Aspects of the Ecology of Gadoid Fish of the West Coast of Scotland.

By

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Adrian Cooper

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ABSTRACT

The distribution, abundance, growth, length-weight relationships and reproductive ecology of whiting, Norway pout and poor-cod populations were studied in inshore and offshore areas around Oban from November 1974 to March 1977.

Planktonic stages and mature adults were found only at offshore sites, the inshore areas being nursery grounds for all three species. Immigration occurred between June and December of the 0-group when the fish were nektonic, with part of the population pelagic and part demersal. In whiting the young fish aggregated for a short period inshore, but in other species abundance was always greater offshore.

Norway pout and poor-cod remained on the nursery grounds for between one and two years, whereas few whiting remained longer than one year. In all species shallower sampling sites were vacated more rapidly than deeper ones. The migration of fish offshore is considered in relation to growth, diet and maturation. The ecological significance and management implications of the migrations are discussed.

The rate of growth in length and weight varied seasonally, being more rapid in summer and autumn in all species. Differences were found between localities in rate of growth and are thought to be due to a preference by older fish for deeper water.

Only the poor-cod spawned in the study area, at Tiree Passage and on the south-west coast of Mull. Spawning occurred between January and May, with a peak in April. Females matured at a mean length of 15.6 cm in the 2-group with only a small proportion of 1-group fish maturing. In males the average age of first maturity was lower (14.0 - 14.6 cm) and a greater proportion of 1-group fish matured, which compensated for a slightly lower survival rate in older fish and equalised the sex-ratio of the spawning population. The success of reproduction was highly **dependent** on a single year-class, since 83.3% of reproducing females belonged to the 2-group.

Although ripe and spent whiting and Norway pout were caught at offshore sites no spawning fish were encountered. The possibility of a spawning migration out of the area and the locality of spawning is discussed for each species.

Length-weight relationships were calculated for each species and significant differences were found between males and females in all cases. Seasonal variations in condition were studied by calculation of condition factors and by analysis of monthly length-weight relationships.

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SECTION 1

INTRODUCTION, MATERIALS AND METHODS

1. 1. INTRODUCTION

The Gadidae are a family of bony fishes belonging to the order Gadiformes (or Anacanthini). The taxonomy and specific characters of the order have been reviewed by Regan(1903), Svetovidov(1948) and Marshall and Cohen(1973). Although there are differences of opinion concerning the taxonomic status and interrelationships of many of the families, the position of the Gadidae seems fairly well established. Regan(1903) and Svetovidov(1948) include both hake-like(Merlucciinae) and cod-like (Gadinae) sub-families in the Gadidae, whereas Greenwood, Rosen, Weitzman and Myers(1966) and Marshall and Cohen(1973) recognise two families, the Gadidae and the Merlucciidae.

The gadoids considered in this study are: Merlangius merlangus (Linnaeus, 1758) (Gadus merlangus), commonly known as the whiting ; Trisopterus esmarkii (Nilsson, 1855) (Gadus esmarkii), commonly known as the Norway pout and Trisopterus minutus (Linnaeus, 1758) (Gadus minutus), commonly known as the poor-cod. These species were chosen because of their abundance in the study area. The Norway pout was the most numerous, although the whiting had the greatest biomass. The poor-cod was the least abundant of the three species.

The opening of the Scottish Marine Biological Association Laboratory at Dunstaffnage in 1969 stimulated extensive surveys of the ecology of fish populations of the inshore areas around Oban. Pemberton(1976a, 1976b) studied trout populations in Loch Etive, while De Silva(1973a, 1973b, 1973c, 1973d) and Gordon(1977a, 1977b, 1977d) found that the inshore areas studied were nursery grounds for young clupeids and gadoids. De Silva found that both autumn and spring-spawned young herring occurred in the area and from the evidence of meristic characters concluded that the autumn spawners originated from the Minch, and the spring-spawners were probably of Clyde origin. The sprat populations were probably derived from a local spawning. Gordon inferred that Norway pout and whiting migrated into the area from the open sea since there was no evidence of local spawning, apart from a small isolated stock of whiting in Loch Etive. The movement of young gadoid fish from offshore areas west of Mull to the inshore areas of Loch Linnhe and the Firth of Lorne forms the basis of this study. Specifically an attempt has been made to :

1. determine (if possible) the origin of the gadoid fish found by Gordon in the inshore areas ;
2. follow and determine the timing of the inshore migration of young fish ;
3. study aspects of the population dynamics of the species during the migration viz. growth, condition factor and length-weight relationships ;
4. study the reproductive biology of each species.

1. 2. MATERIALS AND METHODS

1.2.A. Sampling Area

The chart (Fig.1.1) shows the area studied. Fish populations at five sites (Loch Linnhe, Firth of Lorne, Bloody Bay, Ardalanish Bay and Tiree Passage) were sampled at approximately 3-weekly intervals from November 1974 to April 1977 (weather permitting). In calculations it was sometimes necessary to use week numbers rather than months, for statistical reasons. These weeks were numbered from 1st January and the corresponding dates are given in Appendix 1.1. The sampling sites were chosen to compare inshore and offshore environments, bearing in mind the suitability of the ground for trawling and the availability of ship-time.

Bathymetry

Fig.1.2 shows the bathymetry of the region, with many of the locations described in the text shown in Fig.1.1. The area is comparable to other glaciated shelves, with deep fiords showing complex systems of troughs and ridges. To the south-west the sea floor is shallow and even, apart from the rocky outcrops of Skerryvore and Dubh Artach. Further north between the islands of Coll/Tiree and Mull a central wide shallow ridge separates two deep valleys running north-east to south-west, the ridge forming the Treshnish Isles above sea level. Two shallow lochs cut the Island of Mull almost into three sections. Mull is separated from the mainland by the Sound of Mull to the east, which rarely exceeds a depth of 60m. To the north a deep trough extends almost into the Bloody Bay sampling area. The deep valley of the Great Glen results in deep water at the Loch Linnhe sampling site. North of Lismore Light is a very deep trough which Gordon (1977c) considers may explain the unusual occurrence of juvenile blue whiting (Micromesistius poutassou) at the Loch Linnhe sampling area. Sills separate this deep area from the Sound of Mull to the north and the Firth of Lorne to the south-west.

Fig.1.1. Chart showing the area studied and sampling sites.

	Site	Depth
1.	Loch Linnhe	90m
2.	Firth of Lorne	47m
3.	Bloody Bay	50m
4.	Ardalanish Bay	77m
5.	Tiree Passage	80m

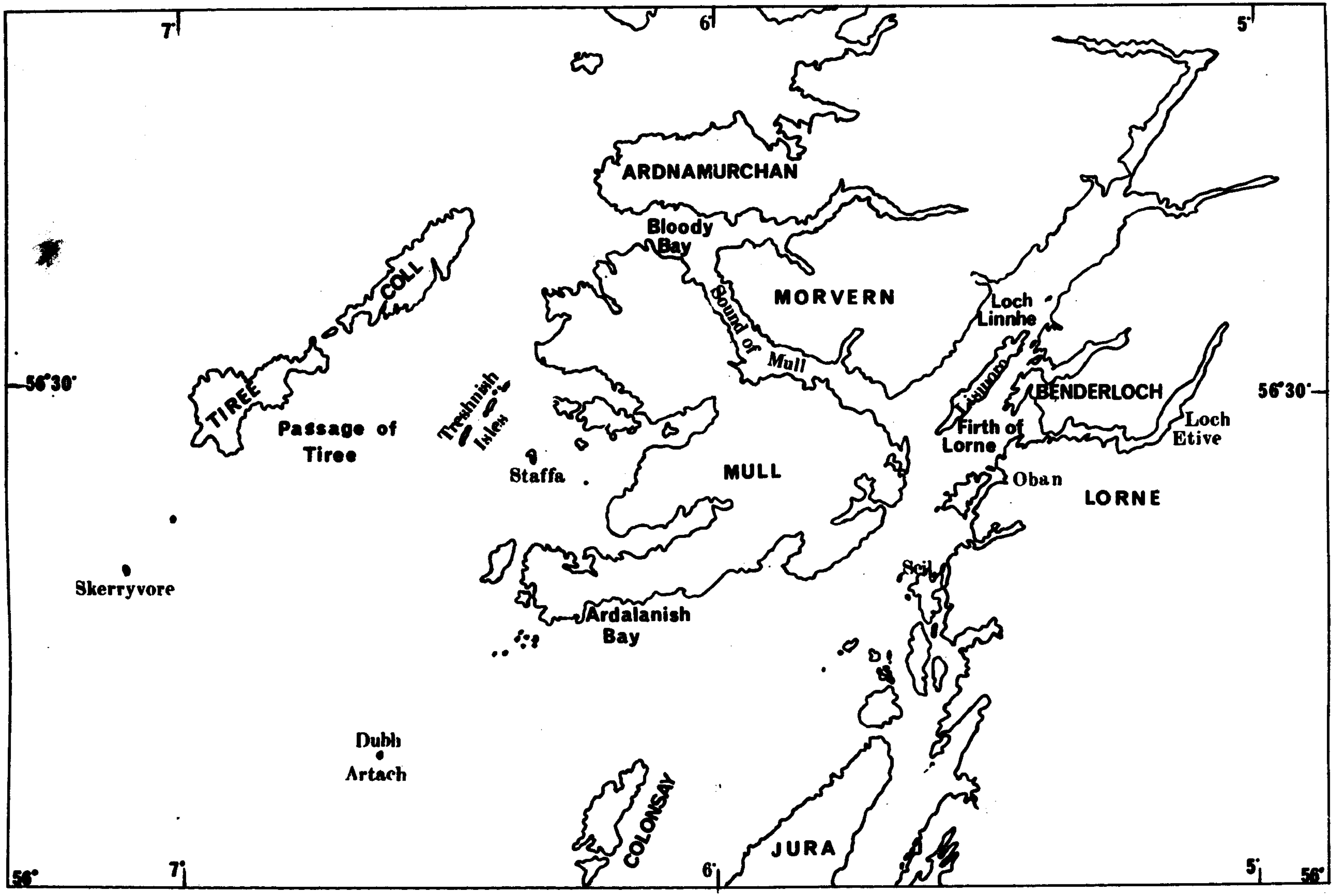
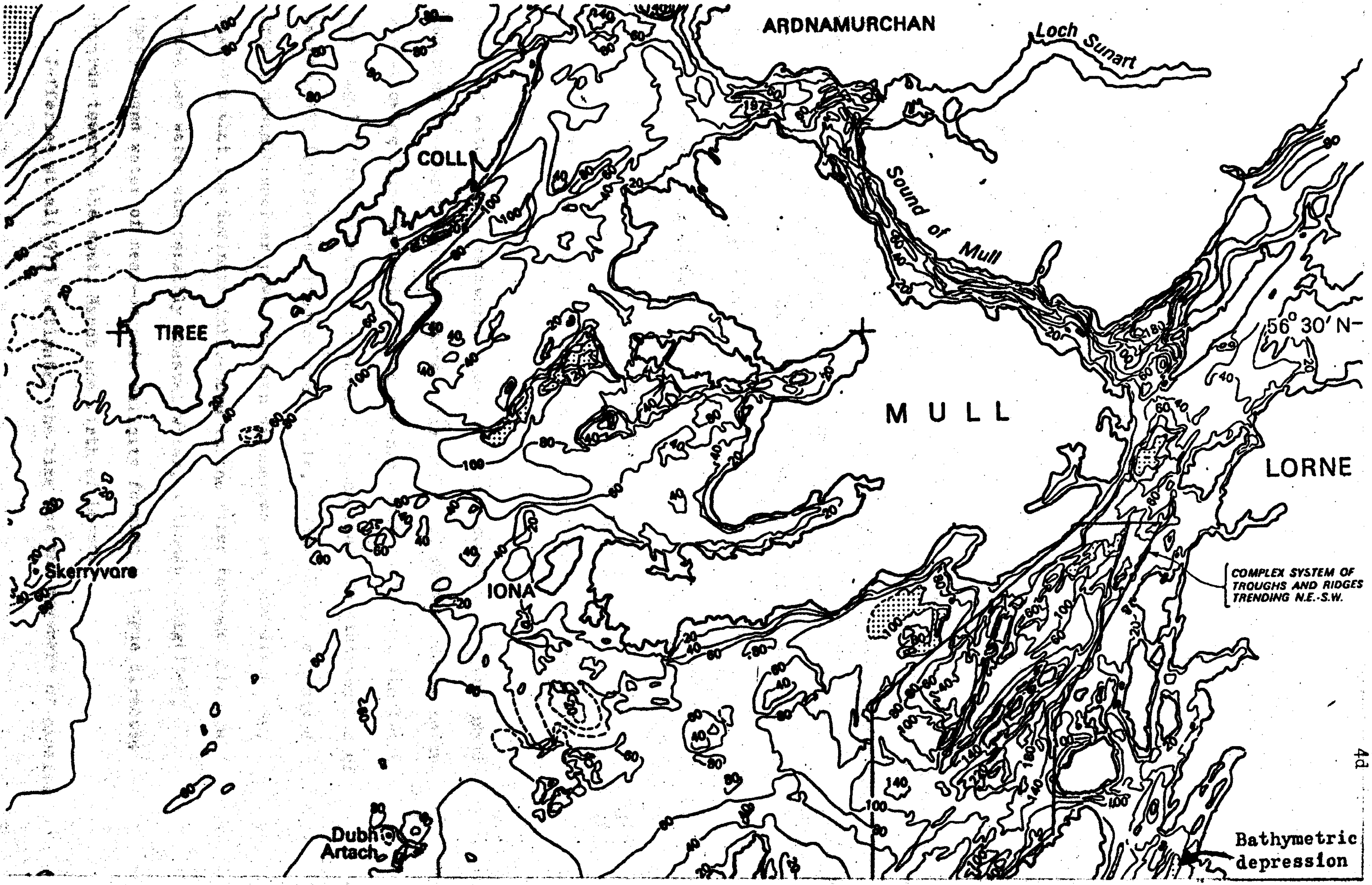

7°
6°
5°
56°30'
56°30'
56°
56°
ARDNAMURCHAN
Bloody Bay
MORVERN
Sound of Mull
Loch Linnhe
Lismore
BENDERLOCH
Loch Etive
Firth of Lorne
Oban
LORNE
COLL
TIREE
Passage of Tiree
Treshnish Isles
Staffa
MULL
Seil
Ardalanish Bay
Skerryvore
Dubh Artach
COLONSAY
JURA

Fig.1.2. Bathymetry of the sampling area. Isobaths in metres below mean sea level. Universal Transverse Mercator Projection.

From (1) I.G.S. Report 73/14 - The Sea of the Hebrides - Bathymetry.

(2) Admiralty Chart 2814A. Loch Linnhe, Southern Part.


ARDNAMURCHAN
Loch Sunart
COLL
Sound of Mull
TIREE
56° 30′ N
M U L L
LORNE
Skerryvore
IONA
COMPLEX SYSTEM OF TROUGHS AND RIDGES TRENDING N.E.-S.W.
Dubh Artach
Bathymetric depression

Between Lismore and Lorne/Benderloch the seabottom is again shallow and even. Further south between Seil Island and Mull there is a complex system of troughs and ridges running in a north-east to south-west direction. To the west and south of Mull the seabottom slopes quite steeply and evenly to a depth of 60 - 80m between Colonsay and Mull, although to the north-west there is shallow water.

Hydrography

The hydrography of the west coast of Scotland has not been studied as a whole, although several authors have deduced circulation patterns based on the limited information available e.g. Tulloch and Tait (1959), Craig (1959) and most recently Ellett (in press). All authors stress the sparseness of the data and lack of long term measurements. It seems fairly well established, however, that three main water types are important in the study area :

(1) Atlantic water derived from the north-east coast of Ireland ;

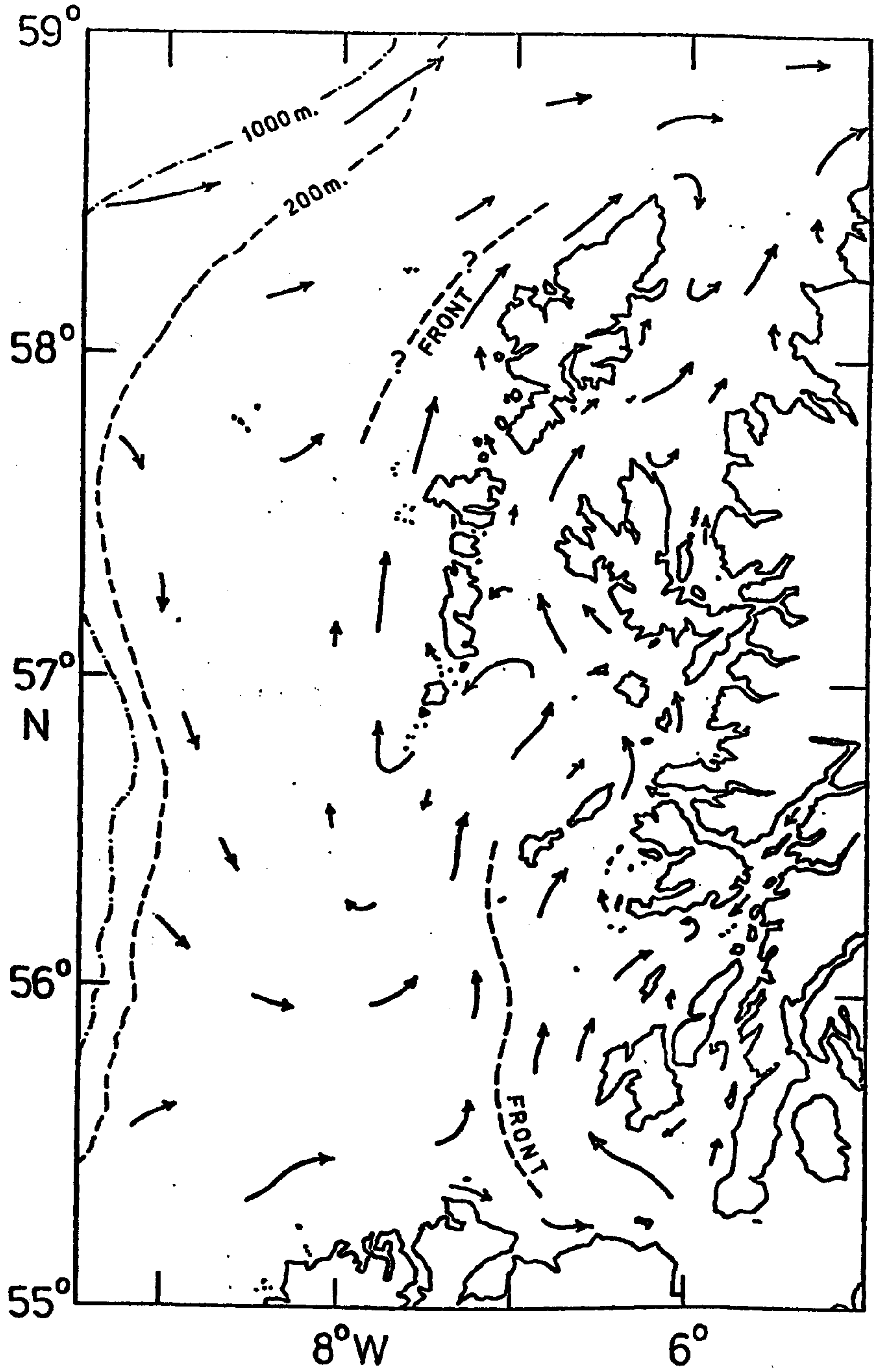
(2) Irish Sea water from the North Channel ;

(3) Coastal water formed locally as a result of rainfall run-off.

Atlantic water flows eastwards along the north coast of Ireland until reaching the North Channel, where it is deflected northwards by northward-flowing Irish Sea water. Some oceanic water turns into the Irish Sea (Fig.1.3 from Ellett, in press). Evidence from the distribution of Caesium 137 (Jefferies, Preston and Steele, 1973), which is derived from Windscale nuclear power station discharges into the Irish Sea, suggests that the dominant influences in the Tiree Passage area are Irish Sea water and possibly coastal water, although Craig(1956, 1959) found water of near-oceanic salinity forming a tongue directed inwards towards the south Minch and Firth of Lorne.

Jefferies et al(1973) estimated the time for the movement of caesium

Fig.1.3. Surface circulation to the west of Scotland in summer (from Ellett, in press).


59°
58°
57°
N
56°
55°
8°W
6°
1000 m.
200 m.
FRONT
?
?
FRONT

from Windscale to the North Channel to be between 1.1 and 1.8 years, from consideration of the ^{137}Cs: ^{134}Cs ratios (^{134} Cs having an appreciably shorter half-life). In contrast Livingston and Bowen(1977) estimated the caesium transit time for the Minch to be 1.6 years and it was suggested that the difference could be a result of the mixing of water in the Irish Sea with older lower-ratio water. A net transit time of two years could be composed of 1.8 years mixing in the Irish Sea and 0.2 years moving from the North Channel to the Minch.

A front is formed west of Islay and south/south-east of Tiree 'As a result of the contrast of density and structure between the two waters' (Ellett,1977; Ellett,in press). Simpson, Edelsten, Edwards, Morris and Tett (in press) show the position of the Islay front in June 1977, from satellite infra-red imagery. Inshore (to the east) of the front the water was found to be vertically mixed while to the west of the front it was thermally stratified (Simpson et al, loc. cit.). The high productivity of frontal areas may influence survival of larval fish, which is frequently food-limited.

The hydrography of the sea lochs opening into the Firth of Lorne (Lochs Eil, Leven, Creran, Etive and Linnhe north of the Corran Narrows) has been described by Milne(1972). Little information is available concerning circulation in the outer Loch Linnhe/Firth of Lorne area, although Craig(1959) found net water movements to be inshore near the bottom and offshore at the surface. This overall circulation is to be expected considering the large freshwater surface run-off, although wind stress and tides will undoubtedly confuse the general pattern of net flow. Craig(loc. cit.) summarised the seasonal temperature structure for the west coast area :

(1) in the area of interest the surface water varies in salinity from 29.2‰ at Loch Linnhe to 35.1‰ at Tiree Passage ;

(2) there is little variation in salinity between surface and bottom water offshore, although inshore (at Loch Linnhe)

salinities rise to 31.5‰ on the bottom, as would be expected in an estuary ;

(3) seasonal variations in salinity are slight, with perhaps slightly lower surface salinities in winter due to increased precipitation ;

(4) winter (February) surface temperatures vary from 3°C inshore to 7°C at Tiree Passage and bottom temperatures from 4.5°C to 7.1°C;

(5) in July the situation is reversed with higher temperatures inshore (16°C at the surface, 13°C on the bottom) compared with Tiree Passage (13°C at the surface, 10°C on the bottom) ;

(6) isolated pockets of cold bottom water below 8°C exist in July in deep trenches between Mull and Jura, between Loch Spelve and the mainland, in Loch Linnhe, parts of the Sound of Mull, Loch Sunart and North of Mull ;

(7) these pockets of cold water lose their identity in October or early November.

There was evidence of a summer thermocline between the south-east coast of Mull and the mainland in June 1977, with salinities higher inshore than offshore and slightly higher closer to the bottom (Edwards, pers. comm.). Presumably this stratification breaks down to the south-east until the Islay front is reached, possibly as a result of the shallower water and the consequent greater effects of winds and tides.

1.2.B. Sampling Gear

Two research vessels were used during the survey: R.V. Calanus for bottom trawling, mid-water trawling and plankton sampling; occasionally R.V. Seol Mara for plankton sampling only. R.V. Calanus is a 23m motor fishing vessel (side trawler), while Seol Mara is an 11m inshore vessel, originally designed for shrimping and light trawling. The dimensions of the nets were standardised from November 1974 onwards, as was the fishing technique, as far as possible (see below).

Bottom Trawl

Throughout the survey a wing trawl was used, with a headline of 58 feet and a foot rope of 76 feet. De Silva (1973a) has described the net in detail, comparing catch composition and variations in fish length and age with catches from other nets. De Silva (loc.cit.) and Gordon (1973a) used a 1½ inch (38.1 mm) mesh cod-end with a ½ inch (12.7 mm) mesh cover and there were losses of the youngest 0-group fish. To obtain better samples of juvenile fish a 5.5 m cod-end extension of ⅝ inch (16 mm) mesh (measured knot to knot) was fitted in this study. All hauls lasted 40 min from the moment that the warps were fully paid out and squared off until the start of hauling.

Mid-water Trawl

Between June and September 1975, and June and December 1976, a Gourock No.1 mid-water trawl was used to collect pelagic juvenile fish. This net had a 90 feet (27.4 m) headline and a 90 feet ground rope, and was fitted with a ⅜ inch (9.5 mm) stretched mesh cod-end. This net has been described by De Silva (1973a). Comparative trawls during June and July 1974 showed that the catch rate was greater when the net was used at night and, since the length composition of day and night catches was the same, this net was subsequently only used during the hours of darkness.

A Kelvin Hughes M.S. 39 F/M Recording Echo Sounder was used to monitor the depth of the sea bottom and to detect pelagic fish. When targets were identified (often in the scattering layer at dusk) the depth of the net was adjusted to fish for them. The depth of the net was determined trigonometrically using an angle meter on the warps and with a knowledge of warp length from the net to the towing block. The accuracy of this method had previously been established by the use of a Netzsonde (Gordon, pers.comm.). The net depth could be varied by either changing the speed of the boat or the length of the warps.

Plymouth 2m Young Fish Trawl

A 2m young fish trawl was used to sample the egg and larval stages between February and August each year. The net, its performance and calibration have been described by Southward (1970). Oblique hauls were made of 20 min total duration at 1½ knots. The net was towed for 5 min with 50 fms (91.5m) and 25 fms (45.75m) of warp from the winch, 5 min at the surface with 5 min allowed for shooting and hauling.

1.2.C. Treatment of Material

Bottom Trawls

When catches were small all fish were separated into species and returned to the laboratory. When catches were large, especially between September and February when the abundance of 0-group fish was greatest, the total number of fish was estimated by sub-sampling and a sample of at least 200 fish of each species returned to the laboratory. Generally the number of 1-group and older fish was small, but occasionally at offshore sites it was necessary to sub-sample these fish. In summer months samples were preserved at sea in Drikold to prevent decay.

All fish were deep frozen in the laboratory for at least one week before they were examined. The total length of each fish from the anteriormost extremity to the end of the tail fin (with the two lobes moved into the position which gives the maximum length measurement) was measured to the nearest millimetre below i.e. the true length of a fish given a length of 113 mm may lie between 113.0 and 113.9 mm. The sex and maturity was determined according to a maturity scale developed for each species. The gut (including the liver and gonads) was then removed and the fish weighed on a Mettler P.160 balance to the nearest 0.1g below, for fish less than 160g. Fish weighing more than 160g were weighed to the nearest gram below. In calculating regression lines of length-weight relationships, lengths were converted to mm and weights to mg in order to avoid difficulties with bar logs. Samples of otoliths were collected for age determination. Initially all the fish were aged but later otoliths from 10 fish were collected from each 10 mm length group.

The method of aging has been described by Williams and Bedford (1973) : each otolith was cut in half, one half being mounted in plasticene with the cut surface uppermost. A Nikon low power zoom lens binocular microscope was used to examine the otoliths. When illuminated from the side, with the surface shadowed by a scalpel, hyaline rings are clear and light with opaque rings dark and shadowy. Difficult otoliths were clarified by brushing the surface with turpineol. The nucleus is opaque and, as with other opaque zones, is laid down in winter. The international convention of designating 1st January as the birthday of North Atlantic demersal fish species was followed. The detailed structure of the otolith has been described by Gambell and Messtorff(1964) for whiting, Raitt(1968b) for Norway pout and Menon (1950) for the poor-cod.

The presence of any large or obtrusive parasites was noted : Norway pout and poor-cod were infected with *Myxobolus aeglefini*, a myxosporidian parasite of the eye, at quite high rates. The presence of capsules in one or both eyes was noted.

Mid-water Trawls

All gadoid fish caught were identified and preserved in 4% formalin. A sample of fish was measured fresh to determine correction factors for shrinkage. At the laboratory all fish were counted and their total lengths measured.

Plankton Hauls

Immediately on hauling the catch was filtered through a plastic tea strainer of rectangular pore-size 0.550 x 0.475 mm, which effectively retained all the eggs and larvae. In summer large catches of Scyphomedusae were sometimes encountered, especially *Cyanea capillata* and *Aurelia aurita*. When this occurred each jellyfish was washed in a large volume of sea water and carefully examined for adhering eggs and larvae before discarding. All other planktonic organisms were preserved in approximately 5% formalin. At the laboratory the fish eggs and larvae were separated and preserved in 2% formalin, for later identification.

1. 3. DISCUSSION OF METHODS USED

1.3.A. Selectivity of Gear

Jones(1954b) discussed some of the limitations of trawls as sampling instruments and considered that variance could be reduced by taking sufficient hauls in a suitable sampling programme. Due to difficulties of detection bias is more difficult to eliminate. In addition to such general considerations as a suitable sampling programme, reliable sub-sampling and suitable methods for analysis Jones(loc.cit.) thought that every limitation of the gear should be known and allowed for. Margetts(1969) pointed out the difficulties of discovering how trawls catch fish ; comparative fishings with different nets give different catch compositions, the reasons for which must be surmised. Even though all nets are selective and it is impossible to determine the absolute density of any species it is still possible to use a gear for comparative purposes, provided it always catches the same proportions of each species in its path when worked under constant conditions (Russell,1931). Barnes and Bagenal(1951) studied catch variability statistically on inshore grounds and found that, as with plankton hauls, the standard deviation of the catch was proportional to the mean. The variance was greater than and increased with the mean, suggesting that the population was aggregated into groups. Jones(1954a) found that the frequency distribution of numbers of fish caught from a large number of trawls to be highly skewed. The logarithmic transformation

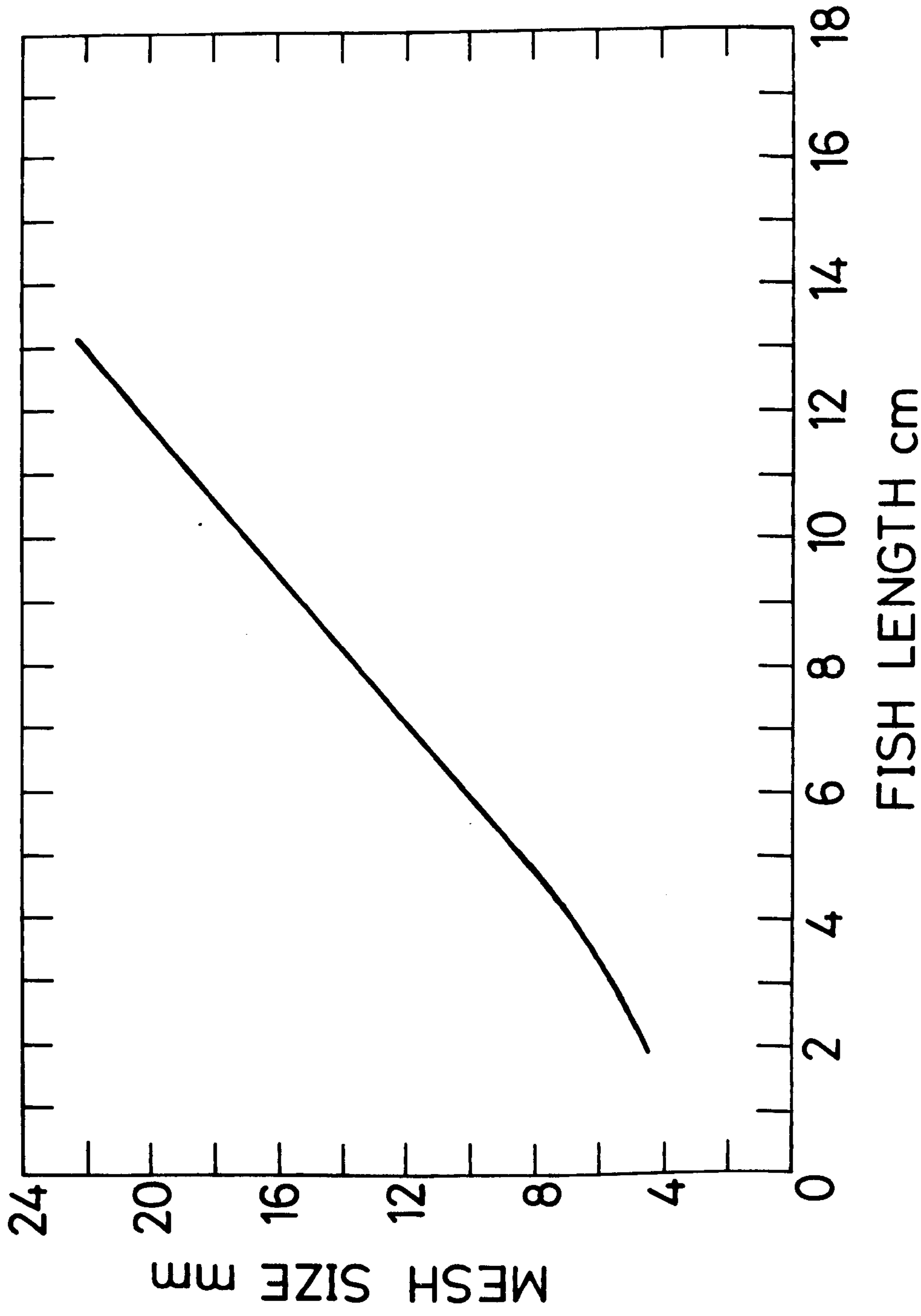
$$\log (n + 1)$$

was recommended (where n = catch rate). This transformation was used in all abundance calculations and graphs.

Among the more obvious causes of variability are the effect of haul duration on catch, diurnal variations in catch and the difference between research vessel and commercial catches. In this sampling programme all hauls were of the same duration (forty minutes for bottom and mid-water trawls, twenty minutes for ring trawls). All plankton hauls and bottom trawls were in daylight and mid-water trawls in daylight and darkness are considered separately. When using the bottom trawl and Young Fish Trawl the speed of the boat was uniform ; with the mid-water trawl this was not possible as this was one of the parameters used to determine the depth of the net (see section 1.2.B). Even so it is possible that some hauls may not be directly comparable e.g. one theory to explain discrepancies in catches is that when the cod-end is full, water flow through the net is reduced. However, this is unlikely to become important in the short hauls used unless the catch is very large. Of more immediate importance is the size selectivity of the different gears : in particular at what size do the young fish begin to escape from the ring trawl and what are the minimum sizes of fish retained by the mid-water and bottom trawls. The relationship between probability of retention of a fish by a cod-end and its length is known as the length-selection curve. It is usually determined by fitting a cod-end cover of considerably finer mesh and comparing the length distribution of the catches in the cod-end and in the cover. Alternatively the catches of repeated trawls over the same ground using the cod-end under consideration followed by one with a much finer mesh are compared. Holden (1971) gives selectivity data for several species (including haddock and whiting), but considers only commercial nets, the minimum mesh size of which is 59 mm. Jensen (1952) gives 50% retention lengths for whiting (Fig.1.4) in cod-ends with different mesh sizes. The 50% retention length was 5.7 cm and 9.5 cm for cod-end mesh sizes of the mid-water and bottom trawls respectively used in the present study. This undoubtedly explains the differences in mean length and size-composition noted later for each species, although other factors may also be important. In particular jellyfish may reduce the 50% length

Fig.1.4. The 50% retention lengths of whiting in cod-ends of different mesh-sizes (from Jensen, 1952).

13b



in summer, especially in mid-water trawls. Sea pens (Pennatulacea) and macroalgae, which are caught in large numbers throughout the year at the Firth of Lorne, Loch Linnhe and Bloody Bay, may choke the meshes of the cod-end and cause the retention of small fish.

1.3.B. Reproductive Studies

Sexing fish

The gonads of whiting and Norway pout have been described by Gokhale (1957), and this description holds good for the closely-related poor-cod. In mature males the testes are 'coiled bodies lying along the median line beneath the air-bladder. There is no well defined vas deferens, but a thin walled triangular sinus runs from the junction of the two testes along the mid-ventral line, joins the ureter and ultimately opens into the cloaca. The size, colour and form of the testes change with the seasons as the organ matures .... The ovaries ... are oblong bodies lying along the median line just ventral to the air-bladder. Their anterior ends are broad and rounded while the posterior ends are narrower and more tapering. The ovaries are fused together towards the middle region, but their ends are free. From the fused region starts the single oviduct which runs posteriorly and joins the common ureter which opens into the cloaca.' In immature males and females the minute gonads are very difficult to distinguish. A small proportion of the youngest fish could be sexed, but it was not until January in the 1-group that this was possible for all fish. This is considered to be the beginning of the breeding season (see sections on reproduction for each species) and even 1-group fish which do not spawn show some gonadal development. This 'pre-spawning maturation' will be discussed in the final section. No unusual, malformed or hermaphroditic gonads were found, despite the large number of fish examined (> 40,000).

Maturation

Many maturation scales have been devised, the most important of which have been listed by Hilge(1977), who recommended the use of four stages to describe all female teleosts. In the present study no attempt is made to compare species and so the main requirements were ease of identification of stages and comparability with earlier work . In addition it was thought desirable to avoid intermediate stages. The system developed for each species is based on that of Bowers(1954) for the whiting and subsequently adapted by Gokhale (1957) for the Norway pout. The latter author describes microscopic changes occurring in the gonads during each macroscopic stage. A similar scale was developed for the poor-cod, bearing in mind the work of Planas and Vives (1952) and after examination of a large number of maturing fish. Basically the scale consists of seven stages in all species. Stage 1 includes immature fish, stage II maturing virgins and recovering spents, stages III and IV developing fish, stage V ripe fish, stage VI running-ripe fish and stage VII spents. It was not possible to distinguish between maturing virgins and recovering spents in stage II.

The seasonal occurrence of maturity stage data can be presented in several ways. The period over which a maturity stage is recorded may simply be given e.g. Gokhale(1957). Planas and Vives(1952) give histograms for each month with maturity stage on the horizontal, and percentage frequency on the vertical axis. Bowers(1954) gives histograms for each maturity stage with months on the horizontal, and percentage frequency on the vertical axis. This is probably the most readily understood form of presentation. The method used is basically that of Bowers (loc. cit.) but with curves drawn by hand through the monthly frequency points, as described by Iles (1964) for herring.

There are several advantages of this method, the chief being that it enables the duration of each maturity stage to be calculated. This is usually less than the period over which a maturity stage is recorded, unless all the members of the population begin to mature at the same time and mature at the same rate. The duration of each stage can be determined from the area under each curve. Iles (loc.cit.) pointed out that a knowledge of the duration of the maturity stages 'allows the evaluation of the growth rates of the gonad and therefore makes possible a comparison of the process of gonad development between different age groups and between male and female within a population, and it throws light on the relationships in time between the maturation process and the act of spawning.'

1.3.C. Growth Studies

Growth has been described as a change in size (length, weight, bulk) with time (Weatherley, 1972), and fish may therefore 'grow larger or smaller '. Ricker (1975) distinguished three types of growth rate :

(1) absolute increase (increment) in a given year

i.e. $w_2 - w_1$ or $l_2 - l_1$;

(2) relative rate of increase

i.e. $\dfrac{w_2 - w_1}{w_1}$ or $\dfrac{l_2 - l_1}{l_1}$ (usually expressed as a percentage);

(3) instantaneous rate of increase

i.e. $\log_e w_2 - \log_e w_1$ or $\log_e l_2 - \log_e l_1$.

Growth curves and length-weight relationships are best fitted to an individual fish measured and weighed throughout life (Ricker, loc.cit.), but this is rarely possible unless fish are kept in artificial environments or are tagged. Weatherley (1972) considered that 'fish growth is essentially indeterminate', depending on feeding conditions; Jones and Johnstone (1977) concluded that there was no such thing as a 'cod growth rate' or a 'haddock growth rate' after showing the range of relationships between annual growth increments and mean weights for populations of the North Atlantic. Work by Kohler(1964) on cod and Jones and Hislop (1972) on whiting and haddock suggests that there is an upper limit to growth in length, whereas growth in weight is limited only by the rate of ingestion of food. Aquarium growth studies can only partially reveal growth rates of natural populations which may be food limited. Tagging experiments were not thought to be worthwhile in the present work considering the small size of the juvenile fish, the limited period of study and the likely low return rate for two of the species (Norway pout and poor-cod), for which there is no fishery in the Oban area.

True growth rate is normally estimated by the well-known back-calculation method. It is, however, only possible to study annual variations in size in this way whereas fish in the present study rarely exceeded two years of age and seasonal variations were thought to be important. Consequently the method used was to follow the mean weight and length of each brood as it grew throughout life. This method is subject to certain inherent sources of bias e.g. gear selection and 'natural selection' caused by size-specific migrations or mortalities. Assuming, however, that the sample obtained is random and not subject to gear selection (which is only likely to occur in O-group fish) the mean size obtained in this way is the best estimate available at any site at any time.

Once the mean size of fish at various ages has been determined, mathematical models of the growth curve are normally constructed. These are used :

(1) to describe the general pattern of growth free from the minor variations shown by the original observations and to facilitate comparisons between species, populations and areas;

(2) to attempt to relate parameters of the model to mechanisms underlying the growth process (Dickie, 1968).

In addition suitable growth curves facilitate the calculation of fishery yield equations. A variety of models have been described, of which the von Bertalanffy is probably the best known. These curves are normally fitted to annual growth of a fairly long-lived species such as cod and haddock. In the present study fish older than the 2-group were rarely caught and the seasonal element was considered to be important in this respect.

Few attempts have been made to construct models of seasonal growth. Lockwood (1974) used von Bertalanffy growth curves for separate age-groups of plaice, using Gulland and Holt's (1959) approximation for data at unequal time intervals. Unfortunately the period of change from one year's growth curve to the next was not adequately covered. Pitcher and MacDonald (1973) devised two modifications of the von Bertalanffy growth curve to account for seasonal growth. In the first 'switched growth' model it was assumed that no growth occurs in winter while in summer growth follows the von Bertalanffy curve. In the second model a smoother change in the growth rate occurs, as a result of modifying the Brody growth coefficient (K), by a sine function of wavelength one year. The second 'sine wave growth' model may exhibit shrinkage in length in winter, but this has been observed for some species e.g. Norway pout (Ursin, 1963). The authors assume that water temperature is important in the timing of growth, and this has also been stressed by Weatherley (1972). In contrast Iles (1974) considered that ' light - acting through photoperiodicity - is becoming accepted as playing a major role in influencing the timing of seasonal physiology, rather than factors such as temperature.' In this regard Ursin (1963) used multiple regression analysis to show that for Norway pout in the Skagerrak, the growth rate depends particularly on day length and less upon temperature.

In the present study the von Bertalanffy equation did not fit the observed data well enough to justify its use. This is thought to be due to the large variation between samples and in particular to local migrations of fish. Growth is therefore plotted by fitting a smooth curve by eye, (for weight), or by drawing lines directly between points (for length, which is less variable).

1.3.D. Condition Factor and Length-weight Relationships

Le Cren (1951) considered that the analysis of length-weight data has been directed toward two objects :

(1) towards describing mathematically the relationships between length and weight, primarily for interconversion;

(2) to measure the variation from the expected weight for length of fish or groups of fish as indicators of fatness, general 'well-being', gonad development, etc.

For the former object the relationship for most species may be represented by the formula

$$w = al^b$$

where w is weight, l is length and a and b are constants. The value of the exponent b normally lies between 2 and 4. When equal to 3 growth is isometric, assuming the density of the fish remains constant (Kesteven, 1947). Le Cren (loc.cit.) used the term 'condition' for analyses of the second type and this convention will be followed in this thesis.

Variations in condition have normally been studied using one of the condition factors of the type

$$K = \frac{w}{l^3}$$

(Fulton's condition factor; Fulton 1911). This factor is often multiplied by 100 to make the numerical value calculated approximately equal to 1. Tesch (1968) points out that allometric growth will cause changes in the relative weight of fish of different length, and recommended the use of an allometric condition factor when an accurate value of b can be determined i.e. $\frac{w}{l^b} \times 100$.

The difficulty here lies in choosing a suitable value for the exponent b, when the calculated length-weight relationship varies with season, age, maturity, area of capture (e.g. Le Cren, 1951; Bagenal, 1957 ; present study). Ricker(1975) considered that b should be 'given a value for the species under standard conditions.' The difficulty lies in deciding what conditions are standard.

Le Cren(1951) and Bagenal(1957) calculated length-weight relationships for separate groups of fish, comparing them by covariance analysis in order to test for significant differences in condition.

In the present study both approaches were used, Fulton's condition factor (henceforward called 'the condition factor') being calculated for individual groups of fish. For the same groups of fish variations in condition were followed by calculating expected weights of fish at a given length from each length-weight relationship. Although theoretically more correct the second approach presents considerable practical difficulties. Residual variances of relationships being compared were frequently heterogeneous, so that analysis of covariance was not always possible. In some cases it is possible to suggest reasons for this e.g. variations in the length range of samples, unequal sample sizes. In general there was good agreement between condition measured by each method, and seasonal trends were obvious.

In calculating length-weight relationships the G.M. (Geometric Mean) functional linear regression of log weight with log length was used, rather than the normal predictive regression (Ricker; 1973,1975). This is particularly important when comparing separate sub-groups of fish e.g. age-groups, in which the length-range of each age-group is less than that pooled.

Condition factors and length-weight relationships may be determined in several ways in order to emphasize different aspects of the ecology of the species e.g. using standard length, total length, total weight, gutted weight with gonads, gutted weight without gonads. In the present study total lengths and gutted weights without gonads were used. Certain disadvantages are inherent in using these parameters e.g. the condition factor thus measured does not include energy stored in the liver or gonads. Energy stored in the gonads may be considered to be lost from the body unless the spawning products are resorbed, but the liver changed in size seasonally. Maximum size was reached shortly after the spawning period in all species, although measurements were not made in any detailed or systematic way. It is important to realise, however, that any estimation of condition based on length and weight is only an approximate guide to the 'well-being' of the fish at any time. More detailed biochemical assays (inevitably based on fewer fish) are necessary to study the seasonal physiological rhythms of fish e.g. Shul'man(1974).

SECTION II.

Trisopterus minutus (Linnaeus, 1758)

POOR-COD

II. 1. INTRODUCTION

The poor-cod occurs in large numbers on the west coast of Scotland, although it is not so abundant as the Norway pout or the whiting. The species is distributed on the European shores of the Atlantic Ocean from Trondheim Fjord to the tip of the Iberian peninsula (Svetovidov,1948). Wheeler(1969) described the distribution as common on all British coasts except in the southern North Sea, where it is occasional. Raitt(1968a) confirmed Schmidt's(1909) reports of larval poor-cod at Rockall Bank. Wheeler(1969) mentioned that the species occurs in the western Mediterranean Sea as T. minutus capensis (Lacepede, 1800), (= Svetovidov's T. minutus capelanus (Risso)). Wheeler(loc. cit.) and Svetovidov(1948) also described the identification, taxonomy and morphology of the species. It is closely related to the Norway pout (Trisopterus esmarkii) and the bib (Trisopterus luscus) with which it is often confused. Smith(1888) reported that the poor-cod had been thought to be an immature form of bib, but considered it unlikely due to differential distributions. Boer(1966), in confirmation, described morphological differences between the two species.

The poor-cod is an unspecialised feeder capable of utilising benthic, epibenthic and pelagic food. The diet is mainly crustacean, including planktonic and free-swimming nektonic animals such as copepods, amphipods, larval decapods, euphausiids and benthic organisms such as squat lobsters (Galathea) and Nethrops. Polychaetes and fish (Gadidae, Ammodytidae and some flat fish) are also taken (Wheeler,1969).

In the Oban area the poor-cod has no commercial importance because of its small size. In the Minch and the North Sea it is probably taken for reduction to fish meal with other industrial species. Svetovidov(1948) reported that the western Mediterranean sub-species is highly-prized but it is not caught in great quantities, and hence its industrial value is comparatively small. Planas and Vives(1952) quoted Andreu and Rodriguez-Roda's(1951) findings that, along with the red mullet the poor-cod is the most common fish caught by the bottom trawl in Castille waters. It is also an important item in the diet of larger fish such as cod, whiting, hake and turbot.

There is a small amount of literature on the biology of the species. The most detailed work is that of Planas and Vives(1952), who described reproduction, diet, growth and length-weight relationsips of the poor-cod in the Plymouth area while Lebour(1917,1919) described the diet of larvae and post-larvae in the same area. In the Irish Sea feeding and reproduction were studied by Nagabhushanam(1965). Boer (1966) described the occurrence of the species in Dutch waters and compared this with the bib. Russell(1976) summarised the literature concerning the development and distribution of planktonic stages.

II. 2. AGE COMPOSITION

Fig.II.1 shows seasonal age-compositions of demersal poor-cod populations at each site, pooling 1975 and 1976 data at bimonthly intervals. 0-group fish were first caught in June/July at Tiree Passage and subsequently this age-group dominated catches at all sites except Loch Linnhe, where the 0-group did not become dominant until October/November. The 1-group dominated catches from January until recruitment of the new year-class was complete, between July and October. 2-group and older fish represented a significant proportion of the population at Tiree Passage and Ardalanish Bay from December/ January to June/July. Although 2-group fish were caught at other sites in December/January they were insignificant thereafter. Fig.II.2 shows the same data plotted in terms of numbers caught rather than percentage frequency. 0-group fish were more abundant offshore than inshore. The observation that 2-group and older fish were more important at Tiree Passage and Ardalanish Bay was further emphasised, since catch rates were greater at these sites. The 2-group was especially important because most fish of this age mature for the first time, and this age-group represented the major part of the spawning population (sections II.5.C and II.5.D).

In addition to position relative to land, depth may be an important factor affecting the age-composition of a population. In this regard 2-group fish were more important at Loch Linnhe (depth 90m) than at the Firth of Lorne (depth 47m). Although the depth of the Bloody Bay sampling site (50m) is similar to that of the Firth of Lorne, some migrating fish may pass through the area.

Since variations between sites and seasons were large and sampling inconsistent between 1975 and 1976, it was not possible to

Fig.II.1. Age composition of poor-cod populations at each site, pooling data at bimonthly intervals from January 1975 to January 1977.

n = number of hauls.

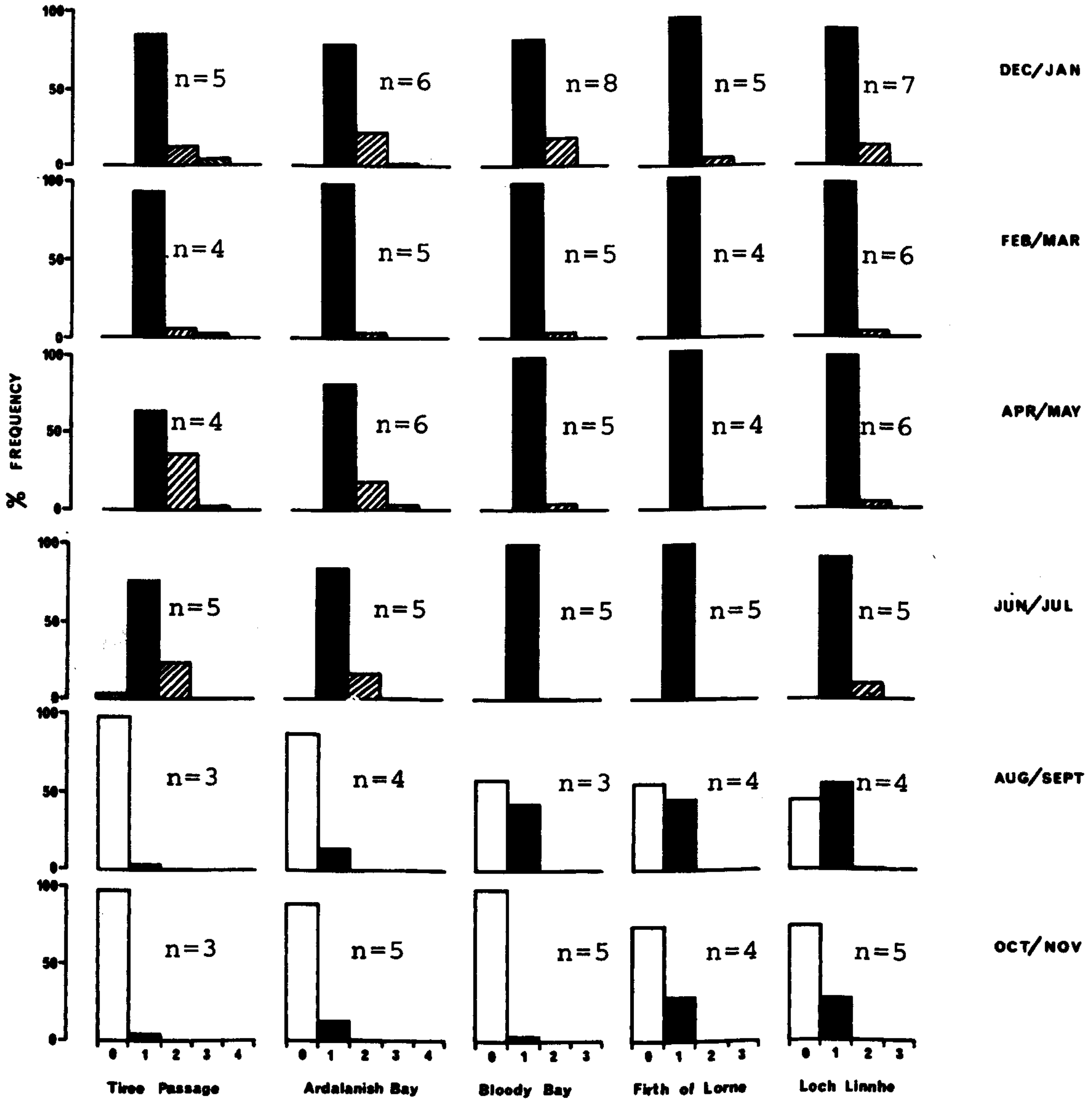
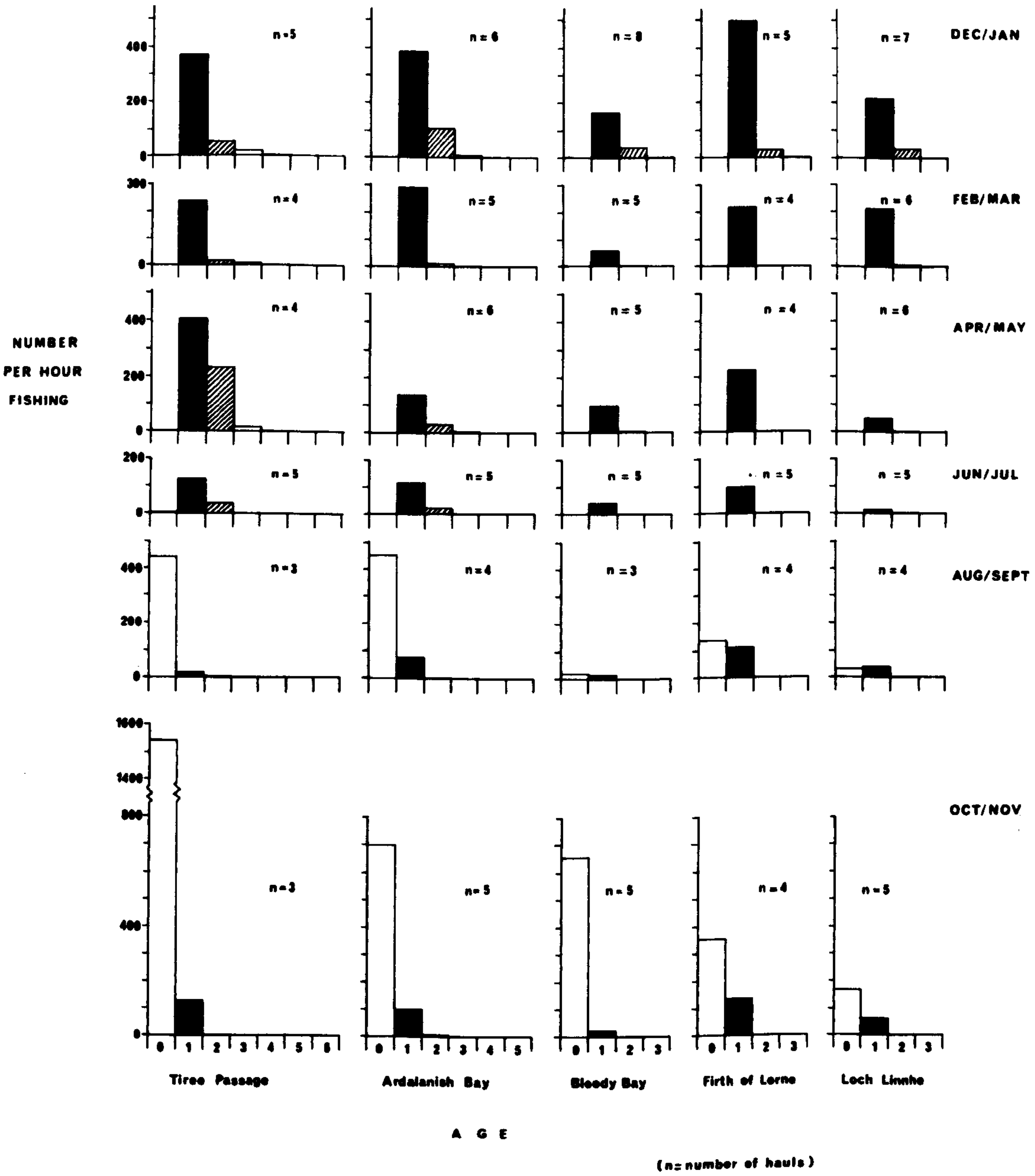

% FREQUENCY
100
50
0
DEC/JAN
n=5
n=6
n=8
n=5
n=7
FEB/MAR
n=4
n=5
n=5
n=4
n=6
APR/MAY
n=4
n=6
n=5
n=4
n=6
JUN/JUL
n=5
n=5
n=5
n=5
n=5
AUG/SEPT
n=3
n=4
n=3
n=4
n=4
OCT/NOV
n=3
n=5
n=5
n=4
n=5
0 1 2 3 4
0 1 2 3 4
0 1 2 3
0 1 2 3
0 1 2 3
Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe

Fig.II.2. Number of poor-cod of each age-group caught per hour fishing at each site, pooling data at bimonthly intervals from January 1975 to January 1977.


NUMBER PER HOUR FISHING
DEC/JAN
FEB/MAR
APR/MAY
JUN/JUL
AUG/SEPT
OCT/NOV
400
200
0
300
0
400
200
0
200
0
400
200
0
1600
1400
800
400
0
n=5
n=6
n=8
n=5
n=7
n=4
n=5
n=5
n=4
n=6
n=4
n=6
n=5
n=4
n=6
n=5
n=5
n=5
n=5
n=5
n=3
n=4
n=3
n=4
n=4
n=3
n=5
n=5
n=4
n=5
0 1 2 3 4 5 6
0 1 2 3 4 5
0 1 2 3
0 1 2 3
0 1 2 3
Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe
A G E
(n= number of hauls)

compare year-class strength directly. Quarterly age-compositions were drawn for each site (Fig.II.3) but only 0-group and 1-group fish were caught in sufficient numbers to make comparison between years worthwhile. Comparing the 1974 year-class in 1975 with the 1975 year-class in 1976 (i.e. 1-group fish), little difference was obvious at Loch Linnhe. At the Firth of Lorne, Ardalanish Bay and Tiree Passage the 1974 year-class was stronger, although at Bloody Bay it was slightly weaker. Comparing the 1975 and 1976 year-classes as 0-group and early 1-group fish, only at Tiree Passage was the 1975 year-class stronger. At Loch Linnhe, the Firth of Lorne and Ardalanish Bay catch rates of the 1976 year-class were much higher with little difference at Bloody Bay. It therefore appears that the 1976 year-class was particularly strong, with the 1974 year-class slightly stronger than that of 1975.

Comparison with other areas

Planas and Vives(1952) looked at the age-composition of poor-cod of the western Mediterranean in winter (Table II.1). The low catch rates of the youngest age-group suggest that they used a net of greater mesh-size than in the present study ; consequently the youngest age-group is not considered in the comparison. In terms of catch/h fishing, age-group 1/2 (measured in December and January) was more important in the Mediterranean than at Tiree Passage. Comparing Mediterranean populations with all of the present sampling sites combined, the parallel was much closer.

Fig.II.3. Catch rates of poor-cod (number / h) of each year-class at each site, pooling data at bimonthly intervals from January 1975 to January 1977.

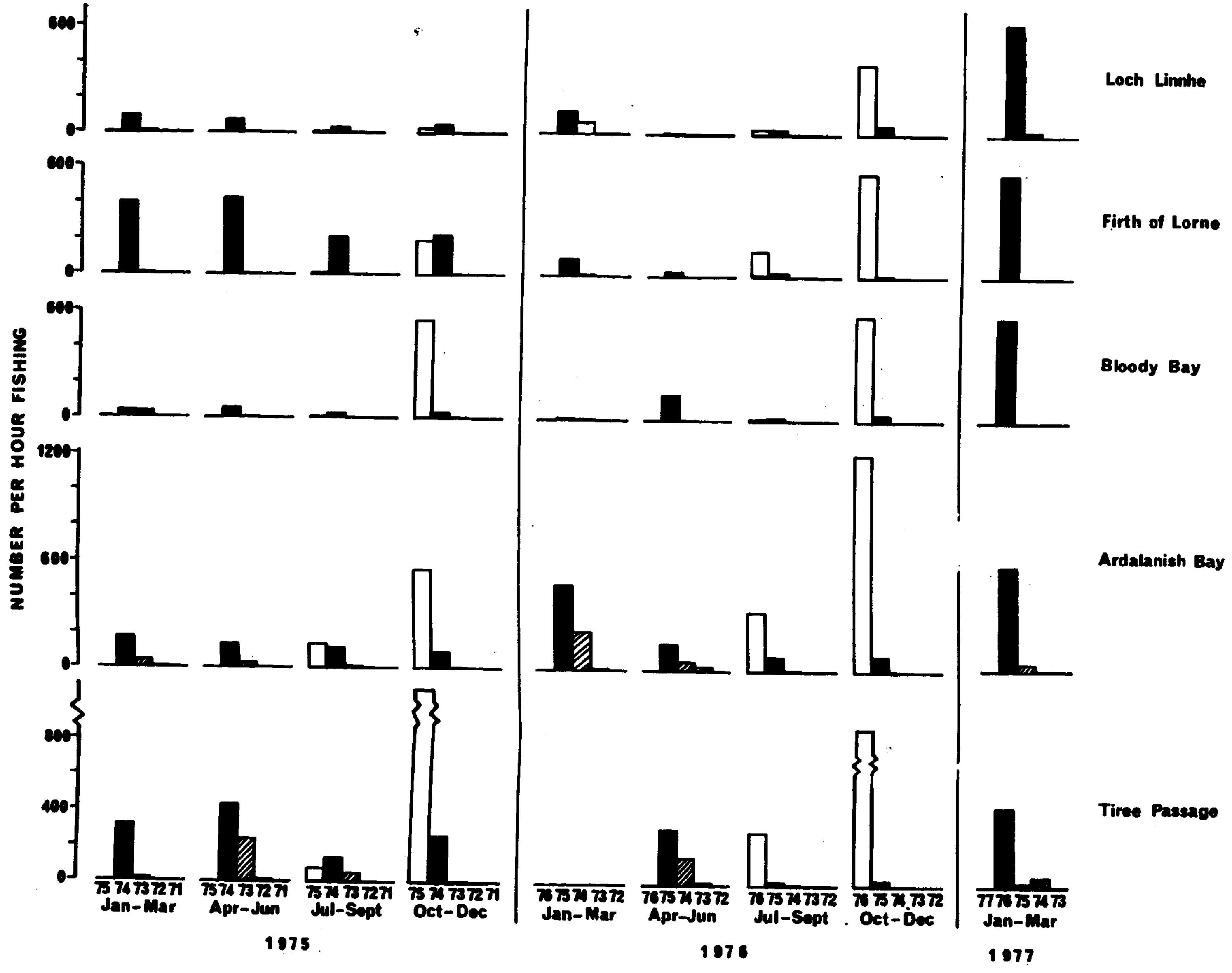

NUMBER PER HOUR FISHING
600
0
600
0
600
0
1200
600
0
800
400
0
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardalanish Bay
Tiree Passage
75 74 73 72 71
Jan-Mar
75 74 73 72 71
Apr-Jun
75 74 73 72 71
Jul-Sept
75 74 73 72 71
Oct-Dec
1975
76 75 74 73 72
Jan-Mar
76 75 74 73 72
Apr-Jun
76 75 74 73 72
Jul-Sept
76 75 74 73 72
Oct-Dec
1976
77 76 75 74 73
Jan-Mar
1977

TABLE II.1. COMPARISON OF CATCH RATES OF EACH AGE-GROUP OF POOR-COD FROM LOCAL WATERS AND THE WESTERN MEDITERRANEAN IN DECEMBER/JANUARY.

AGE	Tiree Passage		All Scottish sites.		Western Mediterranean	
	Catch rate per hour	%	Catch rate per hour	%	Catch rate per hour	%
0/1						
1/2	53.4	72.8	258.8	88.8	226.8	94.5
2/3	17.8	24.3	30.0	10.3	8.9	3.7
3/4	2.1	2.9	2.6	0.9	4.4	1.8

II. 3. MIGRATIONS AND SEASONAL OCCURRENCE

II.3.A. Planktonic Stages

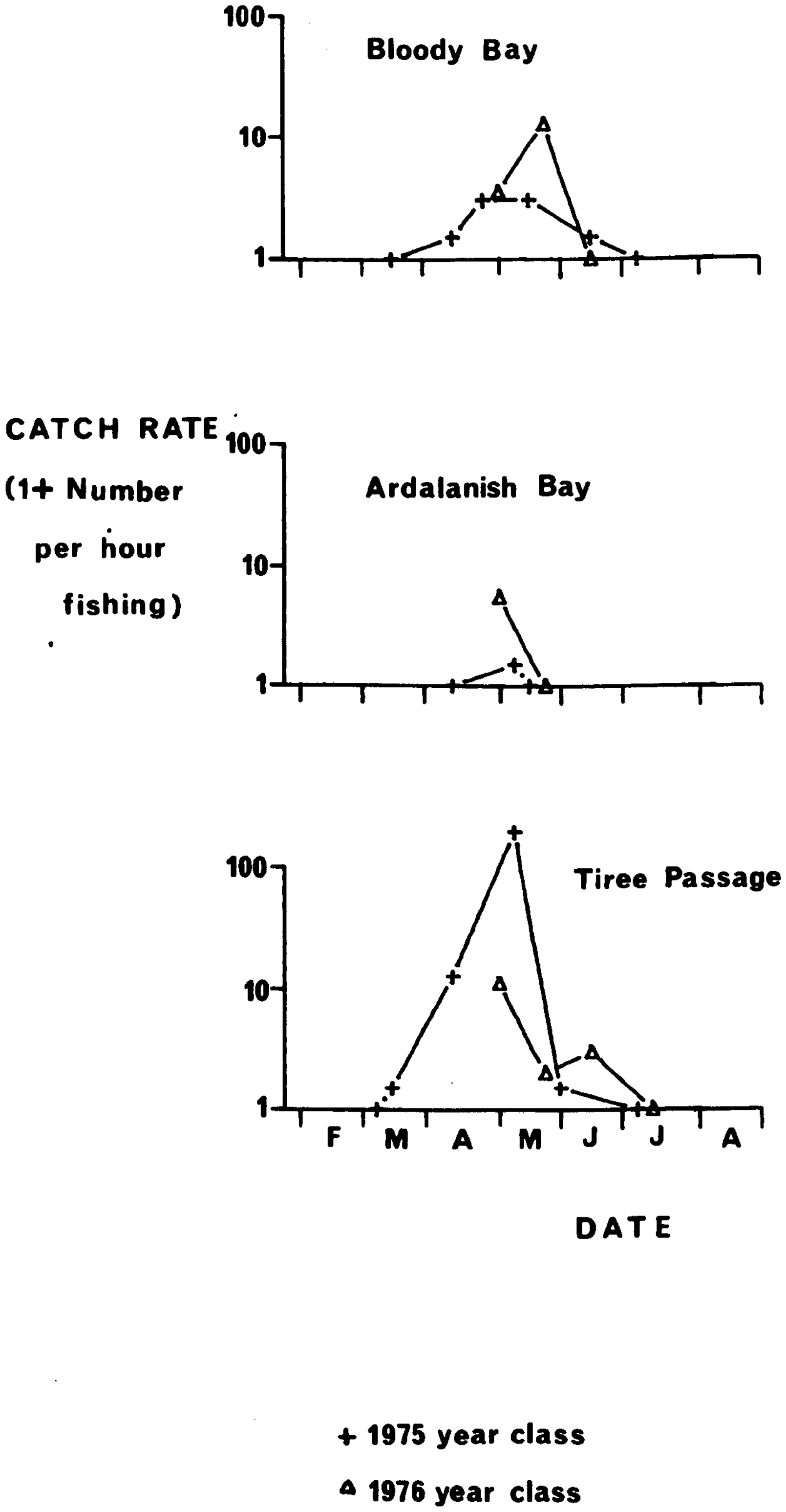
Russell(1976) described the eggs, larvae and post-larvae of *Trisopterus minutus*. It is very difficult to distinguish between the eggs of poor-cod and those of other species, in particular the sprat, bib and Norway pout (Hiemstra,1962; Bal,1941). The larvae are 2.3 - 2.4 mm long when newly-hatched. Between 7.0 and 11.5 mm it is difficult to distinguish between the post-larvae of *T. minutus* and *T. esmarkii*.

Fig.II.4 shows the catch rates of identifiable planktonic stages of poor-cod at each site on each cruise. No planktonic stages were found at the inshore sites of Loch Linnhe and the Firth of Lorne. Post-larvae were first caught in March at Tiree Passage, with a peak of abundance at the end of May and a rapid reduction in numbers in June. This could be due to the young fish reaching a size at which they could escape capture, or due to the rapid adoption of a bottom-living habit described by Russell(1930). Comparing catch rate curves at Tiree Passage with Bloody Bay and Ardalanish Bay the most surprising feature was the scarcity of post-larvae at Ardalanish Bay. This is considered anomalous because running-ripe fish were found at Ardalanish Bay, but not Bloody Bay (section II.5.F). Planktonic stages were only found at Ardalanish Bay when their abundance was greatest at Tiree Passage. The occurrence of post-larvae at Bloody Bay, when no mature fish were found there, is evidence of an inshore drift of plankton. This was presumably passive and due to residual currents.

Comparison with other areas

Russell(1976) summarised the seasonal distribution of poor-cod at Plymouth: as in the present study post-larvae were found between February and July, but the peak of abundance was somewhat earlier (March, April or May). Fives(1970) reported that post-larvae

Fig.II.4. Catch rates (log. scale) of O-group poor-cod in the 2m Plymouth Young Fish Trawl at each site. Although hauls were made on each cruise at Loch Linnhe and the Firth of Lorne no planktonic poor-cod were caught.


Bloody Bay
Ardalanish Bay
Tiree Passage
CATCH RATE (1+ Number per hour fishing)
100
10
1
F
M
A
M
J
J
A
DATE
+ 1975 year class
Δ 1976 year class

occurred along the west coast of Ireland between March and April. Continuous Plankton Recorder surveys showed that to the north-west of Ireland post-larvae were found between March and April (Henderson, 1954). Schmidt (1909) also found large numbers of pelagic poor-cod on the west coast of Scotland in late May, though in the North Sea they were common in July, August and September.

These results indicate a progressively later spawning, moving clockwise round the coast from Plymouth.

II.3.B. Juveniles and Adults

Nektonic pelagic stages

The catch rates of poor-cod in mid-water trawls are shown in Fig. II.5. The earliest appearance of pelagic nektonic fish in mid-water trawls occurs when the fish are both present and large enough to be retained by the mesh of the cod-end (section 1.3.A). The occurrence of poor-cod off the bottom has not previously been reported in any detail. Only 0-group fish were found off the bottom, and these only in the more extensive survey in 1976. Since only night mid-water trawls were made in 1976 it is impossible to tell if this is a diurnal migration. Gordon (pers.comm.) found evidence of vertical migration of 0-group fish in late July at the Firth of Lorne. This vertical movement of fish occurred when they were at their maximum abundance on the bottom (see following section).

Figs.II.6.A and II.6.B show the length-frequency distributions of bottom and mid-water trawl samples. Pelagic fish were only caught in September at Loch Linnhe and Tiree Passage. Standard significance tests rejected the Null Hypothesis that the mean lengths of poor-cod in each trawl were equal (Loch Linnhe, $P < 0.01$; Tiree Passage, $P < 0.001$). This was probably due to differential selectivities of the nets.

Fig.II.5. Catch rates (log. scale) of O-group poor-cod in the mid-water trawl at each site. No poor-cod were caught at the Firth of Lorne although hauls were made on each cruise.

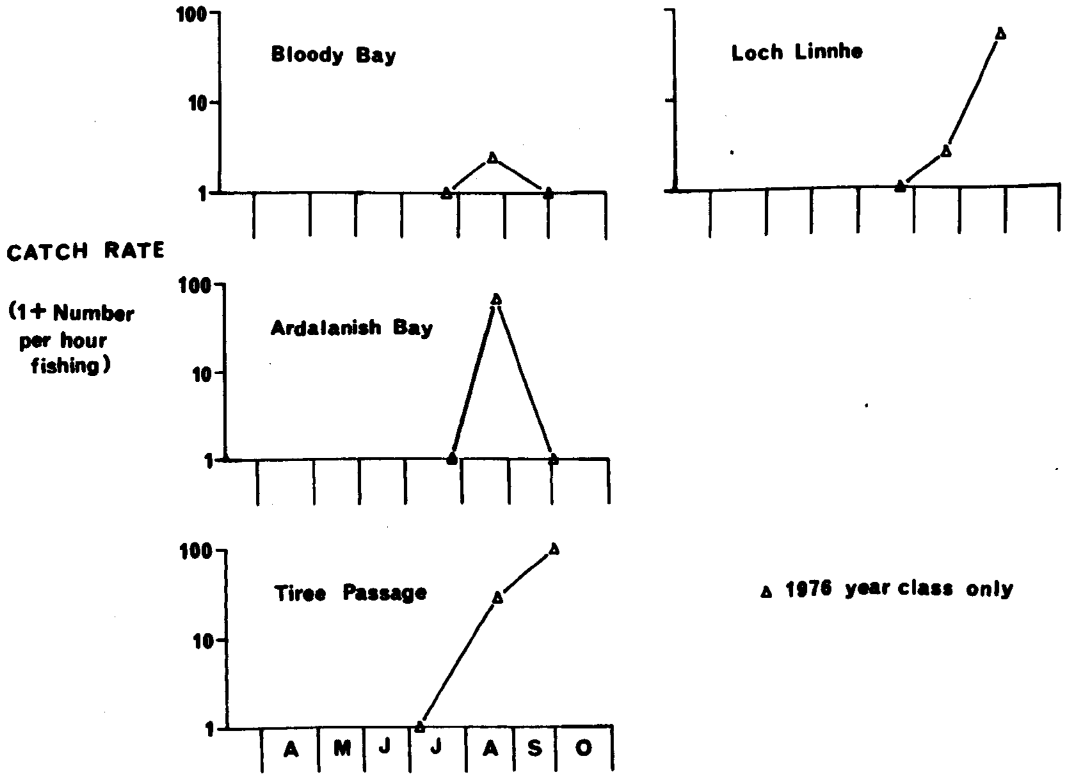
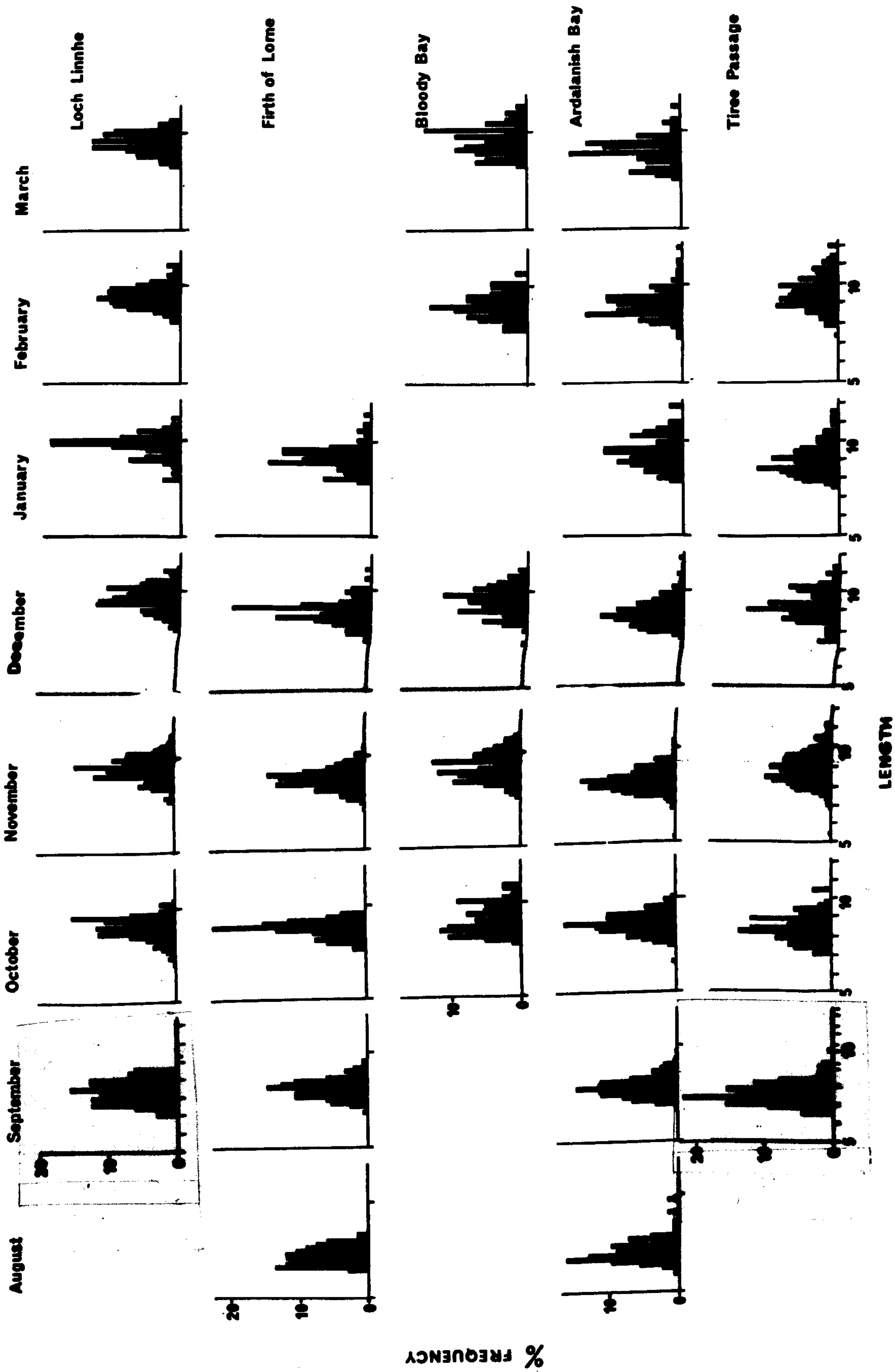

CATCH RATE
(1+ Number per hour fishing)
100
10
1
Bloody Bay
Loch Linnhe
Ardalanish Bay
Tiree Passage
A
M
J
J
A
S
O
▲ 1976 year class only

Fig.II.6.A. Monthly length-frequency distributions of demersal O-group and early 1-group poor-cod, 1976 year-class.

Fig.II.6.B. (**Plastic** sheet). Monthly length-frequency distributions of pelagic O-group poor-cod at each site, 1976 year class.


August
September
October
November
December
January
February
March
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardalanish Bay
Tiree Passage
20
10
0
5
10
LENGTH
% FREQUENCY

Demersal stages.

The catch rates of poor-cod in bottom trawls on each cruise are shown in Fig. II.7. As with pelagic stages catch rates of young fish depend on the fish being present in the area and also being large enough to be retained by the cod-end meshes. For the 1975 year-class this was in July and fish were found at all sites by late August. In 1976 0-group poor-cod were found earliest in August at Tiree Passage, Ardalanish Bay and the Firth of Lorne; at Bloody Bay and Loch Linnhe they were first recorded in late September.

In all cases except the 1975 year-class at Loch Linnhe, the first recorded presence of demersal poor-cod was followed by a very rapid increase in numbers to a maximum, which occurred between September and December. This increase in catch was probably due to an increasing proportion of the population being retained by the net i.e. incomplete recruitment. The maximum density of fish was recorded at Tiree Passage in October. By October/November the net was probably taking a representative sample of the whole year-class; the remaining part of the catch-curve is considered to be a fair representation of the relative abundance of fish at each site.

The catch rates were log-transformed, but there was still a considerable amount of variation around the trend of a reduction in numbers with age. Regression lines were calculated for each site from the beginning of October (Fig. II.8 and Appendix II.1.). In all cases a large and significant part of the variance of catch rates was explained by regression. Bartlett's test for homogeneity of variance showed unexplained variances to be heterogeneous, so comparison of slopes and intercepts by covariance analysis was impossible. This could in part have been due to an increase in the apparent abundance of fish between October in the 1-group and March in the 2-group at all sites. At Tiree Passage and Ardalanish Bay this happened with

Fig.II.7. Catch rates (log. scale) of each year-class of poor-cod in the bottom trawl at each site, against age.

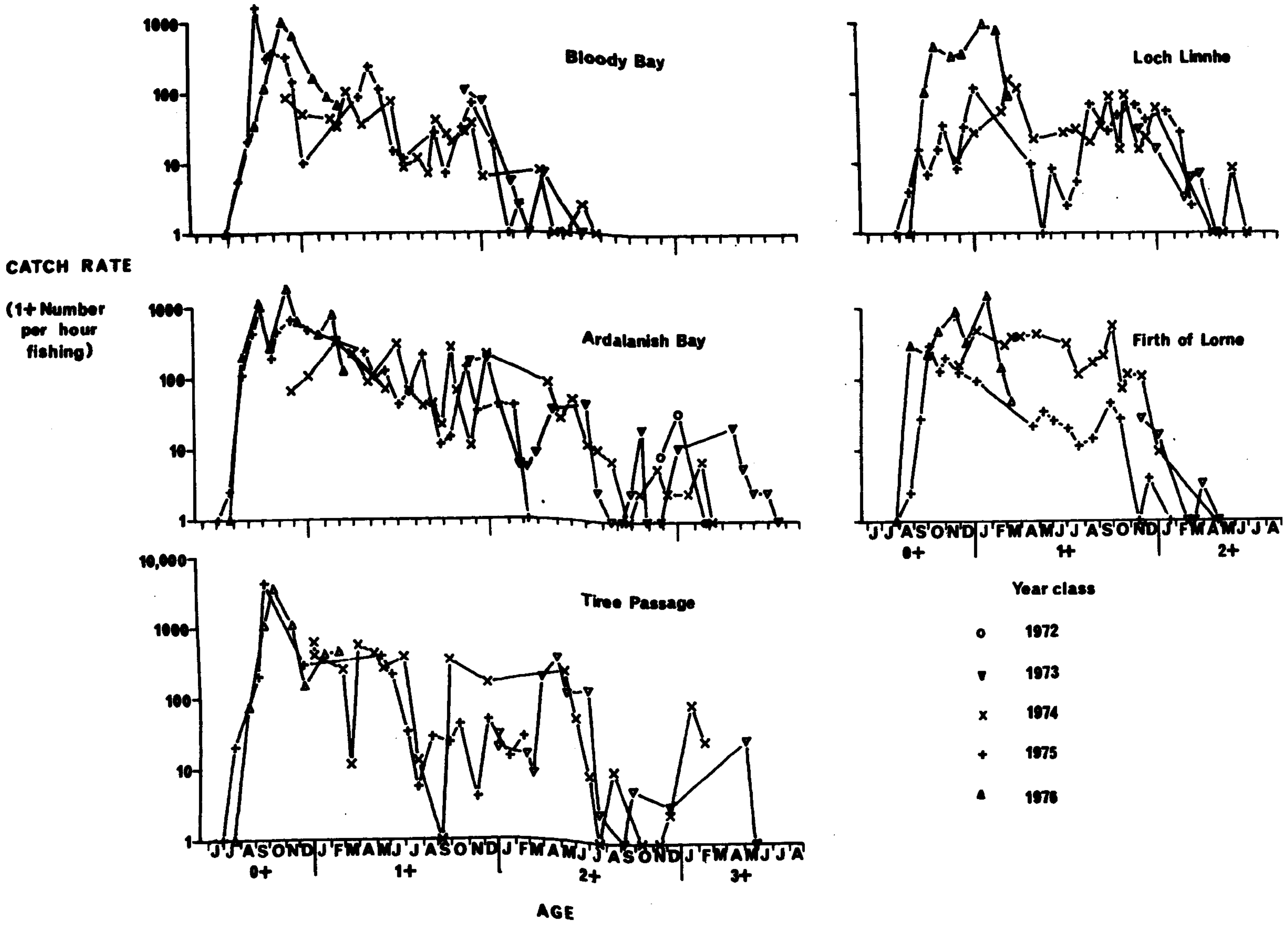
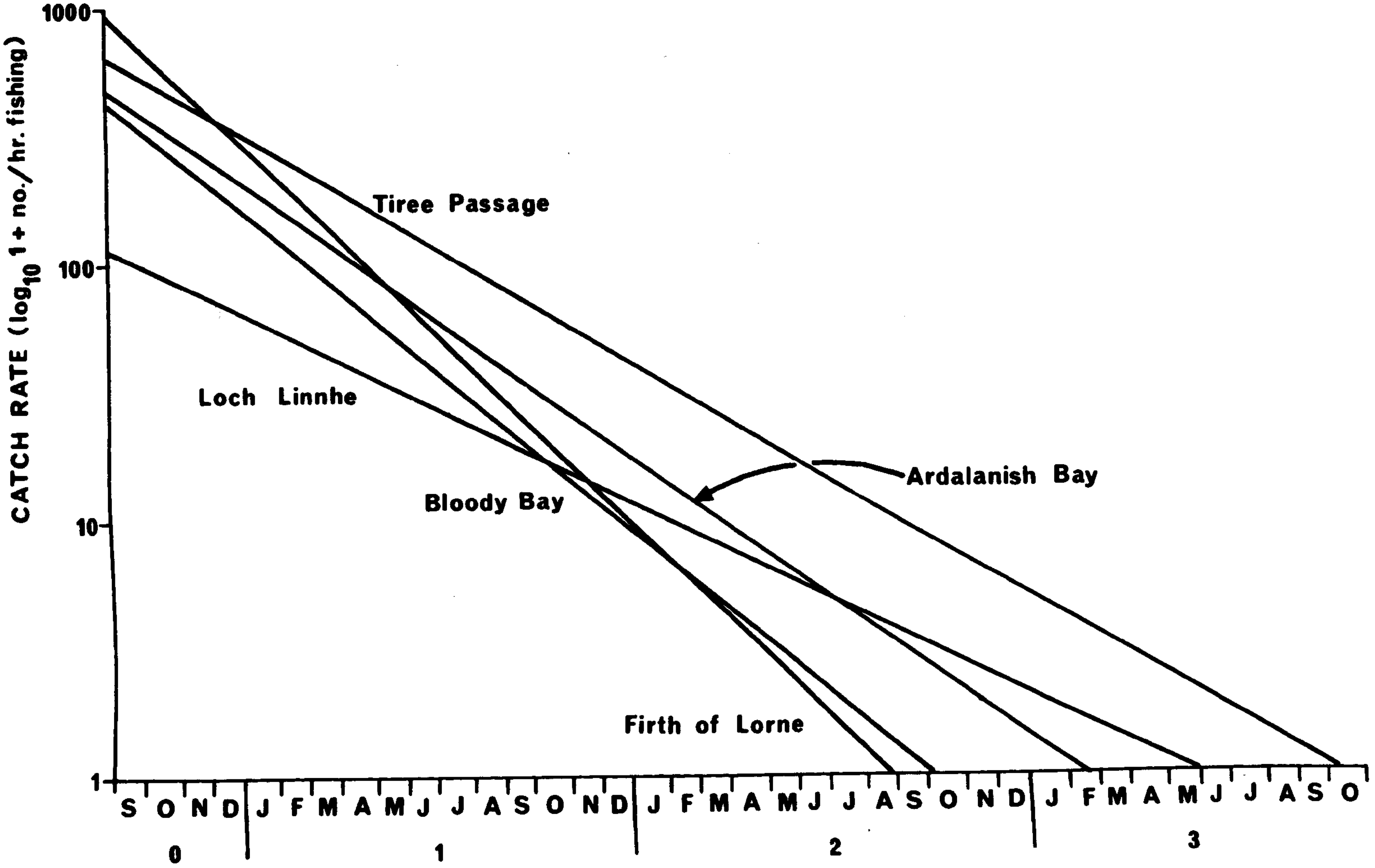

Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
CATCH RATE
(1+ Number per hour fishing)
1000
100
10
1
10,000
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
0+
1+
2+
3+
AGE
Year class
o 1972
▼ 1973
x 1974
+ 1975
▲ 1976

Fig.II.8. Predictive regressions of the catch rate (log. scale) of poor-cod against age at each site, from October (week 39.5) in the 0-group onwards.

Site	Regression
Loch Linnhe	$Y = 2.56 - 0.014X$
Firth of Lorne	$Y = 3.98 - 0.029X$
Bloody Bay	$Y = 3.47 - 0.024X$
Ardalanish Bay	$Y = 3.41 - 0.021X$
Tiree Passage	$Y = 3.41 - 0.017X$

($Y = \log_{10} 1 +$ number / h fishing
$X =$ age in weeks).


CATCH RATE (log10 1 + no./hr. fishing)
1000
100
10
1
Tiree Passage
Loch Linnhe
Bloody Bay
Ardalanish Bay
Firth of Lorne
S O 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 S O
0
1
2
3

fish one year older and could have been due to a seasonal change in habit rendering the fish less susceptible to capture e.g. by moving to rocky ground which could not be trawled. There could also be a migration of fish into the area for breeding e.g. from further offshore.

Catch rates at inshore sites were never greater than at Tiree Passage. Recruitment to inshore nursery grounds may therefore represent a spreading of 0- and 1-group fish over the sea bottom.

Comparison with other areas

Boer(1966) found that the maximum abundance of poor-cod in the Wadden Sea occurred in August and September, owing to the arrival of the new year-class. This was somewhat earlier than in local waters, but may have been due to the selectivity of the gear. There was also a very rapid reduction in numbers in October. Planas and Vives(1952) observed the entry of the new year-class into the population in April, several months earlier than in local waters. In the Mediterranean Sea, however, reproduction also occurs several months earlier (section II.5.G).

Cunningham(1891) describes the occurrence of 200 specimens less than three inches (7.6 cm) long in Whitsand Bay in May (i.e. 1-group fish) and concluded that young fish frequent shallow water and sandy ground. Older fish, 4.5 - 6.4 inches (11.4 - 16.3 cm) and probably belonging to the 2-group, were found near Eddystone. Menon(1950) also found all sizes between 8 cm and 26 cm outside Plymouth breakwater and on the Eddystone grounds.

II. 4. GROWTH

II.4.A. Length-frequency Distribution

The monthly length-frequency distributions of poor-cod in 1975 and 1976 at each site are shown in Fig.II.9. For most of the year the youngest age-group formed a definite peak, from its first appearance in August onwards. 0-group fish were usually distinct from the rest of the population, but from January of the 1-group the length-frequencies of distinct age-groups merged. There were no modes in the length-frequency distributions of 0-group fish (Fig.II.6) which suggests that the stocks were homogeneous. The length-frequency distributions of fish caught in separate years were similar in most cases. There were certain exceptions, however, e.g. at the Firth of Lorne in 1975 the 0-group was much less abundant than in 1976, while the reverse was true at Loch Linnhe.

II.4.B. Growth in Length

Seasonal growth

Seasonal growth in poor-cod caught by the bottom trawl is shown in Fig.II.10. Only when fish from all sites were pooled were there sufficient to measure growth into the 3-group. Growth was markedly seasonal, occurring in summer and autumn. The first fish were caught in August at a length of about 7 cm, though it is unlikely that the catches were a true representation of the population until September/October. Increments between each years growth and the relative rates of increase in length are shown in Table II.2. Intervals were taken between lengths in December. The growth rate decreased exponentially with age.

Comparison between sexes and year-classes

Growth in each sex is shown in Fig.II.11 and Table II.3 for all sampling sites combined. For each year-class females were consistently longer than males, although the 1975 year-class was also

Fig.II.9. Monthly length distributions of poor-cod populations at each site in 1975 and 1976.

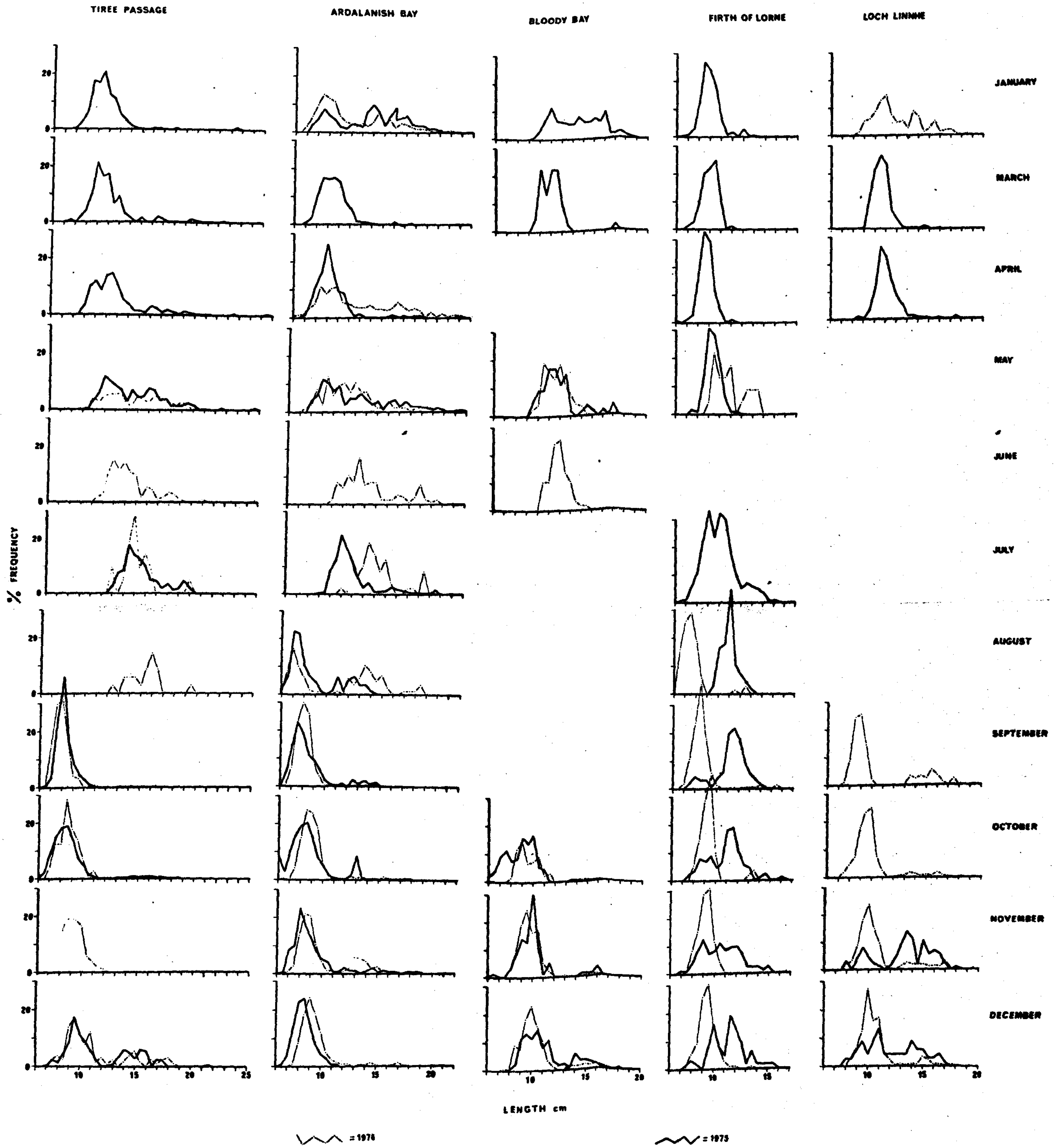

TIREE PASSAGE
ARDALANISH BAY
BLOODY BAY
FIRTH OF LORNE
LOCH LINNHE
JANUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
% FREQUENCY
20
0
10
15
20
25
LENGTH cm
=1976
=1975

Fig.II.10. Seasonal growth in total length (cm) of each year-class of poor-cod at each site and pooling fish from all sites, sexes combined.

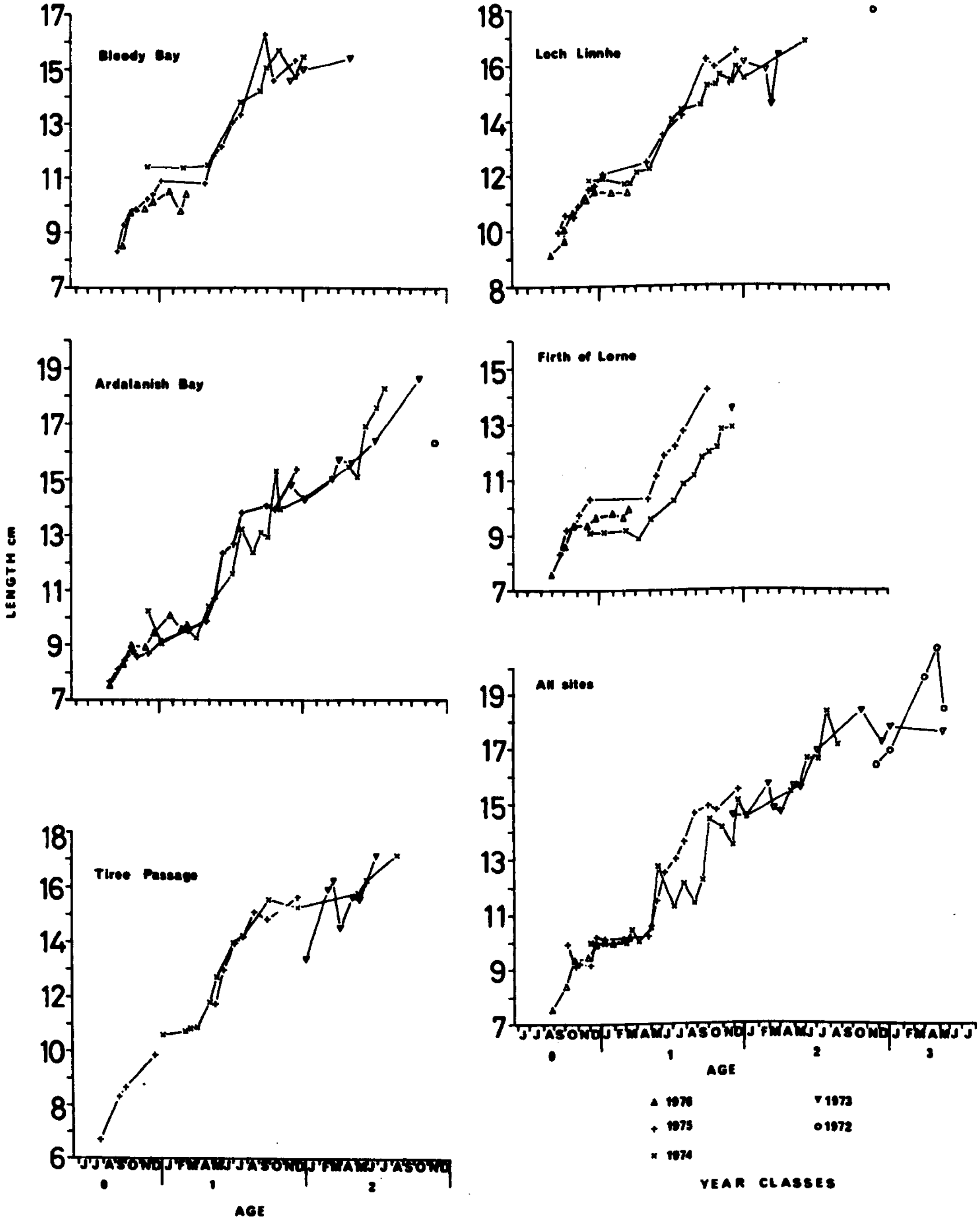

Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
All sites
Tiree Passage
LENGTH cm
17
15
13
11
9
7
18
16
14
12
10
8
19
17
15
13
11
9
7
15
13
11
9
7
19
17
15
13
11
9
7
18
16
14
12
10
8
6
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
0
1
2
AGE
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
0
1
2
3
AGE
▲ 1976
+ 1975
× 1974
▼ 1973
o 1972
YEAR CLASSES

TABLE II.2.A. INCREMENTS AND RELATIVE RATES OF INCREASE IN TOTAL LENGTH (cm) FOR EACH YEAR'S GROWTH (MEASURED IN DECEMBER) IN POOR-COD. FISH FROM ALL SITES AND EACH SEX WERE COMBINED.

Age	Year Class	December l_1	December l_2	Absolute Increase	Mean	Relative Rate of Increase	Mean
0	1976 1975 1974	0 0 0	9.89 10.16 9.95	9.89 10.16 9.95	10.00	- - -	- -
1	1975 1974 1973	10.16 9.95 -	15.46 15.06 14.53	5.30 5.11	5.25	52% 51%	51.5%
2	1974 1973 1972	15.06 14.53	17.10 17.73	2.04 3.20	2.54	13% 22%	18.5%

II.2.B. CALCULATED LENGTHS (cm) OF POOR-COD IN PLYMOUTH WATERS (from Menon,1950).

Age (years)	From Scales	From Otoliths		From supra-occipital		From Size Analysis
				Graphical	L-D formula	
1	8.75	9.75	Female	8.3	7.7	8.0
2	14.25	14.75		13.7	13.5	14.0
3	17.25	17.75		16.9	17.4	17.0
4	19.75	19.25		19.0	19.0	"
1	8.75	9.75	Male	8.2	8.0	8.0
2	12.75	13.25		12.4	12.5	13.0
3	15.25	15.75		14.8	15.4	15.0
4	16.75	17.25		16.4	16.4	"

Fig.II.11. Seasonal growth in total length (cm) of each sex of poor-cod, pooling fish from all sites.

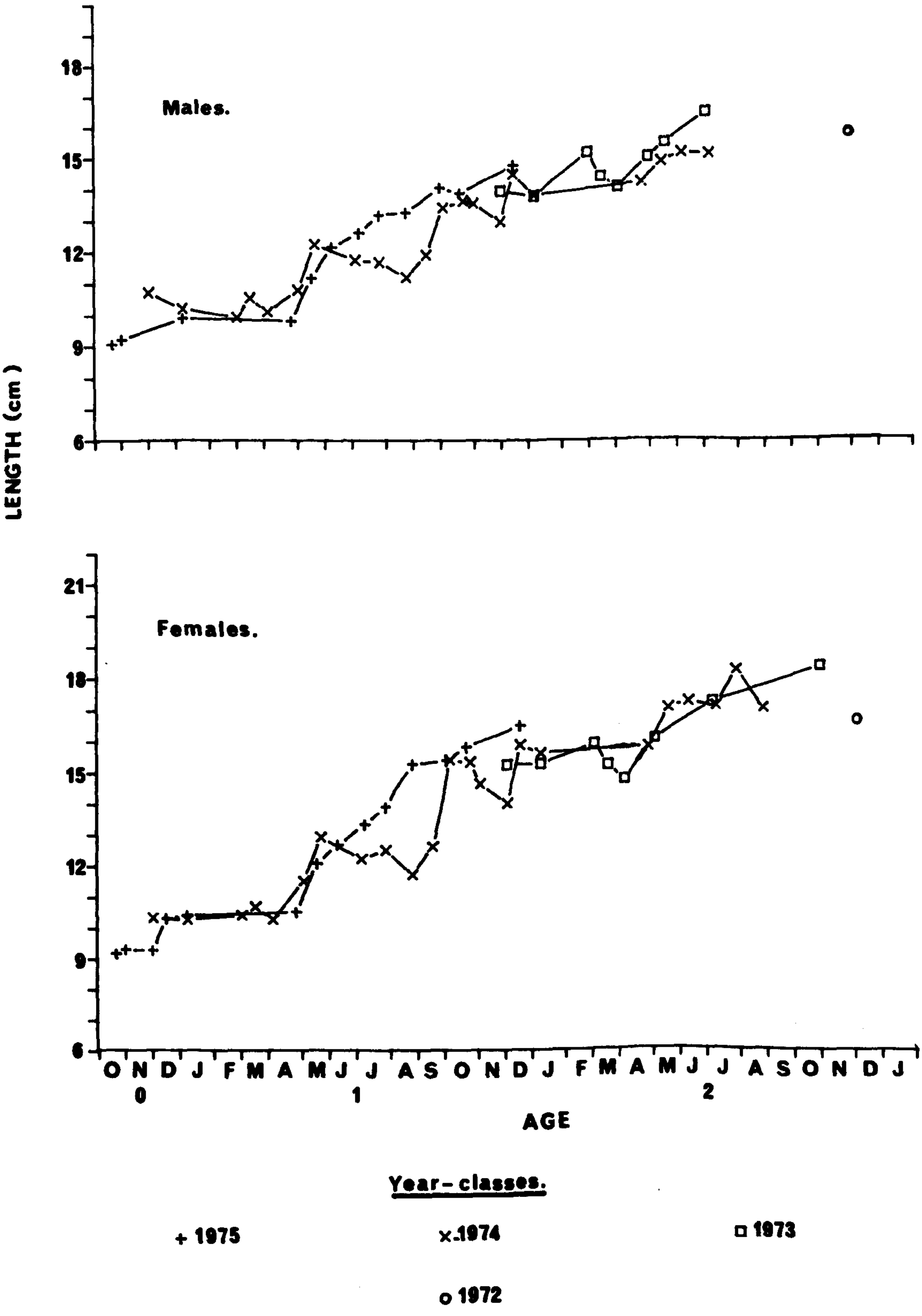

Males.
Females.
LENGTH (cm)
6
9
12
15
18
21
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
0
1
2
AGE
Year-classes.
+ 1975
x 1974
□ 1973
o 1972

TABLE II.3.A. MEAN TOTAL LENGTH (cm) OF POOR-COD AT THE END OF EACH YEAR'S GROWTH AT EACH SITE AND FOR EACH SEX.

SITE AND SEX	AGE		
	0 - 1	1 - 2	2 - 3
Loch Linnhe (all sexes)	10.2 - 11.2	14.3 - 15.5	
Firth of Lorne (all sexes)	9.0 - 10.2	-	
Bloody Bay (all sexes)	10.0 - 11.5	14.3 - 15.7	
Ardalanish Bay (all sexes)	8.8 - 10.0	14.0 - 16.0	
Tiree Passage (all sexes)	10.8 - 11.0	14.8 - 16.0	
All sites (all sexes)	9.5 - 10.5	14.0 - 16.0	approx.19.0
All sites - males	9.8 - 10.2	13.6 - 14.4	-
All sites - females	10.0 - 11.0	15.0 - 16.0	approx.19.0

II.3.B. MEAN STANDARD LENGTH (cm) OF POOR-COD IN THE WESTERN MEDITERRANEAN IN WINTER (from Planas and Vives, 1952).

SEX	AGE		
	0 - 1	1 - 2	2 - 3
Males	9.5	12.4	14.5
Females	10.0	14.4	17.2

consistently longer than that of 1974. Females spawned in 1974 had a similar size to 1975 males of the same age.

The difference in growth-rate between year-classes is evident when the sexes are combined at the Firth of Lorne (Fig.II.10). At other sampling sites the differences in growth rate between year-classes were neither obvious nor consistent ; when sites and sexes are combined the 1974 year-class was smaller in the 0-group during the growing season (June to November).

Comparison between sites

Table II.3.A shows the range of mean lengths of year-classes at the end of each growing season for each site (from Fig.II.10). At the end of the 0-group fish from the Firth of Lorne were about 1 cm smaller than fish from other sites. Insufficient fish were present to estimate the mean length of fish at the end of the 1-group at the Firth of Lorne, although at other sites there was little difference in the length attained.

Discussion

Menon(1950) studied growth in poor-cod by back-calculation of lengths of supra-occipital crests, scales and otoliths ; and by observation of modes in the length-frequency distribution. He also found that females grew faster than males. The lengths of fish at the end of each year's growth are shown in Table II.2.B. The fish caught locally were somewhat larger than those at Plymouth. Menon(loc. cit.) used standard rather than total lengths, although calculation of conversion factors (Appendix II.2) showed that this was insufficient to account for the difference. Menon also noted that the peak period of zone formation occurred between September and November, however, several months before growth ceases. This anomaly is large enough to explain the different sizes attained. Cunningham's (1891) measurements of growth rates at Plymouth agree essentially with those of Menon.

Planas and Vives(1952) measured the lengths of male and female fish caught in winter : females were also larger than males. At the end of the first season's growth there was good agreement with the lengths found locally, although growth in the second and third years was faster (Table II.3).

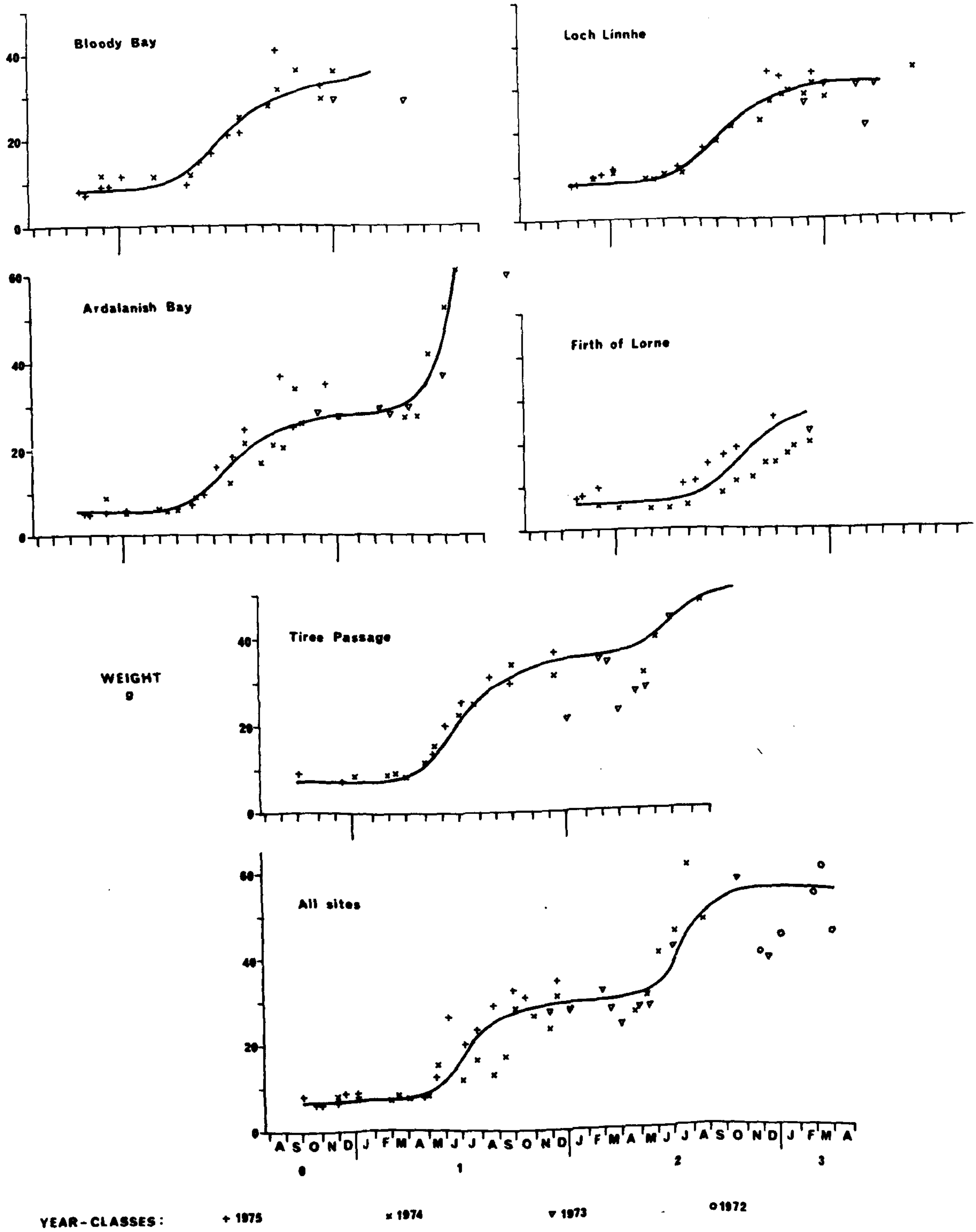
The seasonal length-frequency distributions compared well with those found by Menon(1950), though the new year-class was caught two months earlier locally and completely dominated the catch. This suggests the use of a net of greater mesh-size at Plymouth. In the western Mediterranean the new year-class was first caught in April (Planas and Vives, 1952) compared with August in the present study. It will be shown that reproduction also occurs several months later locally (section II.5.E).

II.4.B. Growth in Weight

Fig.II.12 shows the seasonal growth in gutted weight of poor-cod at each site, and for all sites combined. No attempt was made to separate the growth of different year-classes because of the large variations between samples, especially for older fish. O-group fish at the Firth of Lorne, however, showed marked differences in weight between the 1974 and 1975 year-classes (comparable to the differences in length). Growth in weight was markedly seasonal, occurring between May and October. There was no appreciable difference between sites in timing of the growing season. Table II.4 shows the approximate weights reached by fish at the end of each season's growth (measured between November and March from Fig.II.12). In December of the O-group fish from Ardalanish Bay and the Firth of Lorne were somewhat lighter than at the other sites (as with growth in length). In December of the 1-group differences between sites were not so great as differences between samples.

There was no difference in the timing of the growing season between

Fig.II.12. Seasonal growth in gutted weight (g) of poor-cod at each site and all sites combined. Curves drawn by hand.


Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
All sites
WEIGHT
g
0
20
40
60
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 S O N D J F M A
0
1
2
3
YEAR-CLASSES:
+ 1975
× 1974
▼ 1973
○ 1972

sexes (Fig.II.13). At the end of the second growing season males were lighter than females by about 10g (Table II.4).

Table II.5 shows the absolute increase and relative and instantaneous rates of increase in weight between each year's growth. There is no published information on the growth in weight of *Trisopterus minutus*.

Fig.II.13. Seasonal growth in gutted weight (g) of each sex of poor-cod, pooling fish from all sites. Curves fitted by eye .

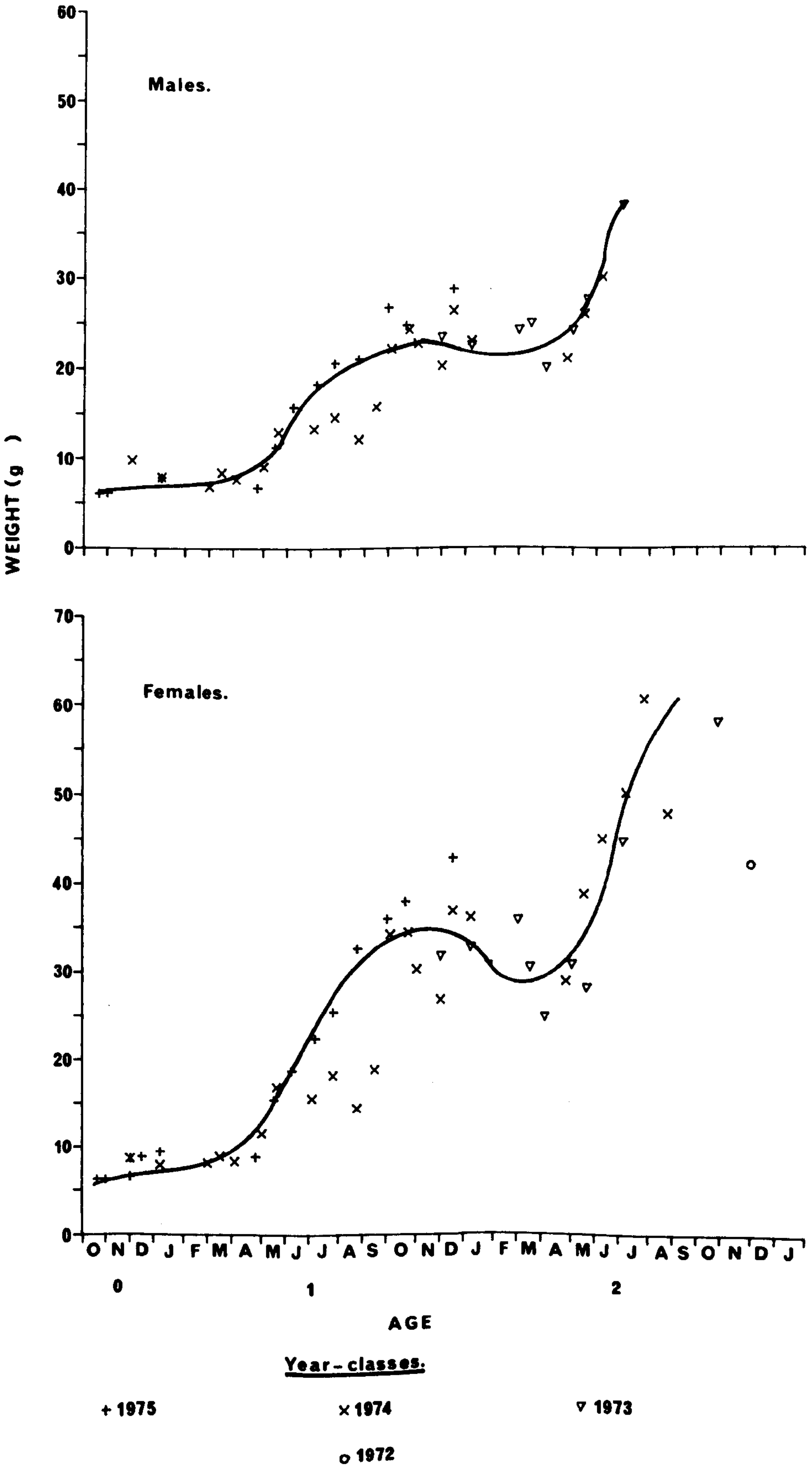

Males.
Females.
WEIGHT (g)
60
50
40
30
20
10
0
70
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
0
1
2
AGE
Year-classes.
+ 1975
× 1974
▽ 1973
○ 1972

TABLE II.4. WEIGHT RANGE (g) OF POOR-COD AT THE END OF EACH YEAR'S GROWTH AT EACH SITE, AND FOR EACH SEX.

Site	Weight (g) at Age:		
	0 - 1	1 - 2	2 - 3
Loch Linnhe	8 - 9	32 - 34	
Firth of Lorne	6 - 7	-	
Bloody Bay	8 - 9	32 - 34	
Ardalanish Bay	5.6 - 6.5	29 - 31	
Tiree Passage	7 - 8	34 - 36	
All sites combined	6 - 8	28 - 30	54 - 56
All sites - males	6 - 8	23 - 24	
All sites - females	6 - 9	32 - 33	

TABLE II.5. INCREMENTS (g) AND RELATIVE AND INSTANTANEOUS RATES OF INCREASE IN WEIGHT FOR EACH YEAR'S GROWTH (MEASURED IN DECEMBER) IN POOR-COD. FISH FROM ALL SITES AND EACH SEX WERE COMBINED.

Age	Year Class	Dec. W_1	Dec. W_2	Absolute Increase	Mean	Relative Rate of Increase	Mean	Instantaneous Rate of Increase	Mean
0	1975	0	8.4	8.4	8.1	-	-	-	-
	1974	0	7.8	7.8					
1	1975	8.4	34.5	26.1	24.5	310.7%	302.8%	1.4128	1.3931
	1974	7.8	30.8	23.0		294.9%		1.3734	
	1973	-	27.2						
2	1974	30.8	60.0	29.2	31.0	94.8%	107.7%	0.6668	0.7294
	1973	27.2	60.0	32.8		120.6%		0.7919	

II. 5. REPRODUCTION

II.5.A. Classification of Gonad Condition

Nagabhushanam(1959) recognised four maturity stages for poor-cod : immature, maturing, ripe and spent. Planas and Vives(1952) defined eight maturity stages for females, and this was modified after observation of a series of samples, the scale shown in Table II.6.A being finally adopted. For males the scale shown in Table II.6.B was developed, based on that of Bowers(1954) for whiting and Gokhale(1957) for the Norway pout and modified after a little use to suit the poor-cod.

II.5.B. Length at Maturity

Maturation of poor-cod began in January and by May fish were recovering (section II.5.E). Results from January to May were pooled to determine the length of first maturity. Since inshore areas represent nursery grounds with few adults, fish from Tiree Passage and Ardalanish Bay only were used in the analysis. It is possible that some fish develop as far as stage II, III or IV without breeding, the ova or sperm being resorbed. Consequently maturation ogives for successive maturity stages were drawn i.e. the curve for stage II includes fish of stage II and over, the curve for stage III includes stage III and over (Fig.II.14).

Females

The point at which the curve crosses the 50% maturity line was taken as the average length of first maturity. The ogives for stages III, IV and V were closely grouped, and separated from stage II. This could possibly be because most fish reaching stage III breed, while a considerable number of fish only develop as far as stage II. The average length of first maturity was about 15.6 cm.

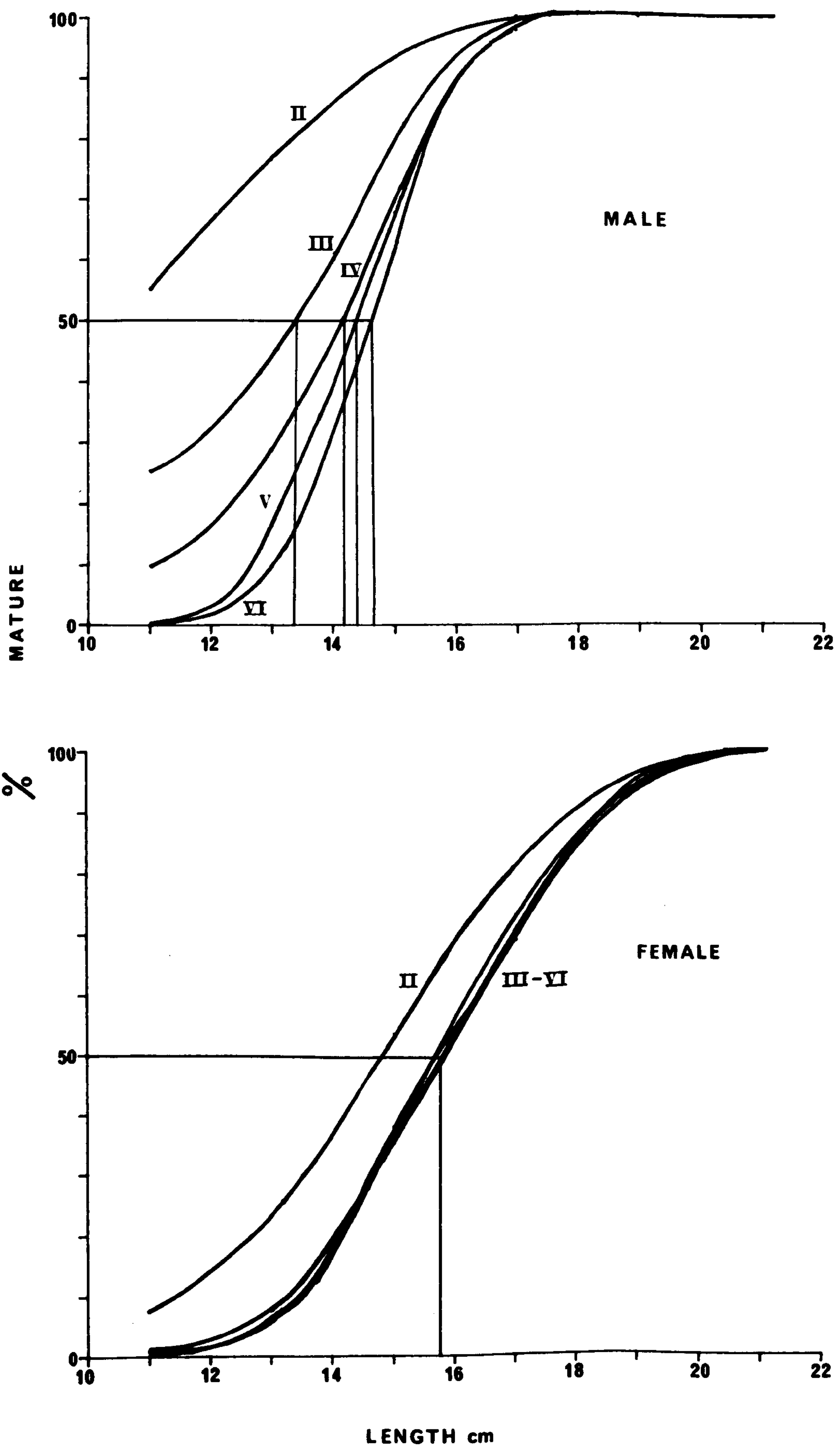
Males

There was greater separation between stages III, IV, V and VI ; and

TABLE II.6. MATURITY SCALE OF THE GONADS OF POOR-COD.

STAGE	A. FEMALES	B. MALES
1	Immature virgin fish. Ovaries small (6-12 mm, majority 8-12 mm) occupying at most one third of the body cavity. They are pink in colour, translucent with no sign of developing ova.	Immature virgin fish. Testes minute and tube-like, transparent and colourless.
II	Virgin-developing and recovered-spents resting. The ovaries are a little larger (10-25 mm , though usually 15-20 mm), but still less than one third of the body cavity is occupied. The colour is more intense and the gonad more turgid. The eggs are still not distinguishable without magnification.	Developing-virgins and recovering-spents resting. The tube-like testes are now loosely-coiled at the anterior and posterior ends and are transparent and dull-white.
III	Maturing and ripening fish. The ovaries are similar to the previous stage, though slightly larger (18-20mm) and may occupy up to half of the body cavity. The colour is more intense. The chief characteristic is that for the first time the opaque eggs are visible as fine points.	Maturing and ripening fish. The chief characteristic is an increase in length to about half that of the body cavity. The coiling may extend along the whole testis, but it is not lobed.
IV	Maturing and ripening fish. The ova are opaque and easily visible. The ovaries are more turgid and their colour a more intense red. Their size is slightly greater than in the previous stage (19-25 mm), usually occupying between half and two-thirds of the body cavity.	Maturing and ripening fish.There is a further increase in length to about three-quarters of the body cavity and coiling is more intense. Lobes develop, which are greyish-white rather than their former white colour.
V	Ripe fish not yet running. The ovaries may be *slightly larger than in the previous stage* (25-40 mm) and occupy about two thirds of the body cavity. They are very swollen and turgid and the tunica bursts easily. Most eggs are opaque and one or two are transparent.	Ripe fish not yet running. No further increase in length. *The lobules are larger, creamy-white and* full of sperm.
VI	Running-ripe fish. Almost all of the eggs are transparent. The ovaries take up about three-quarters of the body cavity. Eggs are extruded easily by slight pressure on the flanks of the fish. This stage includes fish which have lost some eggs but are still capable of extruding fully-ripe eggs which lie free in the flaccid ovary.	Running-ripe fish. The appearance is as in Stage V, but for the first time milt is extruded by slight pressure on the flanks.
VII	Spent fish. The ovaries are orange-coloured, flaccid and shrunken. Any residual eggs are in the process of resorption and do not lie free in the ovary. This stage continues until the characteristics of Stage II are reached.	Spent fish. At the beginning of this stage the testes are shrunken and bloodshot, with a small number of lobes which are yellowish in colour. Towards the end of this stage the testes lose their lobes and become dull-white. Return to Stage II.

Fig.II.14. Maturation ogives for male and female poor-cod. Percentage of fish reaching each maturity stage in each centimetre length group.


100
50
0
MALE
II
III
IV
V
VI
10
12
14
16
18
20
22
MATURE
%
100
50
0
FEMALE
II
III-VI
10
12
14
16
18
20
22
LENGTH cm

as in females stage II fish were distinct. Assuming that only fish over stage IV mature, the average length at first maturity was 14.0 - 14.6 cm.

II.5.C. Age at Maturity

Results from January to May in 1975 and 1976 at Tiree Passage and Ardalanish Bay were used in the analysis. It was impossible to plot maturation ogives for age because the population consisted mainly of only three age-groups. The proportions of fish of each age-group in each maturity stage are shown in Table II.7.

Females

The results from Fig.II.14 suggest that if a fish reaches stage III it is likely to continue development to a fully ripe condition. Only 0.6% of 1-group fish developed beyond stage II, whereas for 2- and 3-group fish the figures were 57.4% and 80.0% respectively. Maturity stages 1 and II may have included some fish at the beginning of the breeding season which matured in time to breed, and also some fish at the end of the breeding season which spawned and recovered to stage II, although the proportion is likely to be quite low. It appears that most fish matured for the first time in the 2-group with a small proportion of 1-group and all 3-group fish.

These results compare well with the length of first maturity. Fig. II.11 shows that the mean length of 1-group fish between January and May was about 10.0 - 10.5 cm; the mean lengths of 2-group and 3-group fish were 14 - 16 cm and 17 - 19 cm respectively. The 1-group therefore contained no fish of a size suitable for maturation. All 3-group fish were large enough to mature, as were a large proportion of the 2-group.

Males

A larger proportion of 1-group fish developed as far as stage III (2.8% compared with 0.6% in females). This is also illustrated in Fig. II.16, showing the proportion of fish of each age in each maturity stage.

TABLE II.7. PERCENTAGES OF POOR-COD OF EACH AGE IN EACH MATURITY STAGE BETWEEN JANUARY AND MAY AT ARDALANISH BAY AND TIREE PASSAGE (RESULTS FROM 1975 TO 1977 COMBINED).

		MATURITY STAGE							
Sex	Age	1	II	III	IV	V	VI	VII	All age group
	1	96.0	3.4	0.1	0.1	0.1	0.2	0.1	85.4
Females	2	13.9	29.7	18.8	8.6	8.6	11.3	9.0	13.3
	3+	4.0	16.0	16.0	24.0	12.0	20.0	8.0	1.2
Males	1	75.6	21.6	2.4	0.3	0.1	0	0	87.0
	2	4.7	58.9	19.1	4.7	3.4	4.7	4.7	11.9
	3+	0	28.5	4.8	9.5	14.2	28.5	14.2	1.1

Number of fish examined = 1997 for females

= 1976 for males .

For 1-group male fish there were marked inflexions in the curves for maturity stages 1, II and III in the breeding season. In contrast the proportions of the 2- and 3-groups reaching stage III were lower (36.6% compared with 57.4% and 71.5% compared with 80.0% respectively). This is surprising in view of the lower age of first maturity, but could be explained by a faster development to maturity or faster recovery of the gonads. A much larger proportion of male fish of all ages developed to stage II.

II.5.D. Sex-ratio and Age-composition of the Spawning Stock

Variations in the percentage sex-ratio by site and season are shown in Fig.II.15 and Appendix II.3. Over the whole period of study the sex-ratio was found to be 1 : 1.1039 (females : males). It appears, however, that in older fish (over the 2-group) there were fewer males. A chi-square test for heterogeneity of sex-ratio among ages, (Table II.8) rejected the Null Hypothesis that both sexes were equally distributed in the population ($p < 0.001$). Standard significance tests showed that the only age-group differing in sex-ratio from 1:1 was the 2+ age-group (including fish of the 2-group and older).

Table II.9 shows the results of a chi-square test for heterogeneity among sites. As there was a lower proportion of males in the 2-group and these were only found at offshore sites, only fish of the 0- and 1-groups were used. Overall the sex-ratio was not significantly different from 1:1, although the ratio varied more than could be expected by pure chance ($p < 0.001$). Standard tests showed that departures from a 1:1 ratio were significant at all sites except Ardalanish Bay. At the inshore sites of Loch Linnhe and the Firth of Lorne there were fewer females than males. At Bloody Bay and Tiree Passage the reverse was true.

Table II.10 shows the age-composition of fish over stage III between January and May i.e. during the breeding season (section II.5.D).

Fig.II.15. Variations in the sex-ratio (% male fish) of poor-cod with age at each site and pooling data from all sites. Fish of indeterminate sex (mainly 0-group) not included.

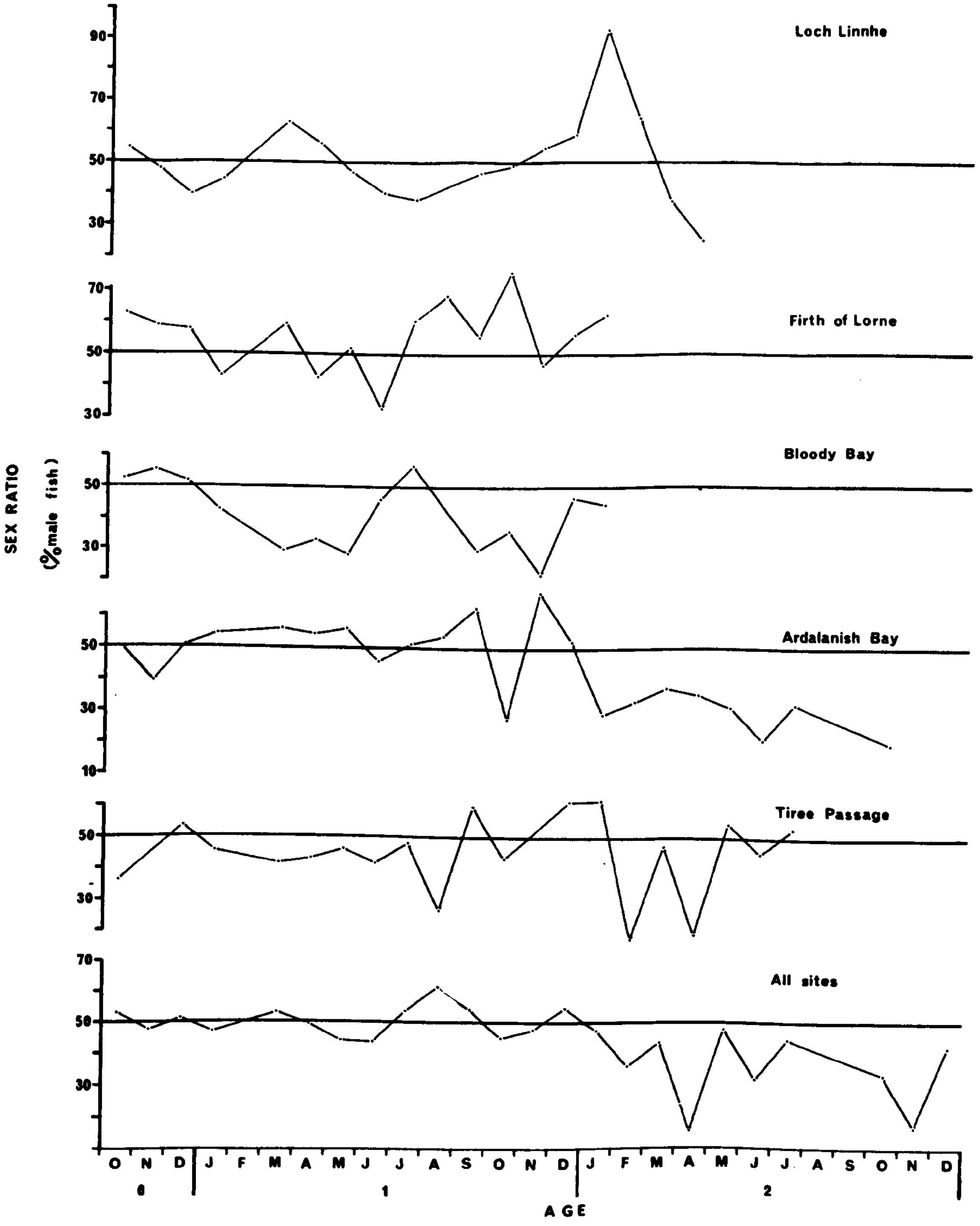

Loch Linnhe
90
70
50
30
Firth of Lorne
70
50
30
Bloody Bay
50
30
Ardalanish Bay
50
30
10
Tiree Passage
50
30
All sites
70
50
30
SEX RATIO
(% male fish)
O N D J F M A M J J A S O N D J F M A M J J A S O N D
0
1
2
AGE

TABLE II.8. CHI-SQUARE TEST FOR HETEROGENEITY OF SEX-RATIO BETWEEN AGES. POOR-COD FROM ALL SITES WERE COMBINED.

		Age:				
	Sex	0	1	2+	Total	
n.	Male	602	2820	453	3875	$\chi^2 = 27.6$
	Female	585	2807	633	4025	d.f.= 2
	Total	1187	5627	1086	7900	$p < 0.001$
%	Male	50.72	50.11	41.71	49.05	
	Female	49.28	49.88	58.29	50.59	
	d	0.4468	0.1734	5.4647	1.6889	
	p	> 0.1	> 0.1	< 0.001	> 0.05	

TABLE II.9. VARIATIONS IN SEX RATIO OF POOR-COD BETWEEN SITES

(ONLY 0 GROUP AND I GROUP FISH USED)

Sex	Site					All Sites
	Loch Linnhe	Firth of Lorne	Bloody Bay	Ardalanish Bay	Tiree Passage	
Male	543	757	375	1080	677	3432
Female	477	557	492	1026	777	3329
Total	1020	1314	867	2106	1454	6761
d.	2.066	5.52	3.97	1.18	2.62	1.25
p.	< 0.5	< 0.001	< 0.001	> 0.10	< 0.01	> 0.10
% Male	53.2	57.6	43.2	51.3	46.6	50.8

$\chi^2 = 57.22$ d.f. = 4 $p < 0.001$

TABLE II.10. AGE COMPOSITION OF THE BREEDING POPULATION OF POOR-COD, BY SEX.

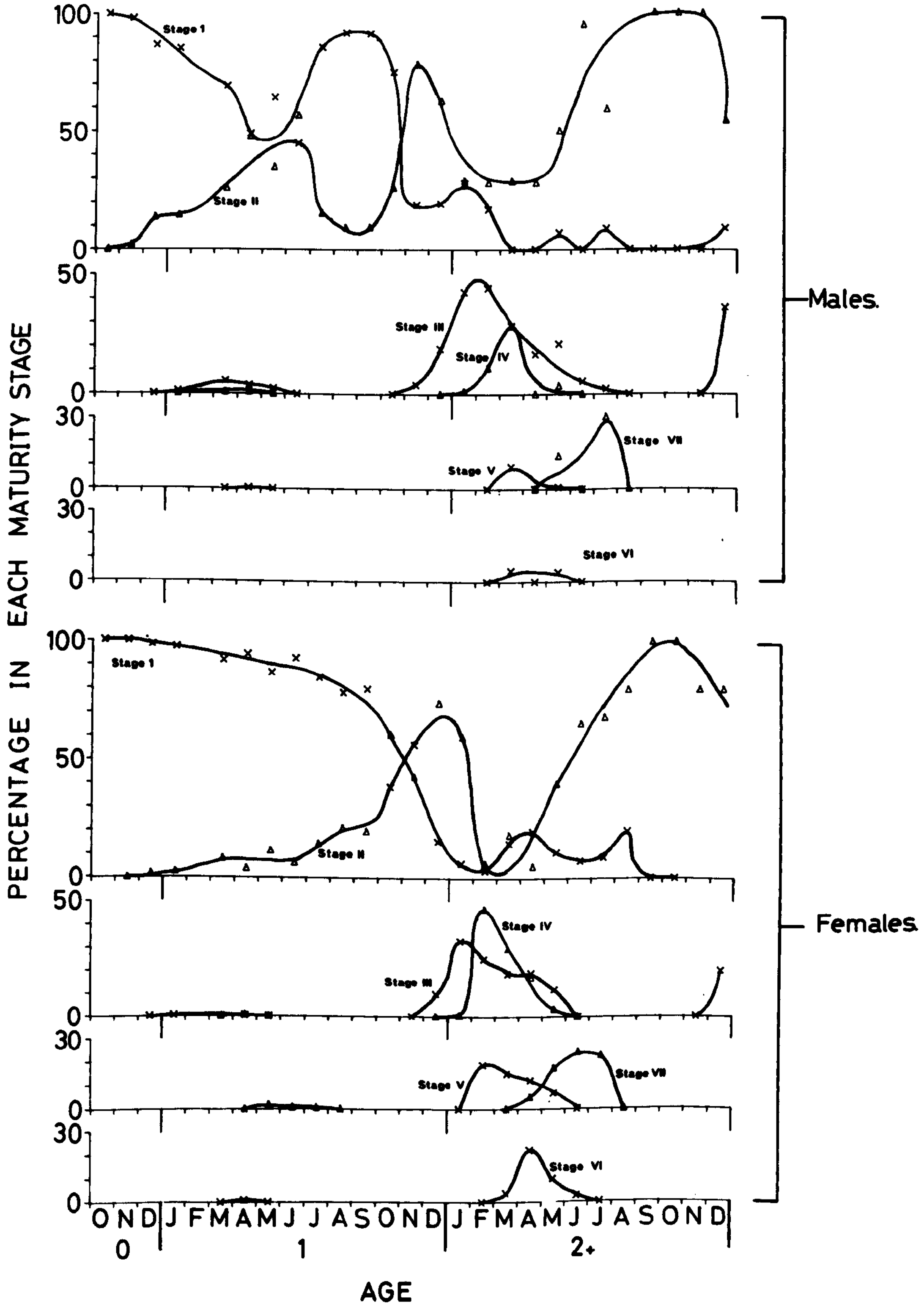
	AGE			Total	
	1	2	3		
n ♂	49	86	15	150	$\chi^2 = 41.5$
♀	10	150	20	180	d.f. = 2
Total	59	236	35	330	$p < 0.001$
% of ♂	14.8	26.0	4.5	45.45	$d = 1.65$
total ♀	3.0	45.4	6.1	54.54	$p > 0.05$

The probability of the ratio differing from 1:1 was greater than 0.05 i.e. not significant. Highly significant differences in sex-ratio were found between age-groups ($p < 0.001$). The chief difference was the greater proportion of mature 1-group male fish compared with females and the lower proportion of mature 2-group fish.

II.5.E. Breeding Cycle and Seasonality of Spawning

Monthly variations in the proportions of fish of each sex in each maturity stage are shown in Fig.II.16, pooling data from November 1974 to March 1977. Immature fish which could not be sexed are not included. It was impossible to detect differences in maturation between 2-group and older fish because of the small number of older fish sampled. The chief difference in the development of male and female fish occurred in the 1-group : more males developed as far as stage II and there was more evidence of development beyond stage II. The proportion of stage 1 males in the population increased after June, however, and the proportion of stage II males decreased with no evidence of development to stage III. This suggests either that virgin fish and recovered spents are indistinguishable, or that those males which mature in time to breed in the 1-group do not recover from the metabolic strain of spawning. The pattern and timing of each stage in the 2-group was almost identical with females, except that there was not such a pronounced peak of stage VI fish. Although male and female running-ripe (stage VI) fish were both found in the period March - May the proportion of males in April was much lower. Recovery of males was also a little faster, 100% reaching stage II by August. It has already been shown (section II.5.D) that there were fewer older males than females in the population. This more rapid recovery may be biased if there are greater mortalities among spawning males.

Fig.II.16. Seasonal change in the macroscopic appearance of the gonads of male and female poor-cod, pooling data from December 1974 to March 1977.


100
50
0
Stage I
Stage II
50
0
Stage III
Stage IV
30
0
Stage V
Stage VII
30
0
Stage VI
Males.
100
50
0
Stage I
Stage II
50
0
Stage III
Stage IV
30
0
Stage V
Stage VII
30
0
Stage VI
Females.
PERCENTAGE IN EACH MATURITY STAGE
O 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
0
1
2+
AGE

II.5.F. Location of Spawning

Table II.11 shows the relative proportions of 2-group and older fish in each maturity stage at each site between January and May. The relative proportions were determined by multiplying the proportion of fish in each maturity stage by the mean catch rate between January and May and adjusting for the sex-ratio. The exclusion of 1-group fish could lead to bias, especially in the case of males, but inspection of the raw data shows essentially the same pattern. Their exclusion increases the proportions of fish which actually take part in breeding and the results are not swamped by large numbers of virgin fish.

Running-ripe fish were found only at Ardalanish Bay and Tiree Passage. At the shallow inshore site of the Firth of Lorne, fish of both sexes were only found in stages 1 and II. At Loch Linnhe fish of both sexes developed as far as stage V (ripe). At Bloody Bay males were found in stages 1 to IV and the development of females reached stage V.

II.5.G. Comparison with Other Areas

Only direct comparisons of similar methods will be made here. Information concerning reproduction gained indirectly e.g. from studies of condition factor or occurrence of planktonic stages, is dealt with in the relevant sections.

Females in the present study matured at about 15.6cm and males at 14.0 - 14.6 cm. Menon(1950) found that the majority of males below 11cm and the majority of females below 13cm were immature, although he did not carry out a survey in any detailed or systematic way. The difference between the two areas cannot be accounted for completely by Menon's use of standard rather than total length (see Appendix II.2). Although there is a difference between the two areas, first maturity in both populations occurred in the 2-group. Planas and Vives(1952) did not give the length and age of first maturity of poor-cod in the western Mediterranean, although their data indicate that fish mature

TABLE II. 11. RELATIVE NUMBER OF 2-GROUP AND OLDER POOR-COD IN EACH MATURITY STAGE DURING THE BREEDING SEASON AT EACH SITE. DATA FROM JANUARY 1975 TO MARCH 1977 WAS POOLED.

Sex	Site	Maturity Stage						
		1	II	III	IV	V	VI	VII
Male	Loch Linnhe	4.47	0.622	2.61	0.871	.122	-	-
	Firth of Lorne	0.289	1.16	-	-	-	-	-
	Bloody Bay	0.370	3.92	1.40	0.188	-	-	-
	Ardalanish Bay	1.20	4.27	6.32	1.54	1.37	1.88	0.51
	Tiree Passage	2.65	24.4	15.1	1.96	0.64	1.96	6.25
Female	Loch Linnhe	0.373	0.621	0.746	0.994	0.373	-	-
	Firth of Lorne	0.577	0.577	-	-	-	-	-
	Bloody Bay	0.678	4.97	1.81	-	0.23	-	0.11
	Ardalanish Bay	3.01	15.41	8.57	2.15	2.41	3.71	1.86
	Tiree Passage	10.53	18.39	9.88	7.56	3.27	3.93	5.89

at somewhat smaller sizes. Cunningham(1891) found 2-group fish breeding in tanks in March 1890 ; these had been caught a year earlier on the Eddystone grounds and were thought to be spawning for the first time. In Manx waters male poor-cod matured at 10 - 11 cm and females at 13 - 14 cm (Nagabhushanam, 1965).

Menon(1950) found an overall sex-ratio of 36% male to 64% female in the Plymouth area while Nagabhushanam(1965) found an overall ratio of 28% male to 72% female (d=9.36, $p < 0.001$) in the Irish Sea. In the present study the ratio was not significantly different from 1:1 overall. It has been shown, however, that the sex-ratio varies with age and sampling ground and this could explain the differences between authors. Nagabhushanam(1959) found fewer males than females in all areas studied, except for fish caught in the January to March quarter on the east side of the Isle of Man. This area supported only small fish between 80 and 140 mm. In the present study fish on the inshore nursery grounds also showed a preponderance of males, in contrast to the offshore sites where the fish had a greater size-range.

Macroscopic observation of the gonads showed that reproduction occurred mainly between March and May with a peak in April. Svetovidov (1948) reports the main time of spawning to be March-April. Günther (1888) found poor-cod ready to spawn in March in the Sound of Sanda (east of the Mull of Kintyre). In Manx waters Nagabhushanam(1959) found ripe individuals between January and June, and spent fish between April and June. In the present study ripe fish were divided into two groups : ripe (stage V) and running-ripe (stage VI). The first occurrence of stage V fish was in February and the last occurrence of stage VI was in July, for males and females. Spent fish were found between April and July for females and May and July for males. It therefore appears that reproduction occurs slightly later in local waters. Cunningham(1891) found that poor-cod in tanks spawned in March at Plymouth.

In the western Mediterranean running-ripe female poor-cod were found between November and May, with maximum occurrence in January (Planas and Vives, 1952). This conclusion was confirmed by measurement of the index of relative fecundity (I.R.F.) , where

$$\text{I.R.F.} = \frac{\text{gonad weight} \times 100}{\text{body weight}} .$$

It appears that reproduction occurs two to three months earlier and lasts for several months longer than in the British Isles.

There was no evidence of older age-groups spawning earlier than younger ones. This was also found by Menon(1950) from direct observation and variations in the condition factor. Measurements of egg size during maturation indicated a single development of eggs rather than serial spawning. This was also found by Scharff(1887).

Svetovidov(1948) reports that 'The main spawning takes place in the English Channel, at the western and northern shores of Great Britain, around Ireland and in the Bay of Biscay ; in small quantity in the North Sea, Skagerrak, at the north-eastern shores of Scotland, at the Faroe Islands. Spawning grounds are mainly at depths of 50 - 100 m, with optimum spawning conditions being not less than 8°C and salinity 32.0 - 35.4 ‰.' In the area studied reproduction only occurred in offshore areas, inshore areas containing juvenile and maturing fish. Nagabhushanam(1959) had only a limited sample of fish but their length ranges indicated that the open sea to the east of the Isle of Man contained young fish (80 - 140 mm long), whereas fish from the west coast and Port Erin Bay had lengths up to 230 mm. Menon (1950) collected mature fish from outside Plymouth breakwater and the Eddystone grounds. Planas and Vives(1952) found running-ripe fish in the western Mediterranean but did not discuss their distribution.

II. 6. CONDITION FACTOR AND LENGTH-WEIGHT RELATIONSHIPS

II.6.A. Condition Factor

Fig.II.17 shows seasonal variations in condition factor with age at each site and pooling data from all sites. Condition factors varied between 0.6 and 1.0, with a general pattern in all age-groups of low condition in the early part of the year and an increase from June onwards. Towards the end of the year condition decreased. The seasonal cycle was essentially the same at each site, although insufficient older fish were caught to show the complete pattern at some sites. Condition was minimal in March in the 1-group at Ardalanish Bay and the Firth of Lorne. Considering all sites combined, however, the spring minimal condition in the 1-group was not appreciably lower than that in the 2- or 3-groups. Similarly the autumn maxima did not differ between the 1 and 2-groups.

Seasonal variations in condition can indicate the spawning season of a fish (section 1.3.D). The results thus imply a spawning season between February and April. Fig.II.18 shows variations in condition associated with each maturity stage, for males and females separately. The pattern was similar in both sexes : condition was low in virgin fish (0.73) and increased to 0.80 - 0.85 (depending on sex) in virgin-developing or recovering-spent fish (stage II). The first ripening stage (stage III) was not associated with much change in condition. Stages IV, V, and VI correlated with minimum condition factors, with increases to stage VII and II.

Table II.12 shows variations in condition with sex, and annual variations. There was no difference in condition between males and females, although immature fish whose sex could not be determined were in considerably poorer condition. Such fish may well belong to a different growth stanza, in which case they are not directly comparable. Fish caught in 1975 had a lower mean condition factor than those caught in 1976. x This could be due to bias caused by differences in sampling between years. Immature 0-group fish were in poorer condition in 1975 but were

Fig.II.17. Seasonal change in the mean condition factor of each year-class of poor-cod at each site and pooling fish from all sites.

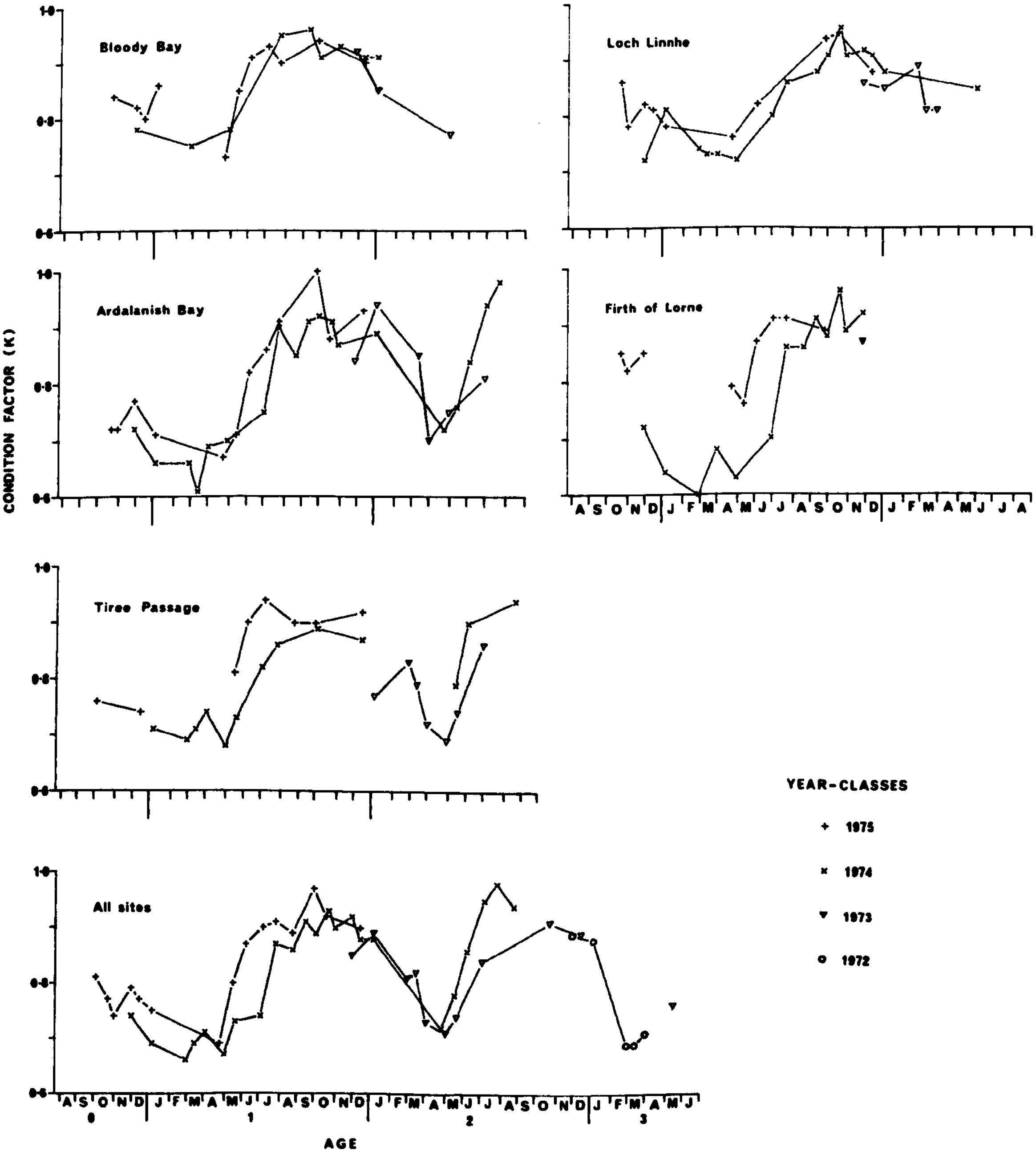

Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
All sites
CONDITION FACTOR (K)
1·0
0·8
0·6
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
0
1
2
3
AGE
YEAR-CLASSES
+ 1975
× 1974
▼ 1973
o 1972

Fig.II.18. Mean condition factor (with 95% confidence limits) of poor-cod in each maturity stage.

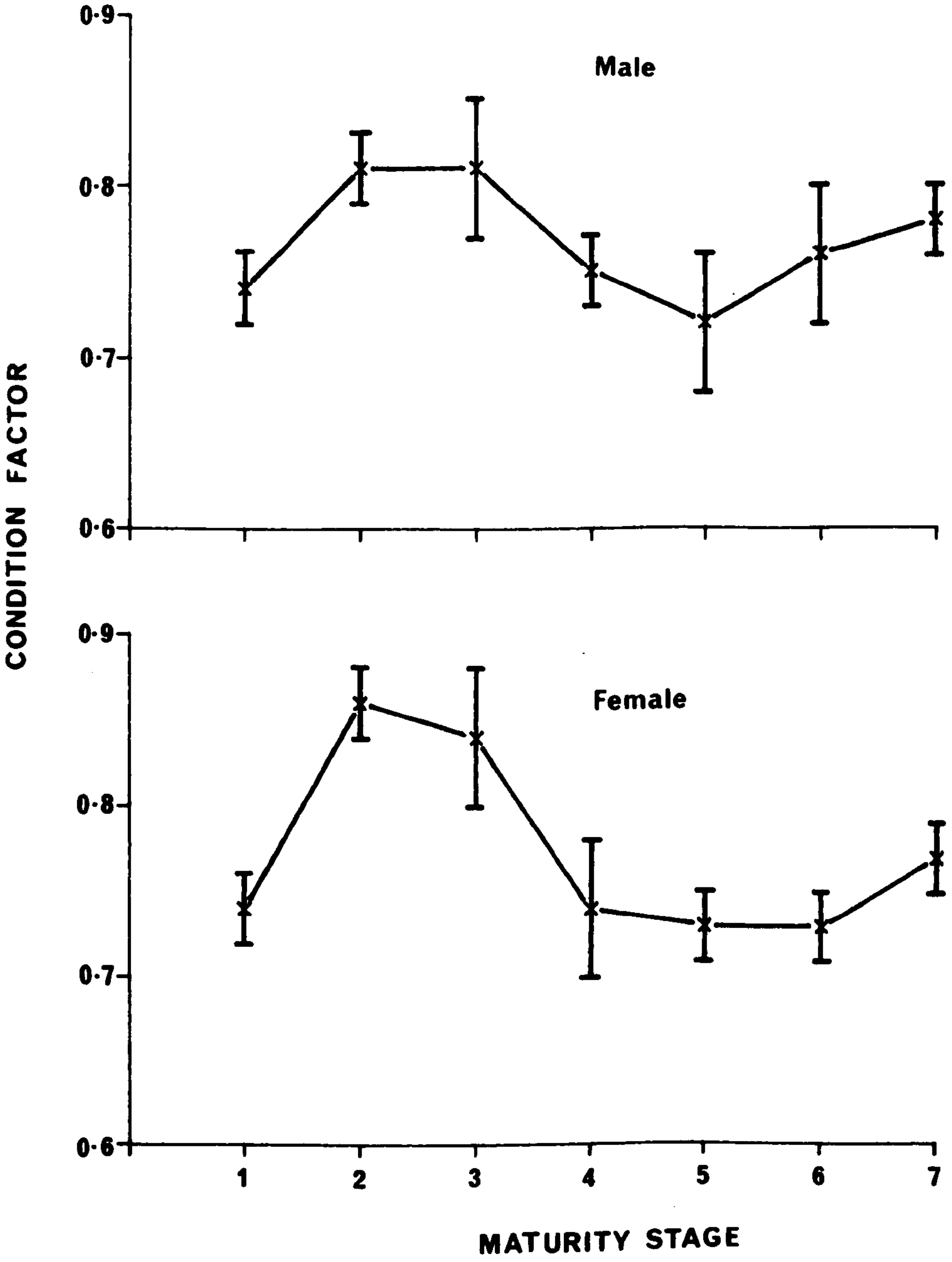

CONDITION FACTOR
0·9
0·8
0·7
0·6
Male
0·9
0·8
0·7
0·6
Female
1
2
3
4
5
6
7
MATURITY STAGE

TABLE II.12. MEAN CONDITION FACTORS OF POOR-COD ACCORDING TO SEX AND YEAR OF CAPTURE, POOLING DATA FROM ALL SITES AND AGE-GROUPS.

Group of fish.	Condition Factor.	Standard Error.
All males.	0.79	0.01
All females.	0.79	0.01
Fish whose sex could not be determined.	0.64	0.01
Fish caught in 1975.	0.76	0.01
Fish caught in 1976.	0.83	0.01
All fish.	0.77	0.01

not weighed in 1976. 1-group fish in 1976, however, were normally in better condition than 1-group fish in 1975 (Fig.II.17). Although the difference was not so clear in the 2-group, the 1974 year-class in 1976 was generally in better condition than the 1973 year-class in 1975.

Fig.II.19 shows seasonal variations in condition for each sex, pooling data from all sites. The seasonal variation was similar in males and females, and in both sexes fish caught in 1975 were in better condition than those caught in 1976.

II.6.B. Length-weight Relationships

A preliminary scatter diagram of log length against log weight showed that, as with most fish, weight varied as a power of length i.e.

$$\text{weight} = \text{a length}^{b} \quad \text{or}$$

$$\log \text{weight} = \log a + b \log \text{length} ,$$

where a and b are constants. The precise relationship was determined by calculation of the G.M. regression of log weight with log length (section 1.3.E and Appendix II.4.A). The relationship for all fish weighed was

$$\log \text{weight} = 3.3939 \log \text{length} - 4.9241 .$$

An analysis of covariance test for comparison of slopes (Appendix II.4.B) showed that there was a significant difference between the length-weight relationships of males and females. Fig.II.20 shows the length-weight relationships of males, females, immatures (fish whose sex could not be determined) and all fish weighed. Ordinary predictive regressions for males and females were also calculated but these were found to underestimate the slopes of the regression lines.

Although the complete curve for immature fish is shown, usually only fish of lengths less than about 10cm could not be sexed. These fish had lower weights than fish of the same length whose sex could be determined. Fish which are in poor condition and are not competing successfully with the rest of the population are unlikely to have much

Fig.II.19. Seasonal variation in the mean condition factor of each year-class of male and female poor-cod, pooling data from all sampling sites.

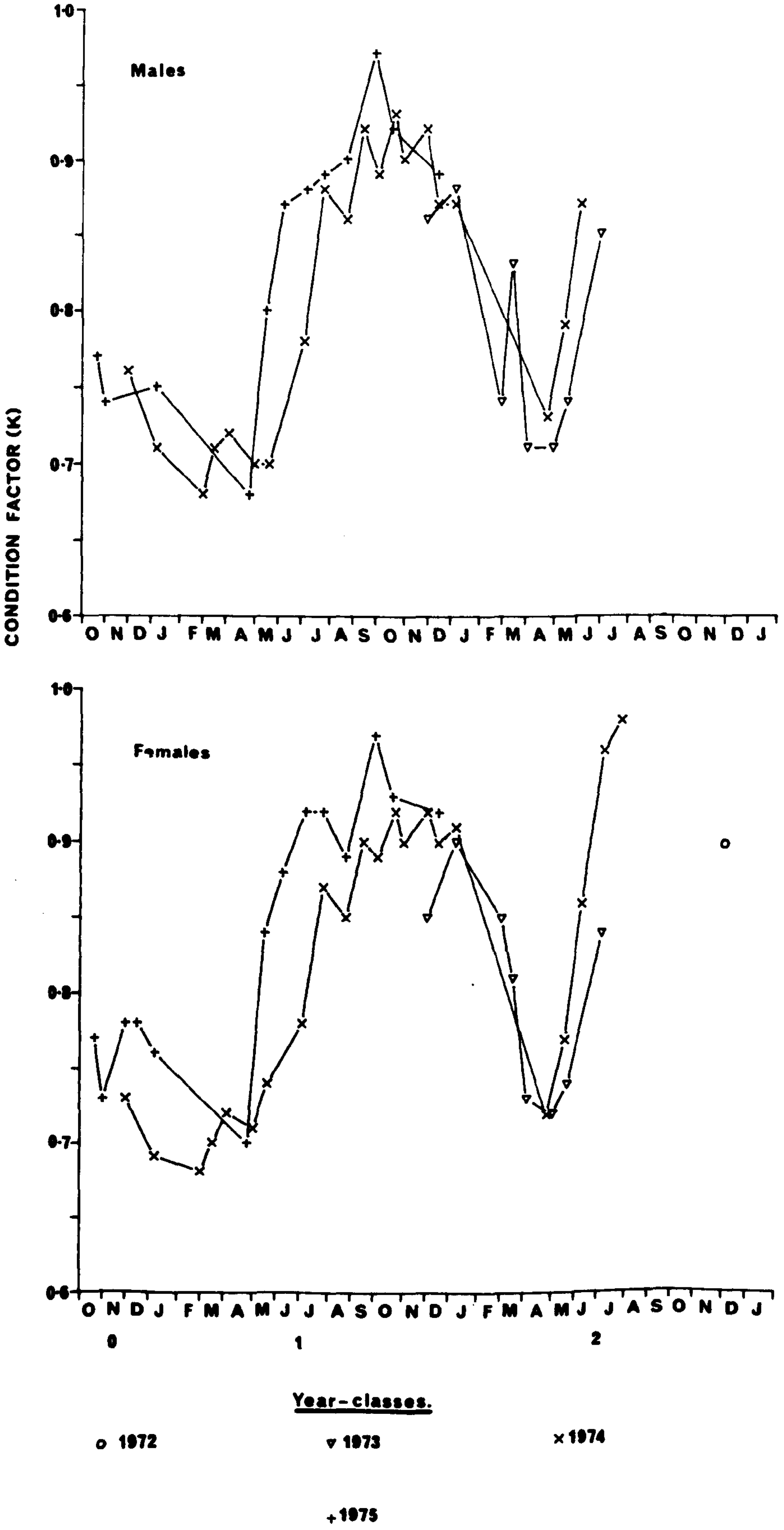
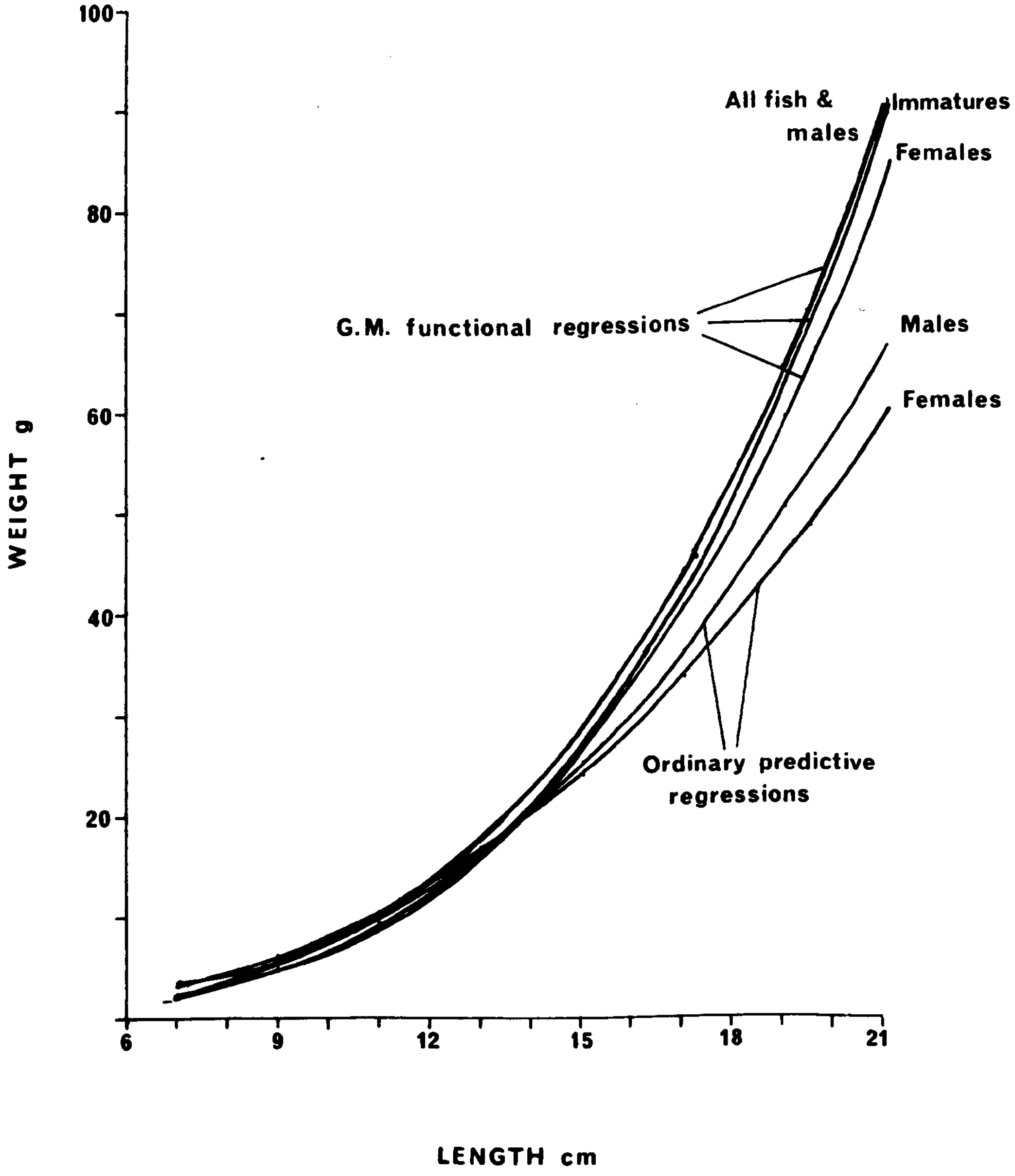

CONDITION FACTOR (K)
Males
Females
1·0
0·9
0·8
0·7
0·6
O N D J F M A M J J A S O N D J F M A M J J A S O N D J
0
1
2
Year-classes.
o 1972
▿ 1973
× 1974
+ 1975

Fig.II.20. Length-weight relationships of poor-cod for each sex, calculated using Ordinary Predictive and G.M. Functional Regressions.


WEIGHT g
100
80
60
40
20
6
9
12
15
18
21
LENGTH cm
All fish &
males
Immatures
Females
G.M. functional regressions
Males
Females
Ordinary predictive
regressions

energy available to put into the development of gonads. Many of the fish whose sex could not be determined were also heavily infected with tapeworms.

Fig.II.21 shows the length-weight relationship of each sex in each maturity stage. Statistics of the regression lines are given in Appendix II.4.C. It was not possible to compare relationships directly because residual variance was significant. Fish in maturity stages IV, V, VI and VII were lighter than fish of the same length in maturity stages 1, II and III.

Seasonal variations (Appendix II.4.D)

Fig.II.22.A shows the calculated G.M. length-weight regressions of fish in each month combining data from 1975 and 1976, for all sites and for all sexes and ages. In smaller fish (less than about 14 cm) the situation is very confused with a great deal of overlap between curves. Between January and May the slope of the length-weight relationship became less steep i.e. fish of the same length were lighter. From June to August changes in the relationship resulted in increases in weight at length. In the remaining four months the situation was not so clear, mainly because of the lower sample sizes. If results for several months are combined, however, there is a further increase in weight at length. In order to equalise residual variances for an analysis of covariance test, results for several months were combined (June and July; August, September and October ; November and December). The resultant curves showed highly significant differences in slope (Appendix II.4.E).

II.6.C. Discussion

Menon(1950) studied variations in the condition of poor-cod in the Plymouth area. Essentially the same pattern was found : a maximum in the period from June to January, a reduction from January to April with an increase to the summer maximum thereafter. The values of the condition factor were lower in the present study than those calculated by Menon

Fig.II.21. G.M. Functional Regressions of the length-weight relationships of male and female poor-cod in each maturity stage.

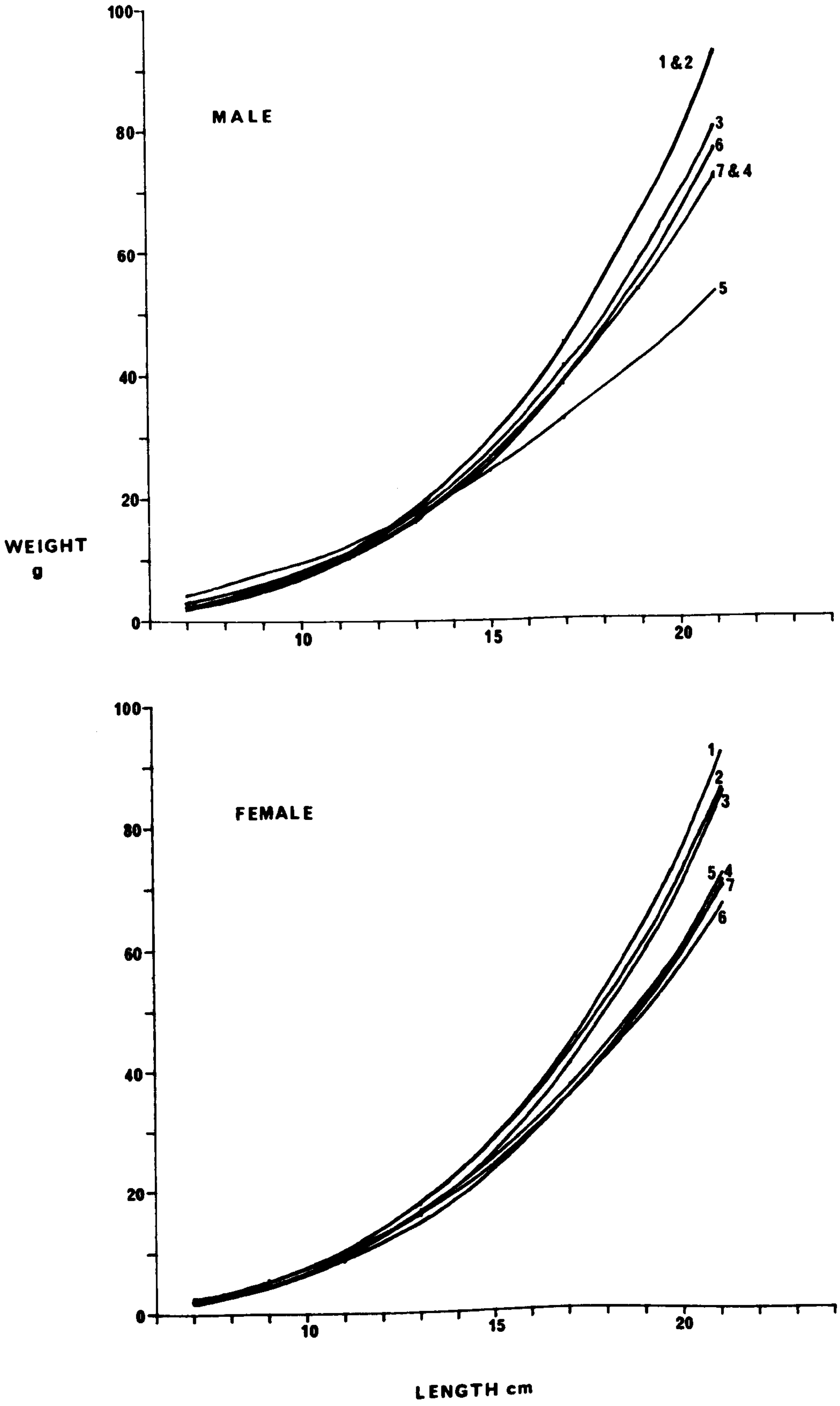
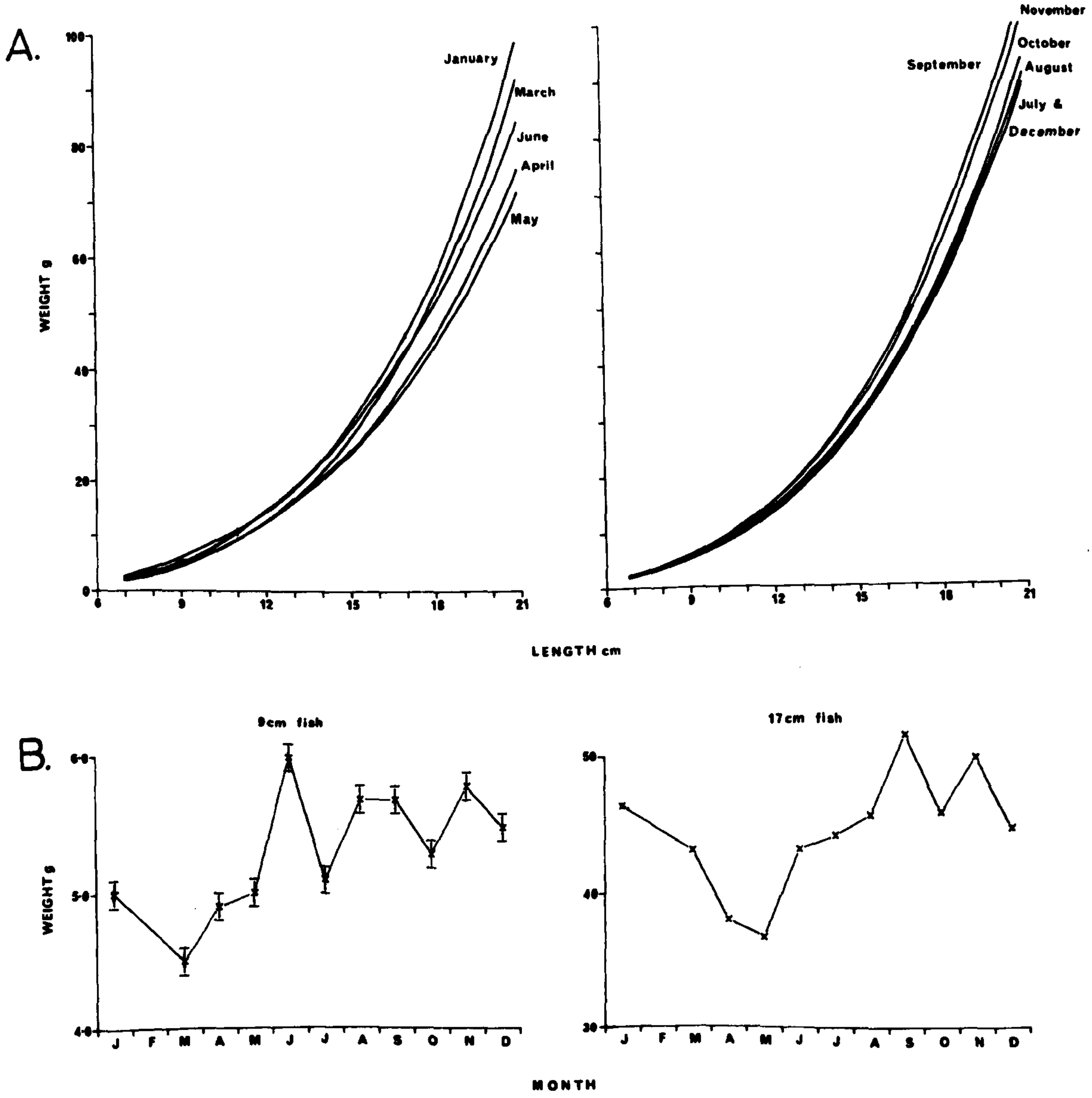

MALE
1&2
3
6
7&4
5
100
80
60
40
20
0
10
15
20
WEIGHT g
FEMALE
1
2
3
5
4
7
6
100
80
60
40
20
0
10
15
20
LENGTH cm

Fig.II.22.A. G.M. Functional Regressions of the length-weight relationships of poor-cod caught in each month.

II.22.B. Seasonal variation in the estimated weight (g) of poor-cod of 9 cm and 17 cm, assuming the above length-weight relationships, with 95% confidence limits.


A.
100
80
60
40
20
0
WEIGHT g
6
9
12
15
18
21
January
March
June
April
May
November
October
September
August
July &
December
LENGTH cm
B.
9cm fish
6·0
5·0
4·0
WEIGHT g
J
F
M
A
M
J
J
A
S
O
N
D
17cm fish
50
40
30
MONTH

(loc. cit.), probably because of the use of total rather than standard lengths, and gutted rather than total weights. At Plymouth slight reductions in condition in August and September were also obvious, but this was not apparent in the present study.

There were significant differences in length-weight relationships between the sexes. This was also found by Menon(1950) from comparison of condition factors. Planas and Vives(1952) plotted length-weight relationships for males and females but, although there were differences, regression statistics were not calculated. Table II.13 shows the weights of poor-cod at three lengths, calculated from the regressions of locally caught fish and from the graphs of Planas and Vives(loc. cit.). Local males and females are consistently lighter. Two reasons for this are suggested :

(1) the use of gutted rather than total weight in the present study ;

(2) the poor-cod of the western Mediterranean belong to a separate sub-species (Svetovidov, 1948) so morphological differences are to be expected.

The relationships between condition and reproduction, feeding and growth in length and weight will be considered in the final discussion (section II.7).

TABLE II.13. COMPARISON OF WEIGHTS OF POOR-COD IN THE WESTERN MEDITERRANEAN WITH LOCAL FISH.

	West Coast of Scotland.			Western Mediterranean Sea.		
Length cm.	13	15	17	13	15	17
Male weight g.	18.09	29.31	44.65	19.5	31.5	-
Female weight g.	16.71	27.02	41.10	19.5	31.0	42.0

II. 7. SUMMARY AND DISCUSSION

Gordon (pers.comm.) found that the inshore areas of the Firth of Lorne and Loch Linnhe were nursery grounds for poor-cod. Fish were first captured by the bottom trawl in August in the 0-group and had left the area by May in the 2-group. The present study confirms these results and answers some of the questions concerning the origin and the rest of the life history of these juvenile fish.

Macroscopic examination of the gonads showed that poor-cod spawn between January and May with a peak in April, at the offshore sites of Ardalanish Bay and Tiree Passage. This was confirmed by the seasonal occurrence of planktonic stages and by analysis of variations in condition factor and length-weight relationships. The breeding season occurs later with increasing latitude, and is also later on the east coast of the British Isles compared with the west coast. This is in agreement with the observations of Orton (1920) who found that species nearer to the colder limits of their range breed during the warmer months of the year.

Considering the reproductive ecology in more detail, females matured at a length of about 15.6 cm in the 2-group, with only a small proportion of 1-group fish maturing. Male fish matured at the slightly smaller size of 14.0 - 14.6 cm; male fish grew more slowly but also a greater proportion of them spawned. There was no overall deviation from a 1:1 sex-ratio, although older age-groups comprised more females than males. If the greater proportion of mature male 1-group fish is taken into account the breeding population did not differ significantly from a 1:1 ratio. It is generally considered that the metabolic strain of spawning is greater in older males than in older females (Menon,1950; Hickling, 1930; Hart, 1946; Ursin, 1963; Beverton and Holt, 1959). This earlier maturation of males counteracts the lower survival rate of older fish. The success of reproduction was highly dependent on a single year-class, since 83.3% of mature female fish consisted of a single age-group (the 2-group).

No evidence was found of serial spawning or the earlier reproduction of individual year-classes. This is in contrast to the conclusions of Qasim (1956) who found that Mediterranean-boreal species in general have a long breeding season. The oocytes of such fish have a wide size-range and are matured and shed periodically, so that larvae are present in the plankton over a long period. This ensures that larvae are ready to take advantage of optimum conditions, which may occur at any time in low latitudes. In contrast artic-boreal species in high latitudes have a short spawning season, with all eggs released in one batch so that the larvae hatch during the short period of maximum production. Perhaps the ecological advantage of this reproductive strategy is lost when a species is divided into a boreal and Mediterranean sub-species, the boreal sub-species becoming adapted to life in an environment where production is seasonal.

The eggs and larvae of poor-cod are planktonic and their distribution therefore depends on the direction and strength of the water currents. Russell (1930) reports that planktonic larval poor-cod of 4-12 mm length occur in water layers between 20m depth and the bottom from February until late April. They then rapidly become demersal, bottom plankton nets catching the fish for a further month at lengths of 12 - 27 mm. The distribution of larvae in relation to water currents will be discussed later, but it should be noted that planktonic stages were only found at Tiree Passage, Ardalanish Bay and Bloody Bay. Movement inshore to the Firth of Lorne and Loch Linnhe therefore occurred after the planktonic stage in July/August. The precise timing of the movement was difficult to determine, because it occurred when the fish were large enough to escape capture by the plankton net and the population was not fully represented in mid-water and bottom trawl catches. Such migrations are not unknown for this species; Poulsen (1937) concluded that the occurrence of poor-cod larvae in the southern Kattegat was due to an inflow and not to a local spawning in the area.

At the time of the migration a large number of individuals are moving from a three-dimensional living space to an essentially two-dimensional sea-bottom. The inshore movement may represent a spreading-out of individuals over the two-dimensional living-space. At the same time as the inshore movement there is also evidence of a limited vertical migration. Unlike the whiting (section III) poor-cod were always more concentrated offshore.

Bottom trawl catch-curves for all sites showed a typical rapid increase in abundance between July and September, when the fish were incompletely sampled. The descending limb of the curve is considered to be a true representation of density of fish at each site. In all cases a large and highly significant part of the regression of log. catch rate was explained by regression with time. There was a lot of variation between samples, however, with some evidence of a reduction in availability (or catchability) of fish in summer. The regressions for the shallow sites of Bloody Bay and the Firth of Lorne showed a very rapid decrease in numbers. At the offshore sites of Ardalanish Bay and Tiree Passage fish survived and remained in the area long enough to mature; at the deep inshore site of Loch Linnhe fish remained longer than at the shallow inshore sites, but not until old enough to breed. It is possible that at sites at which reproduction did not occur the fish just died, but this is unlikely (see section V). It therefore seems probable that the more rapid reduction in numbers was due to natural mortality and emigration, the migrating fish boosting apparent survival rates offshore.

The length-frequency distributions of O-group fish showed no modes. There is no evidence in the literature of separate stocks of poor-cod, although fish at the opposite ends of the distribution may be effectively distinct.

Growth in length and weight was markedly seasonal occurring mainly between March and September, although increases in length may continue until November. Between May and September there was a marked increase in condition factor corresponding to an increase in the slope of the length-weight relationship. This indicated that the fish were increasing in weight at a greater rate than one would expect, either assuming isometric growth or assuming that the fish grew according to the overall length-weight relationship of

$$\log \text{weight} = 3.3939 \log \text{length} - 4.9241.$$

From September to November the condition of the fish reached a plateau, associated with continuing increases in length after growth in weight had terminated. The seasonal variations in length-weight relationship and condition may also be related to variations in feeding. Menon (1950) found that feeding increased between May and July with a reduction to a slightly lower level from August to January. From January to April feeding was minimal. The reduction in condition and reduced slope of the length-weight relationship from November to May occurred when there was little growth in length. Menon (1950) found a reduction in the rate of feeding in this period and at the same time the gonads developed. The maturation of the gonads has been shown to be associated with changes in condition.

These inter-relationships between length, weight, condition and rate of feeding do not take into account energy stored in the liver. Though liver size was not measured in any detailed or systematic way it was observed that the liver increased in size very rapidly in June/July when the increase in feeding and condition, and the recovery of the gonads occurred.

SECTION III

Merlangius merlangus (Linnaeus, 1758)

WHITING

III.1. INTRODUCTION

The taxonomy and distribution of the species have been described by Wheeler (1969) and Svetovidov (1948). The species is found along the European Atlantic Coast within the 200m depth contour from Murman to the Iberian peninsula, at Iceland, throughout the Irish Sea, North Sea, Skagerrak, Kattegat and Belt Sea, and the western Baltic. Occasionally the species occurs in the Mediterranean and Adriatic Seas. A separate sub-species, Merlangius merlangus euxinus (Nordmann, 1830) occurs in the Aegean, Marmara, Black and Azov Seas.

The whiting is an important commercial species, total catches from I.C.E.S. statistical areas 1 to XIV varying between 160,021 and 268,076 tonnes from 1970 to 1977. During this period the total U.K. catch increased from 34,899 to 55,934 tonnes; thus the U.K. catch represented between about 15% and 30% of the total (Table III.1). Denmark landed the greatest catches, usually about half of the total, associated with the 'Industrifisk' fishery while the U.K. and French landings represented the greater part (about 80%) of the U.K. catch, although English and Welsh landings increased markedly in 1974. The whiting varied between fourth and sixth in order of importance to the Scottish fishing industry, after haddock, herring, cod, sprat and in some years, saithe and Norway pout.

The region studied forms part of I.C.E.S. statistical area VI.a (Fig.III.1). Table III.2 shows that landings from this area represent between one-quarter and one-fifth of the total U.K. catch. Several nations fish in the area, Scotland being the most important, followed by France, Ireland and England. The total catch of whiting from the area varied between 11,222 tonnes in 1970 and 20,460 tonnes until 1977, the U.K. catch varying between 6915 and 16,902 tonnes. These figures for area VI.a should be treated with some caution since until 1977 the fishery was unregulated, leading to deliberate mis-reporting

Fig.III.1. Chart of I.C.N.A.F. and I.C.E.S. statistical areas.

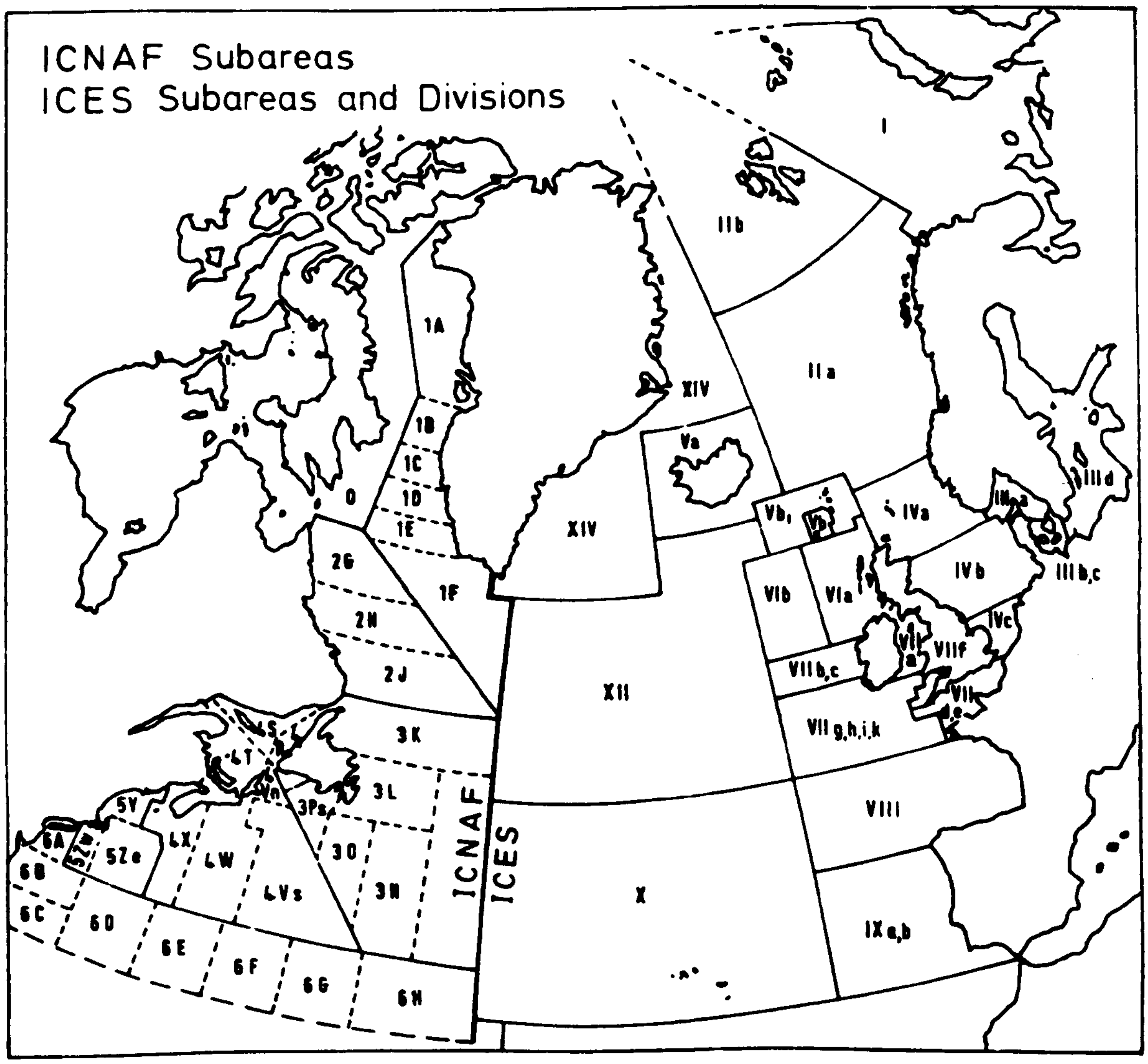

ICNAF Subareas
ICES Subareas and Divisions

TABLE III.1. CATCHES OF WHITING FROM 1970 TO 1974 IN SCOTLAND, ENGLAND AND WALES, N.IRELAND, TOTAL U.K., AND THE TOTAL CATCH FROM ICES STATISTICAL AREAS 1 to XIV. (FROM BULLETIN STATISTIQUE DES PECHES MARITIMES).

Year	Scotland		England + Wales		N.Ireland		Total U.K.		Total
	Catch Tonnes	% of U.K. Catch	Catch Tonnes	% of U.K. Catch	Catch Tonnes	% of U.K. Catch	Catch Tonnes	% of ICES Catch	I.C.E.S. Catch Tonnes
1970	28,225	81.0	5,360	15.4	1,314	3.8	34,899	15.4	226,610
1971	38,392	83.2	5,866	12.7	1,899	4.1	46,157	27.9	165,503
1972	34,739	82.6	5,357	12.7	1,976	4.7	42,072	26.3	160,021
1973	30,997	76.9	6,895	17.1	2,437	6.0	40,329	19.3	268,076
1974	29,627	57.3	21,660	41.9	435	0.8	51,722	19.2	208,458
1975	41,692	80.7	7,683	14.9	2,280	4.4	51,655	23.5	220,100
1976	44,109	79.9	7,790	14.1	3,290	6.0	55,189	24.0	230,174 *
1977	43,872	78.4	9370	16.7	2,692	4.8	55,934	29.5	189,653 **

* Figures from France, Norway and Spain excluded.

** Figures from Portugal and Spain excluded.

TABLE III.2. U.K. CATCHES OF WHITING FROM I.C.E.S. STATISTICAL AREA VIa AS A PROPORTION OF THE TOTAL U.K. CATCH (FROM BULLETIN STATISTIQUE DES PÊCHES MARITIMES.)

Year	Total U.K. catch in tonnes	Total U.K. catch from stat. area VIa tonnes	%
1970	34,899	6,915	19.8
1971	45,157	11,501	24.9
1972	42,072	10,809	25.7
1973	40,329	9,887	24.5
1974	51,722	10,041	19.4
1975	51,655	12,800	24.8
1976	55,189	16,902	30.6
1977	55,934	10,393	18.6

of catches when quota limits for the North Sea were reached (Anon. 1977a). Total Allowable Catches (TAC's) of 22,000 and 17,000 tonnes were recommended for 1977 and 1978 respectively in area VI.a.

As with many demersal gadoids, whiting stocks of the North Sea, Bristol Channel and west coast of Scotland have been classified as overexploited from growth overfishing (Anon., 1977b). In such stocks overfishing has reduced catch rates because of a reduction in the average age of fish in the catch. Although recruitment is not likely to be affected the fishery becomes increasingly unstable due to dependence on a reduced number of age-groups.

The whiting is an active unspecialized predator feeding on most available animals of a suitable size. Although usually an epibenthic feeder whiting also occur in intermendiate and upper layers (Woodhead, 1965), possibly associated with diurnal migrations. Young fish eat small crustaceans and gobies, progressing to small fish (Ammodytidae, sprats, smaller whiting, poor-cod and Norway pout) as they grow.

Because of its commercial importance there is a large amount of literature on the biology of the species. No attempt will be made here to summarise previous work but important papers will be referred to in the relevant parts of the text.

III.2. LOCAL DISTRIBUTION, ABUNDANCE AND AGE COMPOSITION.

III.2.A. Occurrence of Planktonic Stages.

Russell(1976) summarised the literature on the identification of the eggs, larvae and post-larvae of whiting: the eggs are very difficult to distinguish from those of the poor-cod, bib and blue whiting. Since the poor-cod has been shown to spawn in the area considered (section II.5) and Gordon (1977c) has shown that a small number of juvenile blue whiting occur in deeper inshore areas, no attempt was made to identify eggs.

The seasonal occurrence and abundance of larval and post-larval whiting, caught by the Plymouth 2m Young Fish Trawl is shown in Fig. III.2. Larvae were found at the three most offshore sites between April and late July, with a peak of abundance in May. There was little variation between 1975 and 1976 catches, although sampling was more extensive in 1975. The peak of abundance was greatest at Tiree Passage. No planktonic whiting were found at inshore sites in either year. Catches of fish over 2cm long were often associated with catches of the Scyphomedusa Cyanea capillata after May.

Gordon(1977b) also found an abundance of larval whiting west of Mull and significant numbers at Bloody Bay. At the inshore sites sampled (Firth of Lorne, Loch Linnhe, Loch Sunart and Loch Etive) whiting larvae were absent from all except Loch Etive.

III.2.B. Occurrence of Pelagic Stages.

The catch rates of planktonic whiting fell rapidly following the peak of abundance in April and May. Although mortalities undoubtedly affected abundance the main reason for this decrease was probably the growing fish escaping capture by the 2m net. In order to sample such young fish in the pelagic phase the mid-water trawl was used from May onwards. Sampling was only on a limited scale in 1975 due to bad weather but in 1976 continued until the fish became demersal (Fig.III.3).

Fig.III.2. Catch rates (log.scale) of O-group whiting in the Plymouth Young Fish Trawl at each site. Although hauls were made on each cruise at Loch Linnhe and the Firth of Lorne no planktonic whiting were caught.

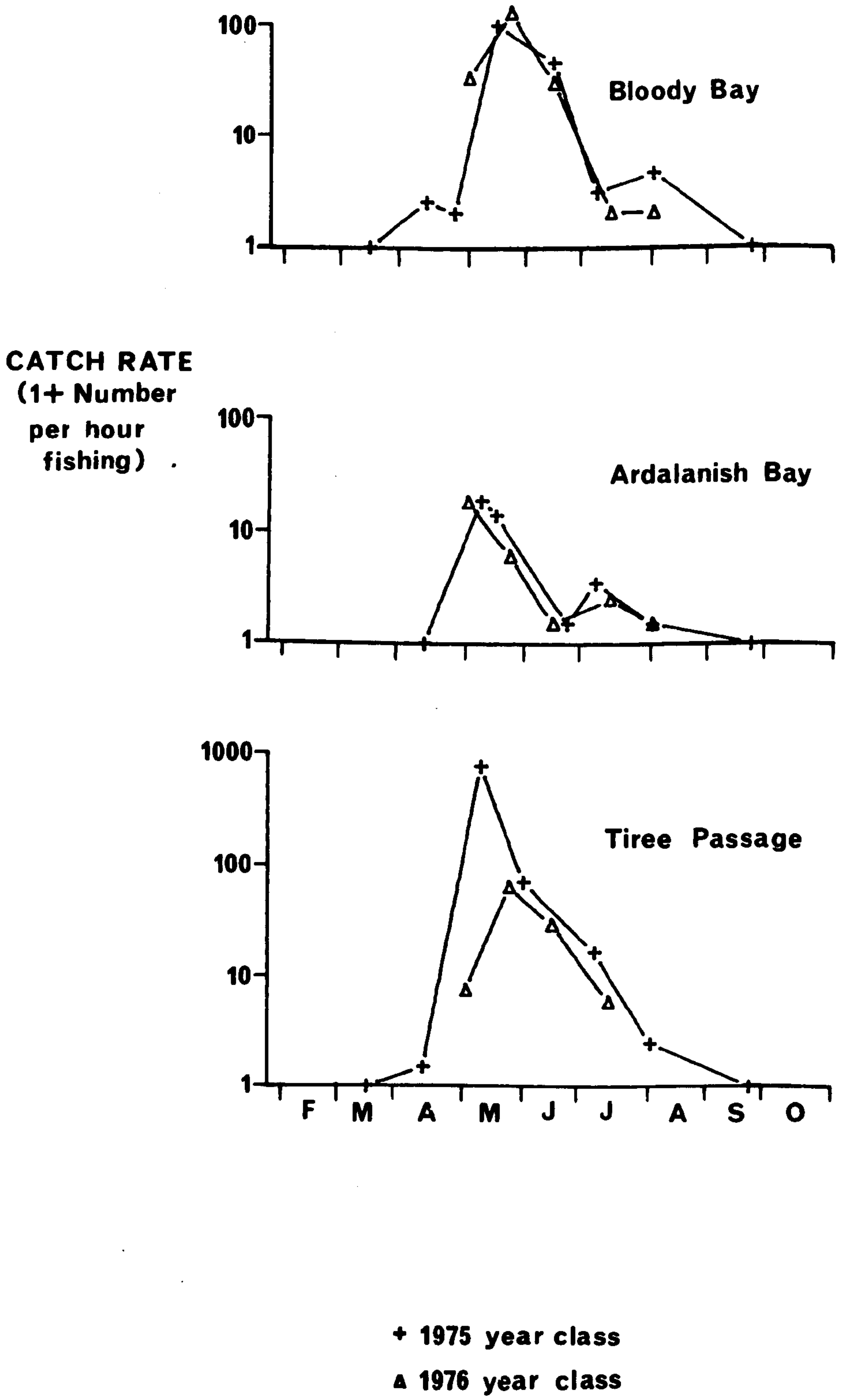
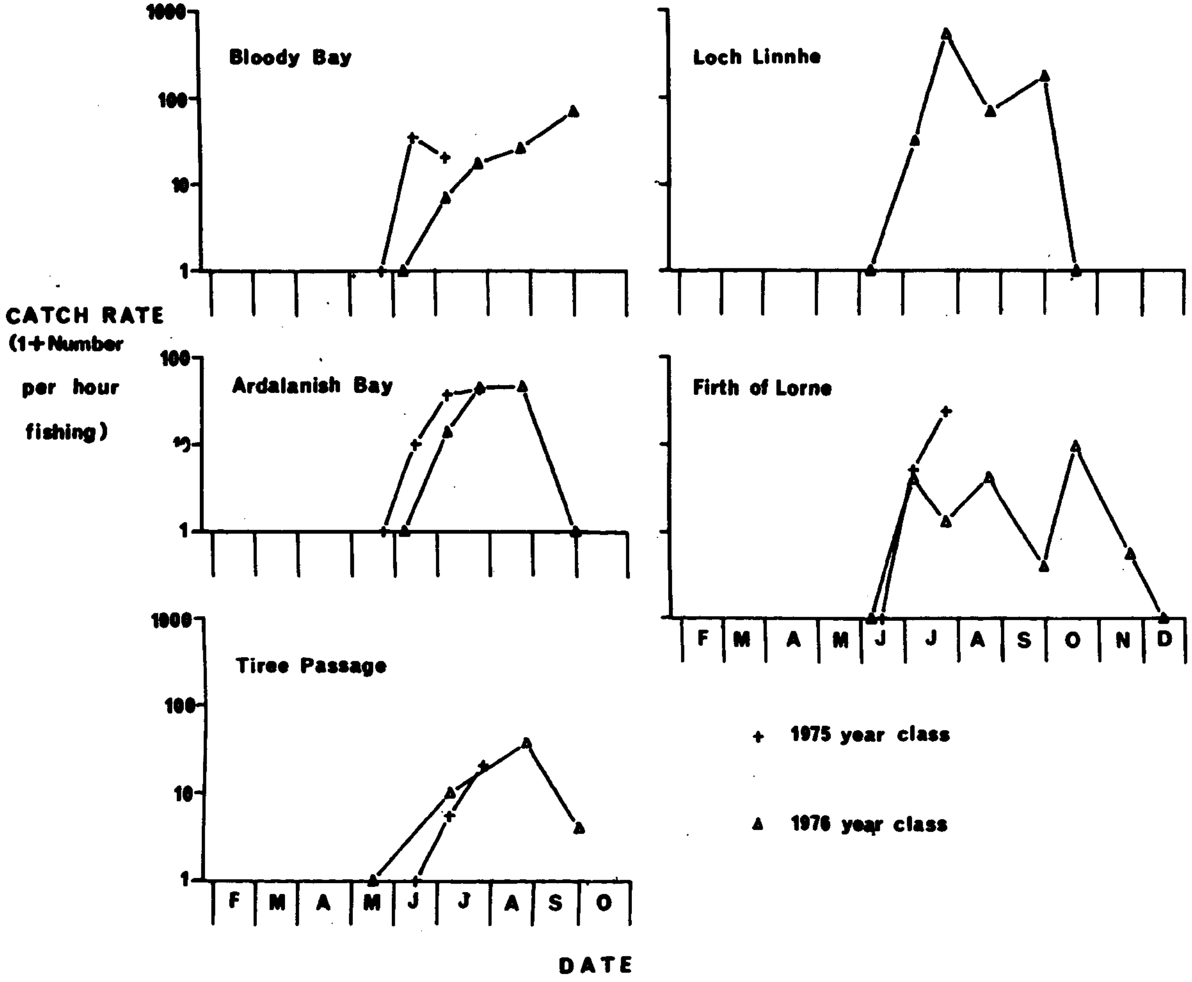

CATCH RATE
(1+ Number
per hour
fishing)
Bloody Bay
100
10
1
Ardalanish Bay
100
10
1
Tiree Passage
1000
100
10
1
F
M
A
M
J
J
A
S
O
+ 1975 year class
Δ 1976 year class

Fig.III.3. Catch rates (log. scale) of O-group whiting in the mid-water trawl at each site.


CATCH RATE
(1+Number
per hour
fishing)
Bloody Bay
1000
100
10
1
Loch Linnhe
Ardalanish Bay
100
10
1
Firth of Lorne
F
M
A
M
J
J
A
S
O
N
D
Tiree Passage
1000
100
10
1
F
M
A
M
J
J
A
S
O
DATE
+ 1975 year class
▲ 1976 year class

Pelagic whiting were first caught in July at all sites. Catch rates were fairly low (10 to 100 per hour fishing) but consistent and continued until about October at most sites. As in the case of the 2m plankton net large catches were often associated with *Cyanea capillata*. The last successful haul at the Firth of Lorne was in November. The mean lengths of fish caught by the mid-water trawl were greater at the inshore sites compared with offshore sites. (Figs.III.4,III.5. and Appendix III.1).

III.2.C. Occurrence of Demersal Stages

The catch rates of fish in the bottom trawl at each site are shown in Fig.III.6. At Bloody Bay, Loch Linnhe and the Firth of Lorne the first occurrence in June was followed by a very rapid increase in catches until about October, when the numbers started to fall. This increase was probably due to an increasing proportion of the population becoming liable to capture. Gordon (1977b) first caught O-group whiting in the bottom trawl at inshore sites in the same area in July, with maximum abundance between August and January. In the present study the cod-end was likely to retain a greater proportion of small fish (see section 1.3). The catch-curve at Ardalanish Bay was similar but the peak of abundance was not as great. At Tiree Passage the ascending limb was not as steep and maximum abundance did not occur until about May.

Mean lengths of fish caught in this early period are shown in Figs. III.4, III.5 and Appendix III.2. Although the differences were not as marked as in mid-water trawled samples, the mean lengths of fish caught offshore were again consistently smaller than those caught inshore. Also fish caught by the bottom trawl were larger than fish caught by the mid-water trawl at the same site. There was, however, some overlap between the larger fish caught by the mid-water trawl (inshore) and the smaller fish caught by the bottom trawl (offshore).

Fig.III.4. Monthly mean total lengths (cm) of 0-group and early 1-group whiting caught by the bottom trawl and mid-water trawl (plastic cover) in 1975.

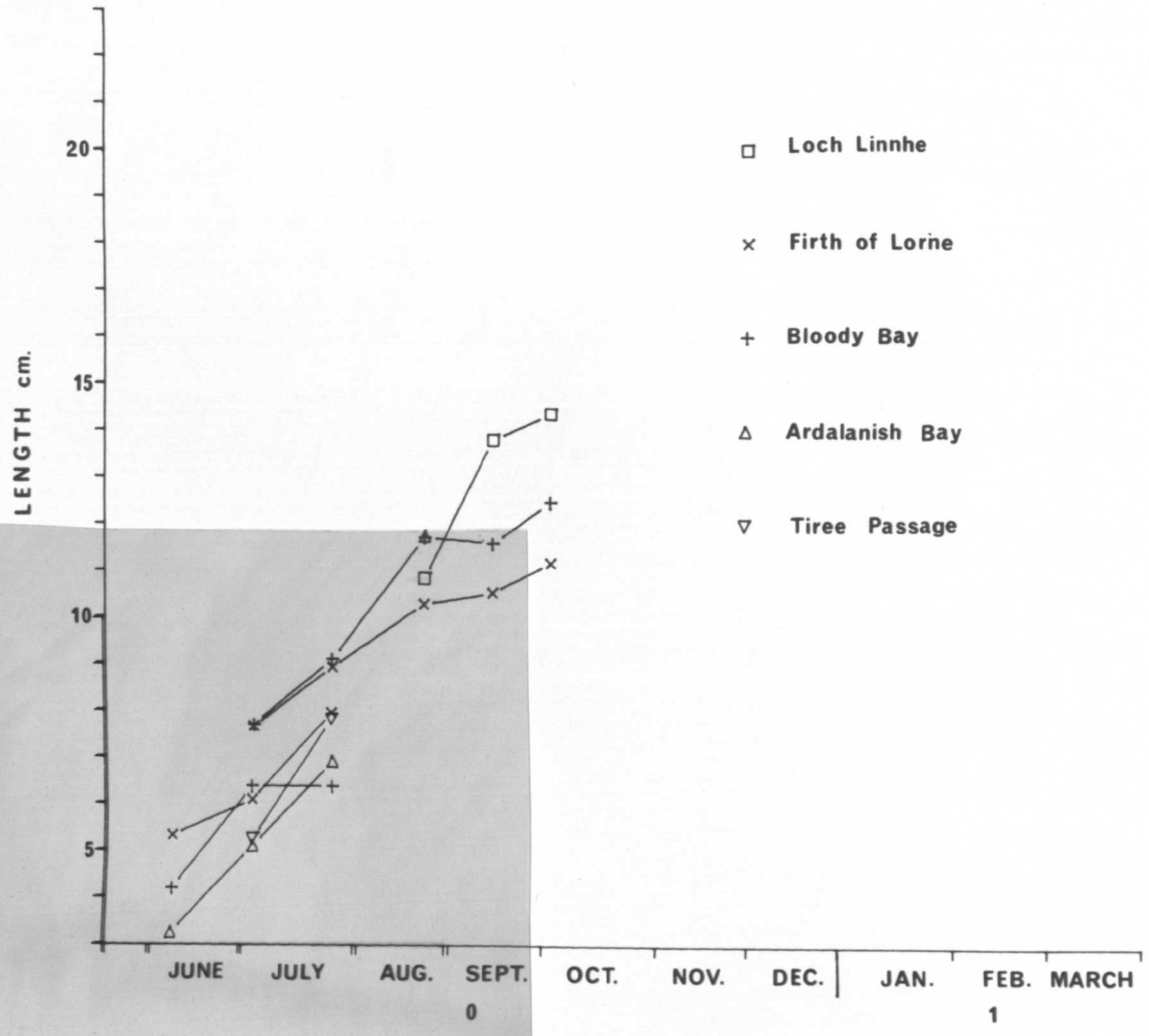
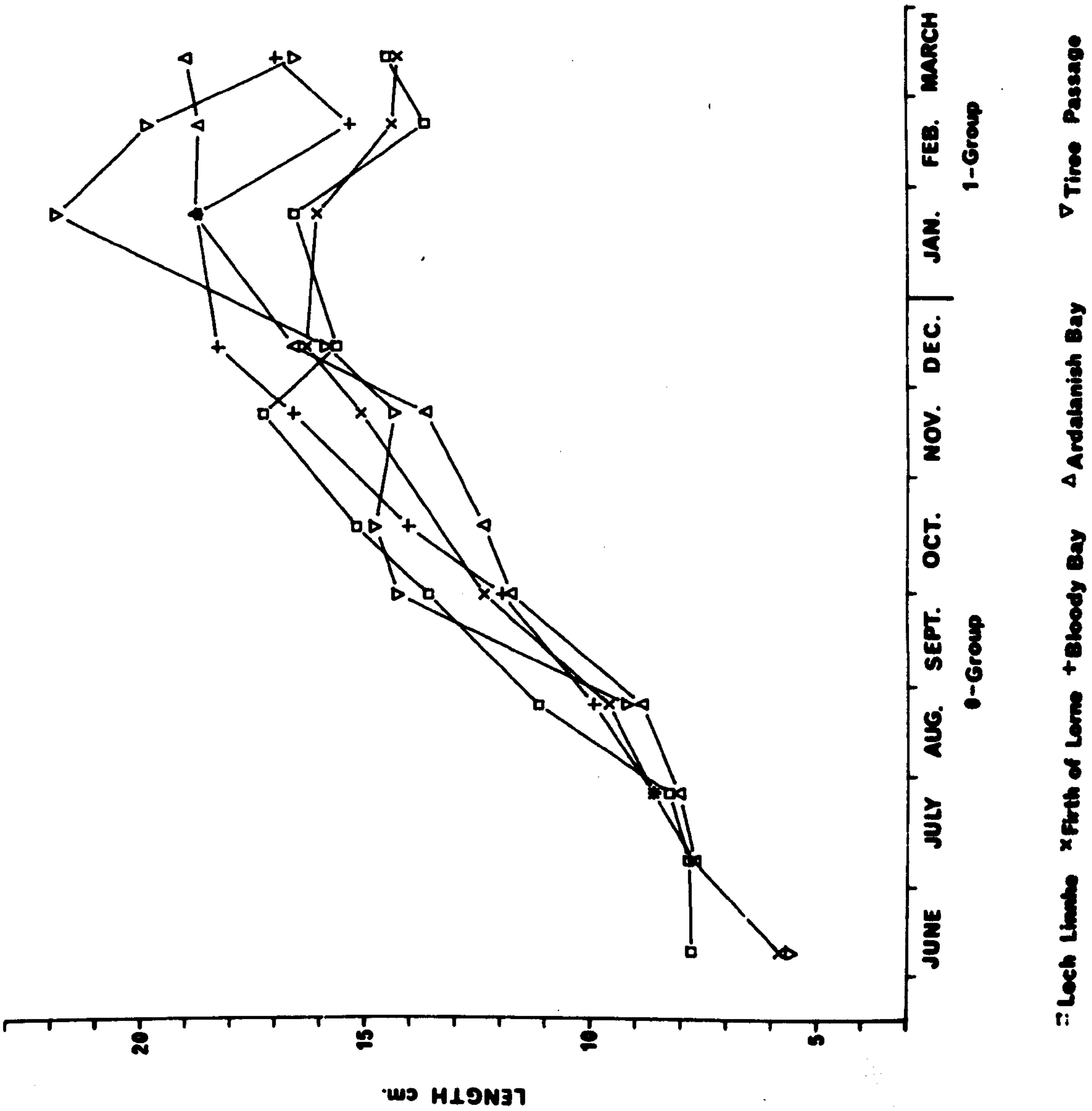
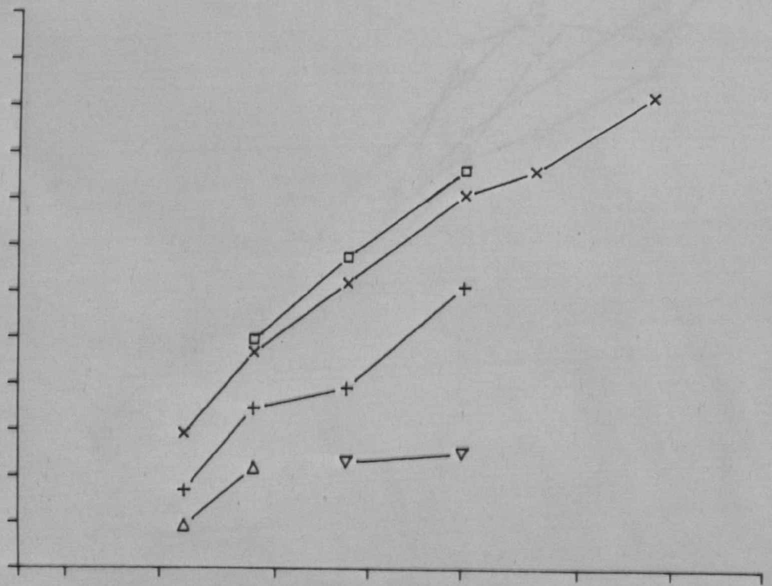

LENGTH cm.
20
15
10
5
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MARCH
0
1
□ Loch Linnhe
× Firth of Lorne
+ Bloody Bay
△ Ardalanish Bay
▽ Tiree Passage

Fig.III.5. Monthly mean total lengths (cm) of O-group and early 1-group whiting caught by the bottom trawl and mid-water trawl (plastic cover) in 1976.


LENGTH cm.
20
15
10
5
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MARCH
0-Group
1-Group
□ Loch Linnhe
× Firth of Lorne
+ Bloody Bay
△ Ardalanish Bay
▽ Tiree Passage



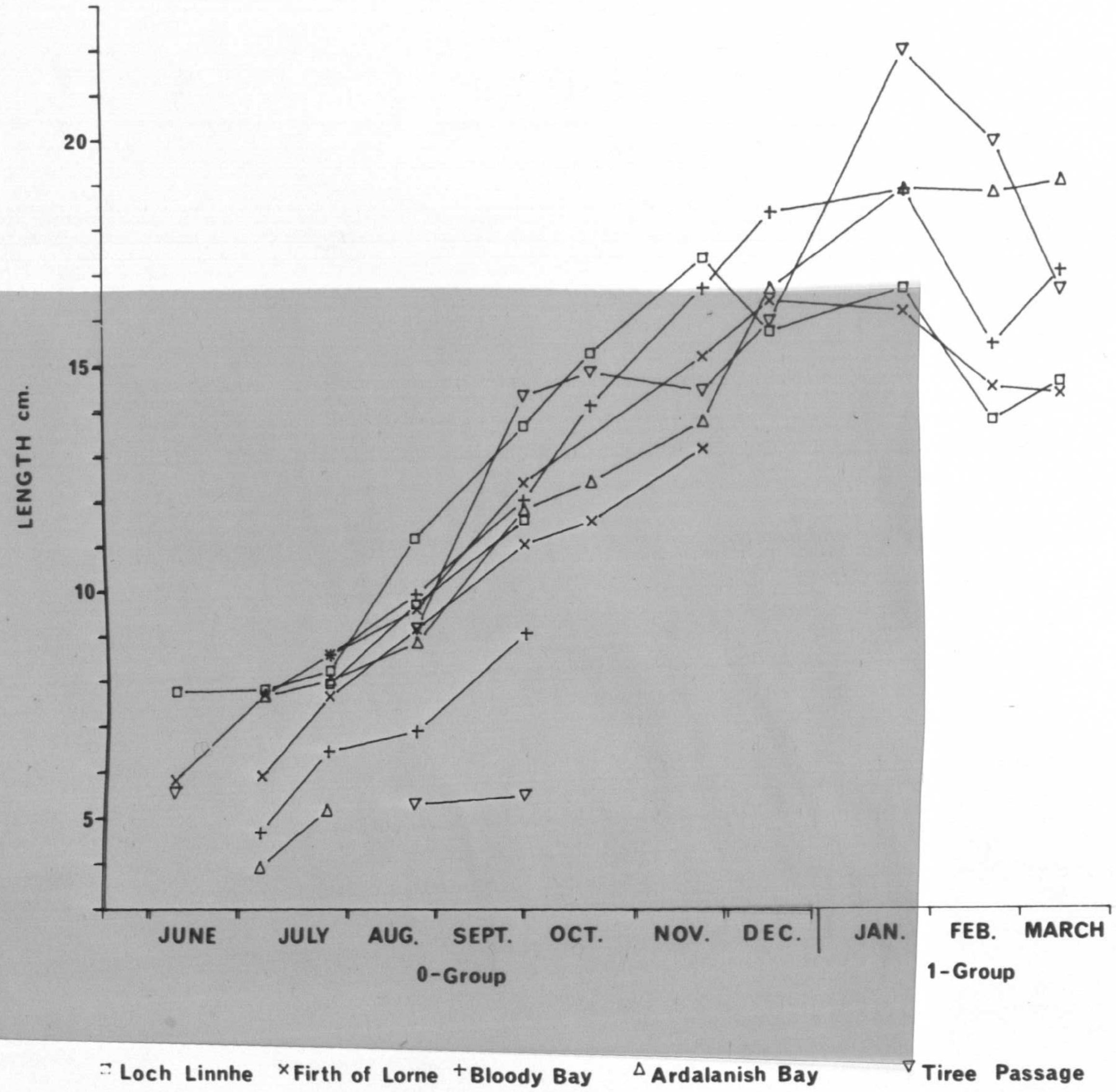
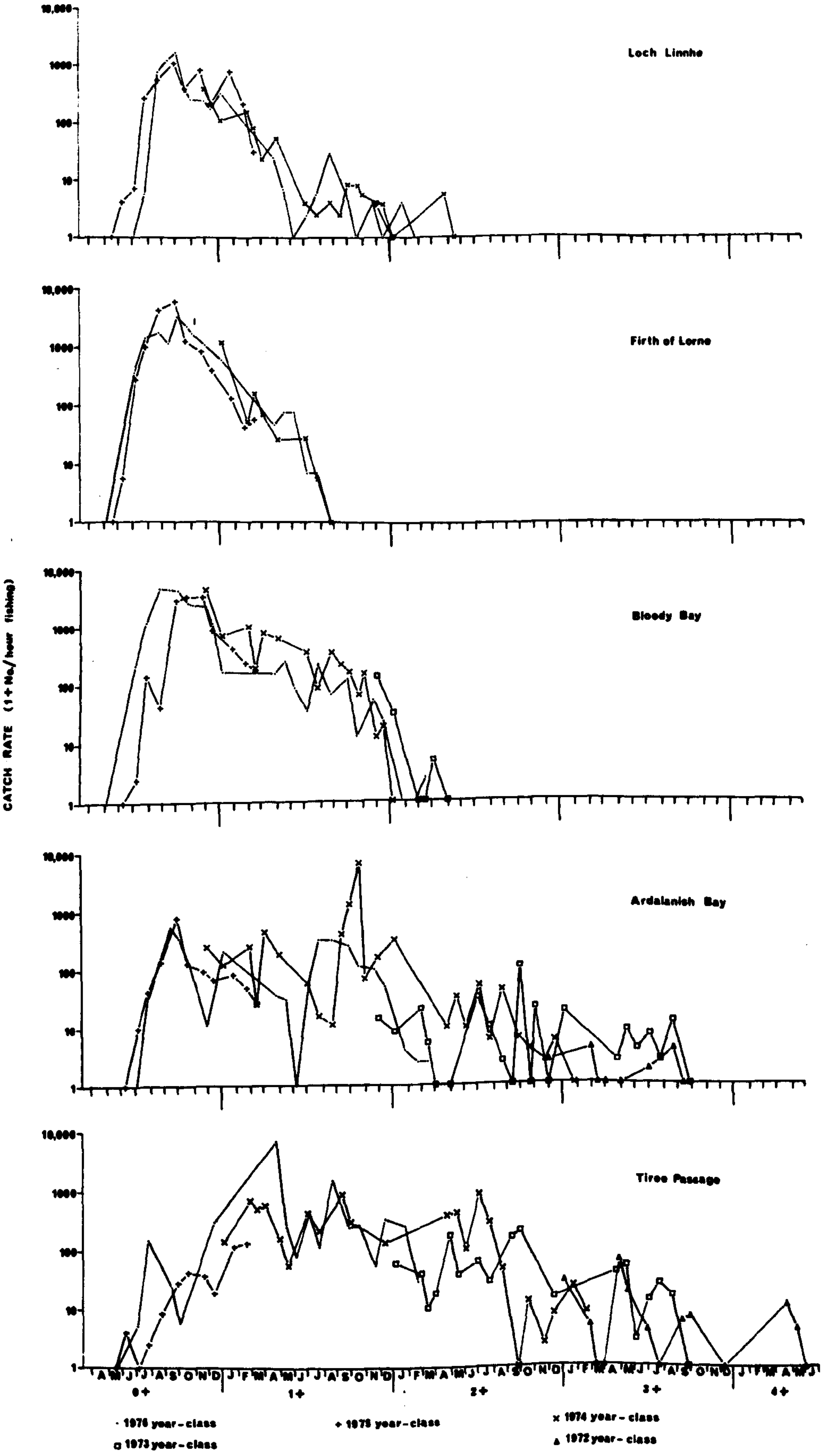

LENGTH cm.
20
15
10
5
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MARCH
0-Group
1-Group
□ Loch Linnhe
× Firth of Lorne
+ Bloody Bay
△ Ardalanish Bay
▽ Tiree Passage

Fig.III.6. Catch rates (log. scale) of each year-class of whiting in the bottom trawl at each site, against age.


10,000
1000
100
10
1
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardalanish Bay
Tiree Passage
CATCH RATE (1+ No./hour fishing)
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 S O N D J F M A M J J A S O N D J F M A M J
0+
1+
2+
3+
4+
· 1976 year-class
+ 1975 year-class
× 1974 year-class
□ 1973 year-class
▲ 1972 year-class

Differences between samples caught by the mid-water and bottom trawls should be treated with caution because of probable gear selection.

III.2.D. Length-frequency Distributions of O-group and Early 1-group Fish.

The length-frequency distributions of juvenile fish caught in 1976 are shown in Fig.III.7. In 1975 the same trends were obvious but samples were smaller and sampling was less frequent. The size-compositions obviously reflect the differences in mean length between sites and gears noted above. Several other trends are also obvious :

(1) several samples in July and August show positive skewness, probably because of selection by the gear of the larger members of the population;

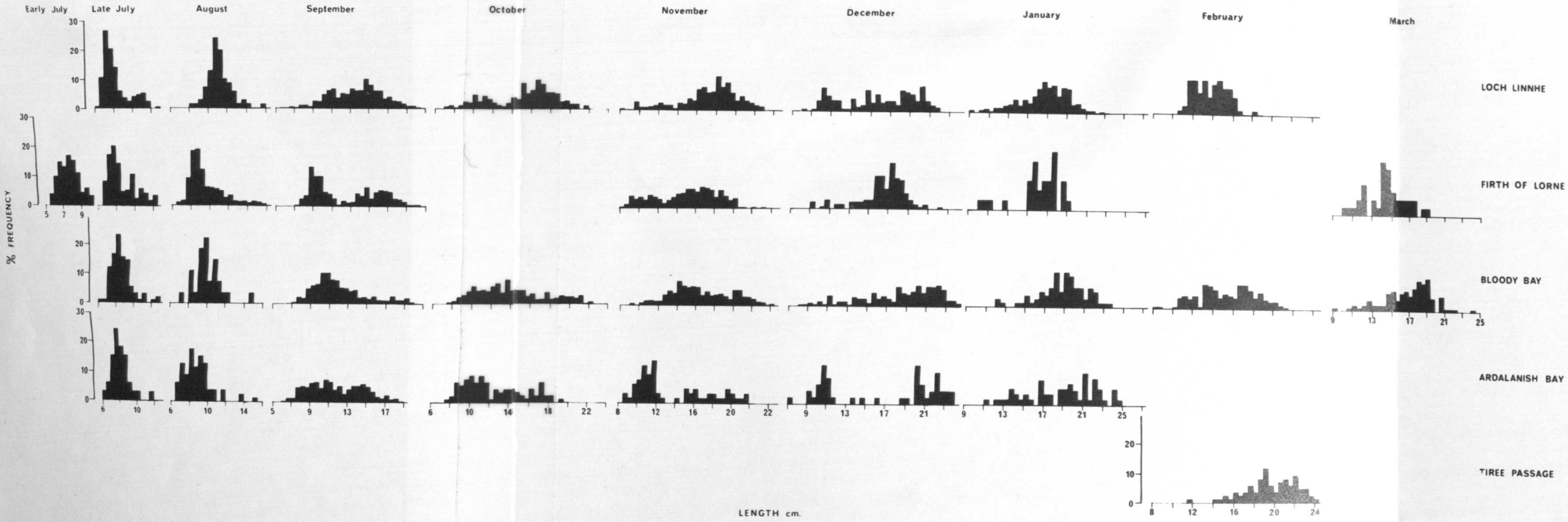
(2) bimodal distributions are obvious at certain sites e.g. Loch Linnhe in October, Firth of Lorne in September;

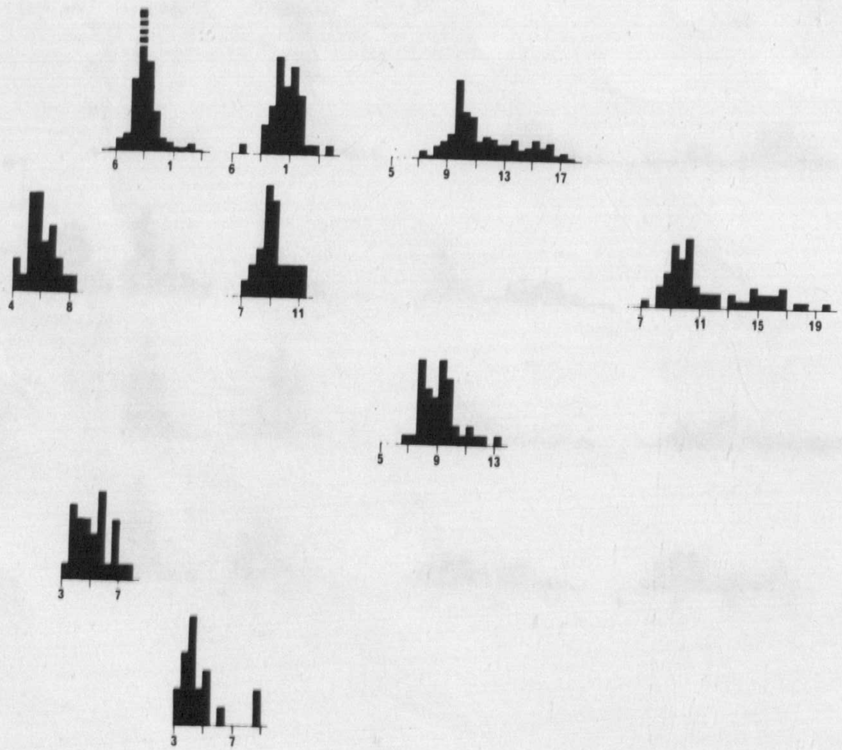
(3) in the October to January period many distributions show platykurtosis (negative kurtosis or less peaked than a normal distribution).

Probit transformations of the length-frequency distributions were also plotted (Fig.III.8) according to the method of Harding (1949). Cassie (1950,1954) has shown that, in addition to facilitating the analysis of polymodal distributions, this method can be used to detect departures from normality. In particular on a probit curve positive skewness appears as increasing steepness and negative skewness as decreasing steepness, from left to right. Platykurtic distributions are S-shaped and leptokurtic distributions reverse S-shaped.

Very few cases of near-perfect normal curves were found e.g. Loch Linnhe in September, Tiree Passage in February. S-shaped curves were especially obvious between September and December. It is difficult to decide whether these curves were due to platykurtosis or whether the populations are bimodal. In practice, however, the conclusions are the same since negative kurtosis always results from overlapping modes. The samples were checked to make sure that no older age-groups

Fig.III.7. Monthly length-frequency distributions of demersal and pelagic (plastic cover) 0-group and early 1-group whiting, 1976 year-class.


Early July
Late July
August
September
October
November
December
January
February
March
LOCH LINNHE
FIRTH OF LORNE
BLOODY BAY
ARDALANISH BAY
TIREE PASSAGE
% FREQUENCY
0
10
20
30
5
7
9
6
10
14
5
9
13
17
6
10
14
18
22
8
12
16
20
22
9
13
17
21
9
13
17
21
25
9
13
17
21
25
8
12
16
20
24
LENGTH cm.


6
1
6
1
5
9
13
17
4
8
7
11
7
11
15
19
5
9
13
3
7
3
7

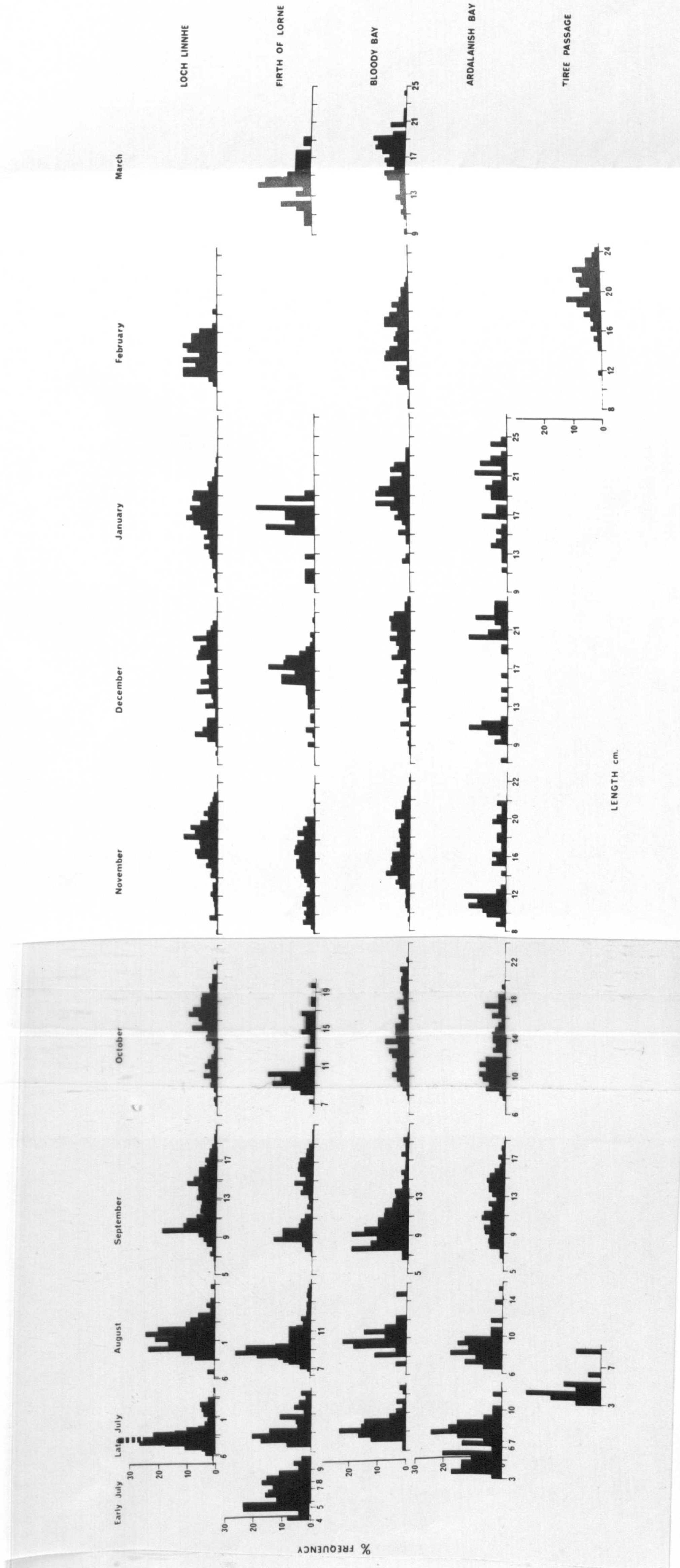
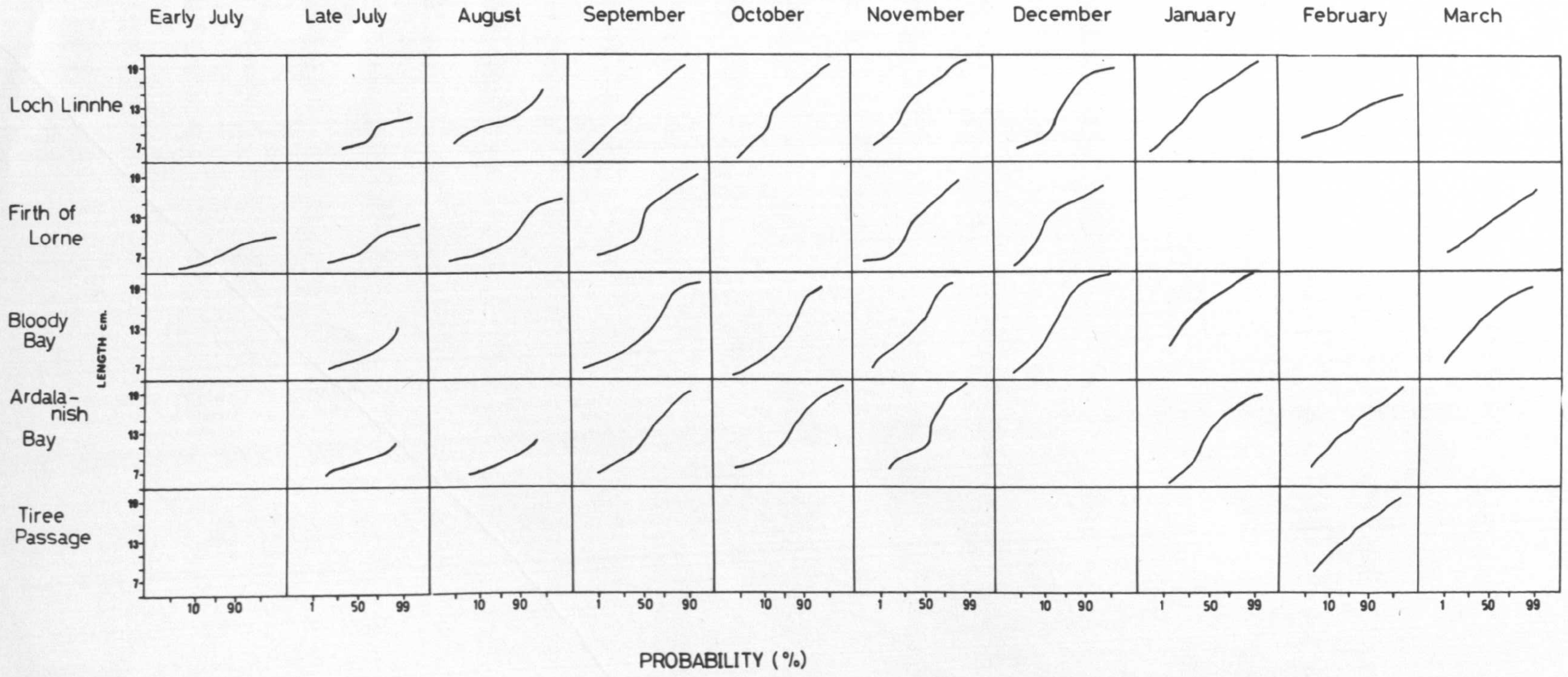
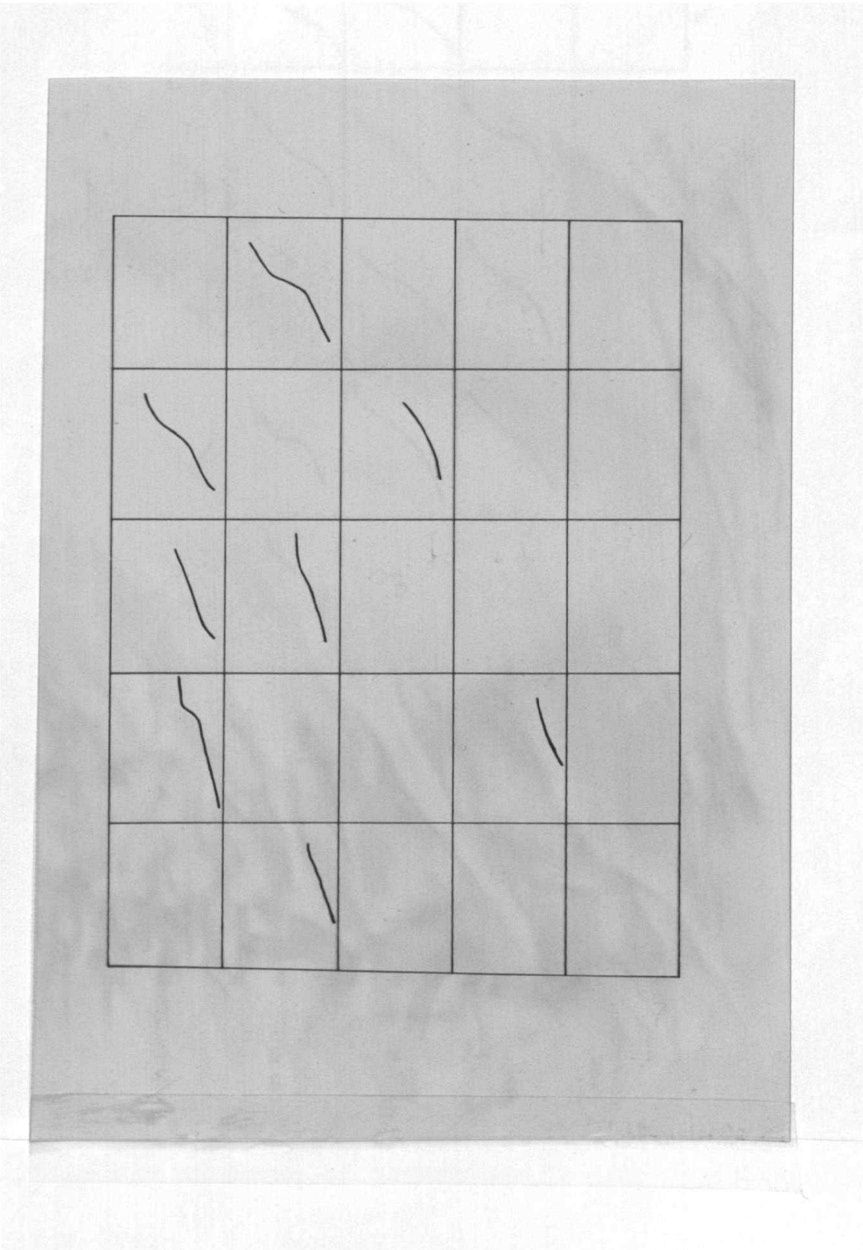
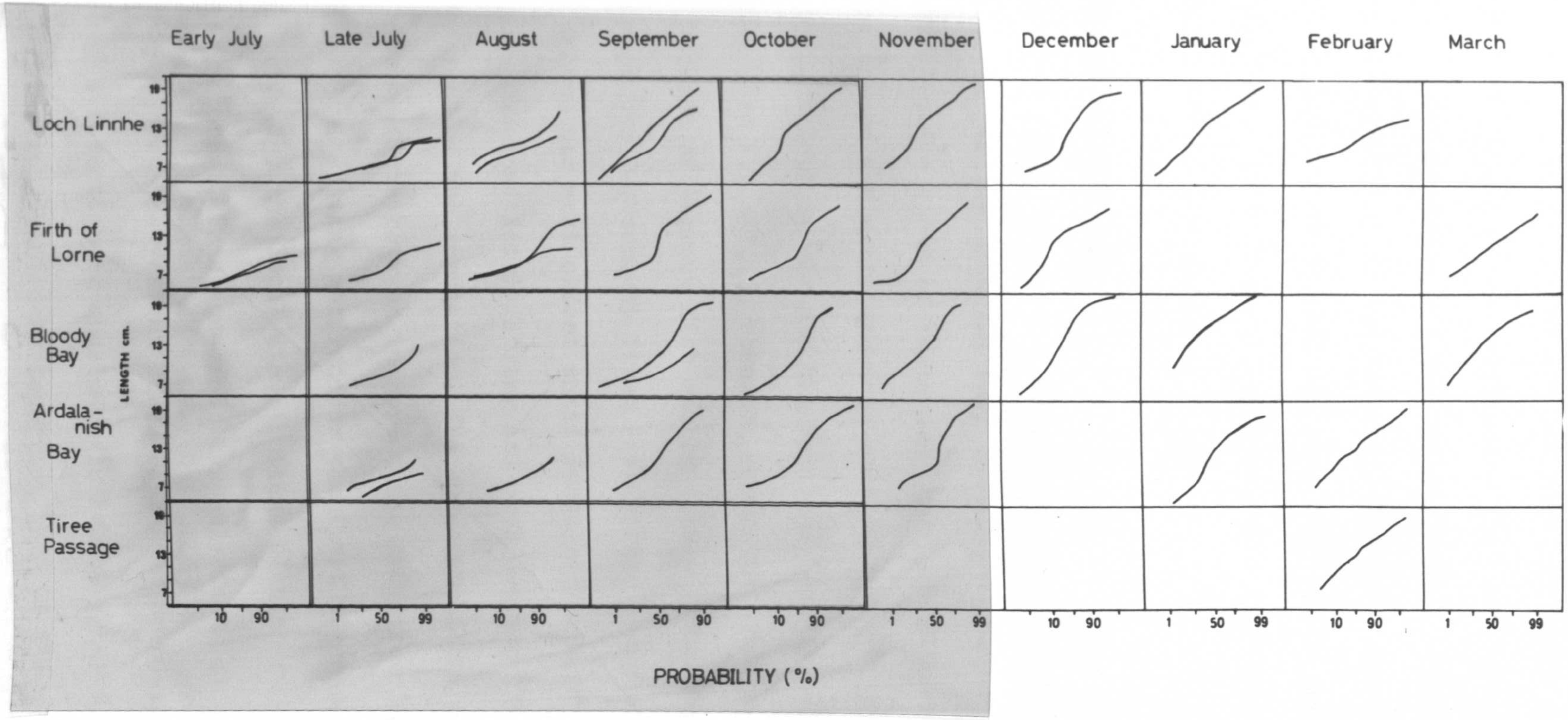

Early July
Late July
August
September
October
November
December
January
February
March
LOCH LINNHE
FIRTH OF LORNE
BLOODY BAY
ARDALANISH BAY
TIREE PASSAGE
% FREQUENCY
LENGTH cm.
0
10
20
30

Fig.III.8. Cumulative monthly length-frequency distributions of 0-group and early 1-group whiting of the 1976 year-class, plotted on probit scales. Plastic sheet shows distributions of mid-water trawled fish.


Early July
Late July
August
September
October
November
December
January
February
March
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardala-nish Bay
Tiree Passage
LENGTH cm.
19
13
7
10
90
1
50
99
PROBABILITY (%)




Early July
Late July
August
September
October
November
December
January
February
March
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardalanish Bay
Tiree Passage
LENGTH cm.
18
13
7
10
90
1
50
99
PROBABILITY (%)

were present, by examination of otoliths. These extended distributions did not occur persistently at any one site, although it was not until February of the 1-group that sufficient fish were caught at Tiree Passage to plot an accurate distribution. Probit transformations of the length-frequencies of mid-water trawled fish showed similar shapes to bottom trawled samples from the same area at the same time. The larger fish were less frequent, however, causing depressions of the right hand side of the curves.

III.2.E. Age Composition.

The age composition of whiting populations at each site is shown in Fig.III.9, pooling data for 1975 and 1976 at bimonthly intervals. At Bloody Bay, the Firth of Lorne and Loch Linnhe the youngest age-group was always dominant. There is some evidence of an increase in the 2-group at Loch Linnhe and the Firth of Lorne in April and May. Comparison with Fig.III.10, however, shows that this was mainly due to the low catches of 1-group fish rather than a greatly increased abundance of the 2-group. At Tiree Passage the youngest age-group did not exceed the next oldest until February/March of the 1-group. The 2-group remained fairly strong and even 3-group fish formed an important part of the population. The age-composition at Ardalanish Bay was intermediate between inshore sites and Tiree Passage.

Since most whiting matured for the first time in the 2-group (section III.4.C), the local distributions of such fish was of particular interest. This age-group was only found in appreciable numbers throughout the year at Tiree Passage. There was also evidence of a reduction in abundance in February/March. At Ardalanish Bay the 2-group represented an important part of the population until June/July in terms of percentage frequency, although catch rates were low.

Fig.III.9. Age composition of whiting populations at each site, pooling data at bimonthly intervals from January 1975 to January 1977.

(n = number of trawls)

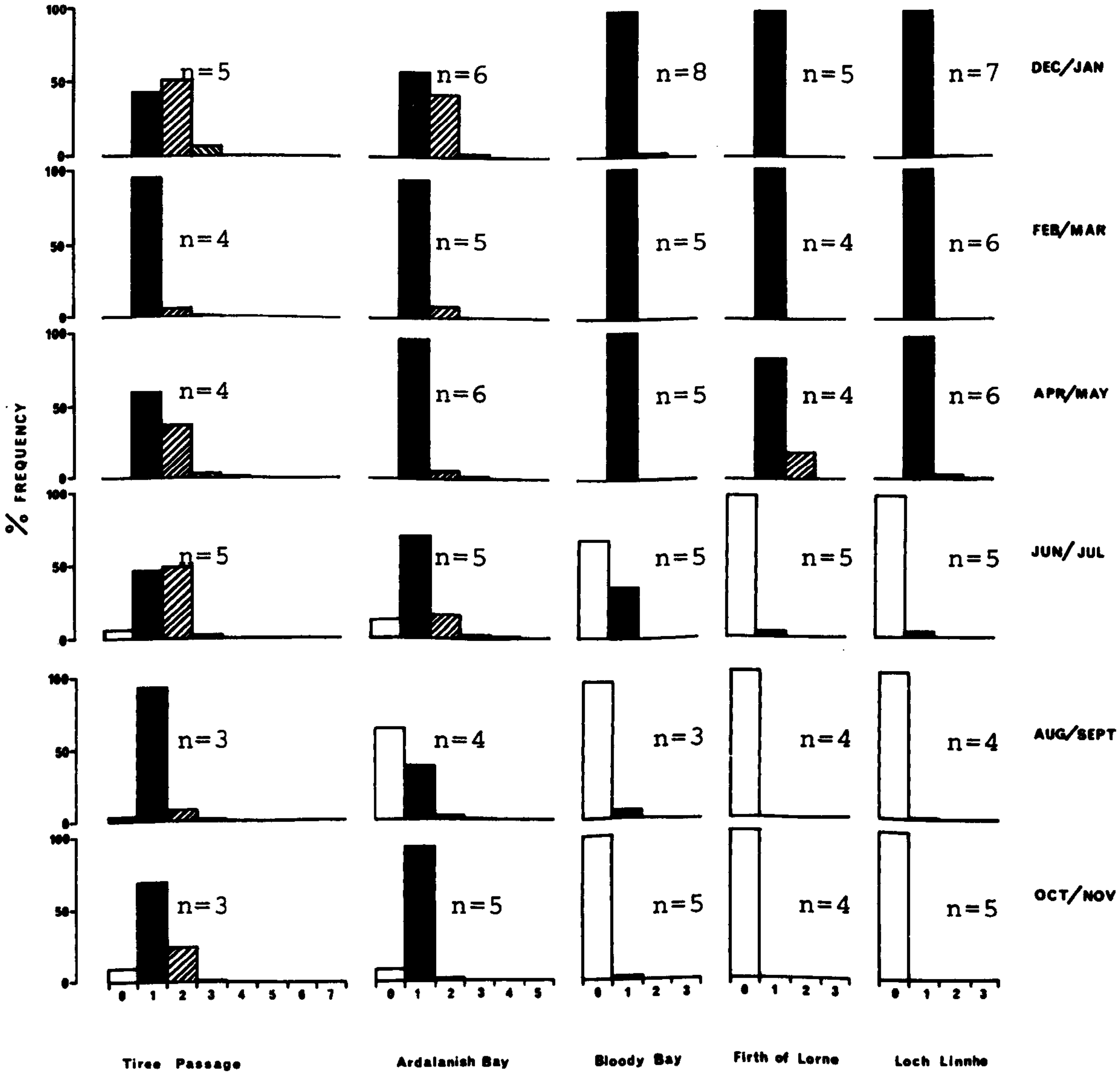
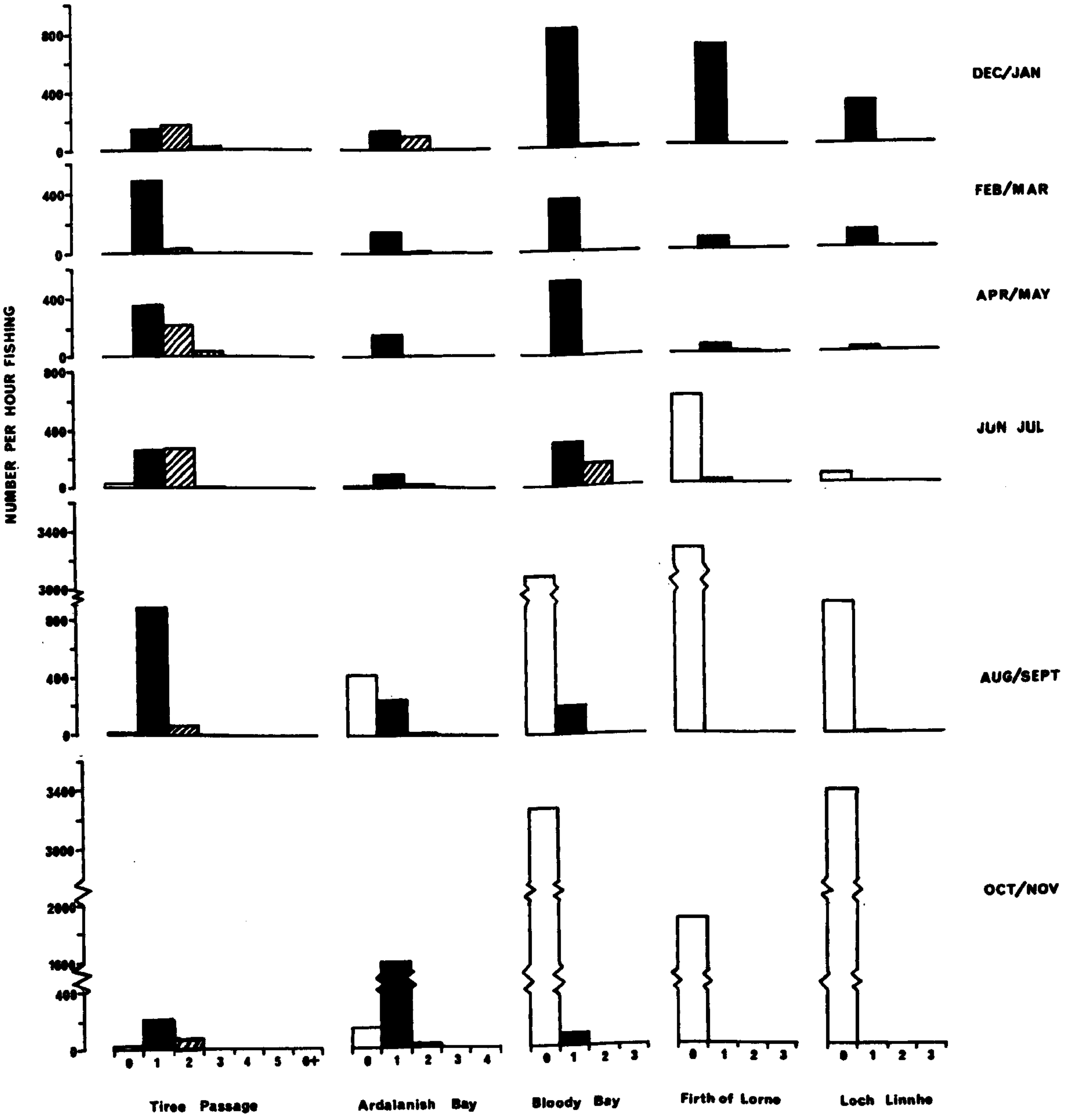

% FREQUENCY
100
50
0
n=5
n=6
n=8
n=5
n=7
DEC/JAN
n=4
n=5
n=5
n=4
n=6
FEB/MAR
n=4
n=6
n=5
n=4
n=6
APR/MAY
n=5
n=5
n=5
n=5
n=5
JUN/JUL
n=3
n=4
n=3
n=4
n=4
AUG/SEPT
n=3
n=5
n=5
n=4
n=5
OCT/NOV
0 1 2 3 4 5 6 7
0 1 2 3 4 5
0 1 2 3
0 1 2 3
0 1 2 3
Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe

Fig.III.10. Number of whiting of each age-group caught per hour fishing at each site, pooling data at bimonthly intervals from January 1975 to January 1977.


NUMBER PER HOUR FISHING
800
400
0
DEC/JAN
400
0
FEB/MAR
400
0
APR/MAY
800
400
0
JUN JUL
3400
3000
800
400
0
AUG/SEPT
3400
3000
2000
1600
400
0
OCT/NOV
0
1
2
3
4
5
6+
Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe

III.2.F Abundance.

The abundance of each age-group at bimonthly intervals is shown in Fig.III.10, pooling data from 1975 and 1976 for statisical reasons. This illustrates the rapid increase in catches of young fish at the inshore sites compared with offshore areas. Maximum abundance occurred in August/September at the Firth of Lorne but in October/November at at Loch Linnhe and Bloody Bay. At Tiree Passage catch rates never exceeded 1000/h compared with over 3000/h at Bloody Bay, the Firth of Lorne and Loch Linnhe. At the 3 inshore sites the maximum abundance was followed by a rapid decline (see also Fig.III.6). This was most rapid at the Firth of Lorne and fish of the 1-group were absent by August. Very few 2-group fish were found after January at Bloody Bay and Loch Linnhe. Gordon(1977b) found similar results for Loch Linnhe and the Firth of Lorne sampling from 1969 to 1973, although the general trend was for fish to persist for slightly longer.

The later reduced peak of abundance of fish at Tiree Passage and Ardalanish Bay has already been noted, as has the presence of mature fish in the population. Fig.III.6 shows that the decline in numbers is much slower compared with inshore sites. The descending limb of the curve is normally considered to represent survival, but difficulties in eliminating the effects of immigration and emigration preclude such estimations in the present study. Reduction in numbers did not begin until March, probably because of recruitment from inshore populations.

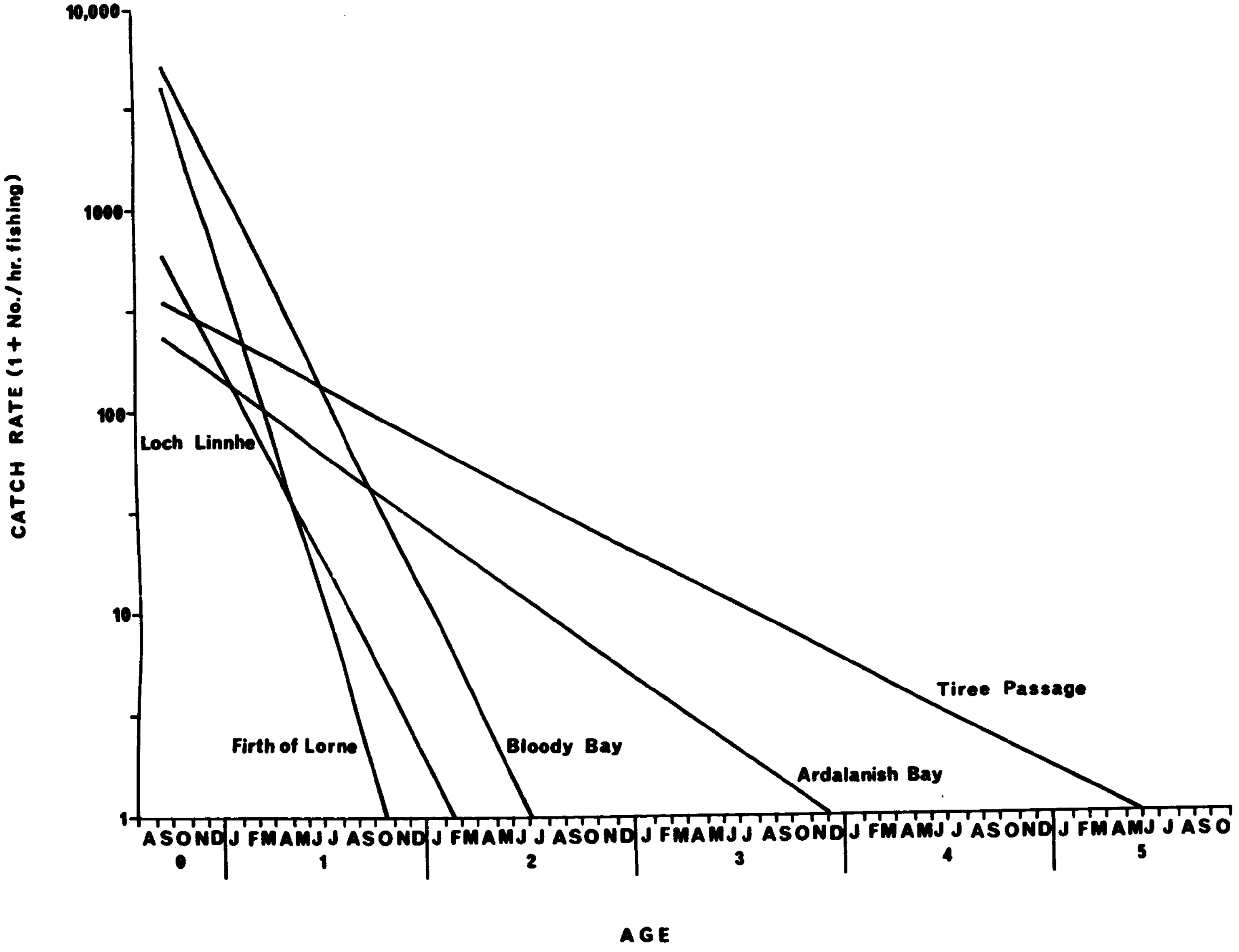
Regression lines were calculated for the reduction in abundance with time for each site from the period of maximum abundance (Fig.III.11, Appendix III.3). In all cases a large and significant part of the variance of catch rates was explained by regression on age. Bartlett's test for heterogeneity of variance was significant, so comparison of slopes and intercepts by covariance analysis was impossible. It seems to be clear, however, that fish were present for longer and

Fig.III.11. Predictive regressions of the catch rate (log.scale) of whiting against age at each site, from September (week 37) in the 0-group onwards.

Site	Regression
Loch Linnhe	Y = 4.1489 - 0.0373X
Firth of Lorne	Y = 5.9366 - 0.0631X
Bloody Bay	Y = 5.1696 - 0.0396X
Ardalanish Bay	Y = 2.8858 - 0.0141X
Tiree Passage	Y = 2.9261 - 0.0104X

(Y = $\log_{10}$ 1 + number/h fishing

X = age in weeks).


10,000
1000
100
10
1
CATCH RATE (1 + No./hr. fishing)
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardalanish Bay
Tiree Passage
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 S O 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 S O
0
1
2
3
4
5
AGE

that older fish were in greater abundance at Tiree Passage and Ardalanish Bay than inshore.

There was a decrease in the mean length of fish during the later part of the inshore life (Fig.III.5 and Appendix III.2). Gordon (1977b) suggested that this was due to the large fish beginning to migrate to the open sea. By the end of the O-group the mean length of offshore fish was certainly greater than those inshore, in contrast to the beginning of the migration.

III.2.G. Discussion

The seasonal occurrence of larval and post-larval whiting was in close agreement with dates given by Russell (1935) for the English Channel. Heincke and Ehrenbaum (1900) frequently found eggs in the plankton near Helgoland between January 28 and May 25. Since the period of incubation is about 10 days (McIntosh and Prince, 1890) larvae occurred from February, somewhat earlier than in local waters. Bal (1941) found eggs of whiting from February to June, also somewhat earlier than on the west coast of Scotland.

The present study confirms Gordon's (1977b) conclusions that :

(1) O-group whiting in inshore areas become established during the summer and autumn, remaining there during their first winter ;

(2) there follows a gradual leakage of all or a proportion of the population to the open sea;

(3) the inshore populations derive from planktonic larvae west of Mull.

The absence of planktonic larvae inshore indicated that a passive denatant migration was unlikely. The distribution of planktonic poor-cod showed a similar pattern. The likely estuarine water movements discussed in Section 1.2 would effectively prevent a passive inshore drift of young larvae at the surface. At the same time, inshore water movements of saline coastal water would reinforce and active inshore migration of young fish at greater depths.

Clearly the vertical distribution of larval and post-larval stages will have an effect on the final horizontal distribution of demersal juveniles. Russell (1976) found that in the daytime post-larvae 5-12mm long were mostly found between 15 and 35m depth (maximum 20-30m) and showed little evidence of vertical migration. Post-larvae from 12mm to about 60mm (between May and August) associated with Scyphomedusae and may migrate with them. This association occurred principally with Cyanea capillata e.g. Heinke (1905), Damas (1909) and Bailey (1975) in the North Sea and Skagerrak; Russell (1935) and Desbrosses (1945) in the English Channel; Bainbridge (1952) in the Firth of Clyde. It seems likely that in Smitt's (1892) observation of an association with Scyphomedusae in the Skagerrak Medusa capillata is synonymous with Cyanea capillata. Rees (1966) reported that association between whiting and Cyanea lamarcki on the south coast of Cornwall. Nagabhushanam (1964) found associations of young whiting with Rhizostoma octopus in Manx waters. Bainbridge (1952) and Rees (1966) described a vanguard position of the fish, above and slightly in front of the bell of the jellyfish as being the more usual and Nagabhushanam (1964) has pointed out that this would increase foraging efficiency. Rees (1966) suggested that the fish adopted the more widely-reported position (beneath the subumbrellar among the tentacles) only when feeding on the jellyfish or when subject to stress. Nagabhushanam (1964) found that whiting feed on Hyperia galba (Montagu), an amphipod parasitic on jellyfish, and possibly also on copepods concentrated by the host. In this regard Jones and Hall (1974) concluded that ' a larval model based on the idea that food density is critical can explain much that is known about the early life history of fish such as cod and haddock'. Concentration of copepods by Scyphomedusae would very effectively increase the searching capacity of the commensal young whiting.

The association of young whiting with Scyphomedusae is clearly of great importance and probably affects the distribution and abundance of young fish. Further work is needed, however, to determine if this occurs generally throughout the range of fish, and to try to quantify benefits to the whiting in terms of feeding efficiency and survival.

Regarding the vertical distribution of whiting after their association with Scyphomedusae, Bailey (1975) found some evidence of a diurnal vertical migration of fish over 10 cm. In the present study bottom trawl catches during the day were consistently more successful than mid-water trawls at any time of day. Bottom trawl catches during the day contained a greater proportion of large fish than those caught using the mid-water trawl at night, although this was undoubtedly partly due to gear selection. This was especially evident later in the year when perhaps the larger fish became completely demersal.

The first whiting to be caught at the Firth of Lorne and Loch Linnhe by the mid-water trawl were larger than fish caught at the same time offshore. This suggests that the inshore fish were older. It seems likely that the fish moved inshore actively during the pelagic and early demersal phases. In the demersal phase there was a clear aggregation of whiting inshore, unlike the Norway pout or the poor-cod. The concentration of O-group fish on the nursery grounds occurred from July onwards (at lengths from 4 cm) at all sites. The maximum age and length of departure varied with site viz. at Loch Linnhe January of the 2-group at 23 cm; at the Firth of Lorne August of the 1-group at 20 cm; at Bloody Bay January of the 2-group at 28 cm. Several authors have suggested that larger fish of each year-class migrate before smaller fish (see section III.3.D). There is also evidence of seasonal migrations between deep and shallow water. At Loch Linnhe (depth 90m) catch rates fell to 2 or 3/h by June in the

1-group, with a slight increase in autumn, fish finally leaving the area in spring in the 2-group (Fig.III.4). At Ardalanish Bay (depth 77m) and Tiree Passage (depth 80m) there was also a reduction in numbers in June in the 1-group. At the Firth of Lorne (depth 47m) there was an increase in abundance in June but fish left the area in autumn. At Bloody Bay (depth 50m) the trend of reduction of numbers with time was interrupted during the summer, with a rapid decrease from autumn to spring. Fish moving offshore may be liable to capture at this site. Knudsen (1968) found that in the Skagerrak in August the 0-group was concentrated along the 40m depth contour, moving to deeper water in winter and below 80m in April. In summer some 1-group whiting migrated to shallow water only to emigrate to deeper water during the following winter. The pattern was similar in the 2-group while fish of the 3-group and over remained below 80m. Knudsen (loc.cit.) also confirmed Gambell's (1963) observation that the availability of fish in the North Sea changed seasonally. Insufficient seasonal studies have been undertaken on the west coast of Scotland to justify the adjustment of catch rates. Decreases in availability would account for the reduced catch rates in June offshore (mentioned above).

There are several reports in the literature of migrations of whiting to inshore nursery grounds. In the Firth of Forth McIntosh (1896) concluded that ' the whiting thus would seem to pass its early post-larval and its young stages chiefly in the deeper offshore waters, -coming inshore in immense swarms in September.' Masterman (1901) working in the same area reached essentially the same conclusions. Ellis and Jones (1956), however, found concentrations of 0-group whiting not only in the Firth of Forth but also in the Central North Sea and approaching the Danish coast. Thomas and Saville (1971), in considering fisheries of the Firth of Forth, concluded that the whiting ' ..... spawn extensively to the north and east ..... The eggs and larval stages are planktonic, so that the population in this coastal area is largely provided by the drift, with a south-going current, of the early planktonic stages into the area ...... Whiting are found as post-metamorphic stages over a wide range of depths and bottom substrates. In other words, they appear to be capable of growing and reaching sexual maturity over much of the North Sea and show no particular dependence on a coastal habitat.' In fact the problem of distributions and migrations of fish in the North Sea is very complex and will be discussed later (section III.6). At this point it will suffice that the Firth of Lorne represents nursery ? grounds for some whiting. Whiting populations of the southern Kattegat, Belt Sea and Kiel Bay are probably derived initially from the Skagerrak and northern Kattegat, and originally from the northeastern North Sea (Knudsen, 1968; Arntz and Weber, 1972; Poulsen, 1937), although in some years a successful spawning may occur in what are normally thought to be nursery grounds. In the Southern Kattegat migration probably occurs in the pelagic or early demersal phase (Knudsen, 1968) while in Kiel Bay it may occur in the 0-, 1- or possible 2-groups (Arntz and Weber, 1972). Hartley (1939) found that 0-group whiting appear in May on the mud flats bordering the Tamar and Lynher estuaries and remain there until the following summer. The Severn Estuary and Bristol Channel area is also a nursery ground for whiting. Fish first appear in July or August, reach a peak in October or November and usually leave after May, although small numbers of fish up to the 3-group are occasionally present (Gardner,D.C., pers.comm.; Badsha and Sainsbury, 1977). In Manx waters immature whiting 77mm long were found in Port Erin Bay from July, remained for several months to a year growing to about 210mm and then moved offshore, where they remained for the rest of their lives (Nagabhushanam, 1964). The distribution of whiting in the Clyde suggests that the inner Firth may represent comparable areas to Loch Linnhe and the Firth of Lorne (Garrod and

Gambell, 1965), with inshore nursery grounds being maintained from spawning grounds off the coast of Northern Ireland.

Comparison of the age composition of catches is subject to three major errors :

(1) gear selection;

(2) age-selective mortality due to fishing;

(3) annual variations due to success or failure of individual year-classes.

Assuming that the figures given by Garrod and Gambell (1965) are typical for each area, the Solway Firth would appear to be similar to the inshore sites of the present study; age-compositions at Tiree Passage are similar to those in the Clyde; the area of the Gonway fishery contains only older fish (3- and 4-groups); the North Lewis, North Coast and West Coast stocks contain a greater proportion of older fish than at any site in the present study. The age composition of whiting populations in the Tiree Passage area is similar to those of the Skagerrak (Knudsen, 1950; Knudsen, 1968)

Many authors have overlapping modes in the length-frequency distributions of O-group whiting e.g. Gordon, 1977b; Hannerz, 1964; Masterman, 1901; Fulton, 1901. Two explanations for this observation are obvious :

(1) populations are derived from separate stocks or spawning grounds;

(2) the extended length-frequency distribution results from a long spawning season.

I have not been able to determine the correct explanation, although one would expect the modes to be consistent if inshore populations were derived from separate stocks or spawing grounds. There is also no evidence in the literature of the subdivision of west coast whiting into distinct stocks (see section III.6). Likewise there are no reports of the existence of separate isolated spawning grounds or or spawning aggregations. In fact there have been no direct observations of running-ripe whiting off the west coast of Scotland (section III.4), although ripe fish occur at Tiree Passage (pers.obs.) and in the Minch (Hislop and Hall, 1974). Gordon (1977b) found running-ripe fish in the deep upper basin of Loch Etive. It has long been known that the whiting has an extended spawning season e.g. Damas (1909), Desbrosses (1945), Nagabhushanam (1964), personal observation (section III.4) and this seems to be the most likely explanation. Bowers (1954) showed that larger fish matured and presumably spawned earlier in the season. Hislop (1975) found that whiting spawn repeatedly for periods up to 90 days in aquaria, releasing eggs of diminishing size in batches of up to 30,000. Jones and Hall (1974) developed a model of the larval stage of common gadoids (principally cod and haddock), based on the idea that cohorts of larvae grow up with and feed on cohorts of copepods. Since the food of larval whiting is very similar (Last, 1978) it is likely that the same factors will affect survival. Cohorts of larvae unsuitably matched with cohorts of copepods would be less successful, producing inconsistent modes in different areas.

III.3. GROWTH

III.3.A. Length-frequency Distribution

Fig.III.12 shows the seasonal variation in length-frquencies of whiting at each site. This confirms conclusions from the previous section concerning the importance of 0-group fish at Loch Linnhe and the Firth of Lorne. Little variation was obvious from year to year although the relative abundance of intra-year-class 'modes' differed.e.g. September and November at the Firth of Lorne, December at Loch Linnhe. At Bloody Bay there is evidence that the 1-group persisted for longer in 1976 than in 1975 (until August compared with May). At Tiree Passage and Ardalanish Bay greater length ranges were found as a result of the mature fish in the population. The youngest age-group remained distinct until about January in the 1-group. Lengths of older age-groups overlapped.

III.3.B. Growth in Length

Seasonal Variations

Mean lengths of fish in each age-group caught by the bottom trawl are shown in Fig.III.13. By pooling data from all sites and sexes sample sizes were large enough to consider growth to the 4-group. Although there was considerable variation between samples a seasonal component was obvious. Recruitment may not be complete until September in the 0-group and this is likely to cause variations in apparent growth rate in the first year of life. This does not seem to occur, however, and growth was uniform until December. There was no further increase in length until about April in the 1-group with some evidence of a reduction in length in this period. This will be considered in the next section, although it should be noted that it is probably because fish were in greater abundance inshore at this time. Growth was slower over the same period in the following year. There appears to be little growth between September in the 2-group and May in the 3-group although this could be due to low sample sizes.

Fig.III.12. Monthly length distributions of whiting populations at each site in 1975 and 1976.

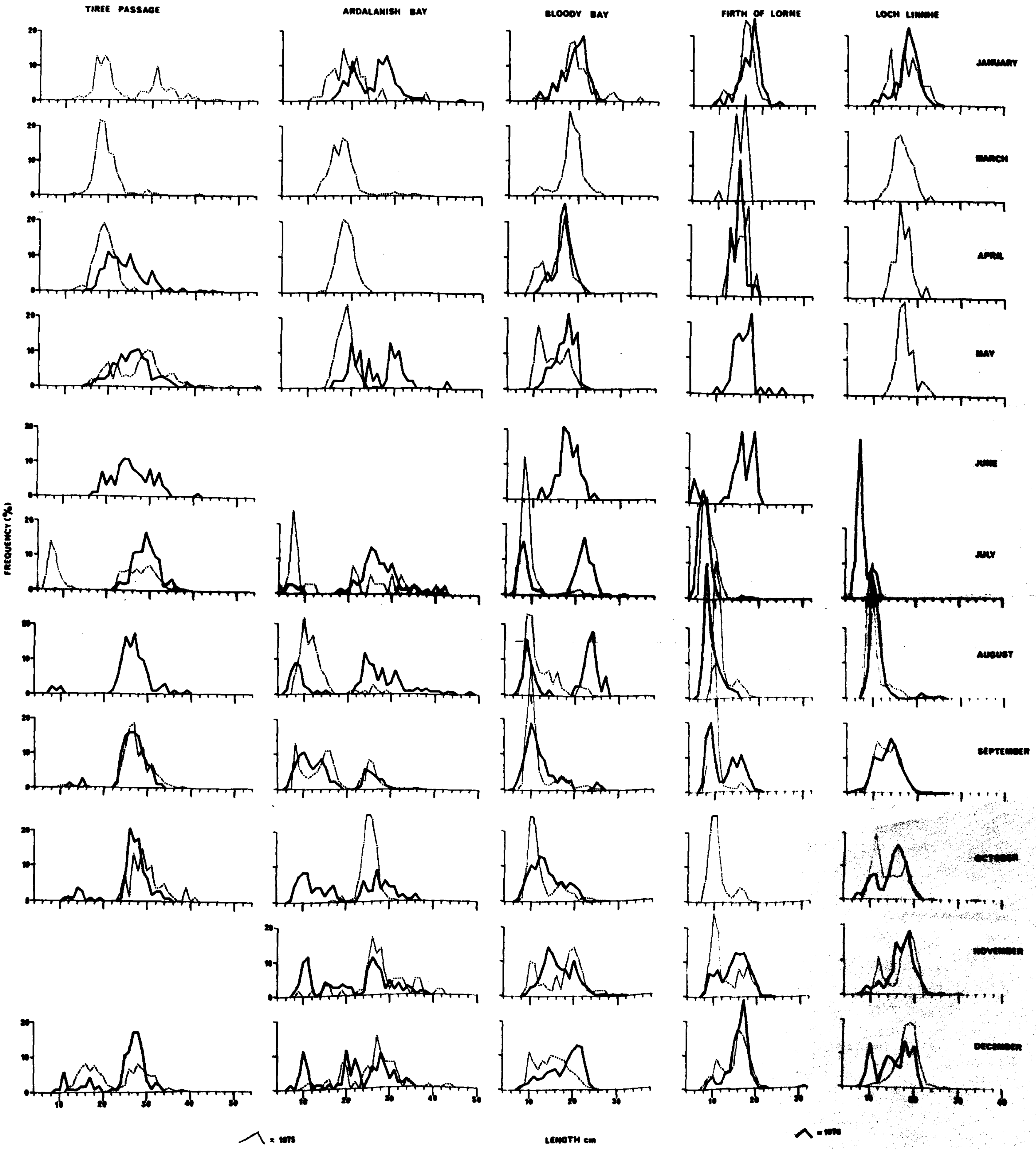
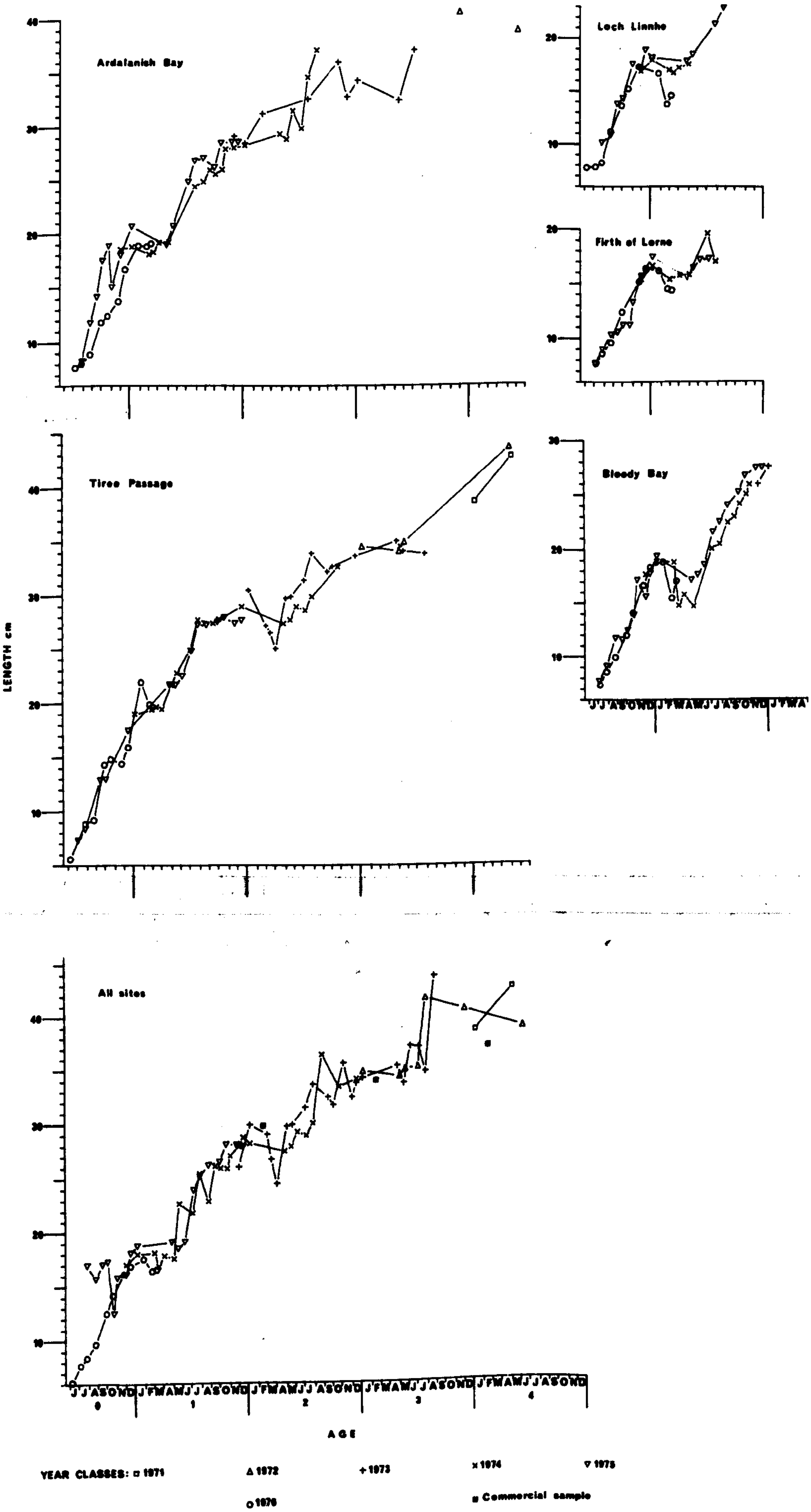

TIREE PASSAGE
ARDALANISH BAY
BLOODY BAY
FIRTH OF LORNE
LOCH LINNHE
JANUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
FREQUENCY (%)
0
10
20
10
20
30
40
50
= 1975
LENGTH cm
= 1976

Fig.III.13. Seasonal growth in total length (cm) of each year-class of whiting at each site and pooling fish from all sites, sexes combined.


Ardalanish Bay
Loch Linnhe
Firth of Lorne
Tiree Passage
Bloody Bay
All sites
LENGTH cm
40
30
20
10
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 S O 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
0
1
2
3
4
AGE
YEAR CLASSES: □ 1971
△ 1972
+ 1973
× 1974
▽ 1975
○ 1976
■ Commercial sample

Variations between sites

There was little variation in length between sites until October of the O-group, when whiting at the Firth of Lorne were smaller than at other sites. The winter maximum length was about 16.5cm compared with 19cm in other areas. At Loch Linnhe, the Firth of Lorne and Bloody Bay there was a reduction in length to about 15cm. At Tiree Passage and Ardalanish Bay growth stopped but there was no evidence of shrinkage. When seasonal growth restarted in May the rate was approximately equal in all areas but the increment gained offshore, where no winter shrinkage occurred, was maintained. The timing of growth did not differ between sites.

Variations between sexes

There was little difference in growth rates between the sexes (Fig. III.14) until summer in the 1-group at about 23cm. Females were then slightly longer, although differences were only of the order of 1-2cm. Because of smaller samples it was only possible to measure growth of males to about the end of the 2-group compared to the end of the 3-group for females. This reflects differences in the 'aparent survival' of fish in the area. The term 'apparent survival' is used since fish density may be decreasing not only because of mortalities but also because of emigration.

III.3.C. Growth in Weight

Seasonal variations

Seasonal variations in weight of each age-group are shown in Fig. III.15, in which curves were fitted by eye. Despite increases in length, weight remained remarkably constant until May in the 1-group. This may be due to gear selection. Growth began in May and continued until December when weight reductions occurred, possibly associated with maturation. A similar pattern was obvious for 2-group and 3-group fish.

Fig.III.14. Seasonal growth in total length (cm) of male and female whiting, pooling fish from all sites.

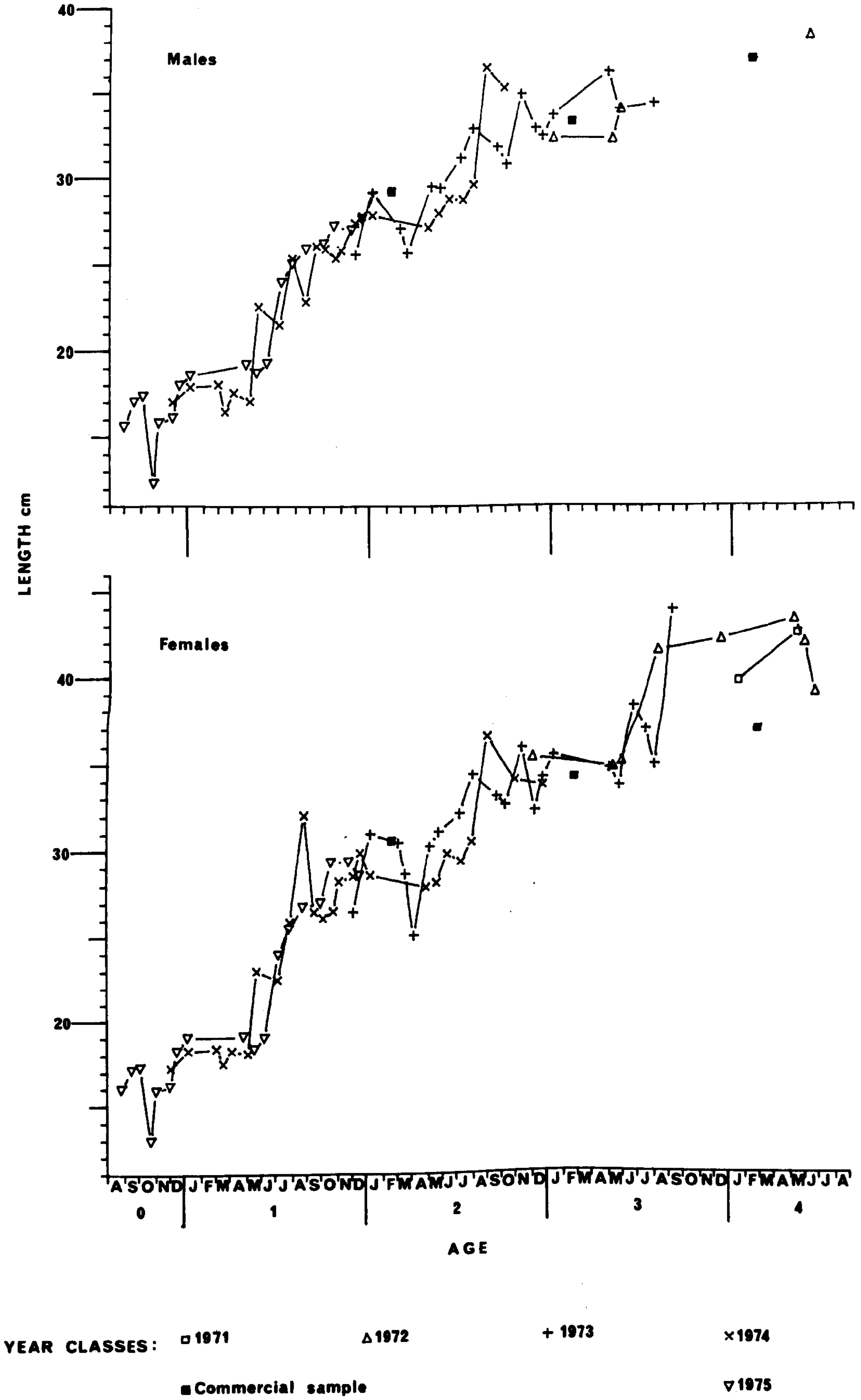
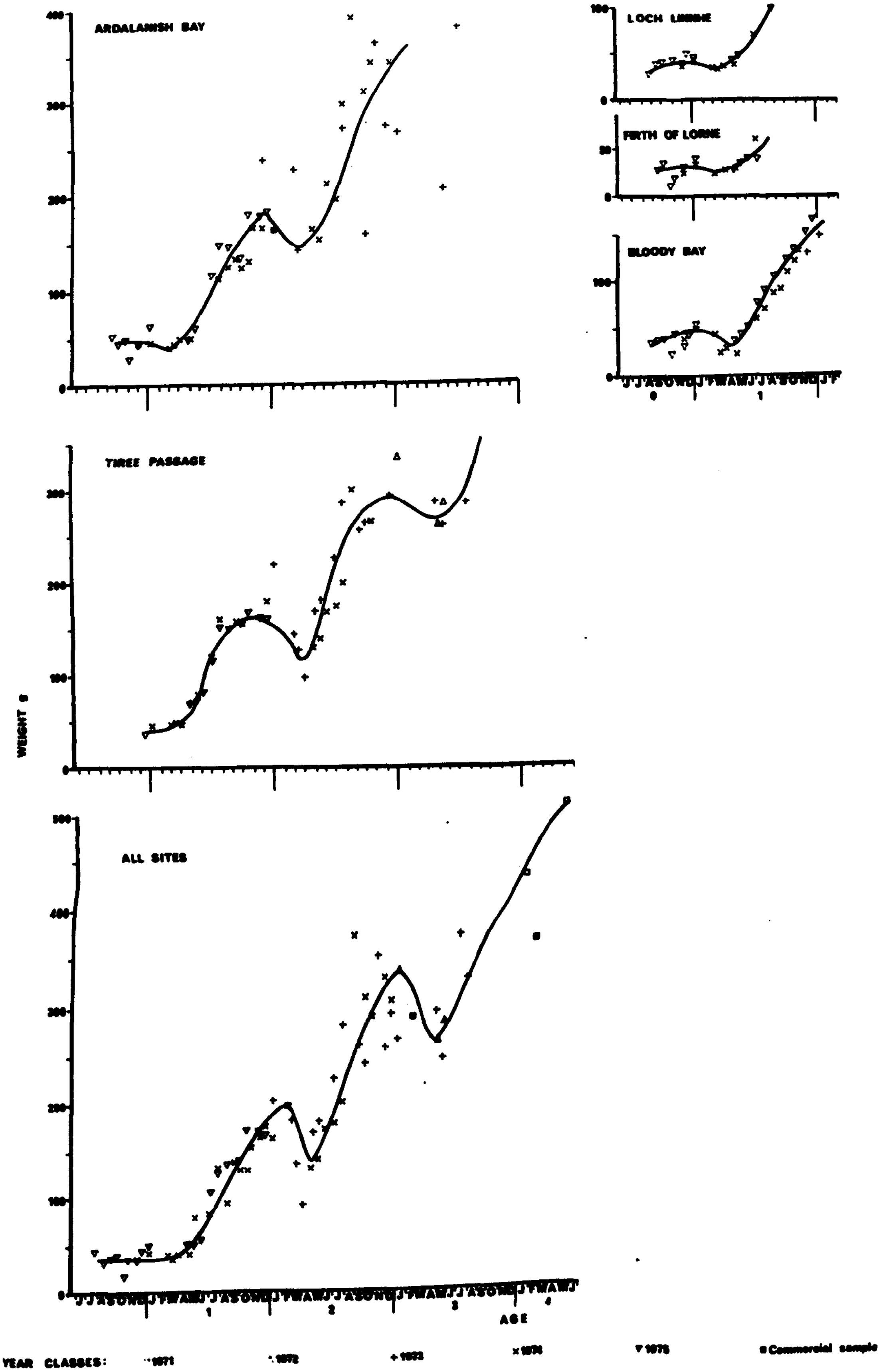

Males
Females
LENGTH cm
40
30
20
40
30
20
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A
0
1
2
3
4
AGE
YEAR CLASSES:
□ 1971
△ 1972
+ 1973
× 1974
■ Commercial sample
▽ 1975

Fig.III.15. Seasonal growth in gutted weight (g) of whiting at each site and all sites combined. Curves fitted by eye.


ARDALANISH BAY
400
300
200
100
0
TIREE PASSAGE
300
200
100
0
WEIGHT g
ALL SITES
500
400
300
200
100
0
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 S O N D J F M A M J J A S O N D J F M A M J
1
2
3
4
AGE
LOCH LINNHE
100
0
FIRTH OF LORNE
50
0
BLOODY BAY
100
0
J J A S O N D J F M A M J J A S O N D J F
0
1
YEAR CLASSES:
1971
1972
+ 1973
× 1974
▼ 1975
■ Commercial sample

Variations between sites

The seasonal timing of growth was essentially the same at all sites. There was evidence of a decrease in weight between November in the O-group and March in the 1-group at some sites, e.g. Loch Linnhe and Bloody Bay, although there was a considerable amount of variation between samples. Differences in mean weight between sites largely reflected differences in mean length.

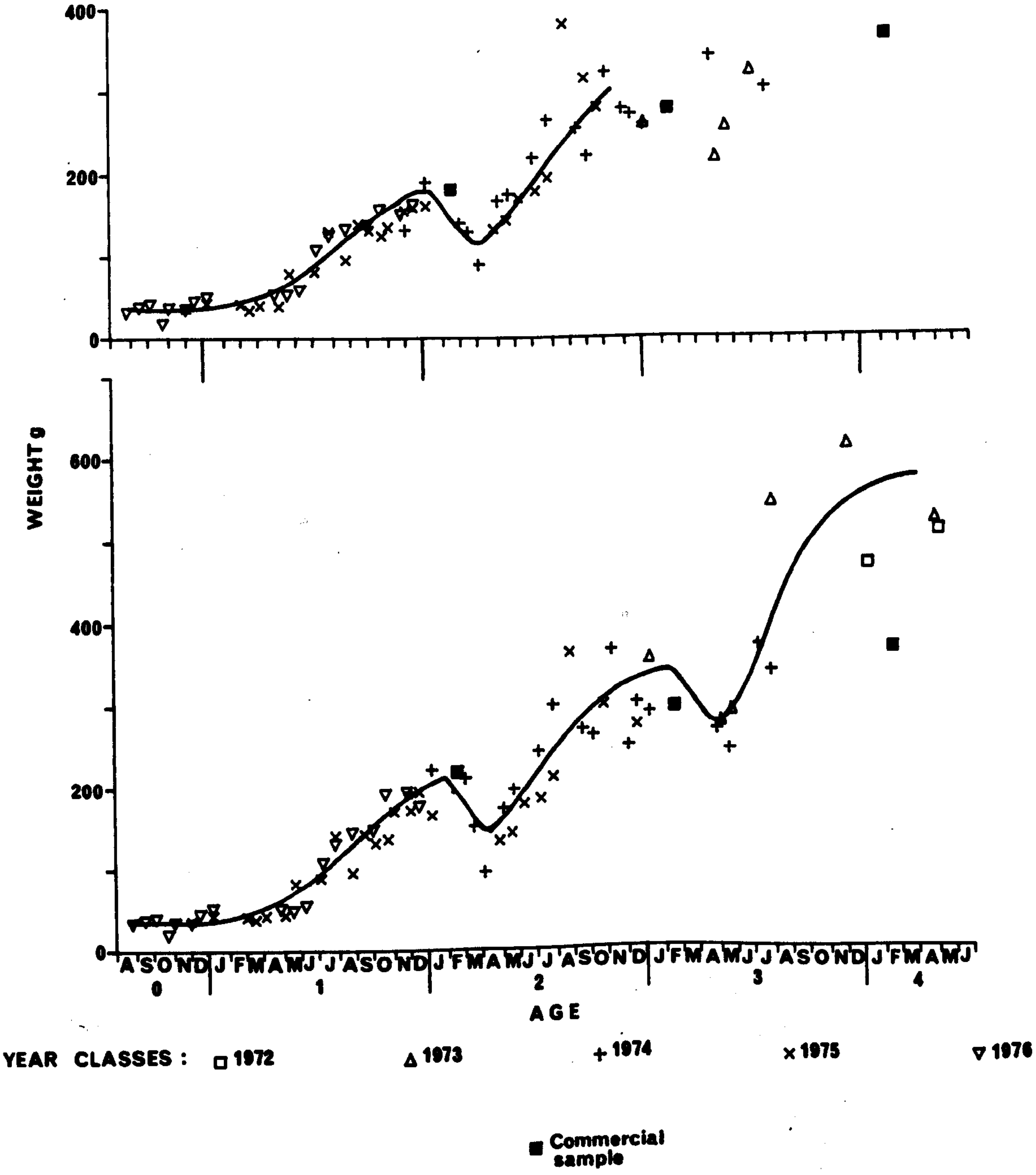
Variations between sexes

Seasonal variations in mean weight of each sex, pooling results for all sites, are shown in Fig.III.16. The timing of seasonal growth was the same and has already been described. Differences in weight were apparent between males and females, again largely reflecting the length differences.

III.3.D. Discussion

The only suitable length-frequency distributions available for comparison are those of Garrod and Gambell (1965) for the Irish Sea and Firth of Clyde. Research vessels fishing with nets with covered cod-ends were used in both areas. Whiting populations of the lower reaches of the Firth of Clyde had similar length-frequencies to those of Tiree Passage and Ardalanish Bay. The Loch Long area, however, had very few O-group fish and an abundance of the 1-group in November. This was a complete contrast to inshore whiting of the present study, in which O-group fish dominated the population, with very few 1-group fish. In the Irish Sea whiting showed an essentially similar size-composition to fish at Tiree Passage. Gambell found that whiting were recruited to the Clyde fishery at a length of 25cm, most fish reaching this length in autumn of the 1-group. This age-group sustained the fishery over the winter and was largely fished out by the following season. The size-composition of whiting at Tiree Passage suggests that the fishery in this area followed the same pattern, since the 2-group

Fig.III.16. Seasonal growth in gutted weight (g) of male and female whiting, pooling fish from all sites. Curves fitted by eye.


400
200
0
600
400
200
0
WEIGHT g
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 S O N D J F M A M J J A S O N D J F M A M J
0
1
2
3
4
AGE
YEAR CLASSES :
□ 1972
△ 1973
+ 1974
× 1975
▽ 1976
■ Commercial sample

mode disappeared in spring. The possibility of a spawning migration out of the area cannot, however, be discounted.(see section III.4.F).

Seasonal variations in the growth in length of whiting have been studied by several workers. In all cases a reduction in growth over winter and early spring was obvious. The lengths achieved at the end of the year varied. Bowers(1954) and Hillis (1968,1971) found that whiting in the Irish Sea reached lengths of about 15cm at the end of the O-group, although in Port Erin Bay fish were slightly smaller. Knudsen (1950) considered growth from early summer to autumn in the Kattegat and found that intermediate lengths approximate winter lengths found by Hillis and Bowers. Mean lengths of the 1-group in January in the present study were greater (17-19cm). Similar results were found by Gordon (1977b) for inshore whiting; and by Hislop and Coul (1975,1974) and Hislop and Jermyn (1973) for populations in the Minches. Fulton (1901) found that whiting in the North Sea overwinter at the end of the O-group at about 13cm. Bowers (1954) considered that disparities between Fulton's results and those of other workers could be due to his use of Peterson's method of age determination.

Differences in the rate of growth in length between inshore and offshore sites have also been noted by Bowers.(loc.cit.), who suggested that this was due to larger fish migrating offshore. Gordon (1977b) and Knudsen (1950) used the same explanation for the reduction in mean length of fish in the Firth of Lorne area and Kattegat respectively. Hillis (1971) concluded that in the western Irish Sea there was 'precocious or selective migration on the part of faster growing fish. Hannerz (1964) found that the growth of the whiting varied over the North Sea and also between years. The rate of growth was slower in the shallow waters of the southeast North Sea than in the deeper northwest North Sea. He concluded that temperature, supply of certain types of bottom food and possibly genetic factors interact in causing regional variations in growth.

The faster growth rate of female whiting is well-established and has also been noted by Saemundsson (1925) in Icelandic waters, Bowers (1954) in the Irish Sea, Desbrosses (1948) in the Gulf of Gascony and by Messtorff (1959) in the North Sea. It was not possible to draw growth curves for comparison with results given by Garrod and Gambell (1965) for other whiting populations in British coastal waters, mainly because only young fish were present (see also section 1.5.C).

Only Hillis (1968) gives details of the growth in weight, for whiting in the Irish Sea. Growth does not appear to differ appreciably from the west coast of Scotland until the 3-group, beyond which samples were too small for accuracy. Large variations between samples were obvious in both studies. Hillis found less evidence of weight reductions in spring. Hislop (1975) found that, when kept in aquaria, most whiting lost weight during spawning.

III.4. REPRODUCTION

III.4.A. Classification of Gonad Condition.

Maturation stages were assigned to each fish measured and weighed. The characteristics used were those of Bowers(1957). Gokhale(1957) correlated microscopic changes in the tissue with these macroscopic changes.

III.4.B. Length at Maturity.

Data from Tiree Passage and Ardalanish Bay between January and May were used to plot the maturation ogives (Fig.III.17). The curve for stage II includes fish of stage II and over. It is assumed that all fish which reach stage III spawn. The point at which the curve crosses the 50% maturity line was taken as the average length of first maturity. Males matured at about 25.5 cm and females at 27.5 cm. Females in the 2-group were 1-2 cm longer than males (section III.3.C).

III.4.C. Age at maturity.

Data from January to May at Tiree Passage and Ardalanish Bay were used to determine the proportions of fish of each age developing to each maturity stage (Table III.3).

Males

A small proportion of fish matured in the 1-group. Most fish matured in the 2-group although a small proportion (6.4%) did not develop as far as stage III in the time period considered. It is possible that some fish in stage 1 at the beginning of the spawning period matured in time to spawn successfully.

Females

The proportions of fish over stage 1 were lower for all ages in females than in males. A small number of fish were found in stage 1 until the 4-group. The general conclusions are the same as for males : a small proportion of fish matured as far as stage III in the 1-group (1.9% c.f. 5.0% for males). Although the majority of fish matured for

Fig.III.17. Maturation ogives for male and female whiting. Percentage of fish reaching each maturity stage in each two-centimetre length group.

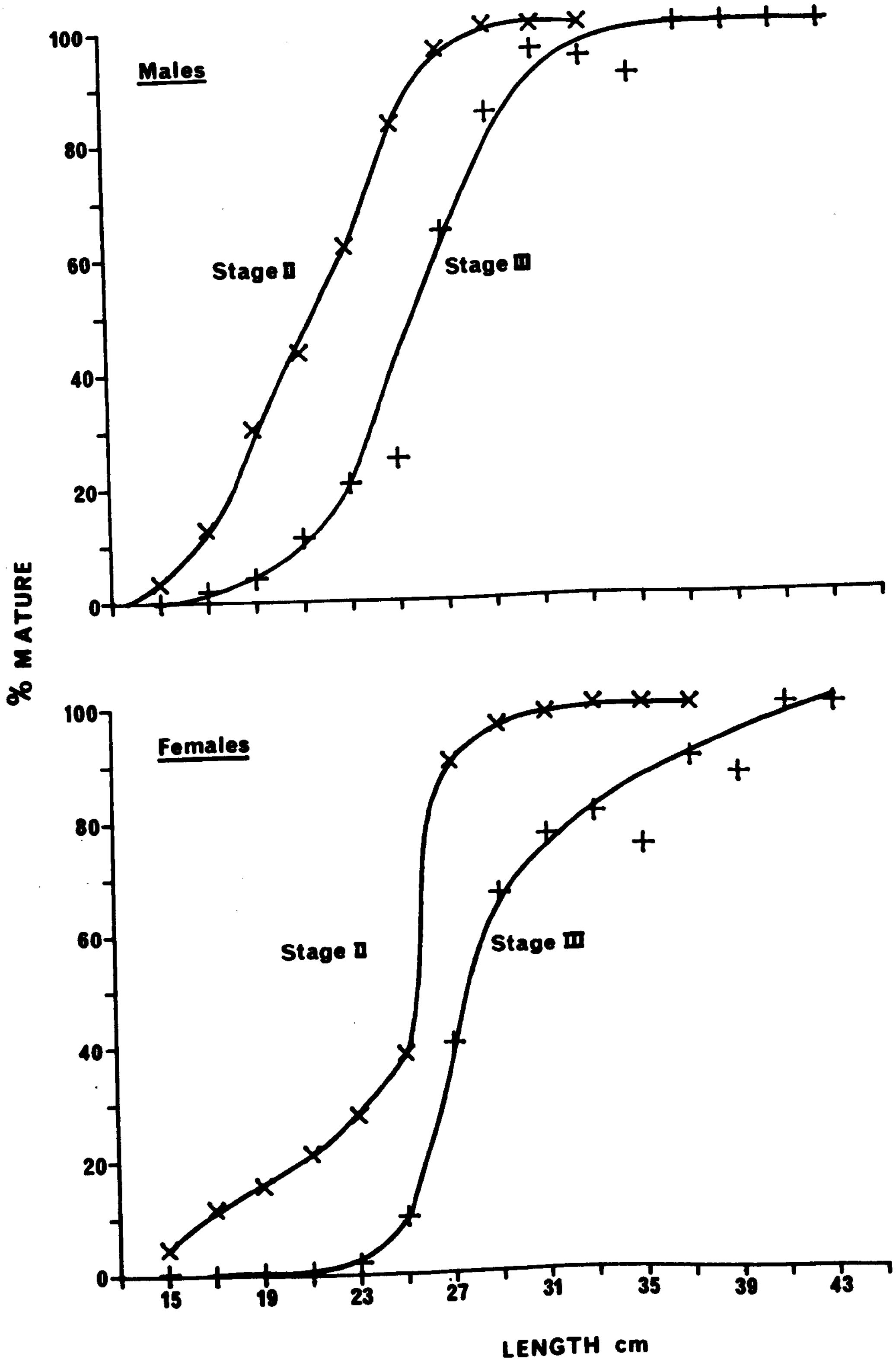

Males
Stage II
Stage III
Females
Stage II
Stage III
% MATURE
100
80
60
40
20
0
100
80
60
40
20
0
15
19
23
27
31
35
39
43
LENGTH cm

TABLE III.3. PROPORTIONS OF FISH OF EACH AGE IN EACH MATURITY STAGE AT TIREE PASSAGE AND ARDALANISH BAY BETWEEN JANUARY AND MAY.

Sex	Age	Percentage No. of fish in each maturity stage.							
		1	II	III	IV	V	VI	VII	No.
Male	1	75.1	19.9	4.3	0.5	-	-	0.2	1813
	2	3.8	23.1	26.5	0.5	7.3	0.4	23.1	234
	3	-	6.4	25.8	15.8	25.8	3.2	22.6	31
	4	-	-	25.0	16.1	-	-	-	4
	No.	1371	417	149	75.0	25	2	64	2082
Female	1	84.9	14.5	0.4	0.5	0.5	-	0.5	1841
	2	9.3	31.6	20.5	11.5	5.0	0.4	21.6	278
	3	1.1	22.6	10.4	14.0	4.3	-	26.9	93
	4	0	5.9	29.4	35.3	5.9	5.9	23.5	17
	No.	1590	377	99	52	20	1	90	2229

Age	Males		Females	
	% in stage II and over	% in stage III and over	% in stage II and over	% in stage III and over
1	24.9	5.0	15.1	1.9
2	96.2	73.1	90.7	59.1
3	100.0	93.6	98.9	76.3
4	100.0	100.0	100.0	94.1

the first time in the 2-group, 40.9% of them and 23.7% of the 3-group fish were in stages 1 or 2 in the time period considered. Three explanations are possible :

(1) that the period of maturity was shorter in females than males and some fish in stage II had spawned and recovered;

(2) females matured more quickly than males;

(3) there was a spawning migration of fish out of the area, with sexual differences in the rate.

It certainly appears that a spawning migration out of the area occurred (section III.4.F), although all three explanations may interact to produce the above anomaly.

The results compare well with the length of first maturity. Mean lengths at first maturity of 25.5cm and 27.5cm for males and females respectively would include most 2-group fish, all 3-group fish and a small proportion of the 1-group.

III.4.D. Sex Ratio

Monthly variations in the sex ratio are shown in Fig.III.18 and Appendix III.4. Excluding only those fish too immature to determine sex, the overall ratio was 1:1.016 (males:females). A standard significance test showed that the probability of this ratio differing from 1:1 was greater than 0.1 i.e. not significant (Table III.4). When fish of each age were considered the same conclusion was reached for the 0- and 1-groups. Fish of the 2-group and over were pooled for statistical reasons. The sex ratio of these fish (1 male:1.219 females) was significantly different to 1:1. A chi-square test for heterogeneity among ages rejected the null hypothesis that both sexes were equally distributed by age.

Fish were present in large numbers at all sites only for a relatively short time (December of the 0-group to May of the 1-group). Standard significance tests showed no departure from a 1:1 ratio at sampling

Fig.III.18. Variations in the sex-ratio (% male fish) of whiting with age at each site and pooling data from all sites. Fish of indeterminate sex (mainly O-group) not included.

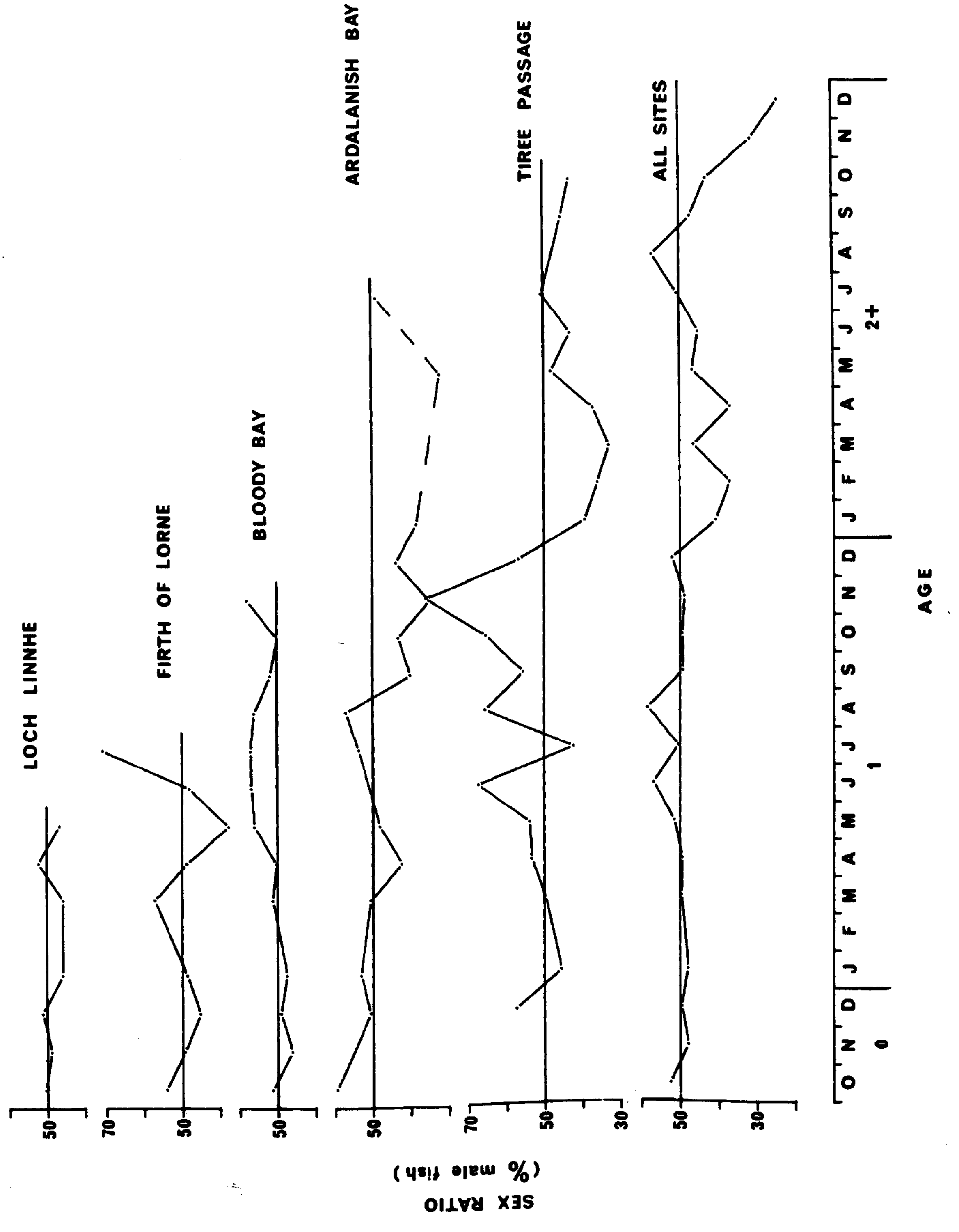

LOCH LINNHE
FIRTH OF LORNE
BLOODY BAY
ARDALANISH BAY
TIREE PASSAGE
ALL SITES
SEX RATIO
(% male fish)
50
70
50
50
50
70
50
30
50
30
O N D J F M A M J J A S O N D J F M A M J J A S O N D
0
1
2+
AGE

TABLE III.4. CHI-SQUARE TEST FOR HETEROGENEITY OF SEX-RATIO BETWEEN AGES. FISH FROM ALL SITES WERE COMBINED.

	Sex	Age				
		0	1	2+	T+1	
	Male	1509	3836	593	5938	$\chi^2 = 12.22$
n	Female	1519	3797	723	6039	d.f. = 2
	TTL	3028	7633	1316	11977	$p<0.01$
%	Male	49.8%	50.2%	45.1%	49.6%	
	Female	50.2%	49.7%	54.9%	50.4%	
	d	0.182	0.446	3.583	0.924	
	p	>0.100	>0.100	< 0.001	>0.100	

sites individually or collectively during this period. Neither was there any heterogeneity of sex ratio between sites (Table III.5).

III.4.E. Breeding Cycle and Seasonality of Spawning.

Monthly variations in the proportions of fish of each sex at each maturity stage are shown in Fig.III.19, pooling data from November 1974 to March 1977. Immature fish which could not be sexed are not included.

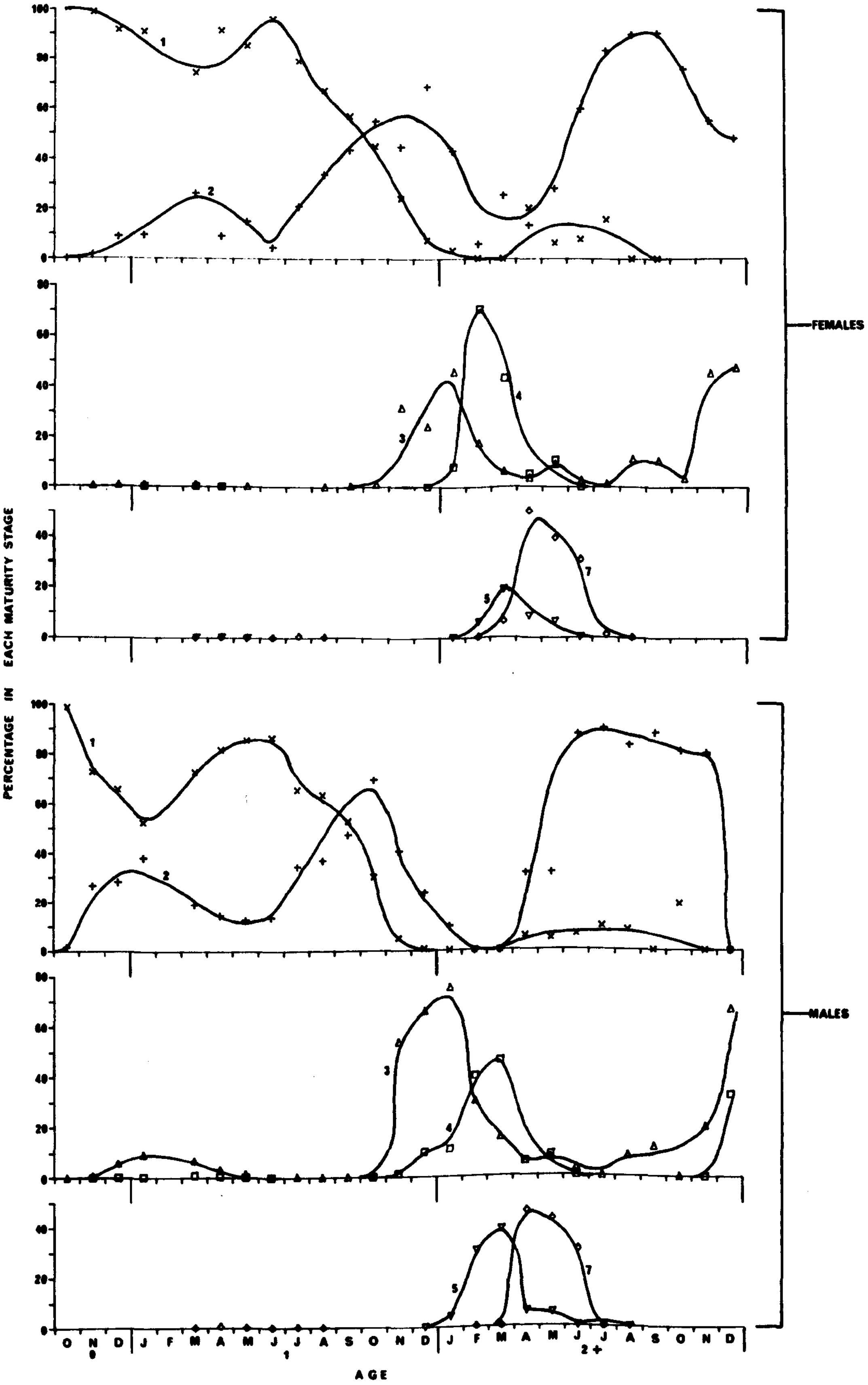
Females

A small proportion of fish developed from stage 1 to II in the 0-group and early 1-group, reaching a maximum in March. Only a very small proportion of fish in the 1-group matured beyond stage II. After March the proportion of stage II decreased and that of stage 1 increased. It is possible that the ovaries regressed to the immature state but neither Bowers (1954) nor Gokhale (1957) mention this. It is also possible that precocious fish suffered greater mortalities following the spawning season. At this time fish were migrating offshore from the inshore nursery grounds (section III.2) and these fish were less mature than those offshore (section III.4.F). A similar increase in the proportion of stage 1 fish occurred in summer in the 2-group, possibly associated with the departure of fish from areas such as Bloody Bay and Loch Linnhe. The proportion of stage II fish reached a minimum in June after which there was a steady development to maturity. The proportion of stage 1 fish fell steadily reaching a minimum in February of the 2-group. Iles (1964) pointed out that the area under the curve representing a single stage is a direct estimate of the mean time spent in that stage by individuals of the population. It follows that the ripe stage (V) was very short for a given fish although members of the population were found in it from January to June, with a peak in May. Only one stage VI (running-ripe) female was found in the sampling area, in May. Bowers (1954) found that the proportion of running-ripe fish

TABLE III.5. VARIATIONS IN SEX RATIO BETWEEN SITES. ONLY 0-GROUP AND EARLY 1-GROUP FISH USED (see text).

				Site			
	Sex	Loch Linnhe	Firth of Lorne	Bloody Bay	Ardalanish Bay	Tiree Passage	All sites
n	Male	572	382	990	499	550	2993
	Female	613	438	964	527	512	3054
	TTL	1185	820	1954	1026	1062	6047
	d	1.19	1.96	0.59	0.87	1.17	0.78
	p	>0.1	>0.05	>0.1	>0.1	>0.1	>0.1
%	Male	48.3%	46.6%	50.7%	48.6%	51.8%	49.5%

Fig.III.19. Seasonal change in the macroscopic appearance of the gonads of male and female whiting, pooling data from December 1974 to March 1977.


PERCENTAGE IN EACH MATURITY STAGE
FEMALES
MALES
1
2
3
4
5
7
100
80
60
40
20
0
O 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
0
1
2+
AGE

in the adult stock varied between 0.5% in February and 7.0% in April.

It seems likely that either the population sampled was not part of the spawning stock or that in some way it became inaccessible to the trawl. This will be discussed in the following section, but it should be noted that a spawning emigration would make estimations of the duration of each stage for individual fish meaningless.

Spent fish (stage VII) were found between February and August with a peak in April. Recovery to the resting condition was obvious as a rise in the proportion of stage II fish from April onwards. Slight increases in the proportions of stage III fish in August and September could be due to recovery of older fish to stage III instead of II.

Males

The breeding cycle was basically similar to females with some evidence for a greater proportion of the 1-group spawning: the stage II maximum occurred earlier (late January) and there was a definite peak of stage III fish. Stages III and V lasted longer in males than females, although the stages are arbitrary and anomalies due to a spawning migration are possible. Recovery of males was faster than females. As with females very few stage VI fish were caught (two 1-group fish in March and one 2-group fish in June).

III.4.F. Location of Maturity Stages.

The mean number of fish in each maturity stage per hour trawling at each site is shown in Table III.6, pooling data from January to July in 1975, 1976 and 1977. In the 1-group few fish over stage III were found at any sampling site. At offshore sites (Ardalanish Bay and Tiree Passage) a greater proportion developed to stage II than inshore, with the exception of Loch Linnhe. This is probably related to the migration of larger fish to deeper water (section III.2).

Most fish of the 2-group or older had developed beyond stage 1 in the period considered. Only a small proportion of maturing males

TABLE III.6. CATCH RATES OF FISH OF EACH MATURITY STAGE AT EACH SITE BETWEEN JANUARY AND JULY, POOLING DATA FROM JANUARY TO JULY, 1975 to 1977.

Sex	Site	Maturity Stage													
		Age 1							Age 2+						
		1	II	III	IV	V	VI	VII	1	II	III	IV	V	VI	VII
Male	Loch Linnhe	29.9	12.2	3.8	0.1					0.1	0.1	0.1	0.1		
	Firth of Lorne	58.0	17.3	3.9											
	Bloody Bay	165.3	23.7	2.6						0.4	1.0		0.4		
	Ardalanish Bay	36.0	26.1	3.9	0.5		0.2			4.4	4.8	1.1	1.0		0.9
	Tiree Passage	101.0	45.1	7.1	1.0			1.0	6.0	47.0	10.6	5.4	1.7	0.2	15.8
Female	Loch Linnhe	50.4	6.5	0.1							0.1	0.1			
	Firth of Lorne	75.9	7.0	0.3								0.3			
	Bloody Bay	154.8	10.9	2.6						1.6	0.6	0.6			
	Ardalanish Bay	48.4	19.8	0.1					0.8	8.6	4.4	1.0	0.5	0.1	1.8
	Tiree Passage	125.2	37.6	0.8		0.2		1.0	11.0	47.0	11.6	8.3	3.3		21.0

and females were found at Loch Linnhe, The Firth of Lorne or Bloody Bay (2.2% of males, 2.7% of females) and no spent fish (stage VII). At Tiree Passage and Ardalanish Bay ripe and spent fish (stages V and VII) were common, but the proportion of running-ripe fish in the adult stock was considered too low to support the population (section III.4.E). In section III.2.E a reduction in abundance of 2-group and older fish was noted in February/March. Gordon (1977c) found running-ripe whiting in the deeper upper basin of Loch Etive, but this localised spawning is not thought to contribute significantly to the populations in the areas studied. It seems likely that ripe fish either migrated out of the sampling area to spawn or in some other way become inaccessible to the bottom trawl e.g. by migrating off the bottom or by moving to rocky ground. Since the latter two observations have not been made by Messtorff (1959) in the North Sea, Bowers (1954) in the Irish Sea or Gordon (pers.comm.) in Loch Etive; the former is considered most likely. Some spent fish at least return to the area.

III.4.G. Discussion

The average length of first maturity was somewhat larger than that found by other workers. Messtorff (1959) found that males mature at 19.3cm and females at 22.0cm total length. Bowers (1954) does not give an average length of first maturity, but found that the smallest male to reach stage V,VI, or VII was 19cm and the smallesr female 21cm (total lengths). In the present study the lengths were 24cm and 23cm. The smallest fish in stage IV was 19cm for both sexes. Nagabhushanam (1964) found running-ripe males at 17cm and females at 18.5cm. All authors found females maturing at larger sizes than males. There was agreement among all authors that most females mature for the first time in the 2-group, while a small proportion of males mature one year earlier.

Bowers (1954) found that 52.8% of fish were male and 47.2% female.

This is significantly different from a 1:1 ratio ($d=3.13$, $p<0.002$). Nagabhushanam (1964) and Fulton (1891) found greater departures from 1:1 (63% and 67.8% male respectively). Bowers pointed out that this was probably because of greater mortalities among large males. This was also found in the present study in which a larger proportion of small fish were sampled than by any of the other authors. No significant departure from a 1:1 ratio was found overall, nor in age-groups 0 or 1. In considering regional variations in sex ratio it was only possible to pool data over a short time period. No departures from a 1:1 ratio were evident at any site nor was there any evidence of heterogeneity between sites. In contrast, Nagabhushanam's figures for nursery area (162 males, 233 females) were significant ($d=3.57$, $p<0.001$). Messtorff (1959) found that in the North Sea the sex ratios were nearly equal overall. Seasonal and regional variations did not show any distinct trend.

The timing of maturity stages agrees very well with figures given by Bowers (1954) and is in good general agreement with Nagabhushanam (1964), both working in the Irish Sea. Many other authors have noted the long breeding season of the whiting e.g. Fulton (1891), Masterman (1901), Debrosses (1945). Storrow (1913), Hawkins (1970) and Hislop (1975) observed the breeding of whiting kept in aquaria, which lasted for between 41 and 90 days and confirmed the long spawning period. All authors noted that the fish spawned periodically, confirming Hislop and Hall's (1974) observation of the serial maturation of eggs in the ovary.

Bowers (1954) and Desbrosses (1945) found evidence of larger fish spawning earlier than smaller ones. No such relationship was found in the present study, although this could be associated with the possible spawning emigration. Such migrations have been observed in several areas e.g. Arntz and Weber (1972) found maturing fish in Kiel

Bay but no running-ripe fish; Knudsen (1964) concluded that the Skagerrak stock undertake a spawning migration to the northeastern North Sea. Hillis (1971) showed the probable migrations of whiting in the Irish Sea; Garrod and Gambell (1965) found maturing fish in the Firth of Clyde but no running-ripe fish, and a decrease in fish density in the spawning season. They inferred from larval surveys that the Clyde whiting population was derived from the north-west coast of Ireland. Arntz and Weber (1972) considered that a successful spawning may occur in their study area (Kiel Bay) in suitable conditions (temperature >3°C, salinity > 25‰). According to results given by Craig (1959) both the Firth of Clyde and Tiree Passage have suitable physical conditions. Bowers (1954) found running-ripe fish at depths between 36 and 80m to the west and south-west of the Isle of Man, where the bottom deposit varied from sandy mud and shell to soft mud with increasing depth. In this study sampling depths varied from 40m to 90m on hard ground (at Ardalanish Bay) to sand (at Tiree Passage) without encountering spawning fish. There are no reports in the literature concerning the locality of spawning grounds of whiting of the west coast of Scotland. Likely areas will be discussed in section III.6.

III.5. CONDITION FACTOR AND LENGTH-WEIGHT RELATIONSHIPS

III.5.A. Condition Factor

Seasonal variations in condition factor are shown in Fig.III.20. When samples from all sites were combined it was possible to look at variations into the 4-group. Condition factors varied between about 0.6 and 0.8. The minimum occurred in spring and early summer with a maximum in August or September. This cycle was common to all age-groups although there is some evidence that in 0-group fish minimal condition extended from October to June of the 1-group. In older fish condition was minimal between April and June. This seasonal pattern was essentially the same at all sites, although inshore it was not possible to plot variations in fish older than the 1-group. Low sample sizes resulted in considerable variations between successive cruises at Loch Linnhe.

The mean condition factor was the same for each sex (0.70 ± 0.02). Fig. III.21 shows seasonal variations in condition factor for each sex, combining data from all sites. The same seasonal pattern is obvious, with an extended period of minimal condition at the end of the 0-group and short periods of minimal condition between April and June of age-groups 1 and 2. In males there was little difference between age-groups in the autumn maximum and spring minimum. In females the spring minimum was lower in mature fish (in the 2- and 3-groups). It is possible that 0-group and early 1-group fish in better condition were being selected by the gear and also fish which could not be sexed (and which may be in poorer condition) are not included.

Fig.III.22 shows changes in condition factor associated with maturation. Virgin immature (stage 1) fish had a lower condition factor than developing and spent-resting (stage II) fish and were found mainly until summer in the 1-group (see Fig.III.19), when condition was low. In males the main decrease in condition occurred after stage V. In females there was an increase in condition between stages II and III

Fig.III.20. Seasonal change in the mean condition factor of each year-class of whiting at each site and pooling fish from all sites.

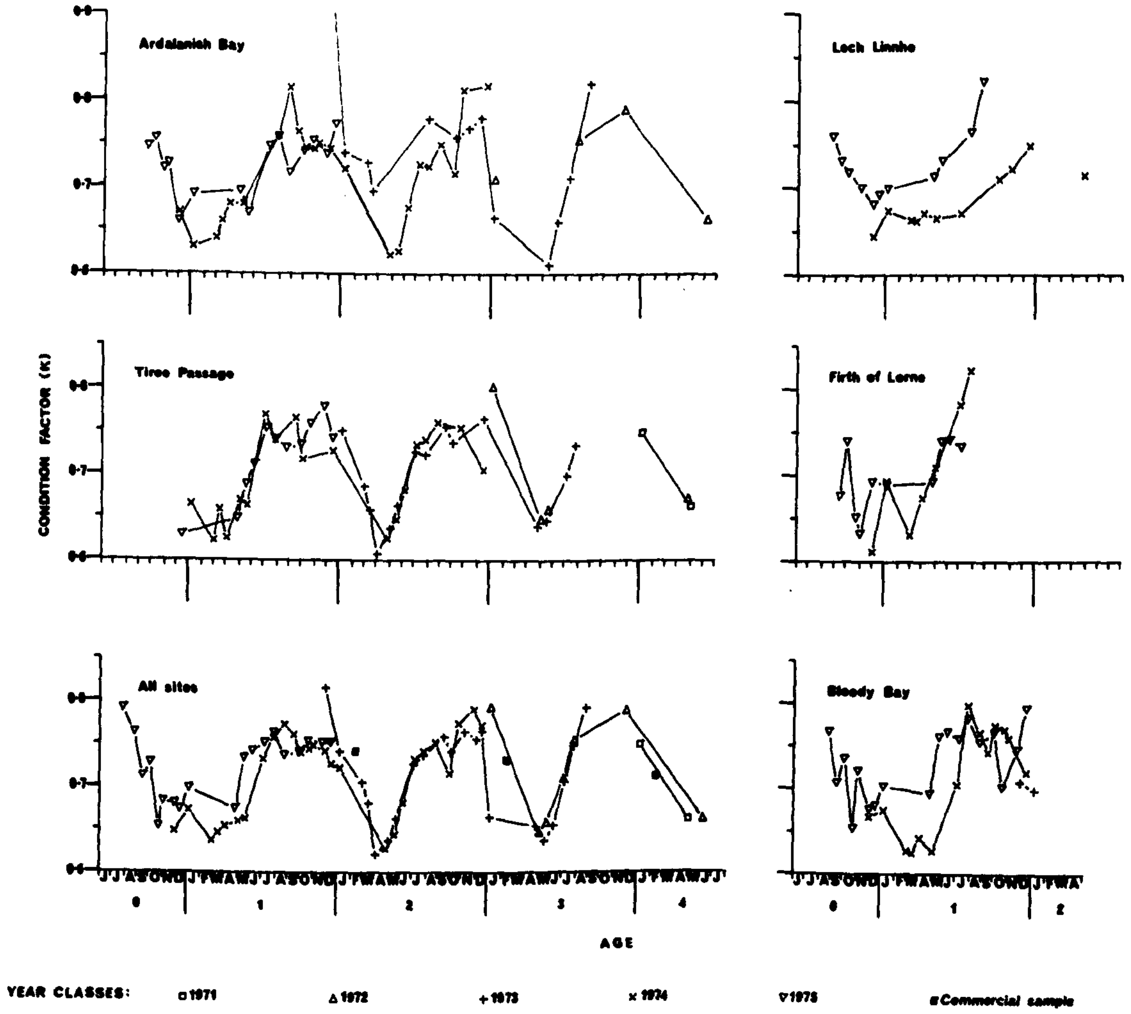

Ardalanish Bay
Loch Linnhe
Tiree Passage
Firth of Lorne
All sites
Bloody Bay
0·9
0·8
0·7
0·6
CONDITION FACTOR (K)
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
0
1
2
3
4
J J A S O N D J F M A M J J A S O N D J F M A
0
1
2
AGE
YEAR CLASSES:
□1971
△1972
+1973
×1974
▽1975
■Commercial sample

Fig.III.21. Seasonal change in the mean condition factor of each year-class of male and female whiting, pooling data from all sites.

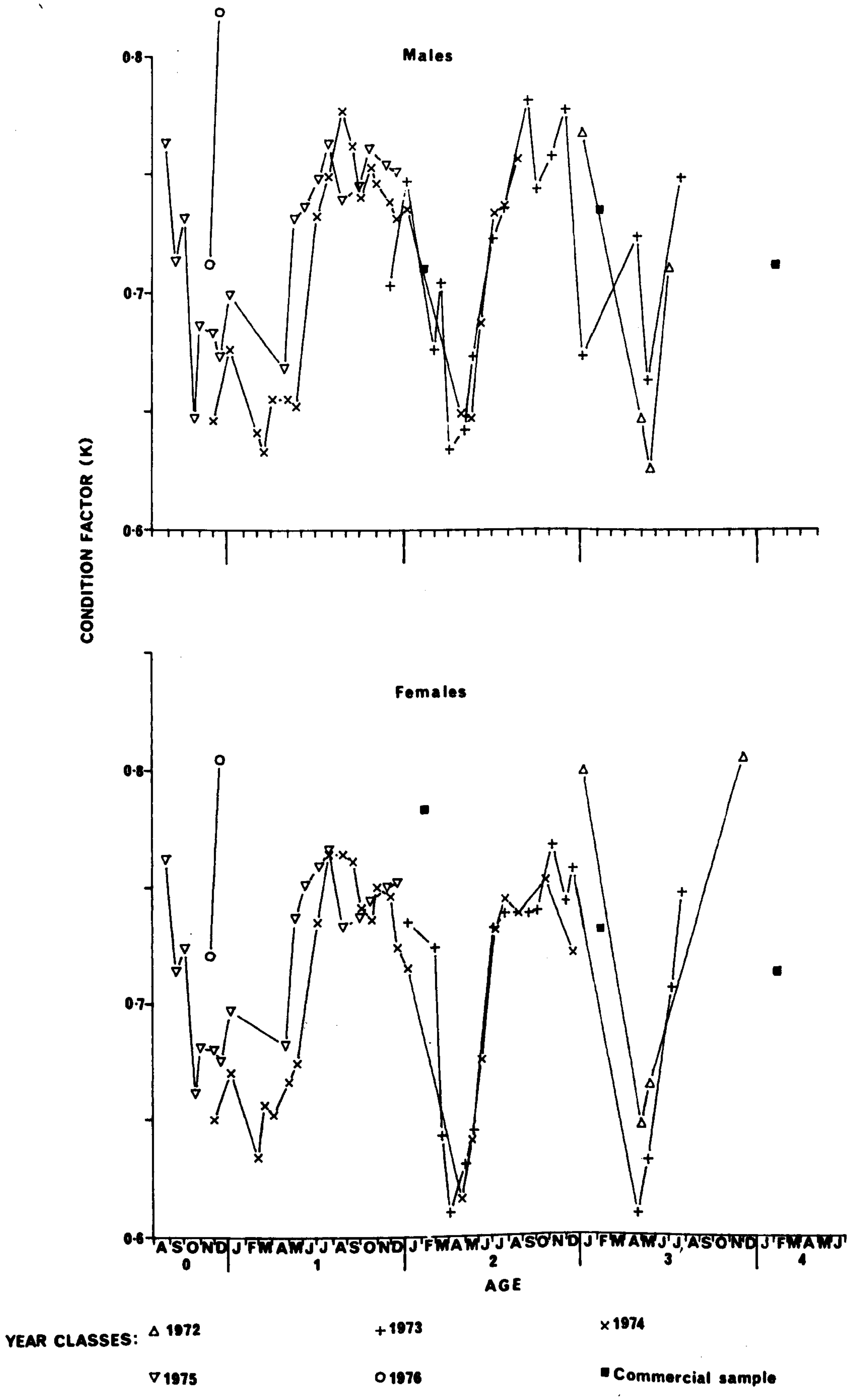
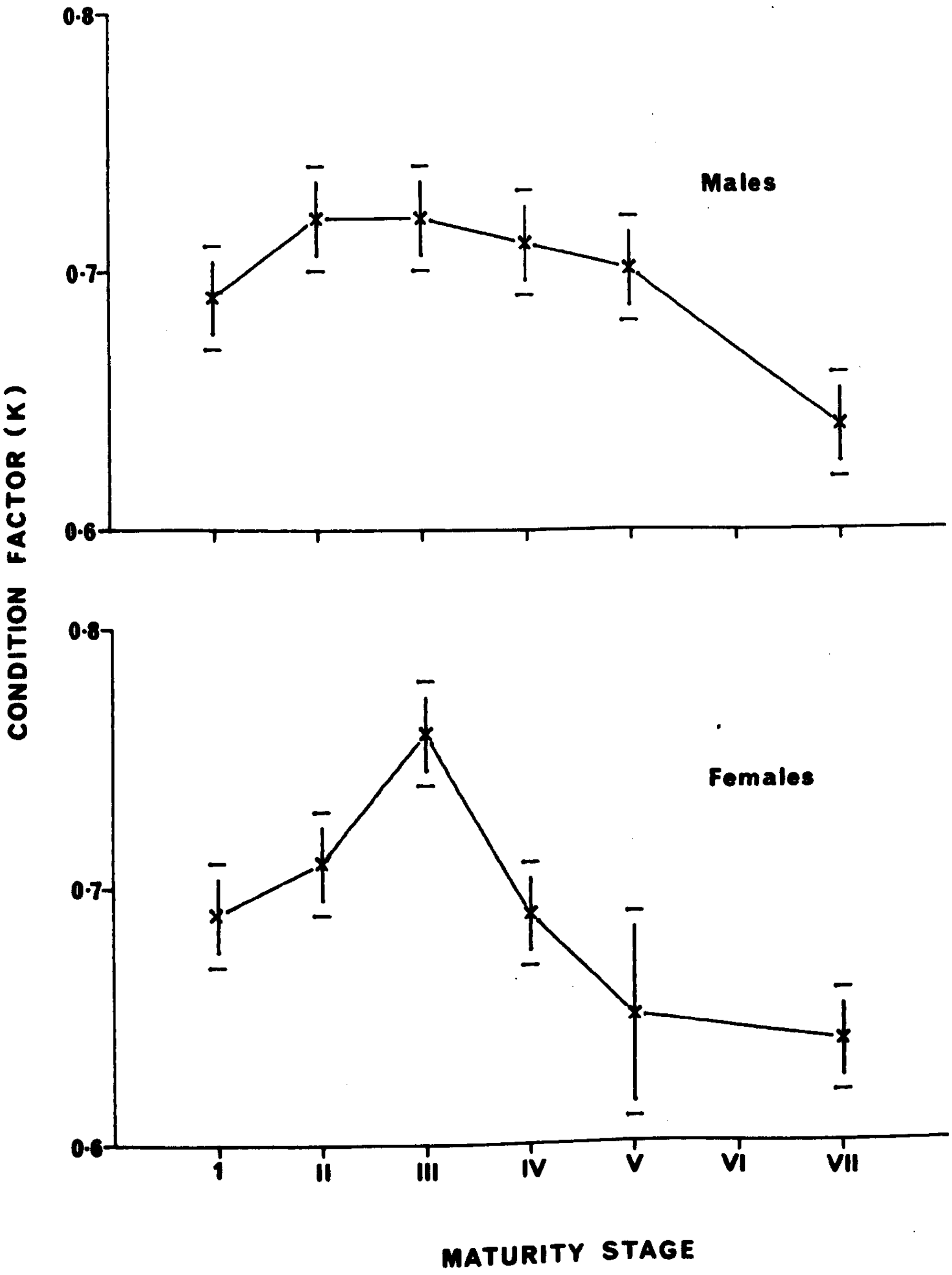

Males
Females
CONDITION FACTOR (K)
0·8
0·7
0·6
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
0
1
2
3
4
AGE
YEAR CLASSES: △ 1972
+ 1973
× 1974
▽ 1975
○ 1976
■ Commercial sample

Fig.III.22. Mean condition factor, with 95% confidence limits, of male and female whiting in each maturity stage.


0·8
0·7
0·6
Males
0·8
0·7
0·6
Females
CONDITION FACTOR (K)
1
II
III
IV
V
VI
VII
MATURITY STAGE

followed by a rapid decline to stages IV and V. In both sexes there was an increase in condition from spent (stage VII) to recovering spent (stage II).

Variations in condition factor with length of males and females are shown in Fig.III.23 pooling data from all months at all sites. Condition increased until a length of about 25cm in both males and females.

III.5.B. Length-weight Relationships

Preliminary scatter diagrams showed that weight varied as a power of length. The G.M. regression of all fish measured and weighed was:

$$\log \text{weight} = 3.1949 \log \text{length} - 4.6055.$$

A large and significant part of the variance was explained by regression (see Appendix III.5.A).

Differences between sexes

Fig.III.24 shows the length-weight relationship of all fish, males, females and fish whose sex could not be determined. In all cases a large and significant part of the variance was explained by regression. Immature fish were heavier at lengths up to about 25cm. In fact all fish over 15cm could be sexed, and most over 10cm. Males and females did not diverge until about 30cm, with females lighter than males. An F-test for comparison of slopes of males and females showed that residual variances were approximately equal ($F = 1.0006$, d.f.= 6115,6176). Comparison of among means variance with within regression variance gave a very highly significant F-ratio ($F = 2{,}038{,}344$; d.f. = 1,12292).

Seasonal differences (Appendix III.5.B)

Fig.III.25 shows the monthly length-weight relationships, pooling data from 1974 to 1976. Fish from Tiree Passage and Ardalanish Bay were used in order to avoid bias in favour of young fish. In both sexes there was a reduction in weight of larger fish at given lengths until about May, followed by increases until the end of the year. This

Fig.III.23. Mean condition factor (with 95% confidence limits) of each 2cm length group of male and female whiting.

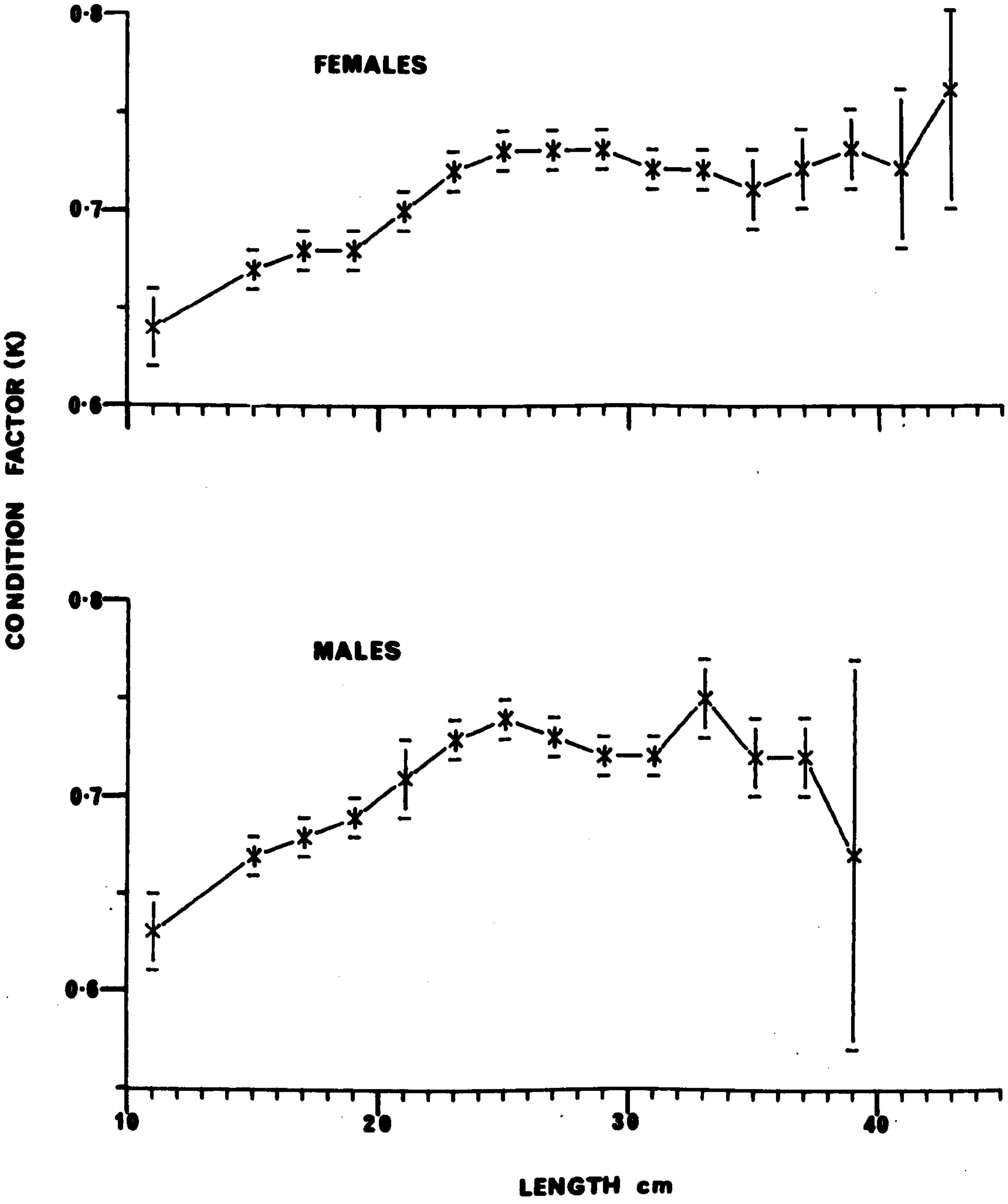

FEMALES
MALES
CONDITION FACTOR (K)
0·8
0·7
0·6
10
20
30
40
LENGTH cm

Fig.III.24. Length-weight relationships of all whiting, males, females and fish whose sex could not be determined, calculated from the G.M.functional regression.

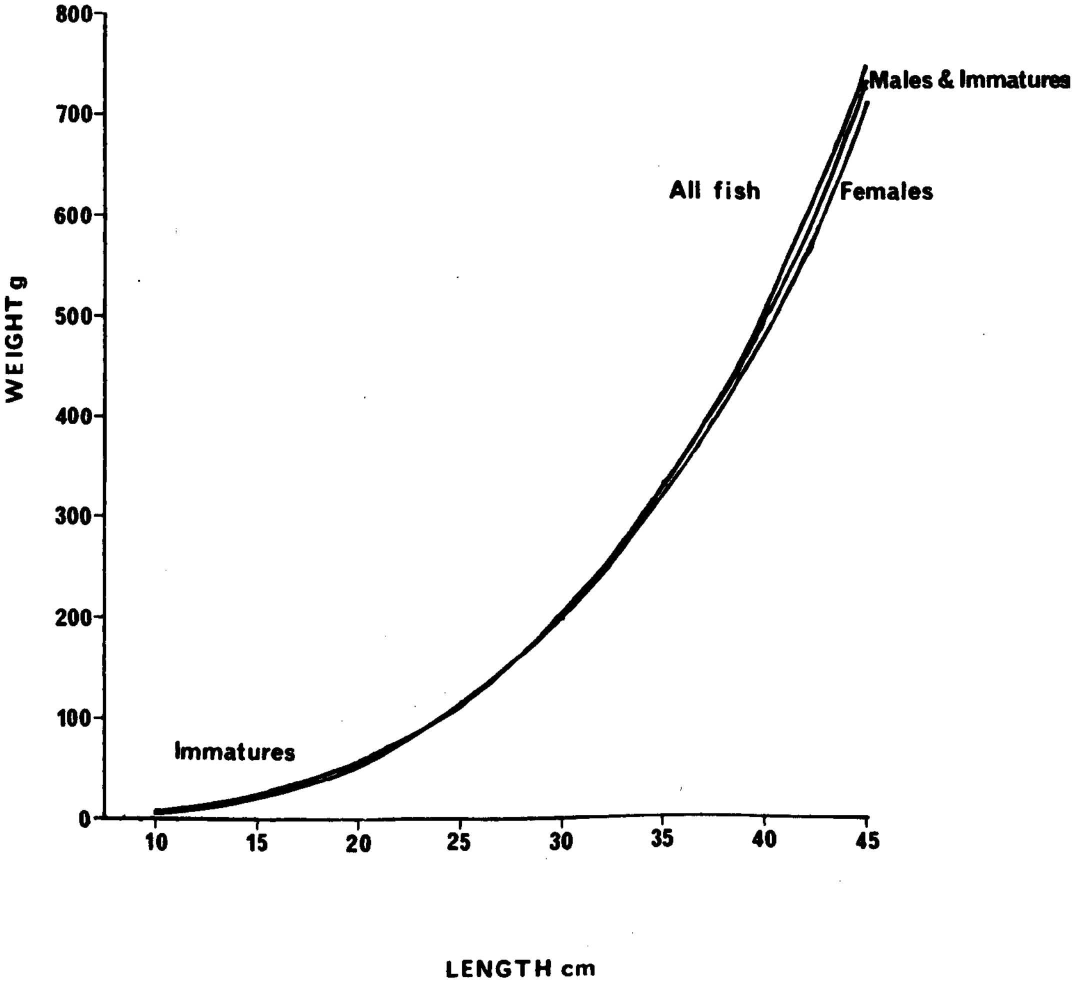
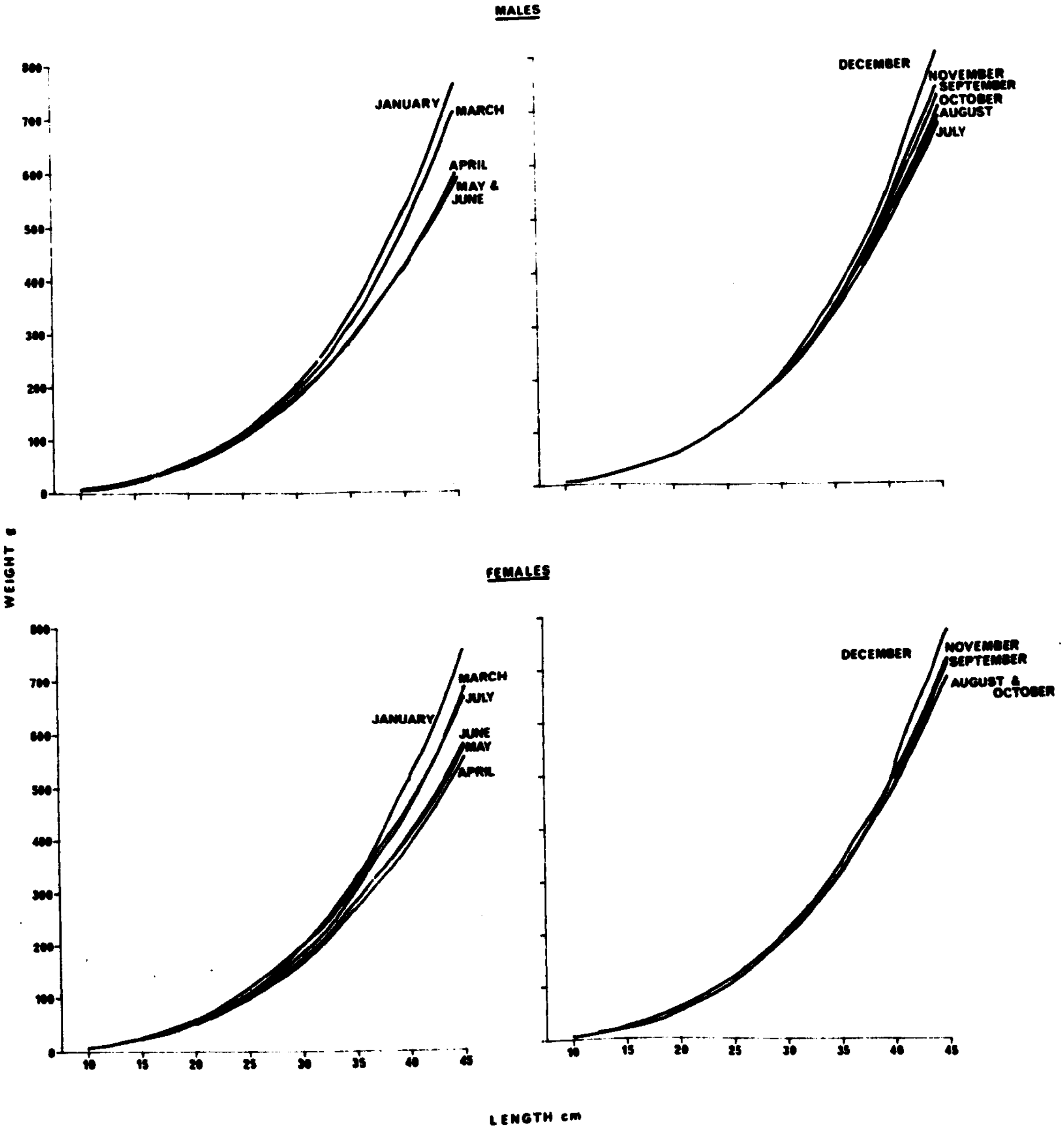

800
700
600
500
400
300
200
100
0
WEIGHT g
10
15
20
25
30
35
40
45
LENGTH cm
Males & Immatures
All fish
Females
Immatures

Fig.III.25. G.M. functional regressions of the length-weight relationships of male and female whiting in each month.


MALES
800
700
600
500
400
300
200
100
0
JANUARY
MARCH
APRIL
MAY & JUNE
DECEMBER
NOVEMBER
SEPTEMBER
OCTOBER
AUGUST
JULY
WEIGHT g
FEMALES
800
700
600
500
400
300
200
100
0
MARCH
JULY
JANUARY
JUNE
MAY
APRIL
DECEMBER
NOVEMBER
SEPTEMBER
AUGUST & OCTOBER
10
15
20
25
30
35
40
45
10
15
20
25
30
35
40
45
LENGTH cm

is illustrated in Fig. III.26 for hypothetical fishes of 15cm and 35cm. Little variation is obvious between the sexes. 95% confidence limits were calculated for each point but the interval was too small to plot (0.1g in all cases). In the immature (15cm) fish mimimal condition occurred between January and March whereas minimal weight of the 35cm fish occurred between April and June.

Variations between maturity stages (Appendix III.5.C)

Fig. III.27 shows that in females there was a fairly regular reduction in weight-at-length with maturation to stage V. Stage VII was associated with an increase in weight of large fish. This could be due to bias in favour of smaller fish however, since few fish over 35cm were sampled. Most maturing fish were between 25cm and 35cm. Table III.7 shows regular reductions in weight of a 30cm fish with maturation from stage III to VII. In both males and females an increase in weight is evident in stage III.

III.5.C. Discussion

Seasonal changes in condition were measured by :

(1) condition factor ($K= 100 \text{ weight}.\text{length}^{-3}$);

(2) monthly changes in the estimated weight of fish of constant length growing according to monthly length-weight relationships.

In both cases immature fish showed an extended period of minimum condition in winter at the end of the 0-group, while maturing and mature fish showed a short period of minimal condition between April and June. Only Gordon (1977b) has considered seasonal variations in condition of such young fish and essentially the same conclusions were reached for immature fish, although no older fish were available for comparison. Hillis (1968), Gambell (1963), Garrod and Gambell (1965) and Messtorff (1959) considered seasonal variations in condition factor of older fish in the Irish Sea, North Sea, Firth of Clyde and North Sea

Fig.III.26. Seasonal variation in the estimated weight (g) of whiting of 15cm and 35cm, calculated from the G.M. Functional Regressions.

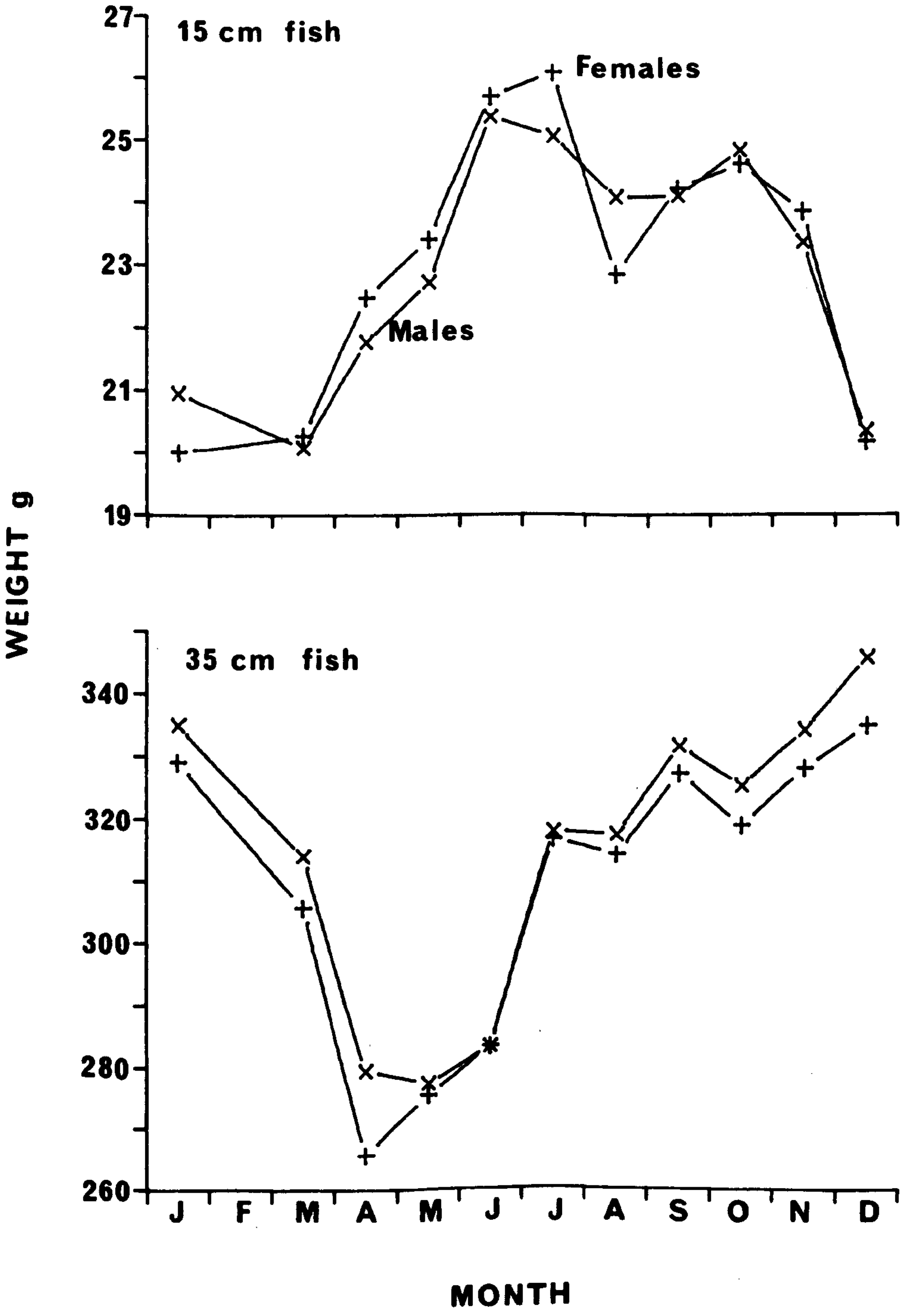

15 cm fish
Females
Males
27
25
23
21
19
WEIGHT g
35 cm fish
340
320
300
280
260
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Fig.III.26. G.M. Functional Regressions of the length-weight relationships of male and female whiting in each maturity stage.

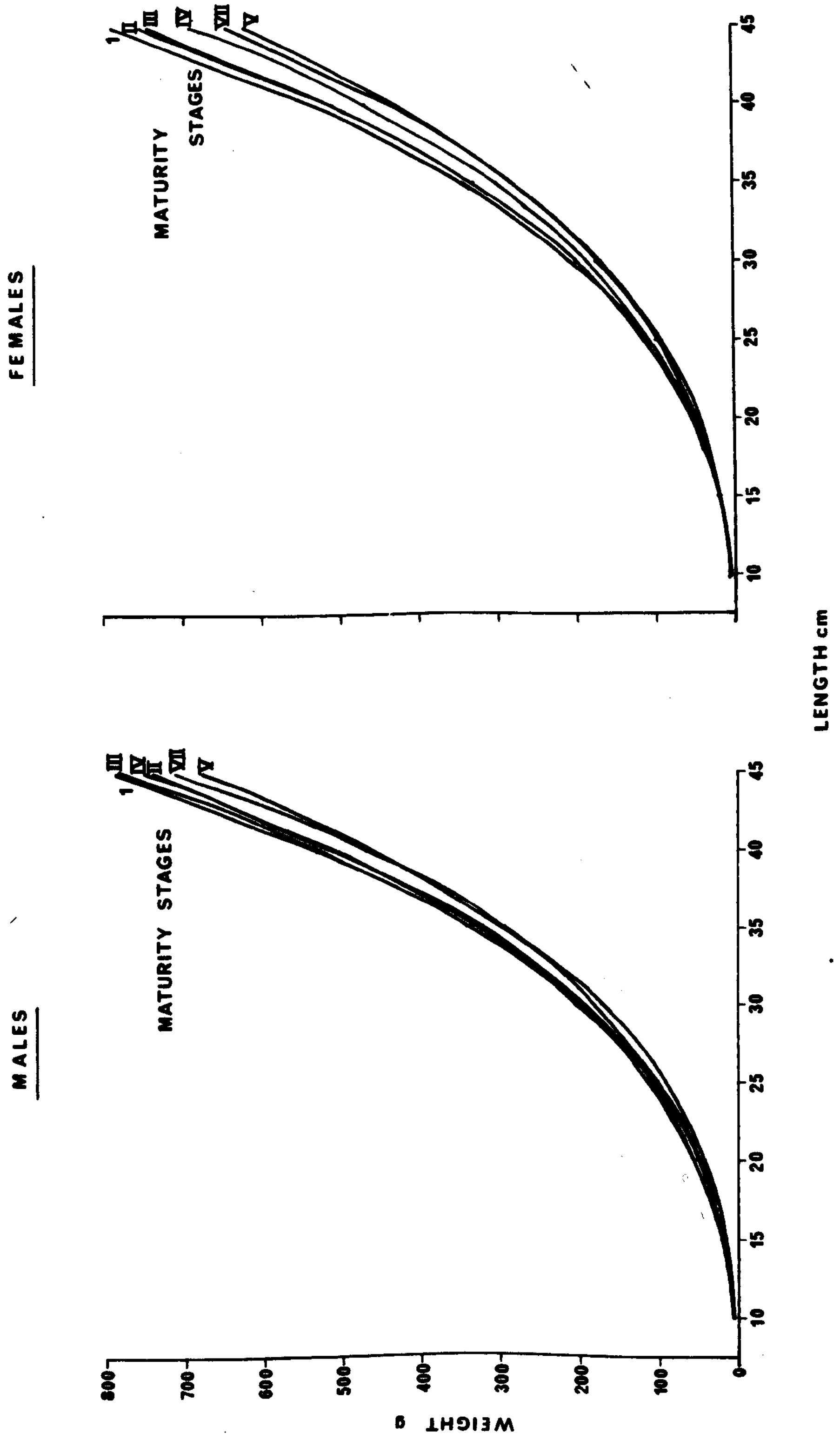

MALES
MATURITY STAGES
I
III
IV
II
VII
V
FEMALES
MATURITY
STAGES
I
II
III
IV
VII
V
WEIGHT g
800
700
600
500
400
300
200
100
0
LENGTH cm
10
15
20
25
30
35
40
45

TABLE III.7. WEIGHT IN GRAMS OF 30 cm FISH ASSOCIATED WITH EACH MATURITY STAGE, CALCULATED FROM LENGTH-WEIGHT RELATIONSHIP

Sex	Maturity Stage					
	II	III	IV	V	VI	VII
Female	197.5	200.1	179.5	174.3	-	168.5
Male	200.7	202.8	192.2	182.2	-	171.3

respectively. All authors noted a short period of minimal condition in spring. Whiting from the Irish Sea and Firth of Clyde were in peak condition in late autumn and winter, whereas condition factors of fish from the North Sea and those in the present study were greatest in late summer and autumn. There were discrepancies between immature and mature fish when considering variations in length-weight relationships: immature fish were in maximum condition in summer and minimum condition for an extended winter period, while mature fish were in maximum condition in early winter and minimum in spring. In the present study variations in condition, measured as condition factor and variations in the length-weight relationship, showed that considerable reductions occur associated with maturation from stage III to VII. Hislop (1975) showed from experiments that reproduction imposes a considerable physiological strain on mature whiting. It is not therefore surprising that in mature and maturing fish there was a short period of minimal condition corresponding to the period of peak spawning (section III.4.E). Most 1-group fish did not mature beyond stage III (section III.4.F). Jones and Hislop (1972) showed that whiting kept in aquaria increase in condition with increasing food supply. O-group and early 1-group whiting aggregated inshore (section III.2) and in studying the same inshore areas, Gordon (1977d) found that the percentage of fish with empty stomachs increases in winter. This may account for the earlier and more extended period of low condition. Differences in the availability and quality of food may also account for regional variations in the timing of the summer maximum in condition.

The spring minimal condition was lower for mature females than males (Figs.III.21 and III.26) and for females in general. Hislop (1975) showed that reproduction places a greater strain on females than males. In contrast,Messtorff (1959) found the length-weight coefficient to be higher in females than males. Several authors have noted that the condition factor increases with fish length e.g. Messtorff(loc. cit.), Gambell(1963), Garrod and Gambell(1965), Hillis(1968). In the present study no increase in condition factor was evident from seasonal studies (Figs.III.20 and III.21). In fact the spring minimal condition was lower for mature than immature females. The mean value of the condition factor increased from the 0-group to the 1-group, however, and up to a length of 25cm for both males and females. Hart(1946) considered the inflexion point to be a good indication of the length of first maturity.

Table III.8 summarises the information available in the literature concerning length-weight relationships. There is good agreement between workers in condition factors although there is considerable variation in the intercept of the length-weight relationships. This is thought to be due to gear selectivity, calculation from limited length-ranges of fish and differences between authors in how length and weight are defined (gutted or total weight, standard or total length).

TABLE III.8. LENGTH-WEIGHT RELATIONSHIPS OF WHITING

FROM DIFFERENT LOCALITIES

Authority	Region	Condition Factor	Length-weight relationship	Comments
Hillis (1968)	Irish Sea	0.63-0.76	-	Commercial data, gutted weight, total length
Nagabhushanam (1964)	Port Erin Bay		$W=0.0074L^{3.002}$	Research data, gutted weight, total lengths
	Irish Sea		$W=0.0024L^{3.346}$	" " "
Hislop (1975)	Aquarium fish	0.65-1.01		Total weight) Fish caught in northern
		0.49-0.84		Gutted weight (estimated)) N. Sea or Minch
Jones and Hislop	"	0.72-0.93		Small whiting) Total condition factor
(1972)	"	0.85-1.07		Large whiting)
Messtorf (1959)	North Sea	0.76		Research vessel data, gutted weight, total length
Gambell (1963)	North Sea	0.64-0.80		Commercial data, gutted weight, total length
Gambell (1965)	Firth of Clyde	0.65-0.84		Commercial data, gutted weight, total length
Gordon (1977b)	Firth of Lorne	0.669	$W=0.0072L^{2.969}$	Research vessel data
	Loch Linnhe	0.708	$W=0.0076L^{2.969}$	Total weight
	Loch Sunart	0.678	$W=0.0035L^{3.342}$	Total length
	Upper Sound of Mull	0.713	$W=0.0035L^{3.272}$	Bulk samples for 1cm length groups
	Loch Etive	0.725	$W=0.0045L^{3.170}$	
	Loch Linnhe	0.64-0.83	logw = 3.4412 log 1 -5.1493	**Research vessel data**
	Firth of Lorne	0.61-0.82	logw = 3.3003 log 1 -4.8274	**Total length**
Present	**Bloody Bay**	0.62-0.80	logw = 2.8480 log 1 -3.8199	**Gutted weight**
Study	***Ardalanish Bay***	*0.61-0.81*	*logw = 2.9235 log 1 -3.9675*	**Ordinary predictive regression**
	Tiree Passage	0.61-0.80	logw = 2.6928 log 1 -3.4206	
	Overall	0.62-0.81	logw = 2.4246 log 1 -2.8346	
	Loch Linnhe		**logw = 3.1962 log 1 -4.6004**	
	Firth of Lorne		**logw = 3.2445 log 1 -4.7130**	**Research vessel data**
Present	**Bloody Bay**		**logw = 3.2947 log 1 -4.8212**	**Total length**
Study	**Ardalanish Bay**		**logw = 3.2135 log 1 -4.6533**	**Gutted weight**
	Tiree Passage		**logw = 3.2044 log 1 -4.6495**	**G.M. Regression**
	Overall		**logw = 3.1949 log 1 -4.6055**	

III.6. DISCUSSION

Summarising the general conclusions from the previous sections, it would appear that the inshore juvenile populations found by Gordon (1977b) are derived in the first instance from planktonic larvae west of Mull. The inshore migration occurred after the planktonic stage at lengths of 2-10cm, a period in the life cycle which has been little studied. The fish at the lower end of the length-range were probably mostly pelagic, many associating with Scyphomedusae. There is some evidence of vertical migration, possibly associated with this commensal relationship. An increasing proportion of the population became demersal with growth, until by October of the O-group few pelagic fish were caught. By this stage also the fish were concentrated in inshore areas. The importance of the association with jellyfish in determining the final distribution is unknown.

Pre-recruit surveys are important in recommending T.A.C.'c (total allowable catches) for roundfish. Those for 1977 and 1978 on the west coast of Scotland were made assuming average recruitment (Anon.1977a). It may be that offshore nursery grounds for whiting occur off the west coast as in the North Sea, but surveys over a larger area are required to determine this. Even so, any future young fish survey should take into account this inshore aggregation of young fish.

The fish remained in the inshore areas for between 1 and 2 years, with some evidence of seasonal migrations in relation to depth. Some large fish probably migrated offshore at the end of the O-group resulting in fish offshore having greater mean lengths and weights. Catch rates were reduced logarithmically with time; the slopes were less steep at offshore sites, presumably due to recruitment of fish from inshore.

Fish matured at the offshore sites, ripe fish being found between January and June, with a peak between April and June. This long spawning season was also indicated by the occurrence of larvae, seasonal variations in the length-weight relationship and the platykurtic length-frequency distributions of 0-group fish. The length and age of first maturity were determined. It appears that most fish matured during spring of the 2-group, but a small number of 1-group males may spawn. Although ripe and spent fish were caught there was a shortage or running-ripe fish, probably due to a spawning migration out of the area. This was also indicated by a reduction in catch rates of 2-group fish in March and April. Localising the spawning grounds of these fish is clearly of great importance. The rest of the discussion will be devoted to considering the location of the spawning grounds and the possibility of the division of western Scottish whiting into separate stocks.

It is now fairly well-established that North Sea whiting are divided into two main stocks, to the north and south of the Dogger Bank. Evidence for this is from:

(1) parasitological studies (Kabata, 1963, 1967);

(2) investigations of vertebral number (Gambell, 1959; Messtorff, 1959; Knudsen, 1964) and number of anal fin rays (Knudsen,1964);

(3) tagging experiments (Hislop and MacKenzie, 1976; Knudsen,1964);

(4) geographical variations in growth rates (Hannerz, 1964; Messtorff, 1959).

The Skagerrak, Kattegat, Kiel Bay and Belt Sea are mainly nursery grounds for fish spawned in the northeastern North Sea (Knudsen, 1964), although some spawning may occur in the area (Anon.,1978). Hislop and MacKenzie (1976) discussed the possible further sub-division of the northern North Sea stock. They concluded from tagging and parasitological studies that:

, (1) fish from the Shetlands move extensively;

(2) there was little interchange between the eastern coastal stock and the offshore stock, although some older coastal whiting may migrate via the Shetlands to offshore waters;

(3) fish from west of the Shetlands move south or south-east after spawning, possibly returning to the same area to spawn;

(4) there was no evidence from tagging of interchange of fish from the northern North Sea and Shetland areas with populations off the north and west coasts.

Wilkins (1971) concluded from serological and parasite studies that whiting off the north coast of Scotland 'do not constitute a single homogeneous population in continuity with those in the Minch and the Orkney/Shetland areas.'

Although there are reports of tagging experiments on the west coast of Scotland (Hislop and Coull, 1974, 1975; Hislop and Jermyn,1973; Hislop and Pirie, 1972) no results for fish tagged in the Minch area have yet been published. Garrod and Gambell (1965) tagged mainly 1-group fish in the Firth of Clyde. Fish remained within the area until the end of the winter fishery, when they moved beyond the outer reaches of the Clyde for spawning. Thereafter they dispersed over a wide area, recaptures occurring in Donegal Bay, the Irish Sea and Tiree Passage. In the Irish Sea it was concluded from evidence of meristic characters, blood groups and tagging that unit stocks are indistinguishable from adjacent stocks outside the Irish Sea. Tagged fish were recaptured off south-east Ireland and near the Firth of Clyde, with a greater proportion moving south than north. The probable movements and migrations of whiting within the Irish Sea have been summarised by Hillis (1971). In contrast Kabata (1967) inferred from parasitological evidence that the stock of whiting in the Irish Sea was a distinct population, although recruitment may be from a spawning ground common with the western Scottish and Clyde whiting. Fish from the north of the Outer Hebrides and north of mainland Scotland were distinct from fish of the north coast of Ireland, with an intermediate mixing zone. Garrod and Gambell (1965) found no variations in growth among west coast populations, apart from the Clyde stock. This anomaly was probably due to emigration of faster growing fish. Hislop and Hall (1974) concluded that fecundity differences could not be used to distinguish between stocks of whiting in British waters.

In summary, whiting from the north coast of Scotland are distinct from those of the North Sea and north coast of Ireland. There is an intermediate mixing zone between the Irish and Scottish north coasts with some interchange between stocks from the Irish Sea, Clyde and mixing zone. The population studied could therefore include fish from the Irish Sea, Clyde, north coast of Ireland and the Minch. The planktonic stages, however, could only be derived from spawning grounds upstream to Tiree Passage, although older fish may migrate actively into the area. Since the water flow to the east and west of Tiree is northwards (section 1.2) and young larvae have been found consistently in the area, it seems likely that the spawning grounds lie to the west and south of Islay, and north of Ireland. It is also possible that fish could be derived from the north-west or even north-east coasts of Ireland. Since the currents in the Sea of the Hebrides and between Barra Head and the mainland are largely unknown, it is also possible that some fish in the Bloody Bay area are derived from spawning grounds in the Minches.

SECTION IV

Trisopterus esmarkii (Nilsson, 1855)

NORWAY POUT

IV. 1. INTRODUCTION

The Norway pout is a small, short-lived gadoid rarely growing longer than 21 cm and older than the 3-group. The distribution is limited to the north-eastern Atlantic: the northern boundary occurs in the Barent's Sea, where it is found to Bear Island in the east and Iceland in the west. In the south it is only found at the western end of the English Channel (Svetovidov, 1948). The depth distribution varies with age, young fish being caught in shallow water with adults mostly between 100m and 250m. The Norway pout feeds mostly on planktonic crustaceans close to the sea bottom (Raitt and Adams, 1965; Gordon, 1977a). Copepods and euphausiids form the bulk of the diet, the food and feeding intensity varying with the season and time of day.

Although normally too small for human consumption, large catch rates led to the development of industrial fisheries for Norway pout in the Skagerrak and North Sea in the late 1950's. More recently fisheries have developed off the coast of Norway, in the North Minch and around the Faroes and Iceland. Catches are reported regularly in 'Bulletin Statistique des Pêches Maritimes', but figures are only approximate due to non-identification of by-catches. The by-catch varies with the area of the fishery, including many whiting in the 'Industrifisk' fishery in the Skagerrak; blue whiting, great silver smelt and silvery pout are important off Norway (Anon., 1978). The fishery is used mainly for the manufacture of fish meal and oil. Annual landings vary according to recruitment of each year-class, since the fishery consists mainly of 1-group and 2-group fish. In addition to its industrial importance the Norway pout is an important link in the food chain for larger commercial gadoids such as cod, haddock and whiting. Raitt (1966) suggested that intra-specific competition may occur, raising difficult problems for management. It should first be decided if an industrial fishery is desirable, to the possible detriment of yield of food species. Even assuming this is so, stocks are vulnerable, since as Anon.(1977b) reports ' stocks with a short life span ..... may be difficult to assess, and management mistakes may be more fatal because of the difficulties in taking corrective actions in time'.

An extensive literature exists on the Norway pout, probably because of this industrial and ecological importance. Raitt (1968a) provided a synopsis of biological data on the Norway pout, which reviewed the literature until that date. More recently Gordon (1977a) worked on the biology of inshore western Scottish populations. Bailey and Hall (1971) considered variations in year-class strengths around Scotland; Smith (1972) studied the occurrence of Diclidophora esmarkii, a monogenean parasitic on the gills while Ostapenko and Malkov (1977) measured growth rate and mortality of populations in the north-east Atlantic.

IV. 2. MIGRATIONS AND SEASONAL OCCURRENCE

IV.2.A. Age Composition

Fig.IV.1 shows seasonal age compositions of Norway pout populations at each site, pooling data from November 1974 to December 1976 at bimonthly intervals. 0-group fish appeared first in June/July and represented a greater proportion of the population offshore than inshore, fish at Loch Linnhe not being caught until August. For the remainder of the year this age-group dominated the offshore populations; at the deep inshore site of Loch Linnhe this did not occur until February/March of the 1-group. The 1-group was the most important at all sites until recruitment of the new year-class. 2-group fish, usually maturing for the first time, were caught at all sites in December/January but represented a greater proportion of the population at the deeper sites (Loch Linnhe, Ardalanish Bay, Tiree Passage). By February/March they occurred only at Tiree Passage and Ardalanish Bay where they were insignificant by August. There was some evidence of a return of 3-group fish in December/January at Tiree Passage.

Considering age compositions in terms of catch rate rather than percentages (Fig.IV.2), reinforces the differences noted above between inshore and offshore areas. Following their first occurrence large catch rates were obvious offshore in the 0-group. Inshore catches approached those offshore only at the end of the 1-group.

IV.2.B. Occurrence of Planktonic Stages

No attempt was made to identify the eggs of T. esmarkii and no planktonic stages were found during the study period. It should be mentioned that the identification of planktonic T.esmarkii is very uncertain, resembling T. minutus very closely (Russell, 1976; Raitt, 1965; Schmidt, 1909; Damas, 1909). In larval sampling surveys from 1970 to 1977 only 14 planktonic Norway pout have been positively identified, 11 of which were taken in 1974. A further 19 have

Fig.IV.1. Age composition of Norway pout populations at each site, pooling data at bimonthly intervals from January 1975 to January 1977.

(n = number of hauls)

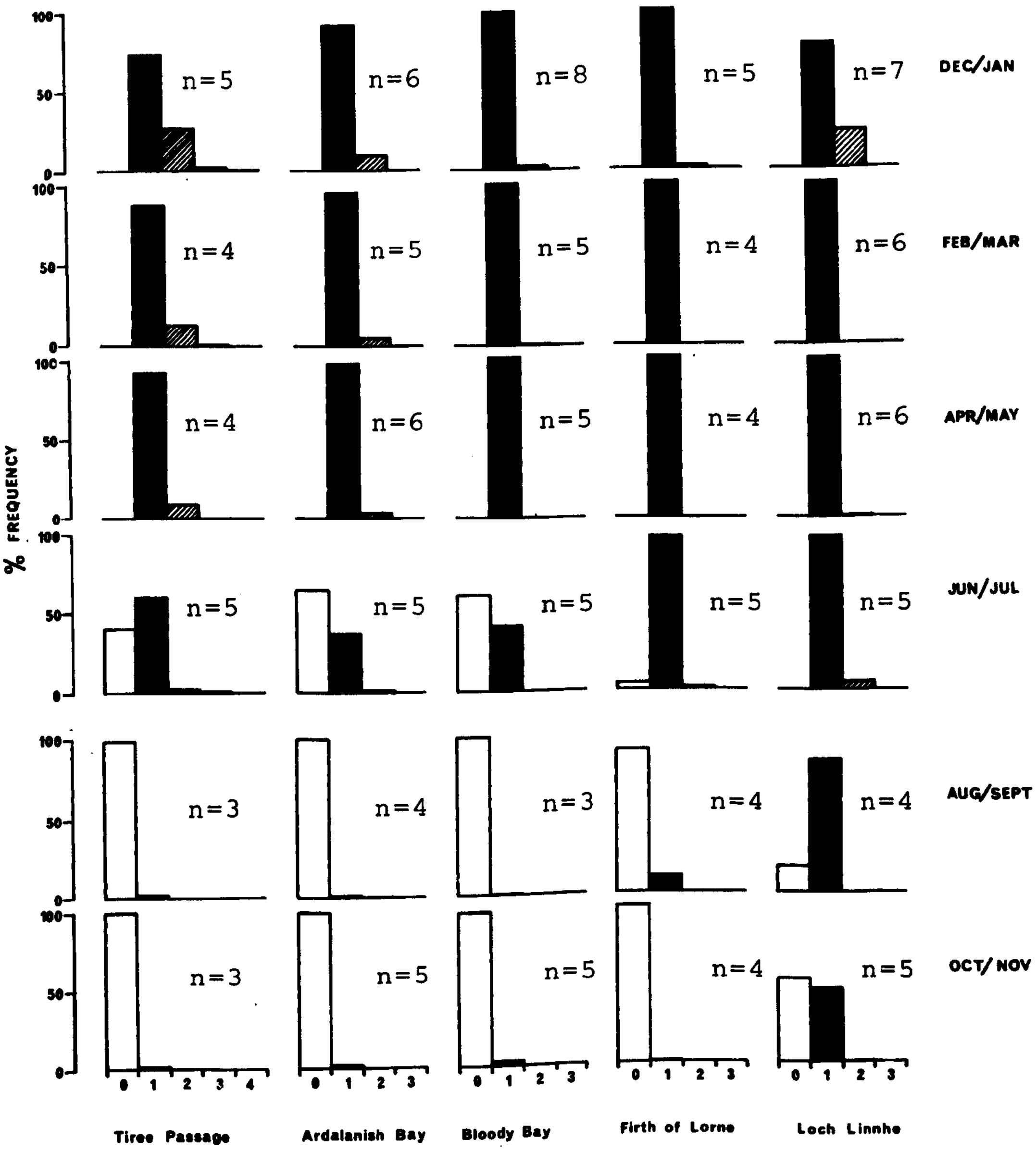
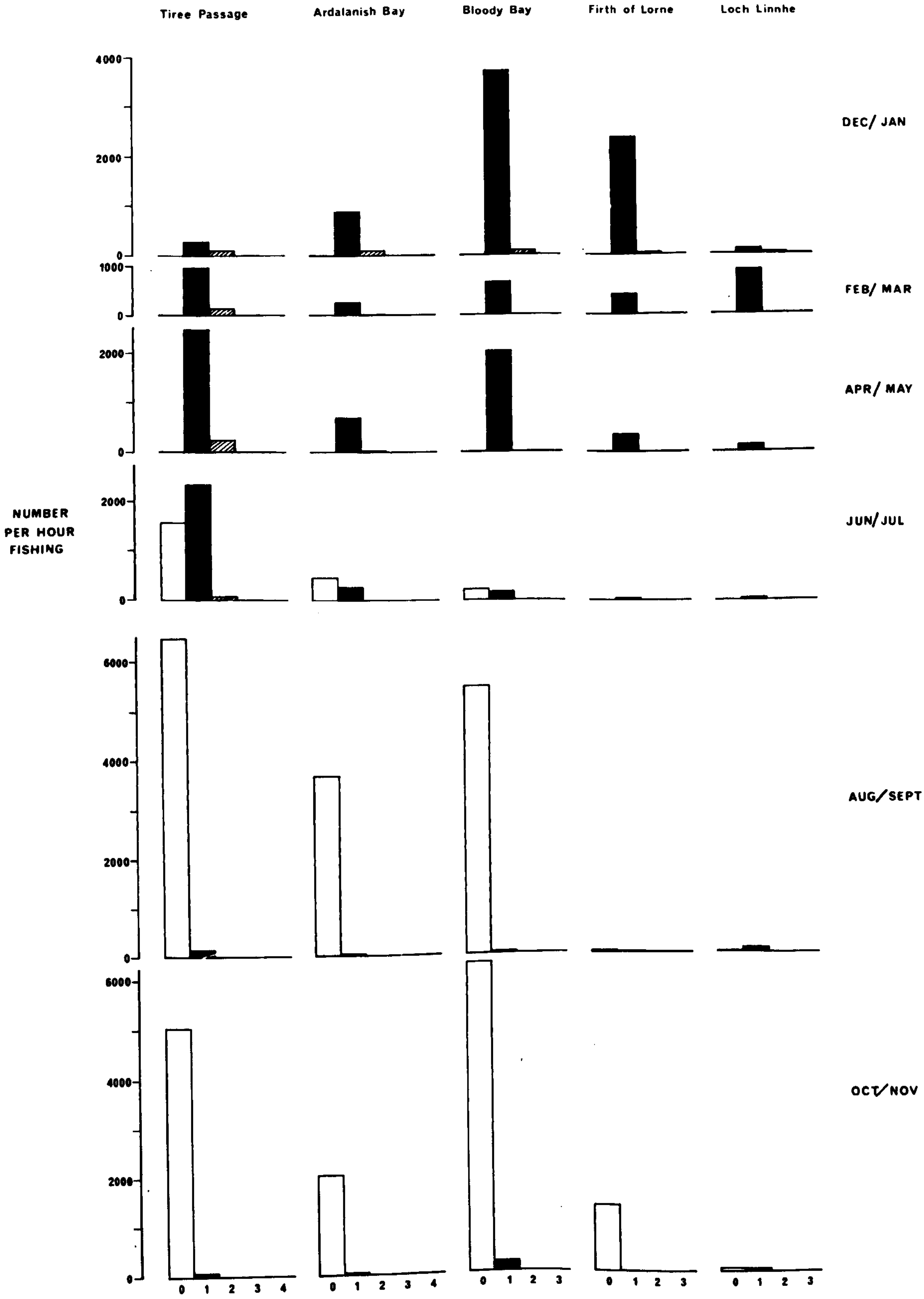

% FREQUENCY
100
50
0
n=5
n=6
n=8
n=5
n=7
DEC/JAN
n=4
n=5
n=5
n=4
n=6
FEB/MAR
n=4
n=6
n=5
n=4
n=6
APR/MAY
n=5
n=5
n=5
n=5
n=5
JUN/JUL
n=3
n=4
n=3
n=4
n=4
AUG/SEPT
n=3
n=5
n=5
n=4
n=5
OCT/NOV
0 1 2 3 4
0 1 2 3
Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe

Fig.IV.2. Number of Norway pout of each age-group caught per hour fishing at each site, pooling data at bimonthly intervals from January 1975 to January 1977.


Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe
NUMBER PER HOUR FISHING
4000
2000
0
1000
0
2000
0
2000
0
6000
4000
2000
0
6000
4000
2000
0
DEC/ JAN
FEB/ MAR
APR/ MAY
JUN/JUL
AUG/SEPT
OCT/NOV
0 1 2 3 4
0 1 2 3 4
0 1 2 3
0 1 2 3
0 1 2 3

been questionably identified and all of these were captured at offshore areas (Table IV.1).

IV.2.C. Occurrence of Pelagic Stages

Fig.IV.3 shows the seasonal variation in catches of Norway pout in the mid-water trawl at each site. No fish were caught at the shallow inshore site of the Firth of Lorne, and Loch Linnhe was not sampled in 1975. Catches were greater at the offshore sites of Ardalanish Bay and Tiree Passage. Fish were caught earlier in 1975 and were also somewhat smaller (Table IV.2). It appears that the pelagic nektonic phase does not last as long as in whiting.

IV.2.D. Occurrence of Demersal Stages

Fig.IV.4 shows the relative abundance of each brood of demersal Norway pout related to age. At Tiree Passage and Ardalanish Bay the first occurrence was followed by a rapid increase in abundance to a maximum in August and September. At Bloody Bay peak abundance did not occur until September or October and at the Firth of Lorne in December. This peak abundance was also somewhat lower than at the former three sites. At Loch Linnhe the increase in abundance was much slower and the maximum catch never approached that found at other sites. The rapid increase found at most sites in July and August was probably due to incomplete recruitment, fully representative samples not being caught until September or October. Since the increase in numbers was slower and occurred later inshore with lower catch rates, it seems likely that the fish were moving inwards from offshore areas.

The mean lengths of O-group and early 1-group fish caught by the mid-water and bottom trawls at each site are shown in Fig.IV.5 and Appendix IV.1 , for the 1975 and 1976 year-classes. Until December of the O-group fish inshore were always longer (and presumably older) than fish at Tiree Passage and Ardalanish Bay. This is also reflected in samples of fish large enough to plot length-frequency distributions (Fig.IV.8).

TABLE IV .1. OCCURRENCE OF *Trisopterus esmarkii* LARVAE IN ROUTINE PLANKTONIC SURVEYS WITH 2m. YOUNG FISH TRAWL FROM 1969 TO 1974. (Reproduced by permission of Dr. J.D.M. Gordon).

Trawl No.	Date	No.	Area	Notes
L/70/32	3/ 6/70	1	Treshnish Isles	Identification questionable
L/71/17	31/ 3/71	3	Opposite Loch Aline, Sound of Mull	''
1/71/22	20/ 4/71	1	Outside Loch Buie	''
L/72/40	13/ 4/72	3	Tobermory	''
L/72/43	8/ 5/72	3	Tobermory	''
L/73/31	28/3 /73	1	Tobermory	
L/73/33	28/ 3/73	2	N. Tiree Passage	
L/73/36	27/ 4/73	2	Off Campbeltown	Identification questionable
L/74/45	17/ 4/74	6	Bloody Bay	''
L/74/46	13/ 5/74	3	Opposite Loch Aline	*T.esmarkii*/*minutus*
L/74/48	13/ 5/74	4	Bloody Bay	
L/74/49	13/ 5/74	2	N. Tiree Passage	
L/74/51	14/ 5/74	1	Opposite Loch Spelve	
L/74/55	29/ 5/74	1	N. Tiree Passage	

Fig.IV.3. Catch rates (log. scale) of O-group Norway pout in the mid-water trawl at each site. No Norway pout were caught at the Firth of Lorne although hauls were made on each cruise.

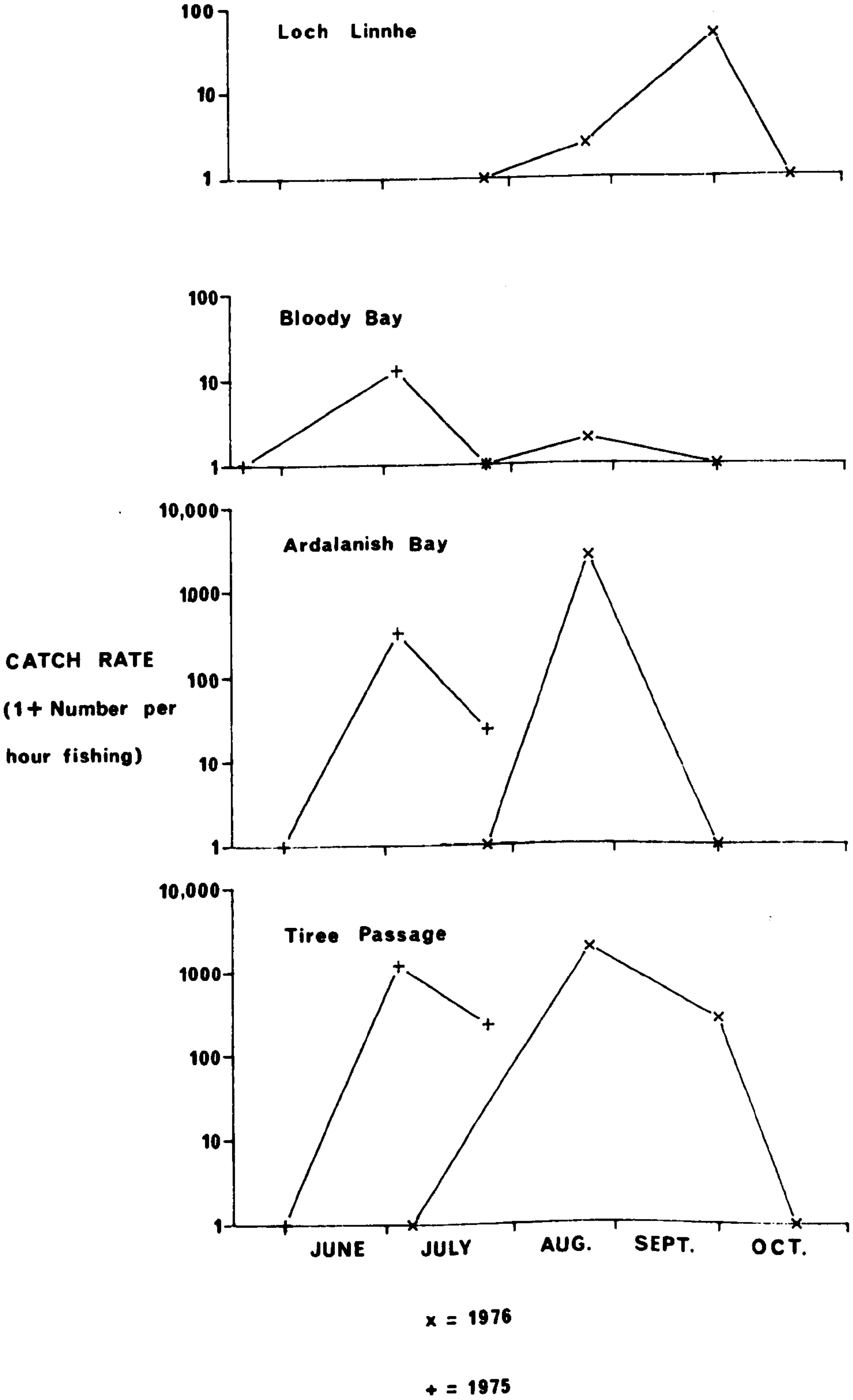

Loch Linnhe
100
10
1
Bloody Bay
100
10
1
Ardalanish Bay
10,000
1000
100
10
1
Tiree Passage
10,000
1000
100
10
1
CATCH RATE
(1+ Number per
hour fishing)
JUNE
JULY
AUG.
SEPT.
OCT.
x = 1976
+ = 1975

TABLE IV.2. MEAN TOTAL LENGTHS (cm) OF 0-GROUP NORWAY POUT CAUGHT BY THE MID-WATER TRAWL AT EACH SITE

Year	Week No.	Site	No.	Length Range cm.	Mean Length cm.	Standard Error
1975	26.5	Bloody Bay	8	5.5 - 7.3	6.46	0.23
		Ardalanish Bay	219	2.8 - 7.2	5.43	0.04
		Tiree Passage	788	4.4 - 7.8	6.08	0.02
	30.0	Bloody Bay	0			
		Ardalanish Bay	15	3.2 - 8.2	5.87	0.34
		Tiree Passage	151	4.4 - 8.4	6.67	0.05
1976	30.0	Loch Linnhe	8	4.8 - 6.1	5.26	0.22
	34.0	Loch Linnhe)	10	6.6 -8.9	8.11	0.20
		Ardalanish Bay)	260	4.8 - 9.8	7.95	0.04
		Tiree Passage)	801	5.7 - 9.6	7.29	0.02
	39.0	Loch Linnhe	4	8.0 -10.4	9.3	-
		Tiree Passage	415	6.0 -10.5	8.18	0.03

Fig.IV.4. Catch rates (log. scale) of each year-class of Norway pout in the bottom trawl at each site, against age.

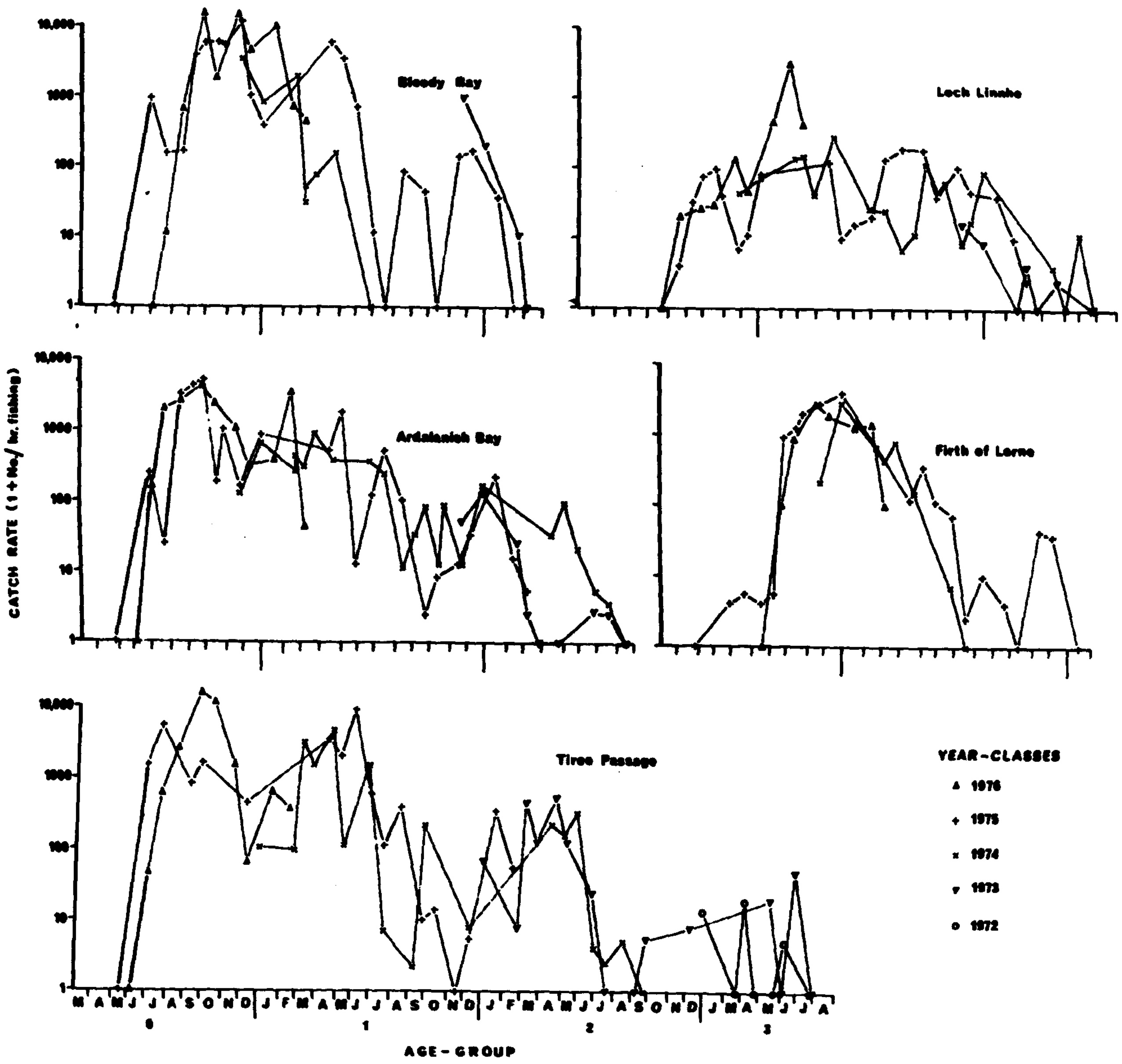
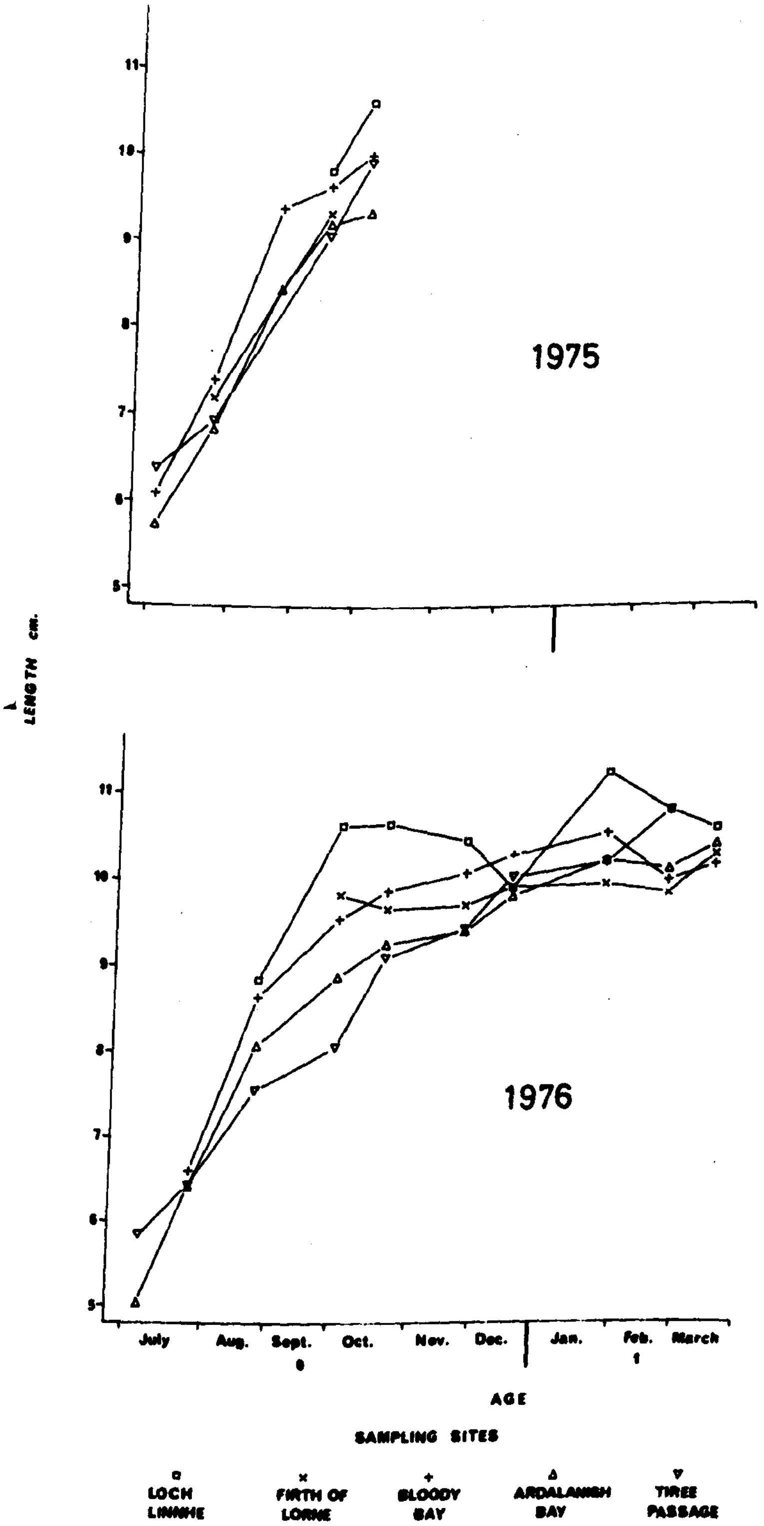
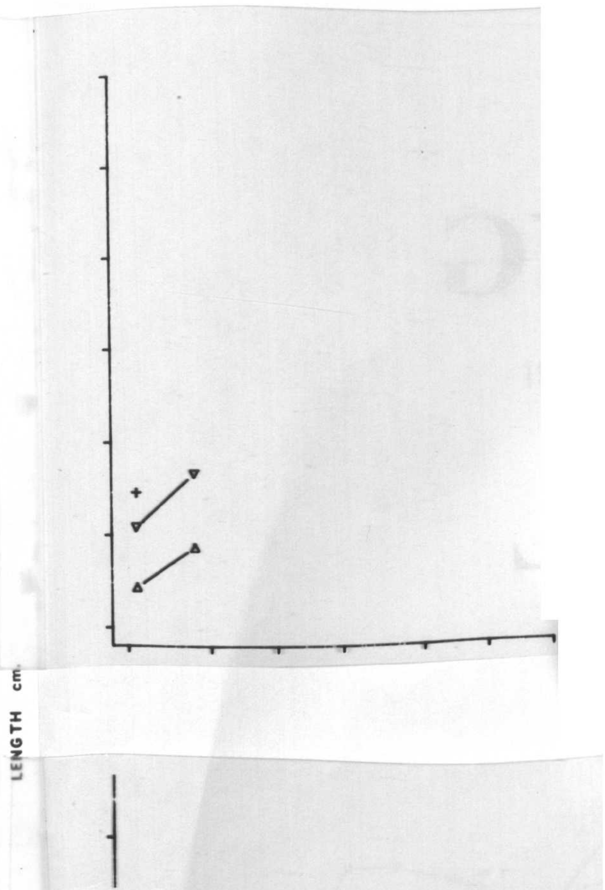

CATCH RATE (1 + No./ hr. fishing)
10,000
1000
100
10
1
Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
YEAR-CLASSES
▲ 1976
+ 1975
× 1974
▼ 1973
○ 1972
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J M A M J J A
0
1
2
3
AGE-GROUP

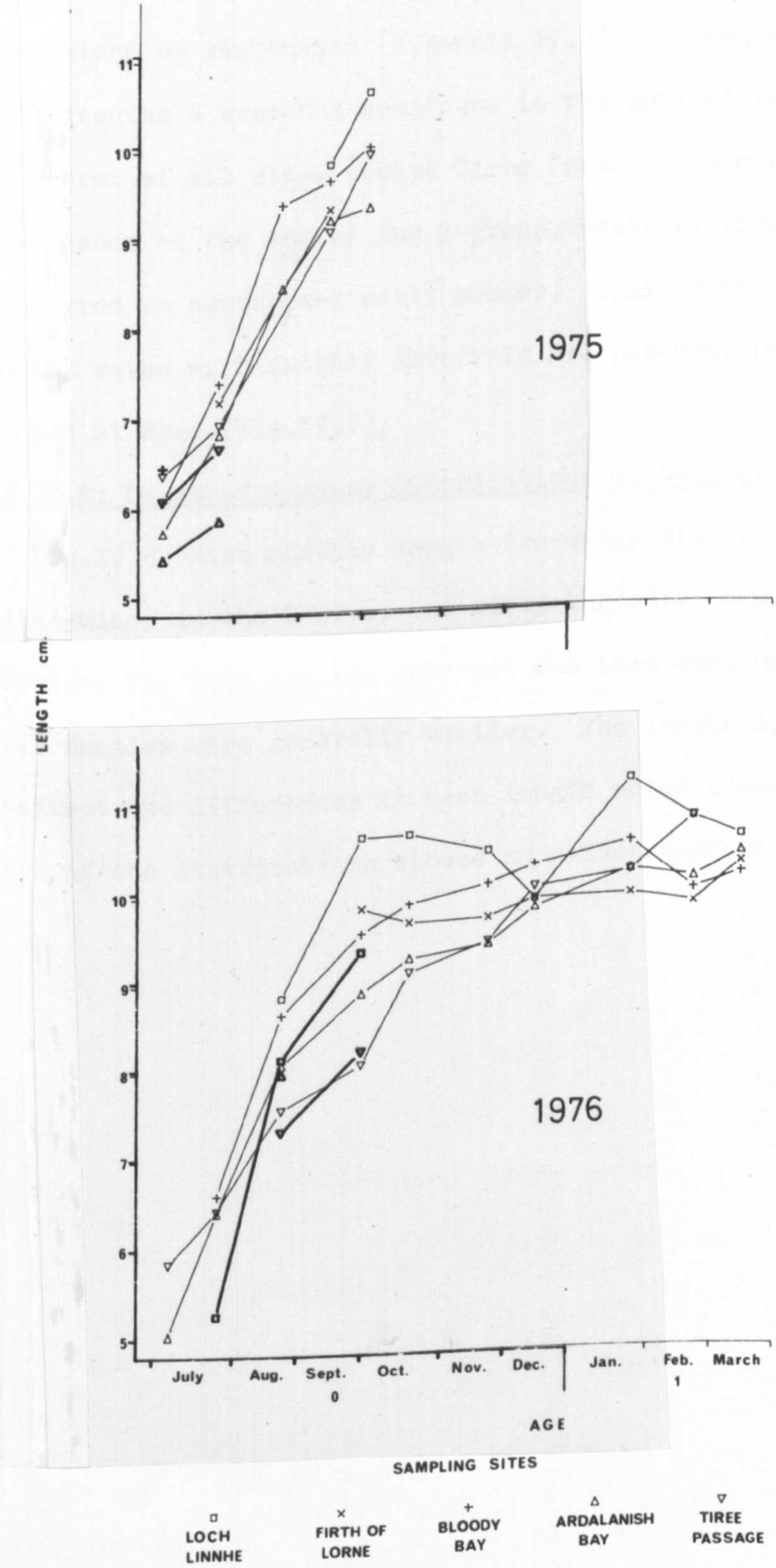
Fig.IV.5. Monthly mean total lengths (cm) of 0-group and early 1-group Norway pout caught by the bottom trawl and mid-water trawl (plastic covers)

A. in 1975

B. in 1976.


1975
1976
LENGTH cm.
11
10
9
8
7
6
5
July
Aug.
Sept.
0
Oct.
Nov.
Dec.
Jan.
Feb.
1
March
AGE
SAMPLING SITES
□ LOCH LINNHE
× FIRTH OF LORNE
+ BLOODY BAY
△ ARDALANISH BAY
▽ TIREE PASSAGE


LENGTH cm.


1975
1976
LENGTH cm.
11
10
9
8
7
6
5
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan.
Feb.
March
0
1
AGE
SAMPLING SITES
□ LOCH LINNHE
× FIRTH OF LORNE
+ BLOODY BAY
△ ARDALANISH BAY
▽ TIREE PASSAGE

Following the maximum at the end of the 0-group catch rates fell at all sites. Regression lines were calculated for the reduction in abundance with time from January of the 1-group (Fig.IV.6). In all cases a large and significant part of the variance of catch rates was explained by regression (Appendix IV.2). It was also possible to distinguish a seasonal component in the general trend of reduction in numbers: at all sites except Tiree Passage there was an increase in abundance at the end of the 1-group, while at Tiree Passage this occurred in spring and early summer. This is more obvious if the mean catch rates at bimonthly intervals are plotted, pooling results for all years studied (Fig.IV.7).

IV.2.E. Length-frequency Distributions of 0-group and Early 1-group Fish

Fig.IV.8 shows monthly length-frequency distributions of the 1976 year-class in the 0-group and early 1-group. Similar trends were obvious for 1975 but the data set was less complete due to bad weather, and samples were generally smaller. The length distributions obviously reflect the differences in mean length noted above. Probit transformation of the distributions showed no evidence of bimodality.

Fig.IV.6. Predictive regressions of the catch rate (log. scale) of Norway pout against age at each site, from December (week 50) in the O-group onwards.

Site	Regression
Loch Linnhe	$Y = 3.56 - 0.024X$
Firth of Lorne	$Y = 5.90 - 0.054X$
Bloody Bay	$Y = 4.73 - 0.034X$
Ardalanish Bay	$Y = 4.37 - 0.029X$
Tiree Passage	$Y = 4.00 - 0.021X$

($Y = \log_{10}$ 1 + number/h fishing
X = age in weeks)

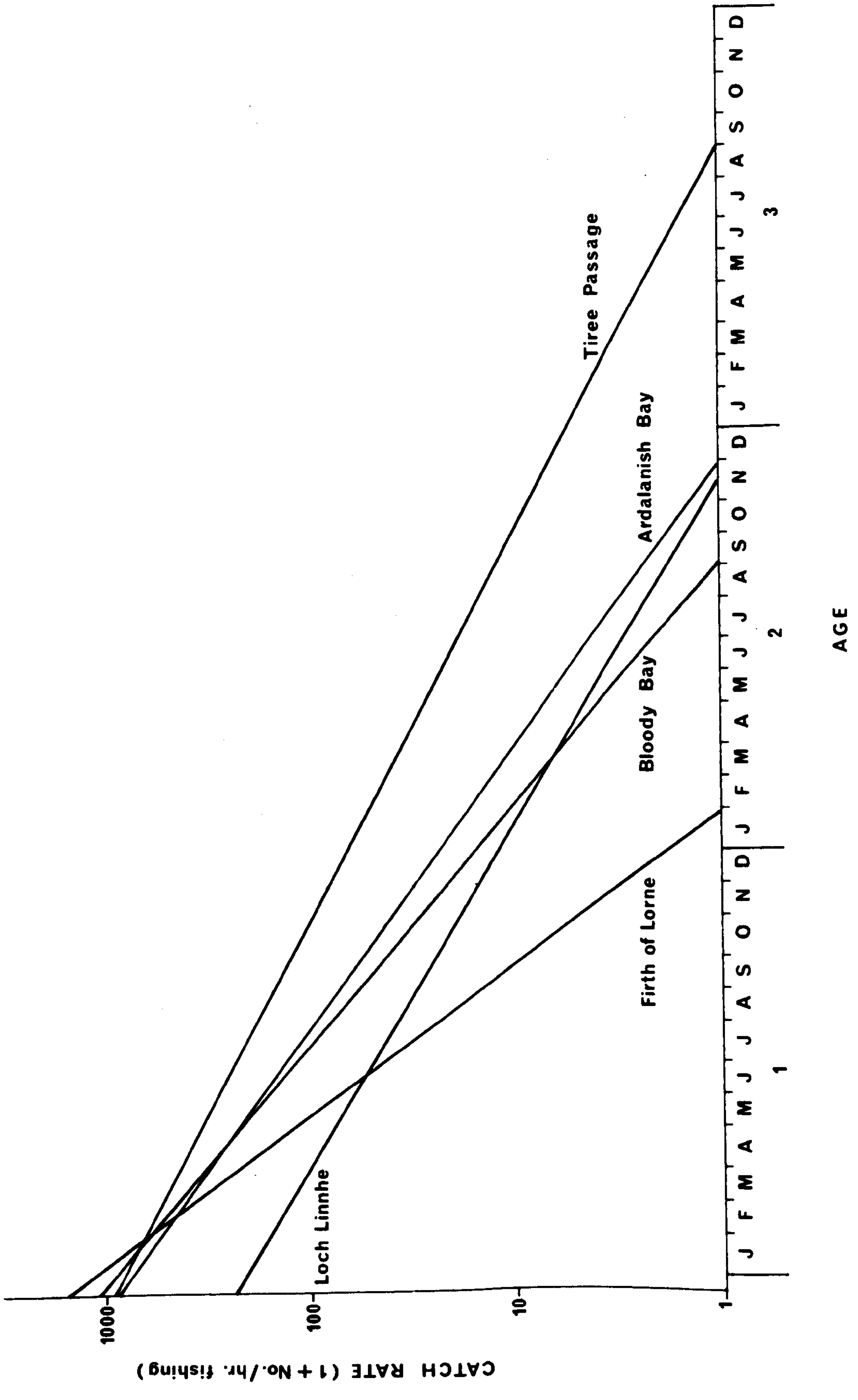

CATCH RATE (1 + No./hr. fishing)
1000
100
10
1
AGE
J F M A M J J A S O N D
1
2
3
Loch Linnhe
Firth of Lorne
Bloody Bay
Ardalanish Bay
Tiree Passage

Fig.IV.7. Catch curve for Norway pout in the bottom trawl pooling data from January 1975 to March 1977 at bimonthly intervals.

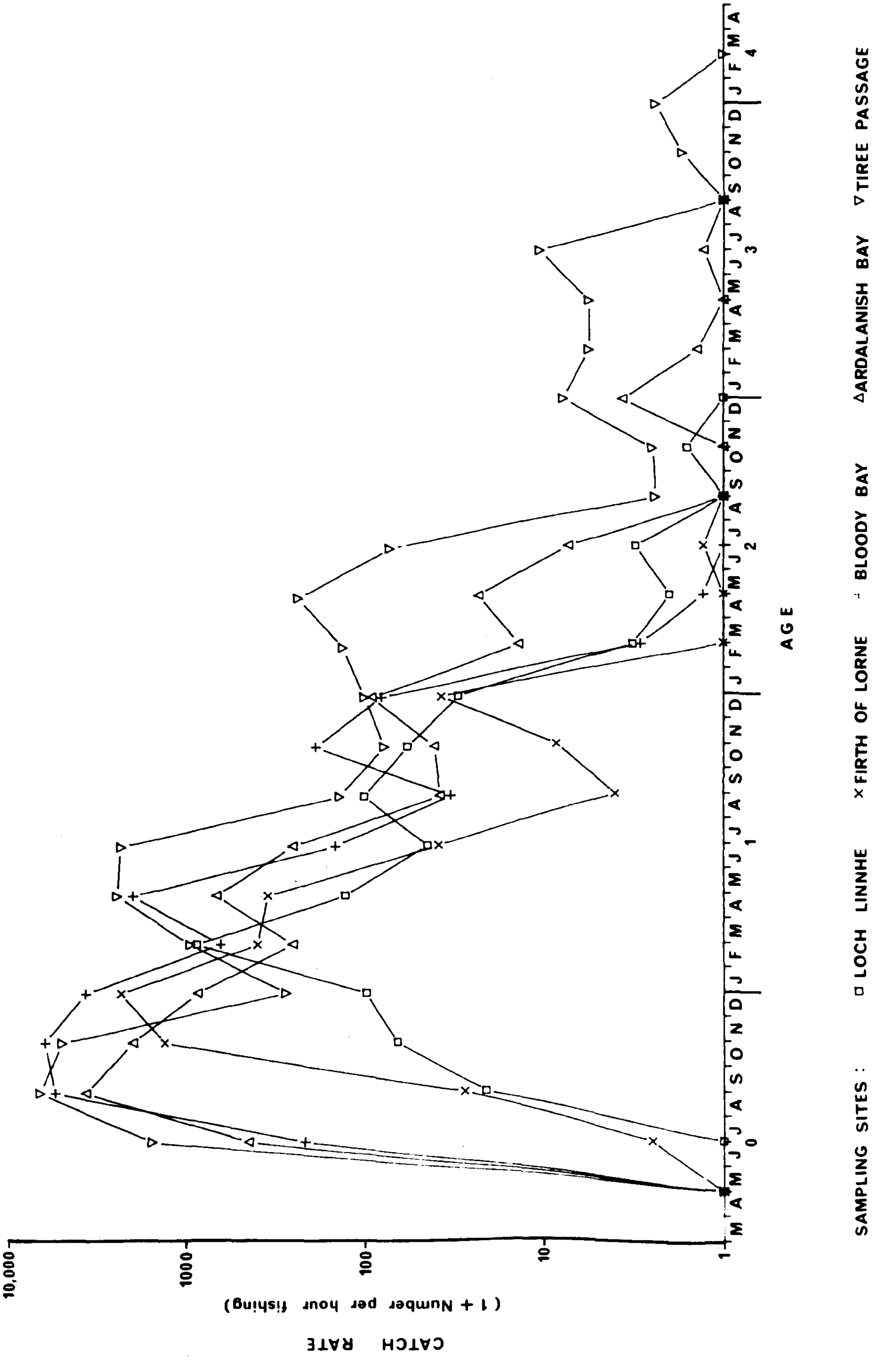
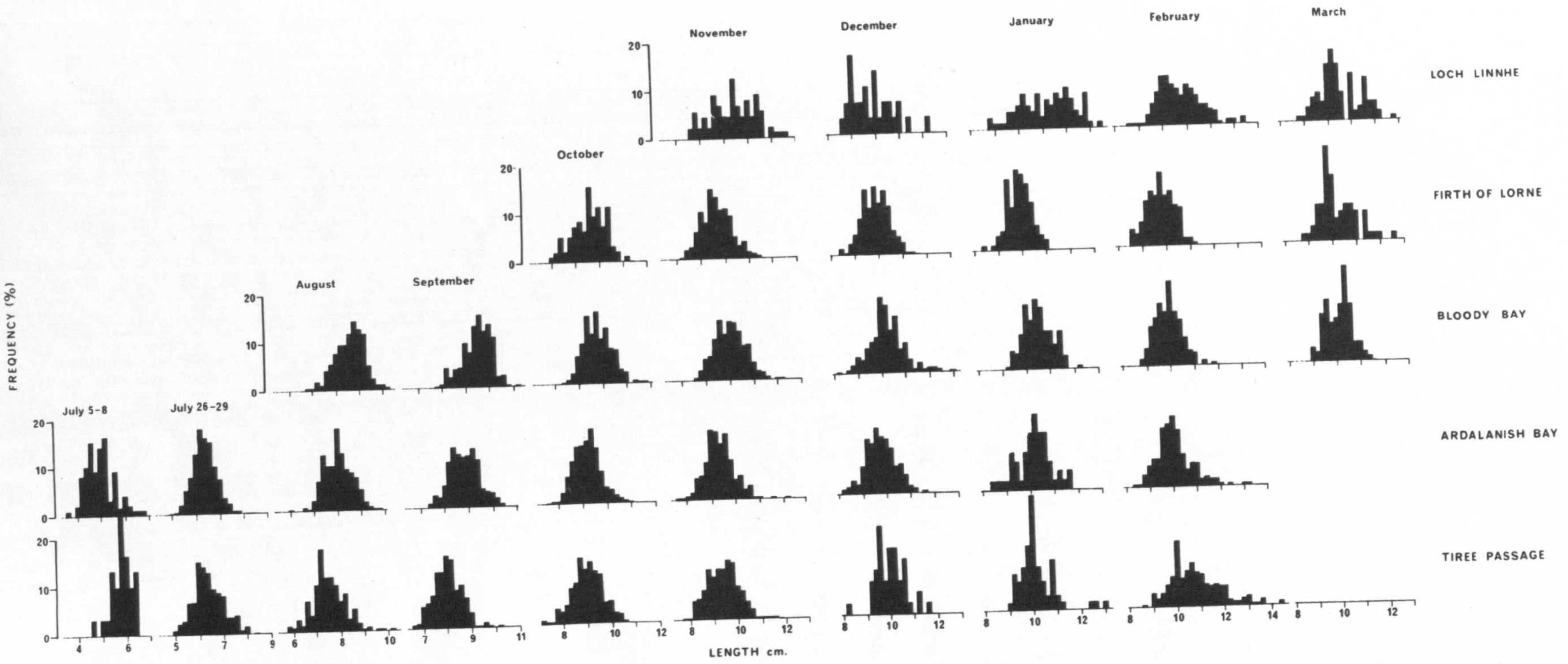
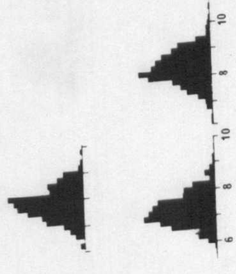
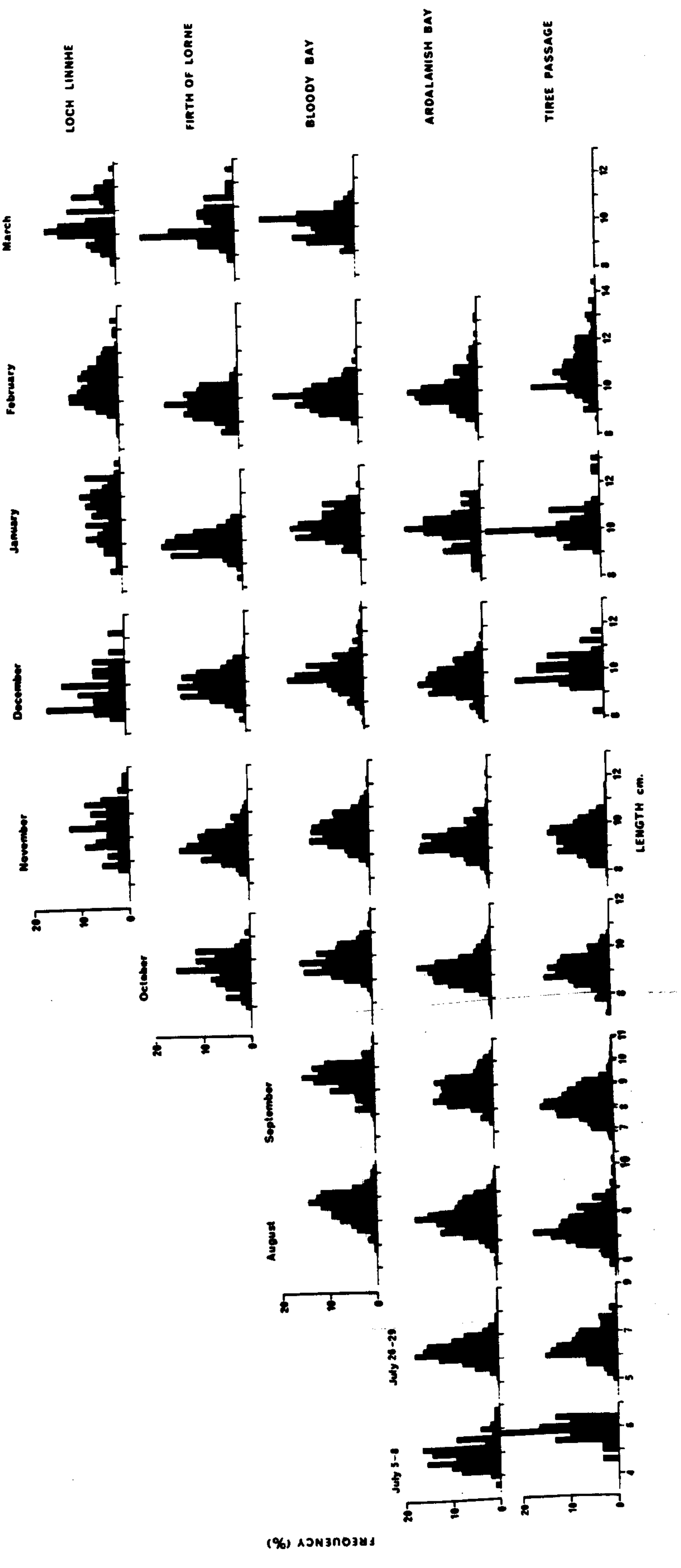

CATCH RATE
(1 + Number per hour fishing)
10,000
1000
100
10
1
M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
0
1
2
3
4
AGE
SAMPLING SITES :
□ LOCH LINNHE
× FIRTH OF LORNE
+ BLOODY BAY
△ ARDALANISH BAY
▽ TIREE PASSAGE

Fig.IV.8.A. Monthly length-frequency distributions of demersal 0-group and early 1-group Norway pout, 1976 year-class.

Fig.IV.8.B. (Plastic cover). Monthly length-frequency distributions of pelagic 0-group Norway pout at each site, 1976 year-class.


July 5-8
July 26-29
August
September
October
November
December
January
February
March
LOCH LINNHE
FIRTH OF LORNE
BLOODY BAY
ARDALANISH BAY
TIREE PASSAGE
FREQUENCY (%)
0
10
20
4
5
6
7
8
9
10
11
12
14
LENGTH cm.


6
8
10
8
10


LOCH LINNHE
FIRTH OF LORNE
BLOODY BAY
ARDALANISH BAY
TIREE PASSAGE
March
February
January
December
November
October
September
August
July 20-29
July 5-8
FREQUENCY (%)
LENGTH cm.
0
10
20

IV.2.F. Discussion

Seasonal variations in the age composition of Norway pout in inshore areas closely resemble figures given by Gordon (1977a), working in the same region from 1969 to 1973. Table IV.3 summarizes the available information on geographical variations in age composition (from Raitt, 1968a) and including data from Bailey and Hall (1971). Only the latter authors and Christensen (1964), cited in Raitt (1968a), gave figures for 0-group fish in autumn. In neither case was the 0-group as important as in the present study. This could be because of gear selection; in addition Poulsen (1966) showed that the abundance of 0-group fish decreased with increasing depth. All of the hauls in the present study were at depths of less than 100m and 0-group fish were much less abundant at Loch Linnhe (depth 90m) than at the Firth of Lorne (depth 47m). Abundance was always greater at offshore sites, however, despite the depth so both factors obviously affect density. Raitt (1963), cited in Raitt (1968a), noted the varying proportions of 1- and 2-group fish in the North Sea, with the 1-group usually the stronger. This is obvious for most areas (from the table). In this study the 2-group was important only at Tiree Passage. This is in contrast to results found by Bailey and Hall (1971) for the west coast of Scotland, where the 2-group was the strongest in spring and was tentatively associated with the lack of a fishery. Since 1973 a fishery for Norway pout in I.C.E.S. statistical area VIa has developed (Anon.,1978) mainly in the North Minch, which could account for the lower proportion of 2-group fish. In addition Raitt (1968b) pointed out the considerable variations in abundance of each brood and Poulsen (1966) showed that the abundance of both 1- and 2-group fish increased with depth. Both age groups were most abundant at depths greater than 200m, which were not sampled.

Gordon (1977a), who found very similar catch curves for demersal

TABLE IV.3. PERCENTAGE AGE COMPOSITION OF NORWAY POUT POPULATIONS.

Region	Time of samples	0	I	II	III	IV	V	Authority
S.W.Iceland	Mar. 1923-4	-	-	31	65	4	+	Saemundsson (1929)
S.W.Iceland	Apri/May 1924	-	-	62	26	12	-	Saemundsson (1929)
Skagerrak	No information	-	86	14	(II and over)			Poulsen (1964)
Skagerrak	Mar. 1961	-	74	23	3	-	-	Hannerz (1961)
North Sea	Feb. 1961	-	94	5	1	-	-	Hannerz (1961)
North Sea	Mar. 1960-63	-	73	25	1	+	-	Raitt (1963)
North Sea	Mar/Apr.1961	-	42	57	1	-	-	Christensen(1964)
North Sea	March 1962	-	100	-	-	-	-	Christensen(1964)
North Sea	June 1960-63	-	72	27	1	-	-	Raitt (1963)
North Sea	Sept/Dec.1961	46	40	14	+	-	-	Christensen(1964)
W.Coast Scotland	Spring 1960-65	-	36.8	51.3	6.4	5.5	-	Bailey&Hall (1971)*
	Autumn 1960-70	10.0	62.8	21.1	6.1	-	-	
Tiree Passage	Feb/Mar 1974-76	-	87.3	12.2	0.4	-	-	
	Oct/Nov 1974-77	98.4	1.5	-	-	-	-	
Ardalanish Bay	Feb/Mar 1974-76	-	95.0	4.9	-	-	-	Present
	Oct/Nov 1974-76	98.0	2.0	-	-	-	-	
Bloody Bay	Feb/Mar 1974-76	-	99.7	0.3	-	-	-	study
	Oct/Nov 1974-76	97.0	2.9	-	-	-	-	
Firth of Lorne	Feb/Mar 1974-76	-	100.0	-	-	-	-	
	Oct/Nov 1974-76	99.4	0.6	-	-	-	-	
Loch Linnhe	Feb/Mar 1974-76	-	99.7	0.3	-	-	-	
	Oct/Nov 1974-76	53.0	46.5	0.5	-	-	-	

* Calculated from Geometric Mean catches

fish at Loch Linnhe and the Firth of Lorne, inferred that the population was derived from spawning grounds in the open sea. In the present study spawning did not occur in the Tiree Passage area (see section IV.4) in spite of the presence of 2- and 3-group fish. The low catch rates of larvae and post-larvae indicated that most fish arrived after the planktonic stage in March and April, slightly later than the peak abundance in the North Sea (Russell, 1976 - quoting the work of Ehrenbaum) and earlier than off the north-west coast of Norway (Baranenkova and Kokhlina, 1968). Fish were caught by the mid-water trawl on only a small number of occasions, usually at lengths between 4 and 10 cm. Norway pout of the same size were caught much more often in the bottom trawl. It would appear that migration into the area occurred towards the end of the pelagic nektonic stage and at the beginning of the demersal stage. Bailey (1975) found fish of this size performing extensive diurnal vertical migrations in August, moving off the bottom at night. In the present work this behaviour did not seem to be determined simply by size: in 1975 the fish were caught in the mid-water trawl earlier than in 1976 and were also smaller. A more concentrated survey over a wider area is required to determine the factors affecting the size and season of migration off the bottom.

Raitt (1965) found Norway pout from the west coast of Scotland heavily infected with Myxobolus aeglefini, a myxosporidian parasite of the eye, whereas in northern North Sea populations it was almost totally absent. He concluded from this and from evidence of larval concentrations that North Sea stocks were distinct from those of the west and north-west Scottish coasts. Smith (1972) found similar infection patterns with Diclidophora esmarkii, but considered that the evidence did not preclude a movement of Norway pout from the northern North Sea westwards. Bailey and Hall (1971) found no correlations of year-class strengths of fish from the North Sea and Scottish west coast and clear differences in apparent mortality rates. They pointed out, however, that the latter evidence could be affected by the lack of a fishery on the west coast and also by the possible westward migration of adults. Gokhale (1953) has suggested that the Irish Sea stock is derived from the north coast of Ireland or west coast of Scotland. Little is known concerning the separation of west coast stocks of Norway pout.

IV. 3. GROWTH

IV.3.A. Length-frequency Distribution

Monthly length-frequency distributions of Norway pout populations at each site are shown in Fig. IV.9, with 1975 and 1976 data plotted separately. At the deeper sites two normally distinct modes were evident at most times of the year, representing the youngest age-group (either 0- or 1-) and the older age-groups combined. The relative importance of the two modes varied seasonally and annually. At the shallower sites the mode representing older fish was only occasionally seen and was always much smaller than that representing the youngest age-group.

IV.3.B. Growth in Length

The mean length of each age-group in populations sampled by the bottom trawl on each cruise is shown in Fig.IV.10. When data were pooled from all sites sufficient fish were available to plot growth into the 3-group. Growth was seasonal, occurring mainly between May and October. It is possible that mean lengths of 0-group fish were biased due to mesh selection (see section 1.3.A). Winter increases in length were between 1 and 1.5 cm while summer increases were 3-4.6 cm.

Differences in the growth pattern were obvious between sites. Comparing the Firth of Lorne and Loch Linnhe (as inshore shallow and deep sites) fish at the latter site were 1 cm larger at the end of the 0-group. This difference was maintained until fish left the Firth of Lorne. At Bloody Bay and Ardalanish Bay the growth curve was intermediate between Loch Linnhe and the Firth of Lorne. The growth curve at Tiree Passage was similar until the 1-group in autumn, when mean lengths were greater than at other sites.

The lengths of different year-classes at various ages differed. In Fig.IV.10 the 1976 year-class at Bloody Bay, Ardalanish Bay and Tiree Passage was consistently smaller than the 1975 year-class in the 0-

Fig.IV.9. Monthly length distributions of Norway pout populations at each site in 1975 and 1976.

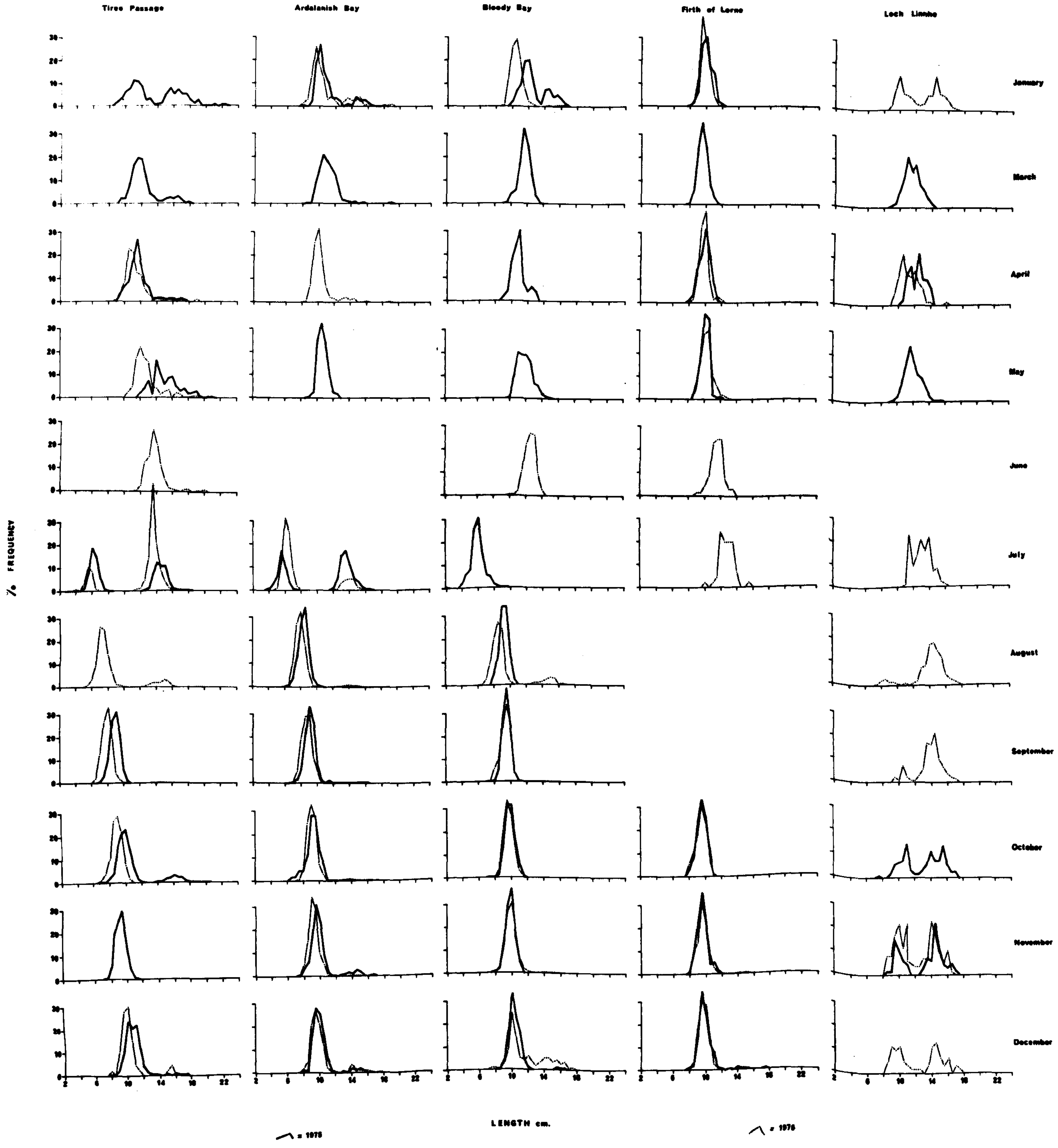
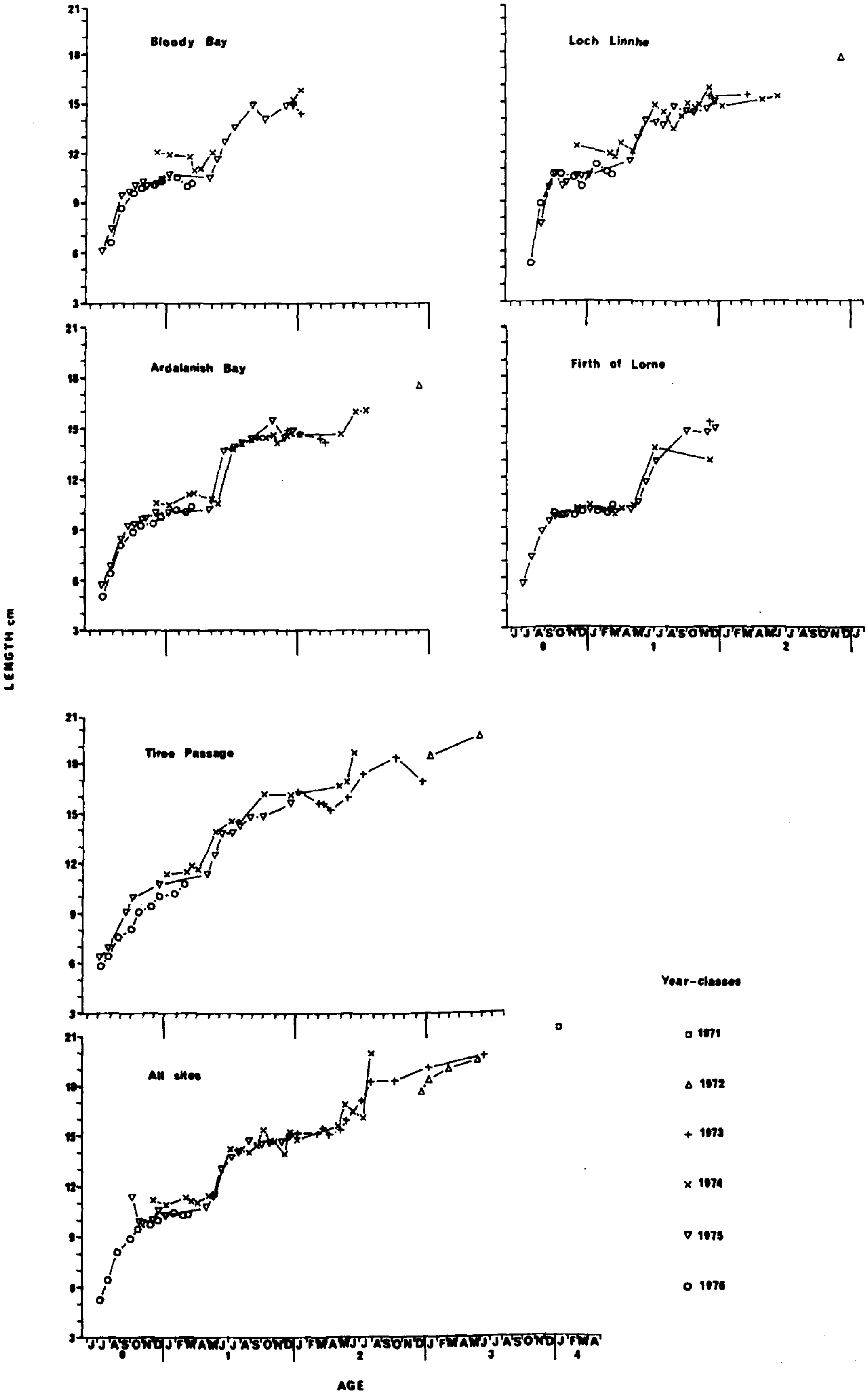

Tiree Passage
Ardalanish Bay
Bloody Bay
Firth of Lorne
Loch Linnhe
January
March
April
May
June
July
August
September
October
November
December
% FREQUENCY
0
10
20
30
2
6
10
14
18
22
LENGTH cm.
= 1975
= 1976

Fig.IV.10. Seasonal growth in total length (cm) of each year-class of Norway pout at each site and pooling fish from all sites, sexes combined.


LENGTH cm
21
18
15
12
9
6
3
Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
All sites
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 S O N D J
0
1
2
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 S O N D J F M A M J J A S O N D J F M A
0
1
2
3
4
AGE
Year-classes
□ 1971
△ 1972
+ 1973
× 1974
▽ 1975
○ 1976

group. In winter at the end of the 0-group the 1974 year-class was larger than either the 1975 or 1976 year-classes. Differences between year-classes were not so obvious inshore or following the growth period in the 1-group.

Fig.IV.11 shows the growth in length of Norway pout of each sex, pooling data from all sites. For fish less than about 10 cm (before October in the 0-group) it was not possible to sex the fish. This undoubtedly caused bias until January in the 1-group, when development of the gonads occurs even in fish which do not spawn (see section V). There were differences in mean length of about 1 cm between September in the 1-group and May in the 2-group, with females larger.

IV.3.C. Growth in Weight

Fig.IV.12 shows mean weights of each year-class at age on each cruise. Variations between samples were large in older fish, in part due to low sample sizes when data from all sites were pooled. Growth in weight was also seasonal, occurring more rapidly between May and July than at any other time of the year. From November in the 1-group to May in the 2-group there was a weight loss of about 5 g, the minimum occurring in March and April. In younger fish in the same months there was a slight weight loss but it was less marked. This is to be expected if weight loss is related directly to size. Variations between samples in older fish were too large to show winter weight losses.

At Tiree Passage and Ardalanish Bay the seasonal timing of growth in weight was similar to the pooled data, although there was no reduction in growth rate at Tiree Passage in summer in the 1-group and weight increased until October. The mean weight was then about 7 g greater than at other sites. This difference was not maintained: the mean weight of 2-group fish in spring was 15-17 g at both Ardalanish Bay and Tiree Passage. There were insufficient 2-group fish to calculate mean weights at other sites. The timing of growth and mean weights

Fig.IV.11. Seasonal growth in total length (cm) of male and female Norway pout, pooling fish from all sites.

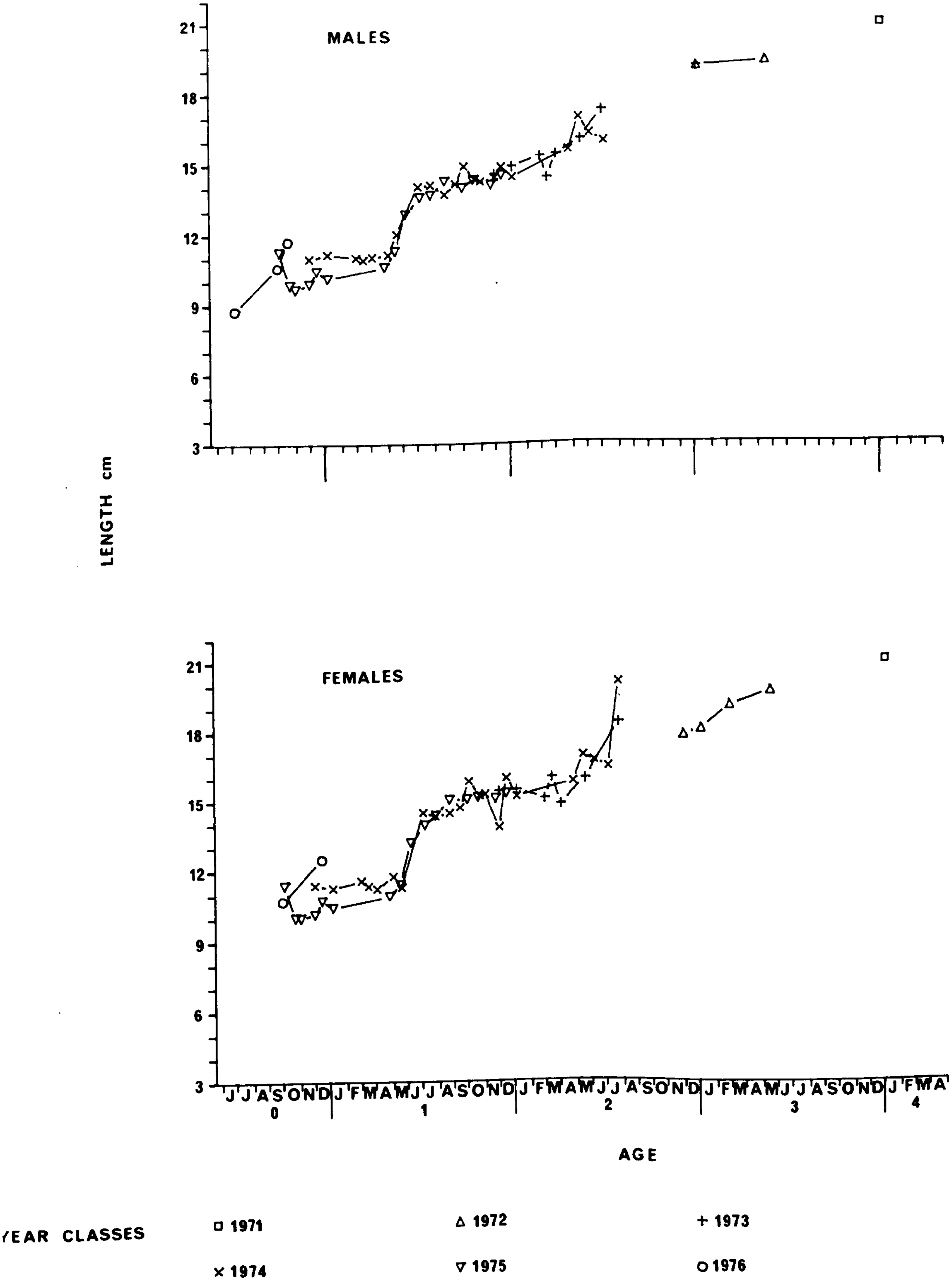
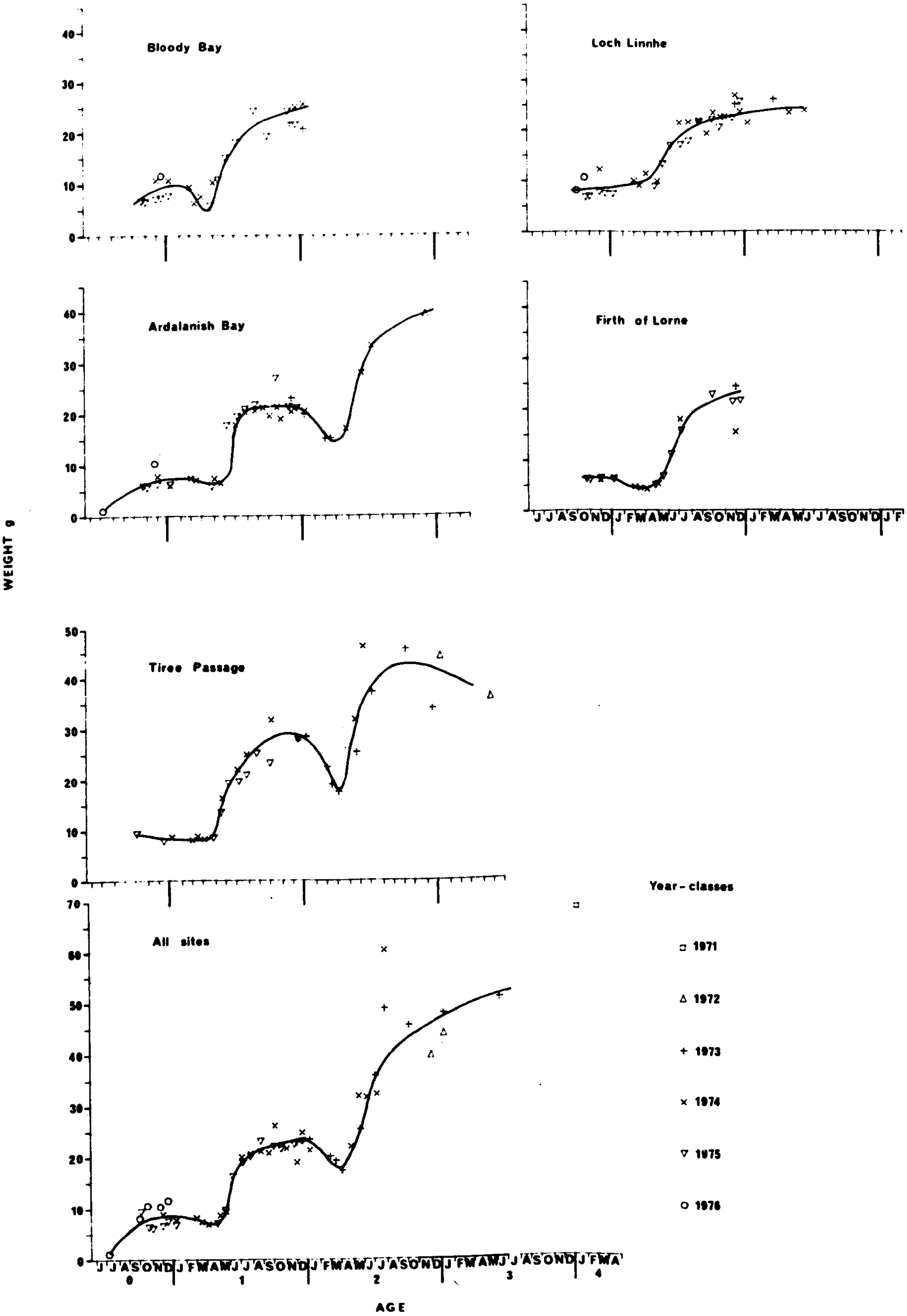

MALES
FEMALES
LENGTH cm
21
18
15
12
9
6
3
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
0
1
2
3
4
AGE
EAR CLASSES
□ 1971
△ 1972
+ 1973
× 1974
▽ 1975
○ 1976

Fig.IV.12. Seasonal growth in gutted weight (g) of Norway pout at each site and all sites combined. Curves fitted by eye.


Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
All sites
WEIGHT g
0
10
20
30
40
50
60
70
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 S O N D J F M A M J J A S O N D J F M A
0
1
2
3
4
AGE
Year-classes
□ 1971
△ 1972
+ 1973
× 1974
▽ 1975
○ 1976

of 0-group and 1-group fish were similar to pooled data. It appears that there was a greater weight loss at the shallower sites of Bloody Bay and the Firth of Lorne in spring of the 1-group.

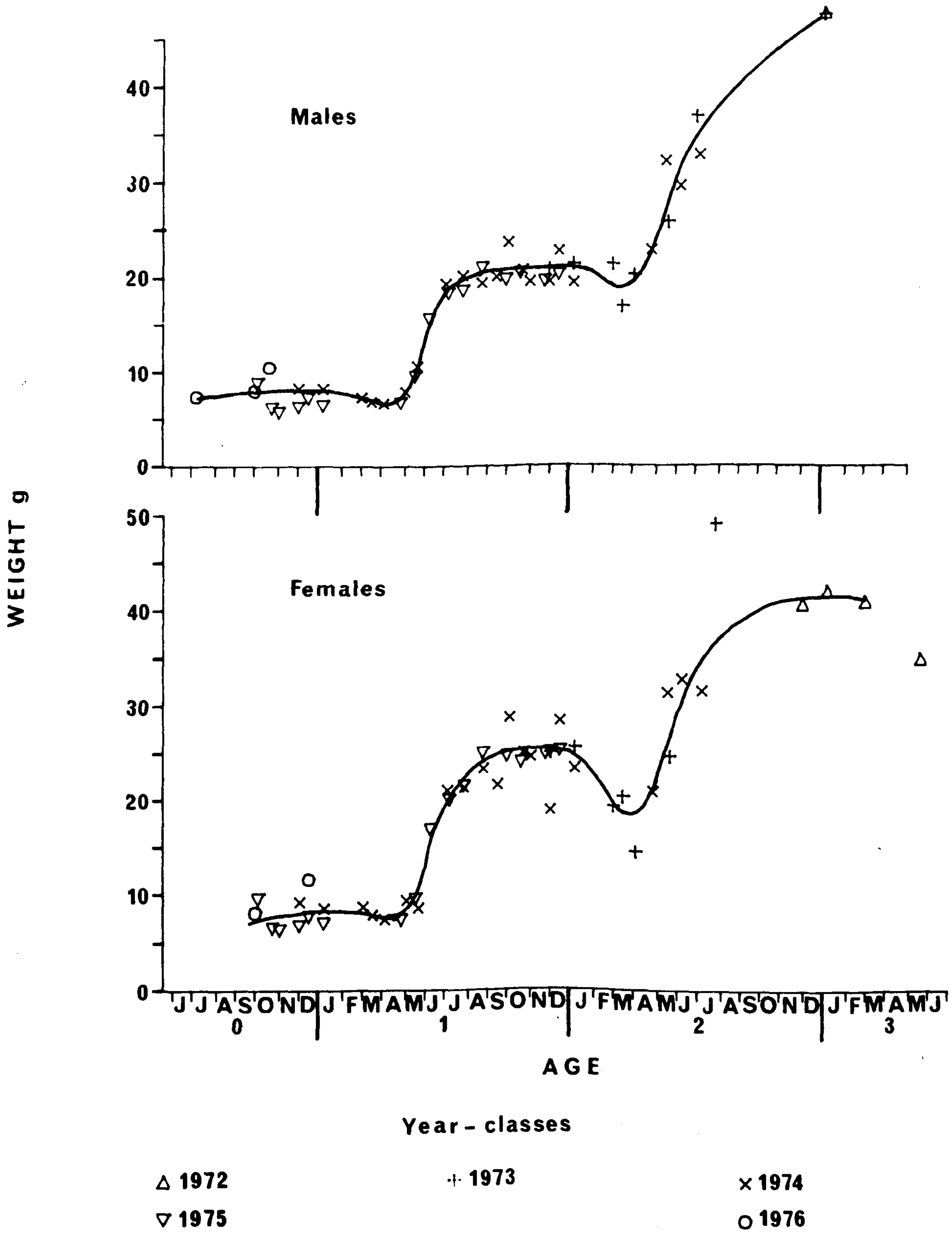
Fig.IV.13 shows the growth in weight of males and females, pooling data from all sites. Bias may again be caused by difficulties in sexing small fish. Sexual differences in weight were similar to differences in length, with females larger between September in the 1-group and May in the 2-group.

IV.3.D. Discussion

The bimodal length-frequency distributions found at the deeper sites are similar to figures given by Raitt(1968b). The shorter mode represents 1-group fish (sampled in March-April by Raitt) and the longer mode older fish. Gokhale(1953) found bimodal size-compositions only rarely in the Irish Sea. Raitt(1968a) also found varying proportions of 1-group and older fish in the North Sea, with the 1-group usually stronger. Modal lengths are inconsistent (Raitt,1968a) and in the present study lay within the range found by earlier authors (Raitt, loc. cit. for summary). Raitt(1966) showed that in the North Sea there was an inverse correlation of length of 1-group fish with abundance, suggesting that growth was density-dependent. The length-range of fish agrees with figures given by most authorities working at similar latitudes ; Saemundsson(1929) found fish up to 24 cm at Iceland and Baranenkova and Khoklina(1966) found fish of 35 cm off the north-west coast of Norway. The absence of the mode representing fish of the 2-group and over at the Firth of Lorne is related to the seasonal migrations discussed in section IV.2.

The seasonal growth in length of Norway pout has been studied by Poulsen(1966) and Ursin(1963) in the Skagerrak, Gokhale(1953) in the Irish Sea and Gordon(1977a) in the inshore waters of the west coast of Scotland. All authors found reduced growth rates in winter and

Fig IV.13. Seasonal growth in gutted weight (g) of male and female Norway pout, pooling fish from all sites. Curves fitted by eye.


Males
Females
WEIGHT g
0
10
20
30
40
50
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 S O N D J F M A M J
0
1
2
3
AGE
Year - classes
△ 1972
+ 1973
× 1974
▽ 1975
○ 1976

spring, with maximum growth after May. Ursin (1963) showed that growth rate depended particularly on day length, since light intensity may be insufficient for feeding at certain times of the year. Gordon (1977a) found that the intensity of feeding varied seasonally, being lower in winter, with some evidence of feeding during the hours of darkness. Poulsen (1966) noted a winter decrease in length from March in the 1-group to September in the 2-group, and concluded that this was either due to the fishery or to a gradual emigration of larger individuals. Ursin (1963) also found length reductions in winter and thought that it may be due to seasonal variation in the state of preservation of the samples. Winter length decreases have not been observed in this study, nor by Gordon (1977a) working in inshore areas in the same region.

Differences in mean length between year-classes at the same age were observed in the present study and also by Gordon (loc.cit.). Raitt (1968b) found that differences in length between year-classes were made before reaching one year of age and were maintained throughout life. In the present study there was little difference between year-classes after the 1-group. This could be due to lower sample sizes, although Ursin (1963) made the same observation with fish in the Skagerrak. This was explained by consideration of the von Bertalanffy growth equation :

$$\frac{dl}{dt} = E-Kl$$

(where E = coefficient of growth anabolism
K = coefficient of growth catabolism
l = length
t = time)

For small fish $E>Kl$ and growth continues in winter whereas in larger fish $Kl>E$. Raitt's (1968b) observation of an inverse correlation of mean length of 1-group fish with abundance of year-classes has already been mentioned.

Differences in growth curves at different sites were also found by Gordon(1977a), who related them to depth. Ursin(1963) assumed a linear regression of percentage length increase upon percentage depth increase. Seasonal migrations of Norway pout in relation to depth have been discussed in section IV.2. Similar differences in length between sexes have also been noted by Gokhale(1953) and Saemundsson(1929), with females always larger.

It appears that only Ursin(1963) has studied weight variations of broods of Norway pout. The weights reached at different ages in the Skagerrak are of the same order as on the west coast of Scotland. Differences in curves of growth in weight between sites and sexes essentially follow length differences.

IV. 4. REPRODUCTION

IV.4.A. Classification of Gonad Condition

Gokhale's (1957) classification was used to assign arbitrary stages to each fish measured and weighed.

IV.4.B. Length at Maturity

It appears that fish leave the area to spawn (section IV.5.F), a small number of spent fish returning. Estimations of the length and age of maturity could be biased if the timing of the migration is linked with maturation or growth.

Males

Fig.IV.14 shows the maturation ogive for male Norway pout. The differences in mean length of fish of stage II and over, and fish of stage III and over could be due to a large number of fish developing to stage II without further maturation ; or could be related to the migration of maturing fish out of the area. The mean length of first maturity was between 13.4 and 16.2 cm.

Females

As with males large differences in mean length are obvious between fish in stage II and over and fish of stage III and over, probably for the same reasons. Females matured at slightly larger sizes (between 14.3 and 16.6 cm).

IV.4.C. Age at Maturity

Table IV.4 shows that 85.7% of the males and 92.6% of the females in the 1-group were in stage 1 during the spawning period. Comparable figures for the 2-group were 5.88% and 12.61% respectively. The more mature fish may have undergone a spawning migration out of the area (section IV.4.F). It seems likely that a small proportion of 1-group and most 2-group fish matured.

Fig.IV.14. Maturation ogives for male and female Norway pout. Percentage of fish reaching each maturity stage in each centimetre length group.

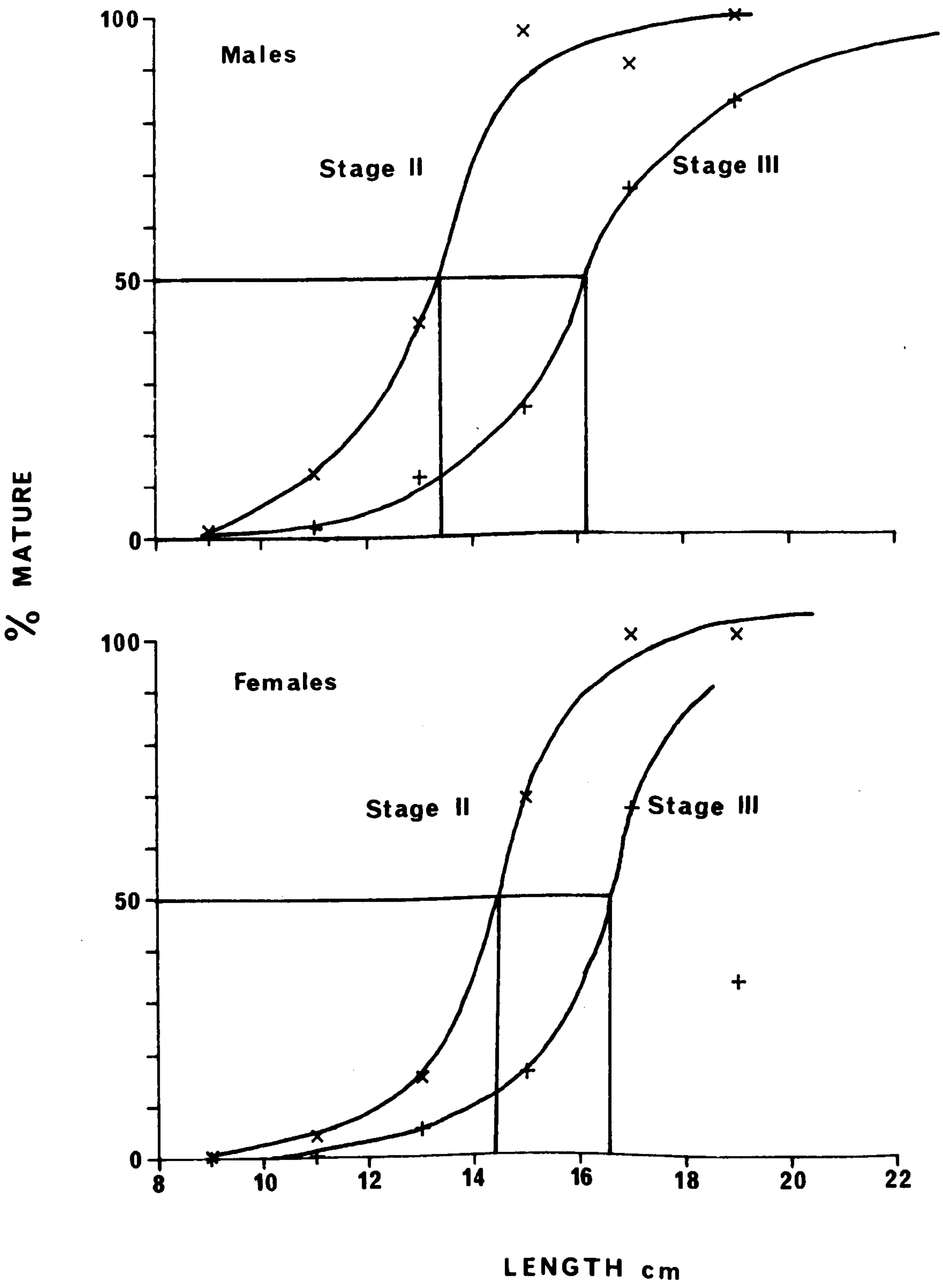

% MATURE
Males
Stage II
Stage III
Females
Stage II
Stage III
100
50
0
100
50
0
8
10
12
14
16
18
20
22
LENGTH cm

TABLE IV.4. PERCENTAGE OF MALE AND FEMALE NORWAY POUT OF EACH AGE-GROUP IN EACH MATURITY STAGE AT ARDALANISH BAY AND TIREE PASSAGE BETWEEN JANUARY AND MAY IN 1975 AND 1976.

Sex	Age	Maturity stage							
		1	II	III	IV	V	VI	VII	n
Males	1	85.71	11.03	3.00	0.23	0	-	0.04	2149
	2	5.88	63.72	14.71	10.78	0	-	4.90	102
	3	0	0	50.0	25.0	0	-	25.0	4
Females	1	92.96	5.25	1.59	0.81	0.04	-	0.08	2456
	2	12.61	56.76	9.01	18.02	0.90	-	2.70	111
	3	0	0	0	100	0	-	0	2

IV.4.D. Sex-ratio

Seasonal variations in sex-ratio at each site are shown in Fig.IV.15 and Appendix IV.3. Over the whole period of study the sex-ratio was 1:1.0854 (males:females). A standard significance test showed that the chance of this ratio occurring in a population in which the sexes were equally distributed was less than 0.001 i.e. a highly significant (d=4.3) departure from a 1:1 ratio. A chi-square test showed that the sexes were unequally distributed among ages (Table IV.5). When each age-group was examined separately only the O-group did not show significant departures from a 1:1 ratio, although many O-group fish could not be sexed.

Table IV.6 shows the sex-ratio of fish between December of the O-group and December of the 1-group, the period when Norway pout were caught in appreciable numbers at all sites. A chi-square test showed that there was highly significant heterogeneity of sex-ratio between sites. Overall there were fewer males than females (47.8%) and this figure was significantly different from 50%. Only at Ardalanish Bay was there no significant departure from a 1:1 ratio. At Tiree Passage there were more males than females, while at the other three sites there were fewer.

IV.4.E. Breeding Cycle and Seasonality of Spawning

Monthly variations in the proportions of fish of each sex in each maturity stage are shown in Fig.IV.16, pooling data from November 1974 to March 1977. A small proportion of 1-group male fish matured to stage III and IV in March. Most 1-group fish matured from stage 1 in autumn/winter, the proportion of stage II fish reaching a maximum in January. Stage III fish first occurred in November, reaching a maximum in March with few fish being caught in this stage after April. Maturity stage IV did not appear to last as long as stage III, possibly because of a spawning migration or because late developers failed to spawn. A small number of stage V and VII fish were found between February and April but

Fig.IV.15. Variations in the sex ratio (% male fish) of Norway pout with age at each site and pooling data from all sites. Fish of indeterminate sex (mainly O-group) not included.

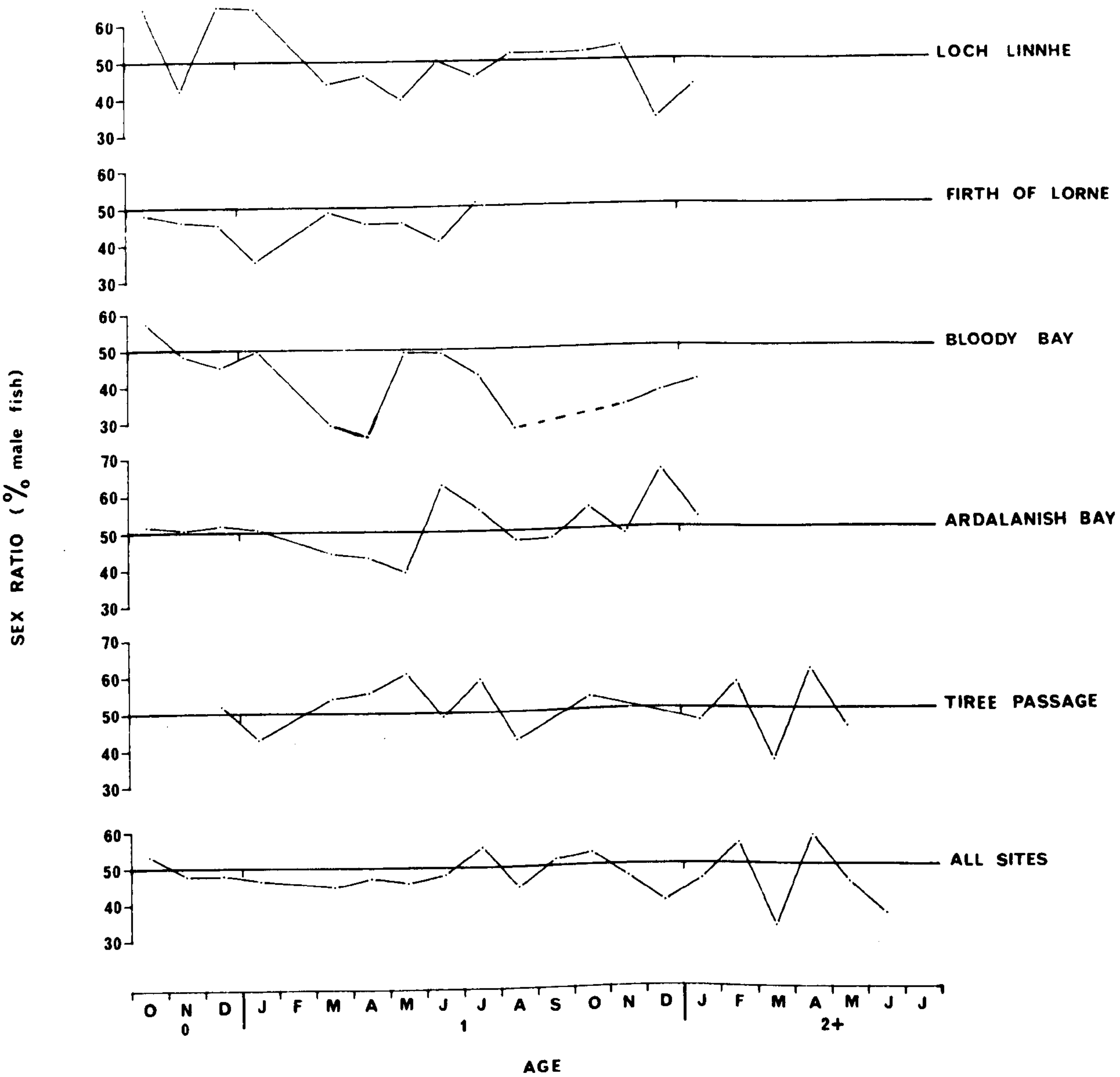

SEX RATIO (% male fish)
LOCH LINNHE
FIRTH OF LORNE
BLOODY BAY
ARDALANISH BAY
TIREE PASSAGE
ALL SITES
30
40
50
60
70
O N D J F M A M J J A S O N D J F M A M J J
0
1
2+
AGE

TABLE IV.5. CHI-SQUARE TEST FOR HETEROGENEITY OF SEX RATIO BETWEEN AGE-GROUPS. FISH FROM ALL SITES WERE COMBINED.

	Sex	Age			
		0	1	2	Total
n	Male	1225	3812	291	5328
	Female	1271	4165	347	5783
	Total	2496	7977	638	11111
%	Male	49.08	47.79	45.61	47.95
	Female	50.92	52.21	54.39	52.05
	d	0.9207	3.9523	2.2171	4.3165
	p	>0.10	<0.001	<0.05 > 0.01	<0.001

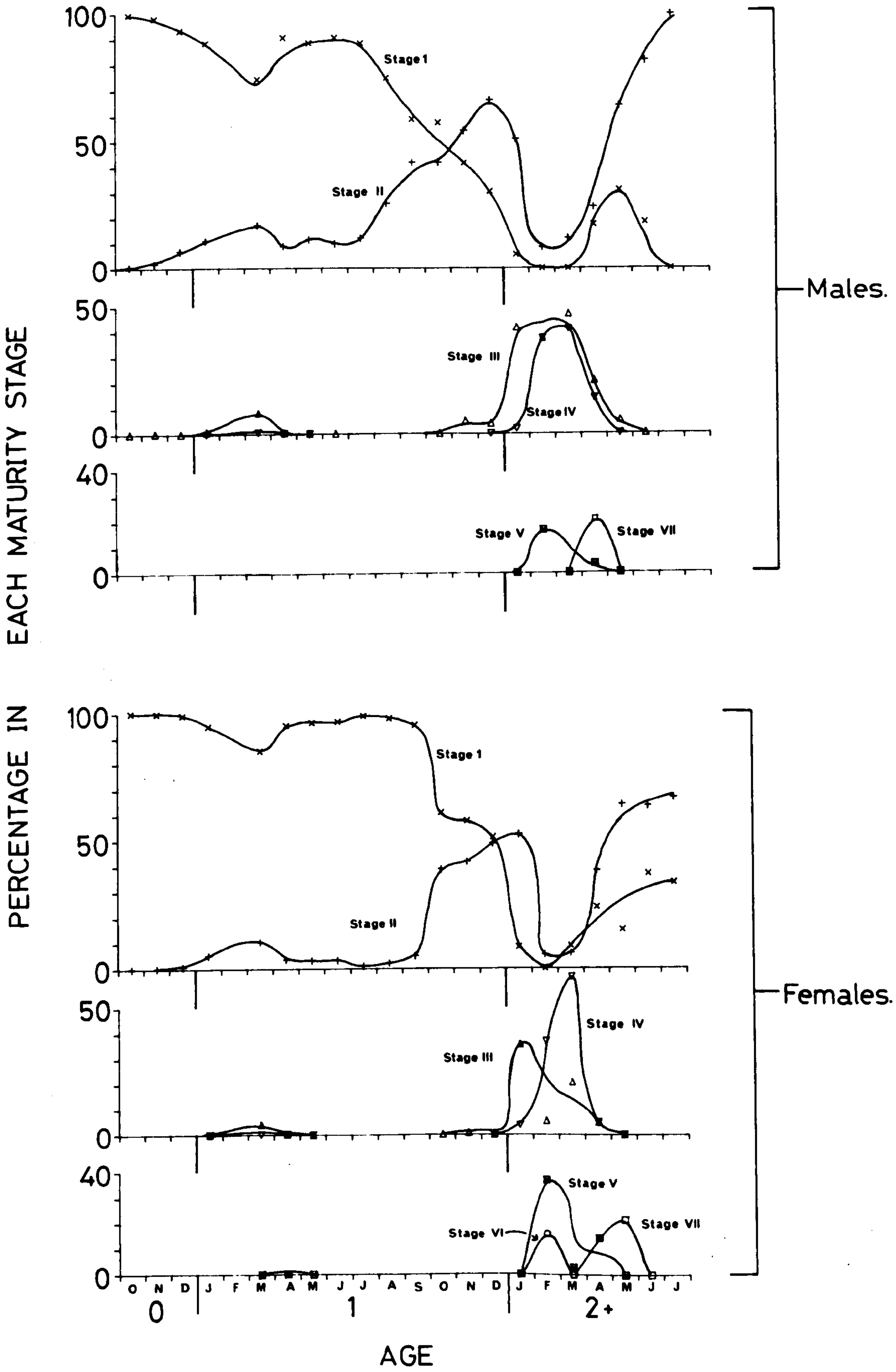
$\chi^2 = 17774229.6$, d. f. = 2 , $p<0.001$

TABLE IV.6. VARIATIONS IN SEX RATIO BETWEEN SITES (ONLY FISH CAUGHT BETWEEN DECEMBER OF THE O-GROUP AND DECEMBER OF THE 1-GROUP USED IN THE ANALYSIS).

	SITE					
SEX	Loch Linnhe	Firth of Lorne	Bloody Bay	Ardalanish Bay	Tiree Passage	All sites
Male	733	657	698	1091	1066	4245
Female	815	843	929	1158	891	4636
Total	1548	1500	1627	2249	1957	8881
d	2.084	4.802	5.727	1.413	3.956	4.149
p	<0.05 >0.02	<0.001	<0.001	>0.10	<0.001	<0.001
% male	47.35	43.80	42.90	48.51	54.47	47.80

$\chi^2 = 60.75$, d.f. = 4 , $p < 0.001$

Fig.IV.16. Seasonal change in the macroscopic appearance of the gonads of male and female Norway pout, pooling data from December 1974 to March 1977.


PERCENTAGE IN EACH MATURITY STAGE
100
50
0
Stage 1
Stage II
50
0
Stage III
Stage IV
40
0
Stage V
Stage VII
Males.
100
50
0
Stage 1
Stage II
50
0
Stage III
Stage IV
40
0
Stage V
Stage VI
Stage VII
Females.
O N D J F M A M J J A S O N D J F M A M J J
0
1
2+
AGE

no running-ripe fish.

The seasonal occurrence of female maturity stages was very similar to males. Stage IV was more leptokurtotic, however, and a small proportion of running-ripe fish were found in February.

IV.4.F. Location of Spawning

In 1975 and 1976 combined no males more mature than stage IV were caught, and only two stage V females. In 1977 five stage V males were caught at Ardalanish Bay and Tiree Passage between February and May, four of which were caught in February. Eleven stage V and three stage VI females were caught in the same period at the same sites, all three stage VI and seven of the stage V fish being caught in February. In 1975 and 1976 sampling was not possible because of research vessel refits. It appears that February was the peak month for spawning although catch rates of stage VI fish were probably too low to suggest an adequate number of spawners to support the local stock. It is possible that the spawning fish moved off the bottom to spawn, or in some other way avoided capture. It seems more likely that a spawning migration out of the area occurred, since so few planktonic larvae were captured. A small number of spent (stage VII) fish were caught at the offshore sites of Ardalanish Bay and Tiree Passage.

IV.4.G. Discussion

The estimations of length and age at first maturity are similar to figures given by Raitt(1968b) for Norway pout in the North Sea. Nagabhushanam(1965), Gokhale(1953), and Raitt(1968a) note individuals smaller than this maturing, but did not give 50% lengths. All authors found females maturing at slightly larger sizes than males. Raitt(loc.cit.) also found that the length-range over which maturity changes take place to be so short as to cause difficulty in estimating the 50% point with precision. From consideration of several years results Raitt noted that in years of low stock abundance there was a significant lowering in the age of first maturity, although the length remained about the same. This change was associated with both an increase in growth (which increases fecundity) and also with an increase in fecundity-at-length.

Table IV.12 summarizes the available information on sex-ratios (from Raitt, 1968a): only Saemundsson (1929) found an excess of males. In O-group fish in the present study there was no significant departure from a 1:1 ratio. It would appear that the lower proportion of males in older age-groups is due to higher apparent mortality rates. Since the whole distribution area was not studied, however, it is possible that some kind of migration out of the area of study occurs which may be sex-selective e.g. through sexual length differences. Ursin (1963) noted that males often have a higher coefficient of growth catabolism, which often correlates with natural mortality. At inshore sites the sex-ratio differed significantly from 1:1 in favour of males; Ardalanish Bay was insignificant and females were in excess offshore. Ursin (loc.cit.) pointed out that 'of two fish of the same species living in different environments (temperature, light, etc.) the one living in the less stable environment will lose in condition more rapidly because the amplitude of the annual weight cycle is bigger.' It has been shown (section 1.2) that annual temperature variations are greater inshore than offshore: the sexual anomalies in K and natural mortality will therefore be more marked. This does not, however,explain the excess of males at Tiree Passage. It is known that the depth distribution of Norway pout varies with age (section IV.2). Size-specific depth selection could cause anomalies in the sex-ratio since females grow faster than males (section IV.3).

The spawning season probably occurs between January and May with a peak in February. The low catch rates of ripe (stage V) and running-ripe (stage VI) fish make it difficult to delimit the extremes of

TABLE IV.7. SEX RATIOS OF NORWAY POUT POPULATIONS

Region	% male	% female	No. in sample	Authority
S.W. Iceland	37.8	62.2	172	Saemundsson (1929)
S W. Iceland	57.5	43.5	421	Saemundsson (1929)
Moray Firth and Shetlands	34.3	65.7	572	Raitt (1961)
North Sea	43.0	57.0	1636	Raitt (1961)
W. Coast Scotland	47.9	52.1	11111	Present study

the season. Gokhale(1957) found running-ripe fish in the Irish Sea in March, April and May. In the same area Nagabhushanam(1959) found running-ripe fish between January and May. This agrees with the seasonal distribution of planktonic stages discussed in section IV.2.

The possibility of a spawning migration out of the area has been considered. Spawning grounds occur off the north coast of Scotland and the Butt of Lewis (Raitt,1965). Little is known about the area to the south of this, although Raitt and Mason(1968) found concentrations of juveniles in the Minch in August and September. Schmidt(1909) found spawning areas over coastal banks or over the upper parts of the slope towards deeper water, with little spawning in more than 200m or less than 50m. As all of the samples in this study were from depths of less than 100m it is possible that the area was too shallow for spawning. Mason(1960) found that Norway pout were only occasionally present at depths of less than 80 - 90m in the North Sea. Although Raitt and Mason(1968) show the distribution of adults on the west coast of Scotland, very few hauls were taken from the area west of Islay and Tiree/Coll, which is slightly deeper.

IV. 5. CONDITION FACTOR AND LENGTH-WEIGHT RELATIONSHIPS

IV.5.A. Condition Factor

Fig.IV.17 shows seasonal variations in mean condition factor at each site, with different age-groups of each year-class plotted separately. When data from all sites were pooled a distinct seasonal trend was obvious : condition was minimal in March and April and reached a maximum in July and August. Condition decreased between August and December with greater decreases from January until April. This cycle occurred from autumn in the 0-group until spring in the 3-group. The range of mean condition factors between April and August was about 0.47 to 0.77. The timing of this seasonal pattern was the same at all sites although the amplitude of the seasonal cycle varied. This is most apparent comparing Loch Linnhe with the Firth of Lorne, since the amplitude was much greater at the latter site.

Fig.IV.18 shows the seasonal variation in condition of males and females. Sexual dissimilarities occurred between January and May in the 2-group, with females in poorer condition. For the rest of the life-span little difference was obvious. Pooling all available data, differences in mean condition factor between the sexes were insignificant (Table IV.8). The overall condition factor was 0.64. The mean condition factor of fish whose sex could not be determined was lower than males or females, but the difference was not significant.

The mean condition factor of fish in each maturity stage is shown in Fig.IV.19. Maturation from stage 1 to II was associated with a slight increase in condition, although at the time of year when these stages occurred condition was falling slowly. Minimal condition occurred when fish were in maturity stage IV, which was at the time of year of minimal condition. Catch rates of fish in stages V and VI were too low to determine mean condition factors with accuracy. The mean condition factor of spent fish was greater than fish in stage IV for both sexes.

Fig.IV.17. Seasonal change in the mean condition factor of Norway pout at each site and pooling fish from all sites.

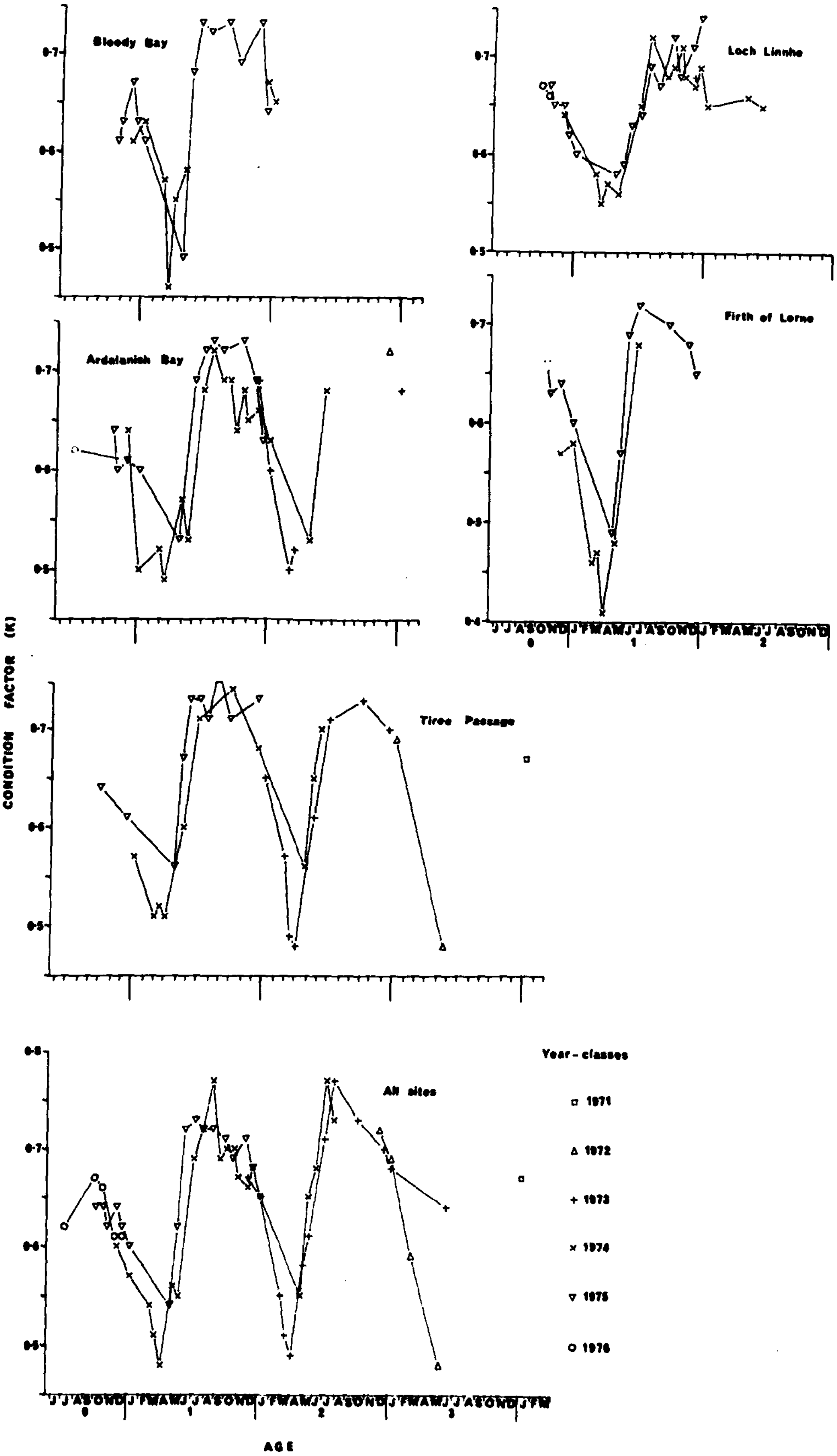

Bloody Bay
Loch Linnhe
Ardalanish Bay
Firth of Lorne
Tiree Passage
All sites
CONDITION FACTOR (K)
0·8
0·7
0·6
0·5
0·4
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
0
1
2
3
AGE
Year - classes
□ 1971
△ 1972
+ 1973
× 1974
▽ 1975
○ 1976

Fig.IV.18. Seasonal variation in the mean condition factor of each year-class of male and female Norway pout, pooling data from all sites.

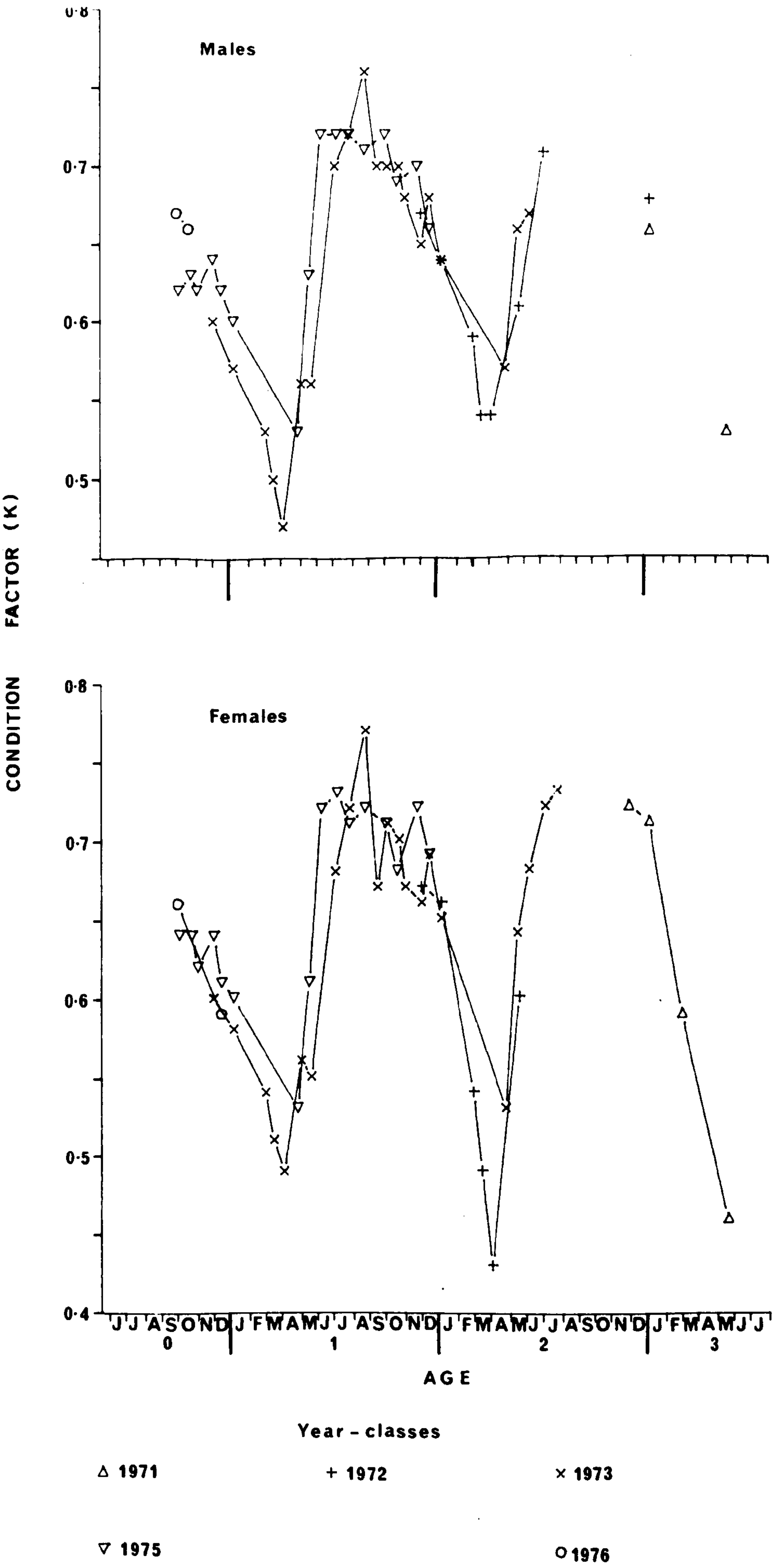
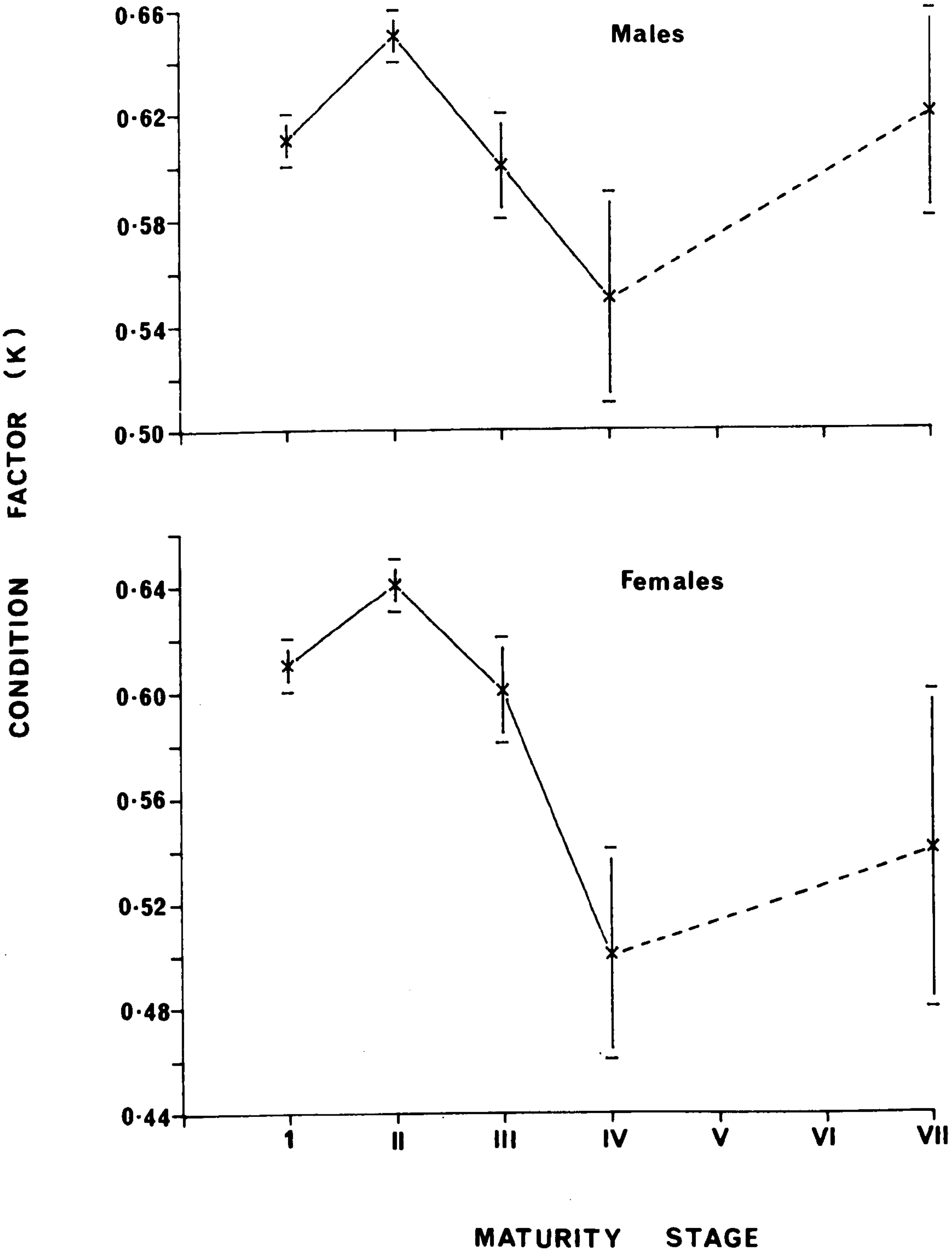

Males
Females
CONDITION FACTOR (K)
0·8
0·7
0·6
0·5
0·4
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
0
1
2
3
AGE
Year - classes
△ 1971
+ 1972
× 1973
▽ 1975
○ 1976

TABLE IV.8. MEAN CONDITION FACTORS, POOLING ALL FISH WEIGHED FROM NOVEMBER 1974 TO DECEMBER 1976, WITH 95% CONFIDENCE LIMITS.

	SEX			
	Males	Females	Immatures	All fish
Number of fish.	5300	5725	461	11486
Mean condition factor.	0.615	0.611	0.577	0.611
95% confidence limits.	± 0.003	± 0.002	± 0.040	± 0.002

(Immatures = fish whose sex could not be dtermined by macroscopic examination.)

Fig.IV.19. Mean condition factor (with 95% confidence limits) of Norway pout in each maturity stage.


Males
Females
CONDITION FACTOR (K)
0·66
0·62
0·58
0·54
0·50
0·64
0·60
0·56
0·52
0·48
0·44
1
II
III
IV
V
VI
VII
MATURITY STAGE

IV.5.B. Length-weight Relationships

Scatter diagrams showed that, as with the other two gadoid species studied, weight varied as a power of length. The G.M. regression of all fish measured and weighed is shown in Fig.IV.20.B. A large and highly significant part of the variance was explained by regression (Appendix IV.4.A).

Differences between sexes

Fig.IV.20.B shows the length-weight relationships of males, females and immatures (fish whose sex could not be determined). Statistics of the regression lines are given in Appendix IV.4.A. Males were slightly heavier than females of the same length. Appendix IV.4.B shows the results of an analysis of covariance test for comparison of slopes of the male and female length-weight relationships, the difference in slope being highly significant. The immature fish were lighter than males or females at the same length but comparison of slopes by analysis of covariance was not possible because residual variances were heterogeneous.

Differences between maturity stages

Fig.IV.20.A shows the progressive reduction in weight of fish at a given length associated with maturation from stage 1 to IV. Stage VII fish may be heavier or lighter than other stages, depending upon sex and length. Statistics of the calculated regression lines are shown in Appendix IV.4.C. It was not possible to compare relationships by analysis of covariance because residual variances were heterogeneous.

Seasonal differences

Monthly length-weight relationships were calculated for fish of each sex, pooling data from 1974 to 1977 (Fig.IV.21). Fish from Tiree Passage and Ardalanish Bay only were used, in order to avoid bias towards very young fish. Statistics of regression lines are shown in Appendix IV.4.D. Fig.IV.22 shows the estimated mean weight of fish of 10 cm and 16 cm in each month, assuming the calculated length-weight

Fig.IV.20. Length-weight relationships of Norway pout, calculated from the G.M. Functional Regression.

A. Fish in each maturity stage for males and females.

B. All fish, males, females and fish whose sex could not be determined.

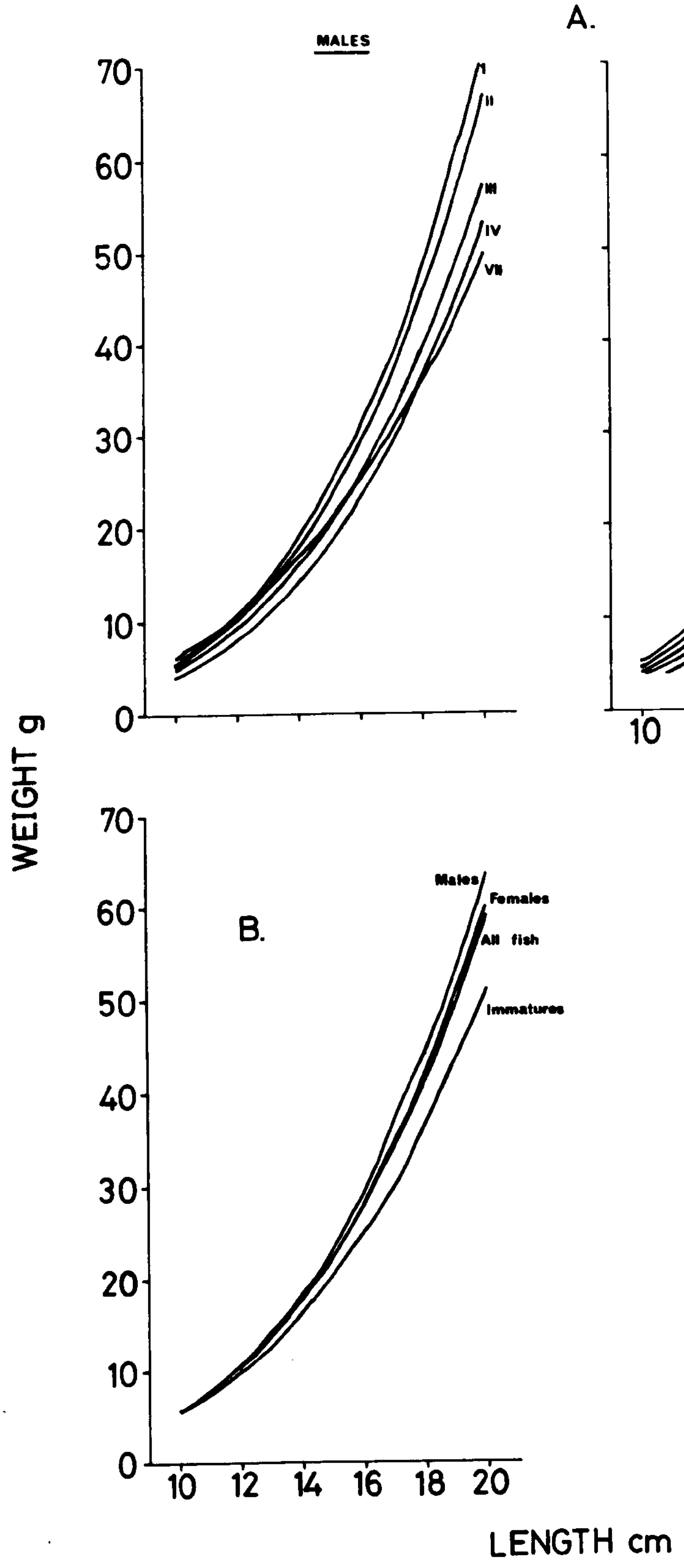

A.
MALES
FEMALES
70
60
50
40
30
20
10
0
I
II
III
IV
VII
1
II
III
VII
IV
10
12
14
16
18
20
WEIGHT g
B.
Males
Females
All fish
Immatures
70
60
50
40
30
20
10
0
10
12
14
16
18
20
LENGTH cm

Fig.IV.21. Seasonal variations in the length-weight relationship of male and female Norway pout, calculated from the G.M. Functional Regression.

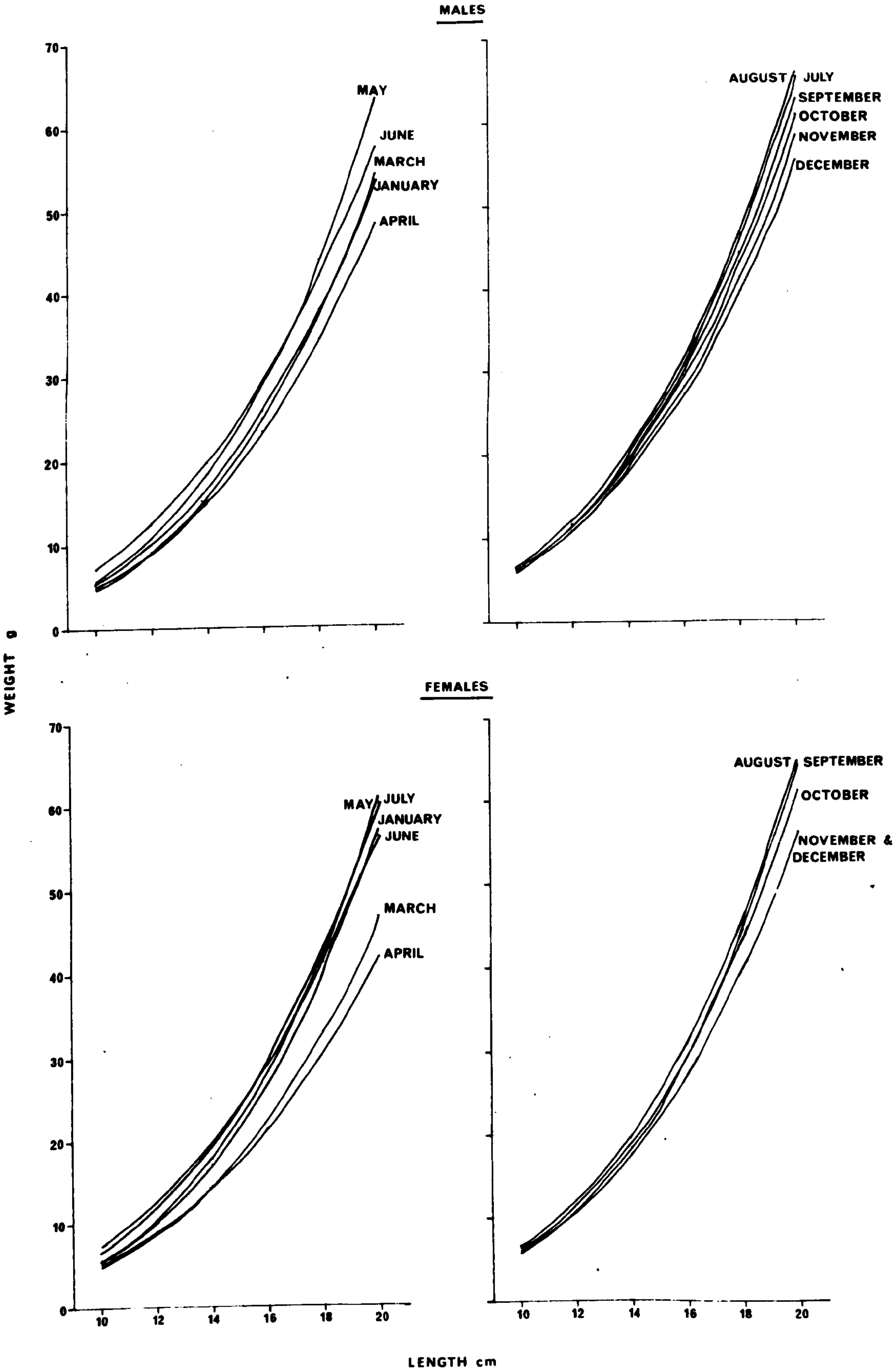
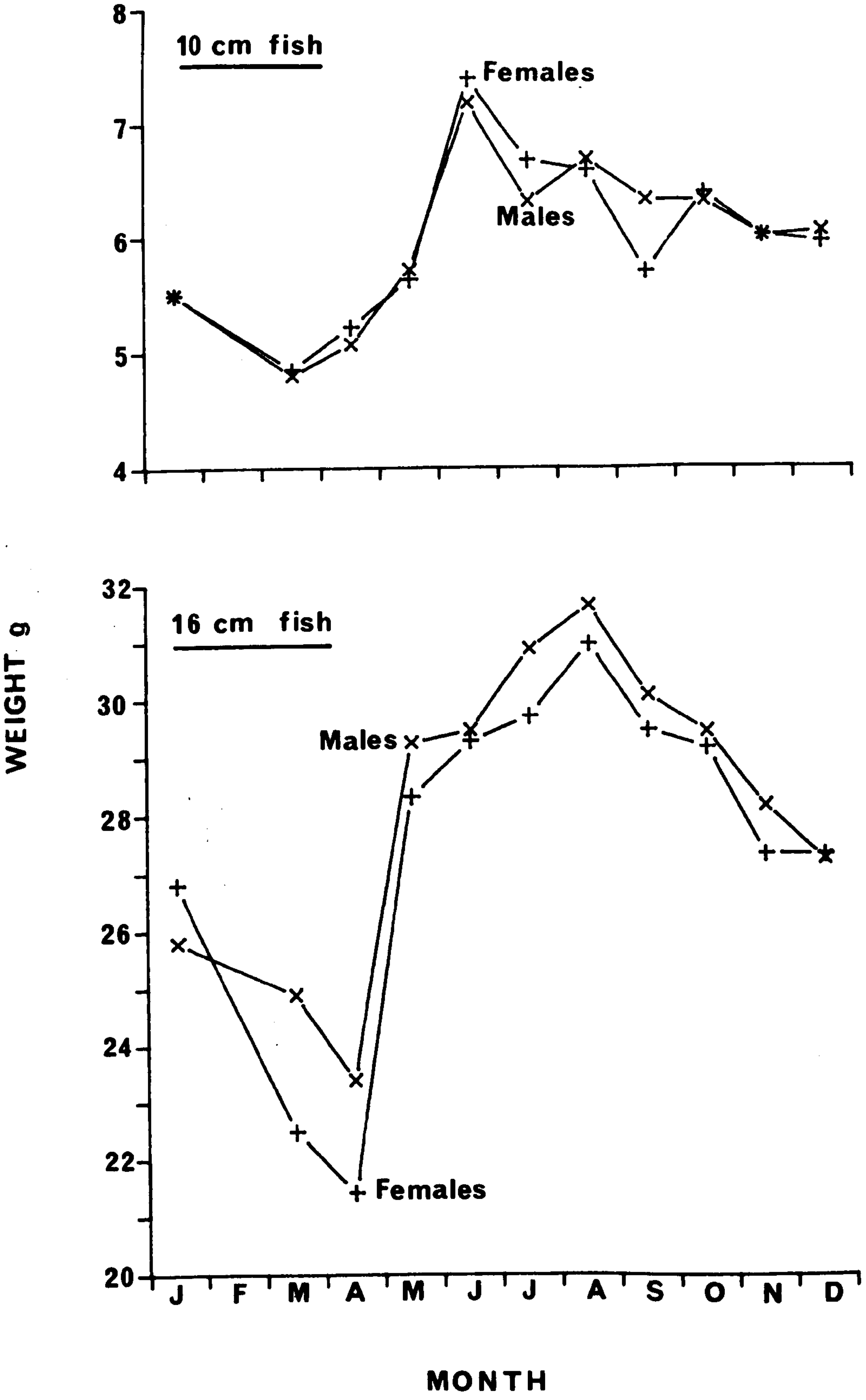

MALES
MAY
JUNE
MARCH
JANUARY
APRIL
AUGUST
JULY
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
FEMALES
MAY
JULY
JANUARY
JUNE
MARCH
APRIL
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER &
DECEMBER
WEIGHT g
LENGTH cm
0
10
20
30
40
50
60
70
10
12
14
16
18
20

Fig.IV.22. Seasonal variation in the estimated weight (g) of Norway pout of 10 cm and 15 cm total lengths, calculated from the G.M. Functional Regressions.


10 cm fish
Females
Males
8
7
6
5
4
16 cm fish
Males
Females
32
30
28
26
24
22
20
WEIGHT g
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

relationships. In all months 95% confidence limits to estimated weight were calculated at ±0.1g. 10cm fish did not spawn (section IV.4.B) and were in either the O-group or the 1-group. Significant differences in weight between males and females of the same length were apparent only at certain times of the year, with neither sex consistently heavier. Most 16cm fish spawned, they belonged to the 1-, 2- or 3-groups and males were heavier for most of the year. The seasonal variations were similar in males and females of the same length, but differences were apparent between lengths. In 10cm fish there was a simple cycle of minimum weight in March, an increase to a maximum in June followed by a gradual loss in condition until the following March. In 16cm fish the spring minimum occurred in April followed by a rapid increase in weight in May ; slight monthly weight increments continued until the summer maximum in August, after which weight was lost until the April minimum.

IV.5.C. Discussion

Gordon(1977a) found similar seasonal variations in condition factor of O-group and 1-group fish, working in inshore areas in the same region. Condition factor values were slightly greater due to the use of whole rather than gutted weight. In the North Sea condition was also highest in summer and early autumn and lowest just after the spawning season (Raitt,1968b). Raitt(loc. cit.) also found that the amplitude of the seasonal variation was greater in females than in males. This was not found in the present study, although Raitt only considered mature fish over 14cm long and did not state if whole or gutted weight was used. In the Skagerrak seasonal variations were similar to those found in the present work (Ursin,1963).

Ursin(loc. cit.) and Raitt(1968b) related variations in condition to spawning and seasonal variations in feeding intensity. In the present study differences in condition associated with maturation did not always correspond with the seasonal occurrence of maturity stages. This was presumably due to differences between fish in the timing of maturation.

Seasonal differences in length-weight relationships and those associated with maturation largely reflect variations in condition factor. Comparable length-weight curves were given by Raitt (1968b) and Gordon (1977a) although only the latter author calculated the equation of the curve. Re-examination shows an error in Gordon's paper, the true relationship being $W=0.003588L^{3.2489}$ rather than $W=0.0003588L^{3.2489}$. On this basis only slight differences were found as would be expected considering the present author's use of gutted, rather than whole weight; and the GM functional, rather than ordinary predictive regression.

IV. 6. DISCUSSION

As with the poor-cod the inshore migration of Norway pout is probably best considered to be a spreading out of fish at a time of peak abundance. Norway pout never become concentrated inshore as in whiting. Fish reached the study area at the end of the nektonic pelagic stage and left the more inshore areas at the end of the 1-group or the beginning of the 2-group. Norway pout were found at Tiree Passage up to the 3-group. Maturing and spent fish were captured but it is not thought that Norway pout normally reproduce in the study area, although they may in some years e.g. 1977 (section IV.4). The emigration of fish from inshore areas undoubtedly boosts 'apparent survival' rates offshore. Such a spawning migration out of the area, with the population being supported by the immigration of larvae and juveniles, is not unknown for this species. Poulsen(1966) suggested that Norway pout populations in the Skagerrak and Kattegat were supported by spawning grounds in the North Sea. Gokhale(1957) considered that the Irish Sea stock was supported by spawning grounds north of Ireland, although some spawning may occur within the area. Nagabhushanam(1959) found running-ripe fish in the Irish Sea in 1958. There was a seasonal trend of a reduction in abundance in late summer at all sites, with an increase in abundance in spring at Tiree Passage and in winter at other sites. Mason(1960), cited in Raitt(1968a), found evidence of a slight northerly migration for spawning in the northern North Sea. Raitt and Mason's (1968) work does not show sufficient detail for west coast stocks to relate the seasonal parameter to an overall migration pattern.

SECTION V

DISCUSSION

The present study confirms Gordon's (1977a, 1977b, pers. comm.) conclusions that Norway pout, whiting and poor-cod on the inshore nursery grounds around Oban are derived initially from planktonic or pelagic nektonic stages west of Mull. Spawning grounds of poor-cod have been located in Tiree Passage and Ardalanish Bay, but for the Norway pout and whiting they are thought to lie outside the study area. Maximum abundance of each year-class inshore occurred at the end of the O-group in all three species. Thereafter there was a rapid reduction in numbers, the rate of which varied with sampling site and species, being much more rapid inshore than offshore. Predation and other natural mortalities undoubtedly accounted for part of this reduction in abundance. The most important predators of gadoids on inshore nursery grounds are probably older whiting, spur-dogs (*Squalus acanthias*) and possibly mackerel. Reef-dwelling fishes such as cod, pollack and saithe may feed on the species studied, but are unlikely to be important because of their low catch rates. Since there is no evidence to suggest that predators are more common inshore (in fact the reverse is true) other factors must be responsible for the more rapid reduction in numbers in these areas. It is possible that the inshore grounds represent sterile expatriation areas (Ekman,1953), the populations being supported by offshore spawning grounds but with no fish returning to spawn. There was no obvious evidence of mass mortalities, however, so it is assumed that a proportion of the population from each site survived to return to the offshore spawning grounds. Inshore catch-curves did not therefore represent survival but survival and emigration ; offshore catch-curves represent survival and immigration from inshore areas.

Harden Jones(1968) defined migration as 'A class of movement which impels migrants to return to the region from which they have migrated.' Since all of the species in the present study were spawned outside the inshore nursery grounds and it is considered that the juveniles moved offshore to spawn, this movement may be termed a migration. In each species young fish reached the nursery grounds after the planktonic stage in June and July, when some fish were pelagic and some demersal. Although the fish at this time can move actively the migration may be aided by the circulation pattern in the Firth of Lorne (see sections 1.2 and III.2.G). Orientated locomotory movements would of course reinforce this effect.

In Norway pout and poor-cod it appears that the inshore migration was a simple dispersal, whereas in whiting there was a greater density of fish inshore for a limited period in the O-group. Harden Jones (loc. cit.) deliberately avoided distinguishing between dispersals and movements between separated defined areas : these are difficult to differentiate in fish since water movements can bias the direction of dispersals and result in shifts in the population density. In the present study, however, this is considered to be an important distinction, since the three species occupied similar areas at the same time of year while eating similar foods, but the final distribution was dissimilar. Hardy(1936) and Russell(1976) have pointed out that different horizontal distributions can result from differences in the vertical distribution, if water currents vary with depth. This is normally considered important only in the planktonic stage, but Harden Jones (1968) notes that whereas larvae <u>must</u> drift, adults <u>can</u>. Also the association of whiting with Scyphomedusae of the genus <u>Cyanea</u> may delay settlement to the demersal phase, thus affecting horizontal distribution. Harden Jones(loc. cit.) considered that, in addition to drift, random locomotory movements operating in an environmental field which affects swimming speed can cause aggregation, as can orientated locomotory movements. Both of these subjects require further study but lie outside the scope of this thesis.

The importance of the inshore nursery grounds to the ecology of each species is thought to be threefold :-

(1) The separation of nursery and adult feeding grounds may be an adaptation towards abundance, since there may not be enough food to support both adults and immatures on the same ground (Nikolsky, 1963). Although referring to large-scale drift migrations in the Barents Sea Marty's (1965) remarks are relevant to the present, more localised study : '...Migrations result in the extension of the species habitat and wider utilization, as feeding areas, of enormous sea spaces which for various reasons cannot be used by a given species for reproduction. Through the resulting extension of the habitat, drift migrations reduce the possibility both for interspecific and intraspecific competition.'

(2) Barnes(1974) argued that a large number of fish use estuaries as nursery areas as they are areas of abundant food supply, much of it unconsumed by resident species. Barnes(loc. cit.) also introduced Margalef's (1963) observation that 'Many animals spend their adult life in mature ecosystems and their juvenile life in less mature ones so that the rapidly-growing young can take advantage of the easily-available 'excess' in the latter.'

(3) McErlean, O'Connor, Mihursky and Gibson (1973) and Gunter (1938) considered that , in addition to a greater availability of food , estuaries allow the escape of juveniles from predators. Perhaps the apparent aggregation of whiting inshore could be due to greater mortalities offshore. This requires further consideration since, if there is such a concentration of young fish inshore, why do predators not also concentrate in the same area. May(1965)

notes that 'Food can be a concentrating factor for commercial fish, allowing them to gather in large numbers *within some part of a favourable temperature and depth range*.' The emphasis has been added, since physiological tolerances and behavioural preferences are obvious ways in which adult fish may be localised offshore.

De Silva(1973b) considered that the movement of young herring from smaller lochs may be a consequence of the availability of a limited food supply common to both herring and sprats, and thereby a means of avoiding direct competition. Other factors e.g. the preference by older fish for deeper water, were also considered to be of possible importance. Small sea lochs were not studied in this investigation, but the possible importance of a limited food supply in determining the timing of emigration from the nursery grounds should not be ignored. In poor-cod (Gordon,pers. comm.), Norway pout (Gordon, 1977a) and smaller whiting (Gordon, 1977d) the diet was mainly crustacean. Polychaetes were also important in younger poor-cod and in Norway pout microcrustacea (mainly copepods) were seasonally important. In both Norway pout and poor-cod stalk-eyed crustacea (mysids, euphausiids and decapods) were the most frequent food items, fish rarely being taken. Clupeid food consisted largely of copepods with mysids and euphausiids important in older fish (De Silva, 1973d). In whiting the crustacean food (chiefly *Meganyctiphanes norvegica* and *Crangon almanii*) of small fish changed to a mainly fish diet with increasing size (Gordon,1977d). There could possibly be competition for stalk-eyed crustacea between Norway pout, poor-cod, older herring and small whiting, although all these fish are opportunist feeders with reserve food sources. In addition the clupeids are more pelagic than all except 0-group gadoids in summer. Gordon(1977d) found that more whiting feed during winter than either clupeids or Norway pout, and thought that this was due to their adequate supply of (fish) food. The possible shortage of crustacean food in winter would account for the seasonal variation in demersal catch-curves for Norway pout (Fig.IV.4) and poor-cod (Fig.II.7). At the time when whiting emigrate most of the population are feeding on fish (mainly shoaling species such as herring, sprats and sand-eels; but also Norway pout and poor-cod). Gordon (1977d) pointed out that the absence of clupeids during winter (De Silva, 1973b) at Loch Linnhe leaves only Norway pout as a suitable food source. Since they are larger than clupeids only the largest whiting are able to exploit them.

Other factors which may affect the emigration of fish include maturation and preferred physical conditions. The low catch rates of fish over maturity stage III at inshore sites have been noted for all species: whether this is a cause of the migration or an effect of a shortage of food when the fish are maturing can only be speculation. Many marine species exist in sterile expatriation areas, the physiological tolerances of adults and for spawning being more restrictive, or different to larvae and juveniles. In all three species a preference for deeper water was observed in older fish. Temperature and salinity preferences may also affect the timing of emigration.

In all species growth in length and weight was seasonal, occurring mainly between May and December. The sigmoid shape of the seasonal growth curves is a common feature in fish and Gerking(1966) gives a number of examples. It was not possible to separate growth in length and weight in time by the methods used, although such differences are illustrated by changes in condition factor and by changes in the length-weight relationship. In all species minimum condition coincided with the spawning season and reductions in condition with maturation from stage II onwards were obvious. Such changes in condition are normally associated with the 'metabolic strain' of spawning e.g. Hart (1946), Hickling(1930), Le Cren (1951), although condition in individual fish may be affected by anything which affects its nutritional status e.g. food availability, disease, parasitism, damage, osmoregulation, growth and aging. Condition thus indicates the general effect on the fish of a wide variety of internal and environmental factors, of which reproduction and feeding intensity are probably among the most important.

Maturation of the gonads began in winter at the end of the 1-group in all species studied i.e. when somatic growth had stopped. Somatic growth occurred when the spawning season was over. This separation of somatic growth and gonadal growth has been discussed by Iles(1974) who gives a number of examples. It appears that in general gonad development is dependent on a nutritional 'store' built up during the feeding and growth periods rather than on material assimilated during maturation, when many fish feed less intently. It may be more realistic to consider that maturation occurs when little food is available in the winter so that the larvae have the optimum chance of survival at the peak of the production cycle in the early spring. Cushing(1969) showed that for four temperate fish species the spawning season is fixed, suggesting that weak and strong year-classes occur when spawning is in or out of phase with production. In the same context a food-limited simulation of the early life history of cod and haddock accounted for the observed variable strengths of year-classes (Jones and Hall,1974). This winter maturation would also allow the maximum food to be available during the growing season and, as Gerking(1966) points out 'The importance of feeding and food supply should not be overlooked. The growth hormone cannot exert its effect unless the fish are able to find adequate food.'

That this seasonal pattern of growth, condition and a 'pre-spawning maturation' occurs in 1-group fish may appear anomalous as these fish do not spawn. This has,however, been observed by several authors. Iles(1974) gives several examples , concluding 'Other activities intimately associated with reproduction have been shown to represent an intensification of rhythms already established in juveniles and adolescents, rather than the appearance of new phenomena.'

The present study has yielded results which may have management implications. Although the importance of the larval stage in determining year-class strength is now well established (e.g. Hjort, 1914; Gulland, 1965; May, 1974), the early juvenile stage should not be ignored. Lucas (1965) thought that ' many more, and more intensive, egg and larval surveys will undoubtedly be needed, but it is becoming evident that much more attention must be paid to the adolescent stages in the life of the fish which follow the first year of its life, and that mortalities should be followed through these as well as the earliest stages.'

Although there have been many intensive studies on large-scale migrations (e.g. Graham, 1924; Trout, 1957; Hickling, 1927; Sette, 1943, 1950) little emphasis has been placed on small-scale local migrations although their importance may be considerable. Apart from the biological importance of understanding the early life history a 'knowledge of ..... pre-recruit stocks is essential in attempts to predict and control fisheries.' (Colebrook, 1965). This stems particularly from difficulties in predicting recruitment from larval surveys, since mortalities are high during this stage. In the North Sea Hislop and Bailey (1974) found good agreement between indices of year-class strength between O-group pelagic surveys and demersal surveys of the 1-group fish in the following year, for whiting and haddock. They considered that a larger data series was required to see if pelagic O-group indices are accurate predictors of year-class strength at recruitment. Such surveys may be of critical importance in recommending maximum catches for such species as Norway pout, where :

(1) there is only a short time period between adopting a demersal habit and recruitment to the fishery ;

(2) the fishery depends on only a small number of year-classes and is therefore subject to great fluctuations due to the strength of each new year-class at recruitment.

In order to avoid setting over-cautious limits which are safe for all years but involve the loss of yield in years of good recruitment, some such reliable predictor of year-class strength is required.

Several countries now cooperate in 0-group gadoid surveys in the North Sea, using pelagic trawls to survey the abundance and distribution of young fish. Such surveys are, necessarily, of limited duration e.g. in 1976 the survey period lasted from 13 - 30 June. Extended seasonal studies, such as the present one, demonstrate the limited period for which fish remain pelagic. Considerable bias could be introduced if comparisons are made between years in which sampling is in separate months. This is obviously appreciated by Hislop and Bailey (loc.cit.) who write 'Recruitment therefore appears to begin in summer as a vertical migration, the fish spending the day on or near the sea-bed to an increasing extent.' Bias could also be introduced by failure to sample the whole area of distribution, including inshore areas. This may be especially important in the case of whiting, in which the fish appear to aggregate inshore (at least in 1975 and 1976) for a short period in the 0-group. There also appears to be an inverse relationship between the abundance of 0-group Norway pout in the Minch and in inshore areas, although several more years results will be required to confirm this. Annual variations in the strength of the inshore migration would seriously affect indices of abundance based solely on offshore stocks.

SUMMARY

1. Whiting, Norway pout and poor-cod populations were studied in inshore and offshore areas around Oban from November 1974 to March 1977.

2. Sampling was at approximately three-weekly intervals using three types of gear at different times of year. A 2m Plymouth Young Fish Trawl was used to sample planktonic stages from about February to August; a mid-water trawl was used from May until December to sample nektonic pelagic stages and a wing trawl was used for sampling demersal fish throughout the year.

3. In all three species inshore areas were nursery grounds, the populations being dominated by 1-group fish until recruitment of the new year-class between July and September. In offshore areas the populations comprised a greater proportion of older fish, and only here were mature fish caught.

4. Planktonic stages of poor-cod and whiting were restricted to offshore areas, recruitment to the inshore nursery grounds occurring when the fish were nektonic with part of the populations pelagic and part demersal. Recruitment of Norway pout occurred in the same stage although no clearly-identifiable planktonic fish were caught.

5. In poor-cod and Norway pout recruitment in inshore and offshore areas occurred simultaneously, whereas in whiting recruitment offshore was masked by a low abundance of fish. It is considered that young whiting aggregate inshore for a short period in autumn and winter at the end of the O-group. Poor-cod and Norway pout were in greater abundance offshore at all ages. These migration patterns are discussed in relation to the local hydrography.

6. The time spent on the nursery grounds varied in each species, whiting leaving before Norway pout or poor-cod. In all three species fish vacated shallow inshore sites more rapidly than deep inshore sites.

7. The growth of fish in different localities was studied and compared. In all three species : (a) growth was seasonal, occurring mainly in summer and autumn ;
   (b) females grew more rapidly than males ;
   (c) differences in growth rate were found between inshore and offshore sites and shallow and deep sites.

   The final observation could be explained if larger fish show a preference for deeper water and a precocious vacation of the nursery grounds.

8. Only poor-cod reproduced in the study area, at offshore sites between January and May with a peak of spawning in April. The average length of first maturity was 15.6 cm for females and 14.0 - 14.6 cm for males. The majority of fish matured in the 2-group although a small proportion of mature 1-group males were caught. The poor-cod is a short-lived species and reproduction was highly dependent on a single year-class, 83.3% of mature females belonging to the 2-group. The overall sex-ratio did not depart significantly from 1:1, although in fish of the 2-group and over there were fewer males than females.

9. Although ripe and spent whiting and Norway pout were caught at offshore sites no spawning fish were encountered. It was concluded that a migration of maturing fish out of the area occurred in both species, and the possible location of spawning grounds are discussed.

10. The average lengths of first maturity, based on maturing and ripe fish were 25.5 cm and 27.5 cm for male and female whiting respectively. For the Norway pout the figures were 13.4 - 16.2 cm and 14.3 - 16.6 cm. In both Norway pout and whiting most fish matured for the first time in the 2-group, although small proportions of 1-group fish were mature. The sex-ratio of whiting was not significantly different from 1:1 overall, although there was a greater ratio of females in the 2-group (1:1.219). The sex-ratio of all Norway pout caught was 1:1.0854 (males:females), a highly significant departure from a 1:1 ratio.

11. Length-weight relationships were calculated for each species. In all cases there was a highly significant difference in slope between males and females. The relationships for each sex were as follows:

male poor-cod $\log w = 3.3665 \log l - 4.8588$;
female poor-cod $\log w = 3.3548 \log l - 4.8687$;
male whiting $\log w = 3.1680 \log l - 4.5425$;
female whiting $\log w = 3.1416 \log l - 4.4852$;
male Norway pout $\log w = 3.4769 \log l - 5.1980$;
female Norway pout $\log w = 3.4047 \log l - 5.0569$;

(where w = weight g
l = length cm).

12. Seasonal variations in 'condition' were studied by calculation of mean monthly condition factors and by analysis of monthly length-weight relationships. In all species a distinct seasonal trend was obvious which was related to maturation and feeding.

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APPENDICES

APPENDIX 1.1. DATES OF CRUISES, WITH DETAILS OF FISHING GEAR USED.

Cruise Number	Year	Date	Weeks into year	Gear used PN	Gear used MW	Gear used OT	Sampling sites LL	Sampling sites FL	Sampling sites BB	Sampling sites AB	Sampling sites TP
1	1974	28 November - 2 December	48	-	-	+	+	+	+	+	-
2		4 - 10 January	1	+	-	+	+	+	+	+	+
3		*	6	-	-	+					
4		1 - 5 March	9	+	-	+	+	+	+	+	+
5		18 - 21 March	11	+	-	+	+	+	+	+	+
6	1	2 - 10 April	13.5	+	-	+	+	+	+	+	+
7		6 - 8 May	18	+	-	+	+	+	+	+	+
8	9	22 - 27 May	20.5	+	+	+	+	+	+	+	+
9a		16 - 19 June	25	+	+	-	+	+	+	+	-
9b	7	3 - 8 July	26.5	+	+	+	+	+	+	+	+
10		28 July - 1 August	30	+	+	+	+	+	+	+	+
11	5	26 - 28 August	34	+	-	+	+	+	+	+	-
12		15 - 18 September	37	+	-	+	+	+	+	+	+
13		1 - 7 October	39.5	-	-	+	+	+	+	+	+
14		21 - 23 October	42.5	-	-	+	+	+	+	+	-
15		3 - 5 November	44	-	-	+	+	+	+	+	-
16		1 - 3 December	48	-	-	+	+	+	+	+	-
17		15 - 18 December	50	-	-	+	+	-	+	-	+
18		6 - 8 January	1	-	-	+	+	+	+	+	-
19		26 - 28 April	17	+	-	+	+	+	+	+	+
20	1	17 - 20 May	20	+	-	+	+	+	+	+	+
21		7 - 10 June	23	+	+	+	+	+	+	+	+
22	9	5 - 8 July	27	+	+	+	+	+	+	+	+
23		26 - 29 July	30	+	+	+	+	+	+	+	+
24	7	23 - 26 August	34	+	+	+	+	+	+	+	+
25		20 - 24 September	39	-	+	+	+	+	+	+	+
26	6	19 - 26 October	42	-	+	+	+	+	+	+	+
27		22 - 25 November	47	-	+	+	+	+	+	+	+
28		13 - 16 December	50	-	+	+	+	+	+	+	+
29		24 - 27 January	4	-	-	+	+	+	+	+	+
30	1977	21 - 24 February	8	-	-	+	+	+	+	+	+
31		8 - 10 March	11	-	-	+	+	+	+	-	-

* = Commercial sample obtained 4 February 1975 off Barra Head.

PN = 2m Plymouth Young Fish Trawl
MW = Mid-water Trawl
OT = Bottom Trawl

LL = Loch Linnhe
FL = Firth of Lorne
BB = Bloody Bay
AB = Ardalanish Bay
TP = Tiree Passage

APPENDIX II.1. STATISTICS FOR REGRESSION OF REDUCTION IN CATCH RATES OF <u>TRISOPTERUS MINUTUS</u> WITH AGE. ESTIMATES OF CATCH RATE FOR ALL YEAR-CLASSES IN EACH YEAR (1975 and 1976) WERE USED TO DETERMINE REGRESSION. AGE IS MEASURED IN WEEKS FROM DATE OF BIRTH (1ST JANUARY OF AGE GROUP 0) AND ALL ESTIMATES OF CATCH RATE FROM WEEK 39.5 ON, WERE USED.

Loch Linnhe $Y = 2.56 - 0.014\,X$

Firth of Lorne $Y = 3.98 - 0.029\,X$

Bloody Bay $Y = 3.47 - 0.024\,X$

Ardalanish Bay $Y = 3.41 - 0.021\,X$

Tiree Passage $Y = 3.41 - 0.017\,X$

Y = Catch rate $\log_{10}(n + 1)$

X = Age from date of birth in weeks.

Site	Source of Variation	D.F.	Sum of Squares	Mean Square	F	P
Loch Linnhe	Explained	1	7.26	7.26	17.52	< 0.005
	Unexplained	49	20.31	0.41		
	Total	51	27.57			
Firth of Lorne	Explained	1	21.26	21.26	60.15	< 0.005
	Unexplained	42	14.84	0.35		
	Total	44	36.10			
Bloody Bay	Explained	1	23.55	23.55	108.78	< 0.005
	Unexplained	50	10.82	0.22		
	Total	52	34.37			
Ardalanish Bay	Explained	1	41.86	41.86	169.86	< 0.005
	Unexplained	75	18.48	0.25		
	Total	77	60.34			
Tiree Passage	Explained	1	22.57	22.57	42.89	< 0.005
	Unexplained	52	27.36	0.53		
	Total	54	49.93			

(i.e.) In all cases a large and highly significant part of the variance of the catch rates has been explained by regression.

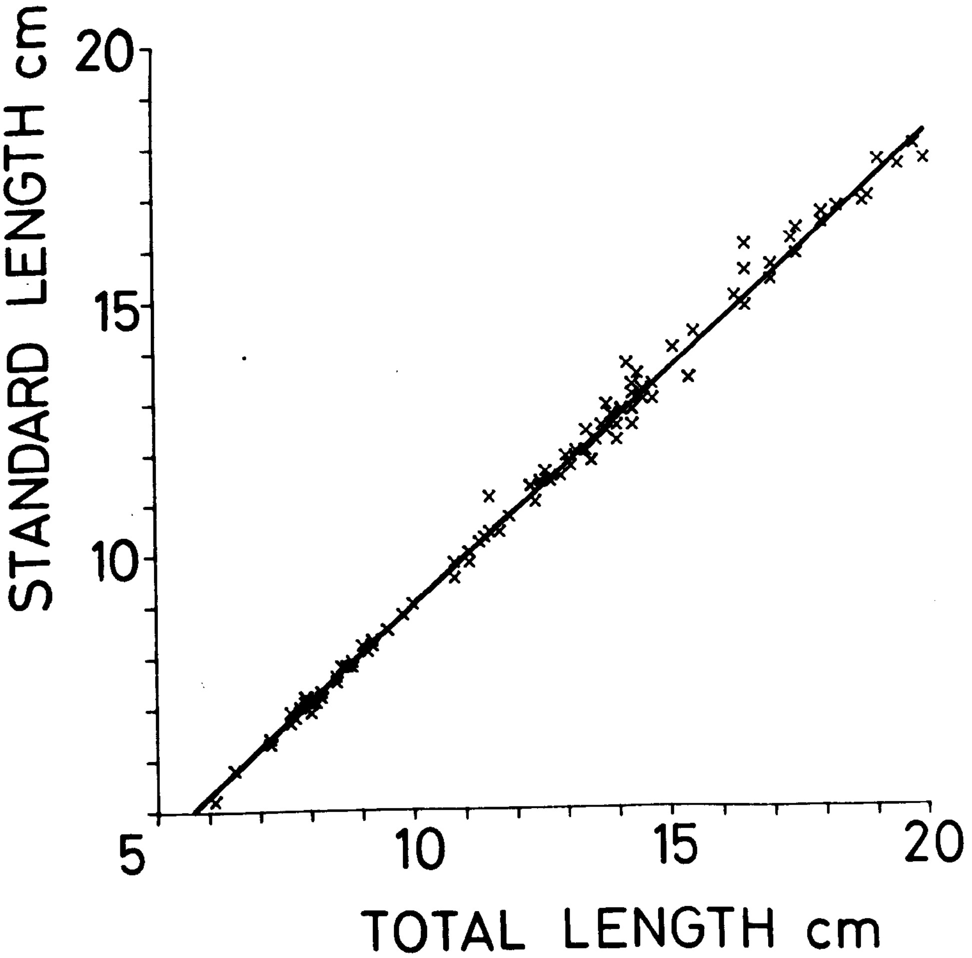
APPENDIX II.2. THE RELATIONSHIP BETWEEN TOTAL LENGTH AND STANDARD LENGTH IN POOR-COD.

Ricker (1973) recommended the use of the GM regression for routine conversions between the different types of lengths used in measuring fish. The equation of the regression line (shown opposite) is:

$$S.L. = 0.9266\ T.L. - 0.2870$$

where S.L. = standard length (cm)

and T.L. = total length (cm).


STANDARD LENGTH cm
20
15
10
5
10
15
20
TOTAL LENGTH cm

APPENDIX II.3. MONTHLY SEX-RATIOS OF ALL POOR-COD EXAMINED, BY SITE (FISH OF THE AGE 2-GROUP OR OVER POOLED).

Age	Month	Loch Linnhe No. ♂	Loch Linnhe No ♀	Loch Linnhe % ♂	Firth of Lorne No ♂	Firth of Lorne No ♀	Firth of Lorne % ♂	Bloody Bay No ♂	Bloody Bay No ♀	Bloody Bay % ♂	Ardalanish Bay No ♂	Ardalanish Bay No ♀	Ardalanish Bay % ♂	Tiree Passage No ♂	Tiree Passage No ♀	Tiree Passage % ♂	All Sites No ♂	All Sites No ♀	All Sites % ♂
0	O	6	5	54.5	27	15	62.8	32	29	52.5	40	40	50.0	4	7	36.4	109	96	53.2
	N	11	12	47.8	30	21	58.8	51	41	55.4	62	96	39.2	1	0	-	155	170	47.7
	D	23	35	39.6	45	33	57.7	87	81	51.8	114	111	50.7	69	59	53.6	338	319	51.4
1	J	52	65	44.4	52	69	43.0	32	43	42.7	100	84	54.3	71	85	45.5	307	346	47.0
	F	0	0	-	0	0	-	0	0		0	0		0	0		0	0	
	M	168	100	62.7	47	32	59.5	18	43	29.5	140	110	56.0	78	110	41.5	451	398	53.1
	A	72	57	55.8	41	55	42.7	12	24	33.3	150	126	54.3	63	83	43.1	338	345	49.5
	M	14	16	46.7	13	12	52.0	44	111	28.4	73	57	56.1	127	148	46.2	271	344	44.1
	J	2	3	40.0	4	8	33.0	31	36	46.3	37	44	45.7	37	52	41.6	111	143	43.7
	J	16	26	38.1	232	151	60.6	12	9	57.1	141	134	51.3	81	87	48.2	472	407	53.7
	A	0	0	-	80	37	68.4	0	1	-	14	12	53.8	4	11	26.7	98	61	61.6
	S	19	22	46.3	85	68	55.6	3	7	30.0	22	13	62.9	9	6	60.0	138	116	54.3
	O	43	45	48.9	60	19	75.9	4	7	36.4	38	99	27.7	69	90	43.4	214	260	45.1
	N	58	49	54.2	14	16	46.7	2	7	22.2	82	39	67.8	1	0	-	157	171	47.9
	D	59	42	58.4	27	21	56.2	47	53	47.0	67	61	52.3	63	39	61.8	263	216	54.9
2+	J	55	5	91.7	5	3	62.5	47	58	44.8	46	111	29.3	18	11	62.1	171	188	47.6
	F	7	4	63.6				0	0		7	14	33.3	3	14	17.6	18	32	36.0
	M	6	10	37.5	-	-		3	2		3	5	37.5	9	10	47.4	21	27	43.7
	A	2	6	25.0	0	1		1	2		24	44	35.3	11	47	19.0	18	100	15.2
	M	0	0		-	-		1	7		22	48	31.4	120	99	54.8	143	154	48.1
	J	0	0		-	-		0	0		7	26	21.2	10	12	45.4	19	41	31.7
	J	0	0		1	1		0	1		13	27	32.5	32	28	53.3	46	57	44.7
	A	0	0					0	0		0	0		0	5		0	5	
	S	1	1	50.0													1	1	-
	O							0	0		2	8	20.0	2	0	-	4	8	33.3
	N	1	1	50.0				0	1		0	3		0	0		1	5	16.7
	D	2	6	33.3	1	0		3	5		4	3		1	1		11	15	42.3
Total		617	510	54.7	764	562	57.6	430	568	43.1	1208	1315	47.9	884	1004	46.8	3875	4025	49.0

Appendix II.4.A. VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF POOR-COD WITH SEX.

	GM Functional Regression	Ordinary Predictive Regression
All fish	$\log w = 3.3939 \log l - 4.9241$	
All males	$\log w = 3.3665 \log l - 4.8588$	$\log w = 2.8343 \log l - 3.7579$
All females	$\log w = 3.3548 \log l - 4.8687$	$\log w = 2.6960 \log l - 3.4802$
Immatures	$\log w = 3.5297 \log l - 4.9241$	

N.B. Immatures = young O-group fish whose sex could not be determined.

Sex	Source of Variation	Degrees of freedom	Sum of squares	Mean square	F ratio	P
All fish	Explained	I	569.2031	569.2031	22341.5	<0.001
	Unexplained	8839	407.6641	0.0461		
	Total	8840	976.8672			
All males	Explained	I	203.3906	203.3906	7004.6	<0.001
	Unexplained	3916	113.7070	0.0290		
	Total	3917	317.0977			
All females	Explained	I	320.6094	320.6094	9807.23	<0.001
	Unexplained	3933	128.5742	0.0327		
	Total	3934	449.1836			
Immatures	Explained	I	16.2893	16.2893	2054.76	<0.001
	Unexplained	867	6.8733	0.0079		
	Total	868	23.1626			

In all cases a large and highly significant part of the variance was explained by regression.

APPENDIX II.4.B ANALYSIS OF COVARIANCE FOR COMPARISON OF SLOPES BETWEEN SEXES.

F ratio for residual variances = 1.1259

degrees of freedom = 3933.3916

P approx. = 0.05

(i.e.) approaching limits of significance

Comparison of slopes :-

Source of variation	Degrees of freedom	Sum of squares	Means square	F ratio	P
Among means	1	134.4194	134.4194	4355.793	<0.005
Within regression	7851	242.2812	0.03086		
Total	7852	376.7006			

(i.e.) very highly significant

APPENDIX II.4.C. VARIATIONS IN LENGTH-WEIGHT RELATIONSHIP OF POOR-COD WITH MATURITY.

Maturity stage	Male GM regression	Female GM regression
All stage I	log w = 3.4305 log l - 5.0036	log w = 3.4305 log l - 5.0036
II	log w = 3.4155 log l - 4.9714	log w = 3.2713 log l - 4.6614
III	log w = 3.1881 log l - 4.5036	log w = 3.4927 log l - 5.1784
IV	log w = 3.0885 log l - 4.3159	log w = 3.2795 log l - 4.7622
V	log w = 2.3506 log l - 2.7393	log w = 3.3155 log l - 4.8394
VI	log w = 3.2766 log l - 4.7288	log w = 3.0132 log l - 4.1685
VII	log w = 2.9496 log l - 3.9983	log w = 2.9852 log l - 4.0836

		Males					Females				
Maturity stage	Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio	P	Degrees of freedom	Sum of squares	Mean square	F ratio	P
Allstage I	Explained Unexplained Total	1 2829 2830	181.2148 53.1836 234.3984	181.2148 0.01879	9644.215	<0.005					
II	Explained Unexplained Total	1 741 742	39.5588 5.2268 44.7856	39.5588 0.00705	5611.177	<0.005	1 553 554	13.8284 3.6636 17.4919	13.8284 0.0066	2087.320	<0.005
III	Explained Unexplained Total	1 101 102	4.0403 0.4678 4.5081	4.0403 0.00463	872.635	<0.005	1 88 89	1.6172 0.4238 2.0410	1.6172 0.0048	335.804	<0.005
IV	Explained Unexplained Total	1 11 12	0.5941 0.0114 0.6055	0.5941 0.00104	571.250	<0.005	1 25 26	0.8783 0.0786 0.9569	0.8783 0.0031	279.357	<0.005
V	Explained Unexplained Total	1 9 10	0.2109 0.0153 0.2262	0.2109 0.0017	124.059	<0.005	1 21 22	0.9444 0.0423 0.9866	0.9444 0.0020	468.851	<0.005
VI	Explained Unexplained Total	1 15 16	0.1998 0.0296 0.2294	0.1998 0.00197	101.421	<0.005	1 40 41	1.0522 0.1152 1.1675	1.0522 0.0288	365.347	<0.005
VII	Explained Unexplained Total	1 43 44	0.4346 0.0813 0.5159	0.4346 0.001891	229.825	<0.005	1 62 63	1.3403 0.1865 1.5269	1.3403 0.0030	445.5689	<0.005

In all cases a large and highly significant part of the variance was explained by regression.

APPENDIX II.4.D. SEASONAL VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF POOR-COD. ALL DATA USED.

Month	G.M. Regressions
January	$\log W = 3.5164 \log L - 5.1761$
March	$\log W = 3.5355 \log L - 5.2509$
April	$\log W = 3.2256 \log L - 4.6148$
May	$\log W = 3.1241 \log L - 4.4028$
June	$\log W = 3.1122 \log L - 4.3054$
July	$\log W = 3.3922 \log L - 4.9204$
August	$\log W = 3.2641 \log L - 4.4216$
September	$\log W = 3.4433 \log L - 4.9698$
October	$\log W = 3.3760 \log L - 4.8696$
November	$\log W = 3.3771 \log L - 4.8370$
December	$\log W = 3.2830 \log L - 4.6738$

Seasonal variations in weight of 9 cm and 17 cm fishes

(Calculated using the above monthly regressions)

	Weight of 9 cm fish (from regression)	Log. variance X 10^{-2}.	95% Confidence limits g.	Weight of 17 cm fish (from regression)	Log. variance X 10^{-2}.	95% Confidence limits g.
January	4.96	9.915	0.100	46.44	10.35	0.100
March	4.55	6.99	0.100	43.12	9.05	0.100
April	4.88	11.14	0.100	37.98	12.17	0.100
May	5.04	6.68	0.100	36.74	6.51	0.100
June	5.98	3.67	0.100	43.25	3.35	0.100
July	5.11	6.49	0.100	44.22	5.80	0.100
August	5.72	0.74	0.100	45.56	0.72	0.100
September	5.74	7.71	0.100	51.30	5.06	0.100
October	5.34	5.06	0.100	45.73	4.98	0.100
November	5.79	2.94	0.100	49.58	3.19	0.100
December	5.52	5.74	0.100	44.52	5.92	0.100

Month	Source of Variation	Degrees of freedom	Sum of squares	Mean Square	F Ratio	P
January	Explained	1	67.2644	67.2644	6902.4	<0.005
	Unexplained	582	5.6716	0.00974		
	Total	583	72.9360			
March	Explained	1	26.3083	26.3083	3827.3	<0.005
	Unexplained	501	3.4438	0.00687		
	Total	502	29.7522			
April	Explained	1	49.5627	49.5627	8824.4	<0.005
	Unexplained	549	3.0835	0.00562		
	Total	550	52.6462			
May	Explained	1	53.6038	53.6038	8535.8	<0.005
	Unexplained	749	4.7036	0.00628		
	Total	750	58.3074			
June	Explained	1	8.5317	8.5317	2648.7	<0.005
	Unexplained	223	0.7183	0.00322		
	Total	224	9.2500			
July	Explained	1	25.6230	25.6230	4681.9	<0.005
	Unexplained	550	3.0100	0.0055		
	Total	551	28.6331			
August	Explained	1	1.7957	1.7957	2446.1	<0.005
	Unexplained	44	0.0323	0.0007		
	Total	45	1.8279			
September	Explained	1	0.8850	0.8850	215.0	<0.005
	Unexplained	49	0.2017	0.0041		
	Total	50	1.0867			
October	Explained	1	52.1680	52.1680	10531.2	<0.005
	Unexplained	397	1.9666	0.0049		
	Total	398	54.1345			
November	Explained	1	16.0588	16.0588	5427.9	<0.005
	Unexplained	193	0.5710	0.0030		
	Total	194	16.6299			
December	Explained	1	58.9431	58.9431	10278.1	<0.005
	Unexplained	445	0.0057	0.0057		
	Total	446	58.9488			

In all cases a large and significant part of the variance was explained by regression.

APPENDIX II.4.E. ANALYSIS OF COVARIANCE TEST FOR SEASONAL VARIATIONS IN LENGTH-WEIGHT RELATIONSHIPS.

Source of Variation	Degrees of freedom	Sum of squares	Mean square	F ratio	P
Among means	6	258.8	43.13	7132.5	<0.005
Within regression	4292	25.9	0.006		
Total	4298				

APPENDIX III.1 Monthly mean total lengths (cm) of O-group whiting caught by the mid-water trawl at each site.

Year-class.	Week	Site	No.	Length range cm.	Mean length cm.	Standard error
1975	23	Loch Linnhe				
		Firth of Lorne	3	4.1 - 6.4	5.30	-
		Bloody Bay	125	2.2 - 7.3	4.17	0.98
		Ardalanish Bay	24	2.5 - 4.5	3.23	1.09
		Tiree Passage				
		All sites	152	2.2 - 7.3	4.07	
	26.5	Loch Linnhe				
		Firth of Lorne	43	3.9 - 8.4	6.07	1.51
		Bloody Bay	13	5.0 - 8.6	6.36	2.60
		Ardalanish Bay	24	4.0 - 7.6	5.07	1.51
		Tiree Passage	3	5.1 - 5.4	5.23	-
		All sites	83	3.9 - 8.6	5.80	
	30	Loch Linnhe				
		Firth of Lorne	157	5.2 -12.6	7.94	0.83
		Bloody Bay	13	5.0 - 8.6	6.36	2.60
		Ardalanish Bay	32	3.9 -10.2	6.89	2.62
		Tiree Passage	13	5.6 -11.0	7.81	4.25
		All sites	202	3.9 -12.6	7.76	
1976	27	Loch Linnhe				
		Firth of Lorne	26	4.2 - 8.0	5.90	0.19
		Bloody Bay	4	3.6 - 5.8	4.67	-
		Ardalanish Bay	8	2.6 - 5.6	3.90	0.36
		Tiree Passage				
		All sites	44	2.6 - 8.0	5.11	
	30	Loch Linnhe	349	5.5 -11.6	7.92	0.05
		Firth of Lorne	8	6.8 - 8.5	7.65	0.21
		Bloody Bay	11	3.7 - 9.8	6.45	0.81
		Ardalanish Bay	29	3.4 - 7.5	5.16	0.22
		Tiree Passage				
		All sites	397	3.4 -11.6	7.67	
	34	Loch Linnhe	44	6.9 -12.7	9.70	0.15
		Firth of Lorne	27	7.3 -11.0	9.15	0.18
		Bloody Bay	25	3.4 -10.8	6.89	0.52
		Ardalanish Bay				
		Tiree Passage	24	3.0 - 9.5	5.30	0.39
		All sites	126	3.0 -12.7	8.09	
	39	Loch Linnhe	173	7.1 -17.5	11.58	0.19
		Firth of Lorne	2	9.3 -12.8	11.05	-
		Bloody Bay	46	6.7 -13.2	9.07	0.20
		Ardalanish Bay				
		Tiree Passage	2	3.7 - 7.3	5.50	-
		All sites	223	3.7 -17.5	11.00	
	42	Loch Linnhe				
		Firth of Lorne	63	7.2 -19.7	11.57	0.38
		Bloody Bay				
		Ardalanish Bay				
		Tiree Passage				
		All sites				
	47	Loch Linnhe				
		Firth of Lorne	3	13.0 -13.3	13.17	-
		Bloody Bay				
		Ardalanish Bay				
		Tiree Passage				
		All sites				

APPENDIX III.2. MEAN TOTAL LENGTHS (cm) OF 0-GROUP AND EARLY 1-GROUP WHITING CAUGHT BY THE BOTTOM TRAWL AT EACH SITE.

Year-class	Week No.	Site	No.	Length range cm	Mean length	St. error
1975	26.5	Loch Linnhe				
		Firth of Lorne	241	5.0 -10.9	7.65	0.06
		Bloody Bay	142	5.2 -10.5	7.69	0.10
		Ardalanish Bay				
		Tiree Passage				
	30	Loch Linnhe				
		Firth of Lorne	946	6.7 -14.0	8.93	0.44
		Bloody Bay	799	6.5 -14.7	9.10	0.44
		Ardalanish Bay				
		Tiree Passage				
	34	Loch Linnhe	475	8.3 -18.0	10.83	0.82
		Firth of Lorne	1194	7.5 -17.2	10.29	0.55
		Bloody Bay	358	7.8 -18.4	11.71	0.13
		Ardalanish Bay	113	8.2 -16.2	11.73	0.18
		Tiree Passage				
	37	Loch Linnhe	798	8.9 -20.7	13.79	0.09
		Firth of Lorne	790	7.8 -19.1	10.53	0.06
		Bloody Bay	1082	8.2 -20.0	11.58	0.08
		Ardalanish Bay	372	7.4 -20.1	14.12	0.15
		Tiree Passage				
	39.5	Loch Linnhe	441	9.2 -21.2	14.35	0.15
		Firth of Lorne	416	7.2 -19.3	11.17	0.11
		Bloody Bay	432	8.1 -26.5	12.47	0.15
		Ardalanish Bay				
		Tiree Passage				
1976	23.0	Loch Linnhe	2	7.5 - 8.0	7.75	-
		Firth of Lorne	6	5.5 - 6.4	5.82	0.17
		Bloody Bay	0			
		Ardalanish Bay	0			
		Tiree Passage	2	5.3 - 5.8	5.55	-
		All sites	10	5.3 - 8.0	6.15	0.29
	27.0	Loch Linnhe	8	6.6 - 8.6	7.80	0.28
		Firth of Lorne	180	5.6 -10.3	7.69	0.08
		Bloody Bay	1	7.4	7.4	-
		Ardalanish Bay	6	6.2 - 9.5	7.67	0.49
		Tiree Passage				
		All sites	195	5.6 -10.3	7.70	0.08
	30.0	Loch Linnhe	173	6.2 -12.5	8.22	0.11
		Firth of Lorne	166	6.7 -12.4	8.58	0.12
		Bloody Bay	91	6.1 -12.8	8.58	0.13
		Ardalanish Bay	33	4.1 -11.9	8.02	0.22
		Tiree Passage	1	8.8	8.8	-
		All sites	464	4.1 -12.8	8.41	0.06
	34.0	Loch Linnhe	71	8.3 -15.8	11.15	0.15
		Firth of Lorne	459	6.7 -15.9	9.58	0.85
		Bloody Bay	27	7.3 -14.5	9.92	0.28
		Ardalanish Bay	79	6.6 -15.3	8.85	0.18
		Tiree Passage	5	8.1 -10.3	9.16	0.46
		All sites	641	6.6 -15.9	9.67	0.07
	39.0	Loch Linnhe	416	5.6 -20.1	13.63	0.13
		Firth of Lorne	276	7.0 -20.4	12.39	0.21
		Bloody Bay	414	6.5 -19.7	12.00	0.14
		Ardalanish Bay	356	6.3 -18.8	11.80	0.15
		Tiree Passage	3	12.7 -15.2	14.30	-
		All sites	1465	5.6 -20.4	12.49	0.08
	42.0	Loch Linnhe	253	7.0 -21.6	15.23	0.21
		Firth of Lorne	141	7.0 -19.6	-	
		Bloody Bay	459	7.6 -22.3	14.09	0.17
		Ardalanish Bay	88	7.5 -19.2	12.41	0.32
		Tiree Passage	12	11.8 -19.8	14.82	0.61
		All sites	953	7.0 -22.3	14.20	0.11
	47.0	Loch Linnhe	262	8.2 -22.9	17.31	0.18
		Firth of Lorne	283	8.3 -23.0	15.15	0.19
		Bloody Bay	447	9.1 -24.4	16.66	0.15
		Ardalanish Bay	64	8.8 -21.6	13.73	0.48
		Tiree Passage	24	9.0 -19.4	14.40	0.66
		All sites	1080	8.2 -24.4	16.20	0.10
	50.0	Loch Linnhe	141	8.0 -21.9	15.70	0.31
		Firth of Lorne	133	9.1 -22.3	16.37	0.21
		Bloody Bay	195	8.1 -24.1	18.33	0.27
		Ardalanish Bay	46	7.4 -23.5	16.65	0.80
		Tiree Passage	12	13.6 -19.3	15.93	0.41
		All sites	527	7.4 -24.1	16.93	0.16
	56.0	Loch Linnhe	248	9.1 -22.7	16.65	0.16
		Firth of Lorne	30	10.3 -19.1	16.14	0.42
		Bloody Bay	77	12.3 -23.5	18.82	0.28
		Ardalanish Bay	56	11.1 -24.5	18.84	0.46
		Tiree Passage	26	13.6 -25.7	21.90	0.47
		All sites	437	9.1 -25.7	17.59	0.14
	60.0	Loch Linnhe	69	10.8 -18.0	13.75	0.19
		Firth of Lorne	7	13.2 -16.0	14.47	0.44
		Bloody Bay	158	8.1 -21.4	15.42	0.22
		Ardalanish Bay	32	11.1 -23.4	18.76	0.52
		Tiree Passage	86	11.9 -26.0	19.88	0.28
		All sites	352	8.1 -26.0	16.47	0.18
	63.0	Loch Linnhe	20	11.2-18.0	14.59	0.46
		Firth of Lorne	38	10.4 -18.7	14.33	0.32
		Bloody Bay	117	9.4 -24.0	17.04	0.24
		Ardalanish Bay	25	15.6 -26.0	19.03	0.95
		Tiree Passage	199	9.4 -26.0	16.61	0.21

APPENDIX III.3. STATISTICS FOR REGRESSION OF REDUCTION IN CATCH RATES OF *Merlangius merlangus* WITH AGE.

ESTIMATES OF CATCH RATE FOR ALL YEAR-CLASSES IN EACH YEAR (1975 and 1976) WERE USED TO DETERMINE REGRESSION. AGE IS MEASURED IN WEEKS FROM DATE OF BIRTH (1st JANUARY OF AGE GROUP 0) AND ALL ESTIMATES OF CATCH RATE FROM WEEK 37 ON WERE USED.

Site	Regression
Loch Linnhe	$Y = 4.1489 - 0.0373X$
Firth of Lorne	$Y = 5.9366 - 0.0631X$
Bloody Bay	$Y = 5.1696 - 0.0396X$
Ardalanish Bay	$Y = 2.8858 - 0.0141X$
Tiree Passage	$Y = 2.9261 - 0.0104X$

Y = Catch rate in log units

X = Age from date of Birth in weeks

Site	Source of variation	D.F.	Sum of squares	Mean square	F.ratio	P
Loch Linnhe	Explained Unexplained Total	1 43 44	35.61 9.07 44.68	35.61 0.21	168.91	<0.001
Firth of Lorne	Explained Unexplained Total	1 25 26	25.52 2.83	25.52 0.11	225.05	<0.001
Bloody Bay	Explained Unexplained Total	1 47 48	48.21 10.57 58.99	48.21 0.22	215.33	<0.001
Ardalanish Bay	Explained Unexplained Total	1 80 81	34.04 34.98 69.02	34.04 0.44	77.86	<0.001
Tiree Passage	Explained Unexplained Total	1 74 75	21.68 35.37 56.95	21.68 0.48	45.50	<0.001

(i.e.) In all cases a large and highly significant part of the variance of the catch rates has been explained by regression.

APPENDIX III.4. MONTHLY SEX-RATIOS OF WHITING, BY SITE. (FISH OF THE 2-GROUP OR OLDER POOLED).

Age	Mth.	Loch Linnhe			Firth of Lorne			Bloody Bay			Ardalanish Bay			Tiree Passage			All sites		
		No ♂	No ♀	% ♂	No ♂	No ♀	% ♂	No ♂	No ♀	% ♂	No ♂	No ♀	% ♂	No ♂	No ♀	% ♂	No ♂	No ♀	% ♂
0	O	97	96	50.3	119	101	54.1	135	128	51.7	19	13	59.4				370	338	52.3
	N	82	86	48.8	99	102	49.2	91	106	46.2	2	5	-				274	299	47.8
	D	252	241	51.1	161	195	45.2	293	304	49.1	100	98	50.5	59	44	57.3	865	882	49.5
1	J	125	148	45.8	137	145	48.6	161	178	47.5	86	76	53.1	54	65	45.4	563	614	47.8
	F																		
	M	137	163	45.7	20	15	57.1	197	188	51.2	113	111	50.4	170	171	49.8	637	648	49.6
	A	24	22	52.2	38	40	48.7	142	140	50.3	95	129	42.4	168	147	53.3	467	478	49.4
	M	34	39	46.6	26	43	37.7	197	154	56.1	105	113	48.2	99	85	53.8	462	435	51.5
	J				25	27	48.1	33	25	56.9				29	14	67.4	87	66	56.9
	J	5	3		17	7	70.8	240	181	57.0	131	113	53.7	226	308	42.3	619	612	50.3
	A	10	10					96	75	56.1	53	40	57.0	63	33	65.6	222	158	58.4
	S	2	1					42	39	51.8	82	123	40.0	138	110	55.6	264	273	49.2
	O	1	1					16	16	50.0	162	212	43.3	91	48	65.5	270	277	49.4
	N	3	1		1	0		11	8	57.9	39	72	35.1	30	7	81.1	84	88	48.8
	D	6	0		1	1		7	8		47	60	43.9	104	79	56.8	161	148	52.1
2+	J	1	0					9	5		48	77	38.4	43	66	39.4	101	148	40.6
	F										1	1		9	16	36.0	10	17	37.0
	M										8	5		5	10	33.0	13	15	46.4
	A	2	2					0	1		2	5	-	31	52	37.3	35	60	36.8
	M				0	1					9	19	32.1	146	157	48.2	155	177	46.7
	J										6	6		25	33	43.1	32	39	45.1
	J	2	0								22	23	48.8	162	158	50.6	186	181	50.7
	A										11	6		1	3	-	12	9	57.1
	S										2	1		15	18	45.4	17	19	47.2
	O	0	1								5	6		16	21	43.2	21	28	42.9
	N	0	1								4	10		1	0	-	5	11	31.2
	D	0	1		0	1					4	8		2	9		6	19	24.0
Total		783	816	49.0	644	678	48.7	1670	1556	51.8	1156	1332	46.5	1687	1654	50.5	5938	6039	49.6

APPENDIX III.5.A. VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF WHITING WITH SEX.

All fish	log w = 3.1949 log l - 4.6055
All males	log w = 3.1680 log l - 4.5425
All females	log w = 3.1416 log l - 4.4852
Immatures	log w = 3.1171 log l - 4.4113

N.B. Immatures = young 0-group fish whose sex could not be determined.

Sex	Source of variation	Degrees of freedom	Sum of squares	Mean square	F.ratio	P
All fish	Explained	1	1166.3125	1166.3125	16845.28	<0.005
	Unexplained	12404	858.8125	0.06924		
	Total	12405	2025.1250			
All males	Explained	1	714.4102	714.4102	15684.33	<0.005
	Unexplained	6176	281.3125	0.04555		
	Total	6177	995.7227			
All females	Explained	1	779.6406	779.6406	17126.75	<0.005
	Unexplained	6114	278.3203	0.04552		
	Total	6115	1057.9609			
Immatures	Explained	1	20.5510	20.5510	7940.32	<0.005
	Unexplained	110	0.2847	0.00259		
	Total	111	20.8357			

In all cases a large and significant part of the variance has been explained by regression.

Analysis of covariance test for comparison of slopes between sexes.

F ratio for residual variances = 1.0006
degrees of freedom = 6115,6176

(i.e.) approximately homogeneous

Comparison of slopes:

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio	P
Among means	1	92802.1875	92802.1875	2038344.0	<0.005
Within regression	12292	559.6328	0.045528		
Total	12293	9839.8203			

(i.e.) very highly significant.

APPENDIX III.5.B. SEASONAL VARIATIONS IN LENGTH-WEIGHT RELATIONSHIP.

FISH FROM TIREE PASSAGE AND ARDALANISH BAY ONLY WERE USED IN ORDER TO AVOID BIAS IN FAVOUR OF JUVENILES.

Month	Male G.M. regression	Female G.M. regression
January	log w = 3.2712 log l -4.7974	log w = 3.3055 log l -4.8923
March	log w = 3.2451 log l -4.7590	log w = 3.2024 log l -4.6621
April	log w = 3.0121 log l -4.2169	log w = 2.9146 log l -3.9907
May	log w = 2.9521 log l -4.0676	log w = 2.9092 log l -3.9614
June	log w = 2.8475 log l -3.7924	log w = 2.8324 log l -3.7540
July	log w = 2.9991 log l -4.1279	log w = 2.9472 log l -3.9974
August	log w = 3.0449 log l -4.2448	log w = 3.0945 log l -4.3755
September	log w = 3.0958 log l -4.3552	log w = 3.0745 log l -4.3068
October	log w = 3.0380 log l -4.2165	log w = 3.0254 log l -4.1930
November	log w = 3.1417 log l -4.4686	log w = 3.0953 log l -4.3586
December	log w = 3.3445 log l -4.9699	log w = 3.3166 log l -4.9127

Month	Source of variation	Degrees of Freedom	Sum of Squares	Mean square	F ratio	P
Male January	Explained	1	21.8879	21.8879	37351.36	<0.005
	Unexplained	211	1.2366	0.000586		
	Total	212	23.1245			
Male March	Explained	1	9.9004	9.9004	1578.442	<0.005
	Unexplained	292	1.8315	0.000627		
	Total	293	11.7319			
Male April	Explained	1	11.8979	11.8979	2113.202	<0.005
	Unexplained	294	1.6553	0.000563		
	Total	295	13.5532			
Male May	Explained	1	24.7749	24.7749	3962.449	<0.005
	Unexplained	351	2.1946	0.000625		
	Total	352	26.9695			
Male June	Explained	1	2.7476	2.7476	2525.053	<0.005
	Unexplained	59	0.0642	0.000109		
	Total	60	2.8118			
Male July	Explained	1	8.6328	8.6328	1611.903	<0.005
	Unexplained	539	2.8867	0.000536		
	Total	540	11.5195			
Male August	Explained	1	3.6392	3.6392	3024.665	<0.005
	Unexplained	126	0.1516	0.000120		
	Total	127	3.7908			
Male September	Explained	1	2.7668	2.7668	878.9404	<0.005
	Unexplained	236	0.7429	0.000315		
	Total	237	3.5098			
Male October	Explained	1	6.8181	6.8181	2053.526	<0.005
	Unexplained	291	0.9805	0.000337		
	Total	292	7.7986			
Male November	Explained	1	3.6340	3.6340	3487.886	<0.005
	Unexplained	74	0.0771	0.000104		
	Total	75				
Male December	Explained	1	27.7061	27.7061	5836.636	<0.005
	Unexplained	228	1.0823	0.000475		
	Total	229	28.7883			
Female January	Explained	1	36.5317	36.5317	4146.417	<0.005
	Unexplained	265	2.3342	0.000881		
	Total	266	38.8660			
Female March	Explained	1	15.4746	15.4746	1679.616	<0.005
	Unexplained	296	2.7271	0.000921		
	Total	297	18.2017			
Female April	Explained	1	17.2112	17.2112	3539.331	<0.005
	Unexplained	331	1.6096	0.000486		
	Total	332	18.8208			
Female May	Explained	1	34.3809	34.3809	7892.769	<0.005
	Unexplained	375	1.6335	0.0004356		
	Total	376	36.0144			
Female June	Explained	1	2.8376	2.8376	3529.698	<0.005
	Unexplained	51	0.0410	0.000080		
	Total	52	2.8787			
Female July	Explained	1	10.7227	10.7227	2490.194	<0.005
	Unexplained	469	2.0195	0.000431		
	Total	470	12.7422			
Female August	Explained	1	2.8330	2.8330	931.201	<0.005
	Unexplained	78	0.2373	0.000304		
	Total	79	3.0703			
Female September	Explained	1	3.2668	3.2668	949.255	<0.005
	Unexplained	251	0.8638	0.000344		
	Total	252	4.1306			
Female October	Explained	1	8.9351	8.9351	2694.182	<0.005
	Unexplained	298	0.9883	0.000332		
	Total	299	9.9233			
Female November	Explained	1	5.8008	5.8008	156962.800	<0.005
	Unexplained	92	0.0034	0.000004		
	Total	93	5.8042			
Female December	Explained	1	30.8755	30.8755	4913.246	<0.005
	Unexplained	208	1.3071	0.000628		
	Total	209	32.1826			

(i.e.) In all cases a large and significant part of the variance has been explained by regression.

APPENDIX III.5.C. VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF WHITING WITH MATURATION.

Maturity stage	Male GM regression	Female GM regression
All stage 1	log w = 3.3017 log 1 - 4.8640	log w = 3.3017 log 1 - 4.8640
II	log w = 3.2184 log 1 - 4.6698	log w = 3.2954 log 1 - 4.8675
III	log w = 3.3177 log 1 - 4.9112	log w = 3.2332 log 1 - 4.7077
IV	log w = 3.3502 log 1 - 5.0151	log w = 3.3195 log 1 - 4.9687
V	log w = 3.2409 log 1 - 4.7674	log w = 3.1283 log 1 - 4.5077
VI		
VII	log w = 3.5126 log 1 - 5.4673	log w = 3.3004 log 1 - 4.9489

Maturity stage.	Source of variation	D. f.	Sum of squares	Mean square	F ratio	P
All stage 1	Explained Unexplained Total	1 2532 2533	165.5156 46.5469 212.0625	165.5156 0.01838	9003.51	<0.005
Male stage II	Explained Unexplained Total	1 1192 1193	61.3320 0.6484 61.9805	61.3320 0.00054	112750.99	<0.005
Male stage III	Explained Unexplained Total	1 327 328	15.7559 1.8059 17.5618	15.7559 0.005523	2852.97	<0.005
Male stage IV	Explained Unexplained Total	1 68 69	2.7751 0.2615 3.0366	2.7751 0.00385	721.63	<0.005
Male stage V	Explained Unexplained Total	1 24 25	1.1038 0.0498 1.1536	1.1038 0.00207	531.95	<0.005
Male stage VII	Explained Unexplained Total	1 78 79	1.1140 0.6035 1.7175	1.1140 0.00774	143.98	<0.005
Female stage II	Explained Unexplained Total	1 1140 1141	79.0391 1.5273 80.5664	79.0391 0.00134	5899.99	<0.005
Female stage III	Explained Unexplained Total	1 214 215	7.0725 1.6113 8.6838	7.0725 0.00753	939.31	<0.005
Female stage IV	Explained Unexplained Total	1 49 50	1.4990 0.1157 1.6147	1.4990 0.00236	634.84	<0.005
Female stage V	Explained Unexplained Total	1 21 22	1.7068 0.0701 1.7769	1.7068 0.00334	511.31	<0.005
Female stage VII	Explained Unexplained Total	1 123 124	3.5928 0.2876 3.8804	3.5928 0.00234	1536.56	<0.005

In all cases a large and significant part of the variance has been explained by regression.

APPENDIX IV.1. MEAN TOTAL LENGTHS (cm) OF 0-GROUP AND EARLY 1 GROUP NORWAY POUT CAUGHT BY THE BOTTOM TRAWL

Year	Week No	Site	No.	Length range cm	Mean length cm	Standard error
1975	26.5	Loch Linnhe	-	-	-	-
		Firth of Lorne	-	-	-	-
		Bloody Bay	712	4.0 -8.8	6.09	0.03
		Ardalanish Bay	165	4.0 -7.2	5.73	0.04
		Tiree Passage	1019	3.2 -8.4	6.38	0.02
	30.0	Loch Linnhe	-	-	-	-
		Firth of Lorne	3	5.8 -9.6	7.2	-
		Bloody Bay	101	5.4 -9.9	7.41	0.07
		Ardalanish Bay	16	4.0 -8.4	6.84	0.23
		Tiree Passage	543	5.0 -8.7	6.94	0.03
	34.0	Loch Linnhe	-	-	-	-
		Firth of Lorne	-	-	-	-
		Bloody Bay	354	8.0 -10.8	9.39	0.03
		Ardalanish Bay	1058	6.0 -10.4	8.45	0.02
		Tiree Passage	-	-	-	-
	37.0	Loch Linnhe	21	8.6 -10.8	9.83	0.12
		Firth of Lorne	3	8.8 -9.9	9.33	-
		Bloody Bay	821	8.4 -11.1	9.65	0.02
		Ardalanish Bay	886	6.9 -11.6	9.21	0.02
		Tiree Passage	689	7.0 -10.7	9.07	0.02
	39.5	Loch Linnhe	50	7.9 -12.2	10.63	0.11
		Firth of Lorne	-	-	-	-
		Bloody Bay	567	7.9 -11.8	10.02	0.02
		Ardalanish Bay	229	6.8 -11.0	9.34	0.05
		Tiree Passage	424	7.3 -12.4	9.93	0.04
	27.0	Loch Linnhe	-	-	-	-
		Firth of Lorne	-	-	-	-
		Bloody Bay	-	-	-	-
		Ardalanish Bay	97	3.6 -6.8	5.03	0.06
		Tiree Passage	30	4.7 -6.5	5.84	0.07
	30.0	Loch Linnhe	-	-	-	-
		Firth of Lorne	-	-	-	-
		Bloody Bay	7	6.2 -6.9	6.61	0.11
		Ardalanish Bay	780	5.0 -8.5	6.42	0.02
		Tiree Passage	415	5.0 -8.4	6.44	0.03
	34.0	Loch Linnhe	13	7.9 -10.0	8.85	0.18
		Firth of Lorne	-	-	-	-
		Bloody Bay	221	6.9 -10.2	8.65	0.04
		Ardalanish Bay	291	6.1 -9.8	8.08	0.03
		Tiree Passage	239	5.8 -10.3	7.56	0.04

Year	Week No.	Site	No.	Length range cm	Mean length cm	Standard error
1976	39.0	Loch Linnhe	17	9.7 - 11.5	10.64	0.12
		Firth of Lorne	11	9.3 - 10.6	9.84	0.13
		Bloody Bay	290	7.9 - 11.2	9.56	0.03
		Ardalanish Bay	340	7.4 - 10.5	8.88	0.03
		Tiree Passage	290	6.7 - 10.3	8.06	0.03
	42.0	Loch Linnhe	19	8.7 - 12.0	10.66	0.20
		Firth of Lorne	95	8.1 - 11.3	9.67	0.07
		Bloody Bay	308	8.5 - 11.8	9.88	0.03
		Ardalanish Bay	401	7.7 - 11.0	9.26	0.03
		Tiree Passage	281	7.2 - 10.6	9.10	0.04
	47.0	Loch Linnhe	87	8.6 - 12.7	10.45	0.10
		Firth of Lorne	300	8.2 - 11.5	9.70	0.04
		Bloody Bay	335	8.6 - 12.3	10.08	0.03
		Ardalanish Bay	238	7.6 - 12.3	9.40	0.04
		Tiree Passage	304	7.8 - 11.6	9.43	0.04
	50.0	Loch Linnhe	30	8.7 - 12.2	9.90	0.16
		Firth of Lorne	306	8.4 - 11.9	9.91	0.03
		Bloody Bay	300	8.2 - 13.1	10.28	0.04
		Ardalanish Bay	210	8.2 - 11.6	9.80	0.04
		Tiree Passage	43	8.3 - 11.7	10.03	0.09
	56.0	Loch Linnhe	81	8.8 - 13.5	11.23	0.12
		Firth of Lorne	100	8.4 - 11.1	9.94	0.05
		Bloody Bay	175	9.3 - 12.2	10.53	0.43
		Ardalanish Bay	50	8.4 - 11.6	10.21	0.10
		Tiree Passage	66	9.0 - 13.0	10.19	0.92
	60.0	Loch Linnhe	210	8.7 - 13.5	10.79	0.06
		Firth of Lorne	200	8.6 - 11.2	9.83	0.04
		Bloody Bay	219	8.8 - 11.5	9.98	0.05
		Ardalanish Bay	204	8.5 - 13.3	10.11	0.05
		Tiree Passage	239	8.6 - 14.2	10.79	0.07
	63.0	Loch Linnhe	100	8.9 - 12.9	10.58	0.08
		Firth of Lorne	65	8.8 - 12.6	10.28	0.09
		Bloody Bay	100	9.0 - 11.4	10.16	0.05
		Ardalanish Bay	29	8.0 - 13.3	10.40	0.26
		Tiree Passage	-	-	-	-

APPENDIX IV.2. STATISTICS FOR REGRESSION OF THE REDUCTION IN CATCH RATES OF <u>Trisopterus esmarkii</u> WITH AGE. ESTIMATES OF CATCH RATES FOR ALL YEAR-CLASSES IN EACH YEAR (1975 and 1976) WERE USED. AGE WAS MEASURED IN WEEKS FROM DATE OF BIRTH (1st JANUARY OF THE 0-GROUP) **AND ALL** ESTIMATES OF CATCH RATES FROM WEEK 50 ON WERE USED.

Site	Regression
Loch Linnhe	$Y = 3.56 - 0.024X$
Firth of Lorne	$Y = 5.90 - 0.054X$
Bloody Bay	$Y = 4.73 - 0.034X$
Ardalanish Bay	$Y = 4.37 - 0.029X$
Tiree Passage	$Y = 4.00 - 0.021X$

(where Y = Catch rate $\log_{10}(n + 1)$
X = Age from date of birth in weeks)

Site	Source of variation	D.F.	Sum of squares	Mean square	F ratio	P
Loch Linnhe	Explained	1	14.14	14.14	40.80	<0.005
	Unexplained	43	14.90	0.35		
	Total	44	29.04			
Firth of Lorne	Explained	1	19.90	19.90	43.31	<0.005
	Unexplained	22	10.11	0.46		
	Total	23	30.01			
Bloody Bay	Explained	1	14.21	14.21	13.94	<0.005
	Unexplained	27	27.51	1.02		
	Total	28	41.72			
Ardalanish Bay	Explained	1	26.47	26.47	72.81	<0.005
	Unexplained	46	16.73	0.36		
	Total	47	43.20			
Tiree Passage	Explained	1	56.45	56.45	80.84	<0.005
	Unexplained	62	43.29	0.70		
	Total	63	99.74			

In all cases a large and highly significant part of the variance of catch rates has been explained by regression.

APPENDIX IV.3. MONTHLY SEX-RATIOS OF ALL NORWAY POUT EXAMINED, BY SITE (FISH OF THE 2-GROUP AND OVER POOLED).

		Loch Linnhe			Firth of Lorne			Bloody Bay			Ardalanish Bay			Tiree Passage			All sites		
Age	Month	No ♂	No ♀	% ♂	No♂	No. ♀	% ♂	No. ♂	No. ♀	% ♂	No. ♂	No. ♀	% ♂	No. ♂	No.♀	% ♂	No.♂	No.♀	% ♂
0	O	43	24	64.2	96	103	48.2	113	84	57.4	60	56	51.7	3	10		315	277	53.2
	N	35	48	42.2	154	179	46.2	157	168	48.3	131	128	50.6	-	-		477	523	47.7
	D	11	6	64.7	84	101	45.4	182	220	45.3	55	51	51.9	101	93	52.1	433	471	47.9
1	J	43	24	64.2	97	177	35.4	161	167	49.8	135	131	50.7	30	40	42.9	466	539	46.4
	F																		
	M	192	244	44.0	158	166	48.8	72	174	29.3	173	218	44.2	172	146	54.1	767	948	44.7
	A	62	72	46.3	115	137	45.6	16	45	26.2	81	108	42.9	168	134	55.6	442	496	47.1
	M	79	121	39.5	137	162	45.8	114	117	49.3	156	244	39.0	121	78	60.8	607	722	45.7
	J	5	5	50.0	28	41	40.6	98	102	49.0	5	3	62.5	94	98	49.0	230	249	48.0
	J	62	74	45.6	26	25	51.0	3	4	42.9	353	280	55.8	278	193	59.0	722	576	55.6
	A	54	50	51.9	1	0	-	16	41	28.1	36	40	47.4	42	57	42.4	149	188	44.2
	S	68	63	51.9	1	1	-	6	3	66.6	11	12	47.8	3	4		89	83	51.7
	O	70	64	52.2	0	0		0	0	-	38	30	55.9	53	46	53.5	161	140	53.5
	N	71	61	53.8	5	11	31.2	21	41	33.9	29	31	48.3	0	0		126	144	46.7
	D	16	31	34.0	5	22	18.5	9	15	37.5	19	10	65.5	4	2		53	80	39.8
2+	J	37	49	43.0	0	0		31	45	40.8	48	43	52.7	47	54	46.5	163	191	46.0
	F	2	1	63.0	0	0		0	0		2	3		20	15	57.1	24	19	55.8
	M	0	3	0	0	0		0	1		3	5		14	25	35.9	17	34	33.3
	A	1	1	50.0	0	0		0	1		11	8		17	11	60.7	29	21	58.0
	M	0	1		0	0		1	0		0	0		38	46	45.2	39	47	45.3
	J	5	2		0	0		0	0		4	11		2	6		11	19	36.7
	J	0	0		0	0		0	0		3	3		2	3		5	6	
	A	0	0		0	0		0	0		0	0		0	1		0	1	
	S	0	0		0	0		0	0		0	0		0	0		0	0	
	O	0	0		0	0		0	0		0	0		1	2		1	2	
	N	1	2		0	0		0	0		0	2		0	2		1	4	
	D	0	0		0	0		0	0		0	0		1	3		1	3	
Total		857	946	47.5	907	1125	44.6	1000	1228	44.9	1353	1777	43.2	1211	1067	53.2	5328	5783	47.9

APPENDIX IV.4.A. VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF NORWAY POUT OF EACH SEX.

	G.M. Functional regression
All fish	$\log w = 3.3541 \log l - 4.9474$
All males	$\log w = 3.4769 \log l - 5.1980$
All females	$\log w = 3.4047 \log l - 5.0569$
Immatures	$\log w = 3.1758 \log l - 4.6013$

(Immatures = young O-group fish whose sex could not be determined.

Maturity stage	Source of variation	Degrees of Freedom	Sum of squares	Mean square	F ratio	P
All fish	Explained Unexplained Total	1 11484 11485	478.4844 474.7070 953.1914	478.4844 0.041336	11575.4	<0.005
All males	Explained Unexplained Total	1 5298 5299	183.3242 183.4336 366.7578	183.3242 0.034623	5294.8	<0.005
All females	Explained Unexplained Total	1 5723 5724	212.8906 197.7969 410.6875	212.8906 0.034561	6159.7	<0.005
Immatures	Explained Unexplained Total	1 459 460	84.9221 6.0962 91.0183	84.9221 0.013282	6394.0	<0.005

In all cases a large and highly significant part of the variance has been explained by regression.

APPENDIX IV.4.B. ANALYSIS OF COVARIANCE TEST TO COMPARE THE LENGTH-WEIGHT RELATIONSHIPS OF MALE AND FEMALE NORWAY POUT.

(1) F test for residual variance

	d.f.	Unexplained sum of squares	Unexplained mean squares	F ratio
Males	5298	183.4336	0.03462	1.0018
Females	5723	197.7969	0.03456	
Total	11021			

Statistical tables do not give F ratios for such large degrees of freedom, but it seems unlikely that this F ratio is very significant.

(2) F test for comparison of slopes

Source of variance	d.f.	Sum of squares	Mean square	F ratio
Among means	1	43887.2109	43887.2109	1268966.0
Within regression	11023	381.2305	0.034585	
Total	11024	44268.4414		

This F ratio is very highly significant ($P \ll 0.001$)

APPENDIX IV.4.C. VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF NORWAY POUT WITH MATURITY. FISH OF ALL AGES FROM TIREE PASSAGE AND ARDALANISH BAY WERE USED TO CALCULATE THE REGRESSIONS.

Maturity stage	Male G.M. regression	Female G.M. regression
I	$\log w = 3.6995 \log l - 5.6614$	$\log w = 3.6821 \log l - 5.6338$
II	$\log w = 3.6911 \log l - 5.6692$	$\log w = 3.7240 \log l - 5.7772$
III	$\log w = 3.5466 \log l - 5.4052$	$\log w = 3.8210 \log l - 6.0242$
IV	$\log w = 3.6872 \log l - 5.7609$	$\log w = 3.5350 \log l - 5.4948$
VII	$\log w = 3.0080 \log l - 4.2255$	$\log w = 4.0954 \log l - 6.7237$

Maturity stage	Source of variation	Degrees of Freedom	Sum of squares	Mean square	F.ratio	P
Male stage 1	Explained	1	141.0781	141.0781	18730.37	<0.005
	Unexplained	1922	14.4766	0.007532		
	Total	1923	155.5547			
Male stage II	Explained	1	21.7356	21.7356	2513.23	<0.005
	Unexplained	460	3.9783	0.008648		
	Total	461	25.7139			
Male Stage III	Explained	1	6.0164	6.0164	3795.21	<0.005
	Unexplained	95	0.1506	0.001585		
	Total	96	6.1670			
Male stage IV	Explained	1	0.5070	0.5070	137.52	<0.005
	Unexplained	15	0.0553	0.003687		
	Total	16	0.5623			
Male stage VII	Explained	1	0.3191	0.3191	108.51	<0.005
	Unexplained	27	0.0794	0.002941		
	Total	28	0.3985			
Female stage 1	Explained	1	141.1406	141.1406	59885.71	<0.005
	Unexplained	2027	4.7773	0.002357		
	Total	2028	145.9179			
Female stage II	Explained	1	17.4023	17.4023	2019.99	<0.005
	Unexplained	286	2.4639	0.008615		
	Total	287	19.8662			
Female stage III	Explained	1	4.6965	4.6965	946.13	<0.005
	Unexplained	72	0.3574	0.004964		
	Total	73	5.0540			
Female stage IV	Explained	1	0.3343	0.3343	102.79	<0.005
	Unexplained	21	0.0683	0.003252		
	Total	22	0.4026			
Female stage VII	Explained	1	0.3122	0.3122	29.21	<0.005
	Unexplained	17	0.1817	0.010688		
	Total	18	0.4939			

In all cases a large and significant part of the variance has been explained by regression.

rees f edom	Sum of Squares	Mean Square	F ratio	P
1 12 13	0.0832 0.0091 0.0923	0.0832 0.000758	109.71	<0.005
1 53 54	16.7014 0.3308 17.0322	16.7014 0.002162	7724.65	<0.005
1 04 05	4.2424 0.0967 4.3391	4.2424 0.000930	4562.66	<0.005
1 78 79	7.0300 0.4536 7.4836	7.0300 0.002548	2758.69	<0.005
1 235 236	21.9312 1.4412 23.3723	21.9312 0.006133	3576.07	<0.005
1 392 393	10.3831 2.0046 12.3877	10.3831 0.005114	2030.42	<0.005
1 257 258	6.0718 1.6045 7.6763	6.0718 0.006243	972.55	<0.005
1 152 153	4.5655 0.3223 4.9878	4.5655 0.002120	2153.14	<0.005
1 116 117	1.7217 0.0540 1.7756	1.7217 0.000465	3698.47	<0.005
1 478 479	2.3105 1.4785 3.7891	2.3105 0.003093	746.99	<0.005
1 96 97	0.7000 0.0747 0.7747	0.7000 0.000778	899.60	<0.005
		0.0632	74.98	<0.005

Month	Source of variation	Degrees of Freedom	Sq
Female November	Explained Unexplained Total	1 99 100	4 0 4
Female December	Explained Unexplained Total	1 157 158	5 0 6

i.e. in all cases a large and signi

explained by regression.

APPENDIX IV.4.D. SEASONAL VARIATIONS IN THE LENGTH-WEIGHT RELATIONSHIP OF NORWAY POUT. FISH FROM TIREE PASSAGE AND ARDALANISH BAY ONLY WERE USED IN ORDER TO AVOID BIAS IN FAVOUR OF JUVENILES.

Month	Male G.M. regression	Female G.M. regression
January	log w = 3.2733 log 1 -4.8031	log w = 3.3703 log 1 -5.0004
March	log w = 3.5018 log 1 -5.3227	log w = 3.2616 log 1 -4.8373
April	log w = 3.2526 log 1 -4.8002	log w = 3.0011 log 1 -4.2841
May	log w = 3.4692 log 1 -5.1808	log w = 3.4329 log 1 -5.1149
June	log w = 3.0020 log 1 -4.1477	log w = 2.9280 log 1 -3.9875
July	log w = 3.3741 log 1 -4.9474	log w = 3.1728 log 1 -4.5207
August	log w = 3.3046 log 1 -4.7836	log w = 3.2916 log 1 -4.7642
September	log w = 3.3128 log 1 -4.8239	log w = 3.4925 log 1 -5.2288
October	log w = 3.2713 log 1 -4.7418	log w = 3.2275 log 1 -4.6494
November	log w = 3.2847 log 1 -4.7908	log w = 3.2178 log 1 -4.6565
December	log w = 3.1984 log 1 -4.6149	log w = 3.2382 log 1 -4.7015

Month	Source of variation	Degrees of Freedom	Sum of Squares	Mean Square	F ratio	P
Male January	Explained	1	18.9021	18.9021	2853.19	<0.005
	Unexplained	229	1.5171	0.006625		
	Total	230	20.4192			
Male March	Explained	1	6.9167	6.9167	1206.58	<0.005
	Unexplained	360	2.0637	0.005732		
	Total	361	8.9805			
Male April	Explained	1	9.3621	9.3621	1610.45	<0.005
	Unexplained	270	1.5696	0.005813		
	Total	271	10.9316			
Male May	Explained	1	5.5630	5.5630	2029.96	<0.005
	Unexplained	178	0.4878	0.002740		
	Total	179	6.0508			
Male June	Explained	1	1.2007	1.2007	2001.17	<0.005
	Unexplained	103	0.0618	0.0006		
	Total	104	1.2625			
Male July	Explained	1	4.0664	4.0664	961.17	<0.005
	Unexplained	636	2.6907	0.004231		
	Total	637	6.7571			
Male August	Explained	1	0.6719	0.6719	466.77	<0.005
	Unexplained	76	0.1094	0.001439		
	Total	77	0.7813			
Male September	Explained	1	0.0832	0.0832	109.71	<0.005
	Unexplained	12	0.0091	0.000758		
	Total	13	0.0923			
Male October	Explained	1	16.7014	16.7014	7724.65	<0.005
	Unexplained	153	0.3308	0.002162		
	Total	154	17.0322			
Male November	Explained	1	4.2424	4.2424	4562.66	<0.005
	Unexplained	104	0.0967	0.000930		
	Total	105	4.3391			
Male December	Explained	1	7.0300	7.0300	2758.69	<0.005
	Unexplained	178	0.4536	0.002548		
	Total	179	7.4836			
Female January	Explained	1	21.9312	21.9312	3576.07	<0.005
	Unexplained	235	1.4412	0.006133		
	Total	236	23.3723			
Female March	Explained	1	10.3831	10.3831	2030.42	<0.005
	Unexplained	392	2.0046	0.005114		
	Total	393	12.3877			
Female April	Explained	1	6.0718	6.0718	972.55	<0.005
	Unexplained	257	1.6045	0.006243		
	Total	258	7.6763			
Female May	Explained	1	4.5655	4.5655	2153.14	<0.005
	Unexplained	152	0.3223	0.002120		
	Total	153	4.9878			
Female June	Explained	1	1.7217	1.7217	3698.47	<0.005
	Unexplained	116	0.0540	0.000465		
	Total	117	1.7756			
Female July	Explained	1	2.3105	2.3105	746.99	<0.005
	Unexplained	478	1.4785	0.003093		
	Total	479	3.7891			
Female August	Explained	1	0.7000	0.7000	899.60	<0.005
	Unexplained	96	0.0747	0.000778		
	Total	97	0.7747			
Female September	Explained	1	0.0632	0.0632	74.98	<0.005
	Unexplained	14	0.0118	0.000843		
	Total	15	0.0750			
Female October	Explained	1	16.9419	16.9419	10263.68	<0.005
	Unexplained	142	0.2759	0.001943		
	Total	143	17.2178			
Female November	Explained	1	4.4053	4.4053	6519.05	<0.005
	Unexplained	99	0.0669	0.000676		
	Total	100	4.4722			
Female December	Explained	1	5.7478	5.7478	2768.96	<0.005
	Unexplained	157	0.3259	0.002076		
	Total	158	6.0737			

i.e. in all cases a large and significant part of the variance has been explained by regression.