traces of 'pure' herring and sprat shoals.

t shoals.


SPRAT
1050 to 1120 hrs
LOCH SPELVE
22-AUG-72
72/85/01
HERRING
1200 to 1245 hrs
LOCH ETIVE
5-OCT-72

intervals with age is given in Fig.6. From these data a few characteristic features of the clupeid populations in this area seem to emerge. When 0-group abundance is considered a definite pattern is evident. In general, the estimates for the 1971 year-class were higher than those for the 1970 year-class and this is thought to be due to an increase in fishing efficiency rather than a difference in the year-class strengths. In 1970, 0-group herring were not obtained in the catches until June, when the mid-water gear was used for the first time. There is evidence, however, from gut analyses of whiting and spur-dogfish (personal communication from Dr. J.D.M. Gordon) that young herring were present in the area in April. The 1971 and 1972 year-classes made their appearance in the catches in April. It is thus evident that there is an immigration of young herring into the area, starting around April. There is a progressive increase in numbers (Fig.4) until about September, reaching values as high as 1700 per hours fishing. During the winter months there is a gradual decrease in numbers and by March-April in the following year the number of herring left in the area is very small. From Fig.5 it is evident that the immigrating fish tend to concentrate in the Firth of Lorne at first and then soon move into the sea-lochs. Loch Etive is the last to be "invaded" probably because of its sheltered, narrow entrance. After the initial movement into the lochs, young herring tend to move out within two months of the smaller sea-lochs, such as Spelve and Creran, and are very rarely caught in them thereafter.

Fig.4. Relative abundance of 0-group herring and sprats (per hour's fishing) of the 1970 and 1971 year classes (log-scale).

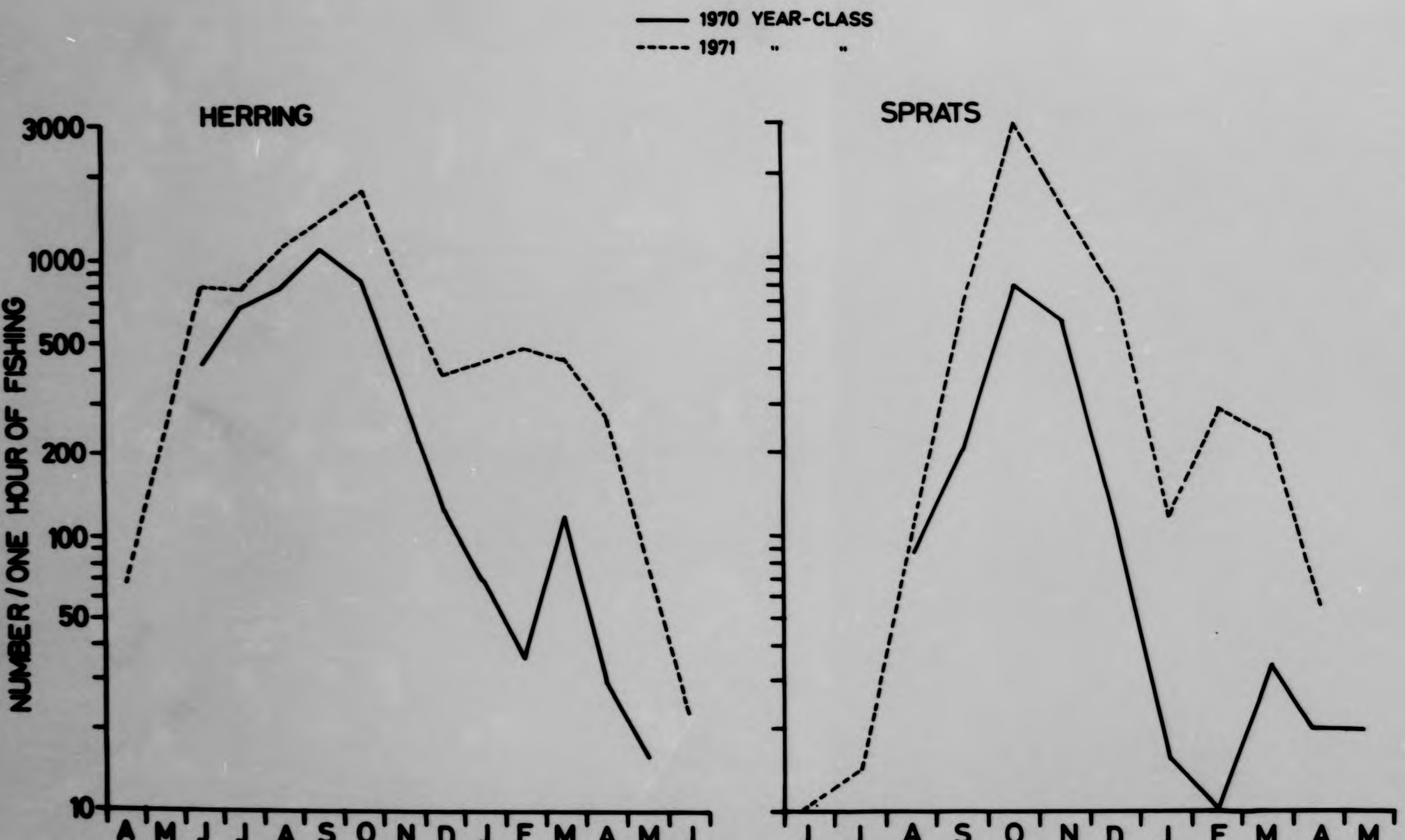
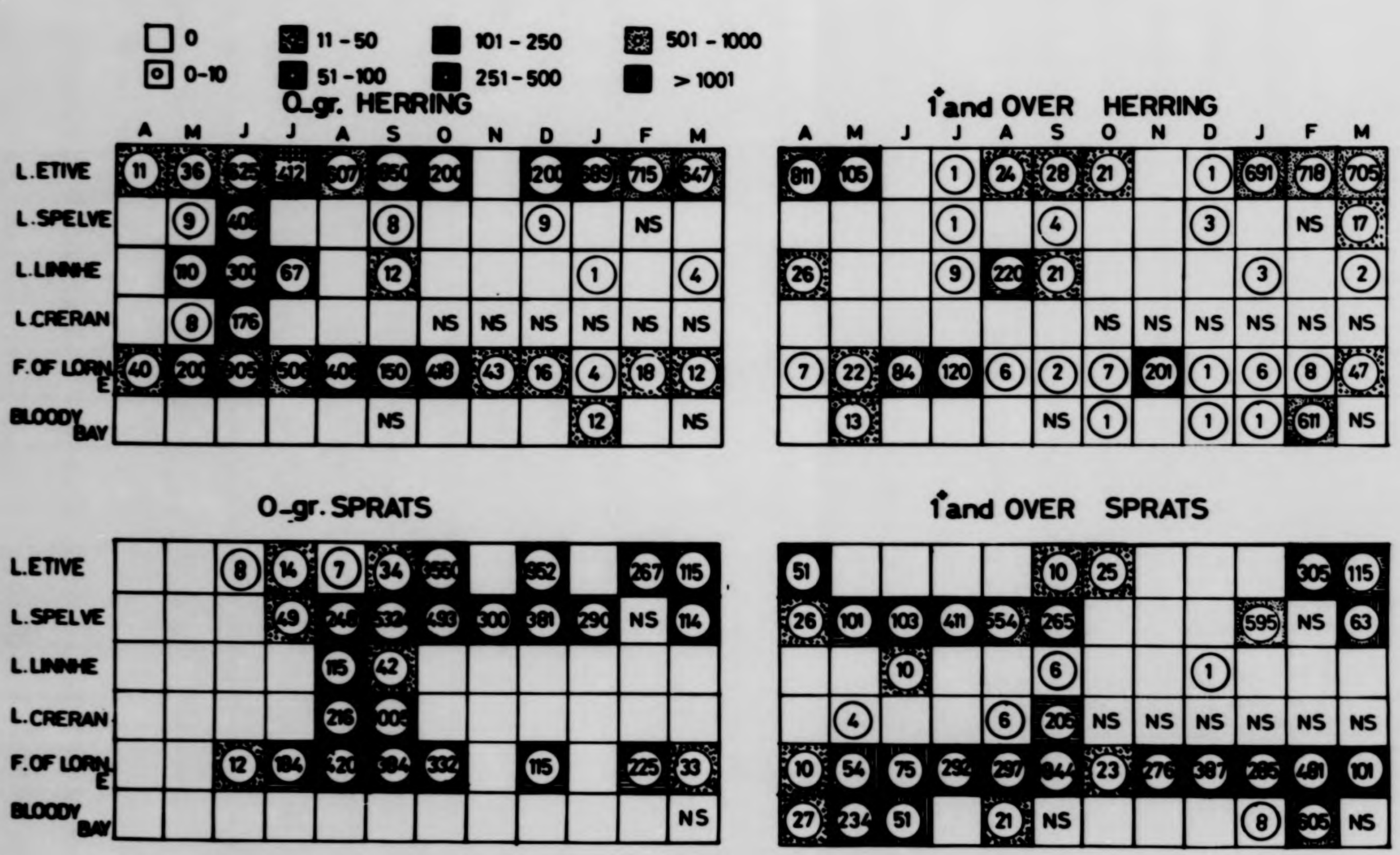

1970 YEAR-CLASS
1971 " "
HERRING
SPRATS
NUMBER / ONE HOUR OF FISHING
3000
1000
500
200
100
50
10
A M J J A S O N D J F M A M J
J J A S O N D J F M A M

Fig.5. Relative abundance (per hour's fishing) of herring and sprats in each locality. (N.S.-Not sampled).

g) of herring

ot sampled).



0-gr. HERRING

	A	M	J	J	A	S	O	N	D	J	F	M
L.ETIVE	11	36	625	412	607	850	200		1200	689	715	647
L.SPELVE		9	406			8			9		NS	
L.LINNHE		110	300	67		12				1		4
L.CRERAN		8	176				NS	NS	NS	NS	NS	NS
F.OF LORNE	40	200	905	506	406	150	418	43	16	4	18	12
BLOODY BAY						NS				12		NS

1^{+} and OVER HERRING

	A	M	J	J	A	S	O	N	D	J	F	M
L.ETIVE	811	105		1	24	28	21		1	691	718	705
L.SPELVE				1		4			3		NS	17
L.LINNHE	26			9	220	21				3		2
L.CRERAN							NS	NS	NS	NS	NS	NS
F.OF LORNE	7	22	84	120	6	2	7	201	1	6	8	47
BLOODY BAY		13				NS	1		1	1	611	NS

0-gr. SPRATS

L.ETIVE			8	14	7	34	9550		952		267	115
L.SPELVE				49	248	532	493	300	381	290	NS	114
L.LINNHE					115	42						
L.CRERAN					216	1005						
F.OF LORNE			12	184	620	984	332		115		225	33
BLOODY BAY												NS

1^{+} and OVER SPRATS

L.ETIVE	51					10	25				305	115
L.SPELVE	26	101	103	411	554	265				595	NS	63
L.LINNHE			10			6			1			
L.CRERAN		4			6	205	NS	NS	NS	NS	NS	NS
F.OF LORNE	10	54	75	292	297	344	23	276	387	285	481	101
BLOODY BAY	27	234	51		21	NS				8	605	NS

During the winter months there is an overall decrease in number of young herring. This could be due to either mass mortality, emigration or both. Predation is thought to be one of the main causes of natural mortality (Section 2.VI) the predators present being spur-dogfish, whiting, mackerel and sea-trout (personal communication Dr. J.D.M. Gordon). There is no evidence of an increase in the number of predators in the winter nor of an increased dependence of these predators on young herring. It is very likely that the decrease in abundance of herring during the winter is mainly due to an emigration, probably into deeper waters.

This decrease is not evident in Loch Etive and large concentrations of herring are found there during the winter. It was also noted that these fish are mainly found in a trench 150 to 180 m deep, which extends from the head of the lower loch well into the upper loch.

0-group herring were found to originate from both autumn-and spring-spawning races (Section 2.VIII). Spring-spawned herring of 1970, 1971 and 1972 year-classes appeared first in June at mean lengths of 44.5, 41.2 and 42.4 mm. The autumn-spawned fish were first caught in April 1971 and 1972 and the mean lengths were 44.8 and 40.4 mm, respectively (Appendices 2 & 3). Thus it is evident that herring from different parental stocks and the same stock in different years arrive in this area at a similar mean and range in length . The timing of the arrival is also the same for all year-classes of any one race.

Unlike herring, 0-group sprats move into the area at different times of the year. In 1970 they were first caught in August and in 1971 in June.

They also show a similar pattern in abundance when the whole area is considered (Fig.4) but are different from herring in their distribution and abundance (Fig.5). Unlike herring they tend to remain for a longer time in the small lochs. From September onwards there is a decrease in numbers in the area as a whole but concentrations of 0-group sprats are also found to occur in Loch Etive.

The 'birthday' of a fish is considered to be on the 1st of January. From Fig.5 it is also evident that after May there is an almost complete absence of 1+ and older herring in the area. Sporadic increases in numbers occurred in the Firth of Lorne in November 1970 and in Bloody Bay in November 1971 and these are thought to be emigrating fish. The increase in numbers in Loch Etive from January to April is due to the 0-group herring, which concentrated in the loch during winter, becoming 1 year old.

Older sprats are found in appreciable numbers throughout the year in the Firth of Lorne and Bloody Bay, while in the sea-lochs mainly one year old fish and a few two and three year olds are found in the spring. The general trends in abundance noticeable are an increase in the numbers of old fish during the winter months and then a gradual decrease from March till June, followed by a slight increase for one or two months and then a decrease coincidental with the arrival of the new year's brood.

The slight increase in the winter is probably a result of the immigration of overwintering sprats, while from March onwards migrations to the spawning grounds of mature fish and also the tendency to move into

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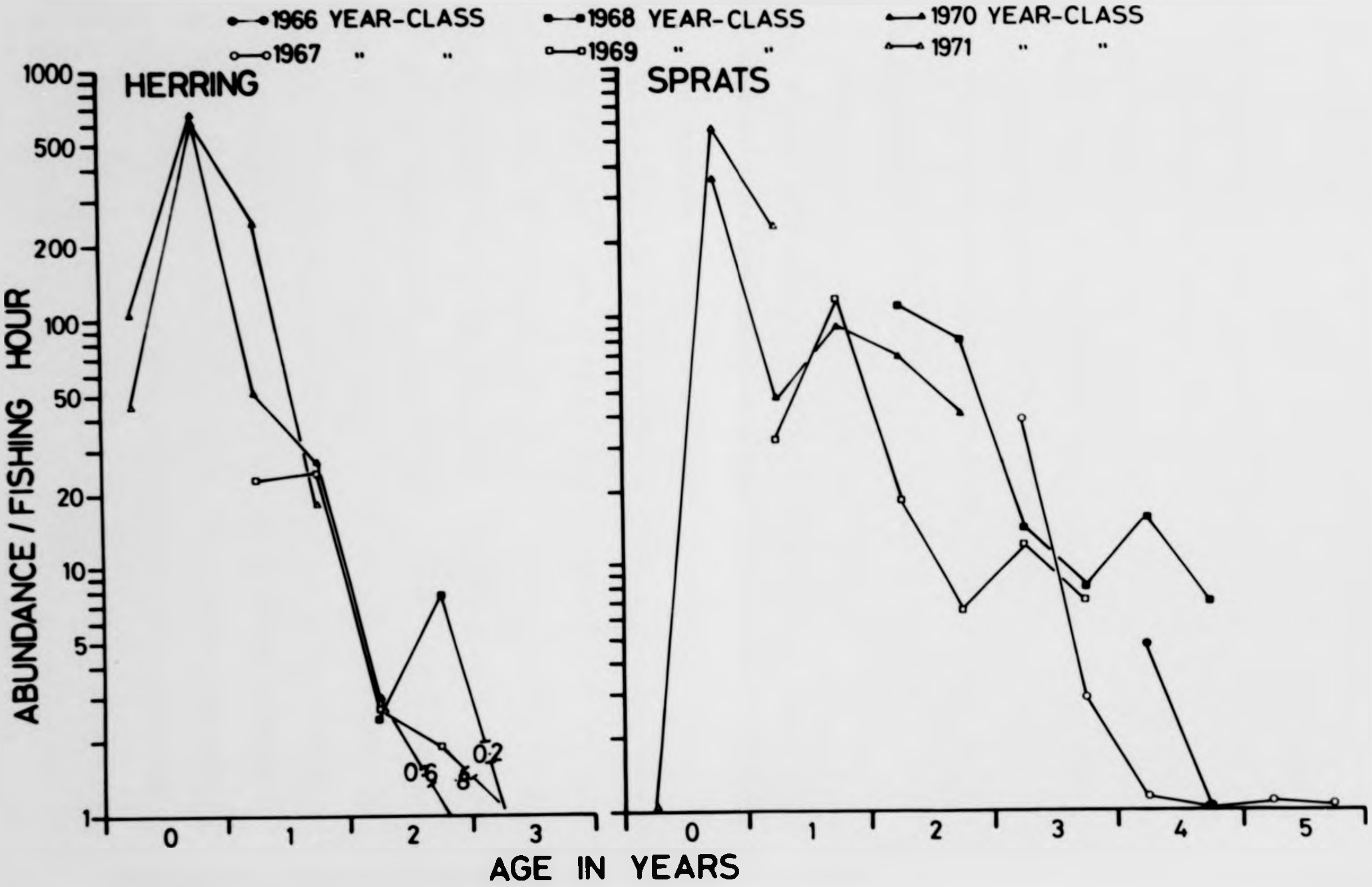
The slight increase in the winter is probably a result of the immigration of overwintering sprats, while from March onwards migrations to the spawning grounds of mature fish and also the tendency to move into deeper waters with age in clupeids would cause a decrease. The return of some individuals in July-August would probably result in a slight increase in numbers. Movement of the 0-group fish into the area would bring about a decrease in the number of older fish, the reasons for which will be given in the final discussion. The 0-group fish will become one year old in January and this together with the overwintering sprats would cause the significant increase in numbers at this time shown in Fig.5.

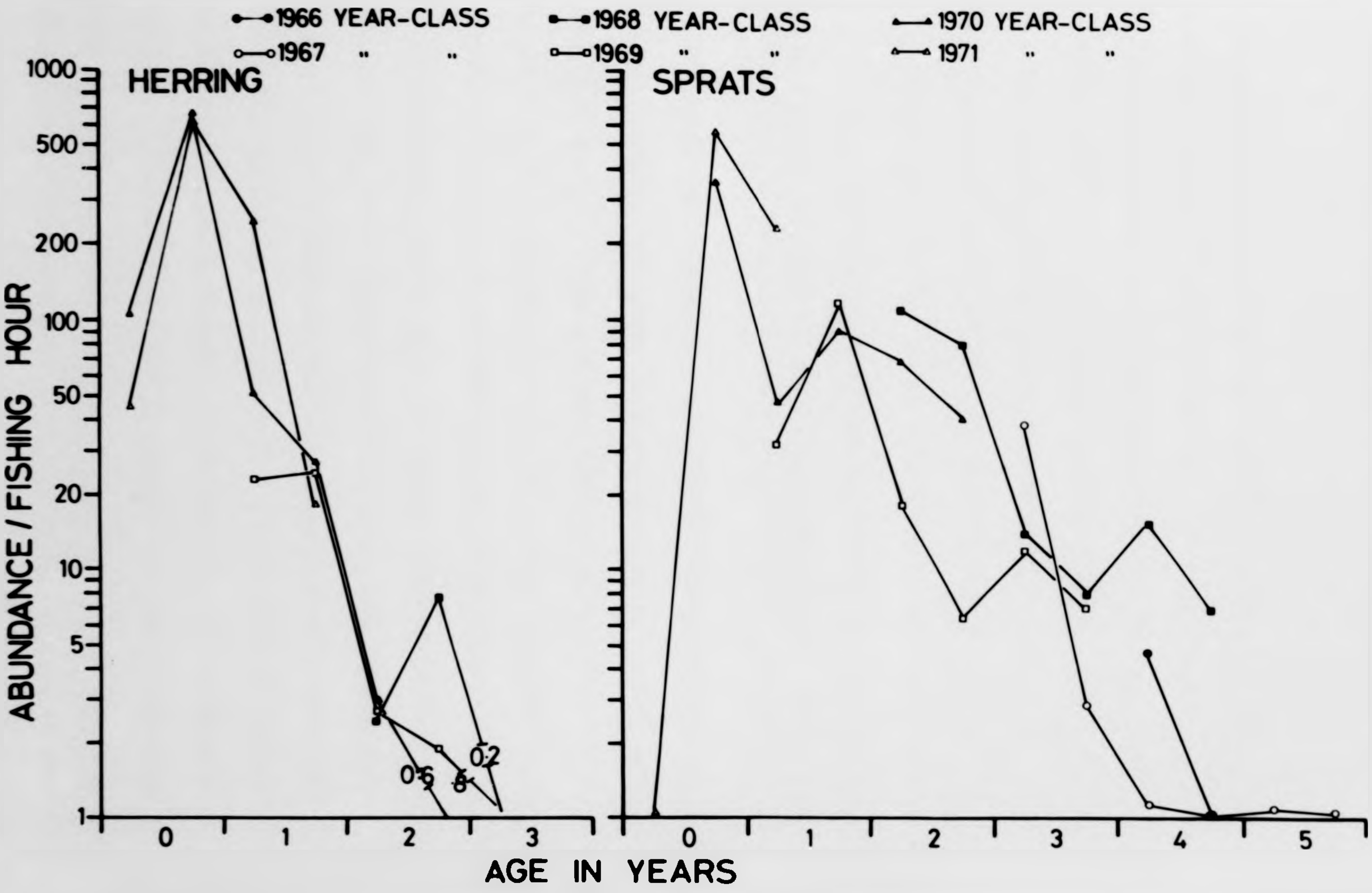
In both species there is a gradual reduction in numbers with age, the most significant being soon after the end of their first year of life (Fig. 6). This is probably due to the tendency in clupeids to move into deeper waters with increasing size and age and has also been noted by other authors (Parrish & Saville, 1965; Dragesund, 1970). This tendency is much less pronounced in sprats, as is evident from comparisons of abundance of corresponding year-classes in the two species. It is also evident that certain year-classes, for example the 1968 year-class, occur in greater abundance even at an older age and it is possible that such a phenomenon may be indicative of the year-class strength. This aspect will be dealt with in detail in the following section.

It has been known for some time that large concentrations of sprats occur in the West Highland sea-lochs and in November 1968, lochs on the mainland north of the Island of Mull were exploited commercially (Langham, 1969). During the 1969-70 and subsequent season, sea-lochs on the West of Mull were again fished. In the area described in this thesis, commercially viable concentrations of sprat were not found but it has been shown that

Fig.6. Year-class abundance of herring and sprats, with age.

ts, with


1966 YEAR-CLASS
1967 " "
1968 YEAR-CLASS
1969 " "
1970 YEAR-CLASS
1971 " "
HERRING
SPRATS
ABUNDANCE / FISHING HOUR
1000
500
200
100
50
20
10
5
1
0·6
0·2
0
1
2
3
4
5
AGE IN YEARS


1966 YEAR-CLASS
1967 " "
1968 YEAR-CLASS
1969 " "
1970 YEAR-CLASS
1971 " "
HERRING
SPRATS
ABUNDANCE / FISHING HOUR
1000
500
200
100
50
20
10
5
1
0
1
2
3
4
5
0·6
·8
0·2
AGE IN YEARS

there is a slight increase in numbers during the time of the fishery. Sprat fisheries around the coast of Britain are dependent on the mass migration of overwintering fish into the shallow coastal waters (Robertson, 1938; Johnson, 1970). It is probable that immigrating sprats find suitable overwintering grounds in the sea-lochs west of Mull and that the island itself acts as a 'barrier' to further easterly movements.

2. IV. Age Structure

Having dealt with relative abundance it is most appropriate to investigate the age structure of the clupeid populations. In temperate regions growth of most organisms is seasonal, with little or no growth taking place during the winter. As a result of this growth check, annual rings are laid down on hard parts of the body, such as scales, otoliths, vertebrae, opercula etc. Graham (1929) deals in detail with the use of otoliths and scales and Le Cren (1947) in the use of opercula, in age determination of fishes. In the otoliths opaque and hyaline substances are laid down alternately during the growing and the non-growing periods. By counting the number of hyaline zones in an otolith, the number of winters it had lived through and thereby its age can be determined.

In arriving at the age distribution of the population, samples obtained in two consecutive months were pooled together. This was done to compensate for errors due to mesh selection and gear selectivity of any one type of gear. Thus a combined sample, obtained from midwater and bottom gear, was expected to give an acceptable representation of the population .

As stated earlier, because of the absence of herring in Lochs Spelve, Creran and Sunart and the similarity in age distribution in the Firth of Lorne, Bloody Bay and Loch Etive, the age composition diagrams are based on pooled data from all the areas (Fig.7). The age composition of herring is dominated by one year old fish until about April-May when the appearance of the 0-group and the emigration of 1+ fish makes the 0-group more dominant. This trend was observed in the two and half years of analysis. Two and three year olds constitute a very small proportion of the population and their occurrence is rather sporadic.

The age composition of sprat populations in Lochs Spelve, Etive, Creran and also those on the west of Mull (Loch Scridain) and in the 'open' areas, Firth of Lorne and Bloody Bay, are given in Figs 8 & 9 respectively from May 1970 to October 1972. For purposes of comparison of the sea-loch and 'open' area populations, with that of the commercial fishery, year-class composition from April 1970-March 1971 and April 1971-March 1972 was calculated separately for the sea-lochs and for the Firth of Lorne and Bloody Bay (Fig.10).

Sprat populations in the sea-lochs are dominated mainly by one year old fish, which gradually becomes replaced by the 0-group of every new year-class. Complete replacement of 1 group fish occurs in two to four months. Fish older than one year are present in small proportion, and enter into the population during the winter months. After the winter there is a gradual decrease and by July-August they constitute an almost insignificant proportion of the population. In the winter months 2, 3 and

Fig.7. Age distribution of the pooled herring populations from April 1970 to October 1972.

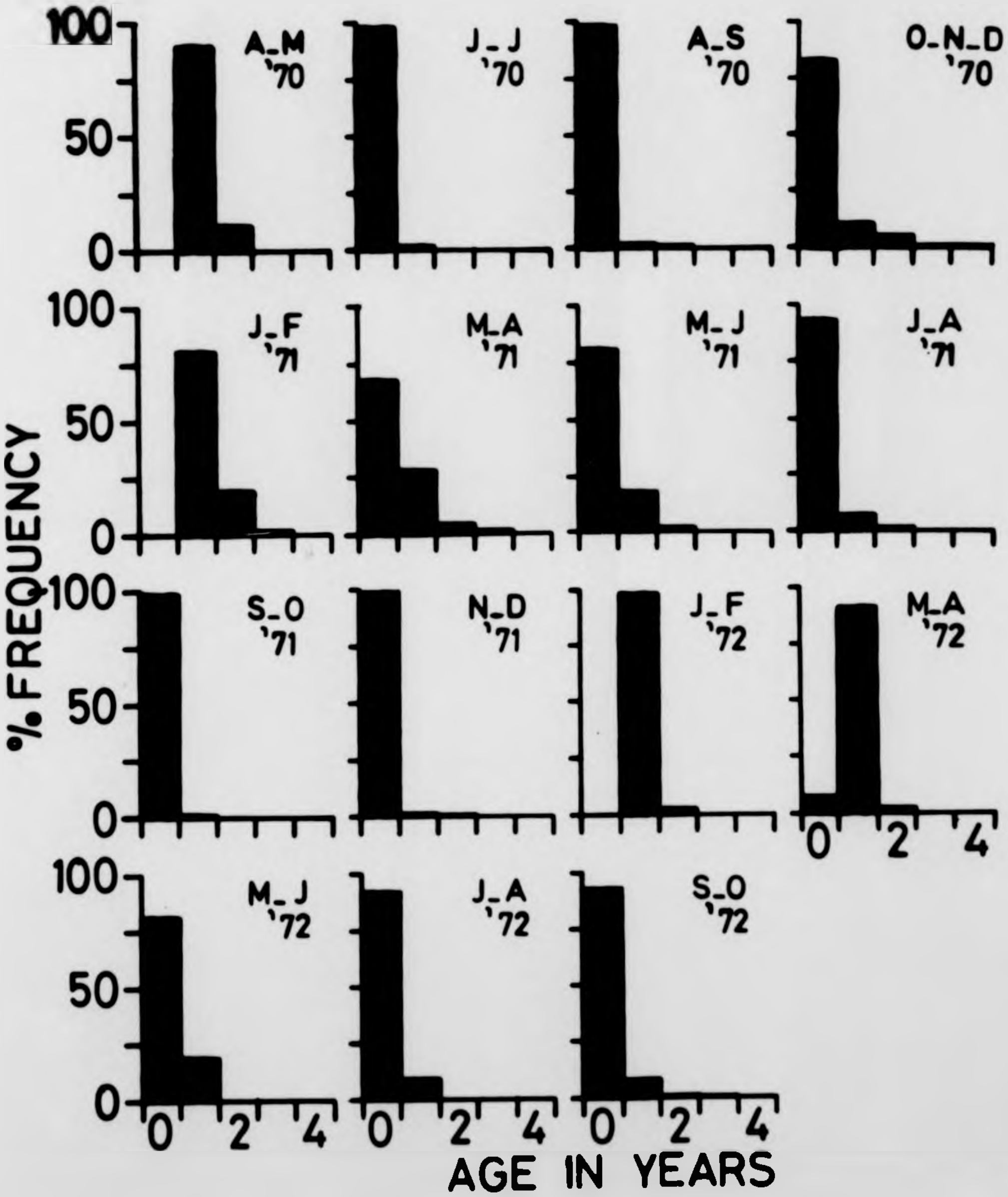

A_M '70
J_J '70
A_S '70
O_N_D '70
J_F '71
M_A '71
M_J '71
J_A '71
S_O '71
N_D '71
J_F '72
M_A '72
M_J '72
J_A '72
S_O '72
100
50
0
% FREQUENCY
0
2
4
AGE IN YEARS

Fig.8. Age distribution of the sprat populations in the sea-lochs from April 1970 to October 1972.

Fig.8. Age distribution of the sprat populations in the sea-lochs from April 1970 to October 1972.

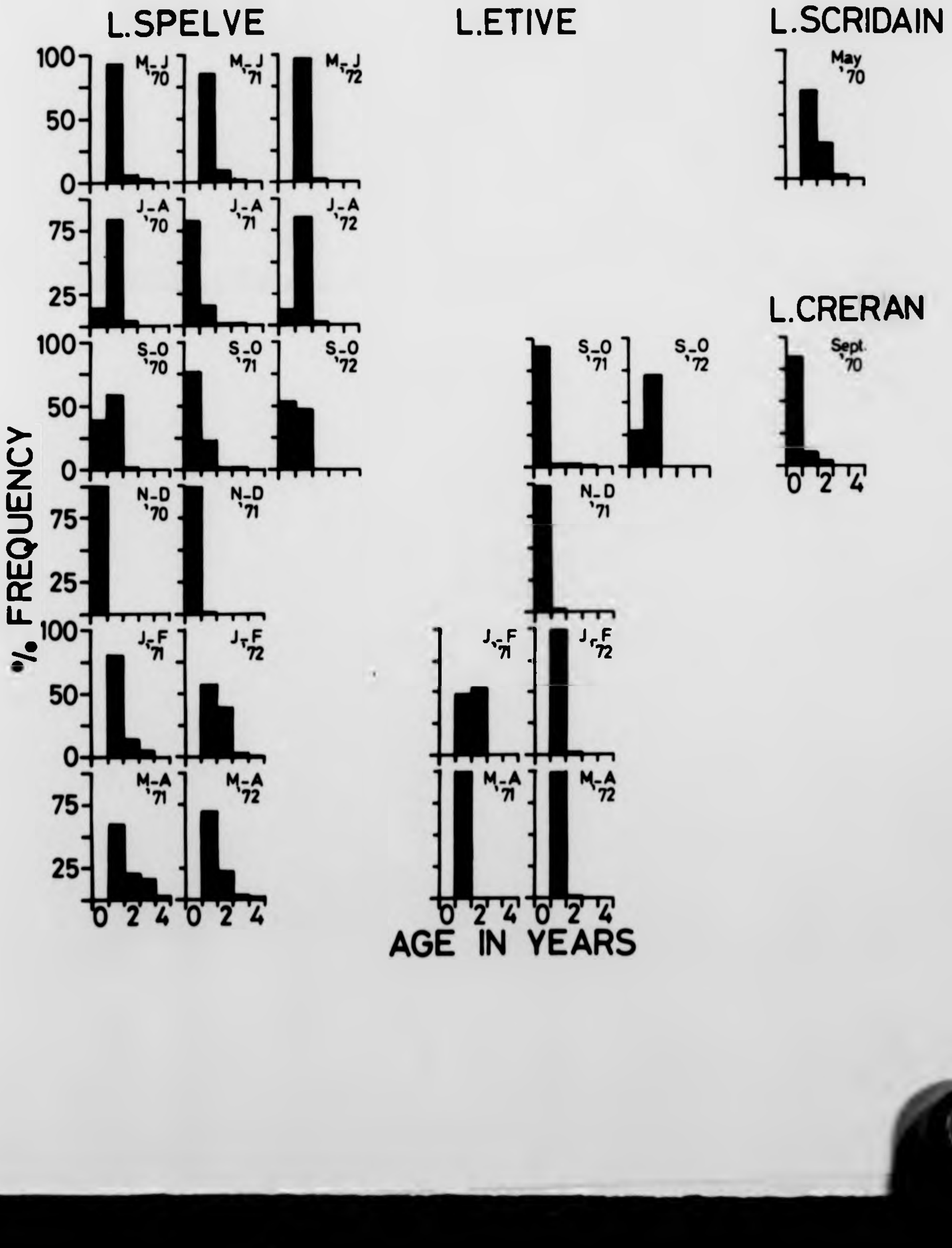

L.SPELVE
L.ETIVE
L.SCRIDAIN
L.CRERAN
% FREQUENCY
100
75
50
25
0
M-J '70
M-J '71
M-J '72
J-A '70
J-A '71
J-A '72
S-O '70
S-O '71
S-O '72
N-D '70
N-D '71
J-F '71
J-F '72
M-A '71
M-A '72
May '70
Sept. '70
0
2
4
AGE IN YEARS

Fig.9. Age distribution of the sprat populations in the 'open' areas from April 1970 to October 1972.

ons in the

r 1972.

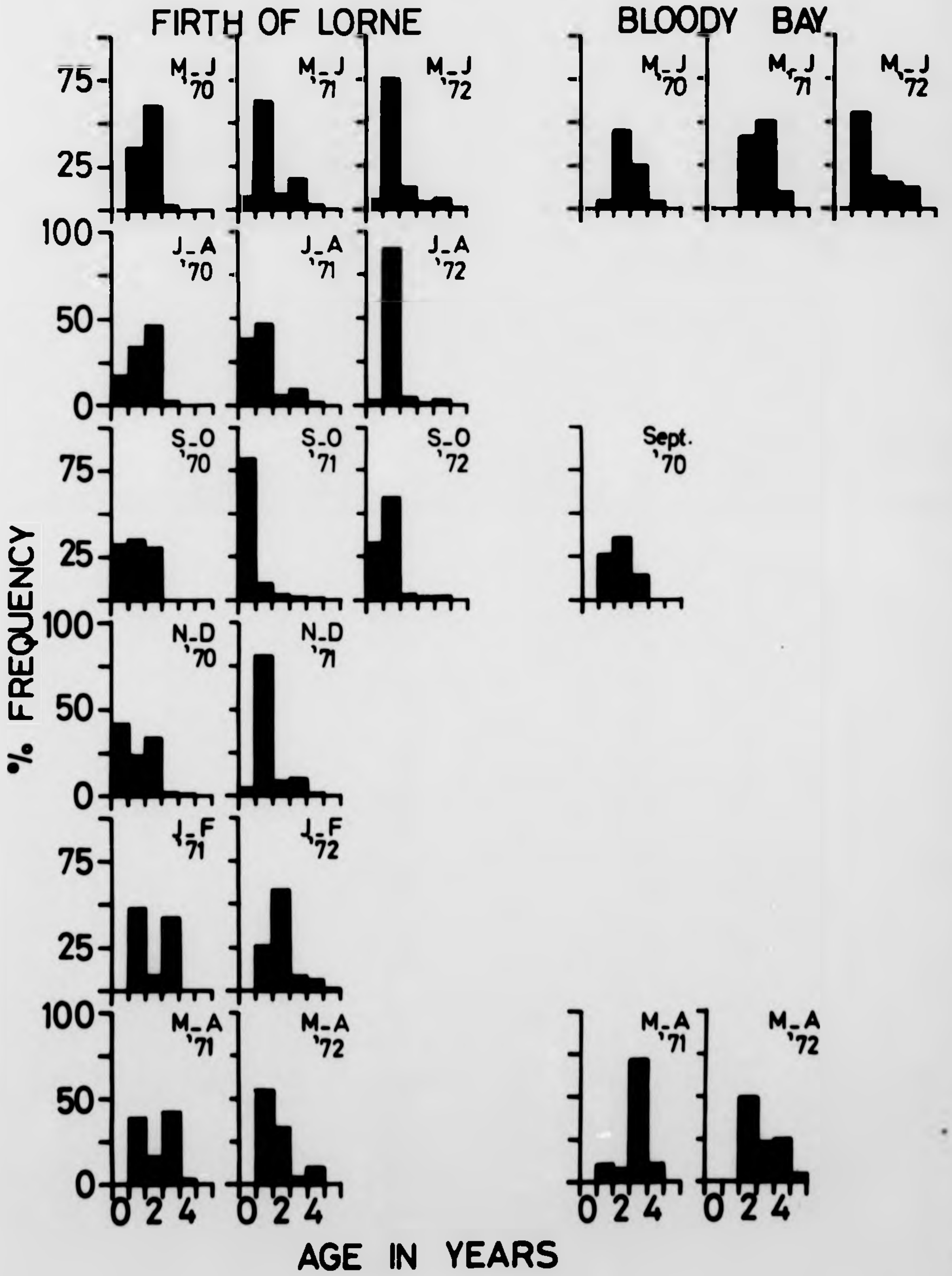
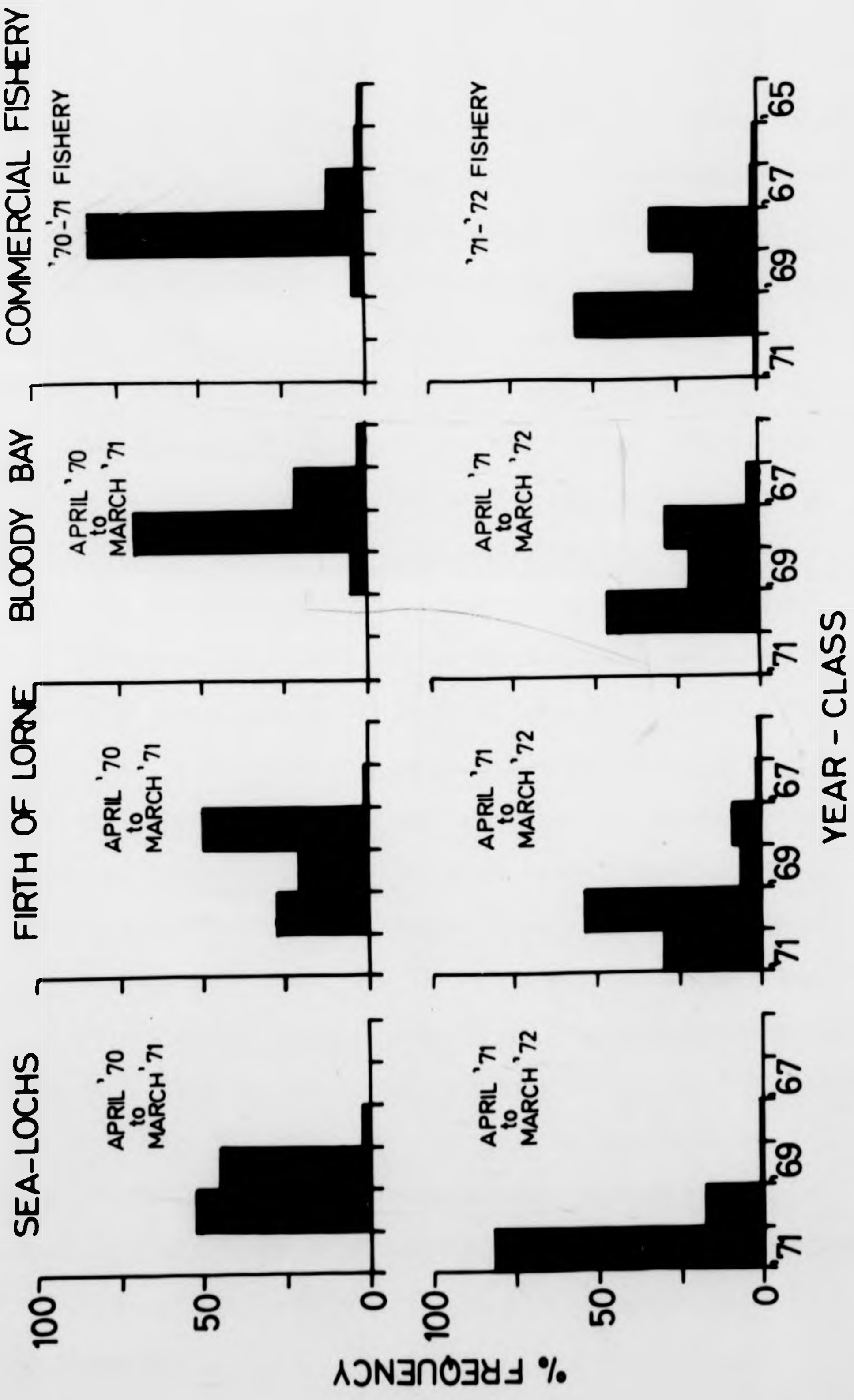


Fig.10. Comparison of the year-class composition of sprat populations in the sea-lochs, the Firth of Lorne and Bloody Bay from April 1970 to March 1971 and April 1971 to March 1972 with that of the 1970-71 and 1971-72 commercial fishery of the Scottish west coast.

on of sprat
h of Lorne
h 1971 and
the 1970-71
Scottish west



4 year old fish enter Loch Spelve but not Loch Etive. An increase in the numbers of old fish is known to occur during the winter and this probably causes the change in age structure in Loch Spelve at this time. It is probable that because of the narrow and sheltered entrance to Loch Etive, these overwintering old fish do not find their way into the loch.

In contrast to the sea-lochs, there is no complete replacement of 1 year and older fish by the 0-group in the 'open' areas. These areas differ, also, in that a high proportion of fish aged 2, 3 and 4 and at times even 5 years old are present in the population (Fig.9). It is evident that the 1968 year-class was dominant as two year old fish in 1970 and as three year old in 1971, in the Firth of Lorne and Bloody Bay.

When the age composition in the Firth of Lorne and Bloody Bay is compared with that of the commercial samples from the 1970-71 fishery, the similarity is apparent. The dominant year-class in the fishery was that of 1968 constituting more than 70% of the catch. The Bloody Bay populations resemble that of the commercial fishery more closely than do the Firth of Lorne populations. Here the 1970 brood constituted a fair proportion and as a result its age structure was less comparable with that of the commercial fishery. The year-class composition of the 1971-2 sprat fishery is also shown in Fig.10. Its similarity to the Bloody Bay populations and also to that of the Firth of Lorne is very evident.

Thus the evidence suggests that, in the 'open' areas, the age structure or year-class composition would give an idea of the composition of the commercial fisheries.

2. V.I. Growth of 0-group clupeids

Growth of 0-group herring and sprats of the 1970, 1971 and a part of the 1972 year-classes was studied by determining the mean length and weight of samples of 80-100 fish, taken at regular intervals. Each year-class of herring was sampled from April to May in the following year, those of sprats were from July-August until September the following year. The length-frequency distribution of each half cm length group in each sample was also calculated. Meristic characters were determined for every sample of herring, on the basis of which they were allocated into either the spring or the autumn spawning race or a mixture of the two races.

The mean length, weight and vertebral number and the keeled scales (K_2) of each sample for the two races of herring, for the 1970, 1971 and 1972 year-classes are given in Appendices 2 & 3. From the mean lengths and the length-frequency distributions of the samples in any one locality it was evident that the rates of growth of the different year-classes were similar. Increase in mean length of 0-group spring- and autumn- spawned herring with time is shown in Fig.11.

This figure shows that growth in length of 0-group herring continues until September-October but ceases during the winter months. Resumption of growth after the winter in autumn-spawned herring takes place in April-May. There was no observable year-class difference in the timing of the growth check nor in the resumption of growth after the winter. There are no data available as to the time of resumption of growth in spring-spawned herring and it is likely that it is similar to that of autumn-spawned

Fig.11. Growth in total length of 0-group herring (autumn- and spring-spawned) and sprats in the different localities.

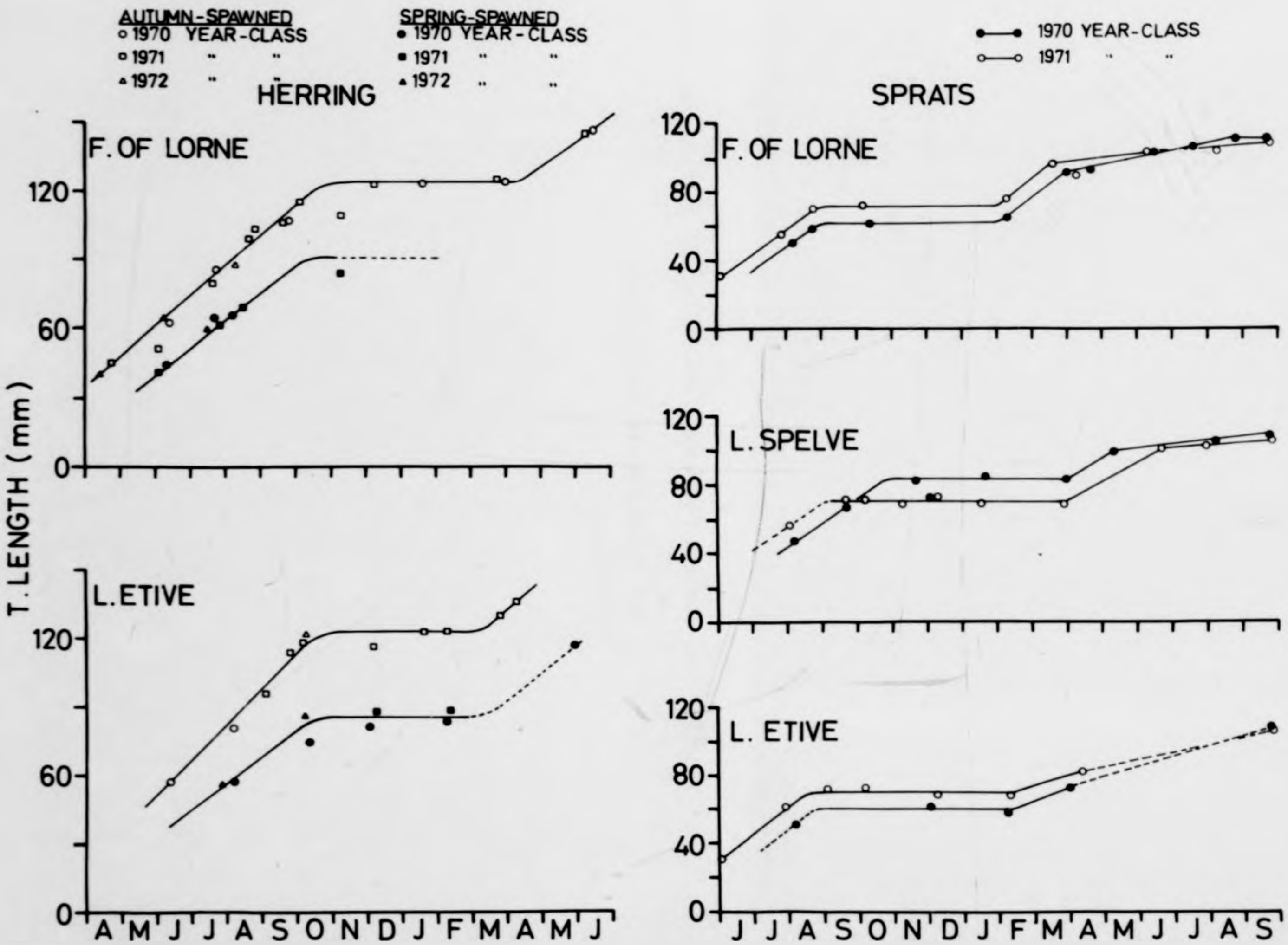
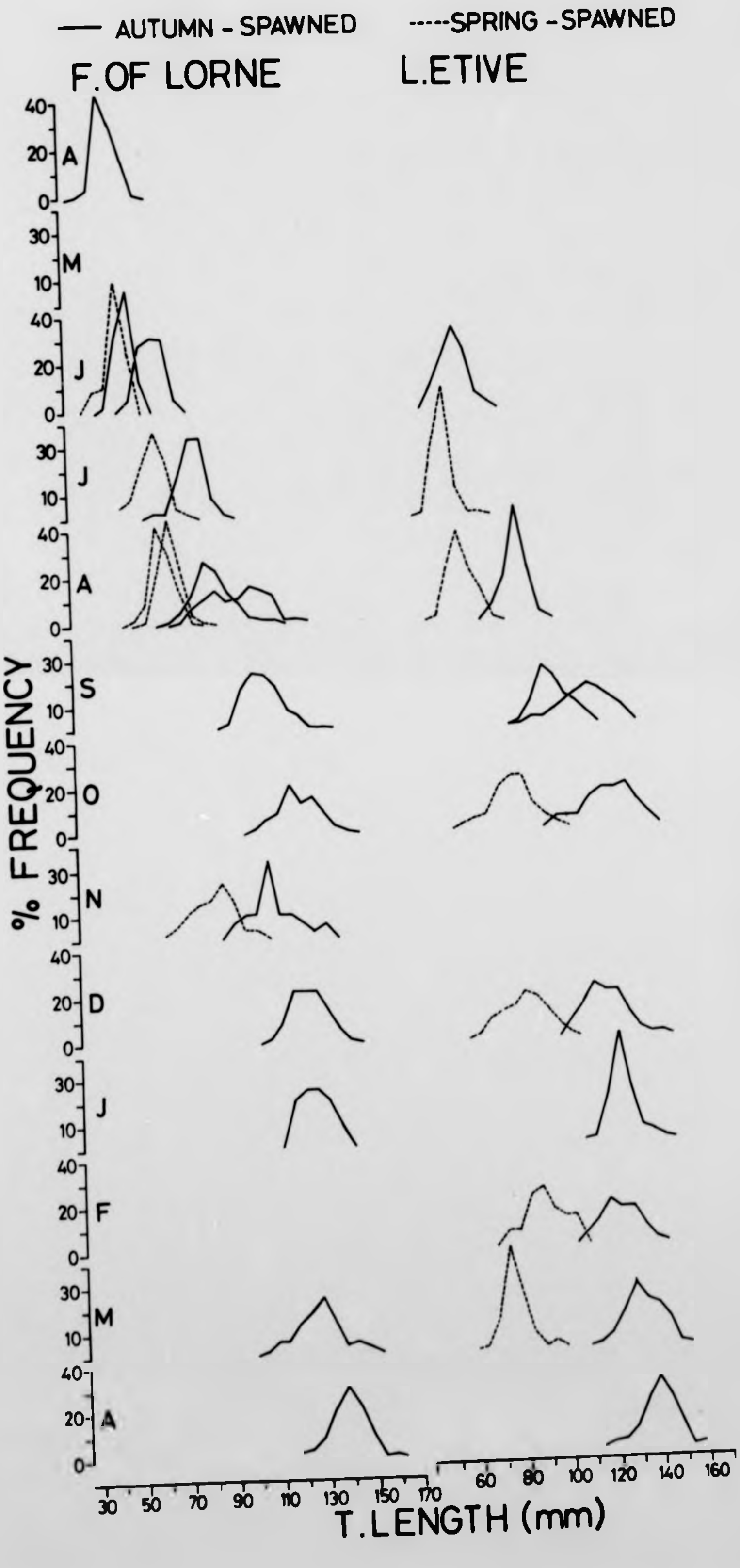

AUTUMN-SPAWNED
○ 1970 YEAR-CLASS
□ 1971 " "
△ 1972 " "
SPRING-SPAWNED
● 1970 YEAR-CLASS
■ 1971 " "
▲ 1972 " "
HERRING
F. OF LORNE
L. ETIVE
T. LENGTH (mm)
0
60
120
A M J J A S O N D J F M A M J
●—● 1970 YEAR-CLASS
○—○ 1971 " "
SPRATS
F. OF LORNE
L. SPELVE
L. ETIVE
0
40
80
120
J J A S O N D J F M A M J J A S

Fig.12. Length frequency distribution of O-group autumn- and spring-spawned herring.

autumn-



— AUTUMN - SPAWNED
-----SPRING - SPAWNED
F. OF LORNE
L. ETIVE
% FREQUENCY
A
M
J
J
A
S
O
N
D
J
F
M
A
0
10
20
30
40
30
50
70
90
110
130
150
170
60
80
100
120
140
160
T. LENGTH (mm)

herring.

The rate of growth was calculated for the two races in the different localities from the slope of the curve during its main growth period before the winter. The growth rate of autumn-spawned herring in Loch Etive and the Firth of Lorne was found to be 3.60 mm/week and 3.3 mm/week, respectively. The growth rates of spring-spawned herring were much lower, with increases of 2.87 mm/week and 2.78 mm/week occurring in Loch Etive and the Firth of Lorne, respectively. The observed difference in the growth rates of each group was not statistically significant, but the differences in growth rate between the two races were significant ($P < 0.01$).

The size-frequency distribution of both groups of herring in each locality is given in Fig.12. Since there was no apparent year-class difference, samples from different year-classes were pooled together, if they were obtained within the same week of each year, if not,separate frequency distributions were drawn. The curves show a gradual increase in length up to October and also that in general the samples were homogeneous and that the size range within a sample did not increase much in the year.

It is evident that the first winter ring in autumn-spawned herring in this area is formed at a mean length of 120-128 mm and that of spring-spawned herring at 85-90 mm. These values are in agreement with those observed from back calculations from otoliths in one year old fish of the respective races (Section 2.VIII).

The mean rate of growth of autumn-spawned herring (3.46 mm/week) in this area is in good agreement with those observations of Marshall et al. (1939) and Ford (1928) for spring-spawned herring of the Clyde and the Plymouth area respectively. The observed mean value of increase in length of 2.82 mm/week, of spring-spawned herring is significantly lower than that of Clyde spring-spawned herring (3.12 mm/week). It has been suggested by the authors themselves that the size of these fish were probably on the larger side, thus resulting in a higher growth rate. A closer study of their growth curves further reveals that except three samples all the rest were unmetamorphosed fish. A curve based on such data may result in erroneous conclusions.

Unlike in 0-group herring, growth curves representing growth in length in 0-group sprats of the 1970 and 1971 year-classes were different from one another (Fig.11). This difference is a result of the change in spawning time in the two years and is discussed in detail in Section 3. Since sprats were caught in the area in 1970 only after August the number of samples obtained during the growth season itself, though far from satisfactory, still allows a fairly smooth growth curve to be constructed, bringing the prominent characteristics to light.

Mean length and weight of sprat samples from the 1970 and 1971 year-classes from Lochs Etive, Spelve and the Firth of Lorne are given in Appendix 4. It is seen that growth in length ceases by late August-September in all instances, except in L. Spelve in 1970, in which growth continued to take place till November. This is thought to be exceptional and it is concluded that the growth check in 0-group sprats occurs in late

August-September. Though there is an early cessation in growth for the winter, resumption of growth takes place much earlier than in herring, by late February-March. Hence, the timing in the growth check and its resumption is different in the two species.

The rate of growth was calculated from the slope of the line during the main growth season for the 1970 and 1971 year-classes and was found to be 3.58, 3.50 and 3.80 mm/week and 3.50, 3.53 and 3.46 mm/week in Lochs Spelve, Etive and the Firth of Lorne respectively. The differences in the rate of growth of any one year-class was not statistically significant from locality to locality nor when one year-class was compared with the rest. It is evident that the rate of increase in length in 0-group sprats in the area is independent of the spawning time and the average increase is 3.55 mm/week. A delay in spawning, however, would effect the mean length at which the first winter ring is laid down, and unlike herring may differ appreciably from one year-class to another depending on the time of spawning.

The length-frequency distribution of each half cm length group for the two year-classes were calculated separately, (Fig. 13) for Lochs Etive, Spelve and the Firth of Lorne. From these curves, the homogeneity of the samples, the increase in length up to August-September and also after the winter check, is evident.

By extending this study well into their second year of life (1+), an interesting feature of growth of sprats became evident. On resumption of

Fig.13. Length frequency distribution of 0-group sprats of the 1970 and 1971 year-classes.

oup sprats of

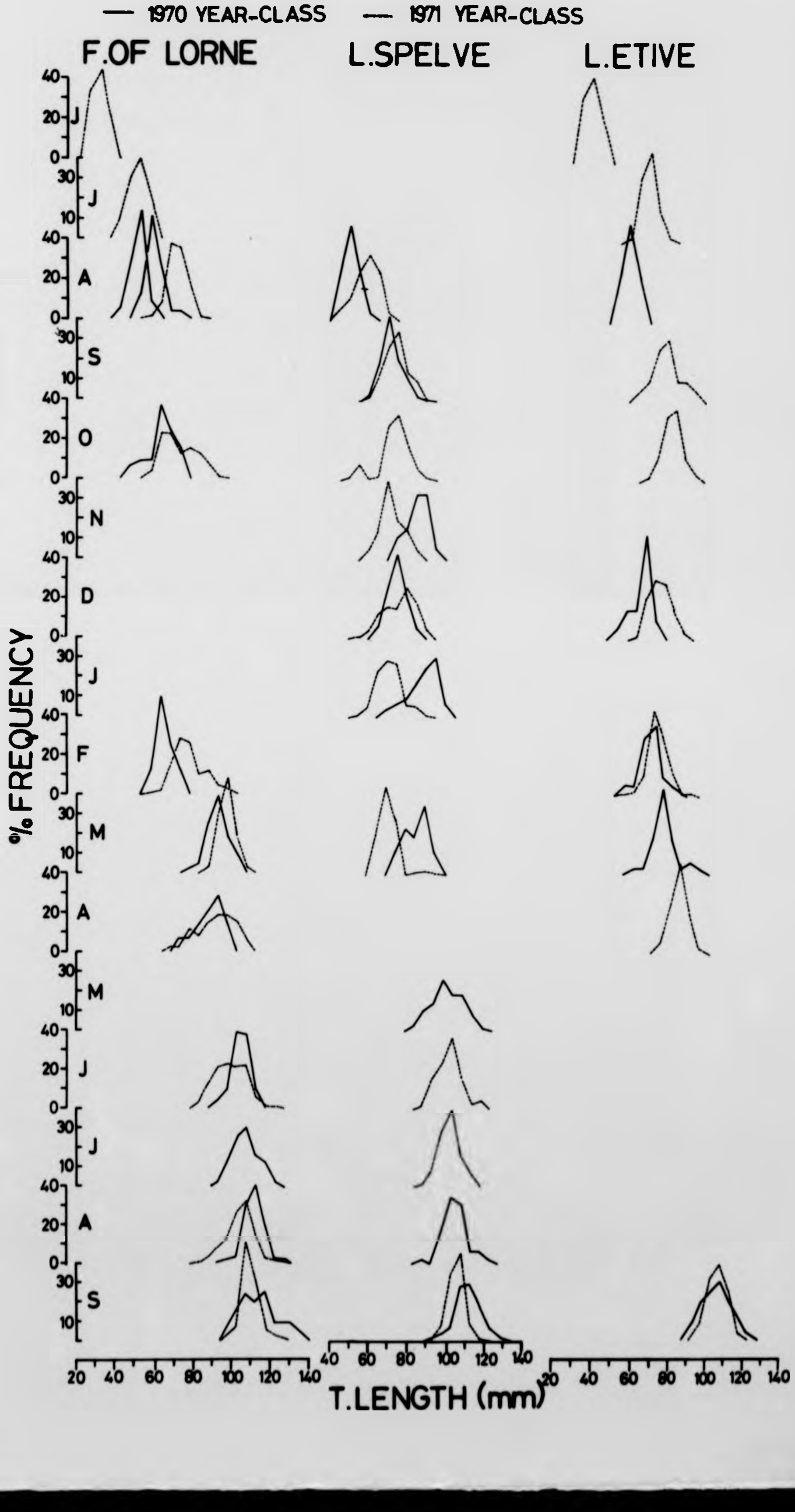
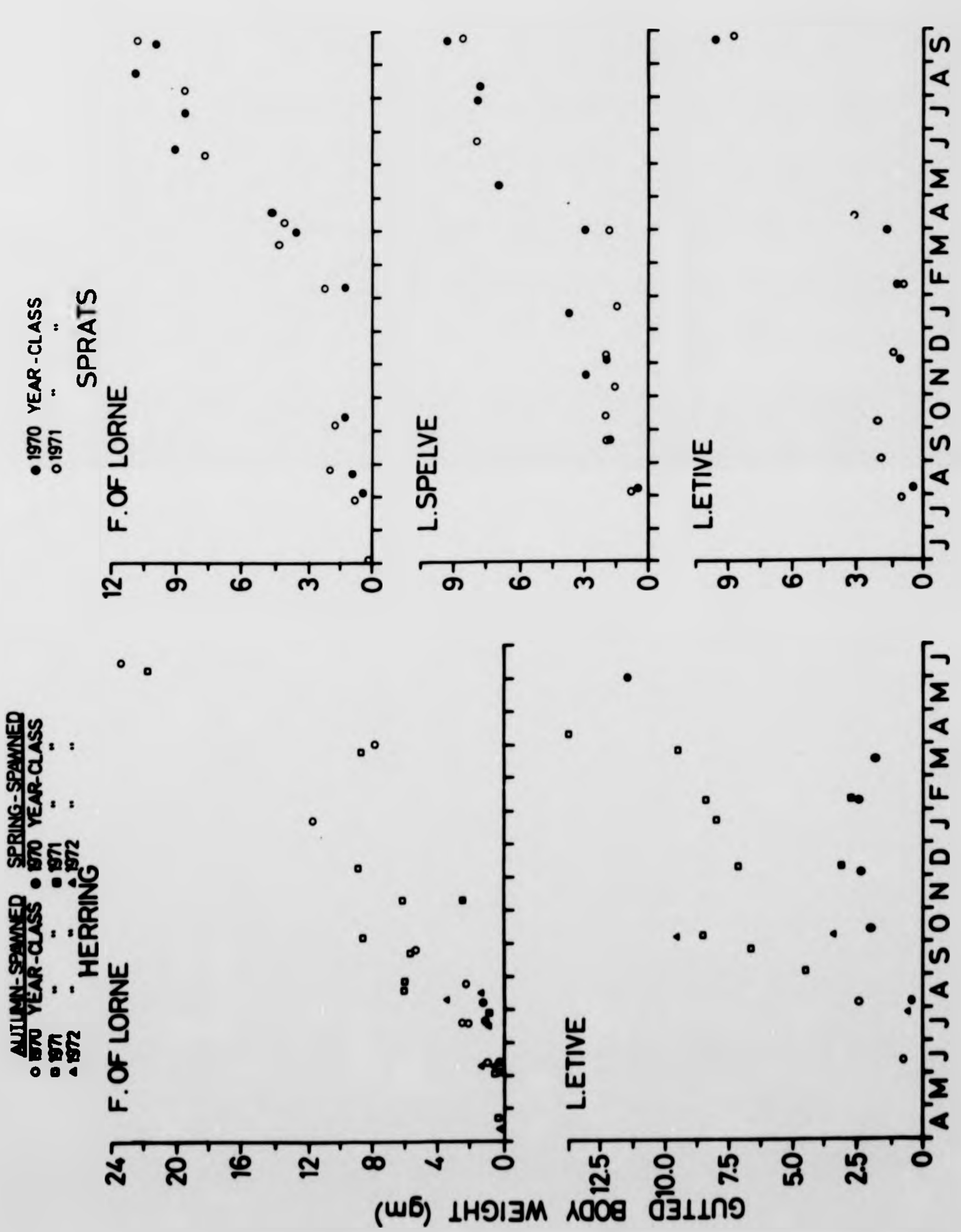


Fig.14. Growth in weight of 0-group herring (spring-and autumn-spawned) and sprats in the different localities.


HERRING
AUTUMN-SPAWNED
○ 1970 YEAR-CLASS
□ 1971 "
▲ 1972 "
SPRING-SPAWNED
● 1970 YEAR-CLASS
■ 1971 "
▲ 1972 "
F. OF LORNE
L.ETIVE
GUTTED BODY WEIGHT (gm)
24
20
16
12
8
4
0
12.5
10.0
7.5
5.0
2.5
0
A M J J A S O N D J F M A M J
SPRATS
● 1970 YEAR-CLASS
○ 1971 "
F. OF LORNE
L.SPELVE
L.ETIVE
12
9
6
3
0
J J A S O N D J F M A M J J A S

growth after the winter a rapid increase in growth in length takes place for a short period of time and then growth is slowed down considerably and maintained at a reduced rate. This increase was observed for both year-classes in all three localities under consideration. The increase is not consistent in its amplitude from year to year or locality to locality. It cannot be caused entirely by a migration of bigger fish into any one area, since a corresponding decrease in length was not observed elsewhere. This is considered to be a growth characteristic peculiar to sprat, the significance of which will be dealt with in the discussion.

Attempts to construct growth curves for increase in weight in herring and sprats were unsuccessful (Fig. 14). Growth in weight is non-linear and rather irregular. Weight is a less reliable criterion of growth because of its wide variation due to changes in condition of the fish. In the present investigation preserved weights were used and it is shown in Appendix 1 that smaller fish tend to lose more weight in 70% alcohol so adding to the irregularity of the data.

2.V.II. Growth of older sprats

The number of one year old and older herring caught in the area after April was so low that sufficient numbers were not obtained to study the growth rates after their first year of life. This was further complicated, since the herring had to be separated into their respective races and such separations, based on meristic characters of small samples, are far from reliable. As a result this and following sections are concerned only with growth in sprats.

The mean length of sprats of the 1968, 1969 and 1970 year-classes, the first two over a period of two years and the last over twelve months, were obtained from Loch Spelve, the Firth of Lorne and Bloody Bay (Fig. 15).

It is evident that there is little or no growth from late August till March, a phenomenon observed in most organisms in temperate regions. A decrease in length was observed for all three year-classes, in March, in Loch Spelve and the Firth of Lorne, while in Bloody Bay it was found to occur in April. This 'apparent' decrease in length is thought to be caused by the emigration of larger fish, which mature early, to the spawning grounds (Section 3). After March, growth begins and the mean length of the population will tend to increase, even though there is a gradual emigration of mature fish to the spawning grounds. It is possible that the decrease takes place a month later in Bloody Bay, because the populations are mainly composed of larger and older fish and hence the movement of a few large fish very early in the spawning season would not effectively reduce the mean length of the population. Evidence in favour of this is obtained from the range in length of a particular year-class in the three localities. It is seen that the lower range in length and the mean at any time of the year is significantly higher in Bloody Bay in comparison with the other two localities.

Compared with the study of growth rates of O-group fish, in older fish it is more useful to construct the general growth pattern observed with age than calculate the rate of growth of year-classes which are in different age groups.

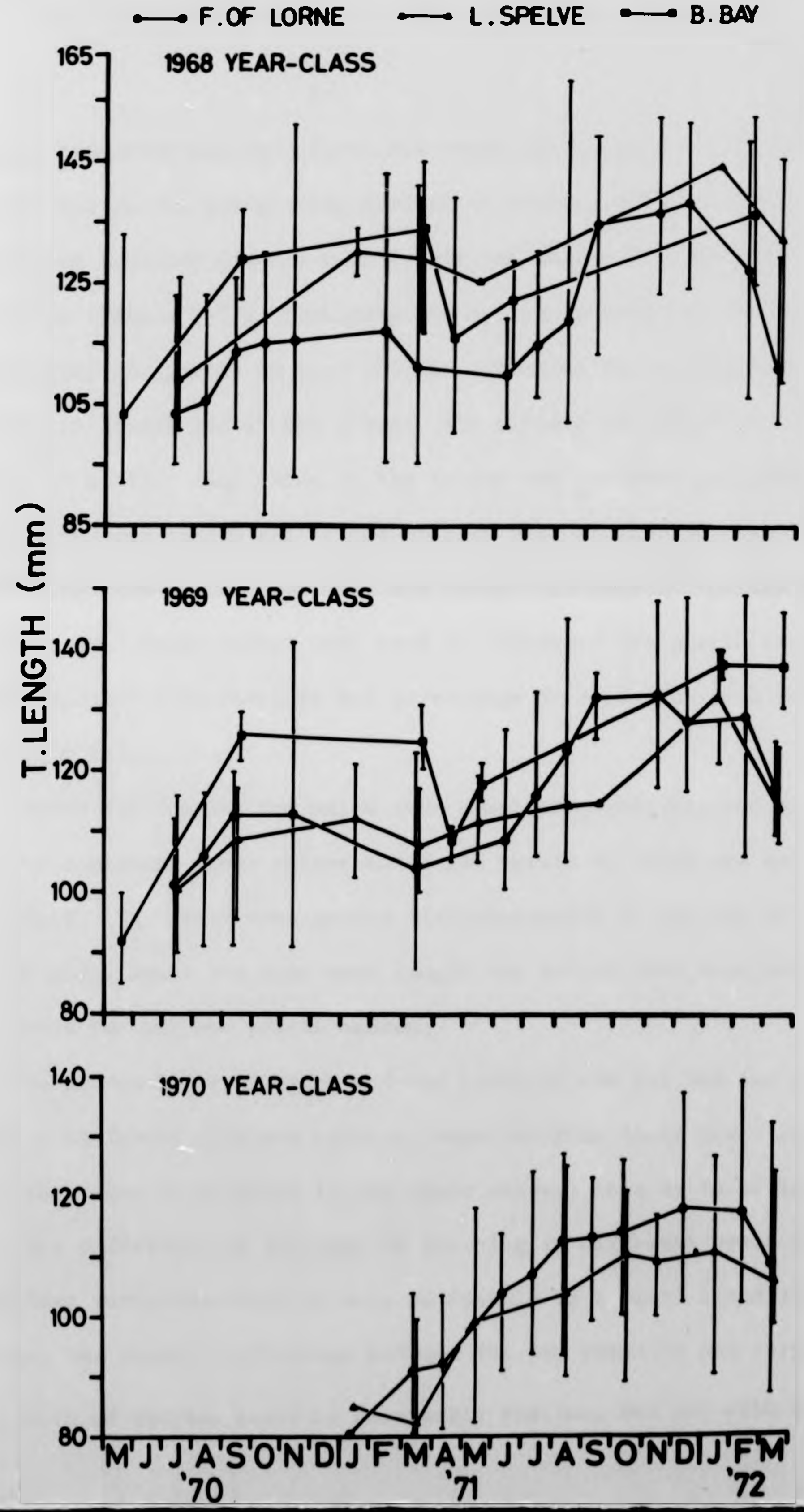
In the preceding paragraphs it was shown that growth of sprats in West

Fig.15. Growth in length of sprats (over a year old) in Loch Spelve, Firth of Lorne and Bloody Bay. Vertical lines show the range in length.

Fig.15. Growth in length of sprats (over a year old) in Loch Spelve, Firth of Lorne and Bloody Bay. Vertical lines show the range in length.

ar old) in Loch

, Vertical lines



Highland sea-lochs and associated sea areas was seasonal. The samples obtained during the non-growing periods of winters 1970-71 and 1971-72 were pooled together and the mean length and weight of each year-class calculated (Tables 7-9). Similarly the average growth for each year-class during the growth season 1971 was estimated by calculating the increase in length and weight between the winters of 1970-71 and 1971-72 (Tables 10 & 11). Also shown in the tables are increase and percentage increase in mean length and weight in each year of life,obtained by subtracting from the mean of each age group the mean of the age group one year younger. These values were used to construct the growth curves for sprats together with absolute and percentage increase for each year of life (Figs 16 & 17).

Curves for females and males were compiled separately and also a third curve by combining these values and a few sprats in which sex was not determined. The sexes were hardly distinguishable at the end of their first year of life, hence the same mean length and weight have been used for all the curves for any one growth season.

The curves for both sexes and the combined one for the two years are slightly different from one another, especially in their lower ranges, while they tend to coincide in the upper range. This is to be expected, since the difference in the time of spawning in different years and also year-class variation would be more noticeable in a short lived species. However, the overall difference between the two years is not very significant. The growth of the two sexes is remarkably similar, but all evidence indicates

Table 7.

MEAN LENGTH AND WEIGHT OF FEMALE SPRATS IN WINTER 1970-71 & 1971-72, INCREASE IN LENGTH AND WEIGHT, AND PERCENTAGE INCREASE FOR EACH YEAR OF LIFE.

WINTER 1970-71

Year Class	Year of life	No.	LENGTH Mean mm	LENGTH Inc. mm	LENGTH Inc. %	WEIGHT Mean gm	WEIGHT Inc. gm	WEIGHT Inc. %
1970	1	-	74.4	74.4	-	2.53	2.53	-
1969	2	96	108.2	33.8	45.43	6.82	4.29	169.55
1968	3	146	126.2	18.0	16.63	11.88	5.06	74.19
1967	4	19	137.3	11.1	8.79	14.93	3.05	25.67
1966	5	3	150.0	12.7	9.24	19.90	5.07	33.95
1965	6	4	151.0	1.0	0.66	17.60	-2.30	-

WINTER 1971-72

Year Class	Year of life	No.	LENGTH Mean mm	LENGTH Inc. mm	LENGTH Inc. %	WEIGHT Mean gm	WEIGHT Inc. gm	WEIGHT Inc. %
1971	1	-	71.4	71.4	-	1.83	1.83	-
1970	2	320	118.9	47.5	66.52	9.72	7.89	431.14
1969	3	38	132.3	13.4	11.26	13.72	4.00	41.15
1968	4	54	135.6	3.3	2.49	14.68	0.96	6.99
1967	5	6	148.7	13.1	9.66	22.54	7.86	53.54

Table 8.

MEAN LENGTH AND WEIGHT OF MALE SPRATS IN WINTERS OF 1970-71 & 1971-72, INCREASE IN LENGTH AND WEIGHT, AND PERCENTAGE INCREASE FOR EACH YEAR OF LIFE.

WINTER 1970-71

Year Class	Year of life	No.	LENGTH			WEIGHT		
			Mean mm	Inc. mm	Inc. %	Mean gm	Inc. gm	Inc. %
1970	1	-	74.4	74.4	-	2.83	2.83	-
1969	2	109	107.1	32.7	43.95	6.36	3.83	151.38
1968	3	85	125.6	18.5	17.27	10.97	4.31	67.76
1967	4	26	135.0	9.4	7.48	13.06	2.09	19.05
1966	5	12	142.5	7.5	5.55	14.60	1.54	11.79
1965	6	-	-	-	-	-	-	-
WINTER 1971-72								
1971	1	-	71.4	71.4	-	1.83	1.83	-
1970	2	271	116.7	45.3	63.44	9.11	7.28	397.8
1969	3	60	130.5	13.8	11.82	12.93	3.82	41.93
1968	4	38	129.4	-1.1		13.11	0.18	1.39
1967	5	7	144.1	14.7	11.36	18.21	5.10	38.90
1966	6	1	148.0	3.9	2.70	18.50	0.29	1.59

Table 9.

MEAN LENGTH AND WEIGHT OF SPRATS (FEMALE AND MALE COMBINED), IN WINTER OF 1970-71, INCREASE IN LENGTH AND WEIGHT, AND PERCENTAGE INCREASE FOR EACH YEAR OF LIFE.

WINTER 1970-71

Year Class	Year of life	No.	LENGTH Mean mm	LENGTH Inc. mm	LENGTH Inc. %	WEIGHT Mean gm	WEIGHT Inc. gm	WEIGHT Inc. %
1970	1	258	74.4	74.4	-	2.53	2.53	-
1969	2	205	108.2	33.8	45.43	6.70	4.17	164.8
1968	3	231	124.7	16.5	15.25	11.37	4.67	69.7
1967	4	45	135.7	11.0	8.82	14.54	3.17	27.88
1966	5	15	146.0	10.3	7.59	16.36	1.82	12.81
1965	6	4	151.0	5.0	3.42	17.60	1.24	7.58
WINTER 1971-72								
1971	1	887	71.4	71.4	-	1.83	1.83	-
1970	2	612	118.0	46.6	65.26	9.41	7.58	414.2
1969	3	116	131.7	13.7	11.61	13.21	3.80	40.38
1968	4	109	133.3	1.6	1.21	13.95	0.74	5.60
1967	5	13	146.2	12.9	9.67	20.18	6.23	44.65
1966	6	1	148.0	1.8	1.23	18.50	-1.68	-

Table 9.

MEAN LENGTH AND WEIGHT OF SPRATS (FEMALE AND MALE COMBINED), IN WINTER OF 1970-71, INCREASE IN LENGTH AND WEIGHT, AND PERCENTAGE INCREASE FOR EACH YEAR OF LIFE.

WINTER 1970-71

Year Class	Year of life	No.	LENGTH			WEIGHT		
			Mean mm	Inc. mm	Inc. %	Mean gm	Inc. gm	Inc. %
1970	1	258	74.4	74.4	-	2.53	2.53	-
1969	2	205	108.2	33.8	45.43	6.70	4.17	164.8
1968	3	231	124.7	16.5	15.25	11.37	4.67	69.7
1967	4	45	135.7	11.0	8.82	14.54	3.17	27.88
1966	5	15	146.0	10.3	7.59	16.36	1.82	12.81
1965	6	4	151.0	5.0	3.42	17.60	1.24	7.58
WINTER 1971-72								
1971	1	887	71.4	71.4	-	1.83	1.83	-
1970	2	612	118.0	46.6	65.26	9.41	7.58	414.2
1969	3	116	131.7	13.7	11.61	13.21	3.80	40.38
1968	4	109	133.3	1.6	1.21	13.95	0.74	5.60
1967	5	13	146.2	12.9	9.67	20.18	6.23	44.65
1966	6	1	148.0	1.8	1.23	18.50	-1.68	-

Table 10.

INCREASE AND PERCENTAGE INCREASE IN LENGTH OF FEMALE AND MALE SPRATS OF EACH YEAR-CLASS BETWEEN WINTERS OF 1970/71 and 1971/72

Year Class	Year of life of increase	FEMALES 1970/71	1971/72	Incr.	% In.	MALES 1970/71	1971/72	Incr.	% In.	COMBINED 1970/71	1971/72	Incr.	% In.
1971	-	-	71.4	71.4	-	-	71.4	71.4	-	-	71.4	71.4	-
1970	2	74.4	118.9	44.5	59.8	74.4	116.7	42.3	56.8	74.4	118.0	43.6	58.6
1969	3	108.2	132.3	24.1	22.3	107.1	130.5	23.4	21.8	108.2	131.7	23.5	21.7
1968	4	126.2	135.6	9.4	7.4	125.6	129.4	3.8	3.0	124.7	133.3	8.6	6.9
1967	5	137.3	148.7	11.4	8.3	135.0	144.1	9.1	6.7	135.7	146.2	10.5	7.7
1966	6	150.0	-	-	-	142.5	148.08	5.5	3.8	146.0	148.0	2.0	1.4

Table 11.

INCREASE AND PERCENTAGE INCREASE IN WEIGHT OF FEMALE AND MALE SPRATS OF EACH YEAR-CLASS BETWEEN WINTERS OF 1970/71 and 1971/72.

Year Class	Year of life of increase	FEMALES				MALES				COMBINED			
		1970/71	1971/72	Inc.	% In.	1970/71	1971/72	Inc.	% In.	1970/71	1971/72	Inc.	% In.
1971	-	-	1.83	1.83	-	-	1.83	1.83	-	-	1.83	1.83	-
1970	2	2.53	9.72	7.19	284.2	2.53	9.11	6.58	260.1	2.53	9.41	6.88	271.9
1969	3	6.82	13.72	6.90	101.2	6.36	12.93	6.57	103.3	6.70	13.21	6.51	97.2
1968	4	11.88	14.68	2.80	23.6	10.97	13.11	2.14	19.5	11.37	13.95	2.58	22.7
1967	5	14.93	22.54	7.61	50.9	13.06	18.21	5.15	39.4	14.54	20.18	5.64	38.8
1966	6	19.9	-	-	-	14.60	18.50	3.90	26.7	16.36	18.50	2.14	13.1

Table 11.

INCREASE AND PERCENTAGE INCREASE IN WEIGHT OF FEMALE AND MALE SPRATS OF EACH YEAR-CLASS BETWEEN WINTERS OF 1970/71 and 1971/72.

Year Class	Year of life of increase	FEMALES				MALES				COMBINED			
		1970/71	1971/72	Inc.	% In.	1970/71	1971/72	Inc.	% In.	1970/71	1971/72	Inc.	% In.
1971	-	-	1.83	1.83	-	-	1.83	1.83	-	-	1.83	1.83	-
1970	2	2.53	9.72	7.19	284.2	2.53	9.11	6.58	260.1	2.53	9.41	6.88	271.9
1969	3	6.82	13.72	6.90	101.2	6.36	12.93	6.57	103.3	6.70	13.21	6.51	97.2
1968	4	11.88	14.68	2.80	23.6	10.97	13.11	2.14	19.5	11.37	13.95	2.58	22.7
1967	5	14.93	22.54	7.61	50.9	13.06	18.21	5.15	39.4	14.54	20.18	5.64	38.8
1966	6	19.9	-	-	-	14.60	18.50	3.90	26.7	16.36	18.50	2.14	13.1

that the females tend to be larger than the males in their early years of life, the difference increasing to about 4 mm in the sixth year of life. It is clear that this difference amounts to less than 3% of an average size sprat in its sixth year of life.

The greatest absolute increase in length takes place in the first year of life and thereafter the increase tends to be progressively smaller from year to year. In general, the curve at the end of the 1970-71 winter was very smooth, exhibiting characters of a conventional growth curve but that at the end of 1971-72 winter showed signs of an inflection between the 4th and 5th year of life.

The curves for increase in weight (Fig.17) with age show an inflection between first and second year of life. The greatest absolute increase in weight in all instances studied takes place during the second year of life. The curve for the 1970-71 winter shows a progressive decrease in absolute and percentage increase in weight after the second year of life. The 1971-72 curves show an added inflection, similar to that of the curves for increase in length between the fourth and fifth year of life. The inflection on the former curve is much more pronounced since the weight is approximately proportional to the cube of the length.

It must be pointed out, however, that these are preserved weights and are thus about 18% lower than the fresh weights (Appendix 1). There are also indications that smaller fish loose more weight than the larger ones, with the result that the shape of the curves may be slightly distorted. Changes in length with preservation are small, amounting to

Fig.16. Curves of growth in length for females, males and the sexes combined, with absolute and percentage increase in length in each year of life (see text for methods of calculation of increments).

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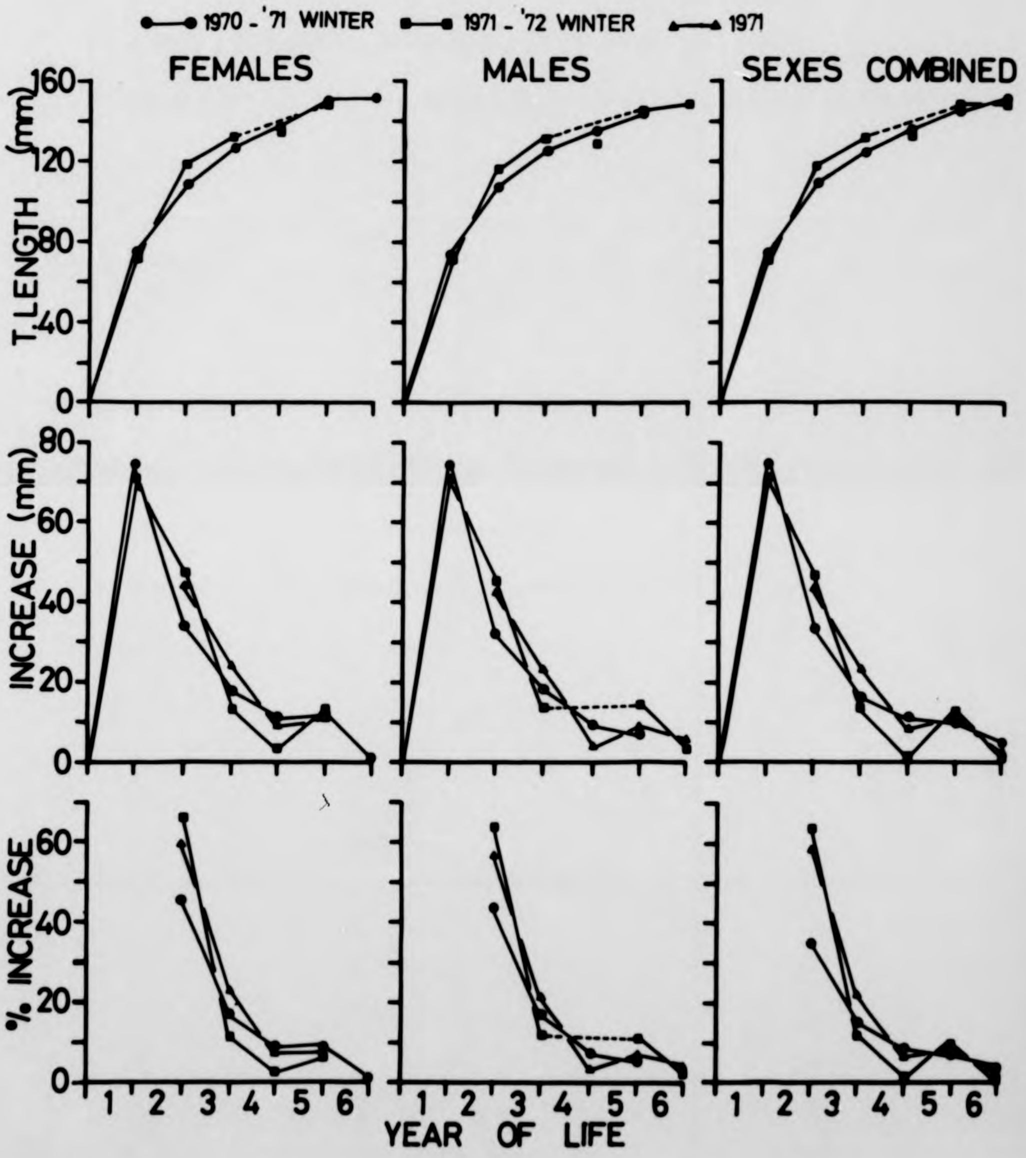

Fig.17. Curves of growth in weight for females, males and the sexes combined with absolute and percentage increase in weight in each year of life (see text for methods of calculation of increments).

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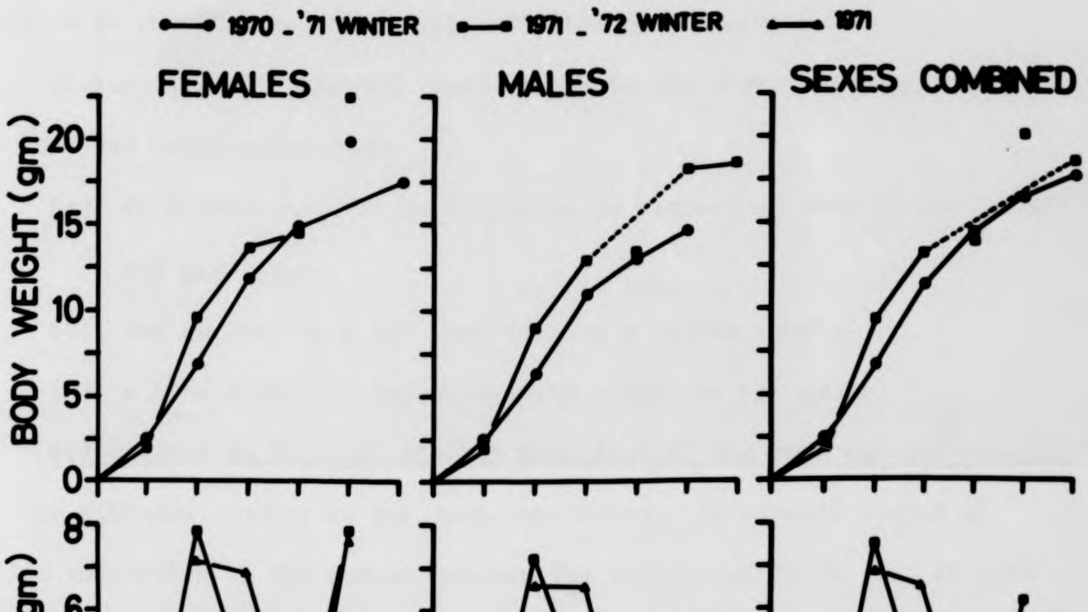

1.5% of the total length, and appear to be the same for all sizes of fish. Thus these results are not greatly affected by preservation.

Ricker (1958) suggested that errors in the above estimates of rate of increase could arise from;

(a) difference between year-classes in respect of rate of growth at any given age,

(b) the sample taken not constituting a random sample,

(c) a size selective mortality rate within an age group.

Differences in (a) will show up when fish of the same age are compared in two different years, as has been done above. As already stated an added inflection in the curves between the fourth and fifth year of life is seen to exist in the growth curve for the 1971 growth season. This is possibly caused by a difference in the growth rates of the 1969 and 1968 year-classes during the 1971 growth season.

Use of multiple gear should result in obtaining an unbiased sample of each age group. As it has been pointed out earlier, the emigration of fish into deeper waters would probably result in a certain amount of bias in the estimates, specially in the older age groups. However, if only larger fish of any one age-group emigrate, then it would give rise to Lee's phenomenon (Lee, 1912) in back-calculated mean lengths or, on the other hand, emigration of only smaller fish would result in a reversal of the above phenomenon.

As regards factor (c), there is no reason whatsoever to believe that a size selective mortality within any age group occurs in populations of sprats in this area.

2.V.III. Back-calculated growth

Lea (1910) arrived at the conclusion that the growth of scales so closely accords with the individual, that it is possible to describe the growth history by means of measurements of the growth zones of the scales. This has been found to be true for other hard structures which show annual markings, such as the otoliths, opercula etc. and these have been used by many workers in determining the past growth history of a particular fish. The principle of the method is to divide the length of each fish into parts for each year, proportional to the lengths of each yearly ring in the scales or otoliths. Thus if the length of the fish at capture is L cm and the length of the first ring v_1, and the total length of the otolith or scale from the centre is V, length l_1 of the fish at the formation of the first winter ring is given by

$$\frac{l_1}{v_1} = \frac{L}{V}$$

Lee (1912) found that sometimes there is a tendency for groups of fish to show a decrease in the back-calculated mean length at each year of life with increasing age. This is referred to as Lee's phenomenon. The possible factors which bring about such a phenomenon are a selective migration of fish, growth of scales due to shrinkage not being proportional to that of the fish, artificial selection due to the gear and erroneous reading of the age of the individuals.

A total of 2747 otoliths, belonging to fish from six year-classes, were aged, measured and the total length at each successive age calculated using the direct proportion method. The mean lengths for each successive age for each year-class are given separately, and from these means the grand mean length at each year of life was obtained (Table 12). From the length-weight relationship the mean weight corresponding to each mean length was also calculated.

A close study of mean back-calculated lengths at the end of each year of life, for all the year-classes investigated, indicated that there was no apparent increase in growth with age, that is there was no regular decrease in the mean length for any one age group with increasing age of the year-classes. Thus there are no indications of the existence of Lee's phenomenon in sprats in this area.

Growth curves were compiled using back-calculated mean lengths and weights (Fig. 18). In Fig. 19 these are compared with the curves from combined empirical data for the growth seasons of 1970 and 1971. The resulting curves are very similar to one another. The back-calculated means obtained for the first and sixth year of life are higher than the corresponding empirical means. Robertson (1938) observed a higher back-calculated mean l_1 in the English east coast sprat samples. Johnson (1970) found the empirical means in the first and second years of life to be higher than the corresponding back-calculated means in Wash sprats.

The reasons for observed differences in the calculated and empirical means lengths cannot be attributed to any one factor. However, the absence

Table 12.

MEAN BACK-CALCULATED LENGTH (mm) OF SPRATS AT THE END OF EACH YEAR OF LIFE FOR DIFFERENT YEAR-CLASSES AND MEANS FOR ALL YEAR-CLASSES COMINED AND THE CORRESPONDING WEIGHTS (gm), OBTAINED FROM THE LENGTH-WEIGHT RELATIONSHIP.

		YEAR OF LIFE					
YEAR-CLASS	No.	1	2	3	4	5	6
1970	1251	77.5	115.0				
1969	628	81.5	110.0	129.0			
1968	745	69.0	102.5	119.0	132.5		
1967	63	81.0	103.0	118.8	125.5	148.0	
1966	15	91.0	123.0	136.1	142.0	147.0	
1965	3	50.5	106.5	125.5	135.5	144.0	152.0
Overall mean		76.5	104.0	121.0	134.0	146.0	152.0
Mean weight		2.27	6.39	10.66	15.04	20.10	23.10

Table 12.

MEAN BACK-CALCULATED LENGTH (mm) OF SPRATS AT THE END OF EACH YEAR OF LIFE FOR DIFFERENT YEAR-CLASSES AND MEANS FOR ALL YEAR-CLASSES COMINED AND THE CORRESPONDING WEIGHTS (gm), OBTAINED FROM THE LENGTH-WEIGHT RELATIONSHIP.

		YEAR OF LIFE					
YEAR-CLASS	No.	1	2	3	4	5	6
1970	1251	77.5	115.0				
1969	628	81.5	110.0	129.0			
1968	745	69.0	102.5	119.0	132.5		
1967	63	81.0	103.0	118.8	125.5	148.0	
1966	15	91.0	123.0	136.1	142.0	147.0	
1965	3	50.5	106.5	125.5	135.5	144.0	152.0
Overall mean		76.5	104.0	121.0	134.0	146.0	152.0
Mean weight		2.27	6.39	10.66	15.04	20.10	23.10

Fig.18. Curves of growth in length for sprats of all year-classes, obtained by back-calculation from otolith growth zones and in weight by substitution of the corresponding weights in each year of life from the length-weight relationship, $W = 0.000001\ L^{3.38425}$ (where W = weight in gm and L = length in mm).

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L = length in mm).

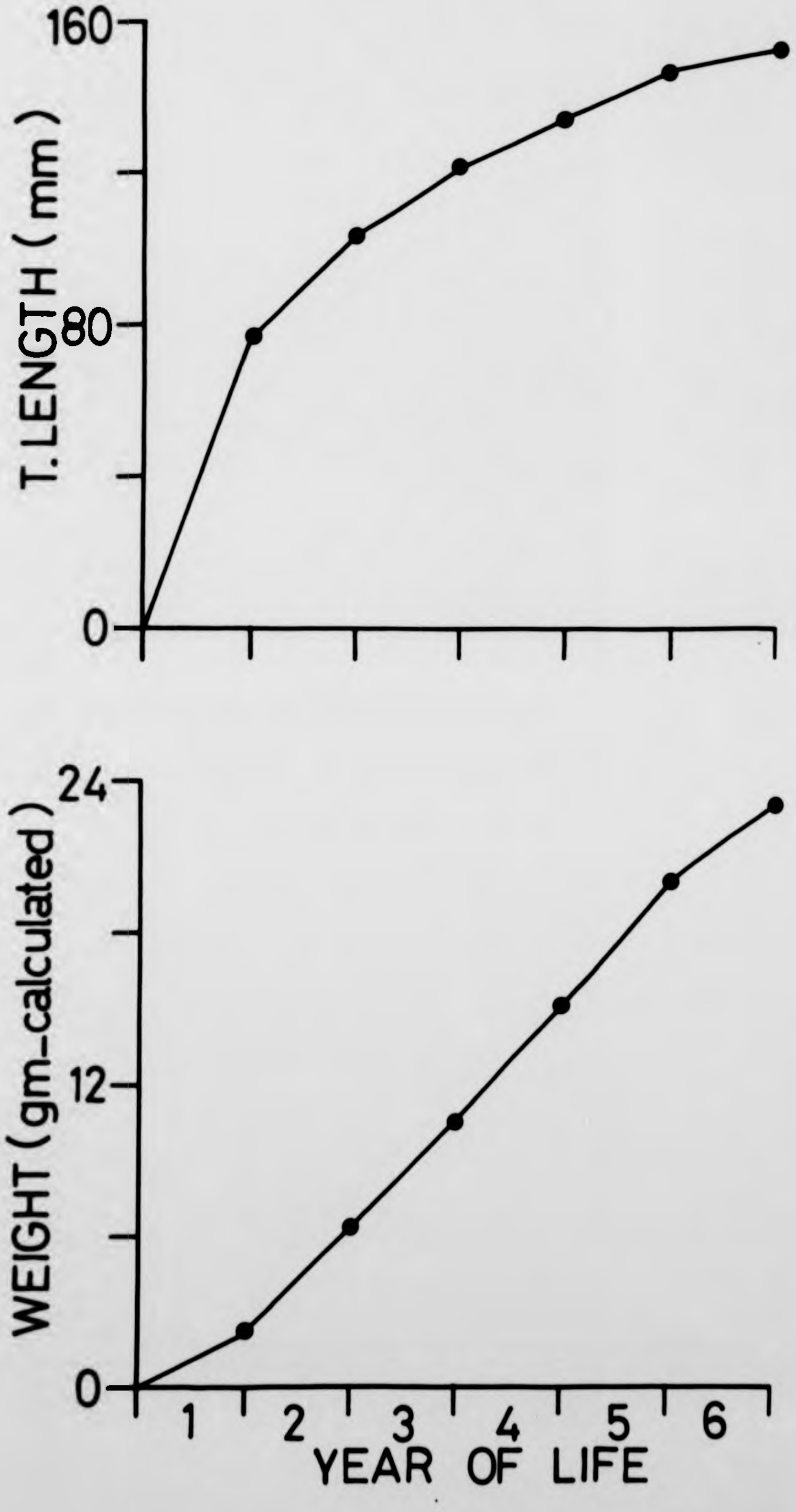

Fig.19. Comparison of curves of growth obtained from empirical data in the winters of 1970-71 and 1971-72 with that obtained from back-calculation from otolith rings.

btained from

1970-71 and

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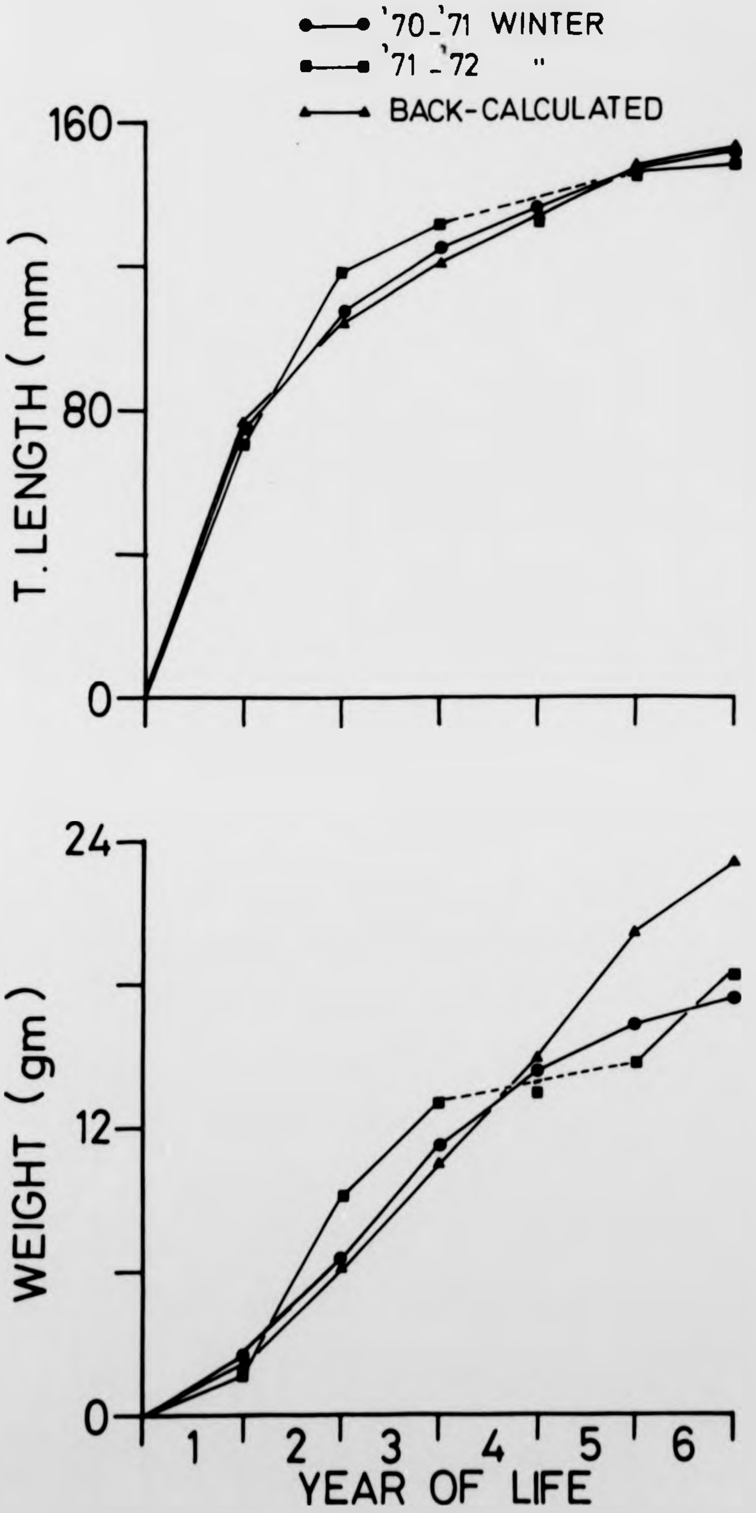

of Lee's phenomenon does indicate that there is no artificial or natural selectivity in the samples.

2.V.IV. Growth in other areas

It is difficult to compare growth and growth potential of different populations and related species when the data are expressed as in the earlier sections. A useful technique was that developed independently by Ford (1933) and Walford (1946), when the length at age n+1 is plotted against length at age n. This plot is now known as the Ford-Walford plot, and the resulting points will normally fall on straight line with slope K, and value of L_∞ where it cuts the 45° diagonal through the origin.

The technique developed by Ford and Walford is essentially a graphical expression of growth by an inverse exponential equation, which in its simplest form is given by von Bertalanffy (1938).

The equation is, $L_t = L_\infty (1 - e^{-K(t-to)})$

where L_t = length at an age t.

L_∞ = asymptotic length.

K = growth constant or rate of growth.

e = natural logarithm.

Ricker (1958) suggested a means of obtaining the best straight line fit to a set of points in a Ford-Walford plot. By plotting $\log_e (L_\infty - L_t)$ against t, one should obtain a straight line of which the linearity is sensitive to changes in L_∞. A few trial plots using different values of Lee's phenomenon does indicate that there is no artificial or natural selectivity in the samples.

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The data obtained from back-calculations are generally suitable for use in Ford-Walford plots, as they are more regular than the empirical data due to being averages over several years of growth at a particular age and being based on large number of observations for each year of life. Furthermore, difficulties arise in fitting statistical growth curves based on empirical data observed over one or two years for short-lived fast growing species which are subjected to varying temperatures and levels of feeding at different times of the year, a phenomenon which has also been noted for Norway pout (Ursin, 1963; Raitt, 1968).

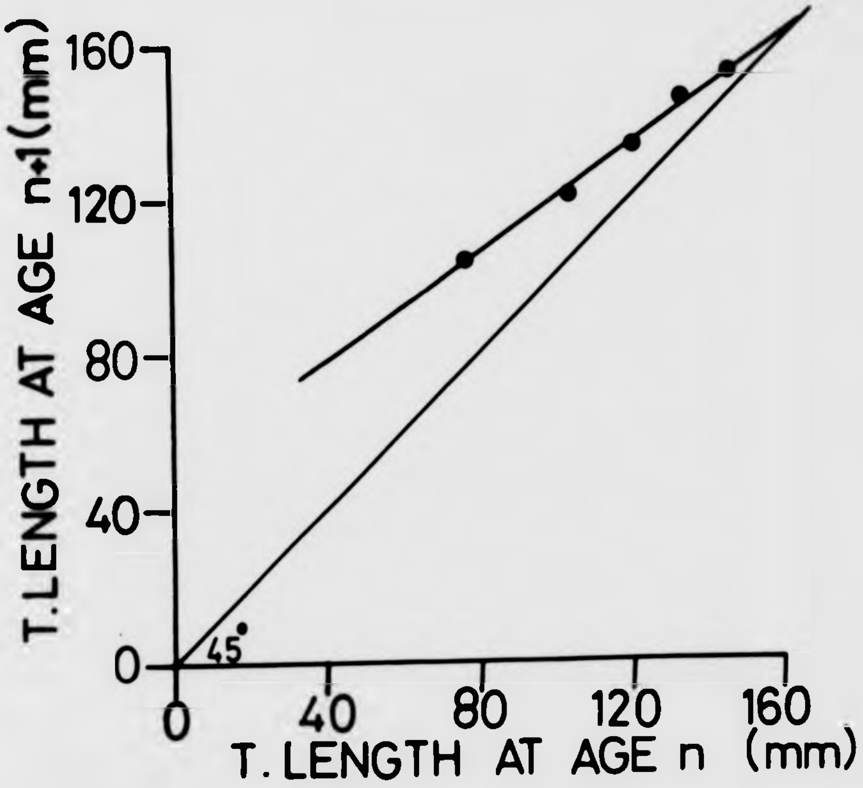
The back-calculated values fall on a fairly good straight line, from which values of 163 mm for L_∞, 0·39 for t_0 and 0.69 for K are obtained (Fig. 20). These values which describe the main growth characteristics of the Scottish west coast populations are comparable to those of other workers (Table 13).

Taylor (1962) showed that the logarithm of K is linearly related to environmental temperature and this has been further supported by work of Kinne (1960). Beverton and Holt (1957) suggested that differences in the food supply greatly modify L_∞ but not K, where as different environmental temperatures affect both L_∞ and K. The bottom sea-temperatures of the area under investigation vary between 16°C in the summer to about 5.5°C in the winter. Temperature is a function of latitude, and when the data for rates of growth from other populations and the present one are considered, there is a general tendency for the growth rate to decrease with increase in

Fig.20.

Fig.20. Ford-Walford plots for back-calculated length and the corresponding weights for sprats.

d length and


T. LENGTH AT AGE n+1 (mm)
160
120
80
40
0
45°
0
40
80
120
160
T. LENGTH AT AGE n (mm)

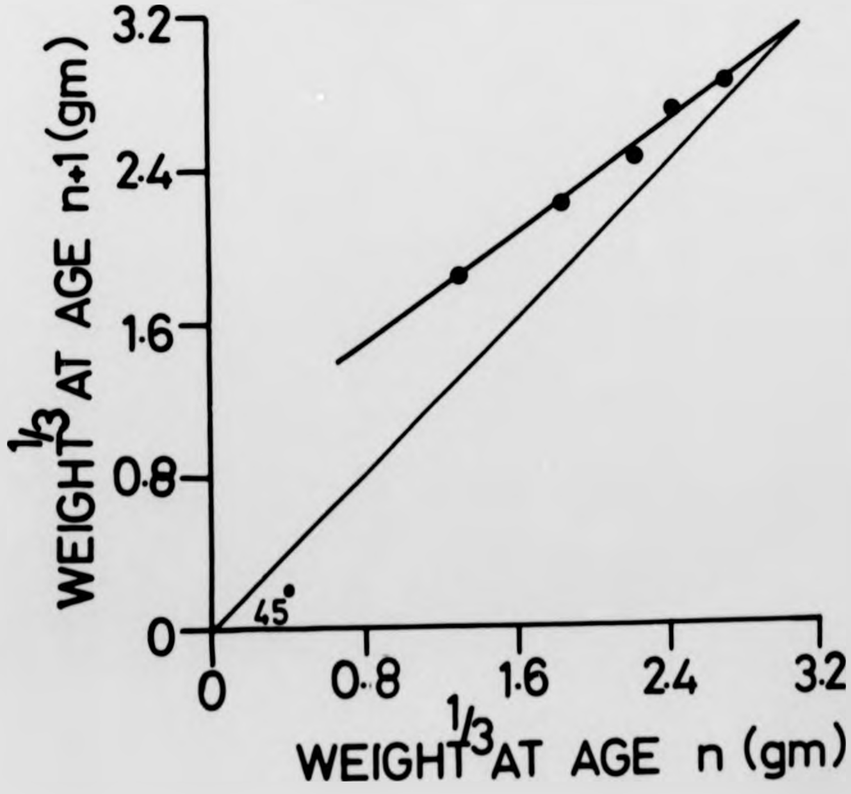

WEIGHT^1/3 AT AGE n+1 (gm)
3.2
2.4
1.6
0.8
0
45°
0
0.8
1.6
2.4
3.2
WEIGHT^1/3 AT AGE n (gm)

Table 13.

ASYMPTOTIC LENGTH $-L_\infty$ AND THE GROWTH FACTOR -K OF SPRAT POPULATIONS FROM DIFFERENT LOCALITIES.

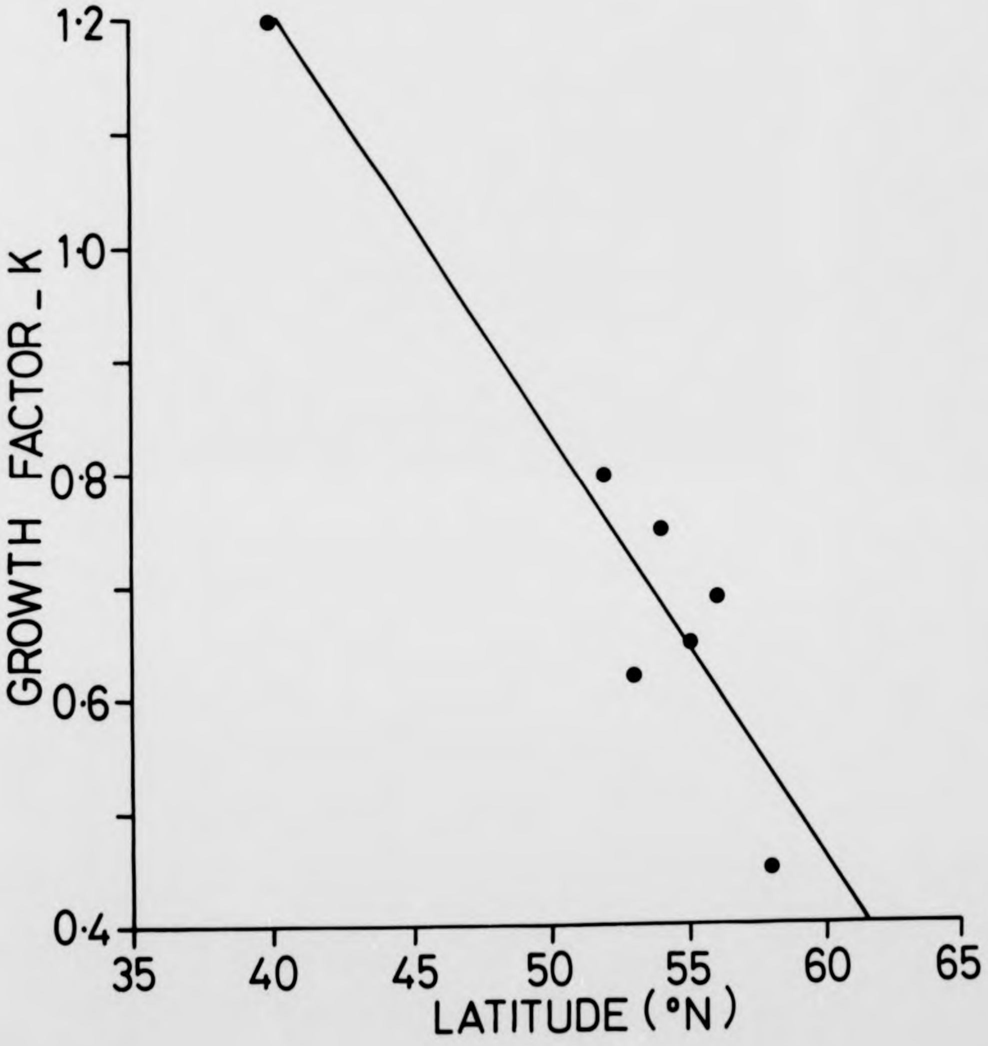
Author	Locality	Approximate Latitude °N	L_∞ mm	K
Sund, 1911	Norwegian coast	55	160	0.65
Robertson, 1938	English east coast	51	140	0.7–0.9
Molander, 1943	Swedish coast	58	162	0.45
Oliver, 1950	Spanish Atlantic coast	40	155	1.2
Elwertowskii, 1961	North Sea	50	155	0.8
Johnson, 1970	the Wash	53	134	0.62
De Silva, 1972	Scottish west coast	56	163	0.69

Fig.21.

Fig.21. Relationship of K (the Bertalanffy growth constant) of different populations of sprats to the latitude (see Table 13).

wth constant)

the latitude



latitude (Fig. 21).

The relationship of the rate of growth to the latitude is,

$$K = -0.038^{\circ}L + 2.716 \text{ (correlation coefficient, 0.953)}$$

In this computation the mean value of K was always used, whenever two values were given by the author. The regression obtained is significant at the 1% level.

Beverton and Holt (1957) applied the von Bertlanffy equation to represent growth in weight by plotting $W^{\frac{1}{3}}_{t+1}$ against $W^{\frac{1}{3}}_{t}$, when a straight line is obtained from which $W^{\frac{1}{3}}_{\infty}$ is read and hence W_{∞} can be calculated (Fig. 20). W_{∞} or the asymptotic weight of the West Coast sprat was found to be 29.8 gm.

During the present study two sprats measuring 161 (5 year old) mm were caught. The highest weight recorded for any individual in this area was 27.5 gms (4 year old). There were many fish which were between 155 and 160 mm in length and over 25.0 gm in weight. The oldest fish recorded during the investigation was 6+ years and was 154 mm in length and 24.6 gm in weight. It is evident, that the asymptotic values obtained theoretically are close to what is observed in nature.

2.VI. Mortality

The standard methods of estimation of mortality are dealt with in detail by Ricker (1958) and Beverton & Holt (1957). As stated earlier sea-loch sprat populations are characterized by a complete replacement every year by the immigration of a new brood and the standard methods of determination of mortality are not applicable to such populations which do not correspond to a steady state. Under such circumstances the natural mortality is almost undeterminable, except by tagging and recapture, before their replacement by a new brood. During the present investigation tagging was not carried out due to lack of facilities for use of an internal tag.

Sprat populations in the 'open' areas have been shown to contain older fish throughout the year and also to reflect year-class strength, thus exhibiting properties of a steady state population. An attempt was made to construct Ricker curves (1948) for the pooled data from the Firth of Lorne and Bloody Bay. Fish caught during the complete investigation were pooled together and the percentage frequency distribution of each age group independent of their year of birth was plotted against the corresponding age (Fig.22). A curve with an ascending limb and a long descending limb was obtained.

The descending right limb when straight is indicative of an uniform survival rate over the range of age groups involved. The rate of survival, S, can be computed from the difference in natural logarithm between age t and t-1, read from the lower descending limb of the catch curve. The negative value is written with a positive mantissa and antilogged giving S, directly. The annual mortality rate, a, and the instantaneous mortality rate i, can be calculated from the equation:

$$a = 1 - S$$

$$i = -\log_e S$$

The annual mortality rate between the second and fourth year of life is 62%. The above interpretation could give erroneous results under certain not correspond to a steady state. Under such circumstances the natural mortality is almost undeterminable, except by tagging and recapture, before their replacement by a new brood. During the present investigation tagging was not carried out due to lack of facilities for use of an internal tag.

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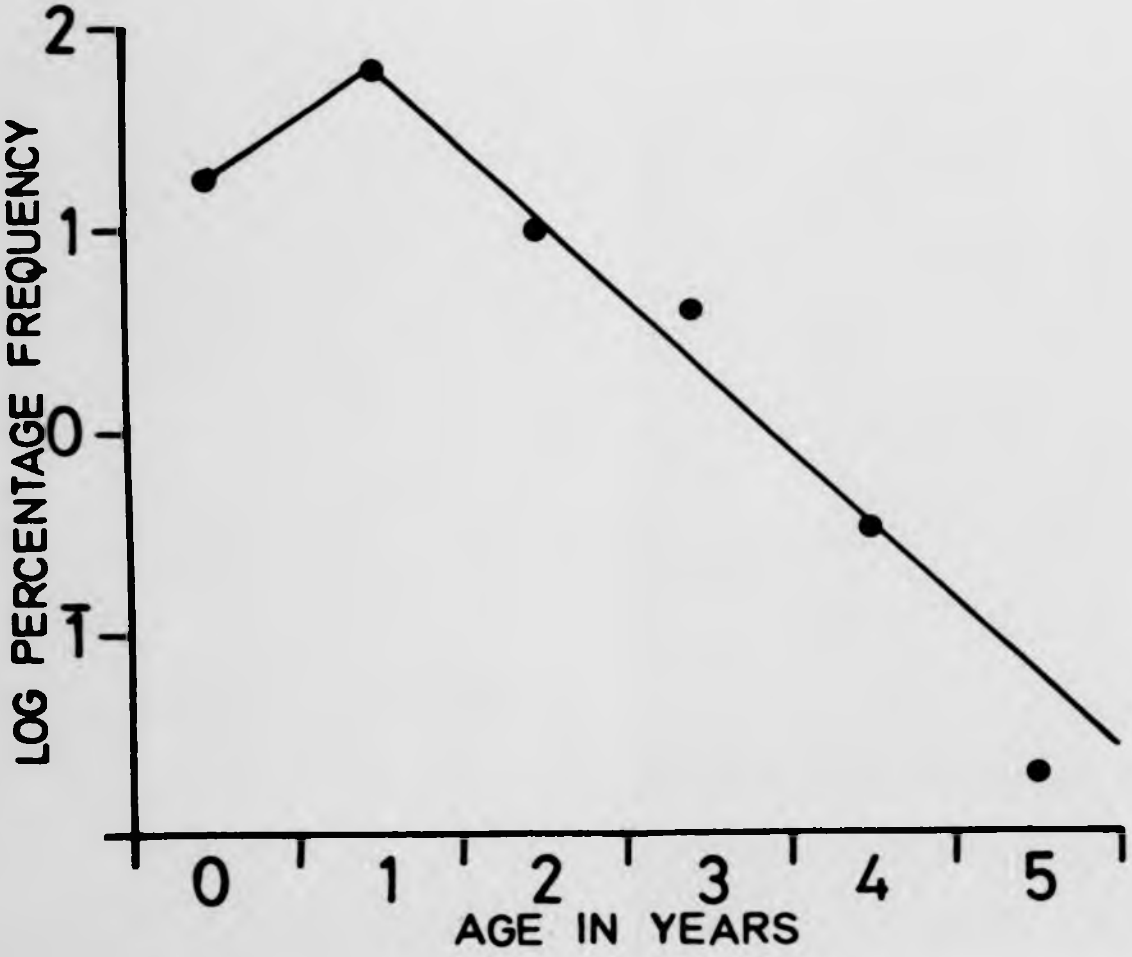
Fig.22.

Fig.22. Catch curves for sprats.


2
1
0
$\bar{1}$
LOG PERCENTAGE FREQUENCY
0
1
2
3
4
5
AGE IN YEARS

circumstances, such as decrease in vulnerability of larger fish due to emigration into deeper waters, which probably takes place to a certain extent in this area, and this is also evident from the fact that five year old fish are represented in a very small proportion compared to the others. Johnson (1970) estimated the natural mortality of Wash sprat to be 57% per annum using the relationship between mortality coefficient and growth constant, a technique developed by Beverton and Holt (1959). This technique cannot be used in the present investigation since a knowledge of the average length and age at recruitment has to be obtained.

In general, species of fish with a short life span tend to have higher growth rate and a high mortality. One of the main causes of mortality in sprats in nature is thought to be predation by other fish, the small size making it vulnerable to its predators throughout most of its life. The data on food and feeding habits of gadoids, spur-dogfish and sea trout were made available for use in this thesis by Dr. J.D.M. Gordon.

Among the gadoids the food of whiting Gadus merlangus was found to be dependent on fish to a large extent. For example in November 1970, 318 whiting were examined, out which 133 were feeding. Among these, 83 had fish remains in their guts. In January 1971, 28 out of 40 whiting examined were feeding and seventeen of these were feeding on fish. The fish taken were 80% to 90% clupeids. During this time the clupeid population in the Firth of Lorne was composed mainly of sprats and it is reasonable to conclude that the whiting is dependent for food mainly on sprats, at least at this time of the year.

Spur-dogfish Squalus acanthias is also an important predator of clupeids and in a sample obtained in June 1969 from Loch Etive, all the individuals were feeding exclusively on clupeids, and in one individual there were 26 clupeids in the stomach.

Sea-trout Salmo trutta is also an important predator of clupeids.

During the summer months, mackerel Scomber scombrus occur in large numbers in the area and they were found to feed on clupeids, mainly 0-group to a large extent. In July 1970, a mackerel caught by an angler was found to contain 48 clupeids, examination of which showed that 31 were sprats between 45 mm - 89 mm in length.

2.VII. Length-weight relationship

The length-weight relationship in fish is usually described by the formula;

$$W = a L^n$$

where W = weight

L = length

a = a constant

n = an exponent in the range of 3.

In this account of the length-weight relationships of herring and sprats values used are those for preserved material and both length and weight are somewhat decreased by preservation (Appendix 1). This should not vitiate relative values since all specimens received the same treatment in preservation.

The length-weight relationships and their significance in fishery biology has come to light in the recent years. Farris (1956) found that the factor 'a' in the above relationship, that is the condition factor, differed significantly when aquarium-reared Sardinops caerulea were maintained on different diets. The exponent 'n' did not vary unless the fish were maintained on either an entirely protein or carbohydrate deficient diet. Ehrlich (1972) observed that the exponent 'n' did not differ significantly in groups of herring larvae fed on diets of rotifers, mixed plankton or nauplii of Artemia salina, but that 'a' did.

The length-weight relationships of 0-group sprats and herring were calculated separately from that of older fish. The weight of all the fish in each mm group throughout the year were averaged and plotted (Fig.23). The length-weight relationships together with the correlation coefficients are given in Table 14.

Covariance analysis showed that the length-weight relationship between 0-group spring-and autumn-spawned herring is significantly different at the 1% level.

For the exponent n,

$$F = 25.81$$

$$F_{0.99}(2,120) = 4.99$$

and similarly for factor a

$$F = 26.78$$

$$F_{0.99}(2,120) = 4.79$$

A similar test to find out whether the length-weight relationships of 0-group and older sprats were significantly different, was found to be negative. Since there was no significant difference a single length-

Fig.23.

Fig.23. Length-weight relationship of herring and sprats.

and sprats.

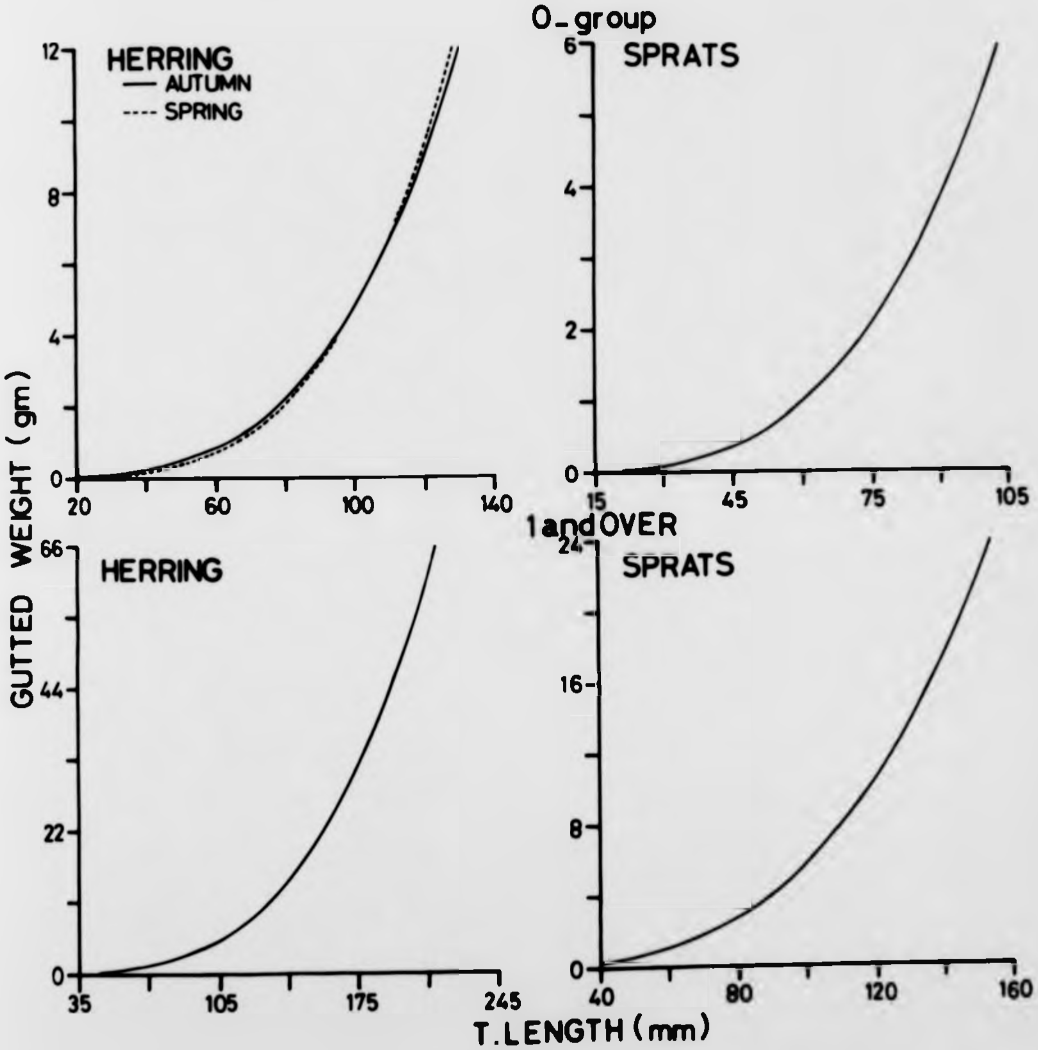

O-group
HERRING
— AUTUMN
---- SPRING
SPRATS
1 and OVER
HERRING
SPRATS
GUTTED WEIGHT (gm)
T.LENGTH (mm)
12
8
4
0
20
60
100
140
6
4
2
0
15
45
75
105
66
44
22
0
35
105
175
245
24
16
8
0
40
80
120
160

Table 14.

THE LENGTH-WEIGHT RELATIONSHIP OF HERRING AND SPRATS AT DIFFERENT STAGES OF LIFE.

	Factor 'a'	Exponent 'n'	Relationship	Correlation c.
* Autumn-spawned herring	0.0000006	3.4855	$0.0000006\ L^{3.4855}$	0.9976
* Spring-spawned herring	0.0000002	3.7419	$0.0000002\ L^{3.7419}$	0.9949
* Sprats	0.000001	3.3612	$0.000001\ L^{3.3612}$	0.9975
Herring over a year old	0.0000004	3.5344	$0.0000004\ L^{3.5344}$	0.9812
Sprats over a year old	0.000002	3.4234	$0.000002\ L^{3.4234}$	0.9898

*0-group.

weight relationship for sprats of all ages was obtained, thus:

$$W = 0.000001 \quad L^{3.38425}$$

The values for 0-group herring of both races are similar to those of Marshall <u>et al</u>. (1937). There are no data available for herring between one and three years old. Fraser (1931), however, found $W = 0.00000337\ L^{3.149}$ for adult herring from the English Channel. Johnson (1970) estimated the length-weight relationship as $W = 0{\cdot}0000029\ L^{3.42}$ for Wash sprats during their non-feeding season. The difference in 'a' between the two populations is probably due to seasonal differences in the analysis. Other local factors such as temperature and nature of feeding grounds may also affect it. It is possible that the differences in both 'a' and 'n' values of autumn and spring-spawned 0-group herring are at least partly genetical.

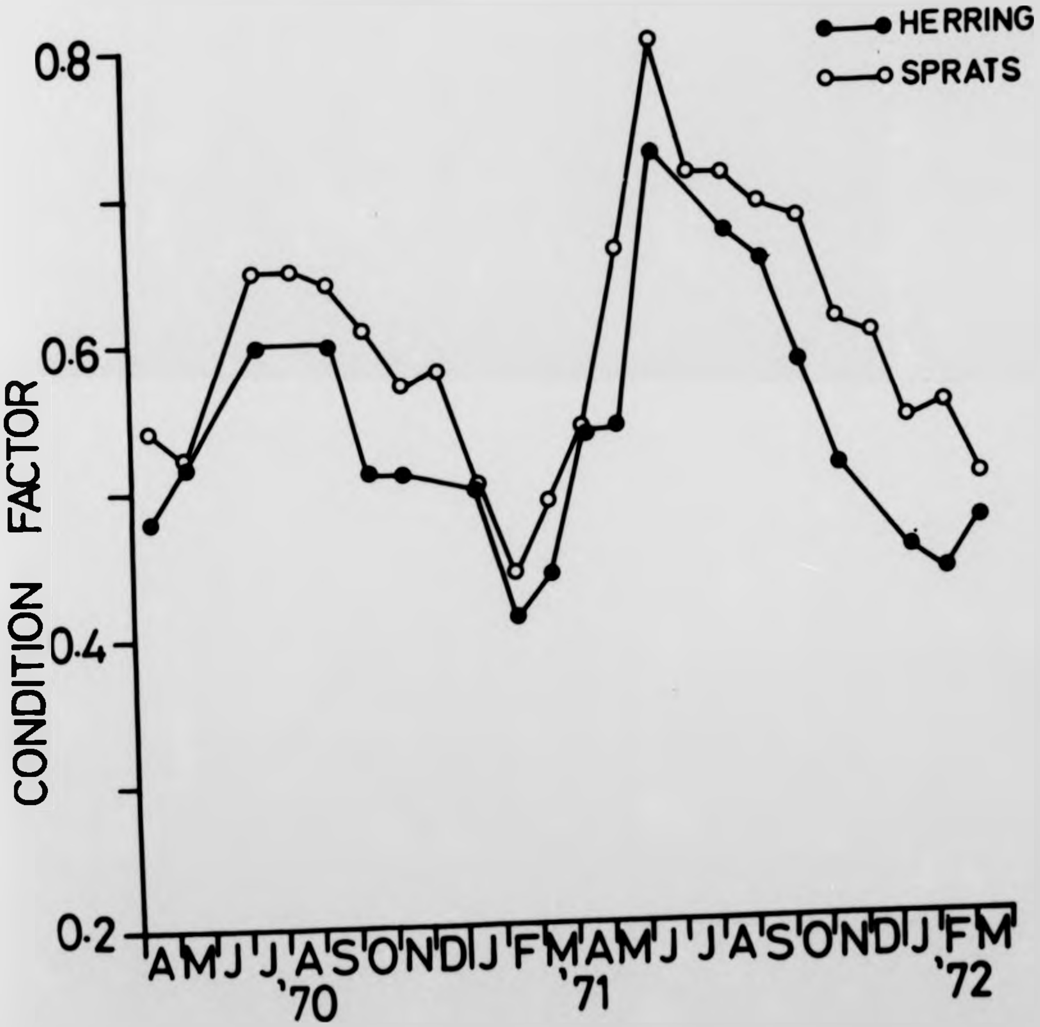
Cyclical change can often be detected in the weight of a fish at a particular body length, in the texture and appearance of the muscles, and in fat storage. These changes are often associated with annual spawning and changes in feeding intensity. Condition has often been measured as the deviation of an individual's weight from the expected weight of a fish of that length. This may be done by finding a 'condition-factor' - K, using the formula $K = 100 \frac{W}{L^3}$, where W is the wet weight in gm, L is the length in cm. This in fact is a comparison of the empirical weight with the weight of a hypothetical ideal fish, where the length-weight relationship follows the cube law.

$$W = KL^3$$

W is multiplied by 100 to avoid the use of small decimals. K was calculated for 50-60 I+ and over fish (gutted & gonads removed), in each monthly sample,

Fig.24.

Fig.24. Seasonal changes in the condition factor of herring and sprats over a year old.

HERRING
SPRATS
CONDITION FACTOR
0.8
0.6
0.4
0.2
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
'70
'71
'72

and the means obtained from April 1970 to March 1972 are shown in Fig.24. In sprats the condition reached a maximum in June and a minimum around February-March. There was a noticeable increase in the condition after the winter and then a gradual decrease up to about September, after which the decrease was more rapid. Condition in herring also followed a similar pattern, with maxima and minima tending to coincide with that of sprat.

2.VIII. Meristics and origin

In the earlier sections factors pertaining to 'population dynamics' in a strict sense have been presented. Without a knowledge of the origin of the clupeid populations that have been investigated the present study would be incomplete.

One of the major tools available to the fishery biologists for the assignment of different biological groups of herring to their respective spawning stocks are the meristic characters. These criteria have been used since the pioneering work of Heincke (1898). In the present analysis the meristic characters of the two species were carried out with different objectives. Mature herring were not caught in the area and therefore spawning was not thought to occur locally. Thus the study was orientated to finding out from which spawning stock or stocks the young herring originated. In the case of sprats, meristic characters have been little studied and the main objective was to examine whether the populations from the different localities showed homogeneity.

Methods used in 'racial' investigations in herring were listed by

Parrish & Sharman (1958). They divided characters used into three categories: morphological, physiological and mixed characters. Tåning (1952), Blaxter (1958) and Blaxter & Hempel (1963) investigated the lability of meristic characters from a point of view of 'racial' problems. Hempel & Blaxter (1961) demonstrated that the myotome numbers of Atlantic herring were fixed before hatching and also that the vertebral counts in German coastal and Clyde spawners differed considerably, which suggests a genetical difference. Kreft (1954, 1958) found a significant difference in gill raker counts of adult spring- and autum-spawned Baltic herring and also that the numbers of gill rakers in juvenile fish were positively correlated to their length. It appears that unlike gill raker or pectoral fin-ray numbers, the numbers of vertebrae are independent of size and will reflect true genetic differences from an early stage in life.

The mean vertebral counts have been used by many workers for complete or partial characterization of young herring to their spawning groups (Marshall et al. 1939; Bowers, 1962 ; Wood, 1960; Symonds, 1964; Saville, 1971). The autumn-spawned herring generally have a lower vertebral count and a higher keeled scale count compared to those of spring-spawned herring.

The mean number of vertebrae of 80-100 young herring from each sample and the keeled scale counts are given in Appendices 2 & 3, together with the mean length and weight of each sample. The mean number of vertebrae falls into two different groups, one with a range between 56.43 - 56.63 and the other with a range of 56.89 - 57.14. A statistical test (Students' t test) proved the differences to be significant at the 1% level. The pattern of distribution of vertebrae of the two groups at their extremes of the range is also markedly different (Fig. 25). Similarly the mean keeled scale counts were divisible into two groups with ranges between 14.18 - 14.34 and 13.75 - 13.96. A statistical test could not be carried out, since the number of observations in the latter group were limited to two. However, the samples with the lower keeled scale counts had high vertebral counts and vice versa.

The significant difference in the mean number of vertebrae in the two groups and also that the mean values observed are in agreement with known autumn- and spring-spawned stocks, indicate that the young herring in the area originate from different racial stocks of herring.

In all the samples except two the mean vertebral count fell within one of the two groups and these two were probably mixed shoals. Even they were separable rather easily into their respective races using external appearances. In June one group was darkly pigmented and the early signs of scale formation were evident, whereas the other group was fairly translucent with much less pigmentation. When they were separated using these characters and the mean vertebral number determined, the means were in agreement with those of 'pure shoals' of autumn- and spring-spawned herring. Length-frequency distributions (Fig. 26) showed only a slight overlap and the mean length of each racial group was determined by using the probability-paper method of Harding (1949).

The meristic characters investigated in sprats were number of vertebrae, keeled scales and anal and dorsal fin-rays. The data are summarised in Table 15. The statistical method used to find out whether the differences in the mean counts from the different localities were significant or not was that of Rothschild (1963). This method was chosen because it is a

Table 15.

MERISTIC CHARACTERS OF SPRAT POPULATIONS FROM DIFFERENT LOCALITITES.

	VERTEBRAE			**KEELED SCALES**			D. FIN RAYS			A. FIN RAYS		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
F. of Lorne	178	45–49	47.75	126	10–13	11.66	126	16–19	16.98	115	18.21	19.10
L. Spelve	200	46–49	47.83	182	11–13	11.52	159	16–18	17.05	211	17–21	19.35
L. Etive	159	46–49	47.81	177	11–13	11.39	126	16–18	16.88	114	17–20	19.07

Fig.25.

Fig.25. Pattern of distribution of vertebrae in autumn-and spring-spawned herring, at the extremes of their respective ranges (See Appendices 2 & 3). The mean vertebral number of each line is (1) 56.36

(2) 56.60

(3) 56.90

(4) 57.22

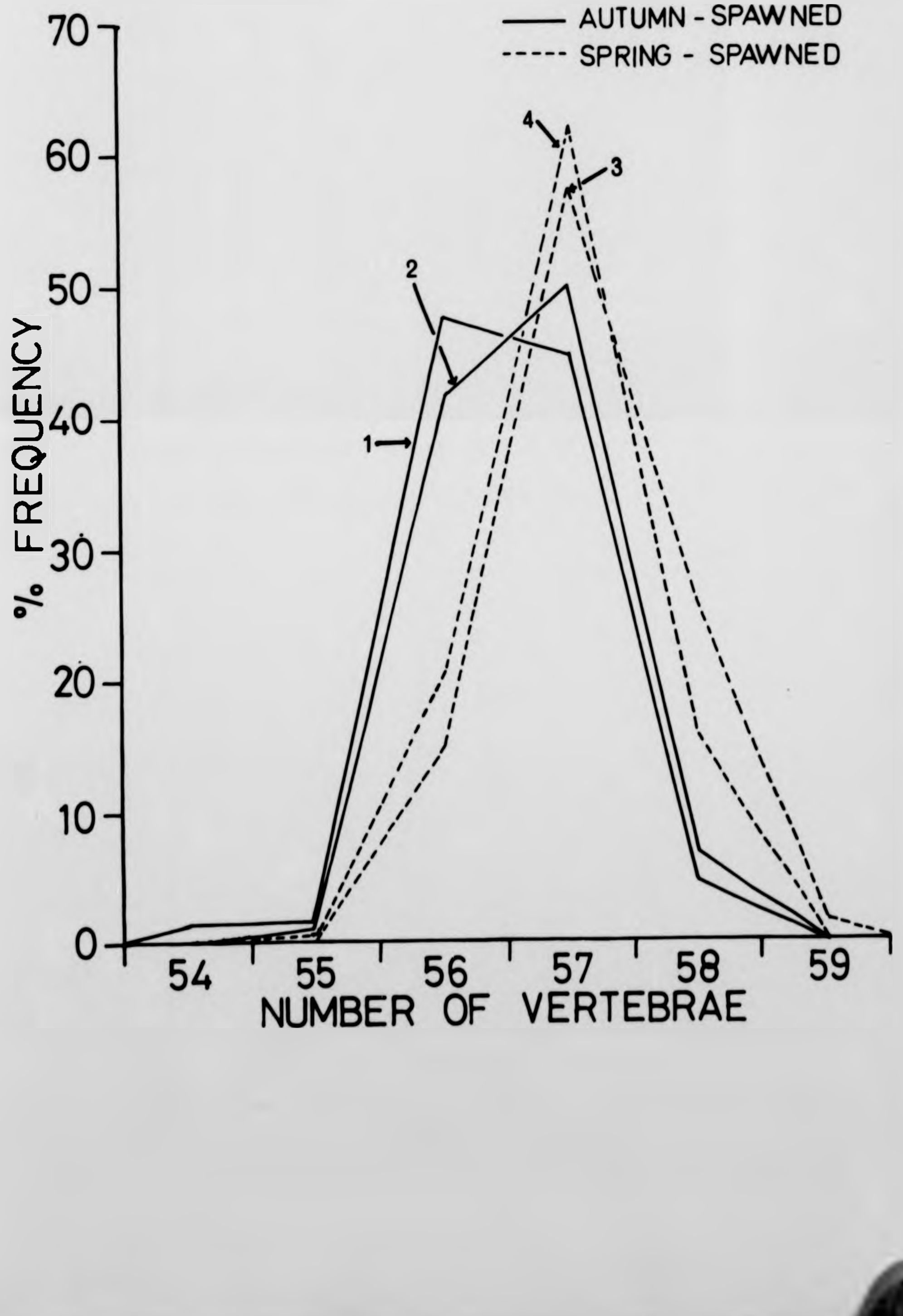
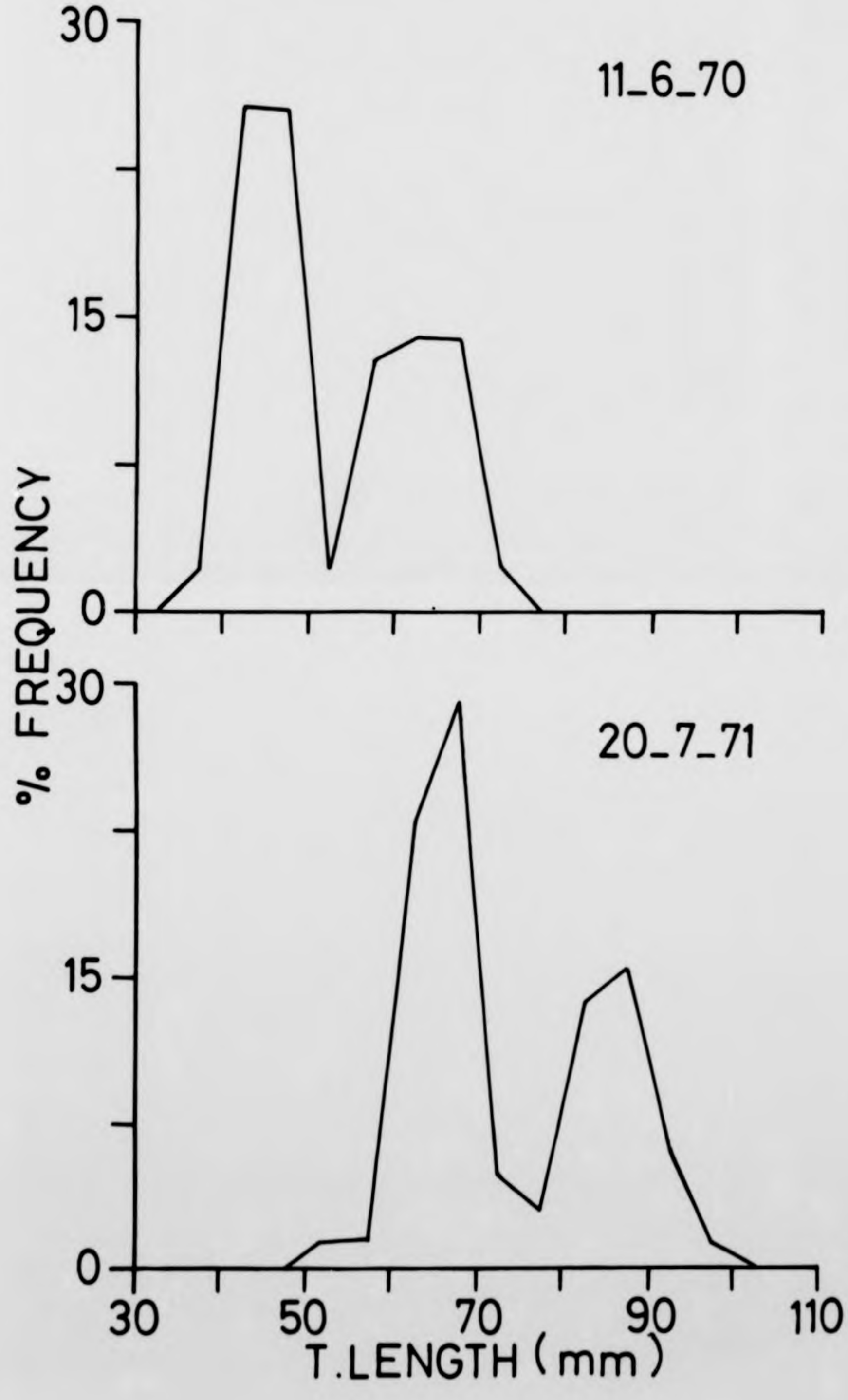

AUTUMN - SPAWNED
SPRING - SPAWNED
% FREQUENCY
70
60
50
40
30
20
10
0
54
55
56
57
58
59
NUMBER OF VERTEBRAE
1
2
3
4

Fig.26.

Fig.26. Length frequency distribution of two 'mixed shoals' of autumn-and spring-spawned 0-group herring caught on the 11th of June 1970 and the 20th of July 1971.


30
15
0
11_6_70
% FREQUENCY
30
15
0
20_7_71
30
50
70
90
110
T.LENGTH (mm)

graphical representation which brings out differences between samples from different areas at a glance.

According to this analysis if the mean of any one sample falls within the range of 2 w of the other sample then it is judged to be not significantly different at the level of significance (1% in this case) fixed by the investigator.

$$2\,w = q\,(p, n_2)\, s_{\bar{x}}$$

where q = is the upper percentage point of the studentized range at the 1% significance level (Snedecor, 1956)

p = number in the sample

n_2 = error degrees of freedom

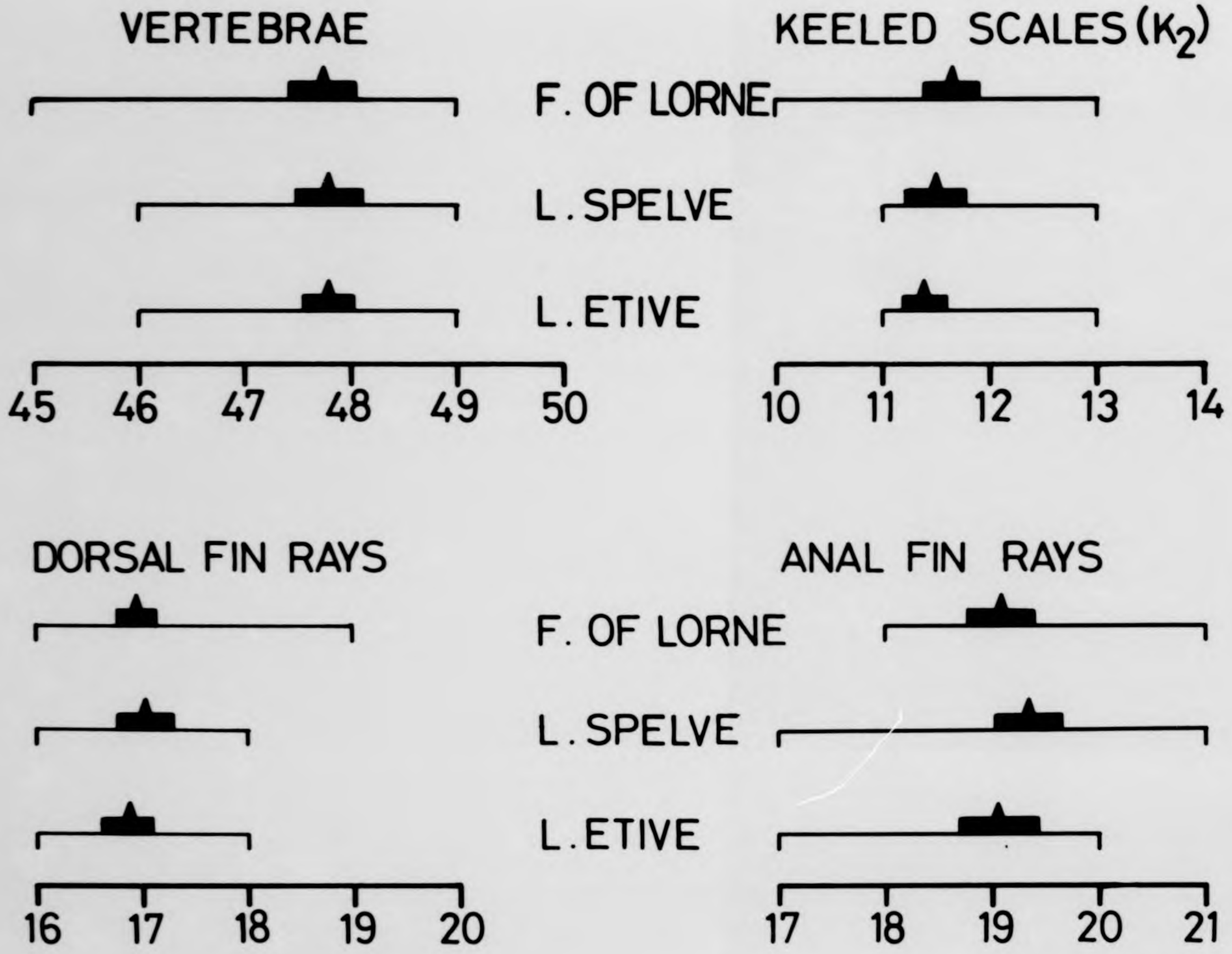
$s_{\bar{x}}$ = is the pooled standard error of the sample means.

It is clear from Fig. 27 that after statistical treatment there is no significant difference in any of the meristic characters investigated in sprats from the different localities. It is thus apparent that populations of sprats in this area are homogeneous and originate from a single breeding stock.

The only observation up to date on the meristic characters of any one population in British Waters is that of Bowers (1949). He determined the mean number of vertebrae in 0-group sprats in Manx Bay and found it to be 47.67. On the other hand Danish (Poulsen, 1950) and Swedish (Molander, 1940; Lindquist, 1968) workers carried out extensive investigations on the meristic characters of different sprat populations from the scandinavian

Fig.27.

Fig.27. Comparison of the number of vertebrae, dorsal and anal fin-rays and keeled scales (K_2) of sprats from different localities (on either side of the mean the broad bar represents 2W and the thin line the range).


VERTEBRAE
KEELED SCALES (K_2)
F. OF LORNE
L. SPELVE
L. ETIVE
45
46
47
48
49
50
10
11
12
13
14
DORSAL FIN RAYS
ANAL FIN RAYS
F. OF LORNE
L. SPELVE
L. ETIVE
16
17
18
19
20
17
18
19
20
21

fjords. Poulsen (1950) recognised five stocks of sprat which he thought to be racially different on the basis of mean vertebral and keeled scale count differences.

Having established that the young herring in the area studied originate from two racial groups or stocks, an attempt was made to define their origin further and allocate them to one or more spawning stocks known to herring biologists. The main spring-and autumn-spawning grounds of herring in British waters are known and the main spawning grounds along the Scottish coasts and in the Irish Sea are shown in Fig.28.

The mean number of vertebrae, keeled scales and the mean l_t value for known spawning stocks are tabulated (Appendix 5). Table 16 is derived from combining the data of the observations for each spawning stock and is used as the final guide for comparison with the present data.

It is seen that the mean vertebral number of autumn-spawned young herring is in very close agreement with that of the Minch autumn-spawning stock while the spring-spawned ones are closest to that of the Minch spring-spawning stock. The mean keeled scale counts of autumn-spawned herring are relatively higher than those of the Minch stock, however, but lie closer to this stock than to any other. Mean numbers of keeled scales for the Minch spring-spawning stocks are not available for any comparisons to be made.

It is clear from Table 16 that the differences in the meristic characters between the races amount to about half a vertebra and keeled scale, and within a race the differences among the spawning stocks is further reduced. Thus, agreement in these characters alone is not adequate to make any definite

Table 16.

THE RANGE IN THE MEAN NUMBER OF VERTEBRAE, KEELED SCALES AND THE MEAN L_1, AND THE RANGE IN L_1 DISTRIBUTION OF SPAWNING STOCKS IN SCOTTISH WATERS AND THE IRISH SEA.

Spawning stock	Mean vert	Mean K.S.	Mean L_1 cm	Range in L_1 cm
Clyde spring	56.97-57.21	14.09-14.25	9.0-12.0	6-18
Manx autumn	56.33-56.49		13.63-14.46	7-19
Minch autumn	56.40-56.62	14.10-14.30	11.9 -13.2	7-19
Minch spring	56.93-57.07		11.0 -13.0	7-18
Buchan autumn	56.32-56.49	14.02-14.53	14.0 -14.8	7-21

Fig.28.

Fig.28. Known spawning grounds of herring in the Scottish waters and in the Irish Sea.

1. Minch - spring-and autumn-spawning grounds (Baxter, 1958).
2. Clyde - spring-spawning ground.
3. Manx - autumn-spawning ground.
4. Buchan - autumn-spawning ground.

(2, 3, and 4 - Parrish & Saville, 1965).


AUTUMN
SPRING
1
1
4
2
3

conclusions as regards the spawning stock.

A total of 1482 otoliths, mainly belonging to 1+ herring of 1969, 1970 and 1971 year-classes were used in l_1 studies. The otoliths of each year-class was classified using the criteria of Parrish & Sharman (1958). The two main characters used were

(a) the nature of the nucleus - whether hyaline or opaque.

(b) the width of the first growth zone.

It was noted that the finer characters such as the ratio of the antirostrum to the size of the rostrum were of little use. The results of the final analysis are given in Table 17.

The back-calculated length at the end of the first year's growth was determined for all individuals which could be classified as either spring- or autumn-spawned with 100% accuracy and the mean for each group obtained. The mean l_1 was also calculated by pooling all the l_1 values and then using the probability paper method, as described by Harding (1949).

When the mean l_1 values are compared with those of known stocks, it is seen that the mean of autumn-spawned herring is in very good agreement with that of the Minch autumn-spawning stock (Baxter, 1963; Saville, 1968), whereas that of the spring-spawned herring is lower than that of the Clyde and Minch spring-spawned stock. The most conclusive evidence as to the origin of young autumn-spawned herring is obtained by a comparison of l_1 distribution of 1970, 1971 year-classes with that of the Minch autumn-spawners (Saville, 1971). The almost complete coincidence (Fig.29) of the l_1 distribution of young herring with that of Minch autumn-spawners indicates that autumn-spawned

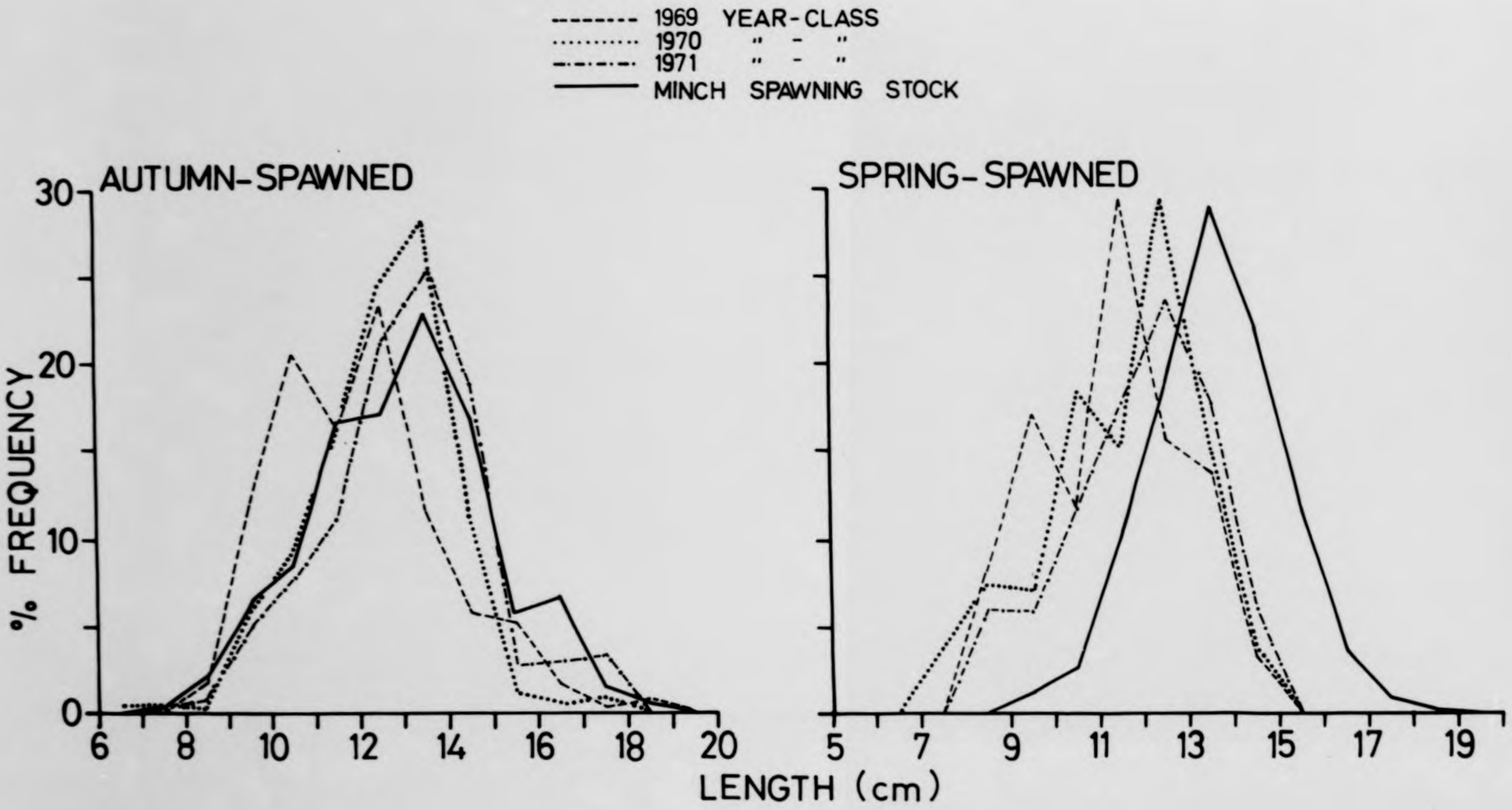
Table 17.

NUMBER AND PERCENTAGE OF OTOLITHS OF HERRING (1^+ AND OVER) OF 1969, 1970 & 1971 YEAR-CLASSES, WITH OPAQUE NUCLEUS/NARROW 1ST GROWTH ZONE, AND HYALINE NUCLEUS/WIDE 1ST GROWTH ZONE, THE RANGE AND MEAN L_1 OF THE RESPECTIVE GROUPS.

Year-class	Total	Number unclassified	Autumn-spawned			Spring-spawned		
				L_1(cm)			L_1(cm)	
			(%)	Range	Mean	(%)	Range	Mean
1969	401	104(25.9%)	(59.6%)	8.1-18.2	12.0	(14.4%)	8.0-14.1	11.3
1970	635	171(26.9%)	(51.8%)	6.6-17.8	12.5	(21.2%)	7.1-14.4	11.5
1971	386	109(28.2%)	(58.5%)	7.2-17.9	13.4	(13.2%)	8.5-14.7	11.8
Range in L_1				6.6 - 18.2			7.1 - 14.7	
Range in mean L_1				12.0 - 13.4			11.3 - 11.8	

Fig.29.

Fig.29. Comparison of l_1, distribution of autumn-and spring-spawned young herring of 1969, 1970 and 1971 year-classes, with those of the respective Minch spawning stocks (Minch autumn-spawning stock l_1 data from Saville, 1971; spring spawning-stock l_1 data re-calculated from Baxter, 1958).



1969 YEAR-CLASS
1970 " - "
1971 " - "
MINCH SPAWNING STOCK
AUTUMN-SPAWNED
SPRING-SPAWNED
% FREQUENCY
0
10
20
30
6
8
10
12
14
16
18
20
5
7
9
11
13
15
17
19
LENGTH (cm)

young herring in this area originate from the former stock. The slight disparity in the mean l_1 and the l_1 distribution is probably a result of emigration of fish in large numbers leaving the small and slow growers behind, and hence would give rise to low mean l_1 values and a slight shift in the l_1 distribution to the left.

A similar comparison of l_1 distribution (Fig.29) of spring-spawned young herring with that of the Minch spring-spawning stock (Baxter, 1958) indicates a big disparity in the l_1 distribution of the two groups.

Observation on larval drift also provides further evidence in favour of a Minch origin of autumn-spawned herring. Baxter (1954) and Wood (1972) observed the presence of large concentrations of larvae on the southern part on the coast of Mull, which are thought to be from the Minch autumn-spawners. There is no evidence on the other hand, of a northwards drift of Clyde spring-spawned larvae (Parrish et al, 1959), but a southern drift of Minch spring-spawned larvae has never been ruled out.

A possible Manx or Buchan origin of the autumn-spawned herring is ruled out because of the dissimilarity in the meristic characters, mean l_1 and l_1 distribution and also since a drift of Manx larvae beyond the lower reaches of the Clyde estuary is not known to occur (Baxter, 1954; Bowers, personal communication) and also a south-westerly movement of Buchan larvae has not been noted.

It is concluded, therefore, that the autumn-spawned young herring in the area originate from the Minch autumn-spawning stock. There is no conclusive evidence to prove the origin of the spring-spawned herring. They are, however, thought to originate from the Clyde spring spawning stocks on the balance of available evidence.

2.IX. Discussion

Studies on the growth of O-group clupeids has shown that the growth rates in any one species are not significantly different from each other in the different localities studied. It is also known that in both herring and sprats maximum growth takes place in their first year of life. Hence factors affecting growth would tend to have a more pronounced affect during this year of life. The environmental conditions and the food supply together with the interspecific interactions are known to be the main factors affecting growth. Environmental conditions in the different localities are similar to one another, possibly indicating that a stable food supply was available in all the localities.

A rapid increase in length in O-group sprats is known to occur after their first winter. This phenomenon is thought to be real and not artificial, in that it is not primarily caused by an emigration of larger fish into only one locality. This rapid increase is probably achieved by a very high increase in feeding activity (Section 4) soon after the winter during the planktonic outburst of the spring.

The mean length of the 1970 and 1971 year-classes at the end of the first winter was 64.0 and 70.0 mm. The sprat is a short-lived species and tends to mature in its second year of life at a minimum size of 90 mm (Section 3). The rapid increase in length after the winter probably enables most of the 1+ individuals to reach maturity in their second year of life.

Year-class variation in the rate of growth of sprats older than a year has been observed, and possibly such variations are more pronounced in species of fish with a short life span and a high rate of growth.

It has been pointed out that more reliable estimates of growth characteristics are obtained from back-calculated values of individuals from a number of year-classes than from empirical data over a few growth seasons. Using the data of previous authors, the dependence of the growth constant, K, on latitude and hence on temperature in the sprat has been demonstrated.

The work of Farris (1956) & Ehrlich (1972) has shown that fish tend to have different condition when maintained on different diets, but the exponent 'n' remains unchanged. The very significant differences in factor 'a' in the length-weight relationship of spring-and autumn-spawned herring is at least partly due to different feeding conditions, probably in their early larval life, while the difference in 'n' is very likely genetical. It may be a worthwhile exercise to find whether significant differences in the exponent exists in different spawning stock of herring.

Section 3.

REPRODUCTIVE BIOLOGY

3.I. Introduction

During the sampling period from April 1970 to August 1972, no mature herring were caught in the area and thus this study is entirely confined to sprats. Most aspects of the reproductive biology of herring are well documented and no attempt is made at present to review this literature.

There has been a serious lack of research on aspects of the reproductive biology of sprat in British waters, except for a few scattered observations made since 1903. Fulton (1904) estimated that there are between 1880 to 3488 large yolked eggs in the ovary of fish of 120-140 mm length. He deduced that some of the reserve oocytes may mature during the spawning season, bringing the total number of eggs shed during any one season to around 5000 in an average sized sprat. On the basis of egg surveys in the Moray Firth, the same author concluded that the 1900 spawning season was of five months duration, extending from March to August. Hefford (1913) found sprat eggs off Plymouth from mid-February to July and also noted that the mean diameter changed from 1.031 mm to 0.912 mm during the period. Holt & Scott (1899) recorded the mean diameter to be between 0.87 - 1.30 mm. Lebour (1921a) found sprat eggs at Plymouth from January to May, being numerous in February and March. Ehrenbaum (1905-1909) concluded that spawning lasts from March to August in the North Sea and is at its maximum in June, which is in agreement with the observations of Tesch (1906-09).

Fage (1920) estimated that the main spawning season on the Atlantic coasts lasts from April to June and also concluded that throughout its range, the sprat is selective as to temperature conditions during spawning and development and that it requires a range of temperature of only 8^{o}-$11^{o}C$. Spawning grounds are known off the West of Ireland, North West of Scotland (Fage, 1920), in the Clyde (Kyle, 1897) and around Faroes Islands (Tåning, 1936). Spawning is also known to occur in the Southern Bight of the North Sea and along the German and Dutch coasts.

Heidrich (1925) was the first author to investigate the spawning process of sprat. He concluded that the sprat sheds its eggs in batches, for apart from small unripe eggs the ovaries contain eggs in different stages of development. He also stated that spawning of an individual fish occupied two and a half to three months and the number of eggs shed in a batch rises to a maximum in May and then declines and also that batches are larger in older fish. On the basis of fecundity estimates he deduced that the sprat sheds its eggs in eight or nine batches during any one season.

The size of the larvae at hatching off Plymouth was found to be 3.0 mm (Lebour, 1921a), 2.25 mm in the Mediterranean and between 3.0 and 3.7 mm in the North Sea (Fage, 1920), emergence occurring only four or five days after fertilization.

Robertson (1938) found that the sex-ratio of sprat was very variable from area to area and from sample to sample with a general preponderance of females in English waters. Johnson (1970) introduced a six-point classification of sprat gonads and also noticed changes in the active development of gonads with climatic changes in Wash sprats.

It is evident that most of the work has been done in the early quarter of this century and that there is no comprehensive knowledge of the reproductive biology of any one stock or population of sprats in British waters. The present study is an attempt to fill this wide gap in understanding its reproductive biology.

3.II. Material and methods

The gonads from fresh fish were classified and a portion from the mid-region was fixed in either formal-saline, Zenker or Bouin's fluid for histological examination. A few ovaries of known maturity stages were brought fresh to the laboratory for egg-diameter measurements.

The fixed tissues were dehydrated, cleared in xylene and embedded in paraffin-wax of melting point 54°C and sectioned at 6 µ using a Jung Rotary microtome. The sections were stained either in Mallory's triple stain or in Haematoxylin and counterstained with eosin. The fresh ovaries were teased out into Ringer solution, a drop of neutral red added and after a lapse of five minutes, a sub-sample (1 ml) was taken and the diameter of 250 eggs was measured along the longest axis under a binocular microscope. From each ovary five such sub-samples were taken and thus a total of nearly 1250 eggs were measured per ovary.

A sample of 80-100 fish were preserved in 70% alcohol each month for macroscopical examination of the gonads. The gonads were removed and weighed to the nearest 0.01 gm. Each pair of gonads was carefully examined and allocated into an appropriate maturity stage.

The maturity scale (Appendix 6) used in this work was a modified version of that proposed by Johnson (1970). Histological examination of fixed material showed that the intermediate stages proposed by Johnson are of short duration, except perhaps for stage VI-II. It is believed that the omission of intermediate stages would not cause an error in the final conclusion drawn from the data. On the other hand, Johnson's scale lacks the stages VI-V and VI-IV, that is those fish that have partially spent their gonads, whereas in the classification used by Russian workers (Aslanova, 1954; Petrova, 1960) such stages are included. In the course of the present investigation, as will be evident later, fish with partially spent ovaries were never captured and therefore would not have resulted in an error by using Johnson's classification. However, the validity of Johnson's scale is doubted when conditions contrary to the present are met with.

The sexes were easily distinguishable by the presence of eggs in the ovaries when the fish were in or after stage II. In most 0-group fish before their first winter, the sexes were hardly distinguishable, specially if they were below 70 mm in length. In fish above this length, but in which active gonadal development had not started, the sexes could be distinguished by their shape. The ovaries were a narrow thin strip of tissue running along about three fourths of the body cavity with slightly tapering ends, while the testes were more flattened, shorter, and with an increasing width towards the anterior part.

Fish in stage IV and late III with enlarged ovaries and a few transparent oocytes were chosen for fecundity studies. The ovarian membrane was removed with a fine forceps and the ovary broken into two or three portions and introduced into Gilson's fluid in a vial and shaken vigorously for a few mintues. The composition of Gilson's fluids was modified as suggested by Simpson (1951).

60% alcohol	100 ml
80% nitric acid	15 ml
Glacial acetic acid	18 ml
Mercuric chloride	20 gm
Water to	1000 ml

The samples were stored in a dark place and shaken from time to time. Gilson's fluid was found to give satisfactory results unlike formalin which has been used by many investigators (Raitt, 1933; Botross, 1959; Scott, 1962). It facilitates the breakdown of the ovarian tissues and thereby making the separation of eggs from the tissue and from one another easier. In addition it hardens the eggs. When most of the eggs were separated from the surrounding tissue, each sample was washed thoroughly in distilled water, remaining pieces of tissue removed manually and then passed through a sieve of 112 µ to remove the reserve oocytes, which would not be used during the present spawning season. The rest of the oocytes were introduced into a 100 ml measuring cylinder and made up to the mark by adding distilled water.

Four to five sub-samples, each of 1 ml, were withdrawn at a time and the number of eggs counted under a binocular microscope. In addition to the total number of oocytes, those in the most advanced state of maturity (by size) was also counted and by averaging the number from all the samples the fecundity and the number of oocytes in the most advanced maturity stage were obtained for a particular fish. Care was taken to ensure that the eggs were uniformly distributed evenly throughout the water column, when withdrawing a sub-sample, by aeration and constant non-rotatory stirring.

In 1970, 1971 and 1972 larval and egg surveys were carried out from February to the end of August using a 2 m stramin net, towed at a speed of 2½ to 3 knots. The duration of each haul was 15 to 20 minutes and the net was towed at three different depths at each station. In 1972 a few night hauls were also made.

3.III. Seasonal changes in gonad condition

Classification of gonads into their respective maturity stages from macroscopic observations were carried out from August 1970 to July 1972. Immature virgin fish which were found throughout most of the year were not taken into consideration.

In the course of this study fish in stage VI-V or VI-IV, that is those that have shed part of their gonads or fish in running condition, were not caught. Only two females and five males in stage V, that is those fish which were very close to a running condition, were caught and therefore stage IV and V have been grouped together in the analysis.

The changes in gonad condition were also assessed semi-quantitatively, in terms of the gonosomatic index or the maturity coefficient, which is the weight of the gonad expressed as a percentage of the body weight of the individual. Gonosomatic index, together with macroscopical observations, are reliable criteria to determine the spawning season of fish and have been used together or singly by numerous workers. Le Cren (1951) found that in perch (Perca fluviatilis L.) the gonosomatic index is not affected by the size of the fish and that it is a measure of change in the gonad condition. West (1970 - unpublished thesis) showed that in the cod (Gadus morhua L.) it is affected by the size of the fish and that true changes in gonad conditions are obtained only by comparing fish of the same size. There was no evidence that the gonosomatic index was affected appreciably by its size in sprats and hence this together with the former criterion has been used to determine the spawning period of West Coast sprats.

Seasonal changes in the macroscopic appearance of the gonads and the mean gonosomatic index in males and females are shown diagramatically in Figs 30 & 31 and Table 18. In the course of the investigation, the end of 1970, the complete 1971 and a good part of 1972 spawning season was covered.

The records show that some 7.5% of all males and 3.5% of females were in an advanced state of maturity by November 1970. In the following months a higher proportion of fish were in a mature condition. By January 60% of males were in stage III and for the first time stage IV-V males appeared in the catches. Females in stage IV-V were first obtained in March and the last in July. The highest percentage of stage IV-V males

Table 18.

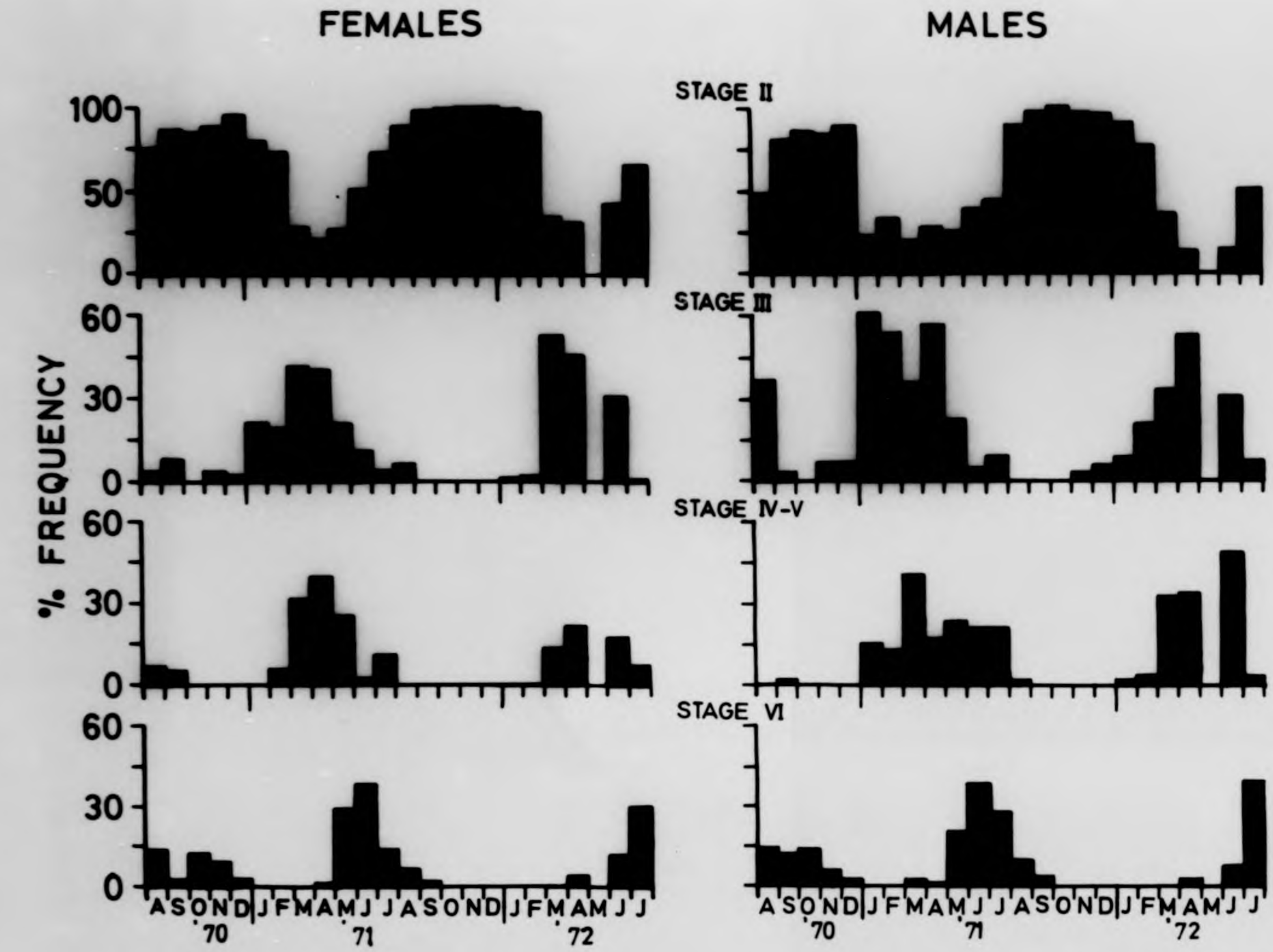
SEASONAL CHANGES IN THE SEX-RATIO AND THE GONOSOMATIC INDEX

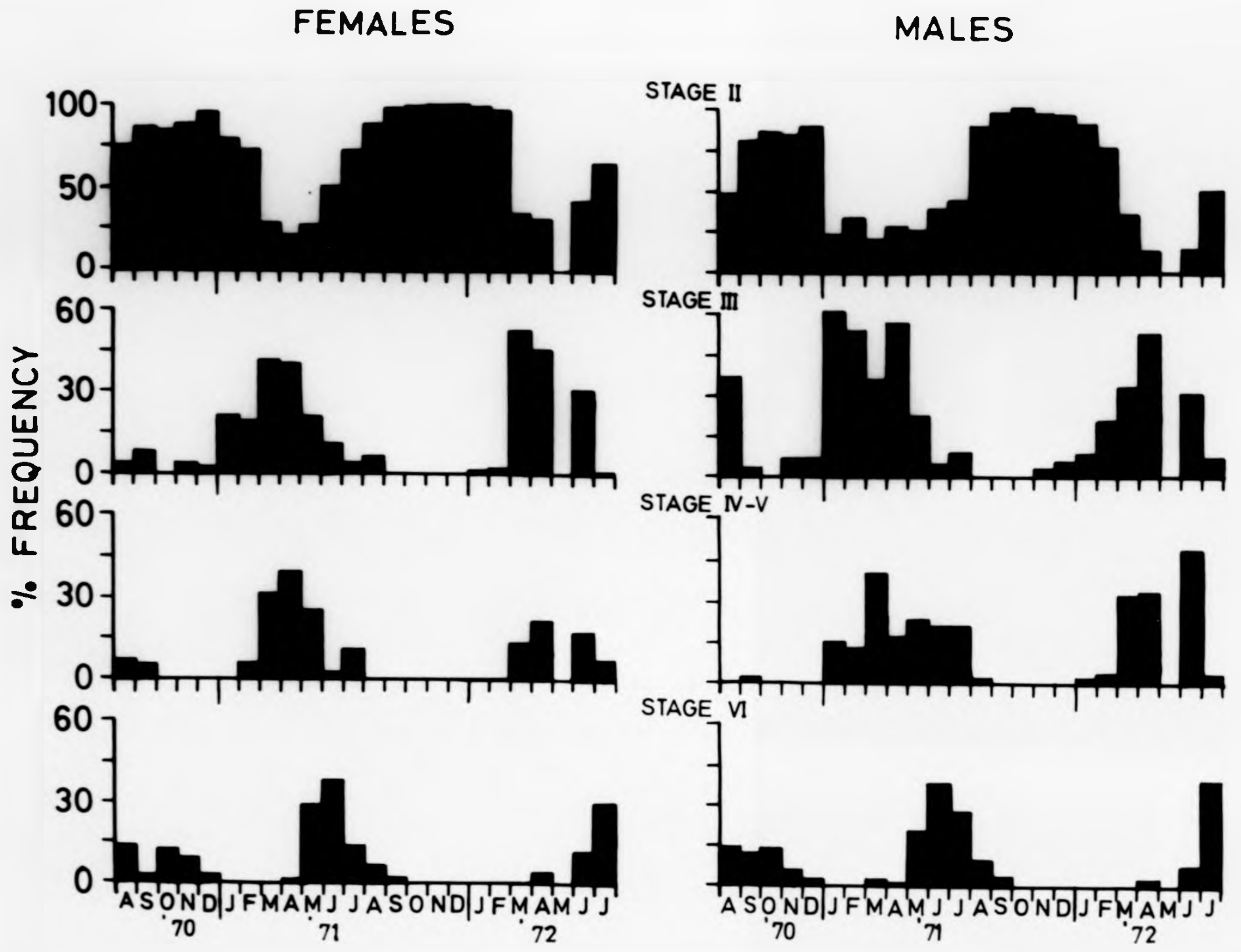
IN SPRATS, FROM AUGUST 1970 TO JULY 1972.

Month	No. Sampled	No. of Females	No. of Males	% Females	GONOSOMATIC INDEX Females	GONOSOMATIC INDEX Males
August	80	34	46	42.5	2.26	1.57
September	162	85	77	52.4	1.07	0.48
October	58	28	30	48.3	1.00	0.68
November	53	33	20	62.2	1.22	0.66
December	139	83	56	59.7	1.43	0.91
January	46	20	26	43.5	1.96	1.64
February	28	22	6	78.6	1.43	2.26
March	136	77	59	56.6	8.94	4.09
April	57	15	42	26.3	9.26	4.63
May	69	35	34	50.7	6.04	2.04
June	59	36	23	61.0	1.93	1.44
July	54	29	25	53.7	2.14	1.70
August	277	149	128	53.8	2.02	1.25
September	117	63	54	53.8	0.93	0.55
October	32	16	16	50.0	0.79	0.47
November	151	79	72	52.3	1.02	0.53
December	162	80	82	49.4	1.01	0.67
January	165	92	63	59.3	1.50	1.49
February	213	89	124	41.8	3.10	3.41
March	235	121	114	48.5	5.79	4.46
April	181	89	91	49.8	7.40	3.90
May		-	NO SAMPLE	-		
June	283	153	130	52.4	5.33	3.55
July	63	34	29	53.9	1.12	0.94

Fig.30.

Fig.30. Seasonal changes in the macroscopic appearance of the gonads of female and male sprats from August 1970 to July 1972.


FEMALES
MALES
STAGE II
STAGE III
STAGE IV-V
STAGE VI
% FREQUENCY
100
50
0
60
30
0
60
30
0
60
30
0
A S O N D J F M A M J J A S O N D J F M A M J J
'70
'71
'72


FEMALES
MALES
% FREQUENCY
100
50
0
60
30
0
60
30
0
60
30
0
STAGE II
STAGE III
STAGE IV-V
STAGE VI
A S O N D J F M A M J J A S O N D J F M A M J J
'70
'71
'72

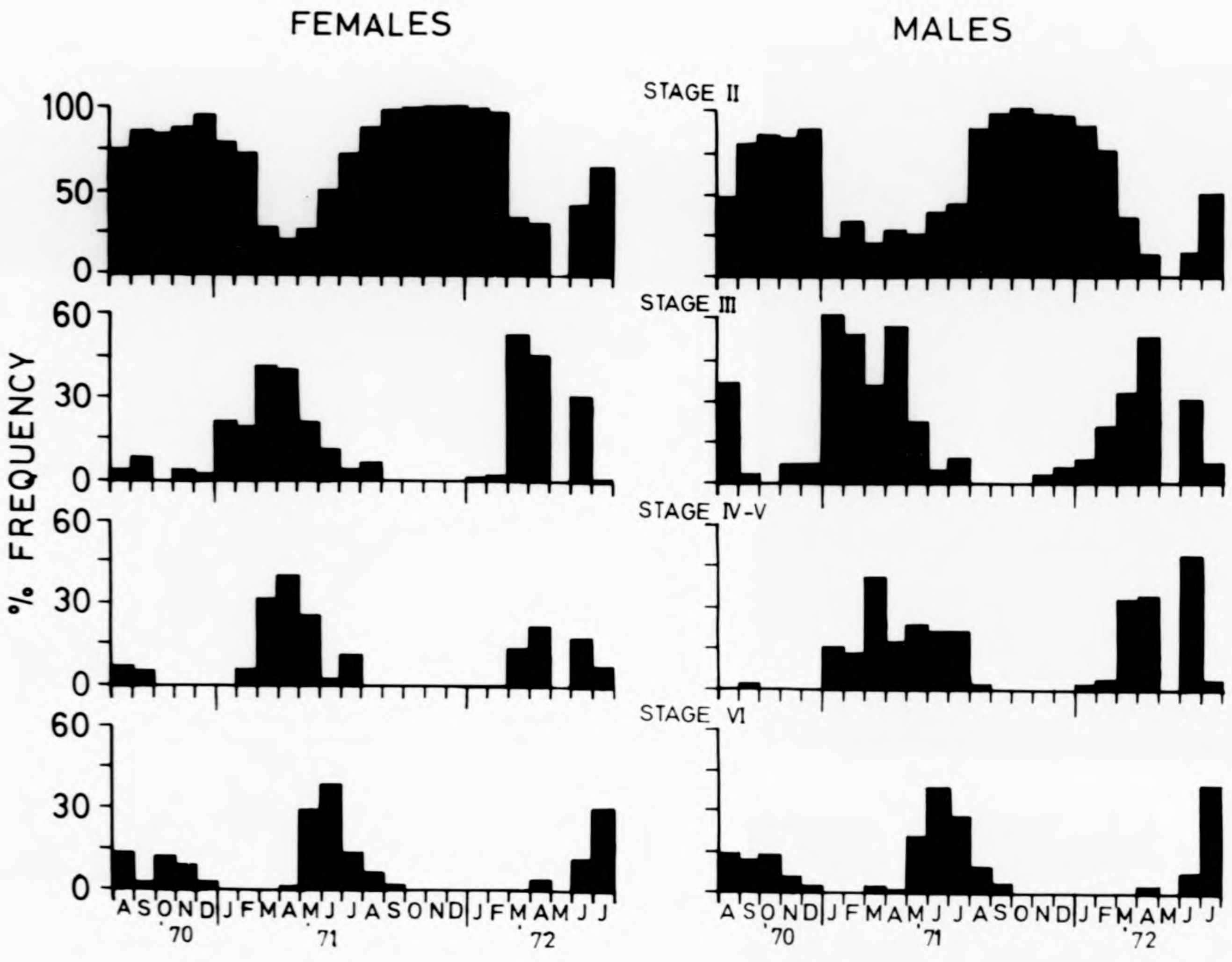
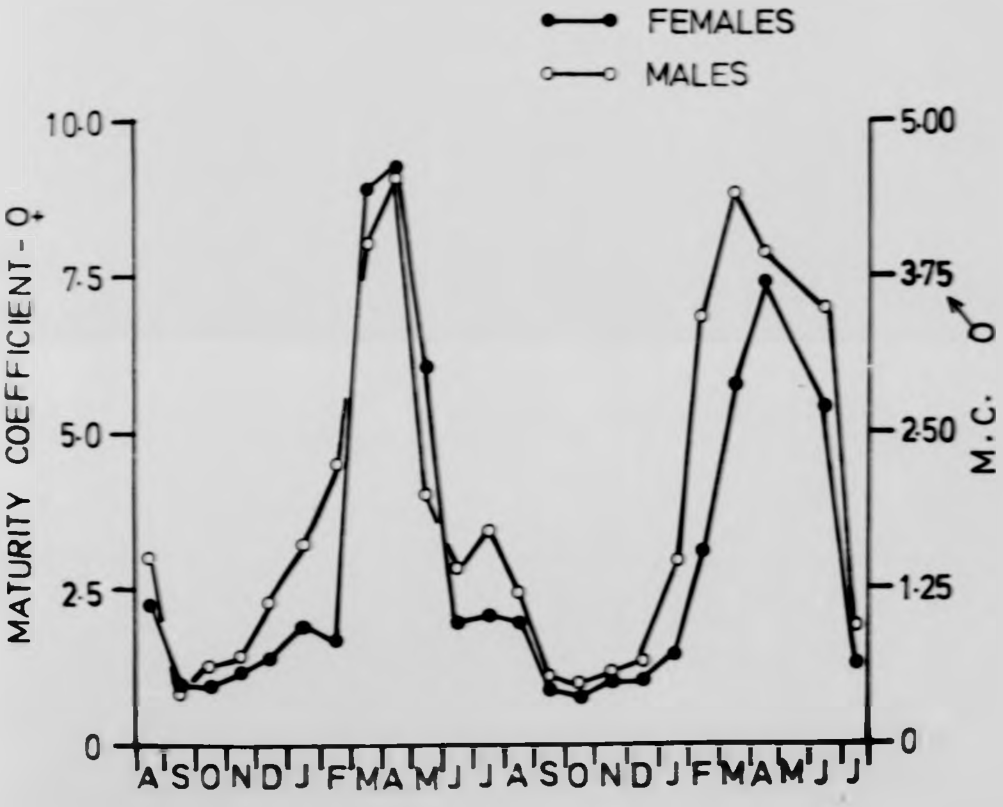
FEMALES
MALES
STAGE II
STAGE III
STAGE IV-V
STAGE VI
% FREQUENCY
100
50
0
60
30
0
60
30
0
60
30
0
A S O N D J F M A M J J A S O N D J F M A M J J
'70
'71
'72

Fig.31.

Fig.31. Seasonal changes in the maturity coefficient or the gonosomatic index of female and male sprats from August 1970 to July 1972.

cient or the

rats from



and females occurred in March and April respectively. Spent fish were caught from March till September. The gonosomatic index in males began to increase from December 1970 and reached a peak in April 1971, while that of females lagged behind at the start, but reached its peak at the same time. By July-August the gonads were almost back to their resting condition.

During the 1970 spawning season, fish in very advanced state of maturity was caught as late as September and newly spent fish until December.

The changes in gonadal maturation during the 1972 season were similar to those of the 1971 season in many respects. Onset of maturity (stage III) occurred as early as November in males but in females first signs of maturity was observed only in January and further maturation did not occur till March when there was a rapid increase in the proportion of stage III fish. The first spent fish were recovered in April. The peak in stage IV-V females occurred in June, while in males, it is probable that it was in May, when a sample was not obtained. The gonosomatic index in females lagged behind that of males throughout the season, unlike in 1971.

3.IV. Spawning period

The almost complete absence of sprat larvae and eggs in the sea-lochs and associated inshore waters (Appendix 7) and also running fish in the catches provides sufficient evidence to conclude that spawning does not take place in this area. However, the presence of fish in very advanced states of maturity and newly spents indicate that spawning does take place close by, probably in the deep waters west of Mull. It is believed from the observations discussed earlier, that the duration, start and termination of the spawning season could be deduced within very reasonable limits of accuracy.

The occurrence of stage IV-V fish as late as September 1970 and spent fish until December in the catches is indicative of a delayed termination in spawning during the 1970 season. It is probable that spawning continued well into October, or possibly into the early part of November, during that year. The 1971 season, on the other hand, was probably terminated by late August, since the last stage IV-V fish were obtained on the 19th of July but none on the 4th of August. The capture of spent fish in late March indicates that spawning was in progress by this time and the peak of spawning was probably in April-May. The start of the 1972 season was in all probability later than that of the 1971 season. Spent fish were first caught only in April, indicating that possibly there was at least a month's delay. Further evidence is obtained when the proportion of stage IV-V fish in the catches in the corresponding months are compared.

Thus it is seen that the 1971 season lasted for a period of nearly six months, from March to August, and this is in general agreement with observations of other workers early in the century. It is also clear that the onset and termination of the three spawning seasons were different from one another.

Maturation of gonads and spawning time is known to be temperature-dependent in fishes for example in whiting (Desbrosses, 1945; Bowers, 1954; Gokhale,

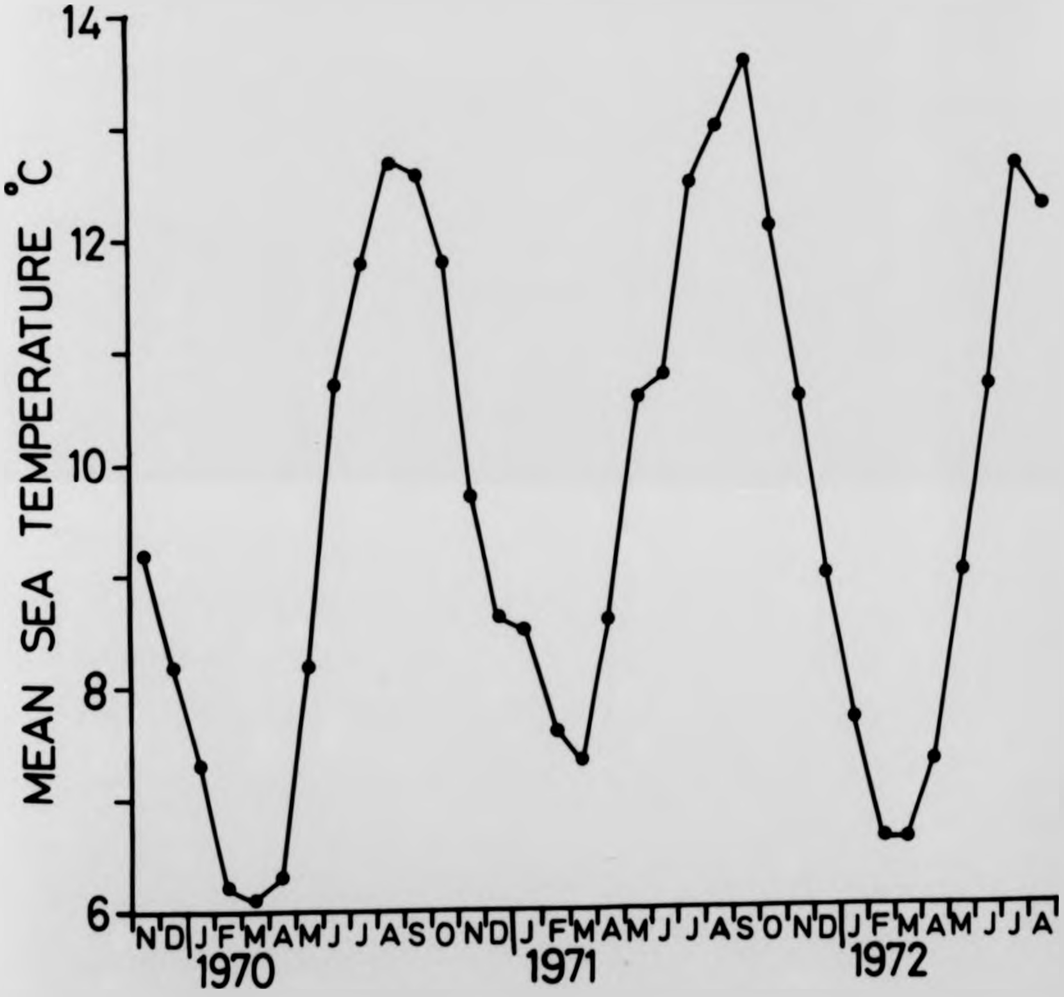
1957) and in Eastern brook trout (Henderson, 1963). Johnson (1970) found a positive correlation between gonadal maturation in Wash sprat and warm winter conditions.

The sea temperature data were taken for Keppel pier in the Isle of Cumbrae. It was known that temperatures here were similar to those in the study area and because regular information was available these data were used. It is seen that the (Fig.32) 1969 winter temperatures were substantially lower than the other two years. The temperatures in the early part of the 1971-72 winter was comparable to that of the previous one, but the temperatures during February and March were much lower than those of the corresponding months of 1972.

The difference in the timing of maturation and hence spawning is in all probability a result of the different winter temperatures. The initial maturation of gonads is seen to take place during the cold period, but exceptionally low temperatures bring about a retardation in maturity. It is probable that the relatively low temperatures during the 1969-70 winter delayed the onset of maturity, ultimately resulting in the observed late termination of the 1970 spawning season. Further direct evidence is obtained from analysis of the 1972 season, when onset of initial maturity was similar to that of 1971 but a cold period in January and February brought about a possible retardation in further maturity and thereby delaying the onset of spawning. It is logical to conclude that in sprat initial maturation takes place at low temperatures and that when it falls below a certain critical level gonadal development is retarded. These conclusions are in agreement with those observations of Page (1920) and Johnson (1970).

Fig.32.

Fig.32. Mean sea-temperature at the Keppel pier in the Isle of Cumbrae from November 1969 to July 1972.


MEAN SEA TEMPERATURE °C
14
12
10
8
6
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
1970
1971
1972

Similar trends have been noted in the Baltic sprat (Petrova, 1960) whereas in the Black Sea sprat maturation takes place in the summer months when the sea temperature is at its maximum and spawning occurs in the winter at temperatures between $5^{o}C-19^{o}C$ (Aslanova, 1954).

3.V. Maturation and size

Fulton (1904) observed that the male sprat matures at 84 mm. Robertson (1938) concluded that around the coast of Britain maturity is reached in the second year of life but he made no reference to the size. Johnson (1970) working on commercial samples from the Wash fishery found that the minimum size of maturation (size at which virgin fish mature) is between 73 and 79 mm and it is not certain whether he refers to standard or total length.

During the present analysis it was evident that maturity took place in their second year of life. The average minimum length at which maturation occurs was calculated using Burd's (1962) procedure for North Shields herring, which involves plotting the proportion of immature fish in each half-centimetre length group. The data for 1971 and 1972 were pooled together (Appendix 8 & Fig.33) and the resulting graph produced a fairly symmetrical ogive, from which the 50% level was read off as the average minimum size of maturation. The graphs for the two sexes were almost identical and the minimum size of maturity (i.e. first signs of gonadal development) was found to be 88–90 mm in both sexes.

This value is higher than that observed by Fulton (1904) and Johnson

Fig.33.

Fig.33. Percentage of 'mature' (reaching late stage II) females and males in each half centimetre length group.

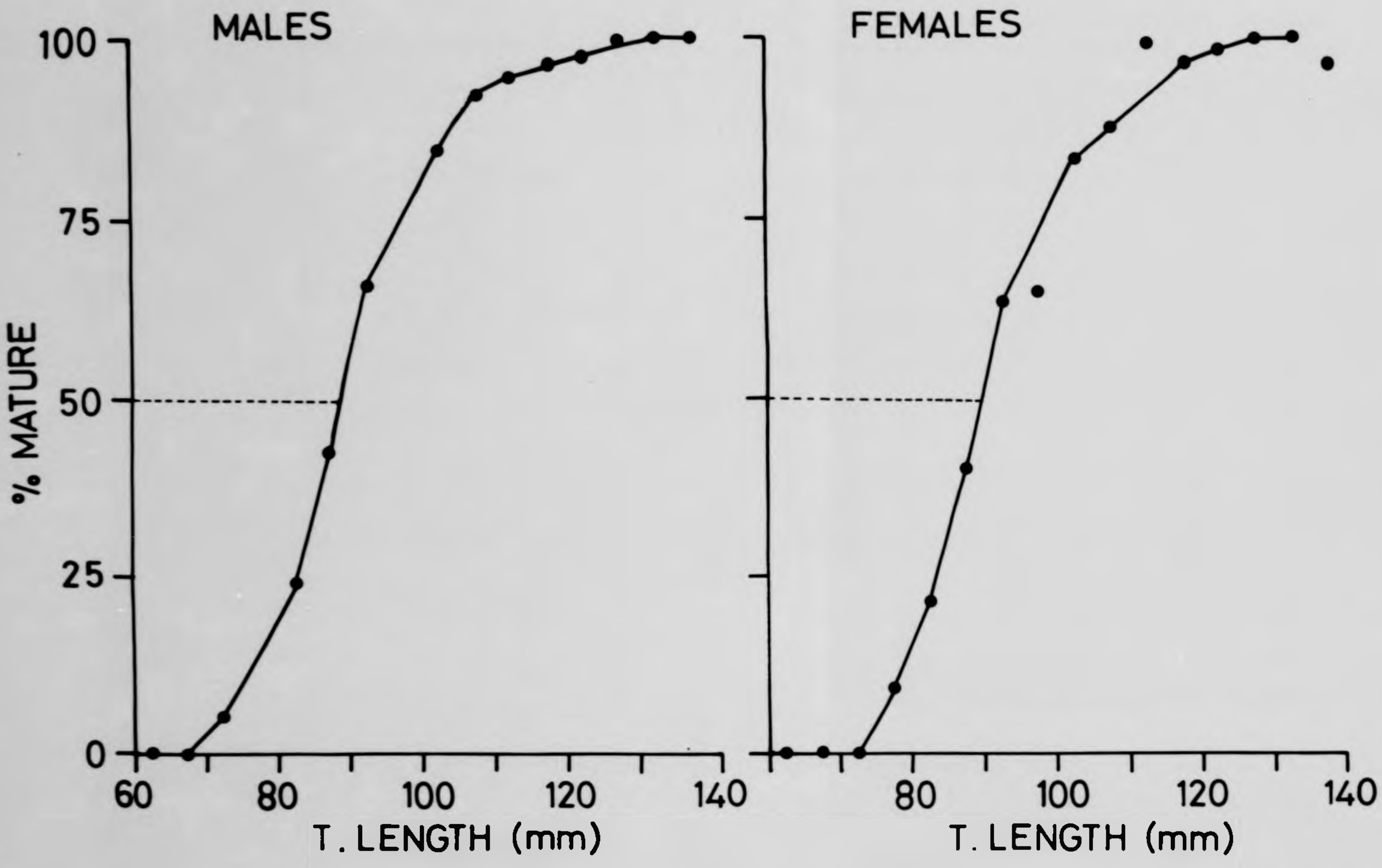

MALES
FEMALES
% MATURE
100
75
50
25
0
60
80
100
120
140
T. LENGTH (mm)
80
100
120
140
T. LENGTH (mm)

Fig.34.

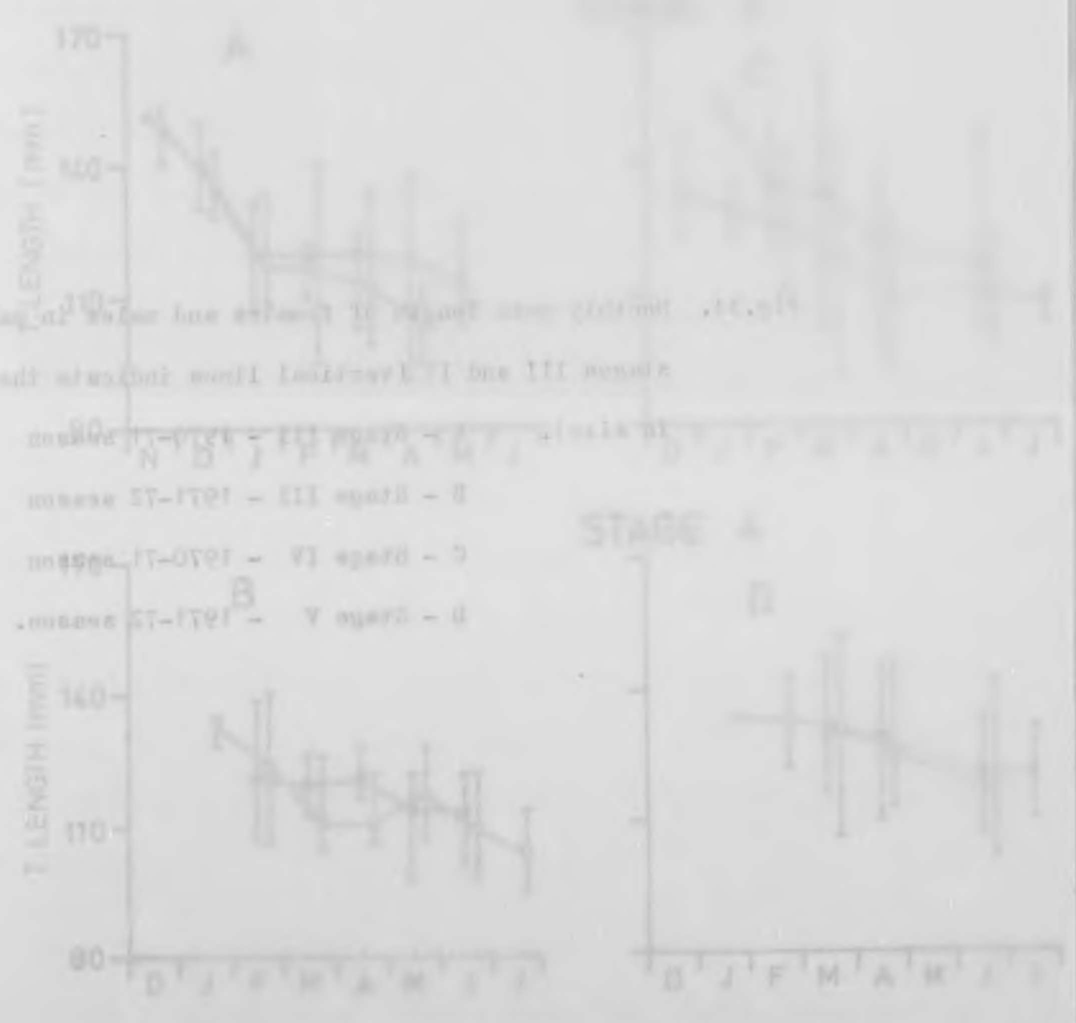
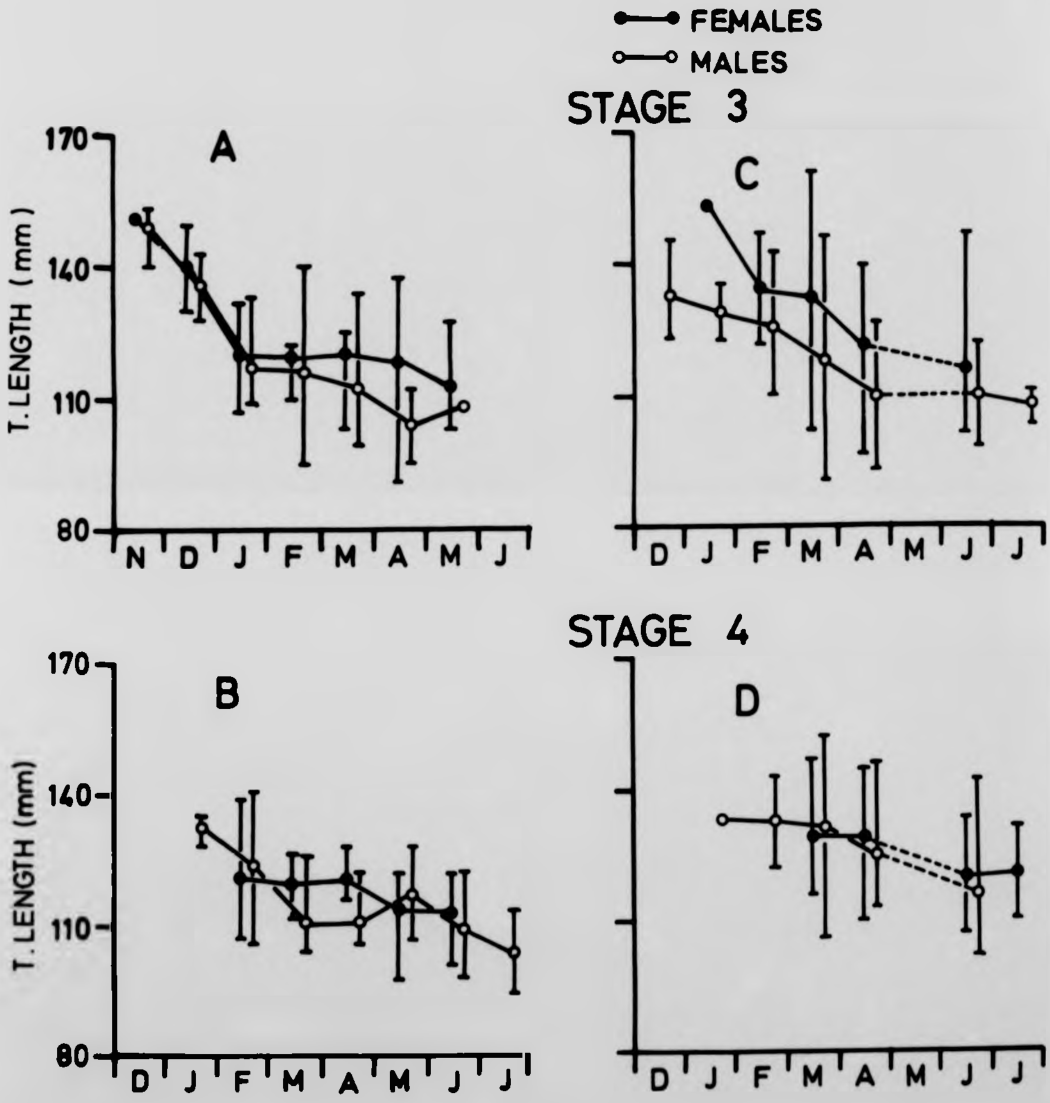


Fig.34. Monthly mean length of females and males in maturity stages III and IV (vertical lines indicate the range in size).

A - Stage III - 1970-71 season
B - Stage III - 1971-72 season
C - Stage IV - 1970-71 season
D - Stage V - 1971-72 season.


FEMALES
MALES
STAGE 3
A
C
170
140
110
80
T. LENGTH (mm)
N D J F M A M J
D J F M A M J J
STAGE 4
B
D
170
140
110
80
T. LENGTH (mm)
D J F M A M J J
D J F M A M J J

(1970), assuming that the latter is referring to total length. Minimum size of maturity is not an independent criterion, but is one that is closely associated with the other features of growth, food supply etc. of a particular stock or population.

It is evident from the data on the seasonal changes in macroscopic appearance of gonads and the gonosomatic index (Figs 30 and 31) that there is a tendency in males to reach maturity (Stage III and upwards) earlier in the season than in females. The mean length at maturity stages III and IV each month for both sexes during the 1971 and 1972 seasons was calculated separately (Fig. 34). It is evident that at any one stage of maturity not only do the males reach maturity earlier but the mean length is higher early in the season and that there is a progressive decrease as the season continues. Also the range in length increases towards the peak of the season. The majority of smaller fish reach maturity late in the season while the reverse is true for larger fish. Though this trend is general, exceptions are evident when some larger fish reach maturity late in the season.

3.VI. Sex-ratio

The overall sex-ratio was 109.16 females for every hundred males or 52.19% of females. This preponderance of females was not observed throughout the year and the seasonal changes in the percentage number of females in the population is shown in Fig. 35A (Table 18). The first appearance of stage IV males and females during the 1971 and 1972 is also shown in the diagram.

Fig.35A & B.

Fig.35A Seasonal changes in the percentage of females(sex-ratio)in the sprat populations (first appearance of stage IV females and males during the 1971 and 1972 spawning seasons are shown by vertical lines).

B Percentage of females in each age group (Pooled data from August 1970 to July 1972).

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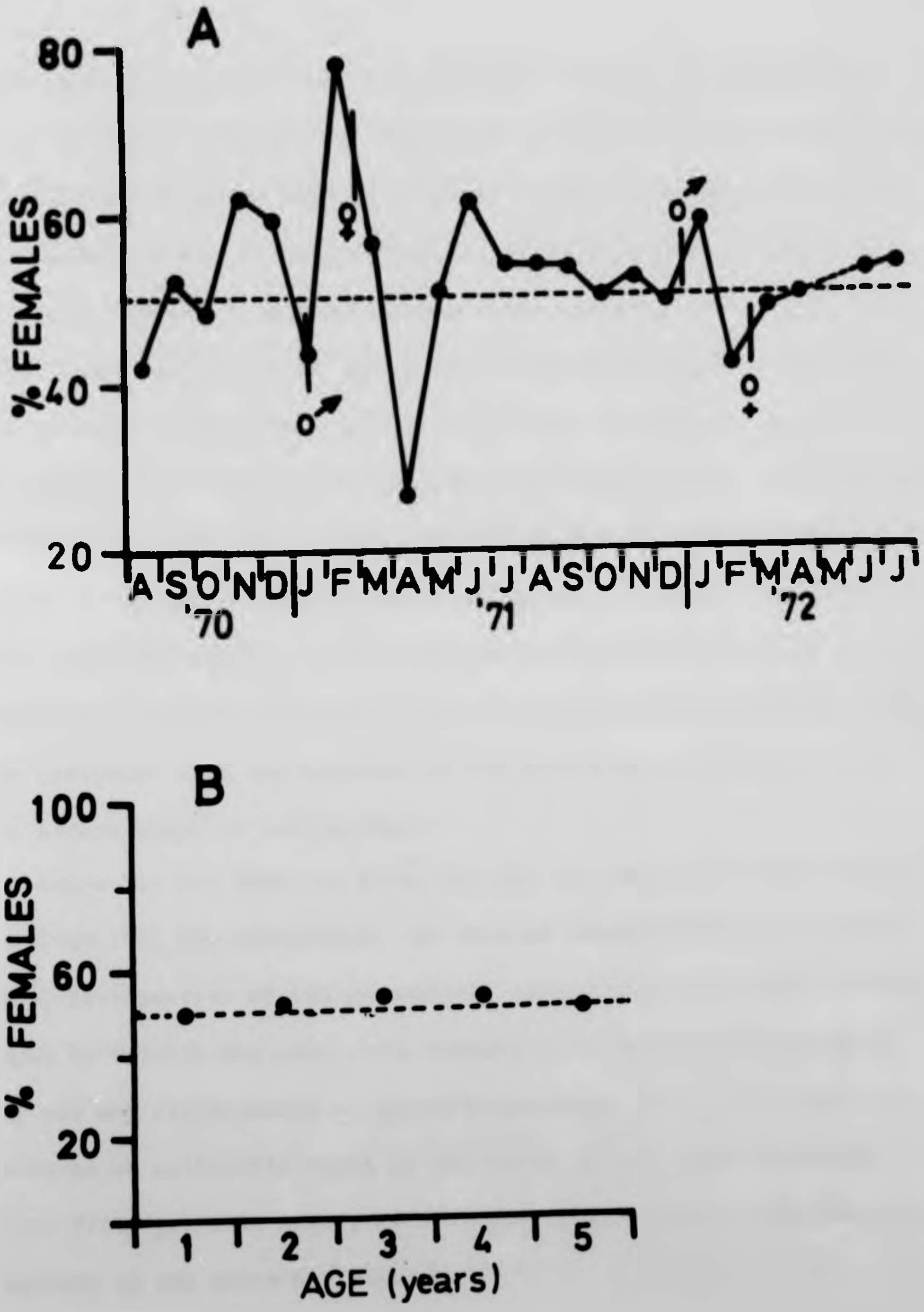
rance

971 and

l lines).

oled data



Since spawning does not take place in the area sampled and also because males tend to mature earlier, an emigration of mature males to the spawning grounds would result in an initial increase in the percentage of females, above the normal level, in the population. Within a short period of time females would emigrate to the spawning grounds and since they would tend to remain longer there because of the nature of spawning, and a simultaneous return of a certain proportion of the males from the spawning ground would cause an increase in the number of males in the population. After the peak of spawning there would be a gradual return of females into the area and since there is a general preponderance of females in sprats, the sex-ratio would reach and fluctuate a little over the fifty percent level of females. Changes in the sex-ratio during the 1972 season, too, showed similar trends with the exception that the decrease in the percentage of females occurred a little before stage IV was reached.

The sex-ratio for each age group for all the samples between August 1970 and July 1972 was calculated. In this computation fish of the same age group, irrespective of its year-class, were grouped together and this is thought to nullify any year-class variation in the sex-ratios, while bringing out any relationship of sex with age (Fig. 35B). It is evident that there is no noticeable trend in the sex-ratio with age, it being around the fifty per cent level, at all ages, from 1 to 5. This shows that the longevity of the sexes are similar.

3.VII. Type of spawning

Hickling and Rutenberg (1936) considered that a long spawning season and the presence of different size groups of yolked oocytes as evidence of multiple spawnings and the problem is discussed in detail by Clarke (1934) and West (1970 - unpublished thesis). In this study three lines of evidence are presented to support the serial nature of spawning.

First, histological examination of ovaries in stage III and IV (Fig. 36) shows that the yolked oocytes have a size range of 0.14 to 1.125 mm and that the nature and amount of yolk is not the same or nearly the same in all the oocytes. When this is compared with histological sections of ovaries of herring at comparable maturity (Bowers & Holliday, 1961) the difference is at once obvious. It is very unlikely that all the oocytes in different stages of maturity would be shed at once.

Second, egg diameter measurements of yolked ova from fish in stage III and IV (Fig. 37) clearly show the presence of more than one distinct mode. If all the eggs were shed simultaneously the eggs destined to mature would be withdrawn from the general egg stock in a single group sharply distinguishable at least by late II or early stage III from the stock of reserve oocytes. But when spawning is serial there will be no sharp separation between the general stock of eggs and the maturing ones and the latter will also show a multimodal distribution because they are not taken out of the general stock all at once.

Third, it has been shown that sprats in this area have a lengthy

Fig.36.

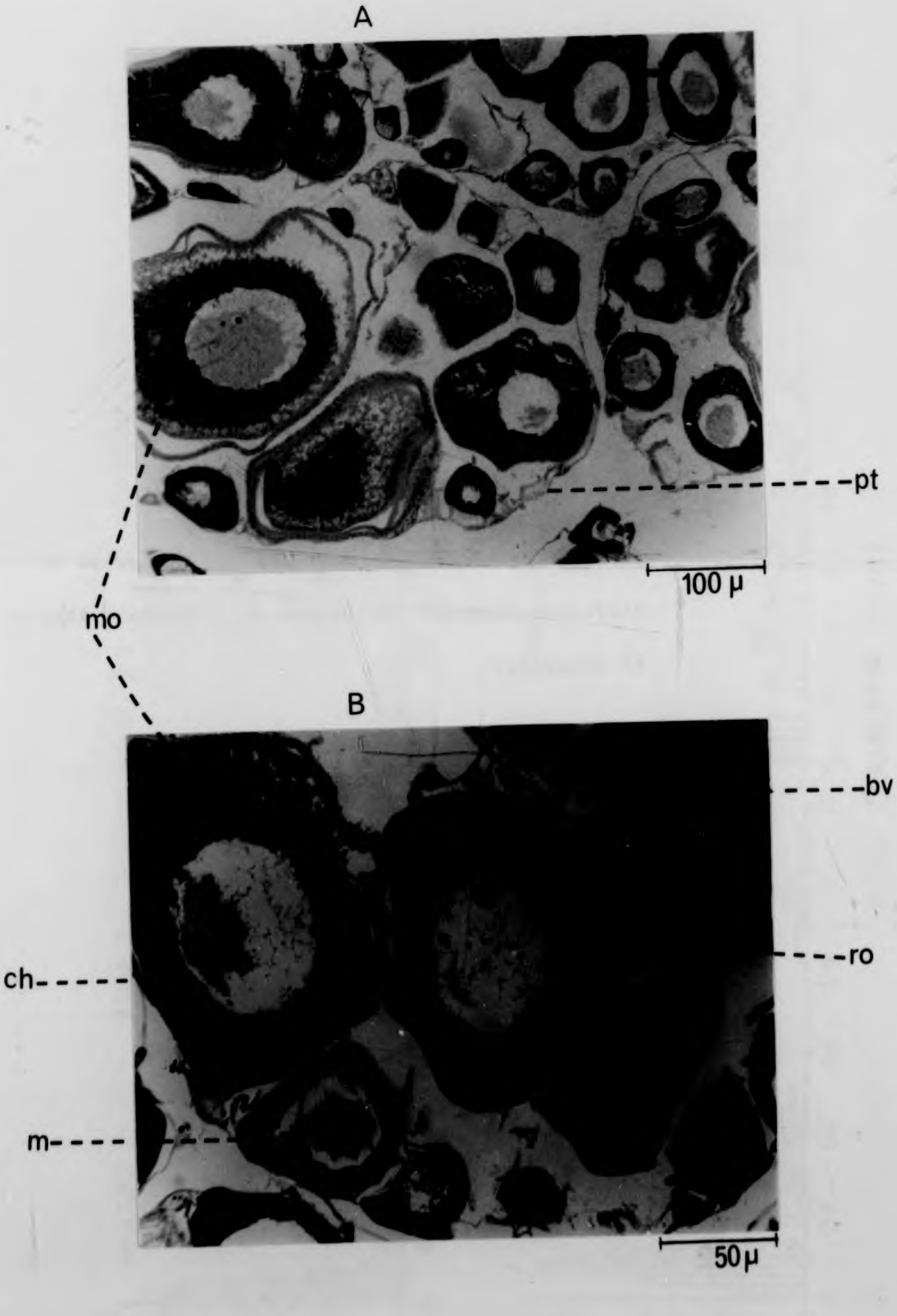
Fig.36.

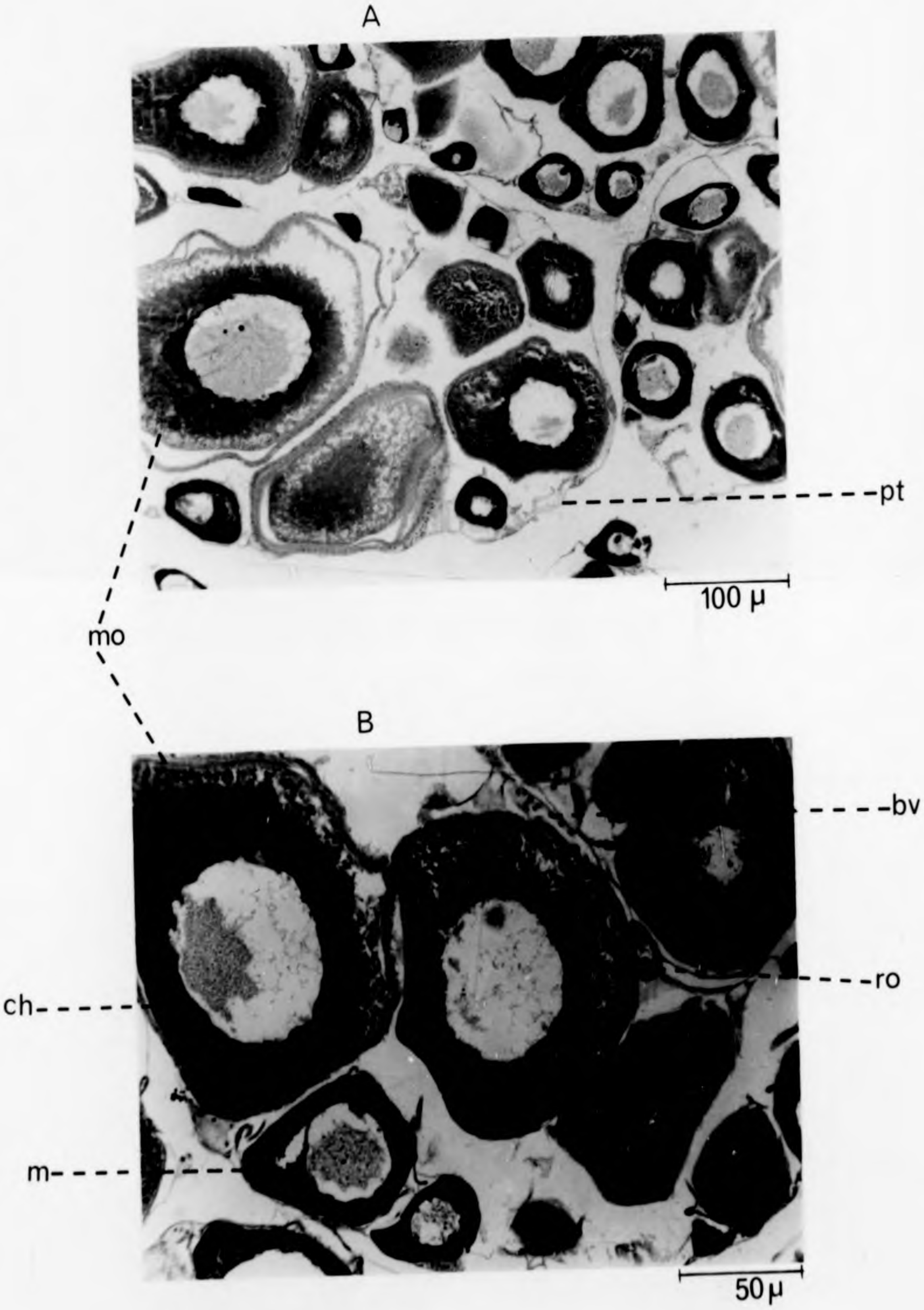
Fig.36. Histological section of ovaries in stage III and IV (Stain - haematoxylin and eosin).

A. Ovary in Stage III

B. Ovary in Stage IV

m - MATURING OOCYTES
mo - MATURE OOCYTES
ro - RESTING OOCYTES
pt - PRIMARY THECA
ch - CHORION
bv - BLOOD VESSEL

A
pt
100 μ
mo
B
bv
ch
ro
m
50 μ


A
pt
100 μ
mo
B
bv
ro
ch
m
50 μ

and IV

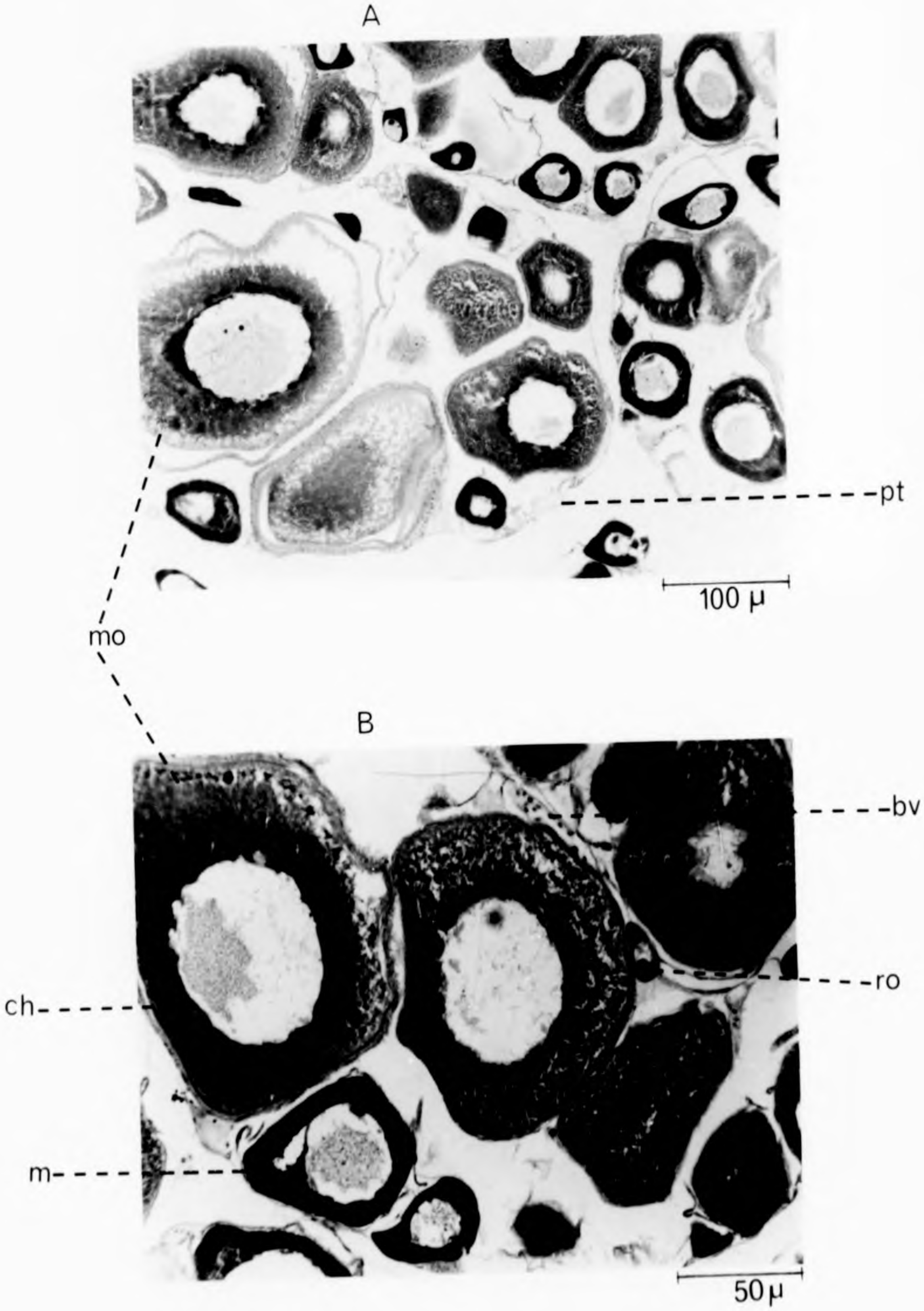
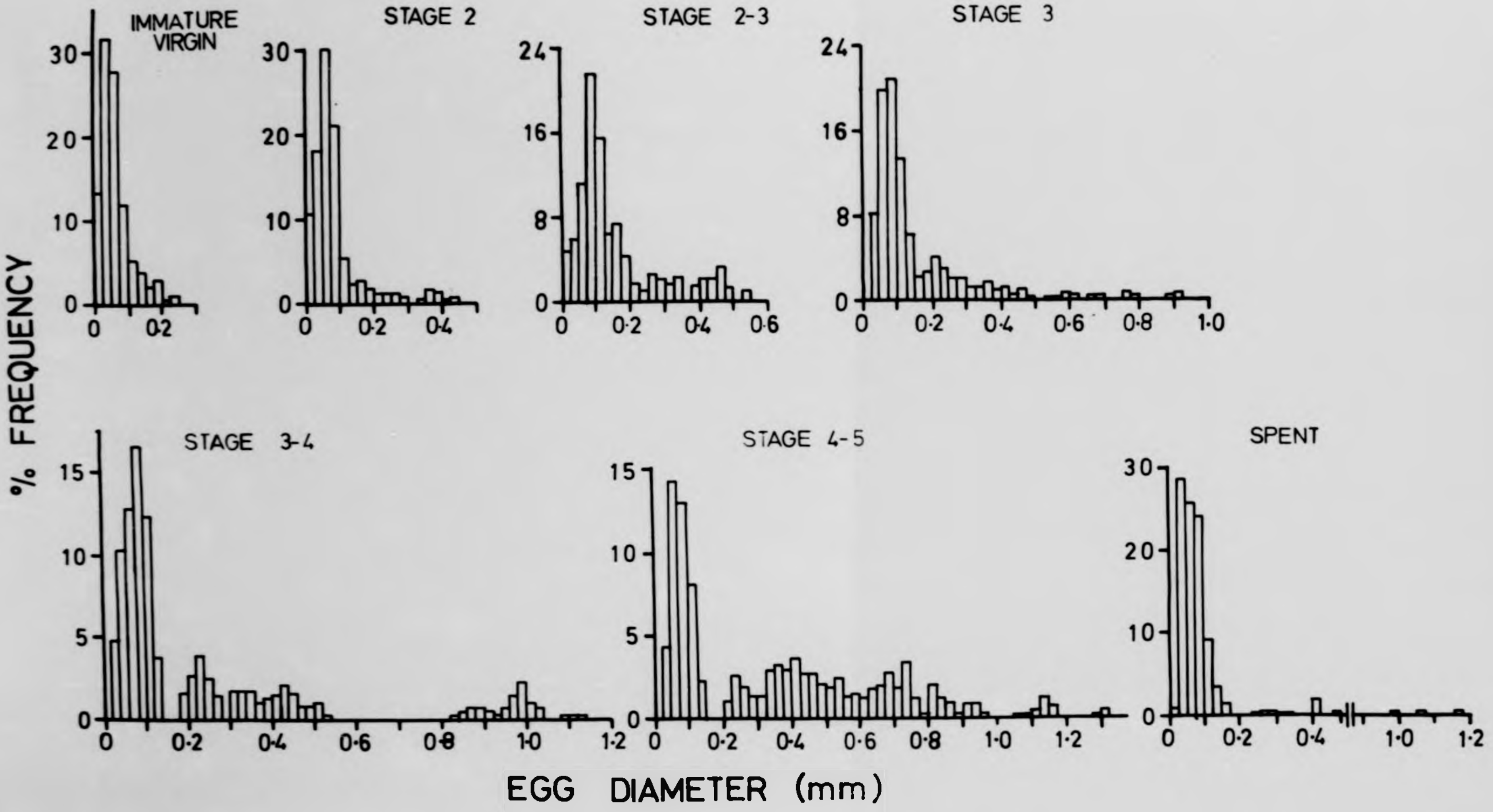


Fig.37.

Fig.37. Percentage frequency distribution of oocytes of different diameter in ovaries at different stages of maturity.

Fig.37. Percentage frequency distribution of oocytes of different diameter in ovaries at different stages of maturity.

Fig.37. Percentage frequency distribution of oocytes of different diameter in ovaries at different stages of maturity.


IMMATURE VIRGIN
STAGE 2
STAGE 2-3
STAGE 3
STAGE 3-4
STAGE 4-5
SPENT
% FREQUENCY
EGG DIAMETER (mm)
0
10
20
30
0·2
0·4
0·6
0·8
1·0
1·2
8
16
24
5
15

spawning season, the duration of which is around six months, and as postulated by Hickling & Rutenberg (1936) this would tend to be associated with serial spawning.

Thus all the evidence confirms that the sprat of the Scottish west coast is a serial spawner like the Black and Baltic Sea sprats.

Having dealt with the evidence in favour of serial spawning in sprat, an attempt is made in the following section to find out how many batches of eggs are shed in a season. To estimate the number of batches of eggs shed, the assumption is made that only ova in the most advanced state of development (size group) are shed at any one time (Clarke, 1934; McGregor, 1957) and the number of eggs in this group is taken to represent the number shed per batch. Therefore the ratio of the total number of yolked oocytes in the ovary to the number in the most advanced state of maturity is regarded as the number of batches of eggs shed per season.

There is no reason to suppose that the older and larger fish would deposit more batches of eggs than the smaller ones, since the older and larger fish are more fecund and have more eggs in any one batch. The fecundity and the number of oocytes in the largest size group were determined in 74 individuals. The data thus obtained were divided into classes and the average number of batches shed in any one season calculated. The results show (Table 19) that the number of batches of eggs shed vary between 7 and 10.

Aslanova (1954) concluded that the Black Sea sprat eggs are released in 7 to 9 batches, and Kazanova (1963) found that the Baltic sprat

Table 19.

RATIO OF THE NUMBER OF OOCYTES IN THE LARGEST SIZE GROUP TO THE TOTAL NUMBER OF YOLKED OOCYTES IN THE OVARIES OF MATURE SPRAT.

Length class cm	Number of observations	FECUNDITY		RIPE EGGS		Number of times of spawning
		Range	Mean	Range	Mean	
10.0 - 10.4	2	8,700 - 10,100	9,400	890 - 1,300	1075	8.74
10.5 - 10.9	6	8,300 - 11,833	10,424	900 - 1,800	1347	7.74
11.0 - 11.4	9	9,550 - 20,033	13,146	966 - 2,637	1474	8.91
11.5 - 11.9	12	12,100 - 20,000	15,347	904 - 3,900	2184	7.03
12.0 - 12.4	10	13,800 - 24,666	20,002	1,666 - 3,700	2841	7.01
12.5 - 12.9	10	17,000 - 34,950	26,242	2,150 - 4,920	3724	7.04
13.0 - 13.4	6	23,650 - 32,000	28,127	3,175 - 5,233	3088	9.10
13.5 - 13.9	8	23,800 - 39,900	32,978	3,025 - 4,500	3476	9.48
14.0 - 14.4	4	33,200 - 46,600	39,212	3,533 - 6,650	4733	8.28
14.5 - 14.9	1	-	41,275	-	4900	8.42

discharges its eggs in about nine batches, while Petrova (1960) concluded that in the latter sub-species the number of batches ranged between six and nine.

3.VIII. Fecundity

Nikolskii (1953), in formulating the laws governing the dynamics of fish productivity, pointed out that fecundity was one of the principal characteristics especially with regard to replacement problems. For species with a definite annual spawning season, such as herring, sprat, whiting etc. fecundity may be defined as the number of ripening eggs found in the female just prior to spawning. This definition will not be valid for most tropical species which breed throughout their lives (Peters, 1963). Lowe (1955) defined fecundity for those species as the number of eggs produced during the life time of an individual.

The term relative fecundity has been used in order to make observations on fish of different size more comparable and is defined as the number of maturing eggs found in the ovary just prior to spawning, per unit weight or length of the fish. Bagenal (1967) discusses the advantages and disadvantages of the use of relative fecundity.

In the present study the first definition of fecundity has been used. Sprat have been shown to shed their eggs in batches and in such species of fish, oocytes destined to mature are not separated from the reserve oocytes all at once and for fecundity studies the mature ones have to be separated from the reserve. A study of distribution of egg diameters at each stage of maturity showed (Fig.37) that separation of oocytes destined to mature and be shed in the current season from the reserve oocytes takes place at late stage III. The resting oocytes have a diameter ranging from 25 – 125 μ and by using a sieve of mesh size 112 μ (allowing for shrinkage in Gilson's fluid) the reserve oocytes were removed from the sample.

Fecundity of 74 fish, 29 in 1971 and 45 in 1972 were determined. The total fecundity varied between 8,700 and 46,600 for fish ranging in length from 95 and 147 mm, and in weight from 4.99 and 22.18 gm. All fish were between one and five years old.

There was a general tendency of fecundity (F) to increase with growth, that is with length (L), and weight (W) and also with increasing age (A). Statistical relationships of fecundity to the above parameters were obtained and are given below with the correlation coefficients (Figs 38 & 39).

(a) To weight:-

$$F = 1644.3788\ W + 85.4374 \quad (r=0.9995)$$

(b) To length:-

$$F = 0.0002\ L^{3.8131} \quad (r=0.8414).$$

or $\log F = -3.6259 + 3.8131 \log L$

*(c) To age:-

$$F = 8719.09\ A - 916.58 \quad (r=0.9989).$$

---

* Age was always determined in whole numbers, for example I, 2, 3 etc. Hence in the equation 'A' refers to a discontinuous entity.

Fig.38.

Fig.38. Relationship of fecundity to body weight (gutted) and total length of sprat.

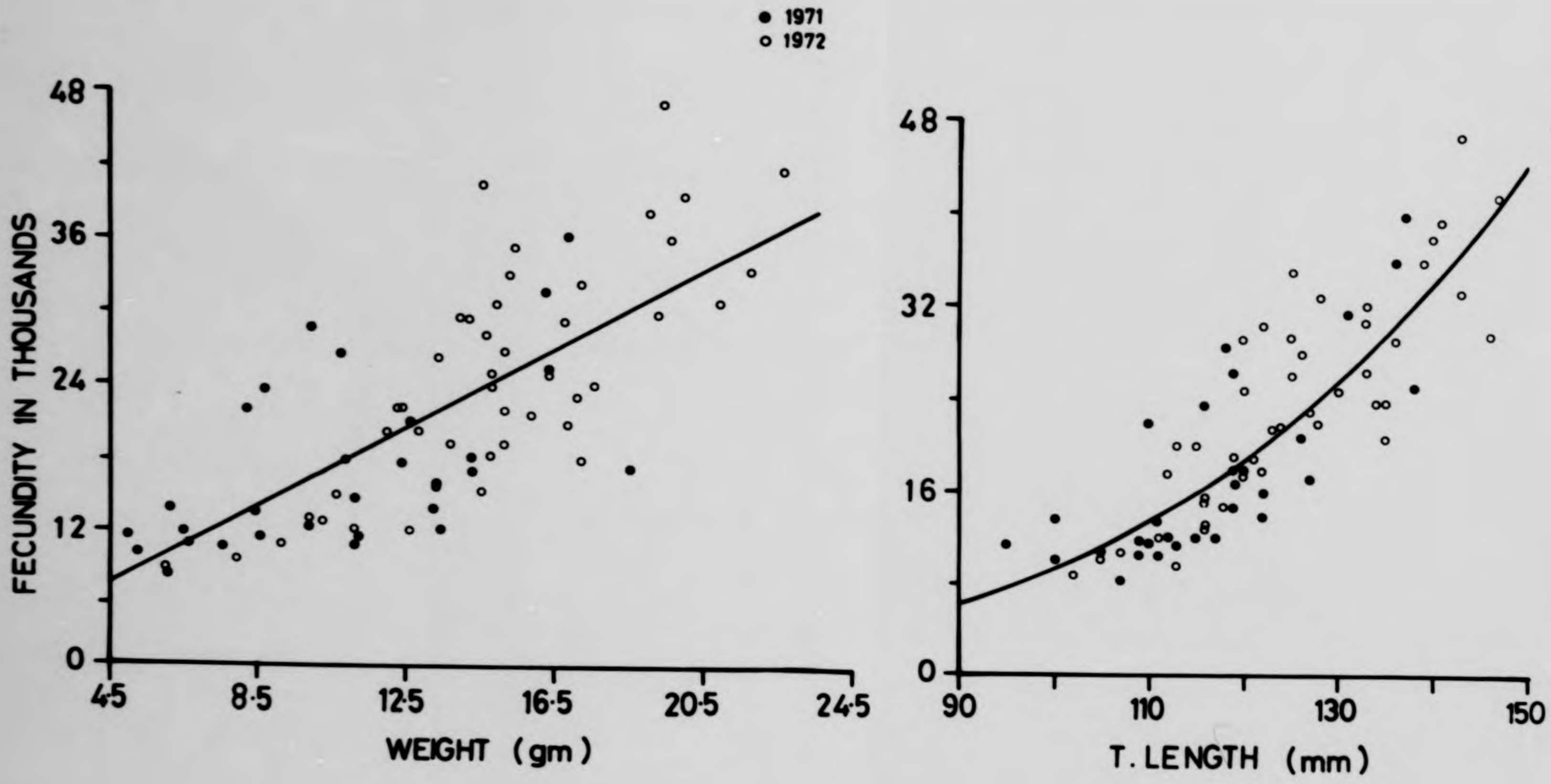
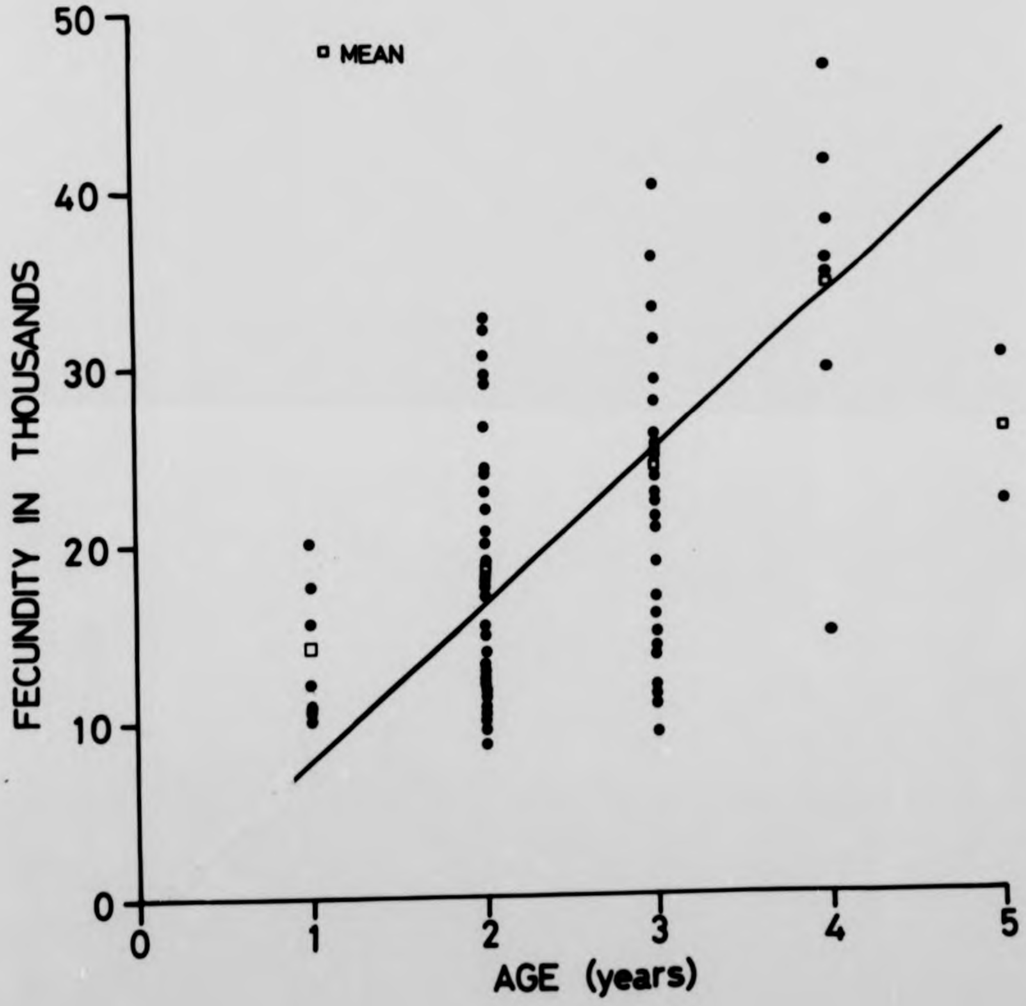

● 1971
○ 1972
FECUNDITY IN THOUSANDS
48
36
24
12
0
4·5
8·5
12·5
16·5
20·5
24·5
WEIGHT (gm)
48
32
16
0
90
110
130
150
T. LENGTH (mm)

Fig.39.

Fig.39. Relationship of fecundity to age of sprats.



□ MEAN
FECUNDITY IN THOUSANDS
50
40
30
20
10
0
0
1
2
3
4
5
AGE (years)

The data also show that fecundity is variable in individuals of the same length or weight or age, the variation being smaller in the smaller than larger specimens.

Though an increase in fecundity with age has been observed for many species of fish, the exact statistical nature of the relationship is available only for a few species. May (1967) found it to be curvilinear for the Atlantic cod, over a range of 27 years, while Bagenal (1957) and McGregor (1957) found it to be linear over a range of 7 years for the long rough dab from the Clyde estuary and the Pacific sardine respectively. It is possible that this relationship is curvilinear when a very wide range of ages are considered, that is in species with a long life-span, whereas in short lived species like the sprat fecundity probably bears a linear relationship to age.

There is conflicting evidence as to whether the observed increase in fecundity with age in species of fish, that age in itself apart from its relation to length,has an effect on the number of eggs. Simpson (1951) showed that age has no effect on fecundity in plaice and the same conclusion was reached by Bagenal (1957) for the long rough dab, but the reverse has been observed for herring (Bridger, 1961; Anokhina, 1963).

In order to examine whether fecundity in sprat is affected by age the data were analysed in two forms. The mean fecundity for each half centimetre length group was calculated for each age group (Table 20) and also its variation within each length group with increasing age was examined (Fig.40).

Table 20.

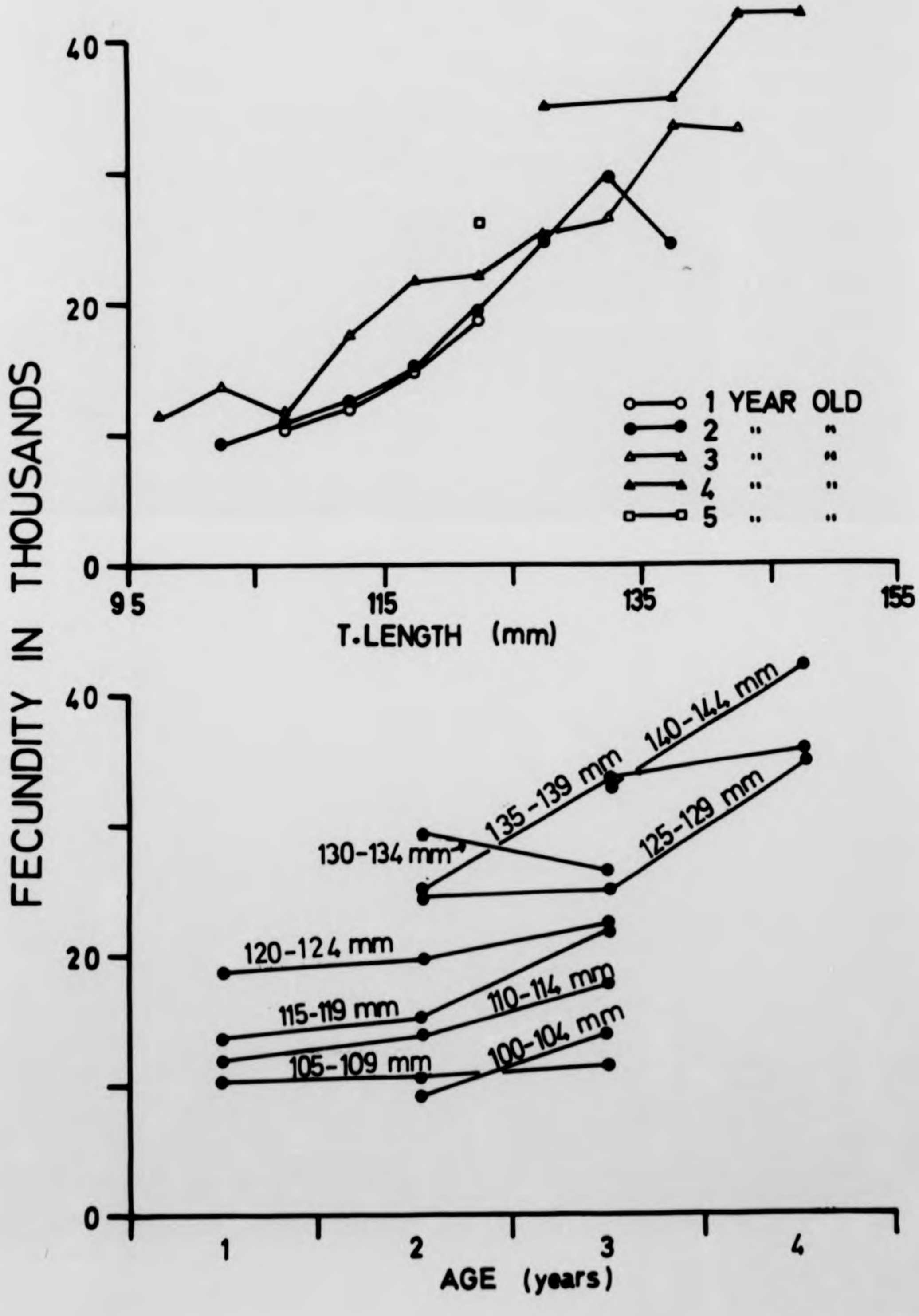
MEAN FECUNDITY AT EACH HALF-CENTIMETRE LENGTH GROUP, IN SPRAT OF DIFFERENT AGE GROUPS.

(Numbers sampled is given in parenthesis).

Length Group—mm	AGE IN YEARS				
	1+	2+	3+	4+	5+
95 - 99	-	-	11,425 (1)	-	-
100 -104	-	9,400 (2)	13,700 (1)	-	-
105 -109	10,458 (2)	10,666 (1)	11,333 (3)	-	-
110 -114	12,000 (2)	13,850 (6)	17,650 (2)	-	-
115 -119	13,800 (3)	15,028 (6)	21,948 (5)	-	-
120 -124	18,920 (1)	19,577 (5)	22,100 (3)	-	26,025 (2)
125 -129	-	24,735 (5)	24,888 (3)	34,950 (1)	-
130 -134	-	29,686 (3)	26,569 (3)	-	-
135 -139	-	24,491 (3)	33,626 (3)	35,700 (1)	-
140 -144	-	-	33,200 (1)	42,200 (2)	-
145 -149	-	-	-	35,400 (2)	-

Fig.40.

Fig.40. Relationship of mean fecundity, to length of fish in different age groups and to age at a given length.


FECUNDITY IN THOUSANDS
40
20
0
95
115
135
155
T.LENGTH (mm)
1 YEAR OLD
2 " "
3 " "
4 " "
5 " "
40
20
0
1
2
3
4
AGE (years)
140-144 mm
135-139 mm
130-134 mm
125-129 mm
120-124 mm
115-119 mm
110-114 mm
105-109 mm
100-104 mm

Though the number of observations in certain categories of Table 20 are far from satisfactory, from Fig.40 very distinct trends become evident. It is clear that fecundity tends to increase with length, but at the same time at any given length fish in the higher age groups had a higher fecundity in 25 instances. Further, it appears that the increase in fecundity from one to two year old individuals, at any given length, is slight, whereas the increase between ages, after two years, is large. It is also evident from Fig.40 that with increasing age there is an increase in fecundity at any given length. The increase appears to be more marked in the older age groups and also at higher lengths. Thus it is evident that in sprat, age by itself effects the fecundity, like in herring.

The fecundity of the Black Sea and Baltic sprat are lower than that of British sprat. In the Black Sea sprat fecundity varies between 1,000-31,000 in fish of 45 mm to 116 mm in length (Aslanova, 1954) while in the Baltic sprat it varies between 5,768-34,290 in fish of 97 mm to 133 mm in length (Petrova, 1960). The higher fecundity in the Scottish west coast sprat is probably due to its bigger size in comparison to the other two sub-species.

3.IX. Discussion

Aspects of the reproductive biology of the sprat have also been dealt with in the earlier sections. It has been shown in section 2 that it has a longevity of 5 to 6 years and an asymptotic length of 164 mm. When its reproductive biology is critically analysed it becomes evident that the main adapative feature is the tendency to increase its reproductive potential and also enhance the survival of the offspring, The sprat reaches sexual maturity in its second year of life, thus making it capable of reproducing during more than 80% of its life span. Beverton (1963) estimated that for herring the ratio of the length at minimum size of maturity to its asymptotic length is 0.80, that is the minimum size of maturity is reached when an individual attains a length of 80% of its asymptotic length. A similar calculation for the West Coast sprat gives a value of 54.9%. Thus it is clear that the sprat reaches sexual maturity when it is just over half its asymptotic length.

Since the sprat has a very high fecundity for its size, if all the eggs were to mature simultaneously, the enormous increase in volume during the final maturation would make it impossible for the ovary to contain all the oocytes. Naturally, if the fecundity is to be maintained at a high level, a maturation of oocytes by groups become an absolute necessity and the eggs must ripen and be extruded intermittently. If the latter is to take place, then time should be given for the immature oocytes to mature, thereby resulting in a prolonged spawning period.

The periodic spawning will have a definite advantage in producing a succession of larval fish, thus allowing time for one batch to disperse from the spawning area before the succeeding batch takes its place. This will avoid overcrowding and competition for food which could possibly become limited under unfavourable conditions. Finally, this would prevent the young being subjected to potentially unfavourable conditions all at once.

The minimum size at maturity in the Scottish west coast sprat is significantly higher than that of either the Wash sprat or that of the two sub-species in the Baltic and the Black Sea. Beverton (1963) demonstrated that in engraulids and clupeids the minimum size of maturity is related linearly to the asymptotic length. Thus it is probable that because of the higher asymptotic length of the West Coast sprat in comparison to others, its minimum size of maturity would be correspondingly higher. In general, minimum size at maturity is also related to the longevity and the rate of growth. When the sexes differ in longevity, one with the lower longevity tend to have a higher rate of growth and lower minimum size of maturity and vice versa. In the West Coast sprat the growth rate and longevity of the sexes have been shown to be almost identical and hence, as expected, both sexes have the same minimum size and age of maturation.

In sprats the spawning season is long and when the winter conditions prior to maturation are unusually cold, maturation and therefore spawning is prolonged. In these circumstances a certain proportion of the larvae will not metamorphose before the winter. It is possible that larval mortality under such conditions is higher than normal. It is suggested that comparative fecundity studies in a year following a late spawning season and in a normal year, would be of special interest. This might determine whether there is an appreciable increase in fecundity in a year following a bad winter, thereby compensating for a low larval survival in the population. In addition, if such an increase does take place, is it achieved by a mean increase in the size of the spawning population or by a decrease in the size of the eggs and a corresponding increase in the number for a fish of a particular size.

Section 4

FOOD AND FEEDING.

4.I. Introduction

Despite more than 50 years of research on the food of fishes, few comparative studies exist on the feeding relationships of species which occur together or of dietary relationships within species at different stages of growth. The little work done up to now has been mainly on species which are found together in fresh water rivers and lakes (Hartley, 1948; Larkin, 1956; Keast, 1970). In the marine environment, Gibson (1968, 1972) investigated the dietary interrelationships of shore fishes.

Of the two species in the present work, the food and feeding habits of herring in their adult stages have been studied extensively by Hardy (1924), Jespersen (1928) and Savage (1931, 1937). Hardy reported that *Ammodytes*, hyperid amphipods, schizopods and copepods were most important in the diet of the English east coast herring. Brook & Claderwood (1886) after an extensive examination of food of herring from the Scottish west and east coast, concluded that copepods were important, and hyperid amphipods unimportant in the diet of the West Coast herring. These results were in agreement with those of Scott (1887).

Hardy (1924) also examined the food of young herring from the Thames Estuary and concluded that the diet was mainly crustaceous. Lebour (1921b, 1924) made a qualitative analysis of the food of herring at different stages of growth from the Plymouth area. Marshall *et al*.

(1939), working on Clyde young herring, found that copepods formed the bulk of the diet, while euphausiids, cladocerans, *Sagitta* and *Oikopleura* were taken in small numbers.

Food of Clyde larval herring was studied by Bainbridge & Forsyth (1971), and that of larval and post-larval was studied by Marshall *et al*. (1937) in the Clyde, Bowers & Williamson (1950) in Manx waters and Bhattacharya (1957) in the northern North Sea.

Lebour (1921b) and Robertson (1938) are the only authors to have studied the food habits of sprat. Lebour (1921b) noted that sprats with yolk-sacs contained diatoms in the gut and after absorption of yolk they also fed on larval copepods. From a size of 80-90 mm the diet consisted chiefly of copepods, larval molluscs and cirripedes. Robertson (1938) based his study on samples from a number of areas, obtained over short periods at different times of the year. In most of the areas copepods constituted the major part of the diet, supplemented by cladocera, balanoid cyprids and decapod larvae. It is evident that there is a serious lack of research of the food and feeding habits of sprat at any stage of the life history.

It has been stated earlier that herring and sprat are two closely related species, and tend to spend their early years of life shoaling together, or in close vicinity of each other, in inshore waters. The present study was made in an attempt to understand the comparative food and feeding habits of juvenile herring and sprats and so to evaluate the existence of any competition for food between the two species either as 0-group or later in life, and also to investigate any change with age in feeding habits. The data for O-group fish are therefore treated separately from that of older fish.

4.II. Material and methods

Fish were obtained and treated as stated in Section 1. IV. Thirty to forty fish of each species per month from each of the O-group and older age groups were gutted. The stomachs were opened, and the contents from both the pyloric and cardiac portions of the stomachs were teased out and stored in 4% formalin in individual vials for examination at a later date.

The contents of each stomach was studied individually under a binocular microscope and identified up to the 'order' level. 'Type' specimens were removed for species identification. When the contents were too large for all items to be counted, those that were found in smaller numbers were identified, counted and removed and the rest was sub-sampled. The total was calculated from four or five such sub-samples.

A stomach was said to be empty if there was no identifiable food material present. Different authors have used different methods to quantify seasonal changes in the dietary composition of fish, see review by Hynes (1950). In the present project the method developed by Hardy (1924) has been used. According to this method, to obtain the relative importance of the food items the size of the individual items are taken into consideration. All the small organisms viz. copepods, cladocera, decapod and bivalve larve, Oikopleura, Sagitta etc. were given unit value

(1 point) per organism regardless of size, while fish larvae, mysids, euphausiids, amphipods etc. were given higher values because they were larger. Depending on the dry weight of fish larvae, mysids, euphausiids and amphipods they were allotted so many copepod points.*

The relative importance of the different organisms in each month was obtained by finding for each food type the percentage of feeding fish containing that species and multiplying by the average number of that species in each fish feeding on it. The resulting figure is then shown as a percentage of the total of all the results for that month. This gives the approximate relative importance of the different organisms in the diet for each month, but it does not allow one to compare the relative importance of different organisms to the fish, taking the year as a whole, since the feeding intensity varies from month to month. This is overcome by weighting these results by the percentage feeding in each month. The percentage of empty stomachs and the average number of points per feeding individual was also calculated for each monthly sample.

In O-group fish the food items were devoid of any fish larvae, mysids, euphausiids and amphipods and as a result all the items were given unit

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* According to the old classification mysids and euphausiids were grouped together as schizopods. This term has been used by a number of workers and in the present study for purposes of comparison and also for convenience mysids and euphausiids were grouped together, as schizopods in Figs 43-46 and Appendices 9-14.

value, thus making the final analysis straightforward. The food of fish one year and older were analysed from April 1970 to March 1972, while those of 0-group herring were from April to March and 0-group sprat from July to March, for year-classes 1970 and 1971. The data for the two years of analysis were pooled together in all instances. A total of 822 1+ and 790 0-group herring and 1018 1+ and 498 0-group sprats were examined. All the samples considered in the analysis were obtained between 1000-1500 hrs.

On the 9th and 10th of August 1972, fish were caught at intervals of 3 to 4 hours to study the diurnal rhythm of feeding activity. The method of capture was by bottom trawling during the daylight hours and by mid-water trawling during the dark hours. When the net was hauled fish were immediately preserved in 70% alcohol. The sample size was varied according to the number of fish caught in each trawl. When more than 100 were caught a random sample of 70 to 80 fish were taken. Each fish was gutted, weighed and the stomach contents teased out into a vial and weighed to the nearest mg. The number of empty stomachs in each sample was also noted. Each trawl was of 40 minute duration and the time of capture was taken to be mid-way between the start and the end of the haul. During the survey, the light at the sea bottom was measured at the end of each haul using an underwater light meter (Craig & Lawrie, 1962).

Evidence for the existence of a diel rhythm of feeding in fish could be obtained either by considering the volume of food taken for a specified number of individuals at given intervals during a 24 hour period (Marshall et al., 1939) or by plotting the mean weight of the stomach contents expressed as a percentage of the body weight with time (Keast, 1970; Edwards et al., 1971) or by estimating the amount of food in different parts of the alimentary canal at given periods of time (Kruuk, 1963). In this investigation, the second method, together with the percentage of empty stomachs at 3 to 4 hourly intervals for a period of twenty four hours, was adopted.

4.III. Seasonal cycle and intensity of feeding

A very high percentage of 0-group fish were feeding throughout the year. Among 790 herring and 498 sprats only 1.8% and 0.7% were not feeding respectively. Among the older age groups 20.9% herring and 22.0% sprats had no food in their stomachs. A seasonal pattern in feeding activity is apparent (Fig.41 and Appendices 11 & 12) at this stage of life in both species. The percentage of feeding individuals tended to decrease from August-September, reached a minimum during the winter months, and thereafter a progressive increase took place during the spring. During the summer months nearly all the individuals tended to feed. Though this is the general pattern observed in both species (Fig.41) there appear to be yearly differences. The biggest discrepancy between the two years occurred in December, when in 1970, 65% of sprats were not feeding while in 1971 only 15% were found to be so.

The percentage of feeding individuals essentially gives an indication of the main feeding season. To study the seasonal changes in feeding intensity or activity in detail, the number of points (see earlier) per feeding individual in both 0-group and older fish were considered.

Fig.41A & B.

Fig.41A. Seasonal changes in the occurrence of empty stomach of clupeids over a year old, from April 1970 to March 1972.

B. Mean monthly percentage occurrence of empty stomachs for a period of twelve months.

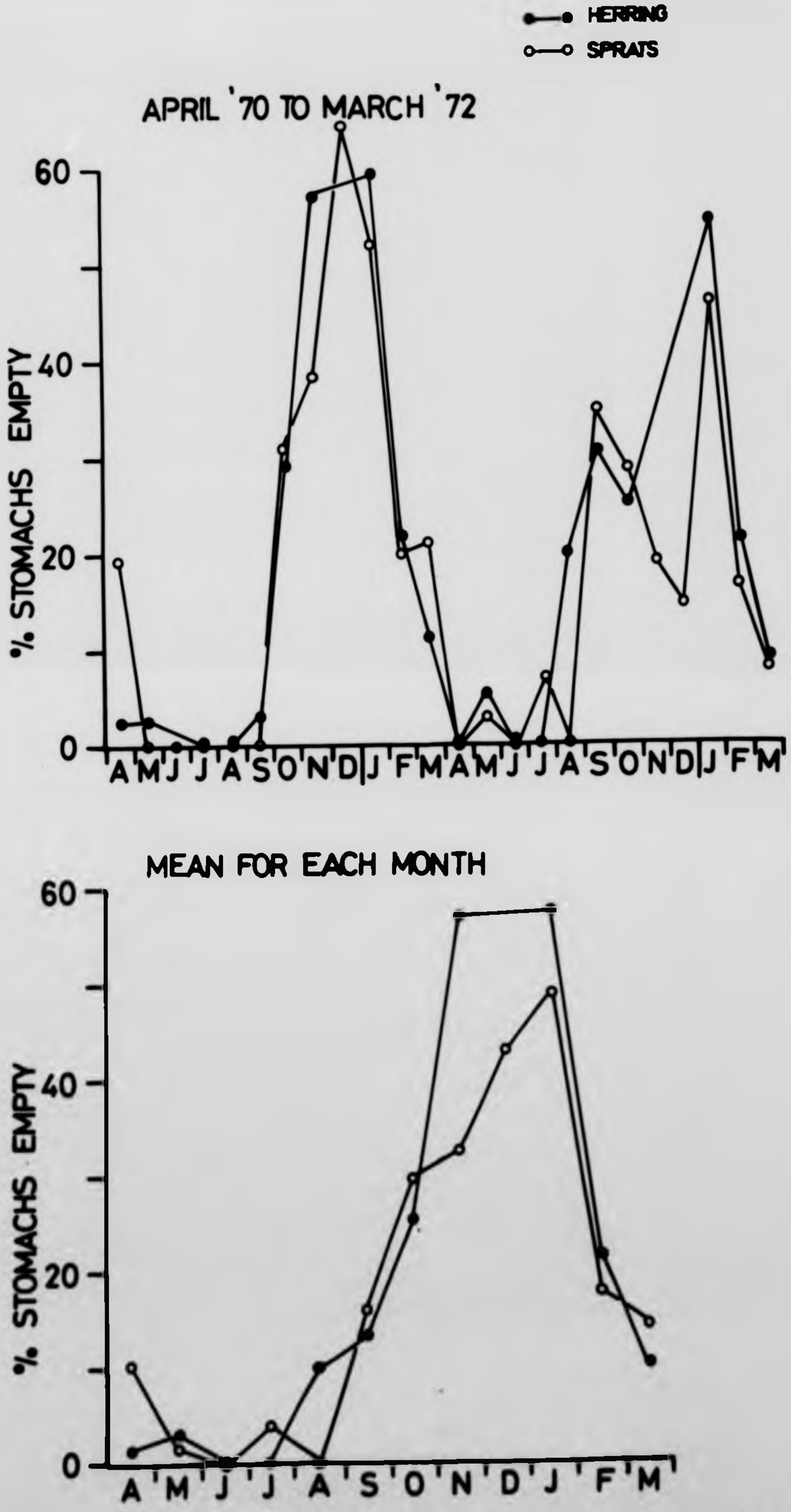
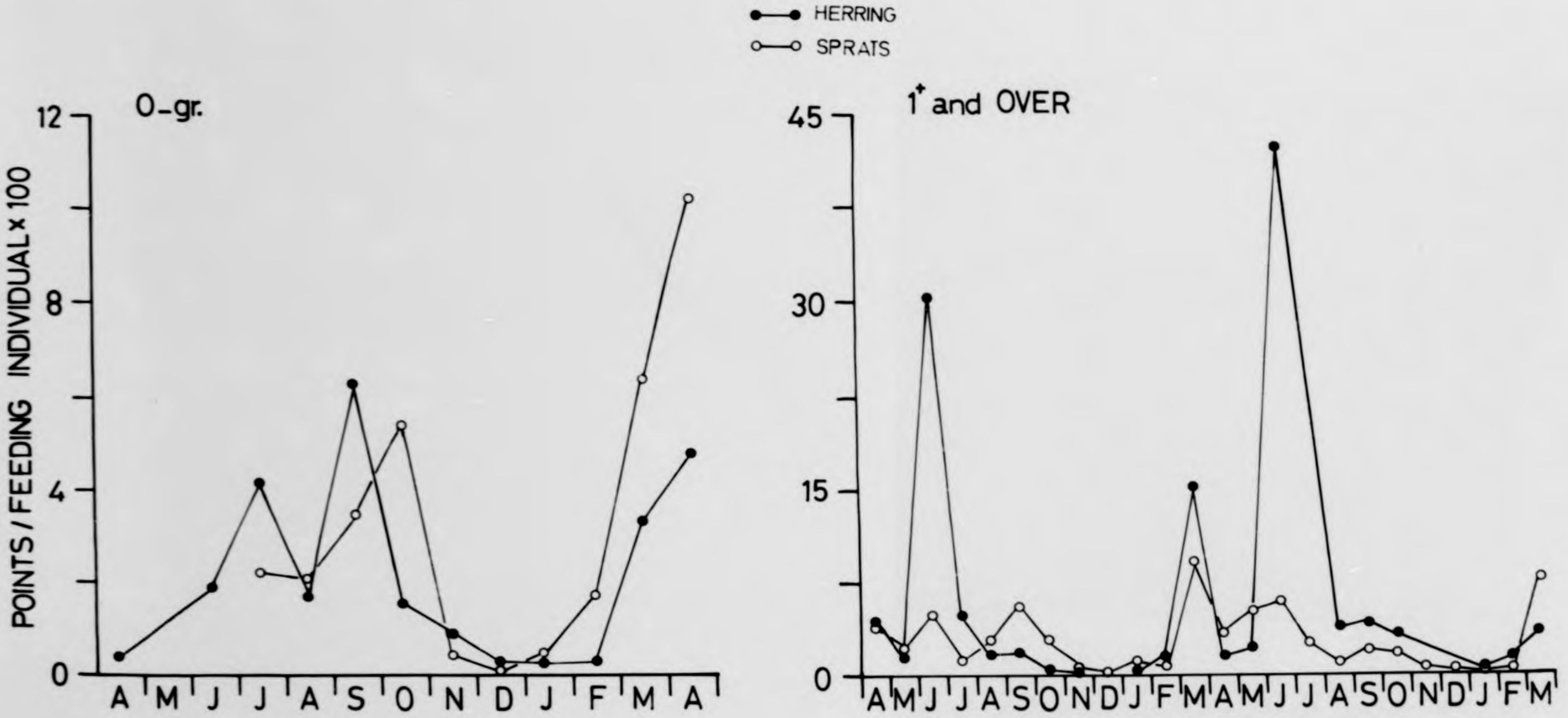

HERRING
SPRATS
APRIL '70 TO MARCH '72
% STOMACHS EMPTY
60
40
20
0
A M J J A S O N D J F M A M J J A S O N D J F M
MEAN FOR EACH MONTH
% STOMACHS EMPTY
60
40
20
0
A M J J A S O N D J F M

Fig.42.

Fig.42. Seasonal changes in the intensity of feeding of 0-group and 1+ and over clupeids.

0-group


HERRING
SPRATS
0-gr.
1⁺ and OVER
POINTS / FEEDING INDIVIDUAL x 100
12
8
4
0
45
30
15
0
A M J J A S O N D J F M A
A M J J A S O N D J F M A M J J A S O N D J F M

In O-group fish, though most of the individuals were feeding throughout the year, the amount of food eaten varied considerably from month to month (Fig.42). In herring there was a progressive increase till July and then a decrease in August. Maximum feeding activity was observed in September, after which there was a gradual decrease towards the winter during which feeding was maintained at a very low level. Feeding activity tended to increase after the winter from February onwards. In O-group sprats a similar trend was seen, with very high feeding activity occurring in October. Unlike in herring intensity of feeding in sprat increased from January onwards reaching a value of 1100 points/individual by March. It appears that peaks of feeding activity in the two species do not coincide, before or after the winter.

In older fish feeding activity is correlated directly with the feeding season (Figs 41&42). During the main feeding season of March to September in both species, activity or intensity of feeding varied from month to month and from year to year. Nevertheless, a pattern in the change of activity seems to emerge. In herring there were two recognisable peaks of increased feeding activity, one very early after the winter around March-April and the other later on, in June-July. In sprats, too, increase in feeding activity took place around a similar time, also with a possible 3rd period of increased activity occurring in September-October. Annual variations are evident in both species. For instance, the last peak during the feeding season in sprats occurred in September in both years, but the intensity of feeding in 1970 was nearly three times as high as that in 1971.

Similarly in herring peak activity in March 1971 was significantly higher than that in 1972. Unlike in 0-group fish there was more overlap in the periods of intense feeding activity of the two species. It is evident from Fig.42 that herring tend to feed very intensely during periods of high activity, the highest observed mean being 4200 points/individual where as in sprats 917 points/individual was the highest observed.

4.IV. Composition and seasonal variation of the diet

The food items were identified as far as possible and the species composition of the diet of 0-group and older fish in both species is tabulated (Table 21). Those items that were present in less than five individuals are also shown in the table. They were not considered to be a regular part of the diet and were omitted from the final analysis.

4.IV.I. Composition of the diet

The range in the composition of the diet is greater in older fish then in the 0-group. In older clupeids, mysids, euphausiids, the copepod Paraeuchaeta and sporadic occurrence of amphipods were observed in the diet in addition to that of the 0-group fish. In older herring, fish larvae were also taken during 1970. The species compositions of the diet in 0-group herring and sprats were identical to each other.

The composition of the diet of 0-group and older fish expressed as percentages of the total food consumed during the full length of the investigation was calculated and expressed as 'segment-diagrams'. The size of the segments represent the proportion of that class of organism consumed during the whole year (Fig.43). It is evident that the diet is

Table 21.

SPECIES COMPOSITION OF THE DIET OF CLUPEIDS

(++ - eaten regularly, + - eaten rarely, (+) - eaten by less than five individuals).

	0-gr. Herring	0-gr. Sprats	1+ and over Herring.	1+ and over Sprats.
Cladocera				
Podon intermedius	++	++	++	++
Evadne nordmanni	++	++	++	++
Copepoda				
Calanus finmarchicus	++	++	++	++
Temora longicornis	++	++	++	++
Centropages typicus	++	++	++	++
Candacia armata	+	+	+	+
Paraeuchaeta norvegica	(+)	(+)	++	++
Amphipoda				
Hyperid type			+	(+)
Mysidacea and Euphausiacea				
Praunus in ermis	(+)	(+)	++	++
Thysanoessa raschii			+	+
Meganyctiphanes norvegica	+		++	+
Decapoda				
Calocaris macandreae			+	+
Crustacean larvae				
Pagurid larvae	++	++	++	++
Pandalus species	++	++	++	++
Jaxea nocturna			(+)	
Balanus nauplii	++	++	++	++
Balanus cyprid	++	++	++	++
Appendicularia				
Oikopleura dioica	++	++	++	++
Chaetognatha				
Sagitta elegans	++	++	++	++
Bivalve molluscan larvae				
Larvae of family Skenidae	++	++	++	++
Fish larvae				
Ammodyte species			++	
Gadoid species			++	

Fig.43.

Fig.43.

Fig.43. The relative importance (see page 76) of the principal food organisms of 0-group and 1+ and over clupeids, as percentages of the total year's food.

76) of the principal

and over clupeids, as

ood.

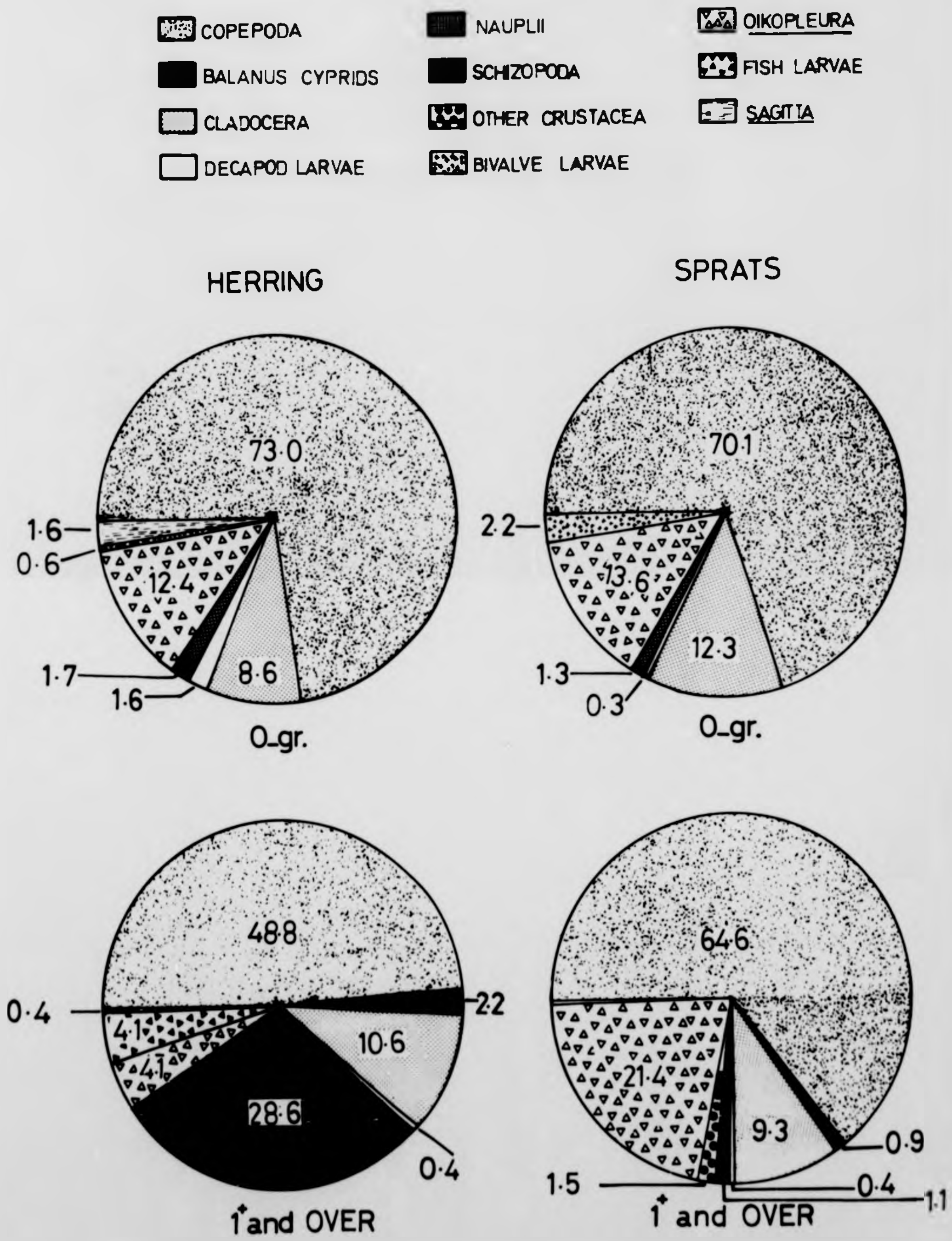
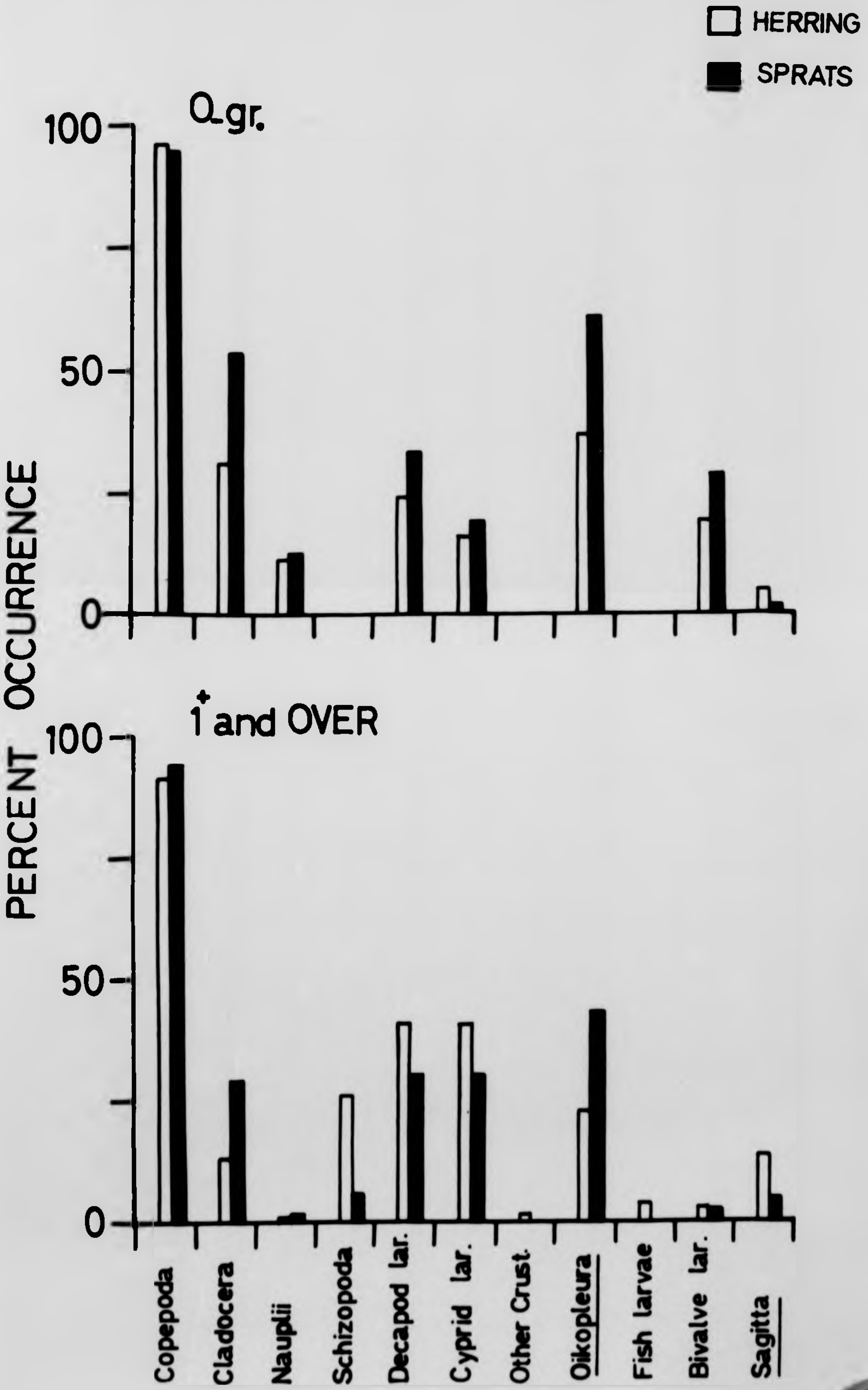


Fig.44.

Fig.44. Percentage frequency of occurrence (see page 81) of food items in 0-group and 1+ and over clupeids.

ce (see page 81) of

over clupeids.



predominantly crustacean in all four instances with copepods accounting for more than 50%, except in herring older than a year. In 0-group sprats, cladocera and Oikopleura were more important than in herring while the reverse was true of copepods. In 0-group herring, Sagitta comprised 1.6% of the diet while in sprat it accounted only for 0.04% and is not shown in the diagrams. Balanus cyprids constituted less than 1% in both species, while the same was found to be so for bivalve larvae in herring and for decapod larvae in sprats.

In older herring, mysids and euphausiids (grouped together as schizopods in Fig.43) constituted 26.8% of the diet in comparison to 1.4% in sprats. The reverse was found in the case of Oikopleura, which constituted 21.5% of the diet in sprat and only 4.18% in herring. Decapod larvae and Balanus cyprids were taken in greater quantity by herring in comparison to sprats.

The percentage frequency of occurrence of individual food items for the whole year in feeding fish were obtained for 0-group and older herring and sprats (Fig.44). In all four instances copepods were found to occur in more than 90% of the individuals. Except Sagitta and copepods the % frequency of all the other items were higher in 0-group sprats in comparison to 0-group herring. It is evident that though Balanus cyprids, decapod and bivalve larvae individually constitute less than 1% of the diet in both clupeids they were eaten more frequently than nauplii, mysids, euphausiids and fish larvae.

4.IV.II. Seasonal variation of the diet in 0-group fish

In order to make a graphical presentation of seasonal variation of the composition of the diet in 0-group fish easier, an arbitrary classification was adopted. Food items were classified into two categories;

(a) items of major importance - those food items that were found in numbers more than 50 per feeding individual for two or more months (Fig.45 and Appendices 9 & 10).

(b) items of minor importance - those food items which did not meet the requirements of (a) (Fig.45).

Accordingly there were only three items of major importance viz. copepods, Oikopleura and cladocerans in both herring and sprats. Except in March following the first winter of the clupeids, copepods constituted the main food item. In March cladocerans took the place of copepods in importance. Oikopleura was eaten in most months and seemed to be more important in the diet of sprats than in herring.

It is evident from seasonal variation in the composition of the diet, the percentage occurrence of various food items, and the qualitative similarity in the species composition, that there is an overlap in the diets of 0-group herring and sprats.

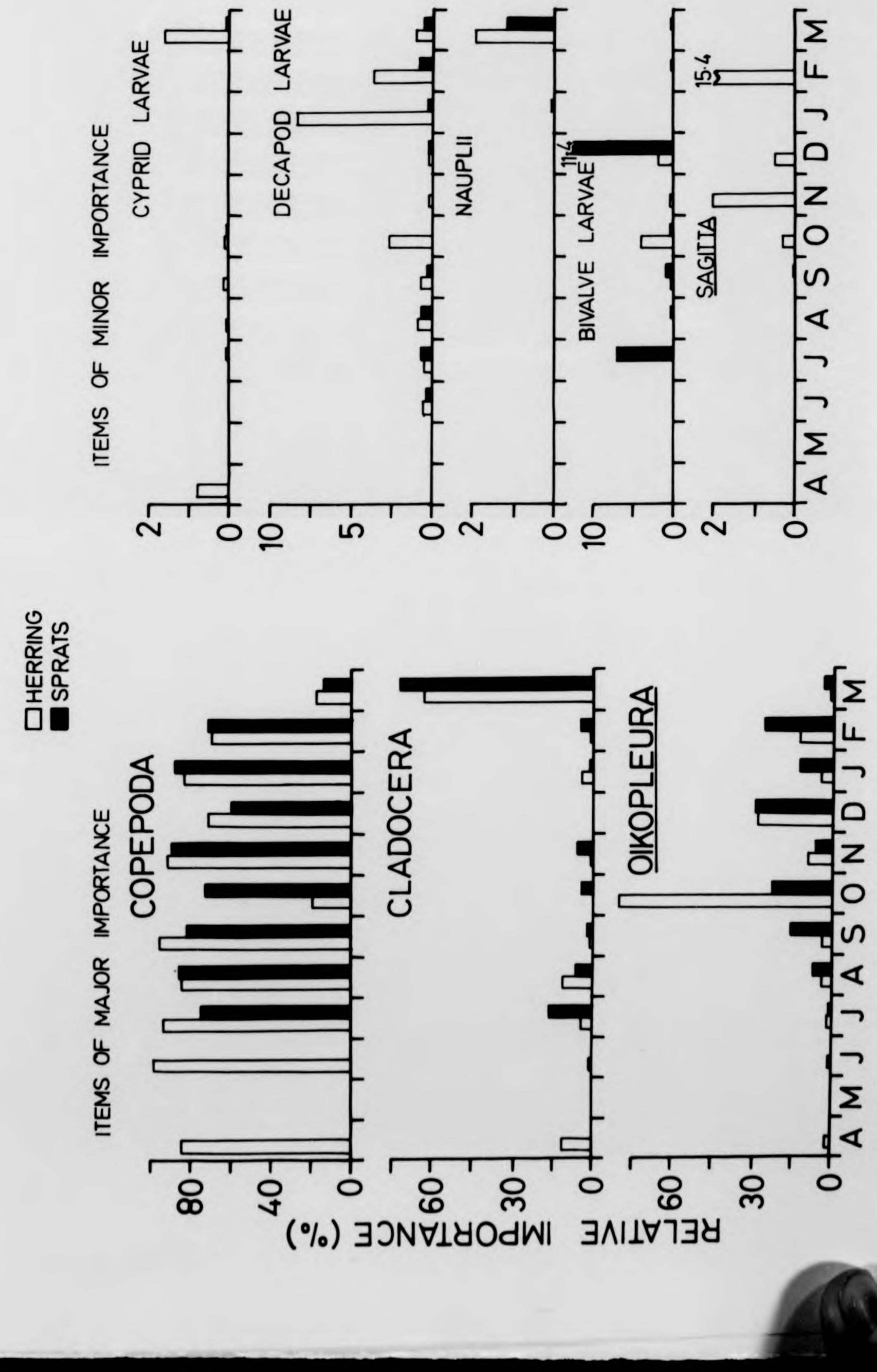
4.IV.III. Seasonal variation in the diet of older fish.

In older fish the relative importance of each food item for each month was calculated (Appendices 11 & 12) and the data for the two years were pooled together and mean relative importance of each item expressed as a percentage of feeding fish in each month (Appendices 13

Fig.45.

Fig.45. Relative importance of food items of 0-group clupeids.

s of 0-group clupeids.



& 14). The final data are represented graphically for herring and sprats in Fig.46. Some important yearly differences in the diet were evident. For example, in herring, fish larvae were eaten in appreciable numbers in April and May 1970, whereas in 1971 they were not eaten at all.

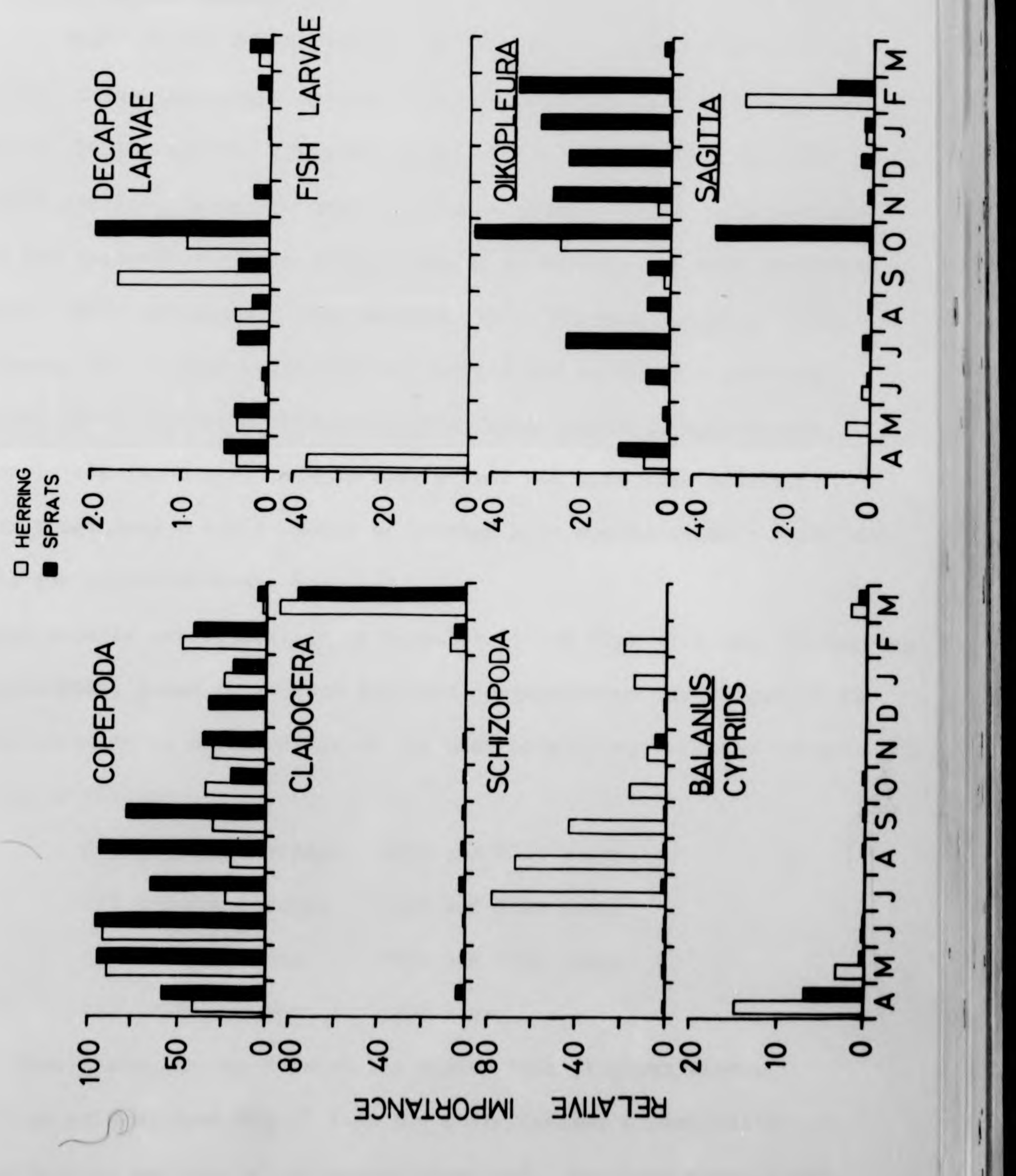
Copepods were eaten throughout the year by both clupeids. During the main feeding season from March to September copepods constituted the bulk of the diet in sprats except in March, when cladocerans were the dominant item. In herring copepods constituted the major portion of the diet from April to June and were replaced by cladocerans in March and by mysids and euphausiids (grouped together as schizopods in Fig.46) from July to September. During the winter the diet of herring was almost entirely composed of copepods, whereas in sprats,copepods were supplemented by other organisms.

Balanus cyprids were taken from March to June by herring and from March to October by sprats. In both clupeids it accounted for only a small proportion of the diet. Decapod larvae on the other hand occurred more regularly in the diet of herring and sprats, but quantitatively it constituted only a very small proportion of the diet of either species.

Among the non-crustacean food types, Oikopleura was the most important and was taken by 65% sprats and 36.2% herring. During the winter Oikopleura was an important food item in sprats, while in herring it was so only in October. Fish larvae were taken only by herring in April. Sagitta was eaten rather regularly by both clupeids in most of the months, but it constituted only a small proportion of the diet in either species.

Fig.46.

ns in each month of
ntage of feeding
ts over a year old
ulation).



4.V. Daily feeding periodicities

Fish species differ widely in their daily patterns of feeding activity. Among the marine species diel feeding behaviour of the plaice (De Groot, 1964), soleids (Edwards et al., 1971) and cod (Arntz, 1972) have been studied. A few records are also available of the fluctuations in the gut contents during a 24 hour period in herring but none in sprats (Lissner, 1925; Jesperson, 1928; Mužinić, 1931; Marshall et al., 1939).

During the 24 hour period survey carried out on the 9th and 10th of August 1972, 0-group sprats and herring were caught in appreciable numbers in all the hauls. Sprats over a year old were also obtained regularly but only a small number of herring were caught in most hauls and none in the 0400-0440 hours haul.

The results are summarised in Appendix 15 and Figs 47 & 48. In 0-group and older fish, peaks in stomach fullness, expressed as the weight of the stomach contents as a percentage of the body weight, are clearly recognisable. They are as follows;

(1) 0-group herring: 1320 and 2220 hours
(2) 0-group sprats: 1320 and 0120 hours
(3) Older herring: 1820 and 1020 hours
(4) Older sprats: 1320 hours.

In all four instances the time of the higher peak is given first.

It is evident from Fig.47 that the daily feeding periodicities of 0-group herring and sprats are almost identical. In older herring and sprats the feeding periodicities appear to be markedly different from each

Fig.47.

Fig.47. Twenty four hour cycle of feeding activity, of 0-group clupeids, measured by the weight of the stomach contents expressed as a percentage of the body weight. Vertical lines represent range in stomach fullness.

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percentage of the
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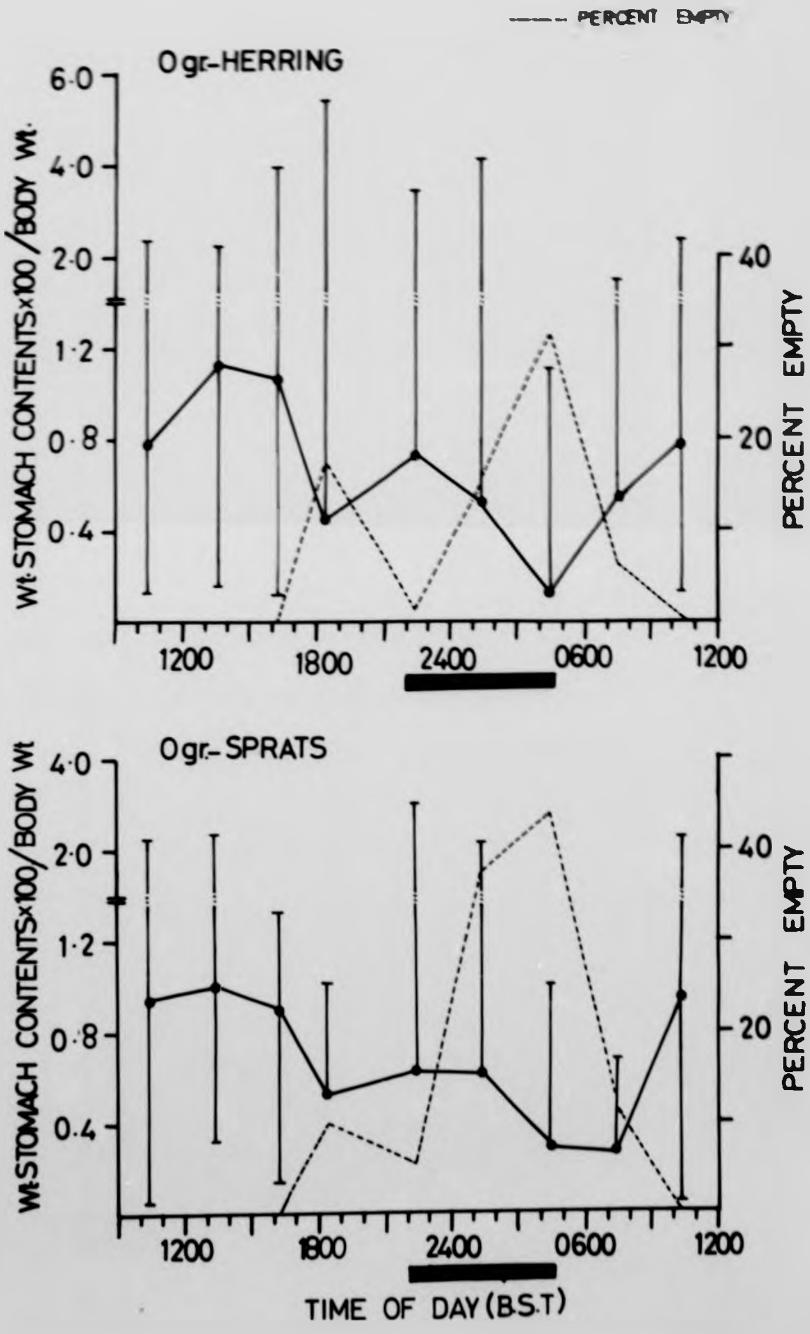


Fig.48.

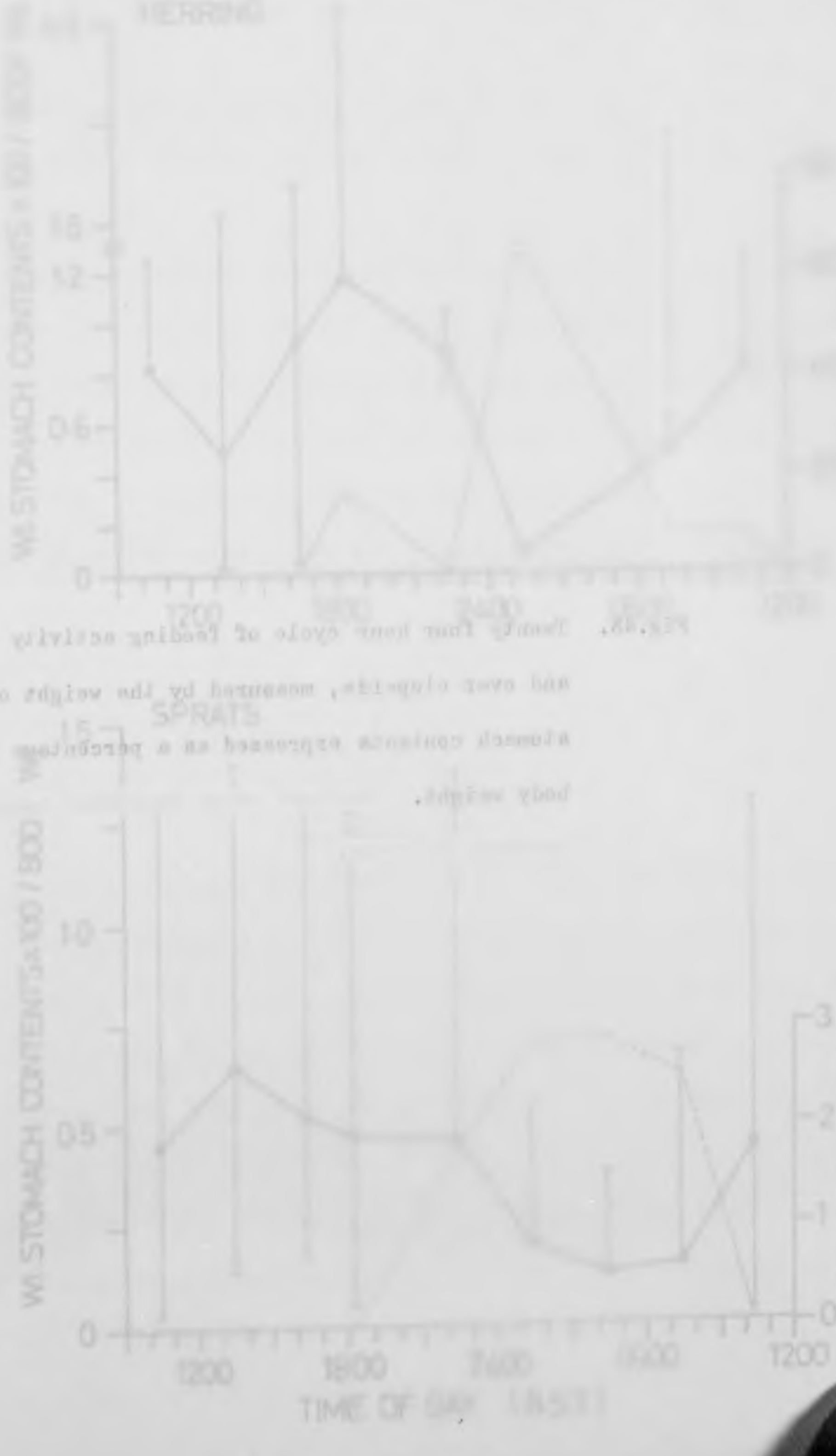

HERRING
W. STOMACH CONTENTS ×100 / BODY W.
1.6
1.2
0.6
0
1200
1800
2400
0600
1200
PERCENT EMPTY
SPRATS
W. STOMACH CONTENTS ×100 / BOD
1.5
1.0
0.5
0
1200
1800
2400
0600
1200
TIME OF DAY (BST)
PERCENT EMPTY
3
2
1
0

Fig.48.

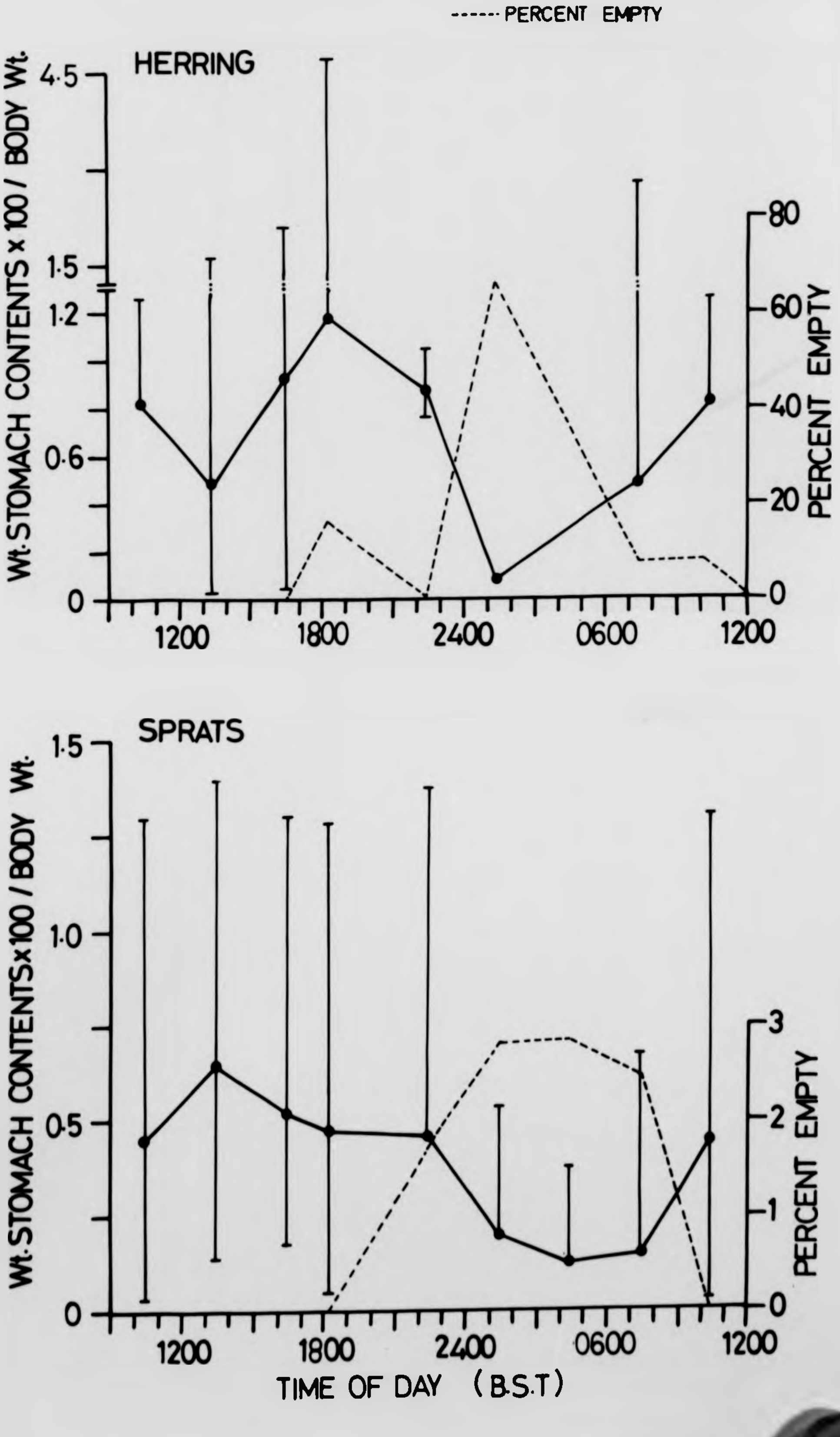
Fig.48. Twenty four hour cycle of feeding activity of 1+ and over clupeids, measured by the weight of the stomach contents expressed as a percentage of the body weight. Vertical lines represent range in stomach fullness.

g activity of 1+

he weight of the

percentage of the

resent range in



other, but the results obtained for herring are far from conclusive because of the small sample size and also the incomplete sampling of the 24 hour cycle.

The feeding periods are those periods when the stomachs are filling rapidly, that is the steeply upward sloping lines prior to the peak. Figs 47 & 48 bring out clearly that, at any peak of stomach fullness, the mean value is considerably lower than that for the individual with the fullest stomach. It is evident that the 'average' stomach is not filled to its maximum potential during a feeding period. Reasons for this may be many fold. An individual that 'over-eats' during one feeding period may consume correspondingly less at the next one. Alternatively, metabolic needs may be adequately met by less than the maximum intake of food, feeding may be rhythmic or the amount of food that can be obtained in a given time might be limited.

It is very likely that in both species the changes in light intensity acts as the main stimulus in initiating feeding. Absence of feeding in the night when the light intensity is below 0.1 mc, considered by Blaxter (1970) to be the best average estimate of a visual feeding threshold, provides further evidence that herring and sprats do not use senses other than vision to locate their food.

Keast & Welsh (1968) used daily feeding period studies to calculate the daily ration, by determining the differences between the main peaks of stomach fullness and the succeeding troughs (greatest emptiness) and added these. The details of the calculations are given in Table 22.

Table 22. CALCULATION OF DAILY FOOD RATION IN HERRING AND SPRATS.

	1st Peak	1st Trough	Difference	2nd Peak	2nd Trough	Difference	Daily Ration*
O-group Herring	1.135	0.447	0.688	0.738	0.126	0.612	1.300
O-group Sprats	1.034	0.528	0.506	0.627	0.261	0.366	0.862
Older Herring	0.834	0.512	0.322	1.180	0.077	1.103	1.425
Older Sprats	0.642	0.129	0.513				0.513

*Expressed as per cent of the body weight.

These estimates are relatively low when compared with those of Keast and Welsh (1968) for Lake Opinicon fish. This is possibly due to the fact that in August the feeding intensity in general is at a low level in both species (Fig.42) whereas the former authors made their observations in the early summer period of accelerated feeding. Even though the present values are obtained during a lean month of feeding they compare well with those of Holliday (unpublished - quoted by Blaxter and Holliday, 1963), who estimated that herring of 10-20 gm required 1.7% of their body weight at 11.4°C to maintain themselves at constant weight.

In general, one would expect the daily ration per unit weight of the body in 0-group fish to be higher than that of the older ones, since the former are still more actively growing. In the present data this is true in the case of sprats but not in herring. It is possible that because of the small sample size the differences between the peak and the succeeding troughs in the degree of stomach fullness have been over estimated.

The above estimates of daily rations are minimal since some digestion must take place whilst some individuals are still feeding and some continue to feed when the mean volume is lessening.

4.VI. Comparison with other areas

The more important work on the food and feeding in herring has been mentioned earlier in the introduction. Lebour (1921 b) studied the food and feeding habits of metamorphosed herring, sprats and pilchard in the Plymouth area and concluded that, though, these species occur together they tend to feed on different organisms. These results are contradictory to the present findings. The difference is probably due to the small sample size used by Lebour and secondly, but more important, that her samples were obtained from estuarine rivers which are entirely different habitats.

Hardy (1924) and Marshall et al. (1939) working on O-group herring from the Thames and the Clyde respectively found a high percentage of non-feeding individuals during the winter months. Jesperson (1928), however, found that young herring off the Danish west coast were feeding voraciously on copepods during the winter. It is probable that these differences are at least partially caused by the time of sampling.

Hardy (1924) did not record the occurrence of Oikopleura or cladocera in the diet of young herring from the Thames and these items were found to occur only occasionally in Clyde herring (Marshall et al., 1939). In general, the diet of O-group herring in the area studied presently is more similar to those from the Clyde than from the Thames.

The food and feeding habits of herring one to two years old have been sparsely worked on. When compared with the composition of the diet of adult herring from the Scottish west coast a basic similarity is evident, the diet itself being somewhat intermediate between that of O-group and adult herring.

Kazanova (1960) noted that in the Baltic sprat that the diet is mainly crustaceous, copepods and cladocerans constituting the bulk. She also found that during the winter and early spring it tends to feed mainly on adult copepods and in late spring changes over to cladocera, mainly Bosmina species.

4.VII. Discussion

It has been clearly shown, that 0-group herring and sprat have much in common in their diets. The species composition is identical and seasonal variation in abundance of food types in their diet is similar to a very great extent. For example, soon after their first winter, cladocerans take the place of copepods in dominance in both herring and sprats. During the same time nauplii are eaten in fair numbers. The greatest number of Oikopleura is present in the diet in both clupeids in October. The small number of food species available and the qualitative and quantitative overlap in the diets of herring and sprat indicate that there could be potential competition for food between the two species. This conclusion is almost entirely contradictory to that of Lebour's (1921b).

In older fish, however, the dependence of herring on mysids, euphausiids and fish larvae is an important deviation from the food of sprats. It has been noted by earlier workers that the food habits of herring change appreciably from one phase of life to the other. For instance, copepods become predominant after the post-larval phase (Lebour, 1921b, 1924; Hardy, 1924; Marshall *et al.*, 1937; Bowers & Williamson, 1952), until in the adult phase, schizopods (on the Scottish west coast) and Ammodytes (on the East Coast) become predominant. It has been shown that in herring of 1 to 2 years old the composition of the diet shows trends towards that of the adults, in that for the first time mysids, euphausiids and fish larvae are added in appreciable quantity to that of the 0-group diet. In sprats, however, changes in food habits are slight between 0-group and older fish.

The tendency of young clupeids to immigrate into inshore waters has been known for many years and during their first year of life they tend to shoal together or at least remain in close vicinity to each other. Gause (1934) put forward the principle of one species to a niche, the niche being defined as the functional status of an organism in its community. Two closely related species could live together in the same habitat but occupy different niches and avoid direct competition. Lack (1945) studied the food habits of two closely related sea-birds, the cormorant and the shag and found that though the habitats were similar their order of preference for species of fish was significantly different, thus avoiding direct competition. On the other hand, the work of Hartley (1948) and Larkin (1956) on fish fauna in fresh water streams has suggested that there is a greater food overlap in species of fish which occur together than in mammals or birds. This violates the accepted concept that animal species from the same or similar habitat show a high degree of 'ecological exclusion'

Competition could occur even when there is a partial overlap of niches and when two species are very closely related. It has been shown that such condition in quality and the quantitative variation of the diet exists in 0-group herring and sprats. This is indicative of the fact that a possible competition for food could occur between these two species, if the food supply was to become limiting.

Direct competition could be avoided by feeding at different times of the day or at different depths. Gause, in his original experiments, demonstrated that Paramecium caudatum and P. bursaria could exist together in a culture medium by feeding on the same type of bacteria but in different parts of the medium. P. aurelia, however, eliminated P. caudatum when introduced into a similar culture medium. It has been shown that in 0-group herring and sprats the daily feeding periodicities are almost identical and it is also probable that they feed at similar depths.

Competition would result in lower growth rates or increased mortality in one or both species. The available growth rates for the different localities where herring and sprats occur together do not indicate a higher or lower growth rate in either species in comparison with localities where only one species occurs. For example, in L. Spelve the growth rate of 0-group sprats, which are found there almost unmixed throughout the year, are not significantly higher than those of L. Etive or the F. of Lorne where sprats and herring occur together. It is possible that when the environmental supply is limiting, competition for food is avoided by adjusting their distribution, that is one species moves out of such an area. This probably is a factor governing the distribution of young herring and sprats in the sea-lochs and will be dealt with in detail in the final discussion.

Section 5

PARASITISM.

5.I. Introduction

Polyanski (1955, 1958) grouped the parasites of teleost fishes into four categories on the basis of the ecology of the fish host and the characters of the parasitic fauna. In this generalisation he concluded that fish which feed on plankton are infected by a few species of parasites and that the incidence and intensity of infection is much lower than in other groups.

In the present study during the routine examination of the samples, both herring and sprat were examined for parasites, on the body and in the coelomic cavity and the stomach. Only fish over a year old were used. No attempt was made to distinguish between species of parasites in the monthly samples.

5.II. Parasitism in clupeids.

A total of 1674 sprat and 1356 herring body cavities were examined. The total percentage infection was found to be 69.5% in sprat and 34.0% in herring. Two species of nematode larvae were parasitic in both sprats and herring, by far the commoner being Anisakis and the other being Contracaecum.

Similarly a total of 1006 stomachs of sprat and 760 of herring were examined for helminth parasites. The percentage infection was found to be 13.4% in sprat and 31.0% in herring. Only one genus of helminth parasite was found and was identified as belonging to the genus Hemiurus.

External body surface was examined for parasites (excluding protozoan) in both herring and sprats. No body surface parasites were found in the case of herring, while in sprats the penant-like copepod parasite of the genus Lernaeenicus was found on 22 individuals out of a total of nearly 5000. The species L. encrasicola (Turton) was found attached to the body of 12 and the species L. sprattae to the eye of 10.

The seasonal variation of the nematode and the helminth parasite fauna in herring and sprat is shown in Fig.49. In the case of sprat there is evidence of a more pronounced seasonal cycle of infection by both nematode and helminth parasites than in herring. Also, in sprat it appears that the maximum infection of helminth parasites is coincident with the minimum infection of nematodes and vice versa. Such a pattern is not so evident in herring.

In both sprats and herring the seasonal cycle of infection by helminth parasites is similar to the cycle of their respective feeding intensities. This similarity is more pronounced in sprat than in herring (compare Figs 49 & 42). On the other hand the seasonal cycle of infection by nematode parasites in sprat coincides to some degree with the seasonal cycle of condition (Fig.24), whereas in herring it does not.

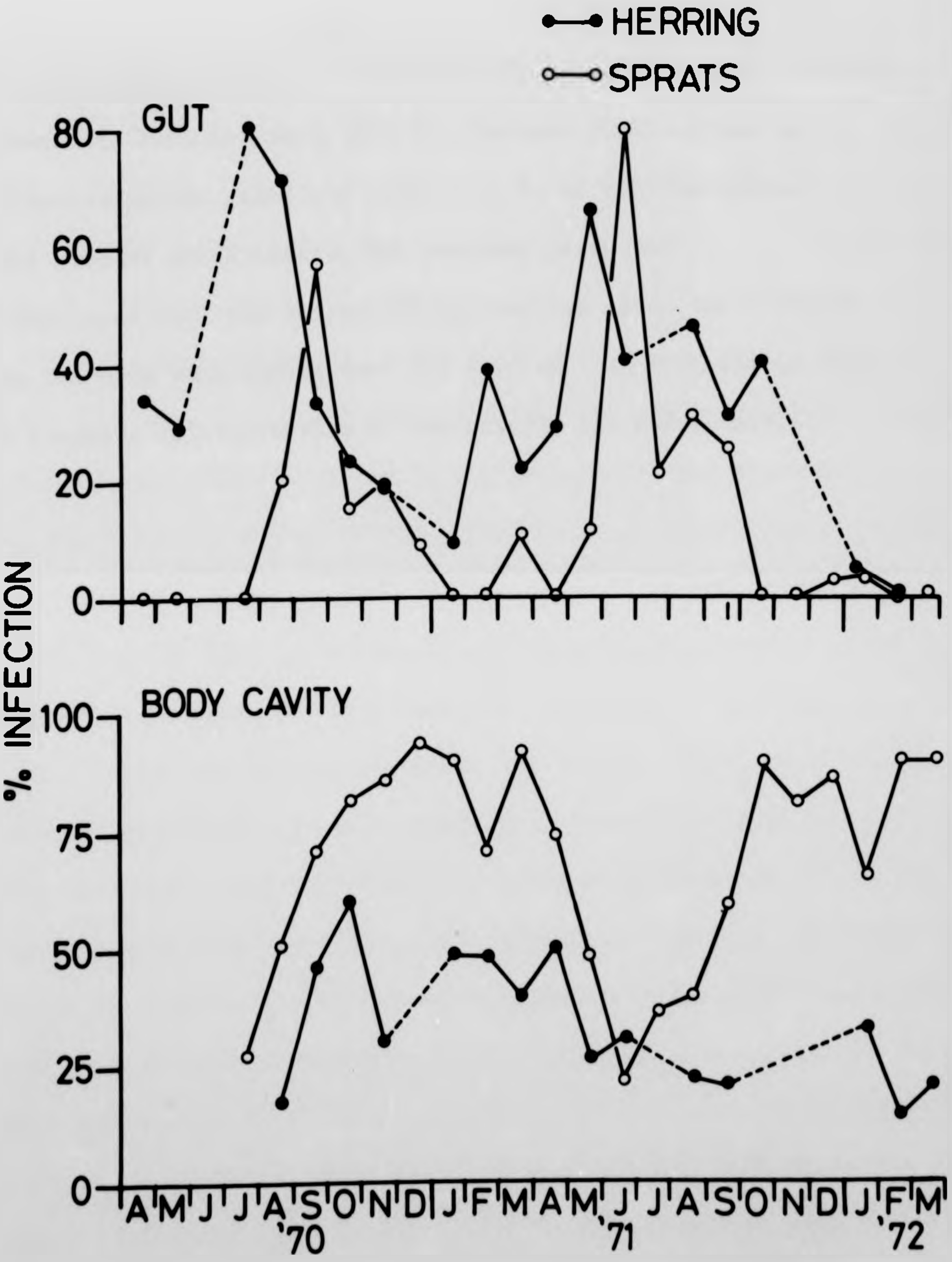
Seasonal fluctuations in the parasite fauna of marine fishes have been much less extensively studied than any other group of vertebrates. Interpretation of seasonal differences in the parasitic fauna is hampered by a lack of knowledge of the complete life cycle of the parasites. For

Fig.49.

Fig.49. Seasonal changes in the percentage infection of 1+ and over clupeids, by nematode and helminth parasites.

of 1+

parasites.



instance, Contracaecum is one of the commonest parasitic genus of marine fishes around the British Coast, however, Berland (1961) after an extensive investigation found its life cycle to be very variable.

In the present investigation the nematode parasites were not separated into the respective species and also the seasonal changes in the mean worm burden were not studied. As a result of these factors a complete interpretation of the results was not possible.

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Section 6

DISCUSSION

It has been shown that young herring begin to migrate into the area investigated in April and sprats around July-August. Careful analysis of herring stocks reveal that the herring which come into the area in April probably originate from the Minch autumn-spawning stock and that those from a spring-spawning stock arrive in June. The mean length when they first appear is 35-38 mm with a range of 30-47 mm. The similarity in the mean length and the time of arrival of the broods in 1970, 1971 and 1972 cannot be rejected as a mere coincidence. Baxter (1954) observed the presence of autumn-spawned larvae off the south-west of Mull in the months of September and October and Wood (1971) observed concentrations of autumn-spawned larvae in the same area in October. Virtual absence of larvae inshore in the Oban area, when their distribution is more liable to be determined by tidal drift etc., seems to indicate more than a passive drift of young herring into the area. The arrival or immigration of young herring is therefore thought to be at least partly due to an active migratory movement. Less is known about the sprats, though they seem to spawn outside the area of investigation and broods from different years move in at different lengths.

The relative abundance estimates of 0-group clupeids give clear indications of importance of this and similar areas as nursery grounds for young clupeids. The Moray Firth has been known to be one of the major nursery areas for young herring in Scottish waters and it has been shown recently that young herring in this area originate from the Minch autumn-spawning stock (Saville, 1971). When abundance estimates of 0-group herring in the Moray Firth are considered (research vessel surveys from 1960-1967) it is seen that except for two catches, all the rest yielded below 500 fish per hour's fishing and in October and December the catches were even smaller. Those obtained in April-May and after that as 1 group fish were much higher in the Moray Firth than in the Oban area. It is therefore evident that at least during the first year of life, Minch autumn-spawned herring are found in larger numbers in the Oban area than in the Moray Firth.

Dragesund (1970) has shown that abundance estimates of 0-group herring in the Norwegian fjords give vital clues of the year-class strength of any one brood long before recruitment to the adult stock. In British waters prediction of stock abundance has been mainly based on larval abundance studies. Such estimates are subjected to much error, because of the extensive mortality rate at this phase of life and also because of its susceptibility to changes in the environmental conditions. It is therefore suggested that long-term research on abundance of 0-group fish in inshore areas similar to those around Oban and correlation of such statistics with those after recruitment may give more reliable estimates of stock abundance and year-class strength.

0-group herring move into the area and then a localisation in their distribution takes place within a very short period of time. On the other hand 0-group sprats tend to remain in appreciable numbers in all the sea-lochs and 'open' areas. A comparison of growth rates of herring and sprats spawning stock (Saville, 1971). When abundance estimates of 0-group herring in the Moray Firth are considered (research vessel surveys from 1960-1967) it is seen that except for two catches, all the rest yielded below 500 fish per hour's fishing and in October and December the catches were even smaller. Those obtained in April-May and after that as 1 group fish were much higher in the Moray Firth than in the Oban area. It is therefore evident that at least during the first year of life, Minch autumn-spawned herring are found in larger numbers in the Oban area than in the Moray Firth.

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0-group herring move into the area and then a localisation in their distribution takes place within a very short period of time. On the other hand 0-group sprats tend to remain in appreciable numbers in all the sea-lochs and 'open' areas. A comparison of growth rates of herring and sprats in their first year of life has shown that they are not significantly different from locality to locality within either species. The growth rate of a population is primarily determined by the food supply and the physical conditions of the environment. The environmental conditions in the sea-lochs and 'open' areas under consideration are not greatly different from one another. It is possible that the similarity in the growth rates of 0-group herring and sprats in the different localities indicates that a stable food supply was available and was not limiting their growth. It is also likely that the total amount of food available is smaller in the small lochs and vice versa. For example, there is evidence that the zooplankton biomass per unit volume in Loch Etive is higher than in Loch Creran (Mauchline, 1972). It has also been shown that 0-group herring and sprats depend on the same food organisms and that when and if the supply is limiting, competition between them is a possibility.

Therefore, if 0-group herring and sprats were to occur at the same intensity in all the localities, food is likely to be a limiting factor for growth and even survival. Thus it is possible that the movement of young herring from the smaller lochs, i.e. Spelve, Creran, etc. may be a consequence of the availability of a limited food supply common to both species and thereby a means of avoiding direct competition. There may be other factors operating, for instance herring prefer deeper waters as they grow older and therefore they may tend to leave the small lochs.

The tendency of young herring, once established in the bigger lochs and 'open' areas, to emigrate during the winter months has been discussed.

The absence of deep waters in most of the areas sampled and the concentration of herring to a certain extent in the deep trench in Loch Etive during the winter provides further evidence in favour of the tendency of young herring to move into deeper water. The greater availability of food in Loch Etive compared to the other areas during the winter months (Dr. Mauchline - personal communication) may also act as a contributory factor. A less pronounced trend is seen in O-group sprats. In sprat, maturation takes place in the second year of life, and the movement to the spawning grounds may also be a contributory factor to the movement from inshore waters. It is probable that herring in particular will have an oceanic phase of life before being recruited to the adult stock, while in sprats recruitment takes place directly much sooner.

The similarity of sprat populations to commercial catches has been shown, but it must be pointed out that the data are far from sufficient for any definitive conclusions to be made. If this phenomenon was found to be true from later long term studies, it is suggested that sampling by research vessels in inshore waters, similar to the one presently investigated should give good indications of year-class strength of sprats and therefore predictions of the yield for the fishery well in advance.

Nikolskii theorised that the total mass of a population and therefore its age structure is governed by the ultimate food supply. The simplicity of age distribution of sprat and the replacement of one year-class by a new incoming brood in the small sea-lochs is also probably a result of the limited food supply available. If there were no replacement of older fish in the small sea-lochs by small and younger fish the food supply would tend to limit growth and survival. Older and bigger fish would require a higher biomass to maintain themselves. The natural and most likely solution would be for either the old or the young fish to move out in search of areas where their demands could be met with. Further evidence in favour of this idea is provided by the appearance of older fish in the sea-loch populations during the winter months when only about 40% of them are feeding; the intensity of feeding is at its minimum and therefore the food supply is not limiting.

A growth curve for West Coast sprats has been constructed and compared with those for other areas. The biology of the sprat is basically different from that of herring. The sprat is a much smaller fish with a growth potential and life span less than half of that of herring.

Parrish & Saville (1965) listed the asymptotic length (L_∞), the von Bertalanffy growth constant (K) and the maximum life-span of Clyde, Minch, Dunmore and Norwegian and Icelandic herring stocks. L_∞ and K of the Clyde herring were found to be 30-33 cm and 0.3-0.4 respectively. L_∞ and K of the West Coast sprat were found to be 16.3 cm and 0.69 from the present data. The maximum age recorded for the West Coast sprat is 7 years (Bailey - personal communication).

Using the von Bertalanffy equation;

$$L_t = L_\infty(1 - e^{-K(t-t_o)})$$

the length of an individual herring and a sprat at the end of each year of life after reaching maturity was calculated. From the lengths so obtained and fecundity data of Baxter's (1963) for Clyde herring and that of sprats from the present investigation the total number of eggs produced by an individual of both species was calculated (Table 23).

It is evident from this theoretical calculation that a herring has a potential to produce 1.53 times the number of eggs produced by a sprat during the course of its life. It should be pointed out, however, that the number of individuals which would live through the maximum number of years would be very small in any one population. Saville, McPherson & Walsh (1972) gave the total catch (monthly) and the age composition for most months for the North and South Minch herring fisheries of 1970. From these data it was calculated that 51.3% of the catch were below 4 years old. It is most likely that these fish would not have reproduced even once before being caught. On the other hand it is evident from the overall age composition of the West Coast sprat fishery (Bailey - personal communication) that only 0.8% were 1 year old and it is probable that the rest (99.2%) of the catch would have reproduced at least once before they were caught.

Herring, and similarly abundant gadoids such as cod, haddock and whiting, show large fluctuations in individual year-class strength but the effects of these large fluctuations on the total adult stock is usually smoothed out by the presence of several year-classes in the population. Generally poor survival in certain years tends to be compensated for by good survival in others. The sprat, with a few year-classes is more sensitive to a year of poor recruitment. Hence populations of such species as the sprat need to ensure a rapid replacement of the stock e.g. fast growth and early

Table 23.

THE NUMBER OF EGGS PRODUCED BY AN INDIVIDUAL HERRING AND SPRAT DURING ITS LIFE SPAN.

	HERRING		SPRAT	
Age in years	Length cm	Fecundity x1000	Length mm	Fecundity x1000
1			100.5	8.58
2			131.0	23.89
3			147.0	36.83
4	24.8	23.57	155.0	41.38
5	26.8	31.86	159.0	49.56
6	28.2	38.91	161.0	51.96
7	29.1	44.39	162.0	53.21
8	29.8	48.72		
9	30.3	51.54		
10	30.7	54.37		
11	31.0	56.31		
12	31.1	57.02		
	Total	406.69		265.41

maturity. On the other hand, relatively long-living herring mature late in life and recruitment each year represents only a small proportion of the population in general.

In the course of this study, an adverse winter (1969-70) and a relatively mild winter (1970-71) were observed. The effects of a severe winter and a mild one on the spawning season of sprat has been demonstrated. Iles & Johnson (1962) showed that even under normal conditions a certain proportion of sprat larvae go through the winter without metamorphosing in the North Sea. The length at metamorphosis is thought to range from 25-34mm. Spawning on the West Coast was shown to continue till August under normal conditions, while it was found to be delayed, (till November) if a severe winter preceeds spawning.

Thus it is evident that under normal conditions a good proportion of the larvae would reach their metamorphic length by winter. If spawning was delayed, due to unfavourable conditions, larvae hatched during the latter part of that season would not reach such a length and would go through the winter without metamorphosing. It is possible that this would result in increased larval mortality and hence effect the year-class strength. It is suggested that a long term study on this basis, together with rate of growth and fecundity, would be of importance.

It would be interesting to find out whether in a short-lived species a bad or unsuccessful year-class would react by an increased rate of growth and fecundity, thereby compensating for its small numbers. It has been pointed out that the 1969 year-class was a poor one compared with the neighbouring ones and that it showed a higher rate of growth,

Early maturity, high (relative) fecundity and serial spawning are all useful adaptations which (a) increase the number of young produced,(b) enable reproduction during more than 80% of the life span and (c) make certain that the complete brood is not subjected to the same environmental conditions.

The food and feeding habits of O-group clupeids have been dealt with in detail and the existence of broad competition for food between the two species established. Cushing & Burd (1957) postulated that the changes in recruitment pattern of Downs herring were probably caused by changes in the food supply during early life. It is known that young herring and sprats tend to shoal together or in close vicinity in inshore waters as O-group fish. In such conditions changes in food supply would influence both species. Retardation in growth would result in a delay in maturity and hence in recruitment.

Competition among species of fish and also between fish and other organisms may not only result in changes in the recruitment pattern, but also in the replacement of species, which constitute established fisheries, by lesser known ones. Most of these replacements have been due to initial over-fishing of the more established fisheries and the subsequent replacement of these by the lesser known species to such an extent that the recovery of the former is inhibited. For example the replacement of the California sardine by the anchovy (Murphy,1966), hake by cephalopods in North-West Africa (Gulland, 1971) and herring by pilchard in the English Channel

(Cushing, 1966). There are also signs that the Norwegian herring are being gradually replaced by capelin (ICES pelagic fish committee 1972). North Sea and other herring stocks are exploited almost to a maximum level while the sprat around the coast of Britain is not. A replacement of herring by sprat is a possibility if the depletion of herring stocks continues and the latter is not 'cropped' in sufficient quantity.

The main emphasis in the present study has been laid on the importance of research on young fish in their nursery grounds, not only in understanding basic biology but also in evaluating potential commercial stocks. It is a pleasing fact that fishery biologists have come to realise the importance of studies on young fish in monitoring the adult stocks.

SUMMARY

1. Population dynamics and some aspects of the biology of both herring and sprats and the reproductive biology of sprat were investigated in the sea-lochs and inshore waters in the Oban area.
2. The method of sampling was by bottom otter trawl used in alternate months with a mid-water trawl.
3. Relative abundances of O-group clupeids, of two year-classes, were estimated and changes in overall abundance and localised distribution are discussed.
4. The age structure of the herring and sprat populations in the sea-lochs and the 'open' areas were studied. The sea-loch sprat populations were found to be mainly composed of 1 year old fish, and these were replaced by O-group fish of that current year. The 'open' area populations contained older age groups, up to 5 years old. The similarity of the latter to the commercial fishery was also shown.
5. The average growth rate of O-group autumn- and spring-spawned herring was 3.46 mm/week and 2.82 mm/week. The average growth rate of O-group sprats was 3.55 mm/week. The differences between the two year-classes of both species and the different localities were not significant.
6. Growth curves of sprat were constructed from empirical data and from back-calculated lengths, obtained from otoliths. Ford-Walford plots were made using the data from back-calculations. The asymptotic length

L_∞ and the von Bertalanffy growth constant K were found to be 163 mm and 0.69 respectively.

7. A Ricker curve was constructed for sprat data from the 'open' areas, and the annual mortality rate was found to be 62%. The main predators of clupeids are listed and their importance discussed.

8. The length-weight relationships were calculated. They were as follows:-

O-group spring-spawned herring-: $W= 0.0000002\ L^{3.7419}$

O-group autumn-spawned herring-: $W= 0.0000006\ L^{3.4855}$

O-group sprats -: $W= 0.000001\ L^{3.3612}$

Herring over a year old -: $W= 0.0000004 L^{3.5344}$

Sprats over a year old -: $W= 0.000002 L^{3.4234}$

Where W=weight in gm, L=length in mm.

9. O-group herring were found to originate from two races. Study of meristic characters, mean l_1 and l_1 distribution of 1+ and over herring, and comparison with that of known spawning stocks, showed that the autumn-spawned young herring probably originate from the Minch autumn-spawning stock, while the spring-spawned ones were from the Clyde stock. Investigation of meristics of sprats from the different localities with in the Oban area indicated that the populations were homogeneous in origin.

10. Seasonal changes in the macroscopic appearance of gonads and the maturity coefficient of sprat were studied. Spawning in sprat was shown to last a period of five to six months. Minimum size of maturity was found to be 88-90 mm in both sexes. Males mature earlier in the season. In both

sexes, the bigger fish tended to mature early in the season.

11. The overall sex ratio of the West Coast sprat was 109.16 females for every 100 males. The seasonal changes in the sex ratio were studied and the probable causes discussed. Sex ratio was not significantly different from one age-group to another.

12. Evidence in favour of serial spawning in sprat is presented and its significance discussed. From the number of ova in the most advanced stage of development and the total number in the ovary, the number of batches of eggs shed in any one season was calculated. The number of batches shed was found to be between 7-10.

13. Fecundity was determined in 74 individual sprat and the relationship to weight, length and age obtained. These were:

$$F = 1644.37\,W + 85.43 \quad \text{(to weight)}$$

$$F = 0.0002\,L^{3.81} \quad \text{(to length)}$$

$$F = 8719.09\,A - 916.58 \quad \text{(to age)}$$

Where F=fecundity, W=weight in gm, L=length in mm, A=age in years.

14. 99.3% and 91.2% of 0-group herring and sprats respectively but 79.1% and 78.0% of older herring and sprats were found to feed throughout the year. In older clupeids the main non-feeding period was during the winter.

15. The species composition of the diet of 0-group herring and sprats were identical. In both 0-group and older fish the diet was predominantly crustacean with copepods contributing the major share. Among the non-

crustacean items Oikopleura was found to be important in both herring and sprats.

16. Daily feeding periodicities of O-group herring and sprats overlapped to a great extent. Older sprats were found to have only one peak in stomach fullness during a 24 hour cycle,older herring had two.

17. 30.0% of the older herring and 13.4% of sprats were infected by the helminth gut parasite Hemiurus. Two species of nematode larvae were parasitic in the body cavity of both clupeids. They were Anisakis sp. and Contracaecum sp., 34.0% of herring and 69.5% of sprats being parasitised.

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APPENDICES

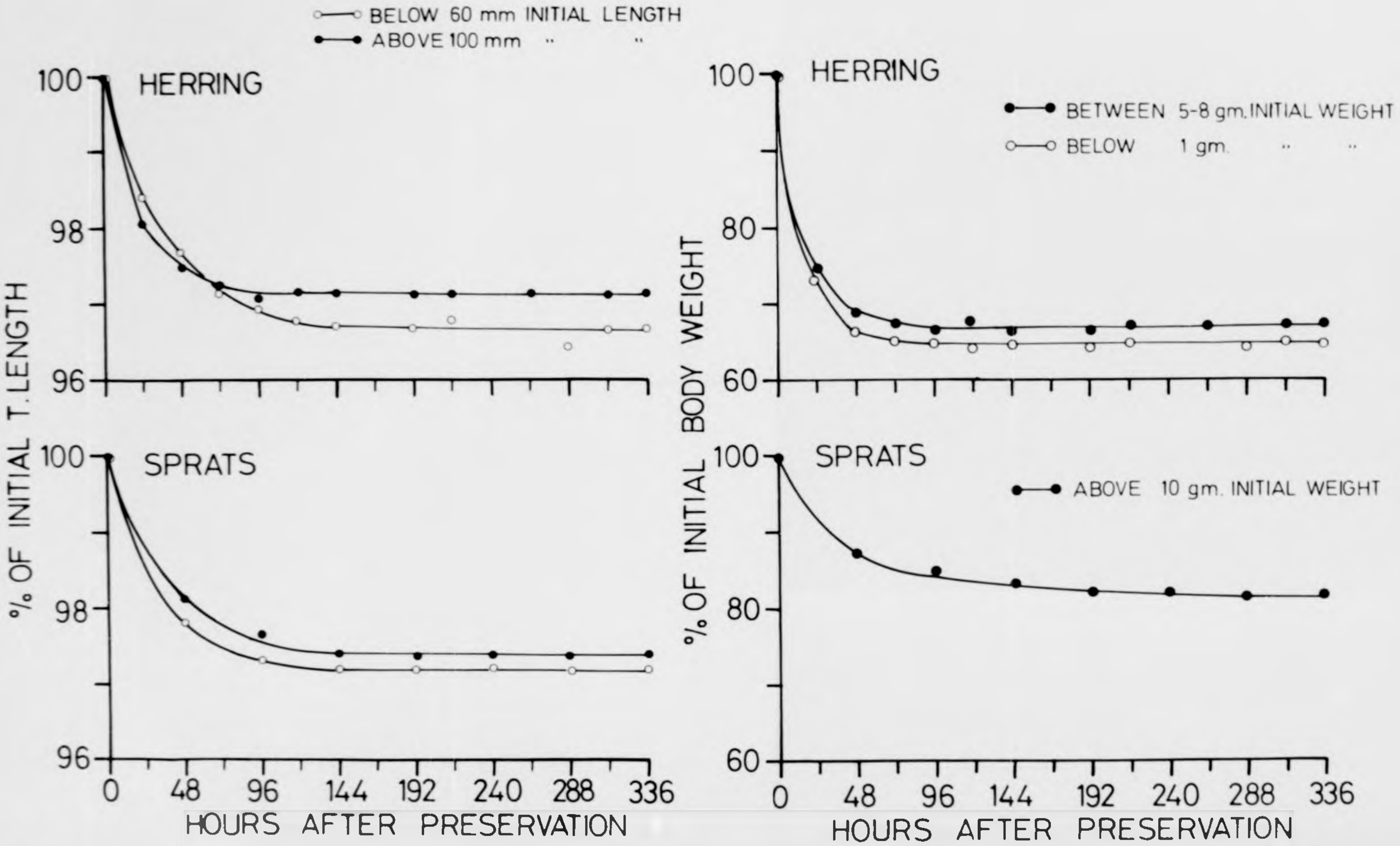
APPENDICES

APPENDICES

APPENDICES

Appendix 1.

Appendix 1. Shrinkage in length and weight in herring and sprats in 70% alcohol.


BELOW 60 mm INITIAL LENGTH
ABOVE 100 mm " "
HERRING
SPRATS
% OF INITIAL T. LENGTH
100
98
96
0
48
96
144
192
240
288
336
HOURS AFTER PRESERVATION
HERRING
BETWEEN 5-8 gm. INITIAL WEIGHT
BELOW 1 gm. " "
SPRATS
ABOVE 10 gm. INITIAL WEIGHT
% OF INITIAL BODY WEIGHT
100
80
60
0
48
96
144
192
240
288
336
HOURS AFTER PRESERVATION

Appendix 2. MEAN LENGTH, WEIGHT, VERTEBRATE AND KEELED SCALES OF AUTUMN-SPAWNED, O-GROUP HERRING OF THREE YEAR-CLASSES (SAMPLES OVER 40 HAVE BEEN ANALYSED).

	FIRTH OF LORNE								LOCH ETIVE							
	Length mm			Weight gm			Mean Vert.	Mean K.S.	Length mm			Weight gm			Mean Vert.	Mean K.S.
Date	1970	1971	1972	1970	1971	1972			1970	1971	1972	1970	1971	1972		
11th Apr.			40.4			0.198	56.46									
22nd Apr.		44.8			0.216		56.44									
3rd June		50.8			0.562		56.36									
8th June			64.8			1.32										
11th June	62.1			1.04			56.51		57.4			0.801			56.57	
14th July																
19th July		80.8			2.39		56.48									
20th July	85.7			2.18			56.56									
7th Aug.									81.8			2.39			56.49	
9th Aug.			86.2			3.75	56.48									
19th Aug.		103.0			6.04		56.55									
24th Aug.	85.3			2.29			56.46									
25th Aug.		104.3			6.02		56.54	14.18								
3rd Sept.										96.1			4.46		56.53	14.33
21st Sept.		106.4			5.72		56.43									
24th Sept.	106.3			5.53			56.63			113.5			6.67		56.54	
5th Oct.											121.7			9.55	56.54	14.25
6th Oct.		115.4			8.63		56.48			118.5			8.59		56.45	
9th Nov.		109.9			6.17		56.44									
8th Dec.		123.7			8.91		56.49	14.19		116.5			7.06		56.60	
20th Jan.	124.1			11.84			56.54			123.5			7.98		56.51	
10th Feb.										123.2			8.42		56.55	14.18
25th March		125.5			8.73		56.45	14.24		130.4			9.59		56.58	14.32
30th March	125.0			7.94			56.48									
10th April										136.4			13.81		56.39	14.17
10th June		146.6			21.78											
15th June	147.1			23.4			56.60									
23rd Aug.		166.6					56.53									

Appendix 3. MEAN TOTAL LENGTH, WEIGHT, VERTEBRAE AND KEELED SCALES OF SPRING-SPAWNED, O-GROUP HERRING OF THREE YEAR-CLASSES.

	FIRTH OF LORNE								LOCH ETIVE							
	Length mm			Weight gm			Mean Vert.	Mean K.S.	Length mm			Weight gm			Mean Vert.	Mean K.S.
Date	1970	1971	1972	1970	1971	1972			1970	1971	1972	1970	1971	1972		
3rd June		41.2			0.18		56.96									
8th June			53.6			0.56										
11th June	44.5			0.20			56.99									
14th July			59.1			0.84	57.09									
20th July	64.8			1.01			57.00									
26th July		60.5			0.86		56.90				56.30			0.70	57.22	
6th Aug.	64.4			1.04			56.91		57.2			0.62			57.14	
16th Aug.			67.5		1.29		56.90									
5th Oct.											86.2			3.39	56.94	
11th Oct.									74.9			2.03			56.93	
9th Nov.		83.1		2.44			56.97	13.75								
2nd Dec.									81.8			2.36			56.85	
8th Dec.										88.5			3.12		56.94	
8th Feb.									82.7			2.46			57.16	13.94
10th Feb.										88.3			2.73		57.04	
16th March									75.1			1.86			56.90	13.96
31st May									117.4			11.43			57.00	

Appendix 4.

MEAN LENGTH AND WEIGHT OF O-GROUP SPRATS OF THREE YEAR-CLASSES

	T. LENGTH mm						WEIGHT gm					
	F. OF LORNE		L. SPELVE		L. ETIVE		F. OF LORN		L. SPELVE		L. ETIVE	
Date Y.Class	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971
31st May		31.6				31.4		0.13				0.13
27th July		55.0				61.2		0.75				1.07
4th August	50.03			56.0			0.49			0.79		
6th August			47.4		51.1				0.43		0.49	
22nd August	58.8						0.84					
24th August		70.0						2.01				
3rd September						71.2						2.03
22nd September			68.4	70.9					1.83	1.81		
6th October		71.5				73.0		1.76				2.08
12th October	61.5			70.1			1.28			2.03		
9th November				69.0						1.56		
20th November			82.3						2.92			
2nd December			71.6		61.0				1.90		1.23	
7th December				73.0		69.3				1.93		1.42
16th January			85.5						3.67			
21st January				68.2						1.48		
10th February	65.1	76.7			67.5	69.4	1.20	2.29			1.26	1.11
18th March		96.5						4.38				
29th March	91.8		82.6	68.4	7.31		3.50		2.87	1.72	1.71	
10th April		91.1				81.6		4.11				3.10
20th April	92.4						4.63					
10th May			99.2						6.85			
8th June		102.9						7.61				
15th June	104.0						9.01					
20th June				100.5						7.88		
19th July	106.6						8.64					
28th July				101.0					7.89			
5th August			104.4						7.81			
10th August		103.9						8.62				
24th August	111.4						10.8					
22nd September	111.4		109.5		111.0		9.83		9.11		9.68	
23rd September		109.1		105.1		106.8		10.64		8.43		8.51

Appendix 4.

MEAN LENGTH AND WEIGHT OF O-GROUP SPRATS OF THREE YEAR-CLASSES

	T. LENGTH mm						WEIGHT gm					
	F. OF LORNE		L. SPELVE		L. ETIVE		F. OF LORN		L. SPELVE		L. ETIVE	
Date Y.Class	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971	1970	1971
31st May		31.6				31.4		0.13				0.13
27th July		55.0				61.2		0.75				1.07
4th August	50.03			56.0			0.49			0.79		
6th August			47.4		51.1				0.43		0.49	
22nd August	58.8						0.84					
24th August		70.0						2.01				
3rd September						71.2						2.03
22nd September			68.4	70.9					1.83	1.81		
6th October		71.5				73.0		1.76				2.08
12th October	61.5			70.1			1.28			2.03		
9th November				69.0						1.56		
20th November			82.3						2.92			
2nd December			71.6		61.0				1.90		1.23	
7th December				73.0		69.3				1.93		1.42
16th January			85.5						3.67			
21st January				68.2						1.48		
10th February	65.1	76.7			67.5	69.4	1.20	2.29			1.26	1.11
18th March		96.5						4.38				
29th March	91.8		82.6	68.4	7.31		3.50		2.87	1.72	1.71	
10th April		91.1				81.6		4.11				3.10
20th April	92.4						4.63					
10th May			99.2						6.85			
8th June		102.9						7.61				
15th June	104.0						9.01					
20th June				100.5						7.88		
19th July	106.6						8.64					
28th July				101.0					7.89			
5th August			104.4						7.81			
10th August		103.9						8.62				
24th August	111.4						10.8					
22nd September	111.4		109.5		111.0		9.83		9.11		9.68	
23rd September		109.1		105.1		106.8		10.64		8.43		8.51

Appendix 5.

RANGE IN MEAN NUMBERS OF VERTEBRAE, KEELED SCALES AND L_1, AND ALSO RANGE IN L_1 DISTRIBUTION, OF KNOWN SPAWNING STOCKS OF HERRING.

Author	Vert.	K.S.	Mean L_1 cm	Range in L_1 cm	Stock
Wood (1936)	57.03-57.21	-			Clyde Spring Spawners
Wood (1951)	-		9-12		Clyde Spring Spawners
Wood (1960	56.98-57.21	14.09-14.25			Clyde Spring Spawners
*Marshall et al. (1937)	55.97-55.16	-			Clyde Spring Spawners
* " "	55.40-55.65	-			Origin not given
Bowers (1964)	56.9 -57.2	-			Clyde Spring Spawners
" (1962)	56.36-56.41	-			Manx Autumn Spawners
Symonds (1964)	56.33-56.49	-	13.63-14.46	7-19	Manx Autumn Spawners
Baxter (1958)	56.93-57.07	-	10.5 -13.43	7-18	Minch Spring Spawners
Baxter (1958)	56.40-56.52	-	11.9 -13.2	7-19	Minch Autumn Spawners
Saville (1971)	56.59-56.62	14.19-14.30	-	-	Minch Autumn Spawners
Saville (1971)	56.32-56.49	14.02-14.53	14.0 -14.8	7-21	Buchan Autumn Spawners
Saville (1963)	56.98-57.13	14.20-14.25	9.3 -11.7	6-18	Clyde Spring

*Urostyle not taken into account.

Appendix 6.

MATURITY SCALE USED IN THE CLASSIFICATION OF SPRAT GONADS (MODIFIED AFTER JOHNSON, 1970).

		Males	Females
Stage I.	- Immature	Gonads thin and thread like and sex determination by inspection is almost impossible at this stage	
Stage II. A	- First signs of development. - encountered in O-gr. fish during the winter months.	The gonads occupy about half the body cavity and is flattened and greyish in colour. It widens towards the distal end.	The gonads are greyish in colour and larger and taper gradually towards the anterior end.
Stage II. B	- Resting phase.	Testes are firm and flattened tend to occupy almost the full length of the cavity.	May be colourless or reddish, eggs hardly visible on the outside.
Stage III.	- Advanced development	Testes show increased vascularisation and are wider.	Opaque, yellowish, large oocytes visible.
Stage IV.	- Mature	The testes are at their maximum size and are very soft. They show increased signs of vascularisation.	Ovaries swollen fully and translucent eggs are present.
Stage V.	-	Testes fully developed and slight pressure produces milt.	Ovaries very soft and swollen, slight pressure produces eggs.
Stage VI.	-	Testes very flattened and thin	Ovary small and wrinkled; very red.
Stage VI-II	- Recovery phase	Testes filling out slightly and becoming firmer.	Ovary gradually becoming smoother and rounded.

Appendix 7.

RESULTS OF THE LARVAL SURVEYS OF 1969, 1970, 1971 AND 1972 IN WHICH CLUPEIDS WERE OBTAINED.

Year	Total no. of samples	Date	Clupeids*	Herring	Sprats
1969	3	-	-	-	-
1970	42	16 April	2	-	-
		2 June	1	-	-
		3 June	4	-	-
		20 Aug.	-	-	2
1971	56	31 March	-	1	1
		10 May	-	-	1
		8 May	-	-	1
1972	56	15 March	-	-	3
		12 April	-	2	9
		8 May	-	-	2

* When herring and sprat larvae were not identified individually they were grouped together as clupeids.

Appendix 8.

PERCENTAGE OF IMMATURE MALES AND FEMALES IN EACH HALF CENTIMETRE LENGTH GROUP (SPRATS)

(Pooled data from the 1971 and 1972 Spawning seasons).

Length Group mm.	MALES		FEMALES	
	No. Sampled	% Immature	No. Sampled	% Immature
70-74	39	94.6	46	100%
75-79	67	93.7	47	90.7
80-84	66	75.5	50	78.1
85-89	54	57.9	56	60.0
90-94	78	34.1	108	36.4
95-99	136	38.1	78	34.1
100-104	157	15.3	145	16.5
105-109	187	7.2	129	7.5
110-114	211	4.6	179	1.1
115-119	161	3.7	155	3.8
120-124	95	2.1	115	1.8
125-129	60	0.0	84	0.0
130-134	83	0.0	92	0.0
135-139	41	0.0	48	3.5

Appendix 9.

RELATIVE IMPORTANCE OF FOOD ITEMS OF O-GROUP HERRING, WEIGHTED BY THE TOTAL FOOD CONSUMED

Month	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total	%
Type														
Copepoda	84.9		98.2	93.4	83.9	95.2	19.4	91.2	70.5	82.0	68.7	16.3	803.7	73.00
Cladocera	12.1		0.3	4.2	11.3	0.4	-	0.3	-	4.0	0.1	62.5	95.2	8.64
Balanus cyprids	0.8		-	-	0.03	0.1	1.0	-	-	-	-	1.6	3.53	0.32
Decapod larvae	-		0.6	0.5	1.1	0.7	2.7	0.1	0.1	8.0	3.6	0.9	18.3	1.66
Nauplii	-		-	-	-	-	-	-	-	-	-	18.5	18.5	1.68
Oikopleura	2.1		0.9	1.8	3.6	3.2	72.5	8.0	28.5	4.0	12.1	0.2	136.9	12.43
Bivalve larvae	-		-	-	-	0.3	4.0	-	0.3	2.0	-	-	6.6	0.60
Sagitta	-		-	-	-	-	0.3	2.0	0.5	-	15.4	-	18.2	1.65
													1100.93	

Appendix 10.

RELATIVE IMPORTANCE OF FOOD ITEMS OF O-GROUP SPRATS, WEIGHTED BY THE TOTAL FOOD CONSUMED IN EACH MONTH.

Month	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total for the year	%
Type											
Copepoda	74.0	85.2	81.0	72.6	88.5	59.4	86.5	70.0	13.5	630.7	70.1
Cladocera	16.6	6.7	1.6	3.8	5.6	-	0.6	4.2	71.5	110.6	12.3
Balanus cyprids	0.6	-	0.2	0.2	-	-	-	-	0.3	1.3	0.14
Decapod larvae	0.4	0.7	0.6	0.2	-	-	0.1	0.7	0.4	3.1	0.34
Nauplii	-	-	-	-	-	-	0.6	-	11.1	11.7	1.30
Oikopleura	1.3	7.3	15.6	22.6	5.9	29.2	12.1	25.0	3.1	122.1	13.57
Bivalve larvae	7.0	0.02	1.0	0.6	-	11.4	-	0.1	0.01	20.1	2.23
Sagitta	-	-	0.03	-	-	-	-	-	-	0.03	
										899.6	

Appendix 11 THE MEAN MONTHLY PERCENTAGE OF 'FEEDING' HERRING AND THE RELATIVE IMPORTANCE OF THE FOOD SPECIES CONTAINED IN THE MONTHLY SAMPLES FROM APRIL 1970 TO MARCH 1972.

Month	April			May			June			July		
Year	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean
No. Sampled	44	35		34	36		54	22		30		
% Feeding	97.72	97.14	98.28	94.1	94.4	94.28	85.18	100		100		
Copepods	29.84	72.85	41.07	87.02	95.9	93.9	99.3	99.5	99.5	22.17		
Cladocera												
Balanus cyprid	17.24	8.50	14.96	9.60	1.60	3.40	0.07	0.006	<0.01			
Decapod larvae	1.00	2.20		0.60	0.20	0.30	0.09	0.03	0.04			
Schizopod		1.2	0.31	2.40	0.80	1.20	0.27	0.18	0.20	77.82		
Other Crustaceans	0.05		0.04									
Fish larvae	50.51		37.31									
Oikopleura	1.37	15.13	4.96	0.10	0.60	0.50	0.07					
Sagitta				0.20	0.70	0.60	0.18	0.24	0.22			
Mollusc	.01	0.10	0.04		0.04	0.03		.002				
Pts/Indiv. feeding	412.67	142.57	375.04	156.56	219.3	382.9	3004.0	4217.17	3594.6	487.6		

Month	August			September			October			November			December	
Year	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'7
No. Sampled	28	45		32	63		17	25		42				
% Feeding	100	80.0	87.67	96.8	66.15	76.28	70.58	80.00	74.57	42.85				
Copepods	67.02	0.36	21.88	22.5	43.5	38.4	28.60	43.63	43.36	71.76				
Cladocera														
Balanus cyprid														
Decapod larvae	1.40		0.44	4.90	1.39	2.24	-	22.90	22.48					
Schizopod	31.32	99.6	77.55	71.7	52.27	57.03	70.20		1.28	20.52				
Other Crustaceans														
Fish larvae														
Oikopleura	0.26		0.08	0.88	2.78	2.31								
Sagitta								33.45	32.84					
Mollusc							1.3		0.02					
Pts/Indiv. feeding	164.6	378.0	271.3	182.0	401.3	291.65	28.0	322.08	175.04	17.0				

September			October			November			December			January			February			March		
'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean
32	63		17	25		42						64	44		46	42		54	33	
96.8	66.15	76.28	70.58	80.00	74.57	42.85						40.60	45.50	42.60	78.2	78.50	78.40	98.90	90.90	89.68
22.5	43.5	38.4	28.60	43.63	43.36	71.76						92.50	4.40	57.40	76.68	30.80	60.90	0.89	9.20	1.63
															14.80		9.64	96.2	89.80	95.68
																		2.3	0.47	2.11
4.90	1.39	2.24	-	22.90	22.48							0.34		0.20	0.48		0.05	0.18	0.22	0.18
71.7	52.27	57.03	70.20		1.28	20.52						6.82	66.60	35.00	0.76	68.80	25.29			
													26.6	6.11	1.3		0.29			
0.88	2.78	2.31																		
				33.45	32.84							0.39	1.30	0.82		0.14	0.08		0.25	0.38
			1.3		0.02								0.88	0.40	5.50	0.28	3.67		0.40	
182.0	401.3	291.65	28.0	322.08	175.04	17.0						22.53	22.5	22.52	142.97	127.88	135.42	1521.09	311.8	819.02

Appendix 12 THE MEAN MONTHLY PERCENTAGE OF 'FEEDING' SPRATS (OVER A YEAR OLD) AND THE RELATIVE IMPORTANCE OF THE FOOD SPECIES CONTAINED IN THE MONTHLY SAMPLES, FROM APRIL 1970 TO MARCH 1972.

Month	April			May			June			July			August			September			October			November			Decembe
Year	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70
No. Sampled	41	51		45	70		44	32		19	56		40	36		54	46		52	42		52	26		45
% Feeding	80.48	100	91.30	100	97.15	98.27	100	100		100	92.80	93.80	100	100	100	100	65.26	84.00	69.20	71.42	70.2	61.53	80.17	67.96	35.55
Copepods	57.84	67.70	64.12	88.35	98.10	95.40	91.30	97.60	94.20	78.5	67.90	69.91	93.60	81.90	92.10	98.20	71.57	92.33	57.90	17.30	26.42	27.26	64.26	52.36	89.49
Cladocera	3.93	4.40	4.24	2.75	0.07	0.80	0.07		0.04	10.97	0.07	2.57	1.44	2.90	1.62	0.25	0.08	0.21		0.14	0.10	0.47		0.13	
Balanus cyprid	5.34	8.50	7.40	2.06	0.20	0.70	0.12	0.01	0.07				0.10		0.09	0.02	0.47	0.12		0.56	0.43				
Decapod larvae	0.38	0.60	0.55	1.45	0.09	0.40	0.14	0.04	0.09	0.95	0.29	0.41	0.24		0.21	0.48	0.29	0.44	1.75	3.09	2.79	0.95		0.28	
Schizopod					0.90	0.70		0.22	0.10	9.50	0.88	2.48		3.75	0.47	0.10	1.68	0.45	1.35		0.30	14.35	3.51	8.37	8.28
Other Crustaceans	32.49		11.52													0.08		0.06							
Fish larvae																									
Oikopleura		18.70	12.04		0.50	0.30	8.30	0.04	5.49		30.58	24.92	4.52	11.01	5.34	0.81	25.8	6.34		78.87	61.19	56.80	30.85	38.76	0.55
Sagitta								2.06	0.02		0.21	0.18	0.06		0.06				22.31		5.00		1.36	0.13	1.66
Mollusc		0.04	0.02		0.01	0.01					0.21			0.37	0.04		0.08	0.06	16.60						
Pts/Indiv. feeding	386.44	355.27	355.27	228.87	506.64	367.75	489.4	558.31	523.8	102.9	232.7	167.8	288.6	81.48	185.04	542.4	186.15	364.27	269.76	173.1	221.44	50.95	58.73	56.06	10.4

September			October			November			December			January			February			March		
'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean	'70	'71	Mean
54	46		52	42		52	26		45	34		50	52		30	48		47	50	
100	65.26	84.00	69.20	71.42	70.2	61.53	80.17	67.96	35.55	85.30	56.90	48.00	53.84	50.98	80	83.30	82.0	78.70	92.60	85.50
98.20	71.57	92.33	57.90	17.30	26.42	27.26	64.26	52.36	89.49	48.80	56.22	33.26	98.30	36.31	83.47	22.06	50.20	6.90	4.56	5.78
0.25	0.08	0.21		0.14	0.10	0.47		0.13							14.56	0.47	6.90	90.50	88.05	89.67
0.02	0.47	0.12		0.56	0.43													1.35	0.59	0.97
0.48	0.29	0.44	1.75	3.09	2.79	0.95		0.28								0.47	0.20	0.30	0.32	0.31
0.10	1.68	0.45	1.35		0.30	14.35	3.51	8.37	8.28		1.60									
0.08		0.06										6.33		6.06					2.01	0.55
0.81	25.8	6.34		78.87	61.19	56.80	30.85	38.76	0.55	51.04	41.76	59.97	1.70	57.25		76.98	41.60	0.90	4.33	2.71
			22.31		5.00		1.36	0.13	1.66	0.13	0.42	0.41	0.40	0.40	1.95		0.89			
	0.08	0.06	16.60																	
542.4	186.15	364.27	269.76	173.1	221.44	50.95	58.73	56.06	10.4	26.48	21.08	101.16	4.21	48.96	79.16	34.16	56.6	917.22	617.5	767.3

Appendix 13 RELATIVE IMPORTANCE OF FOOD ITEMS IN EACH MONTH OF THE YEAR IN HERRING (1+ AND OVER) STOMACHS, AS WEIGHTED BY THE PERCENTAGE OF FEEDING INDIVIDUALS

Type	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total for Year	%
Copepoda	40.54	88.52	91.37	22.17	19.18	29.29	33.33	30.74		24.4	47.74	1.46	428.74	48.8
Balanus cyprids	14.77	3.20	0.01								1.89		19.87	2.26
Cladocera											7.50	85.80	93.30	10.63
Decapod larvae	0.36	0.37	0.03		0.38	1.7	0.95			0.08	0.03	0.16	4.06	0.46
Schizopoda	0.30	1.13	0.18	77.82	67.82	67.98	43.51	16.76	8.79	14.90	19.82		251.19	28.61
Other Crustacea										2.60	0.09		2.69	0.30
Fish larvae	36.83												36.83	4.11
Oikopleura	5.89	0.47	0.06		0.07	1.76	24.48	3.29		0.34	0.04	0.34	36.74	4.18
Sagitta		0.56	0.20				0.01			0.17	2.87		3.81	0.43
Bivalve larvae	0.04	0.28											0.32	0.04
												Total	877.55	

Appendix 14

RELATIVE IMPORTANCE OF FOOD ITEMS IN EACH MONTH OF THE YEAR IN SPRAT (1+ AND OVER) STOMACHS, AS WEIGHTEDBY THE PERCENTAGE OF FEEDING INDIVIDUALS

Type	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Total for year	%
Copepoda	58.60	93.75	94.20	65.47	92.10	77.51	19.54	35.57	32.02	18.51	41.16	4.91	633.34	64.63
Balanus cyprids	6.75	0.68	0.07		0.09	0.10	0.30					0.83	8.82	0.90
Cladocera	3.87	0.78	0.04	2.41	1.62	0.17	0.07	0.08			5.65	76.66	91.35	9.32
Decapod larvae	0.50	0.39	0.09	0.38	0.21	0.36	1.96	0.19			0.16	0.26	4.50	0.46
Schizopoda		0.68	0.10	2.32	0.47	0.37	0.24	5.68	0.91				10.77	1.09
Other Crustacea	10.51									3.08		1.72	15.31	1.56
Fish larvae														
Oikopleura	10.99	1.29	5.49	23.07	5.34	5.32	43.96	26.29	22.78	29.17	34.11	2.31	210.12	21.44
Sagitta			0.02	0.17	0.06		3.51	0.09	0.24	0.20	0.73		5.02	0.51
Bivalve larvae	0.02		0.01		0.04	0.01	0.63						0.71	0.07
												Total	979.94	

Appendix 15 RESULTS OF THE SURVEY ON THE 9TH - 11TH OF AUGUST TO STUDY THE DAILY FEEDING PERIODICITY OF HERRING AND SPRATS*

		O-GROUP HERRING				O-GROUP SPRATS				HERRING 1+OVER				SPRATS 1+ OVER			
Time B.S.T.	Gear	n	% Empty	Mean a	Range in a	n	% Empty	Mean a	Range in a	n	% Empty	Mean a	Range in a	n	% Empty	Mean a	Range in a
0700-0740	OT	33	6.06	0.559	1.88-	18	16.60	0.261	0.676-	40	7.50	0.487	2.750-	80	2.5	0.147	0.689
1000-1040	OT	52	00	0.788	2.387- 0.134	20	00	0.944	2.477- 0.047	11	8.33	0.834	1.738-	75	00	0.452	1.295- 0.031
1300-1340	OT	31	00	1.135	2.209- 0.156	44	00	1.034	2.678- 0.380	6	00	0.512	1.515- 0.029	75	00	0.642	1.409- 0.131
1600-1640	OT	68	00	1.070	3.978- 0.118	24	00	0.903	3.409- 0.077	12	00	0.930	2.074- 0.052	78	00	0.519	1.305- 0.179
1800-1830	OT	46	17.40	0.447	5.428-	30	10.00	0.528	1.033-	6	16.70	1.180	4.712-	80	00	0.471	1.284- 0.066
2200-2240	MT	66	1.50	0.738	3.444-	36	5.55	0.637	3.001-	3	00	0.881	1.054- 0.706	56	1.7	0.467	1.370-
0100-0140	MT	59	15.20	0.533	4.090-	48	37.50	0.627	2.180-	3	66.66	0.077	0.077-	34	2.8	0.202	0.534-
0400-0440	MT	76	31.60	0.126	1.103-	50	44.00	0.284	1.058-	-	-	-	-	70	2.85	0.129	0.380-
Total Analysed		431				270				81				548			

*

OT - Otter trawl

MT - Mid-water trawl

n - the number sampled

a - weight of the stomach contents expressed as a percentage of the body weight.

II