VARIATION IN LIFE HISTORY, ECOLOGY AND RESOURCE UTILIZATION BY ARCTIC CHARR *SALVELINUS ALPINUS* (L.) IN SCOTLAND

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I hereby declare that this thesis has been composed entirely by me and that all the work herein was carried out by me alone, except where otherwise acknowledged.

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ABSTRACT

A study was made of three populations of Arctic charr, *Salvelinus alpinus* (L.), from different habitats. Differences were found in morphology, feeding habits, growth, energetics and reproductive tactics. A pelagic, planktivorous, rather than benthic, life history was adopted by populations in competition with other salmonids. Measurements showed morphological coincidence with these life styles. Growth rate in body length was similar among the populations but growth in weight was related to the productivity of the habitat. Final body size was determined by the onset of sexual maturity. Large, deep, lowland fjord-like lochs produced bigger, heavier charr than a smaller,less temperate hill loch and a meso-eutrophic Hebridean loch. Body resources (lean, lipid, energy), expressed as values for fish of a standard size, were greater in the lowland loch population. These charr invested more resources in somatic sexual dimorphism while the hill charr invested more in gonad tissue. The age at maturity and fecundity were greater in the lowland charr but egg size was smaller. The size of offspring at the onset of feeding was directly related to egg size.

It is hypothesized that the requirement for yolk to ensure alevin survival may initiate adaptation of the life history. The lowland charr (hypermorphic, large, old, fecund with small but variable egg size) resemble the root stock of post-glacial colonization. Large egg size, early maturity (with its demographic advantages), and small body size with reduced fecundity represent a chain of responses to more stringent environments.

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CHAPTER 1

INTRODUCTION AND GENERAL METHODS

1.1 INTRODUCTION: The Arctic charr, *Salvelinus alpinus* (L.), is a salmonid fish with a remarkable ability to adapt to exacting environments through morphological plasticity and variation of life history tactics. Recent major reviews of the species (Balon 1980; McCart 1980; Johnson *et. al.*, in press) allow the observation that variation may be more typical of the species than any particular phenotype. This is highlighted by the considerable debate that still centres around the taxonomic status of populations worldwide (Behnke 1980; Savvaitova 1980). The problem is exacerbated by the fact that the fish reproduce and often spend their lives in islands of fresh water, each imposing its own special set of environmental criteria on the fish. Thus, one is working with a problem in island biogeography (MacArthur and Wilson 1967) and not a more continuous distribution as one might observe in terrestrial or marine organisms.

The island environments also influence the life history tactics employed by the populations of charr. Considerable variation has been found in the species' feeding ecology (Nilsson 1978 with references; Barbour, in press), and reproductive tactics (Frost 1965, McCart, 1980). The demography of the species varies with latitude (Johnson, 1980) and also from population to population (Johnson 1980). Analysis of these variations in tactics allows one to apply life-history strategy theory to foster an understanding of the species' ecology.

In Chapter 2, I examine the colour and morphology of the charr and try to provide functional reasons for the observed variation. The data are analysed classically and by more recent numerical methods.

Chapter 3 describes the food, parasites and predators of the charr I have studied. The feeding especially seems to have a profound effect on the life history of the fish.

Chapter 4 details the ageing and growth of the fish. The differences found between two of the populations are further explored in Chapter 5, which is a study of the proximate composition of and resource partitioning by the fish. Chapter 6 follows naturally by showing how reproductive investment is spent to ensure the survival of the progeny of the charr.

Chapter 7 attempts to demonstrate that the variations described in the preceding chapters comprise a suite of life history tactics that adapt the population most beautifully to its environment.

The populations I have studied are situated in three lochs in Scotland. Scottish charr have been greatly neglected by science. Two brief papers by Friend (1956 1959) and a review of the natural history and status of the charr by Maitland *et. al.* (in press; with obscure references) are the only literature on Scottish charr. Fortunately, for comparative purposes, one of the most thoroughly studied lacustrine ecosystems in the world, Windermere, which contains well studied populations of charr, is only one degree of latitude due south of my study lakes. This thesis is an attempt to fill a surprising gap in Scottish natural history, and also hopes to explain some very startling variations among the populations in terms of ecological adaptation.

1.2 GENERAL METHODS

Three lochs, Meallt, Isle-of-Skye, Builg, Banffshire, and Doine, Perthshire (Plate 1.1) were the principal sites for this study while small collections were made from Loch Earn, Perthshire. The work in Loch Earn was discontinued, because catches of charr were sporadic, and transferred to Loch Doine. The sites were chosen to represent a range of charr habitats. Loch Meallt was chosen because it contains no other salmonid fish species. It has a mild maritime climate and is totally isolated from the sea. Loch Builg was chosen to represent a hill loch and because it is in the harshest climatic region of Britain. Eels and perhaps sea trout penetrate to this loch. Loch Earn was chosen to represent the large fjord-like lochs which typify Scottish freshwaters with their self-buffered (because of their huge volume) lowland climate. Loch Doine was chosen to replace Loch Earn because it is nearby and, although much smaller, was originally part of fjord-like Loch Voile before being cut off by the Monachyle Burn delta (Murray and Pullar 1910). The climate at Loch Doine is similar to Loch Earn's, but slightly wetter. Sea trout, salmon, eels and lampreys migrate throughout the Loch Doine catchment area.

The physical, chemical, geological and climatic parameters of the lochs are summarised in Tables 1.1 to 1.5. Plate 1.1 depicts the three main study lochs. Samples of charr were obtained using monofilament gill nets set and retrieved from a small boat. Each net was a standard survey type (Lundgrens Fiskredskaps-Fabrik, Stockholm, Sweden) comprised of eight panels, each one of a geometric series of mesh sizes. The net was 122m long with each panel 15.2m long, and 1.8m deep. The mesh series was 8, 10, 12.5, 16 19, 22, 25, 30 mm bar measure, as recommended in Johnson (1980).

The sampling dates and catches of charr are summarised in Table 1.6. The dates are of the day the net was raised and the fish removed. The net was bottom set in the early afternoon of the previous day and fished for 24 hours. It was usually set perpendicular to the shore across depth contours of 10 to 20 metres of water. Charr were usually taken in all panels of the net, except in Loch Earn, where the fish tended to be taken from deeper than 20 metres. Loch Meallt was a special case, as its maximum depth is 3

A

B

Plate 1.1 - The three lochs of the study.
A - Loch Meallt
B - Loch Builg
C - Loch Doine

Table 1.1 - The physical characteristics of the four lochs in the study.

Loch	Location	Elevation (m)	Area (ha)	Depth Mean (m)	Depth Max (m)	Volume ($\times 10^6$ m^3)
Meallt	57 36 N/6 10 W	53	8.2	2	3	.16
Builg	57 7 N/3 20 W	483	31	8.5	26	2.6
Doine	56 21 N/4 27 W	126	54	10	20	5.5
Earn	56 24 N/4 10 W	97	1013	42	88	408

Table 1.2 - The physical environments of the four lochs in the study.

Loch	Geologic base	Soils	Surrounds
Meallt	Boulder clay drift on basalt. Jurassic limestone outcrop on east shore	Organic soil. Podzolized soil.	Peat Pasture Truck farming
Builg	Moraine dams at each end. Quartzite and granite base. limestone outcrop on east shore.	Organic soil. Podzolized soil.	Peat Grouse moor Wet meadow
Doine	Dalraidian schists	Organic soil. Podzolized soil.	Coniferous plantations Pasture
Earn	Dalraidian schists	Organic soil. Grey-brown podzolized soil.	Coniferous plantations Pasture

Table 1.3 - Trophic status of the four lochs of the study.

Loch	pH	Total P	Trophic Status
Meallt	7.4	16	meso-eutrophic
Builg	5.8	6	oligotrophic
Doine	5.9	7	oligotrophic
Earn	7.2	5	oligotrophic

Table 1.4 - The climates of the four lochs of the study.

Loch	Climate	Rainfall mm/yr	Ice cover	Temperature mean*	
				Feb.	July
Meallt	maritime temperate	1500	nil	4.1	12.9
Builg	Sub-arctic	927	annual	0.7	12.4
Doine	Sheltered glen micro-climate	2000	occasional in severe winters	2.6	14.2
Earn		1599	nil	2.6	14.2

* same stations as Table 1.5.

Table 1.5 - Monthly mean temperatures (°C) recorded at weather stations near the four lochs of the study. *

	Meallt	Builg	Doine/Earn
Station	Stornoway	Glenmore Lo.	Ardtalnaig
Elevation(m)	3	341	130
January	4.1	0.6	2.4
February	4.1	0.7	2.6
March	5.6	2.9	4.6
April	6.9	5.3	7.1
May	9.1	8.3	10.1
June	11.7	11.3	13.3
July	12.9	12.4	14.2
August	12.9	12.1	13.8
September	11.6	10.5	11.8
October	9.5	7.7	8.9
November	6.4	3.3	5.3
December	4.9	1.9	3.7
Annual Mean	8.3	6.4	8.1

* courtesy of the Meteorological Office, Edinburgh.

metres, and the net was found to do better when set across the direction of the wind.

The fish were removed from the net as quickly as possible. Live fish were placed in a dark bucket filled with water while dead ones were put into empty buckets which were kept drained. Excess live fish were released in Loch Builg, but all fish were retained from Loch Doine. The capture and care of broodstock is described in Chapter 6. Every effort was made to keep the samples cool and, if possible, they were packed in snow or ice.

The surface water temperature was recorded when the net was raised. The deep end of the net was raised first and the internal temperature of the first fish was taken. This usually agreed with the surface temperature and was ignored as a parameter. Early in the study water samples were taken for analysis, but no limnologic sampling program was undertaken.

The laboratory treatments of the fish samples are described in the appropriate chapters.

Table 1.6 - Dates of sampling and the numbers of charr removed from the four lochs.

Loch	Date	Day*	n
Meallt	5 to 22.6.81	156-173	103
	15.10.81	288	51
	1. 9.82	244	42b
Builg	8. 7.81	189	20p
	13. 9.81	256	48p
	24.10.81	297	19p
	20. 5.82	140	70p
	10. 9.82	253	47
	21. 9.82	264	21b
	25. 9.83	268	221bd
Doine	17. 9.81	260	16p
	20.10.81	293	55p
	11.12.81	345	24p
	13. 5.82	133	4p
	22.11.82	326	12b
	24.11.83	328	239bd
Earn	19.11.80	323	7
	11. 3.81	70	27
	6.12.83	340	25b

* number of days after January 1.
b broodstock collection
d demography collection
p proximate analysis sample

CHAPTER 2

THE MORPHOLOGY OF CHARR

2.1 APPEARANCE OF THE FISH:

2.1.1 INTRODUCTION: In the following paragraphs I describe the general appearance of the arctic charr from the different lakes. The intention is to introduce the biological variation that is evident even to casual observation, and to ponder the adaptiveness of such a spectrum of characteristics. In a later section, I report on a detailed study of morphometric and meristic variation among the populations.

2.1.2 GENERAL SHAPE: Arctic charr have the typical salmonid fusiform shape with a terminal mouth. The head is relatively small and the tail often appears disproportionately large. Younger fish tend to have a rather blunt snout, inferior mandible, and a thin body with the maximum girth just behind the head. Older fish tend to develop a more pointed snout and the mandible often lengthens to equalise the length of the jaws. The body becomes more robust and the maximum girth is shifted toward the origin of the dorsal fin.

Many charr populations become sexually dimorphic with maturation. Females tend to alter little except for distention of the abdomen due to the enlarged gonads. The males, however, may show varying degress of progression toward the archetypal male salmonid secondary sexual characteristics shown by the genus *Oncorhynchus*. (Figure 2.1).

Male charr from Loch Earn are the most developed in this respect, having a lengthened head and jaws with a pronounced kype on the mandible. The maxillary extends well behind the eye. The body is laterally compressed and deepened. The epidermis is thickened and spongy with the scales deeply buried and concealed within it.

Males from Loch Doine are also laterally compressed and deeper bodied with lengthened jaws, but there is rarely a kype on the mandible. The maxillary extends well behind the eye. The epidermis is thickened, but not spongy.

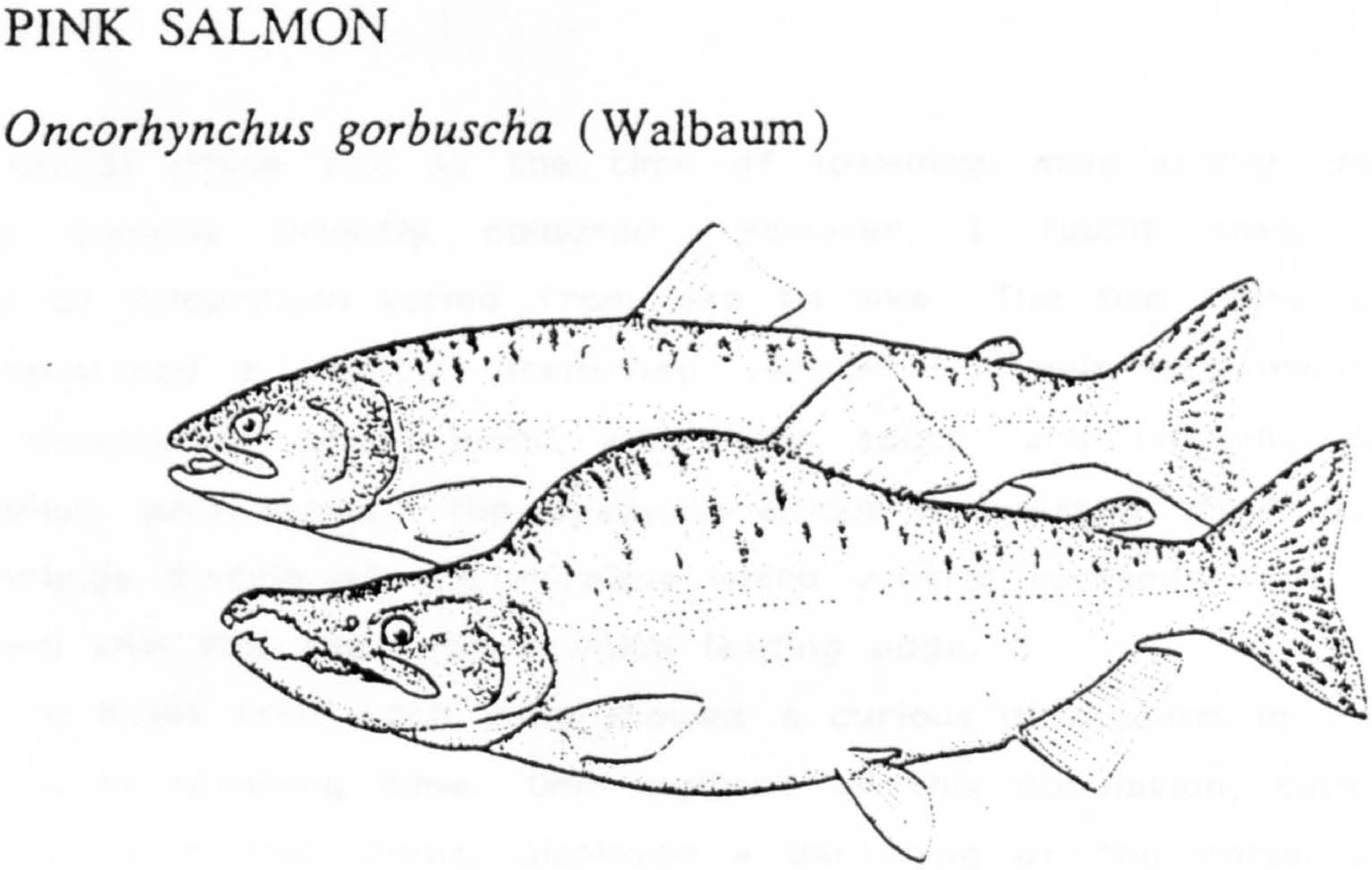


Figure 2.1 - External morphology of the pink salmon.
Background: Immature fish showing typical salmonid fusiform shape.
Foreground: Breeding male. Note lengthened and hooked jaws (lower hook with distal knob is the "kype"), humped back, deepening of body with associated lateral compression. (from Scott and Crossman 1973).

Bright males (see below) from Loch Builg are laterally compressed, but not noticeably deeper bodied. The shape of the head is not altered except for lengthening of the maxillary to behind the eye. The skin does not become spongy.

Loch Meallt males show almost no change in morphology with maturity. Some males have slight lateral compression, but this is not obvious to the casual observer. The maxillary does, however, lengthen to well behind the eye.

2.1.3 COLOUR:

2.1.3.1 MALES: (Plate 2.1) At the time of spawning, male arctic charr generally become brightly coloured. However, I found that the intensity of colouration varied from lake to lake. The fish from Loch Meallt developed a slightly intensified version of their non-breeding colours dorsally of brown-black with light spots, and laterally pale with obvious parr marks. The spawning colour manifested itself as a pinkish-orange tinting of the normally white ventral surfaces with the paired and anal fins red with a white leading edge.

Mature males from Loch Builg showed a curious dimorphism in their appearance at spawning time. One segment of this population, termed "bright" males in this thesis, displayed a darkening of the dorsal and lateral surfaces, which partially obscured the parr marks, and a moderately intense "international orange" colouration of the ventral surfaces. The paired and anal fins were blood red with white leading edges. The second segment of the mature male population, which I call "cryptic" males, looked similar to female charr and could only be identified by the expression of milt. These fish were dorsally dark (purple-black) with silvery flanks and obvious parr marks. The paired and anal fins were red with white leading edges (Plate 2.2).

The male charr from Loch Doine become very intensely coloured at spawning time. Dorsally they are a solid brown-black which becomes increasingly blotched and mottled ventrally. An intense orange suffused the ventral surfaces and tinted any light areas or spots dorsally. Parr marks were discernible on some specimens. The paired and anal fins were, serially from the leading edge, white then black, blending to red. The leading edge of the ventral lobe of the caudal fin was often white.

A

B

Plate 2.1 - Sexually mature male charr from four Scottish populations.
A - Loch Meallt C - Loch Doine
B - Loch Builg D - Loch Earn

A

B

C

Plate 2.2 - Phenotypes of sexually mature male charr.

A - Bright male from Loch Builg.

B - Cryptic (female imitator) male from Loch Builg.

C - Sexually mature female charr from Loch Builg.

D - Cryptic (female imitator) male from Loch Builg.

E - Precocious males (d,f-i) compared to immature (a,e) and bright (b) male charr from Loch Doine. Fish `c' has features of both bright and precocious phenotypes.

As in Loch Builg, there is a segment of the male population in Loch Doine that matures sexually, but does not develop obvious secondary sexual characteristics (Plate 2.2). However, as they tend to be very small and resemble immature fish more than they do mature females, I have designated them as "precocious" males. Their dorsal surface is dark blue-black or grey, the flanks have obvious parr marks and are often suffused with a vague orange cast along the lateral line. The ventral surface is off-white but may be a light orange in larger specimens. The paired fins are a dull yellow darkening distally to grey-black. The body is more laterally compressed than immatures and the skin is thickened and slimy.

Breeding male charr from Loch Earn were the most spectacularly coloured of the populations I examined. They were dorsally and laterally black with a few cream coloured spots on the flanks. The ventral surface was bright orange-red, but only extended to just above the paired fins. The paired and anal fins were black with white leading edges. The distal two thirds of the leading edge of the caudal fin was also white.

2.1.3.2 FEMALES: (Plate 2.3) Breeding female charr tended to develop orange, pink or red colouration of the ventral surfaces and fins, but did not achieve the spectacular livery of the males from lochs Builg, Doine or Earn. The dorsal and lateral body surfaces usually resembled those of immature fish. They were always difficult to identify except when very gravid or when ova could be extruded. Usually, when collecting broodstock, I would mistake one or more immature males (which often were developing modest colouration) for unovulated females. Plate 2.3 is of females from which I actually stripped viable ova.

2.1.3.3 IMMATURES: (Plates 2.4) Immature (or non-breeding) arctic charr from all the lakes I studied had similar colouration. The back was usually a blue-black, but often brown or green. Loch Meallt fish had many obvious light spots on the dorsal surface. The flanks were always silvery and parr marks were usually visible as blue-black blotches. The fish from all lakes had many small cream coloured spots on the lateral surfaces. The belly was always creamy white with a pink cast on larger fish. Very small fish had virtually transparent

A

B

Plate 2.3 - Sexually mature female charr from three Scottish populations.

A - Loch Meallt
B - Loch Builg
C - Loch Doine

A

B

C

D


E

Plate 2.4 - Immature charr from three Scottish populations.
A-Loch Meallt **B-Loch Builg** **C-Loch Doine**
D-a yearling from Loch Meallt E-fry at the onset of feeding reared in the laboratory from Loch Builg eggs.

paired and anal fins, the dorsal fin being the colour of the fishes back. Larger fish had fins ranging from yellowish to brown to blue-black and often had a purple-mauve cast over the entire body.

2.2 MORPHOMETRY

2.2.1 INTRODUCTION: The original philosophy behind the taxonomic distinction of organisms was to create order out of chaos by specifying each creature and plant by an unique name coupled with a detailed description of its morphology. Once the theory of evolution had been embraced, scholarship quickly turned to exploring the phylogenetic relationships of organisms through the examination of their structural similarities and contrasts. More recently, attention has been directed toward explanation of functional design in morphology through the detailed analysis (using powerful statistical methods and computer technology) of more or less classical taxonomic data.

Fish biologists have been able to distinguish most species through the use of about twenty standard parameters (Hubbs and Lagler 1964; Scott and Crossman 1973). However, these may mask individual and population variation especially in cases where island biogeographical phenomena may be operating. This is the case with the charr, which has a patchy distribution among freshwater "islands" as well as a continuous distribution along arctic sea coasts. The current opinion among some scientists is that the charr is a species complex of diverse morphs, each rapidly adapted to its particular habitat (Savvaitova 1980). Others (Behnke 1980) believe that variation among populations is the result of several waves of invasion of differing morphs, at different climatic periods, leaving relict populations exhibiting features of the founding population.

Scotland, in fact most of Britain, was completely covered by ice during the most recent glaciation. Thus the fish fauna would have been extinguished. Therefore any morphological variation in charr must have arisen since the glacial retreat, (assuming only one recolonization occurred). Thus, Britain with up to 15 species of charr (Regan 1911) provides a useful opportunity to measure the potential short term variability (or plasticity) in this species.

The object of this section is to describe, and possibly distinguish, the populations under study through detailed measurements of body morphology. An attempt is made to explain functional variation among the populations.

2.2.2 METHODS: Specific collections of at least fifteen charr from each loch were made from the general samples outlined in section 1.2. Superficially undamaged apparantly sexually immature specimens were selected at the lake shore and immersed in 10% formalin. Care was taken that the attitudes of the fish were as "normal" as possible. They were fixed in vessels large enough that they were not bent. At the lab, after more than 20 days in fixative the specimens were washed for 12 hours and then stored in 70% ethanol.

Measurements were made using dividers and a metal ruler graduated to 0.5 mm. Measurements were recorded to .1 mm by close examination of and interpolation from the graduations. Some measures were effected with a vernier caliper. These are recorded in section 2.2.3 (definitions).

Sixty-five separate measurements were made of each specimen. These are listed and defined below.

2.2.3 DEFINITIONS: A total of fifty-five morphometric measurements were taken from each speciman. Forty-one given by Hubbs and Lagler (1964), and McGlade and MacCrimmon (1979) while the remainder were devised specifically for the present study. All are listed below in order to prevent any confusion about the results. All measurements are linear measures and were taken with dividers except where otherwise stated. All longitudinal measures were made on the left side of the fish.

1 Total length: Tip of the snout to the end of the longest caudal fin ray. Measured on a measuring board.

2 Fork length: Tip of the snout to the end of the shortest median caudal ray. Measured on a measuring board.

3 Standard length: Tip of snout to the caudad edge of the wrinkle that forms near the end of the lateral line when the caudal rays are deflected laterally.

4 Anterior end of the snout to the end of the lateral line scales.

5 Anterior end (upper) of the operculum to the fork of the tail. (figure 2.2a). Care must be taken to avoid measuring gill net damage at the emergence of the operculum.

6 Head length: anterior tip of the snout to the most distant caudad edge of the opercular bone.

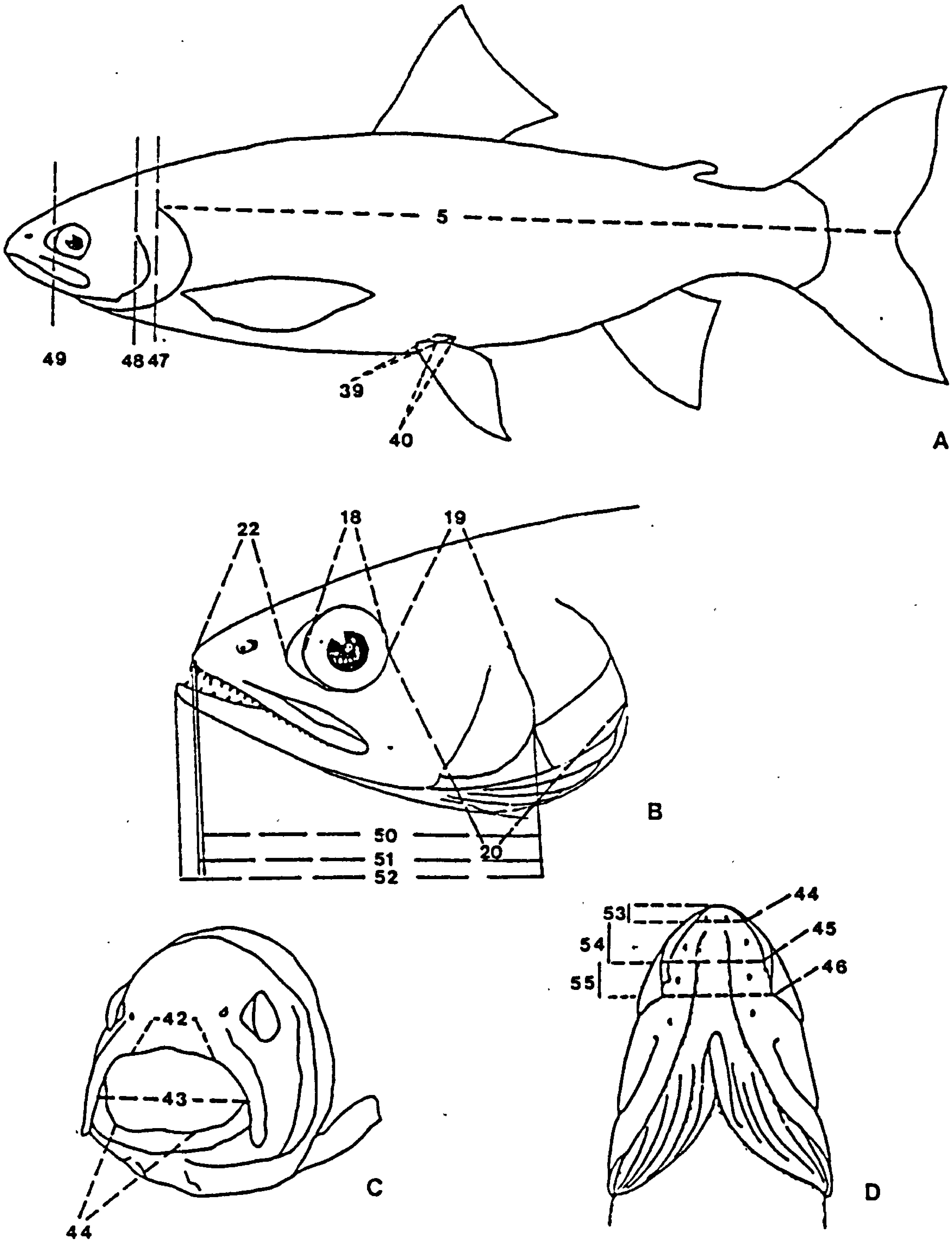


Figure 2.2 - Illustrations of some of the morphometric measures made on charr from the three populations.
A - lateral view of fish.
B - lateral view of head.
C - anterior view of head.
D - ventral view of head.
(A and B after Regan 1911; D from Scott and Crossman 1973)

7 Predorsal fin length: Tip of the snout to the origin of the dorsal fin. The origin is defined as the unconformity on the skin (a line) just anterior the first dorsal ray.

8 Insertion of the dorsal fin to the fork (see 2, fork length) of the tail. The insertion is defined as the point where the last dorsal ray contacts the body of the fish.

9 Insertion of the dorsal fin to the standard length.

10 Insertion of the anal fin to the fork of the tail.

11 Insertion of the anal fin to the standard length.

12 Origin of the pelvic fin to the origin of the anal fin.

13 Insertion of the adipose fin to the fork of the tail.

14 Insertion of the dorsal fin to the origin of the adipose fin. There is no distinction of the adipose fin. This study used the point where the angle of the origin was most acute.

15 Anterior tip of the lower jaw to the origin of the pelvic fin.

16 Maximum body depth. (measured with vernier calipers)

17 Origin of the pectoral fin to the origin of the pelvic fin. The origin of the pectoral fin was sometimes hidden under the the operculum.

18 Eye diameter (Figure 2.2b). The antero-posterior distance across the eye between the edges of the surrounding membrane. Thus the actual eyeball was not measured.

19 Posterior margin of the eye to the preopercle (Figure 2.2b). The eye membrane was pinched against the orbital bone to give a "bony" distance.

20 Postorbital length or bony head length (Figure 2.2b). As in 19, but to the most distant point on the caudal edge of the opercular bone.

21 Interorbital width. The shortest distance across the dorsal surface of the head between the eyes. The calipers were tightened as much as possible without distorting the bones.

22 Snout length (Figure 2.2b). Excludes the anterior orbital membrane.

23 Length of the maxilla.

24 Height of the maxilla.

25 Length of the premaxilla.

26 Length of the upper jaw. The mouth was opened by insertion of a finger. The point of the dividers was inserted into the corner of the mouth, just behind the end of the maxilla, and forced

caudally along the jaw until it stopped in the hinge. The measure was from this point to the anterior end of the toothed surface of the premaxillary bone.

27 Length of the lower jaw. As in 26, but to the anterior tip of the dentary bone.

28 Anterior tip of the lower jaw to the origin of the pectoral fin.

29 Base length of the dorsal fin. The distance from the defined origin to the defined insertion.

30 Height of the dorsal fin at the origin. This was measured from the origin to the tip of the longest fin ray.

31 Height of the dorsal fin at the insertion. This was changed from Hubbs and Lagler's (1964) measure to the distance from the insertion to the tip of the posterior fin ray.

32 Base length of the adipose fin. As in 29.

33 Height of the adipose fin. A measure from the mid point of 32 to the most distant edge of the adipose fin.

34 Base length of the anal fin.

35 Height of the anal fin at the origin. As in 30.

36 Height of the anal fin at the insertion. As in 31.

37 Height of the pectoral fin. As in 30.

38 Height of the pelvic fin. As in 30.

39 Length of the axillary process (Figure 2.2a). The dorso-ventral breadth of the axillary process measured at the point of its insertion.

40 Height of the axillary process (Figure 2.2a). The distance from the origin (the junction of the process with the pelvic fin) to its distal end.

41 Height of the caudal peduncle.

The following group of measurements was designed to demonstrate the observed differences in head and jaw shape among the three charr populations. They are illustrated in Figure 2.2. The objective was not to measure skeletal dimension per se, but to measure functional apparatus presumably used for feeding.

42 Width of gape (upper jaw) at origin of the maxilla. This was measured between the outer edges of the toothed surfaces of the upper jaw. The idea was that an object striking the jaw

within this measure would be directed into the fishes mouth.

43 Width of gape where maxilla crosses or touches (but is not inserted by) the mandible-maxillary fold.

44 Width of mandible at insertion of mandible-maxillary fold. This includes the thickness of the membrane (see 42 final comment).

45 Width of mandible at point of caudad gape measure (43).

46 Width of mandible at posterior end of maxilla.

47 Greatest horizontal width of head on a transverse plane through the dorsal insertion of the opercle (measured with vernier calipers).

48 Greatest horizontal width of head on a transverse plane through the dorsal insertion of the pre-opercle (vernier calipers).

49 Greatest horizontal width of head on a transverse plane through the anterior edge of the visible part of the eyeball (vernier calipers).

50 Tip of the snout to the intersection of the opercular - sub-opercular suture with the posterior edge of the pre-opercle.

51 Anterior tip of the premaxilla to intersection defined in 50.

52 Anterior tip of the mandible to intersection defined in 50.

53 Anterior tip of the mandible to 44, the insertion of mandible-maxillary fold.

54 Distance along mandible from 44 to point where parameter 45 was measured.

55 Distance along mandible from 45 to point where parameter 46 was measured.

The following group of parameters are standard (Hubbs and Lagler 1964) counts of serial, or meristic, structures on the fish. Fin rays were counted without dissection for rudiments. All the gill rakers on an arch, including rudiments, were counted.

56 The number of branchiostegal rays (left).

57 The number of branchiostegal rays (right).

58 The number of gill rakers on the first left arch.

59 The number of pyloric caecae.

60 The number of anal fin rays.

61 The number of dorsal fin rays.

62 The number of pectoral fin rays (left).

63 The number of pelvic fin rays (left).

64 The number of mandibular pores. The total on both sides of the jaw.

65 The number of parr marks.

2.2.4 DATA ANALYSIS

The values of morphometric and meristic measures may change during the lifetime of a fish. Morphometric characters may change as a function of body size (Gould 1966) while meristic counts may increase during early ontogeny (Balon 1980). The latter problem can be solved by collecting data from fish that are beyond the juvenile stage, as was done in the present study. The former problem can be solved by correcting for allometric growth (Thorpe 1976). In the present study, allometry was detected by regression of the log value of the character in question on the log of the standard length. If the slope of the regression was significantly different from unity (t-test comparing slopes, $p<.05$, Sokal and Rohlf 1981) the growth of the character was considered allometric. The allometry was corrected to a standard size of fish using the equation (Thorpe 1975):

$$\hat{Y}_i = 10^{\hat{Y}_i} \qquad 2.1$$

where:

$$\log\hat{Y}_i = \log Y_i - b\,(\log X_i - \log\bar{X}) \qquad 2.2$$

where:

b is the pooled slopes of the population regressions of character Y on X,
$\hat{Y}_i$ is the adjusted character value,
Y_i is the unadjusted character value,
X_i is the standard length of the specimen,
$\bar{X}$ is the grand mean of the standard lengths.

Stepwise discrimnant function analyses were performed using the programs of Nie *et. al.* (1975). The value of Wilks' lambda was the criterion by which a variable entered the analysis at each step. The maximum Mahalanobis distance (D^2) was the measure of separation among the groups of charr. The success of the discrimination was tested by reclassifying each specimen according to the calculated canonical variables. A selection of the morphological characters was made after the initial discrimination in order to eliminate highly correlated variables. Only a single representative of a bloc of correlated variables should be included in the analysis in order to avoid a biased result (Thorpe 1976).

2.3 RESULTS

The discrimnant analyses were 100% successful in separating the three populations of charr, and in reclassifying individuals into the correct population. The same result was acheived with the populations paired into the three possible combinations (for example, Meallt - Doine). However, the discriminating variables often differed among pairs and some of these with the variables used by the three-way analysis. Purely morphometric characters were more successful (100%) at discriminating the populations than meristic characters (97%). A combination of both types of measures achieved greater separation of the populations. Most of the variables included in the analysis were required for the separation of the populations from lochs Builg and Doine. Usually only two or three were required to account for the Loch Meallt charr. Sets of nine morphometric, six meristic, or five variables of the two classes combined were required for successful separation of the populations. These are listed, with their standardized discrimnant function coefficients in Table 2.1. Discrimnant analysis plots using these variable sets are given in Figure 2.3.

Descriptive statistics of the meristic counts and selected morphometric characters are given in Tables 2.2 and 2.3 respectively. They illustrate the distinguishing features of the three populations. The meristic characters show no pattern of variation among the populations. Loch Meallt charr have a longer and broader head, bigger mouth, and shorter tail relative to Loch Doine charr. Loch Builg charr are intermediate. Both data sets fall within the ranges described for the species *Salvelinus alpinus* (L.) (Vladykov 1954; Scott and Crossman 1973; Behnke 1980).

Table 2.1 - Sets of minimum numbers of characters required to successfully discriminate the three populations of charr, with standardized discrimnant function coefficients for the first two canonical variables.

Set	Variable	Coeff. 1	Coeff. 2
Morphometric	44 distal mandible width	0.84241	-0.62478
	35 anal fin height, origin	-0.19295	0.71542
	46 proximal mandible width	0.14659	1.02502
	25 premaxillary length	0.05039	0.96674
	12 pelvic to anal fins	0.17097	0.74863
	33 adipose fin height	-0.25519	0.32990
	31 dorsal fin height, ins.	-0.28189	-0.60109
	18 eye diameter	0.41331	0.47478
	48 head width at preopercle	0.35178	-0.41570
Meristic	62 pectoral fin rays	0.95543	0.00997
	64 mandibular pores	-0.10552	1.00308
	57 branchiostegals, rt	-0.30706	-0.18585
	63 pelvic fin rays	0.31359	-0.43202
	61 dorsal fin rays	-0.23199	0.31209
Combined	62 pectoral fin rays	-0.86128	-0.17748
	64 mandibular pores	-0.40113	-0.88620
	12 pelvic to anal fins	0.37646	0.86527
	*19 eye to propercle	1.08561	-0.03237
	46 proximal mandible width	0.59369	0.39294

* additional variable

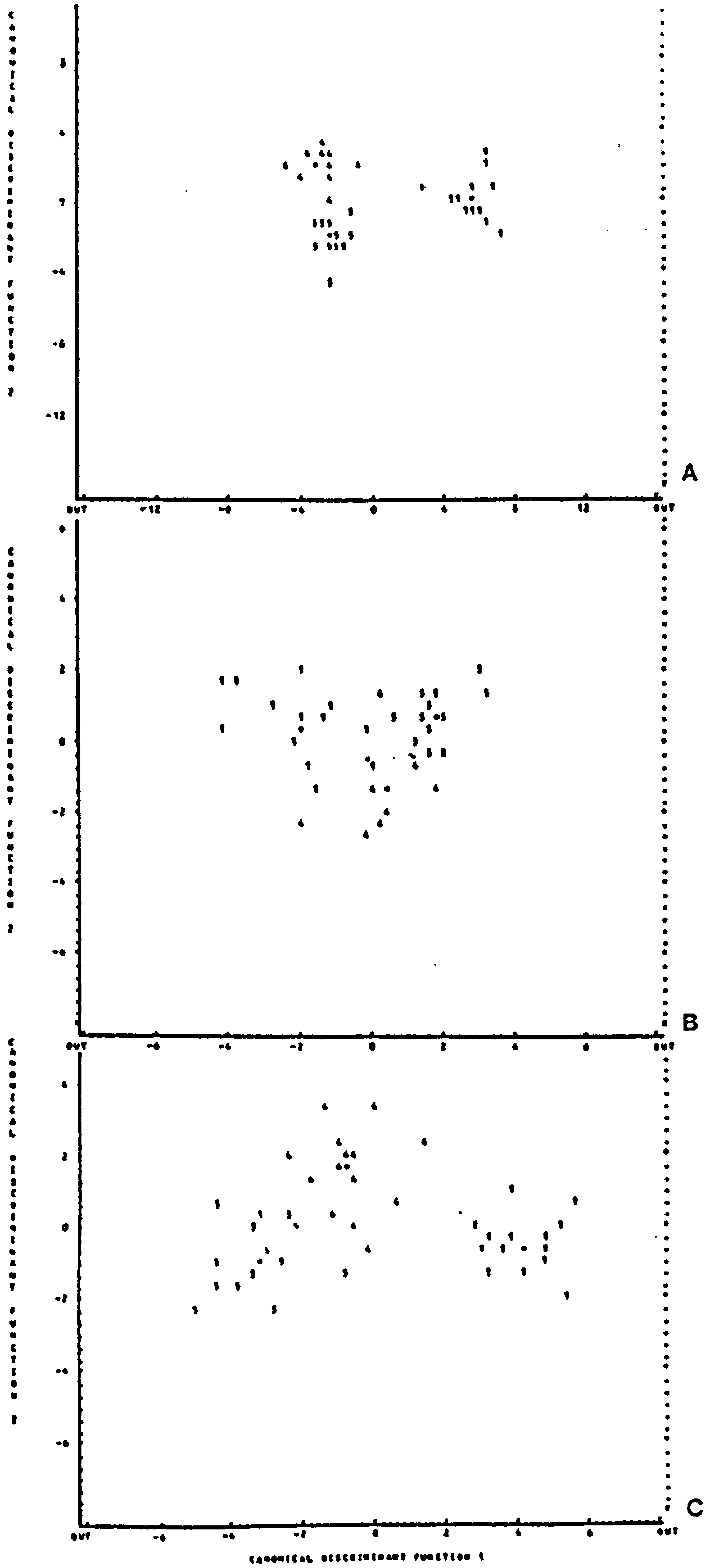


Figure 2.3 - Discrimnant analysis plots of morphometric (A), meristic (B), and combined sets of variables from charr from the three lochs.
Symbols: 1-L. Meallt 4-L. Doine 5-L. Builg *-group centroid.

Table 2.2 - Descriptive statistics of meristic characters.

Character		Meallt			Builg			Doine		
		mean	sd	range	mean	sd	range	mean	sd	range
branchi-	L	11.8	(.86)	10-13	10.7	(.80)	10-12	11.8	(.77)	11-13
ostegals	R	11.2	(.86)	10-13	10.7	(.80)	9-12	11.0	(.85)	10-13
gill rakers		24.5	(1.77)	21-28	25.7	(.95)	24-27	22.4	(1.36)	20-24
pyloric caecae		30.4	(3.48)	25-37	39.2	(3.14)	34-44	37.2	(3.42)	29-40
dorsal rays		11.1	(.52)	10-12	11.0	(.38)	10-12	10.9	(.26)	10-11
anal rays		10.4	(.51)	10-11	9.8	(.41)	9-10	10.1	(.27)	10-11
pect. rays	L	12.1	(.64)	11-13	14.1	(.46)	13-15	13.3	(.59)	12-14
pelvic rays	L	9.7	(.46)	9-10	10.0	(-)	10	10.0	(-)	10
mandibular pores		13.5	(1.25)	12-16	14.4	(.99)	13-16	12.1	(1.30)	11-15

Table 2.3 - Descriptive statistics of selected standardized morphometric characters.

	Meallt		Builg		Doine*	
	mean	sd	mean	sd	mean	sd
3 standard length	152.3	-	152.3	-	152.3	-
6 head length	39.6	(1.19)	36.0	(1.97)	36.2	(1.56)
22 snout length	9.4	(.42)	8.3	(.64)	8.2	(.52)
20 post-orbital head length	20.2	(.53)	20.1	(1.03)	18.7	(3.17)
48 head width at preopercle	20.0	(1.43)	17.0	(.89)	17.1	(.64)
46 proximal mandible width	14.6	(1.47)	9.5	(1.01)	10.0	(1.05)
44 distal mandible width	10.2	(.54)	7.3	(.32)	6.6	(.57)
26 upper jaw length	19.1	(1.55)	15.8	(1.22)	16.7	(1.18)
27 lower jaw length	18.4	(1.37)	15.2	(1.57)	16.6	(1.13)
18 eye diameter	8.8	(.48)	8.0	(.27)	8.2	(.30)
28 tip of mandible to pectoral fin	35.5	(1.37)	33.1	(1.61)	32.5	(1.18)
15 tip of mandible to pelvic fin	84.4	(2.28)	80.7	(3.64)	78.4	(1.98)
17 pectoral to pelvic fins	50.3	(3.00)	49.3	(4.60)	46.9	(1.92)

* n=14

2.4 DISCUSSION

The colour of the charr from the four lochs in which this was examined varies considerably. This applies to both the cryptic colouration of immature charr and the bright colouration of the breeding populations.

Immature charr in Loch Meallt tend to be mottled on the dorsal surfaces, with silvery flanks and white underparts. This is typical of fish which inhabit shallow waters with good cover such as weeds. Immatures from lochs Builg and Doine have a dorsal surface of solid blue-black, silvery flanks and white or pale pink ventral surfaces. Loch Doine charr are also laterally compressed. These features are typical of pelagic planktivores and are the best camouflage against predation from beneath (Alexander 1974). Charr from Loch Earn were similarly but darker coloured. They were most often captured from deeper water where there is less light (Wetzel 1975).

The pink bellies of immature charr from Loch Doine and Loch Earn require comment. Red light is absorbed very quickly by water (75% extinction per metre depth, 100% extinction by 3 metres depth) and the greatest penetration is by green light (Wetzel 1975). Green is the complementary colour of red and so would be absorbed by a red object. Thus, the pink bellies of the pelagic charr should produce grey tones which could adjust the ventral camouflage of the charr at midwater depths. A similar effect is achieved using bioluminescence by deepwater marine fishes (Denton *et. al.* 1972).

Sexually maturing charr exhibit an intensification of their colouration which is variable among populations. Male charr are highly territorial at spawning time. Frontal display is the signal of aggression against intruders (Johnson 1980; personal observations). These males are usually intensely red, and, in the light of the above argument, should appear black, especially since spawning tends to occur in poor light (Frost 1965). It may be that the male charr achieve the effect of a massive black body outlined by the fishes dorsal silhouette and the ventral white margins of the jaw and fins. Rather than being cryptic, they would become very obvious, especially from beneath. However, since they should be near the substrate, their vulnerability to predation may not be greatly increased.

Mature female charr tend to have more muted breeding colouration. The colour they do achieve may actually be an artefact caused by increased levels of sex hormones and therefore may be of no functional value. Female charr have not been observed to engage in agonistic behaviour and tend to hide their red ventral surfaces against the substrate when entering a male's territory (Johnson 1980). The need for a such a social signal is therefore questionable.

The shape and structure of the charr proved to be quite variable among the populations. The meristic data show no patterns such as consistent addition or reduction of structural elements. There does not appear to be any functional value to the observed variations.

I do not believe this to be true of the morphological measures. These features can be grouped into body, head, jaw and fin descriptors. The standardized data show Loch Meallt charr to have smaller bodies, larger heads, longer and much wider jaws and slightly larger fins located slightly further back on the body. Loch Doine charr have a longer tail and the pelvic fins slightly closer to the pectoral fins. Loch Builg charr tend to be similar to those of Loch Doine except in the buccal region. Loch Doine fish have longer and wider heads with longer but narrower jaws. Not only that, the base of the mandible is wider than in Loch Builg charr! Loch Meallt charr have much larger mouths in all respects.

I have hypothesized that the differences in jaw morphology are functional and related to the size of the food particles consumed by the fish (Barbour, in press). The results of the present study lend support since Loch Doine charr have jaw proportions similar to those of the Loch Earn fish measured in the previous study and also eat the same food (zooplankton). Furthermore, Loch Builg charr have just been shown to have jaw widths intermediate between lochs Meallt and Doine and have more generalized feeding habits (Chapter 3). Loch Meallt charr have very large jaws and eat large benthic organisms.

The variation in body morphology among populations may also be functional. The Loch Doine charr have longer tails, bigger, more compressed bodies and smaller heads and jaws. These features are characteristic of pelagic, planktivorous fishes (Alexander 1974). Conversely, Loch Meallt charr have shorter tails, smaller, cylindrical bodies and large heads and jaws. These are characteristics of less active fishes. The weedy habitat and sluggish but cryptic prey organisms of this population favour a predator of this type. The charr in Loch Builg are generalist feeders and have an intermediate morphology. I suggest the charr in each of the lochs of the present study have evolved a body morphology to suit their respective habitats. The evolution of the populations is discussed in Chapter 7.

2.5 SUMMARY

1. The colouration of adult and juvenile arctic charr varies among populations.

2. The colouration of immature charr is cryptic.

3. Adult colouration appears to be for display and is adapted to the particular breeding system within a population.

4. The morphology of arctic charr varies among populations.

5. Morphology is distinctive and can be used to classify individuals into their populations of origin.

6. The morphological characteristics of a population appear to be adaptive.

CHAPTER 3

TROPHIC INTERACTIONS

3.1 FOOD OF CHARR

3.1.1 METHODS: The contents of the stomachs of 478 charr were examined. During the dissection of each fish, the stomach was transversely sectioned and the contents extruded into a petri dish. The contents were swirled in water, which was changed several times by careful decantation if it became murky. The dish of separated food organisms was examined under a binocular microscope over a dark background. The entire dish was examined and all taxa were identified to the appropriate level and recorded on the fish's scale envelope. Each taxon was recorded only if, and as, present. The data were then collated on to a frequency table for each sampling date.

3.1.2 RESULTS and DISCUSSION: The results are summarised in Table 3.1, which gives the absolute and relative frequencies of occurance of each food category in each sample. For example, Trichoptera larvae occurred in 70 stomachs (68%) of charr sampled from Loch Meallt in June 1981. This method was used because the examination of samples and recording of data are very quick. The results from this method have been shown to be accurate as long as sample sizes are sufficient (Hynes 1950). This, and other simple methods, are recommended by Nilsson (1965) for behavioural, rather than production, studies and he successfully used them for his studies of feeding interactions between trout and charr in Sweden.

Several points should be noted from Table 3.1.

1. The dominant food items in Loch Meallt charr contrast with those in Lochs Builg and Doine.
2. The dominant food item within a loch population may change with the age of the fish.
3. The foraging habits of the three populations appear to differ.

I shall deal with each of these points in turn.

Table 3.1 - Absolute and relative frequency of occurance of food items in the stomachs of Arctic charr from the three lochs.

	MEALLT						BUILG										DOINE							
Date	June'81		Sept'82		Oct'81		May'82		July'81		Sept'81		Sept'82		Oct'81		May'82		Sept'81		Oct'81		Dec'81	
Sample Size	n=103		N=42		n=35		n=70		n=23		n=48		n=49		n=12		n=4		n=17		n=50		n=25	
	f	%	f	%	f	%	f	%	f	%	f	%	f	%	f	%	f	%	f	%	f	%	f	%
Rotifera	1																							
Hirudinea																							1	4
Arthropoda																								
Crustacea																								
Copepoda	2	2			8	23	1	1			3	6	9	18							1	2	2	8
Cladocera							56	80	13	57	45	94	40	82	12	100			14	82	30	60	3	12
Gammarids	14	14	8	19	2	6	5	7																
Insects																								
bits							7	10			1	2							1	6	2	4	1	4
Ephemeroptera							3	4																
Plecoptera							5	7																
Hemiptera	2	2																						
Trichoptera	70	68	10	24	2	6	7	10	1	4	1	2												
Diptera																								
other							3	4					3	6										
Chironomidae	1	1	2	5			38	54	14	61	1	2					4	100	3	18	6	12	3	12
Coleoptera			1	2			1	1																
Hymenoptera							1	1																
unspecified terrestrial	6	6	2	5	3	9	2	3	8	35	7	15	1	2										
Arachnida											1	2	1	2										
Mollusca																							1	4
Gastropoda	20	19	28	67	2	6	1	1																
Pelecypoda	5	5	2	5	1	3	23	33	5	22	12	25												
Vertebrata																								
Osteichthyes																								
Salmonidae (ova					1	3					x		x										10	40
Gasterosteidae	4	4	12	29																				
Empty	17	17	3	7	21	60	2	3			1	2	9	18					3	18	20	40	11	44

The charr in Lochs Builg and Doine fed mainly on Cladocera, with chironomid larvae and pupae (Diptera) seasonally (spring and early summer) dominant. These two prey taxa are available in the water column. They were almost never associated with benthic detritus in the stomachs of Loch Doine fish, while about 25% of Loch Builg fish were found to have *Pisidium* (pea mussels) and pebbles associated with pelagic (planktonic) organisms. In contrast, Loch Meallt fish were found to feed mainly on benthic organisms at all times of the year. Trichoptera nymphs and their cases were dominant in June with snails dominant in September. Various benthos were taken in October with a slightly higher than usual frequency of terrestrial insects. Fish (Sticklebacks - *Gasterosteus aculeatus*) were found in the stomachs of larger charr in both spring and autumn, and in autumn also in the stomachs of smaller charr, presumably when 0+ sticklebacks had grown to a size appropriate for eating. Small charr were found to feed on copepods while they were very rarely found in larger fish. Charr ova were found in representatives of all three populations at spawning time.

The dominant food items of a charr population appear to conform to a type although some segments of each population may differ. In Loch Doine the food of large fish was almost exclusively pelagic zooplankton, while smaller fish appear to have eaten benthos. In Loch Builg zooplankton were always dominant but a third of the population was found to have consumed some benthos. In Loch Meallt the food consisted almost exclusively of benthos except among certain charr that had become piscivorous and the very small fish which ate copepods.

Because these differences in feeding habits might be size related, the feeding data were broken down by the age classes of the charr in each loch.

In Loch Meallt, this analysis revealed little except that the same food items were dominant through all the age classes captured in a sample. The only exception to this was fish of age 0+ (1981 cohort) which became catchable in October 1981. All of these fish fed on copepods with two individuals also taking Gammarus or small insects. The June 1981 sample of age 1+ (the 1980 cohort) were all feeding on benthos in the same proportions as older fish. One might surmise that

Loch Meallt charr undergo a change in feeding behaviour during their first winter of life. The only other revelation was that spawning fish in Loch Meallt usually were not feeding and that a large proportion of spent fish had an empty gut in June. Piscivory was not age related.

In Loch Builg the analysis gave a similar result in that age made no difference in the proportions of food items taken by the fish. None of the very few young fish captured were consuming different food. However, many mature fish captured on the spawning grounds had empty stomachs.

In Loch Doine there was a considerable sampling bias, in that all except four individual fish were captured in the autumn. The number of young fish captured was also very small. The food of the fish was almost uniformly planktonic regardless of age. However, a sample of fish taken in weed beds near the lake inlet contained a number of small charr which were feeding on copepods and *Pisidium*. These fish were measured, but not aged, and their size indicates that they were 2+ or less years old. Mature fish tended to have empty stomachs until spawning was in progress, when there was heavy predation by spawning fish on charr eggs.

In spite of the difficulties with sampling in Loch Doine, there is some evidence that a change occurs in the life history of the charr as they age. Small charr were virtually absent from catches made in the deeper areas of the loch over a stony substrate. Also, small charr were not eating charr eggs as was occasionally found in Lochs Meallt and Builg. Charr of age two and older were captured in all areas of the loch and were eating cladocera with a very few taking *Pisidium*. It seems that a change from a benthic to pelagic habit may occur in the charr of this loch between the ages of two and four. A similar pattern was found in Lake Lone, Norway, where charr aged 2+ or less fed on benthos, while older fish lived pelagically and fed on zooplankton (Jonsson and Ostli 1979).

Charr may be considered to operate on the "principle of the smorgasbord" (Johnson 1980). This is stated:

> "If the crowd is large and the table long, one moves to a position where the maximum consumption with the least interference can be effected, but if few others are present one can pick and choose with greater discrimination."
>
> (Johnson,1980)

This principle seems to be operating among the populations in the present study. Adult charr in Loch Doine are pelagic planktivores, while in Loch Builg the stomach contents indicate that nearly a third of the population is feeding on benthos. In Loch Meallt, the charr eat benthos almost exclusively, apart from a few piscivorous individuals. If one looks at the community structure of each loch this "smorgasbord" behaviour begins to be explained.

The charr in Loch Doine share their loch with trout (*Salmo trutta*), possibly salmon (*Salmo salar*), minnow (*Phoxinus phoxinus*), lamprey (*Petromyzonidae*, up to 3 spp), and the eel (*Anguilla anguilla*). The feeding habits of trout (Frost and Brown 1967), eels (Hussein 1983), and emigrating salmon smolts (Jones 1959) would bring them into intense competition with charr for littoral and/or benthic invertebrates. Thus, according to (Nilsson 1965) the charr should adopt a pelagic habit. Johnson (1980), dicussing Frost (1946, 1977) notes that small charr from Windermere, where the adult fish are predominantly pelagic planktivores, were oriented towards bottom feeding. I speculate that the charr may spend their first few years as benthic or littoral fish living in good cover. Their cryptic colouration would support this idea. This niche may be open to small charr because trout and salmon of a similar size would still be in their nursery streams. Larger trout were numerically dominant in the littoral area of Loch Doine and appeared to have displaced larger charr. This agrees with Johnson's (1980) contention that charr are a fairly unaggressive species (Frost 1977) able to avoid a "head-on confrontation with brown trout by avoiding direct competition for resources." Adult charr sidestep competition by occupying the pelagic zone and becoming planktivorous.

In Loch Builg, the charr share the loch only with trout and eels. Charr are numerically dominant (catch data, this study) and appear to be feeding from all niches in the loch. I hypothesize that they may be able to coexist with trout, even in littoral waters where trout usually do better, because of a low recruitment to the trout population due to a lack of good spawning habitat. This has been shown to affect the population densities of rainbow trout (*Salmo gairdneri*) in British Columbian lakes (Larkin, c.1958). Trout prefer to spawn in running water (Frost and Brown 1976). Although suitable areas of Lake Builg were investigated and were found to hold trout fry, there was very little suitable spawning area available because the loch is a headwater with very few inlet burns and a small outlet.

Loch Meallt holds no other fish species, except sticklebacks (*Gasterosteus aculeatus*), and larger charr should have very little competition. Charr grow larger than most sticklebacks (certainly their mouths are bigger) by the end of their first growing season, and it is interesting to note that this corresponds to the age at which young charr stop feeding on cyclopoid copepods and switch to much larger benthos. Habitat displacement appears to be operating in this situation as I always caught young-of-the-year charr in weed-free areas of the loch further from shore than the dense population of sticklebacks. Once the change from copepods has been made, the charr become the dominant predator in the loch and can select the largest food particles available to them, including suitably sized sticklebacks.

Nilsson (1965), reviewed a long series of his own papers on the feeding habits of charr and trout in allopatric and sympatric situations. He found a general rule operated in which allopatric charr fed on benthic or surface insects, primarily Trichoptera, while sympatric populations were pelagic planktivores. He explained that anomalies in this principle were due to sudden gluts of a food organism (i.e. chironomid hatches) which allowed the breakdown of niches. These generalizations agree almost exactly with my observations of Scottish charr.

3.2 PARASITES

The degree of parasitism in 465 charr was visually assessed and noted as a scale from 0 to 5. Criteria for assessment of these parasite index values were:

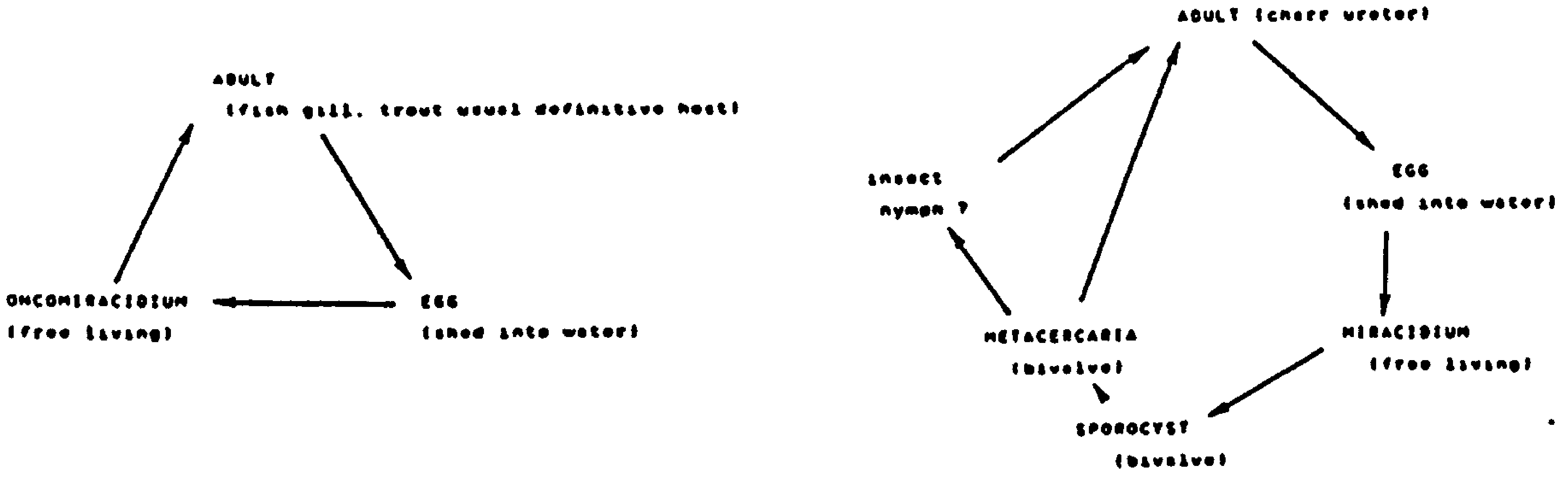
0 - No parasites found.
1 - One or two cysts or worms in the viscera or gut lumen.
2 - Many cysts but none in liver or gonads.
3 - Presence of cysts in liver. Cysts widely scattered on viscera, massed under spleen.
4 - Cysts in liver, gonads. Viscera heavily encysted with adhesion of internal organs. Worms free in body cavity.
5 - Viscera completely obscured by cyst material. Cysts in organs outside the peritoneum. Many worms free in body cavity. Viscera adhered into solid mass.

It was difficult to asses the tapeworm content of the gut as they did not obviously increase or vary among individual fish. No charr was found with the gut distended by a mass of tapeworms as is often found in other salmonids. Thus, tapeworms were lumped with plerocercoid cysts in the parasite index. This was probably an error as the tapeworms would represent the major energy cost by parasitism to the charr.

Parasites were sampled for identification from fish freshly killed on the lakeshore. The affected organ was quickly removed from the fish, dropped into boiling water and cooked for several minutes. After cooling the sample was drained and preserved in 70% ethanol.

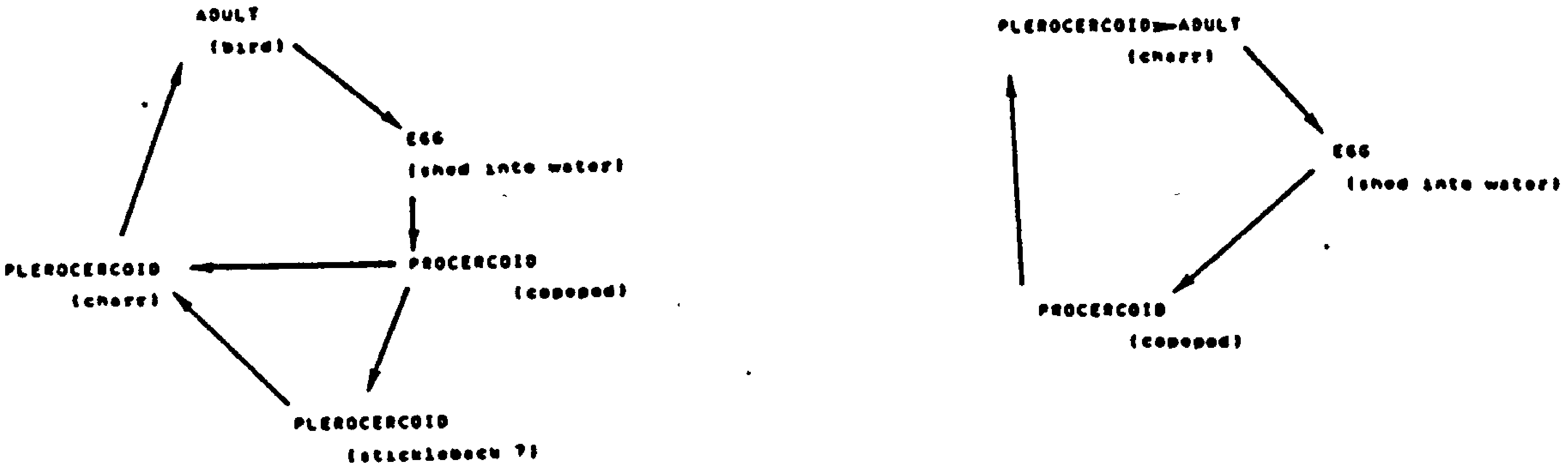
The parasites recorded in this study are given in Table 3.2. Their life cycles are diagrammed in Figure 3.1.

The data for the parasite index are related to the age of the fish in each population and are presented in Figure 3.2. The fish accumulate parasites as they grow older. In the case of the plerocercoids of *Diphyllobothrium* this is to be expected, as the parasites are recruited several times a year to the charr (their second intermediate host) and may live in the fish for several years before the death of the fish (Henricson 1977).



DISCOCOTYL ?SAGITTATA (MONOGENEA)

PHYLLODISTOMUM ?FOLIUM (DIGENEA)



DIPHYLLOBOTHRIUM DENDRITICUM (CESTODA)

EUBOTHRIUM SALVELINI (CESTODA)

Figure 3.1 - The life cycles of parasites recorded from Arctic charr in this study.

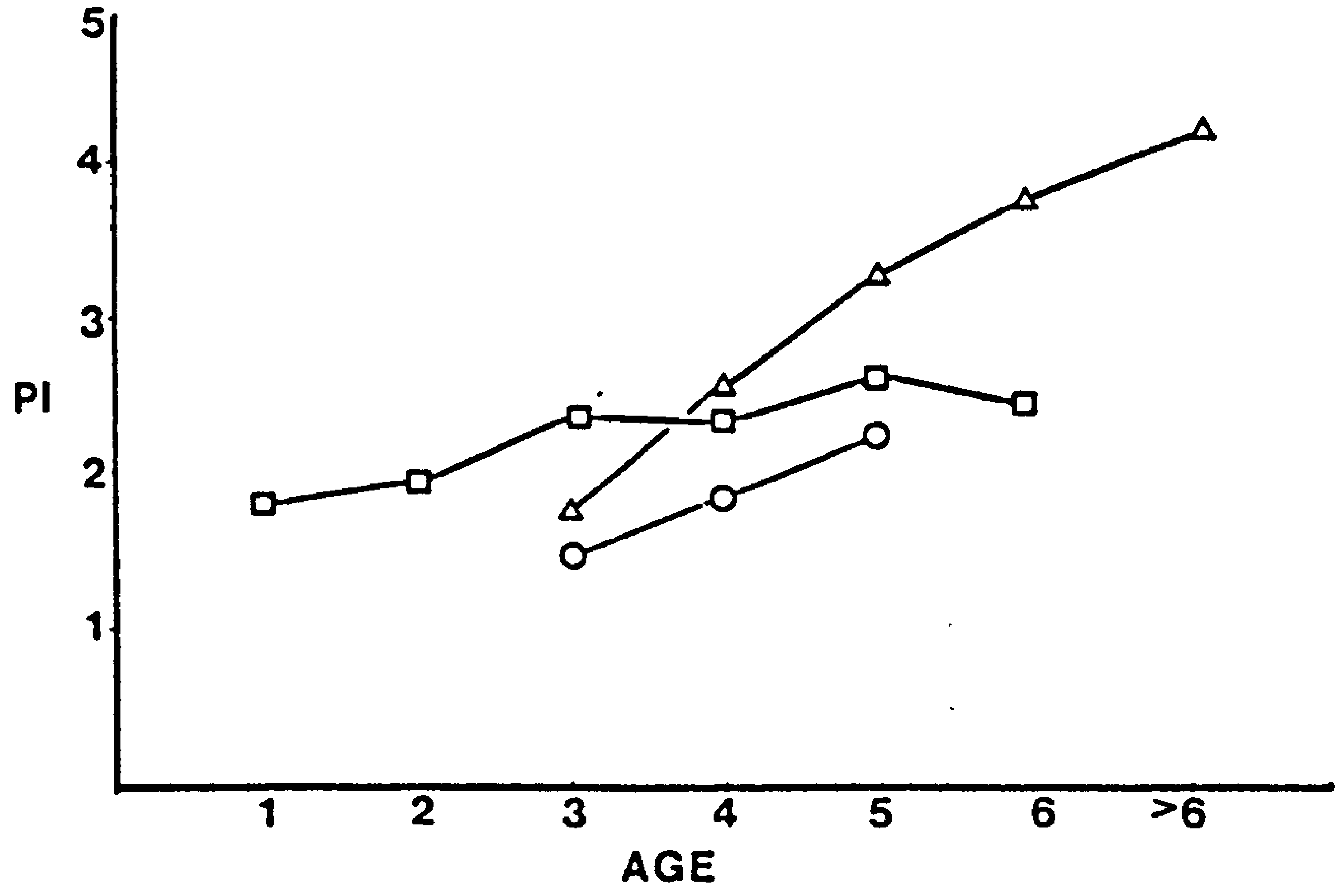


Figure 3.2 - A plot of the mean parasite index against age in three populations of Arctic Charr.
□ Meallt
△ Builg
○ Doine

Table 3.2 - Parasites, and the affected organ, recorded from Arctic charr during this study.

	Meallt	Builg	Doine	Voile	Earn
Monogenea					
Discocotyl ? sagittata		gill			
Digenea					
Phyllodistomum ? folium		ureters	ureters	ureters	
Cestoda					
Diphyllobothrium sp (plerocercoids)	viscera	viscera	viscera	viscera	
Eubothrium ? salvelini		gut			gut

There is a good case for thinking that the parasites may affect the mortality rate of their host. It is essential to the completion of the parasites' life history that the intermediate host be eaten by the parasites' final host. Henricson (1977 & 1978) discusses this and presents good evidence to show that charr heavily infected by *Diphyllobothrium* plerocercoids have a higher mortality rate than those lightly or not infected. He argues that a weakened host is more susceptible to predation by the final host and that the invasion of vital organs by the plerocercoids should provide the necessary stress.

3.3 PREDATORS

3.1.1 OBSERVATIONS: Charr were collected from the stomachs of trout (*Salmo trutta*) in both Loch Doine and Loch Builg. The trout in Loch Doine was a male "ferox" (Campbell 1979) and was associated with a shoal of charr caught over a spawning area. It was 541mm FL, weighed 2125 grams and was aged 12+ years. Two partly digested charr were retrieved from its stomach and they measured approximately 13cm FL (a precocious male!) and 17cm FL respectively. A smaller trout (464mm FL, 1041 g, 6+ years) thought to be a lake dwelling trout, yielded several minnows (*Phoxinus phoxinus*) from its stomach, but no charr.

The trout from Loch Builg appeared to be lake dwelling brown trout. Several were captured that contained charr, but there was no way of identifying predators without actually examining the stomach contents. These trout were usually about 30 cm FL (2 lb size) and were eating charr of about 12 cm FL.

3.3.2 ATTACKS ON NETTED CAPTIVE CHARR: Often when I raised gill nets, a number of charr were found to have been attacked while in the net. In Loch Meallt this was always by leeches (*Haemopsis sanguisuga*), which attached themselves to the ventral surface, located the vent and proceeded to eviscerate the fish.

In Lochs Builg and Doine netted charr were attacked by eels (*Anguilla anguilla*). This was determined by the characteristic twisting and tearing of the victim which made removal from the net a long and tedious operation. Occasionally, an eel would wrap itself in the net and be captured.

In Loch Doine, I captured two sea trout alive and in perfect condition. I hypothesize that these fish saw the charr go past as the net was being raised and attempted to feed. They were always caught by the teeth or kype and so had not been in the net for more than a short time (trout caught in a net fight strongly and violently and twist or roll up the net into a complicated tangle.)

Table 3.3 - Potential predators of Arctic charr sighted on the lochs during the course of the present study.

Species	Location	Circumstances
Black-headed gull *Larus ridibundus*	Builg	colony nearby, roost on loch; gull parasites in charr.
Various gulls *Larus spp.*	Meallt	roost on loch; gull parasites in charr.
Heron *Ardea cinerea*	Meallt	observed fishing along shore
Otter *Lutra lutra*	Meallt Builg	observed diving in loch; spraint on lakeshore

3.3.3 POTENTIAL PREDATORS: During the course of this study, many other species of animal were sighted. Some of these are piscivorous by habit or opportunism. The details are given in Table 3.3. None were actually seen to be eating charr and they are listed here for information only.

3.4 SUMMARY

1. The food habits of arctic charr vary among populations. The habits of a particular population appear to be a response to the presence or absence of competition.

2. Charr may alter their feeding habits at points in their life history.

3. Most charr were found to carry parasites. The degree of infestation was positively correlated with age. Four taxa of parasites were identified.

4. Few incidences of predation were documented. Direct evidence came from other fish while potential predators included birds and mammals.

CHAPTER 4

AGE AND GROWTH

4.1 INTRODUCTION: In the study of population dynamics, the most useful parameters are those specific for age (Caughley,1977). The whole concept of life history strategy is based on the analysis of how an organism disposes of its resources in relation to time, and therefore, its age.

This chapter is concerned with the determination of the ages of charr and then the calculation of age specific growth parameters. Later chapters will tap this information repeatedly as the life history of the charr is revealed.

4.2 AGEING OF CHARR

4.2.1 METHODS: The ageing of Scottish charr proved at first to be difficult. However, I found that by using the otoliths and a scale sample, a reliable estimate of a fish's age could be made. The task became much easier when I was able to capture a sample of 0+ charr from two of the three lakes. With these fish I was able to show that young of the year (0+) develop scales in their first summer, and I was able to pinpoint the actual zero point of growth in the otoliths.

The method used in determining age was as follows. During the dissection of the fish, a sample of scales was taken by plucking them individually from the two scale rows above and below the lateral line, usually directly dorsal to the anus. This region is where scales first develop on young salmonids (Power 1969; this study) and thus should have the most circuli and give the best indication of the first annulus. The scales were cleaned by peeling off the epidermal layers with needles and then arranged on a wetted glass slide. A cover slip was dropped onto them and cellotaped at the edges to make a more or less permanent mount. The slide was labelled with the fish's number only and stored dry. The scales could then be examined when convenient.

The otoliths were removed by splitting the skull of the fish antero-posteriorly along the mid-cranial suture. The brain was deflected and the sacculus plucked from the inner ear cavity with fine forceps. The sagitta was removed and cleaned by peeling off any membranes. It was then viewed under direct light against a black background using a binocular microscope at 20x magnification. The dark hyaline bands were counted, the outer edge of these bands, where the opaline material began, being considered arbitrarily as the fish's anniversary. Fish collected in May were considered to have passed their birthday and were assigned an age without plus growth. Opaline material on the outer edge of the otolith at other sampling times was considered to be plus growth. The otolith age was recorded on a data envelope and the otoliths stored within and allowed to dry. Subsequent examinations were made after soaking the otoliths overnight in a 2:1 solution of benzyl benzoate and methyl salicylate (Johnson 1983).

Scale ages were determined independently from the otolith ages. The previously mounted scales were viewed wet (water having been introduced under the cover slip) on a microprojector at 55X magnification. The criterion for an annulus was the first complete circulus surrounding and overcutting previous partial circuli. Annuli were usually located by examining the outer edge of each band of closely spaced circuli of winter growth. Several scales from each fish were examined in order to be sure no annuli were missed.

After a careful comparison of scale ages with otolith ages, and the introduction of the benzyl benzoate-methyl salicylate clearing solution, I concluded that otolith ageing was more reliable by far. Therefore, the entire collection of charr was re-aged by this method. I and a colleague examined each otolith sample independently and then immediately compared our secretly noted results. Disagreements were resolved by immediate re-examination of the material by both parties and discussion of the quality of the growth checks. Scales were used to clarify doubtful results.

These data, along with those collected during dissection of the fish, were tabulated and filed in the University of Edinburgh ICL 2900 computer. Analyses of the data were performed using appropriate programs from Nie et al.(1975).

4.2.2 CORRECTION FACTORS: The ages of the fish were recorded as the number of anniversaries passed by the fish. In order to allow for progress through the growing season current at capture, the expired proportion of this season was added using the equation:

$$\text{Age} = \frac{(A \times Ny) + (Nc - Na)}{Ny} \qquad 4.1$$

where:

A=number of anniversaries,

Nc= number of days elapsed from Jan. 1 to the date of collection,

Na= 91= the day number of April 1, an arbitrary birthdate, for the fish, and

Ny= the number of days in the year.

Age was expressed as number of years to two decimal places.

The fork lengths of the fishes were found to change with freezing, in that the fish became shorter by up to five percent. Several lots of fish were measured when killed and then frozen for up to eighteen months. More than 90% of the shrinkage occurred within a month of collection; therefore all samples were stored for at least that length of time before being processed. The equation

$$FL = (1.0256\ OFL) + 2.5719 \qquad 4.2$$

where:

FL is fresh fork length, and

OFL is observed frozen fork length

was used to compute the body lengths used in the analyses.

The weights of the fish used in the analyses are the wet weights recorded at dissection. Wet weight is an inherently imprecise measure in fish due to the fact they are wet when captured, they secrete large amounts of mucus after death, they soak up fresh water if they die in a net before it is raised, or they begin to dry if they cannot be stored quickly after capture. Observations on the change in wet weight of fish stored for up to eighteen months in sealed polythene bags revealed no pattern of weight change; in fact, some fish gained weight while others in the same bag lost weight. The magnitude of weight change was small (1 to 2%), so no correction was made to the recorded weights.

4.3 RESULTS

4.3.1 AGE FREQUENCY: The frequency of occurence of each age class for each sex in each loch is presented in Figure 4.1 for the total sample of charr taken in this study. The frequency is also shown for all fish captured in the autumn only in Figure 4.2. Separate captures are not shown as they revealed little about the populations. The distributions tend to have strong modes, usually at age 4+. It should be noted, and is intuitively obvious, that a strong mode at an advanced age does not imply a lack of fish at younger ages. It is a perennial problem for fish biologists that gear selection will always take place, especially in large, open water systems such as lakes or the sea. In this study the modal capture tends to fall at age 4+, but the younger fish must be somewhere in at least the numbers of the age 4 sample plus those lost to escapement and natural mortality. An explanation of their absence could be:

(1) physical net selection
(2) behavioural differences
(3) geographic separation

I do not believe that physical net selection is a problem except for very small (<100 mm) and very large fish (>300 mm). Section 4.3.2 on length frequencies discusses this.

I feel there is a case for behavioural differences and geographic separation of age classes. Section 2.1 on feeding in charr discusses a shift from benthic to planktonic food in Loch Doine. Younger fish may well be more cryptic and less mobile than older fish, thus reducing their chances of capture. Finally, much of the fishing effort would preferentially take planktivores as the nets were set away from inlet streams, weedy, and littoral areas (in most cases) to avoid killing trout and salmon.

The unimodal age distribution is weakest in the Loch Meallt population. Both figures show the mode at age 4+ in female fish, but males have the mode at age 2+. When the sexes are combined, the mode remains at 2+, but it is not well defined. It appears that the age structure of the two sexes in this loch are quite different, with females surviving roughly twice as long as males.

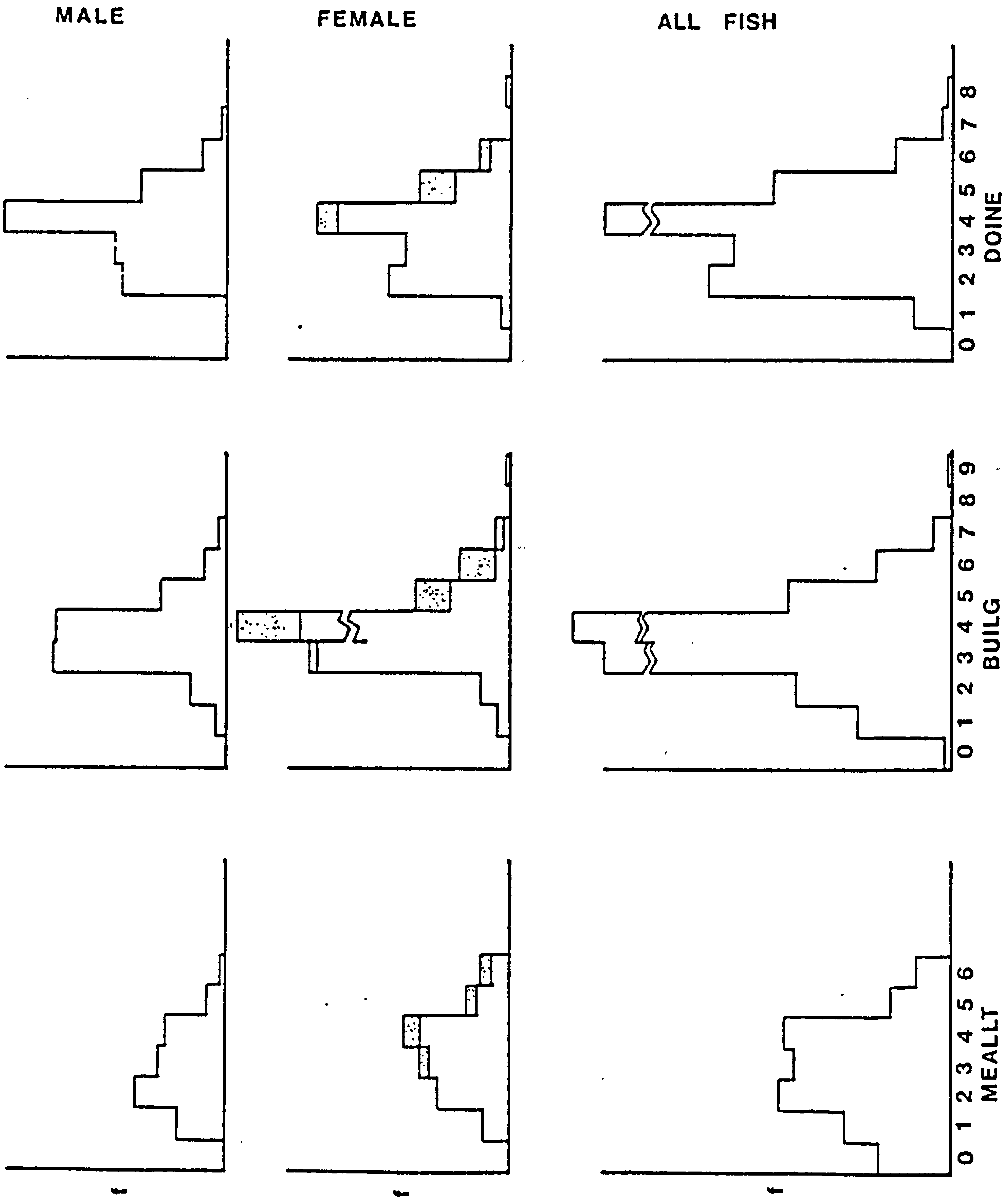


Figure 4.1 - The frequency of occurrence of ages for each sex and the total catch of charr from each of the three lochs. Stippled area represents repeat spawners.

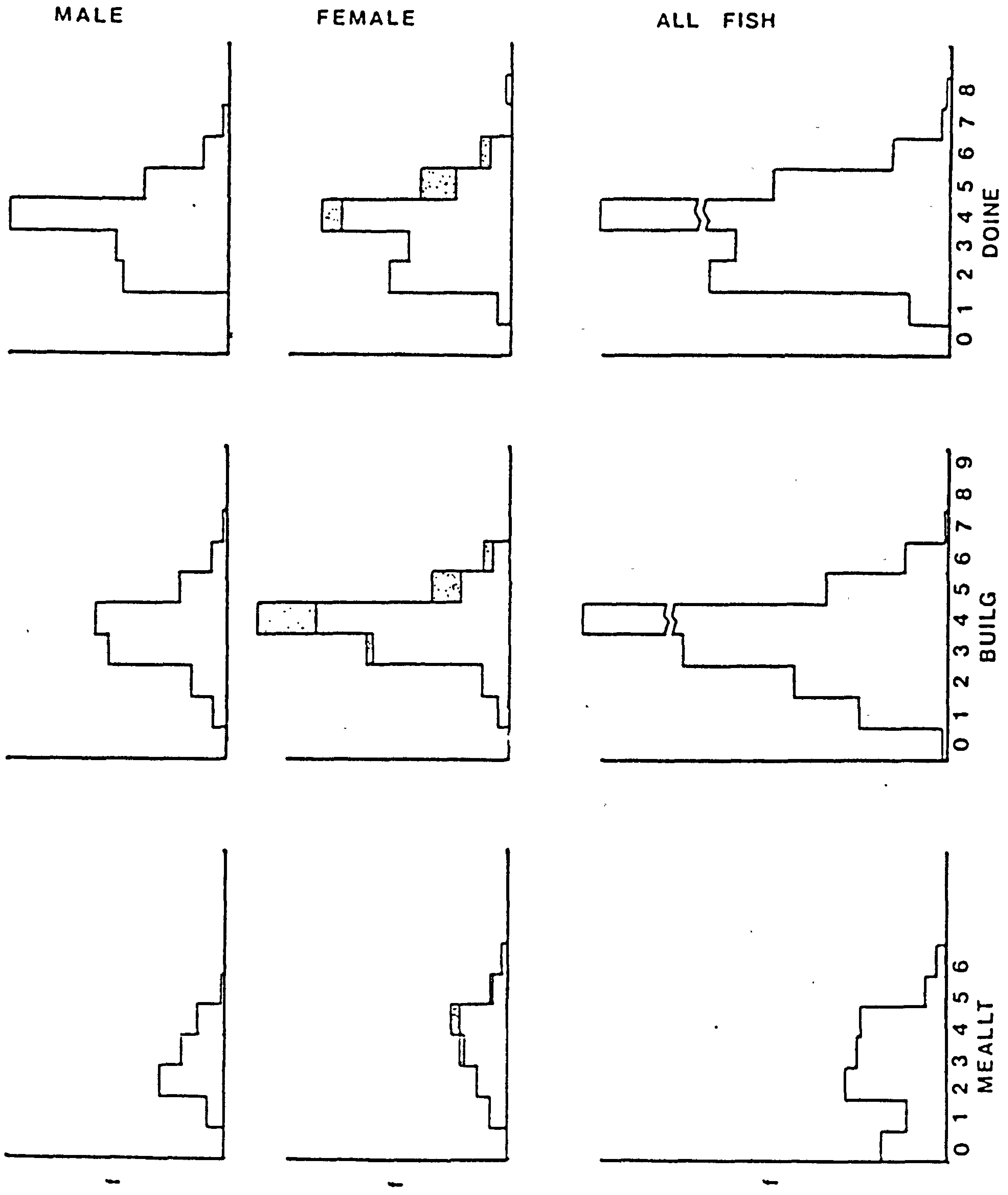


Figure 4.2 - The frequency of occurrence of ages for each sex and the total catch of charr taken in the autumn and winter from each of the three lochs. Stippled areas represent repeat spawners.

It is noteworthy that the number of repeat spawning females is reduced in the autumn sample in this loch. This implies that the fish may overwinter after spawning, but suffer high mortality the following summer, when they would have to start to feed and cope with warmer conditions. However, it may be that my fishing removed most of the spent fish in the spring and the autumn reduction is an artefact of this.

The pattern in Loch Builg is similar in both figures. Female fish have a strong mode at age 4+, but males were caught in approximately equal numbers at ages 3+ and 4+. In Loch Doine, the two figures are almost identical as only 4 fish were caught in the spring. This population has a very strong mode at age 4+ for both sexes. This is the loch that appeared to have the greatest geographic and behavioural separation of old and young fish (section 2.1).

The frequency distribution of age for the autumn samples is presented because these are the data used (in conjunction with Figure 6.1 -- age frequency of spawners) in the demographic calculations in Chapter 7. The autumn samples only were used as this eliminated the confounding effects of any variation in seasonal mortality. The samples from all years were lumped, as there were no apparent differences among their distributions and sampling was kept to a minimum until the end of the field study. Therefore, I believe the descending limb of the frequency distribution probably represents the true relative sizes of the age classes in each lake. The ascending limb can only be ignored as has been the case in most demographic analyses of fish populations (Caughley 1977).

4.3.2 LENGTH FREQUENCY: The total frequency of occurence of one centimetre length classes in each population of fish is given in Figure 4.3. The subdivisions of the histobars represent the age classes from which each length class is drawn. Two points can be made from this figure. First, length frequency is not a valid method of separating age classes as no one age class strongly dominates a length class. Therefore it cannot be used to verify ages determined from otoliths or scales. Second, the modes of the distributions are markedly different among the lochs. This means that the gangs of gill nets used in this study were not size selective (except at the extremes) and that the apparent differences in the sizes of the fish in the

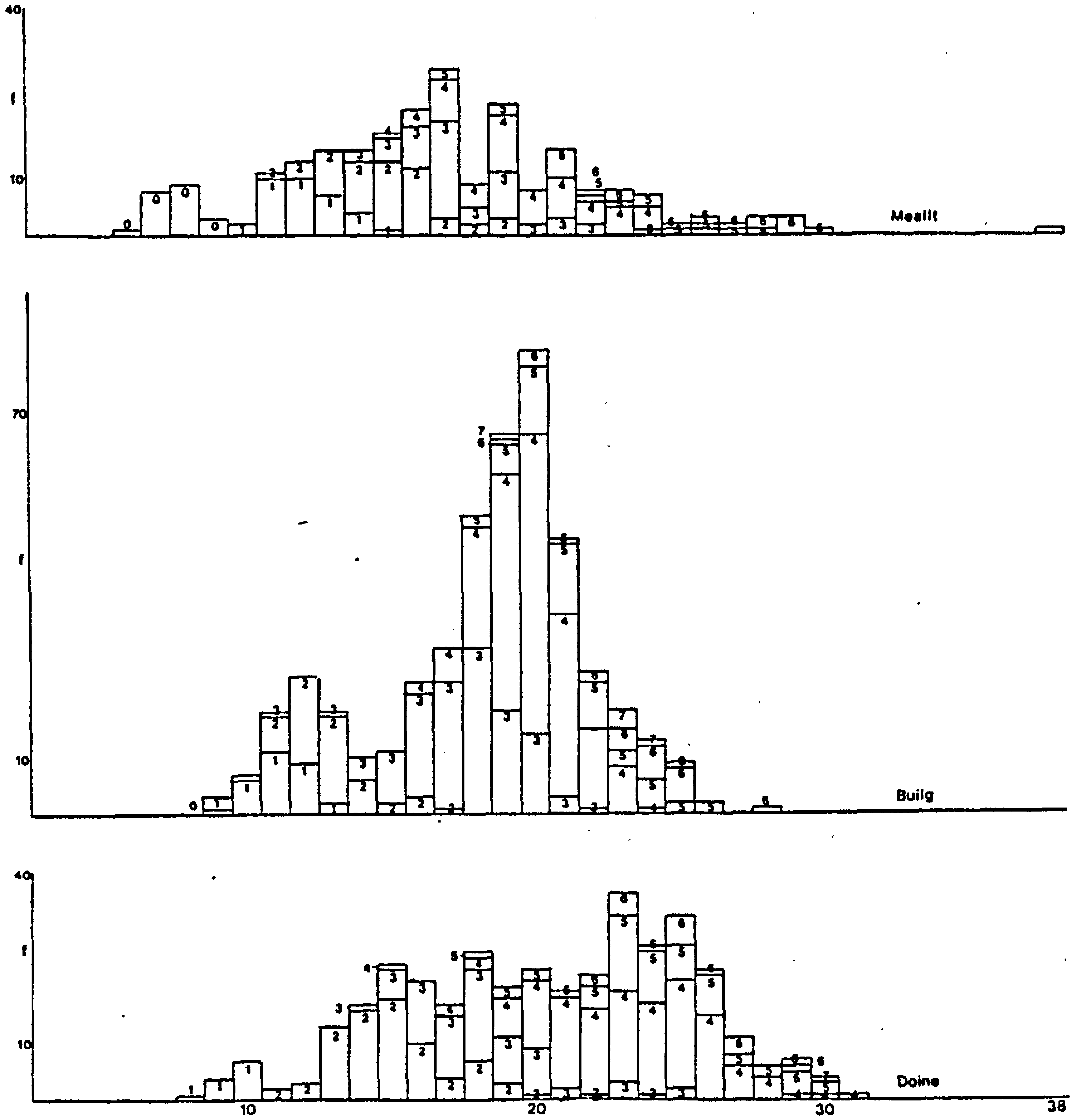


Figure 4.3 - The frequency of occurrence of one centimetre length classes of charr in each of the three lochs. The histobars are subdivided into their component age classes.

populations are probably real. Small fish would be under represented because they probably remain cryptic and do not move much. Also, small fish swim more slowly and so would be less likely to encounter a fixed net during a fixed time. Very large fish may not have been captured because the mesh sizes were too small to take them. Larger sizes were considered and rejected so that salmon and sea trout would not be taken. Nevertheless, a very large (38 cm) charr was caught, by its teeth, in Loch Meallt.

The histogram for Loch Meallt (Figure 4.3a) has the mode at 17 cm with the distribution skewed to smaller fish. This agrees with the findings of the age frequency distribution (section 4.3.1) where this population tends toward a short life history (but see section 4.3.5 hypothesizing a fast growing segment of the population).

In the Loch Builg population, (Figure 4.3b) the modal length falls at 20 cm with some skewing of the distribution toward smaller sizes. The second mode at 12 cm was caused by a single sample caught in an experiment in net placement which happened to locate a shoal of small fish.

The Loch Doine population has the mode at 23 cm with skewing toward smaller fish (Figure 4.3c). However, many more large fish were captured than in the other two lochs, even though the age distributions are similar. This indicates a paucity of large fish in the other two lochs, as the capability of the net to take these fish is demonstrated in Loch Doine.

All three frequency distributions (Figure 4.3 a,b,c) were found not to be non-normal (Kilmogorov-Smirnov one tailed test for normality).

4.3.3 LONGEVITY: The maximum age recorded from an Arctic charr in this study was 9 years, from an immature female fish caught in Loch Builg on May 20 1982. The maximum age recorded from Loch Doine was 8+ years for a ripe female captured on November 24 1983. In Loch Meallt the oldest fish taken were 6+ years old; an age achieved by eleven fish (females=90%) taken in several samples.

Table 4.1 summarises the biological data for the oldest fish taken for each sex in each lake.

4.3.4 GROWTH IN LENGTH: Growth of the Arctic charr in this study showed great variation amongst individuals and this made it difficult to reveal differences among the groups of fish.

Table 4.1: Biological data for the oldest fish taken of each sex from each loch.

LOCH	SEX	MAXIMUM AGE	FL	WW	n
Meallt	M	6	257	220	1
	F	6	282	235	4
	F kelt	6	265	209	6
Doine	M	7	325	351(n=1)	2
	F	8	298	294	1
	F kelt	6	236	155	3
Builg	M	7	243	119	2
	F	9	252	157	1
	F kelt	7	226	96	2

General growth curves for all the fish sampled from the three lochs of the study are presented in Figure 4.4. Growth in Loch Meallt appears indeterminate (open-ended) while that of the other two populations more closely resemble the logistic growth curve (Weatherley, 1972). The fish in Loch Doine tend to grow the fastest and those of Loch Builg the slowest of the three populations.

In Loch Builg, female charr (repeat spawners excluded) were found to be larger than males at all but the youngest (1+) and oldest (6+) ages (Figure 4.5). The difference in length was significant at ages 3+ (t-test, p=<.01) and 4+ (t-test, p=<.01), but not significant for ages 2+ and 5+, where sample sizes were small. Males from Loch Meallt were significantly smaller (t-test, p = 0.03) at age 2+ but not at older ages, where they were greatly reduced in numbers. No differences were found between the sexes in Loch Doine.

If the sexes are broken down by state of maturity, it can be seen that maturing female fish tend to be larger than immatures of the same age (Figure 4.6). This observation is usually statistically significant especially at the younger ages. However, it does not hold for males in any loch, as any differences in mean length at age are almost always statistically nonsignificant and there were no clear trends(Figure 4.7).

I could detect no differences in growth between year classes within a loch.

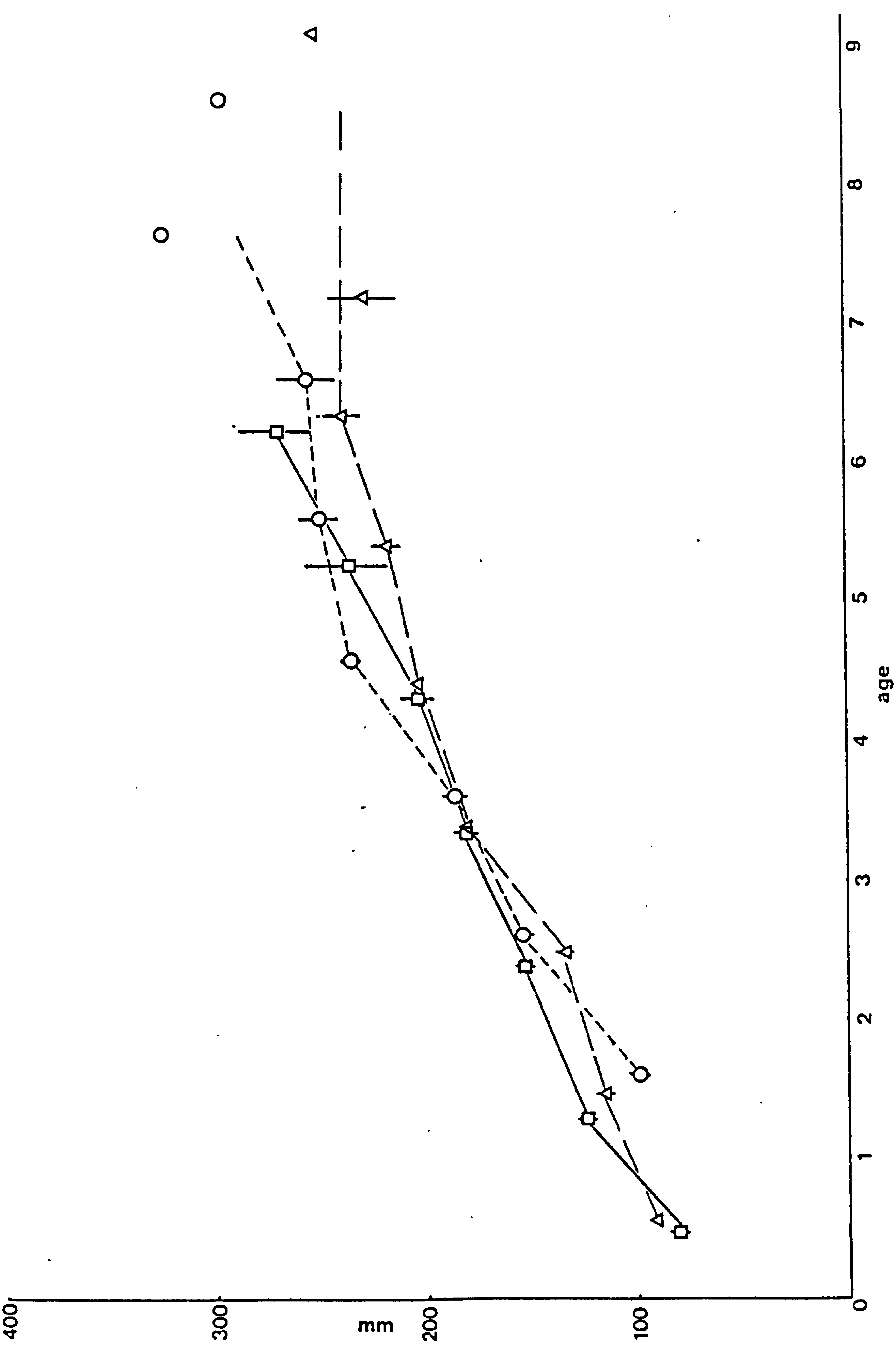


Figure 4.4 - Growth curves of charr in each of the three lochs. Vertical bars represent 95% confidence intervals.

□ Meallt

△ Builg

○ Doine

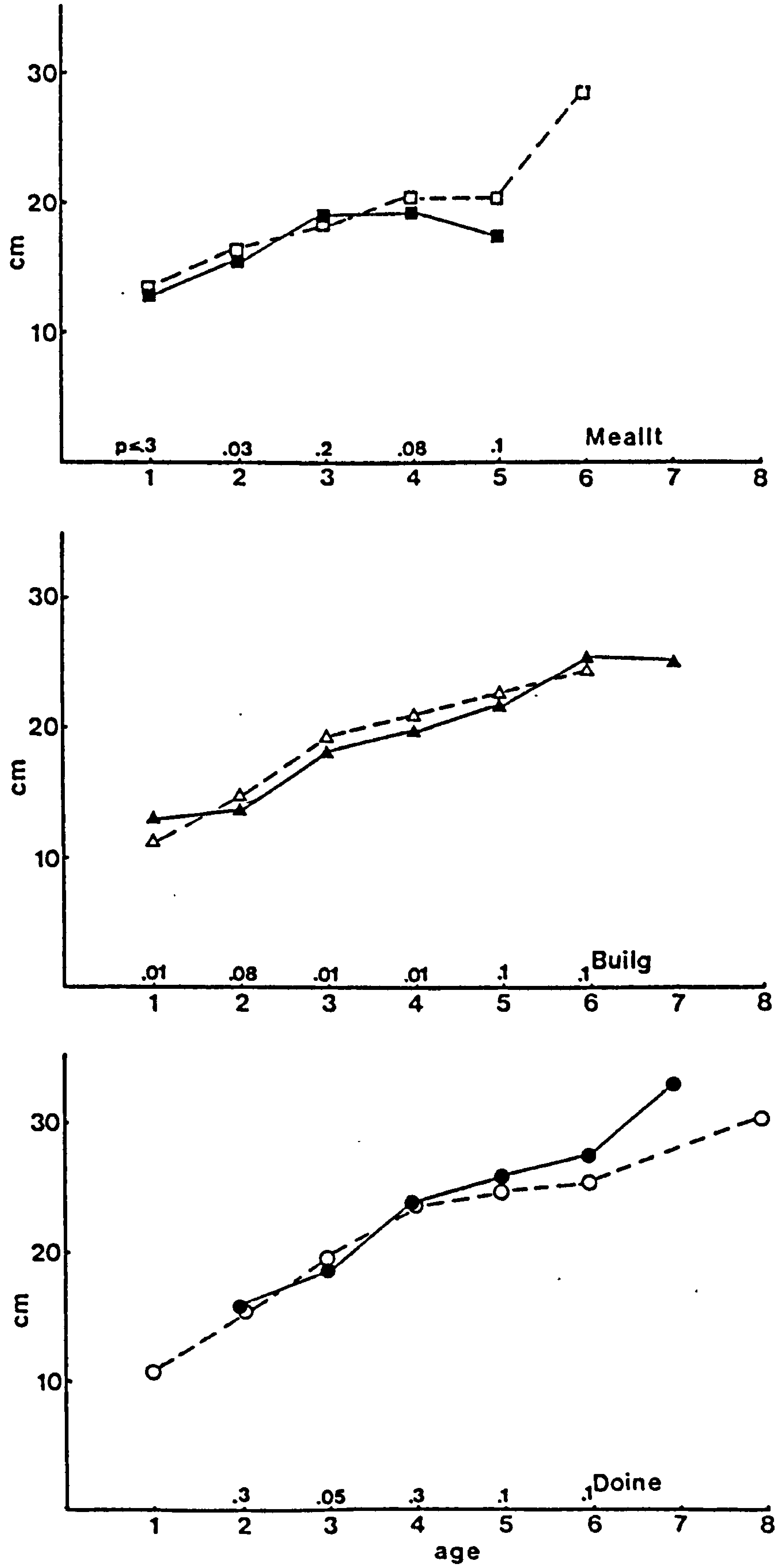


Figure 4.5 - Growth curves of the sexes (excluding repeat spawning females) in each of the three lochs. Probabilities are for one tailed t-test between the sexes within an age class. Solid symbols: males, open symbols: females.

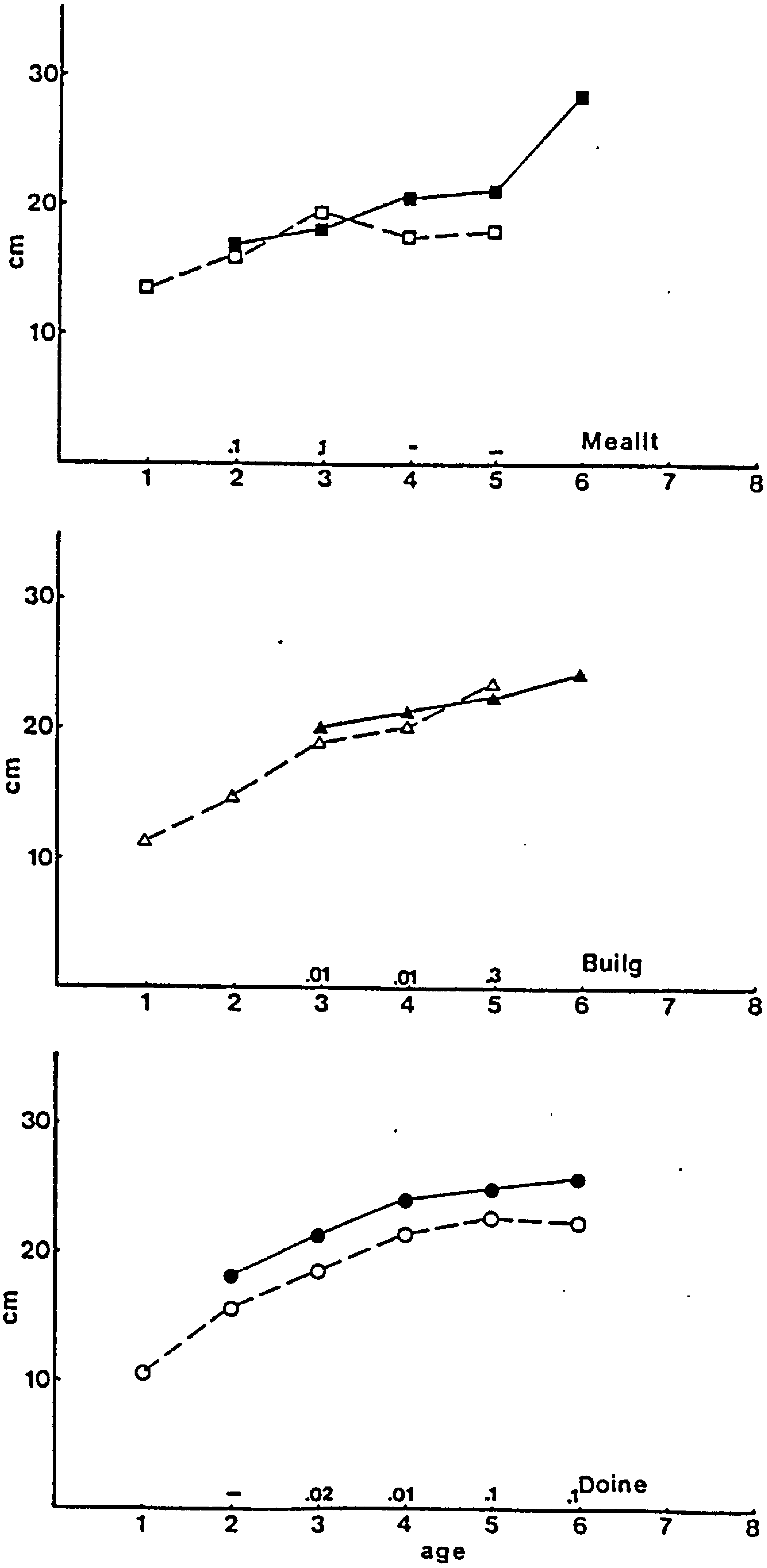


Figure 4.6 - Growth of maturing and immature females in each of the three lochs. Probabilities as in Figure 4.5 but between maturation classes. Solid symbols: matures, open symbols: immatures.

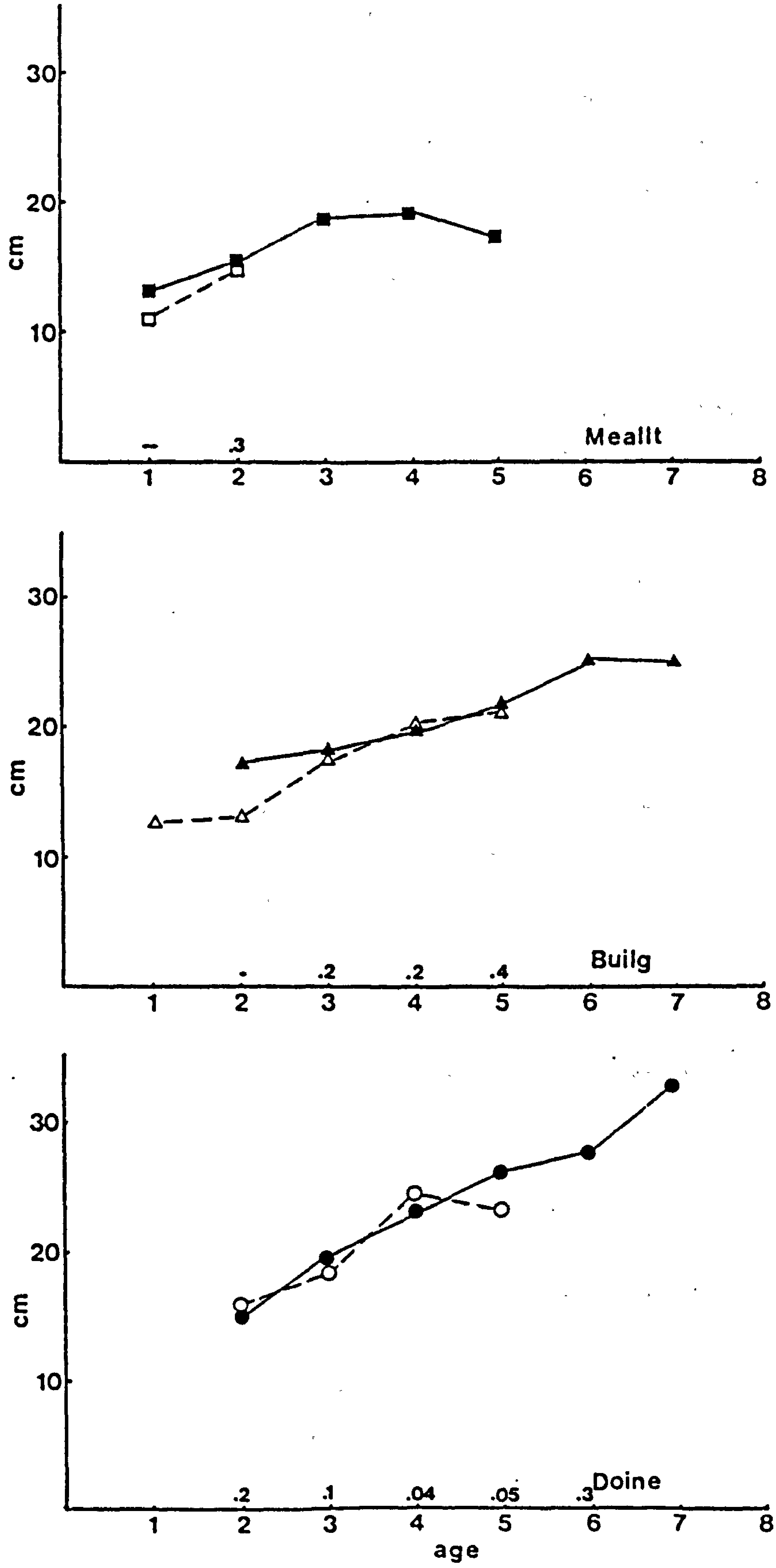


Figure 4.7 - Growth of maturing and immature males in each of the three lochs. Probabilities and symbols as in Figure 4.6.

4.3.5 BIMODAL GROWTH IN LOCH MEALLT: There appears to be a dichotomy in the growth of the charr in Loch Meallt. Most of the fish taken from the Loch were quite small and young. In comparison with the other two lakes of this study, the life history seems to be truncated. However, several very large and older fish were captured in this lake, one individual being the largest captured in the study. This suggests that some members of the population grow more quickly and, by virtue of their larger size, are able to break into a new niche where growth and longevity can be enhanced. However, support for this contention is difficult to find in my data. Inspection of length frequency within an age class shows more large individuals than one might expect in a normal distribution. This contrasts with my findings from the same frequency distributions for the other two lochs. This suggests a bimodal size frequency distribution may exist that is not apparent due to insufficient sample sizes.

4.3.6 GROWTH IN WEIGHT: Growth curves of body weight with age for each population are presented in Figure 4.8. The most striking observations are that the charr from Loch Builg remain very small, while, in contrast, those from Loch Doine show a tremendous weight gain during their fifth growing season. Some fish from Loch Meallt are capable of great weight gain in their sixth and seventh year but mortality has removed most of the population by then. I shall return to this point in Chapter 7.

In each loch, the mean weights of the various samples within an age class were rarely significantly different from one another. Therefore, the samples were pooled for each age and the mean weight of the pooled sample calculated. These data are used in the growth curves given in Figure 4.8.

This figure shows that growth in weight is similar among the lakes up to age 4. During the fifth growing season, growth in Loch Doine accelerates. During the sixth growing season growth of some of the fish in Loch Meallt accelerates, while the remainder (consider the very wide error bars for these fish on Figure 4.8) and the charr of Loch Builg are significantly smaller for the rest of the life span.

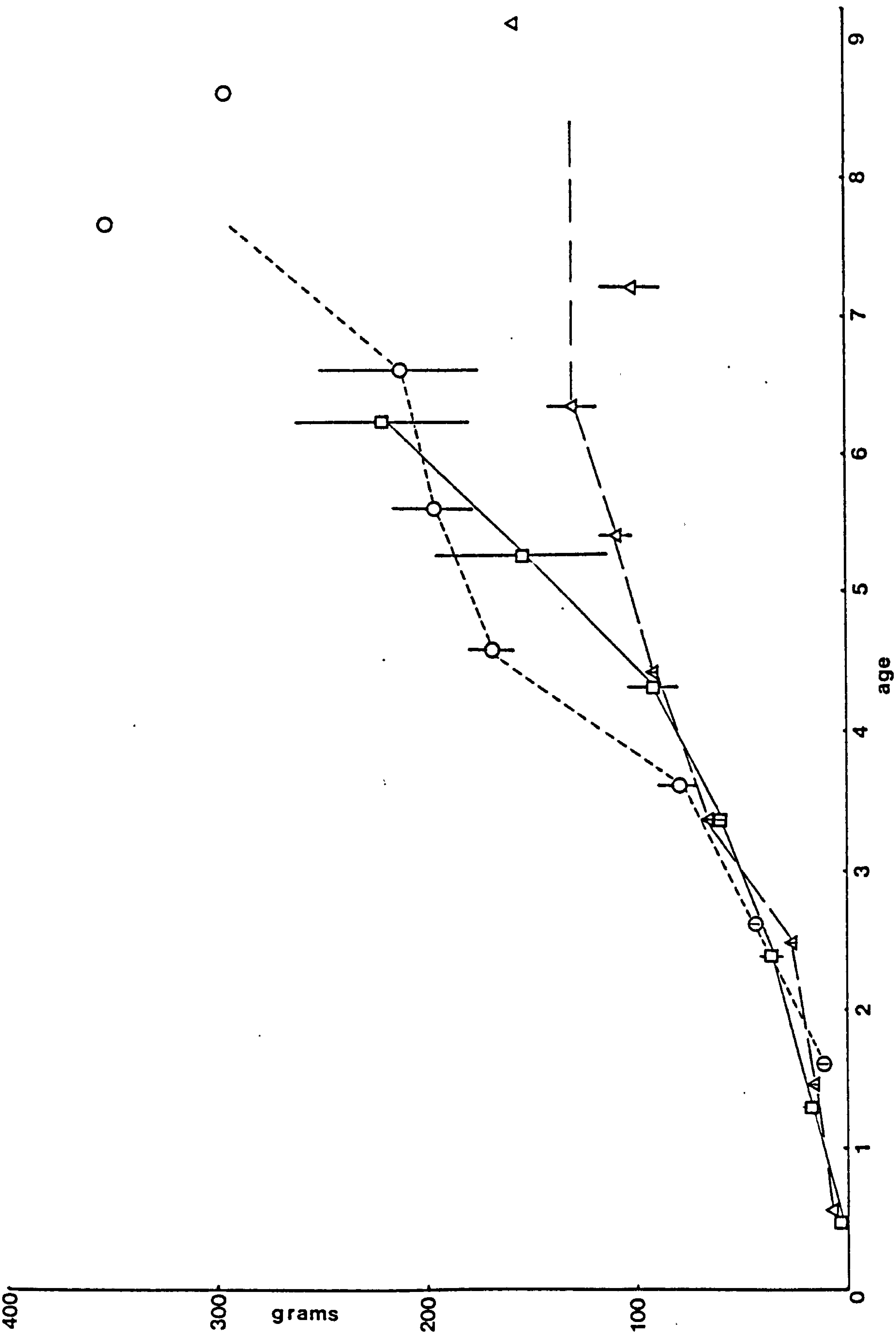


Figure 4.8 - Growth curves of grand mean wet weight of charr in each of the three lochs. Vertical bars are 95% confidence intervals.

□ Meallt
△ Builg
○ Doine

4.3.7 LENGTH-WEIGHT RELATIONSHIPS: The coefficients of the regressions of log weight on log fork length satisfying the equation:

$$W = aL^{b} \tag{4.3}$$

which in practice is:

$$\log W = \log a + (\log L \quad \log b) \tag{4.4}$$

are given in Table 4.2 for the three populations of charr sampled in the early summer and the autumn. It can be seen that on the whole the fish in Lochs Meallt and Doine are more robust (slope (b) >3) than those in Loch Builg (b<3).

The absolute values of the coefficients change with the seasons and reflect improved fitness and the growth of the gonads in the fish toward the end of the growing season.

Loch	Sex	Slope		Intercept		r		n	
		sum.	aut.	sum.	aut.	sum.	aut.	sum.	aut.
Meallt	all fish	3.15	3.15	-5.36	-5.34	.993	.990	104	62
	♂	3.17	3.31	-5.39	-5.68	.990	.988	41	22
	♀ virgin	3.09	3.22	-5.22	-5.51	.992	.975	44	3
	♀ kelt	3.31	-	-5.74	-	.992	-	11	3
Builg	all fish	2.87	2.98	-4.72	-4.94	.990	.989	95	359
	♂	2.72	2.90	-4.38	-4.73	.989	.986	40	114
	♀ virgin	2.93	2.83	-4.87	-4.59	.988	.965	41	156
	♀ kelt	2.66	2.23	-4.24	-3.18	.942	.884	12	34
Doine	all fish	3.07	3.12	-5.11	-5.21	.996	.991	4	327
	♂	-	3.13	-	-5.22	-	.991	2	157
	♀ virgin	-	3.15	-	-5.28	-	.990	2	139
	♀ kelt	-	2.65	-	-4.09	-	.862	0	20

Table 4.2 - Seasonal coefficients for the regressions of weight on length for the various sub-populations of charr from the three lochs.

4.4 DISCUSSION: The age frequency distributions of charr sampled from the three lochs are similar (except for males from Loch Meallt), but the length frequency distributions differ. This implies that there is a genuine difference in growth among the lochs. It also demonstrates that gear selection is not a problem in this study and that the catches from each loch are comparable.

Johnson (1980 and 1983) obtained similar results in studies of many lakes in the Canadian arctic and discusses at length the relationships of these age and length distributions to his equipment. He concluded that a geometric series of gill net mesh sizes provides a powerful tool for sampling open water fish populations. The specifications of my net met this requirement.

The life spans of the charr in this study are similar to those of other populations of British charr. Figure 4.9 shows growth curves from the present study and for several populations from around Britain. These tend to terminate at age 6+ or 7+. The observed length of a population's life span may be influenced by sampling effort. The number of fish in age classes older than 4+ may be quite small (Figure 4.1) and they could be missed by a low effort.

Assuming a life span of about 7+ years (maximum 9+), British charr have a normal longevity in comparison with other temperate zone populations (curves 1 to 4, Figure 4.10) but a short life history when compared with both freshwater resident (curve 7) and anadromous (curves 5 and 6) Arctic populations. Two mechanisms may operate here. First, temperate zone fish are warmer than their Arctic counterparts and presumably metabolically more active. Also, the growing season is longer in the temperate zone. These conditions would allow greater annual growth and, therefore, reproduction at an earlier age (Alm 1959). This may account for the differences between temperate and arctic freshwater resident populations. The arctic anadromous populations are able, additionally, to exploit marine production and (coupled with high marine survivorship, Johnson 1980) acheive a size at reproduction which is much larger and, as size is a function of growth rate, much older.

The rate of growth by the charr in the present study is intermediate by the standards of British populations. Figure 4.9 illustrates growth by a selection of populations ranging from the slowest, Loch Awe (Maitland *et. al.* in press) to the fastest, Loch Insh

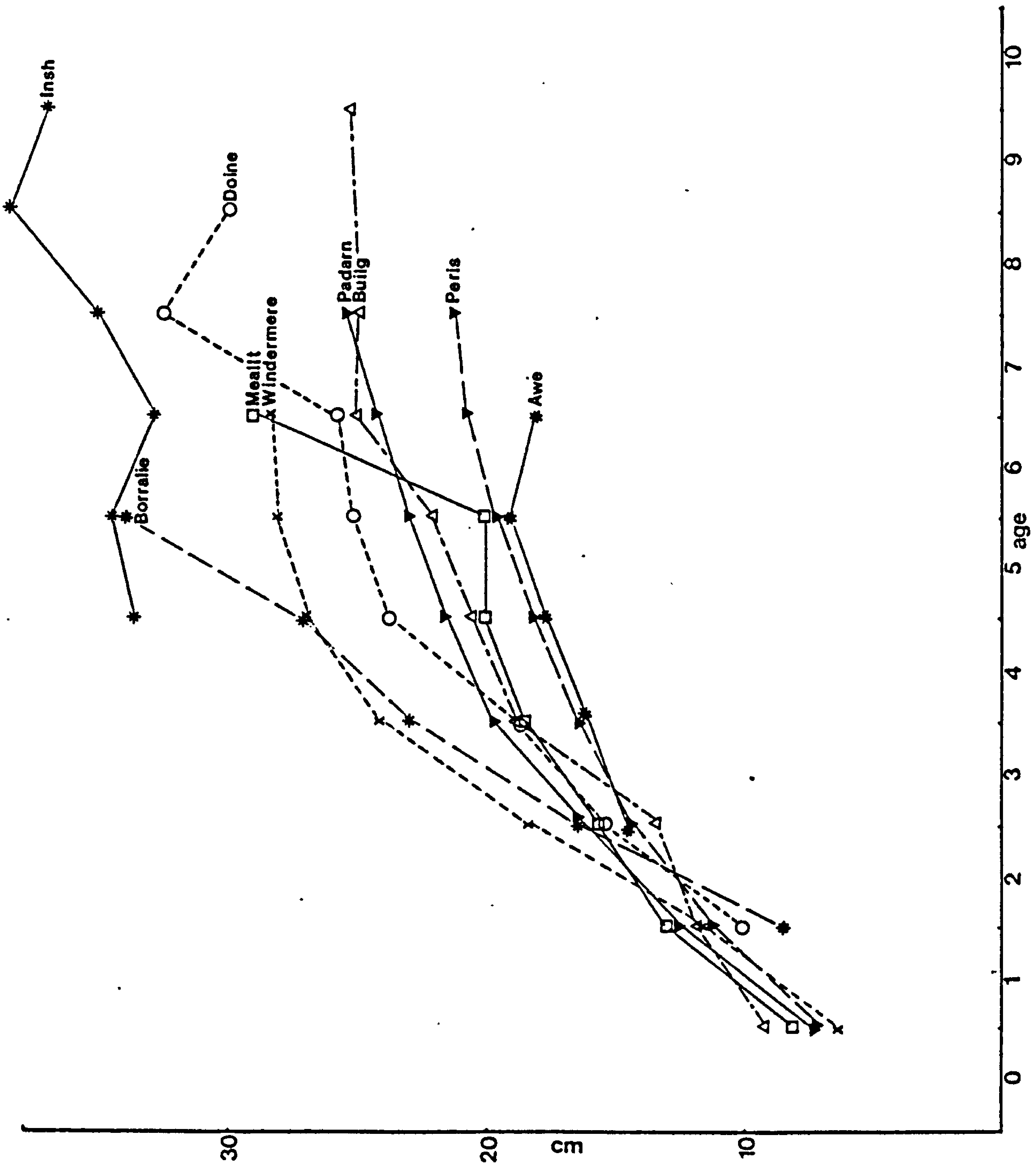


Figure 4.9 - A selection of growth curves (FL) for populations of charr from British lochs. Data from present study, Butterworth 1980, Frost and Kipling 1980, and Maitland *et. al.* in press.

□ Meallt	✱ Scottish
△ Builg	× English
○ Doine	▼ Welsh

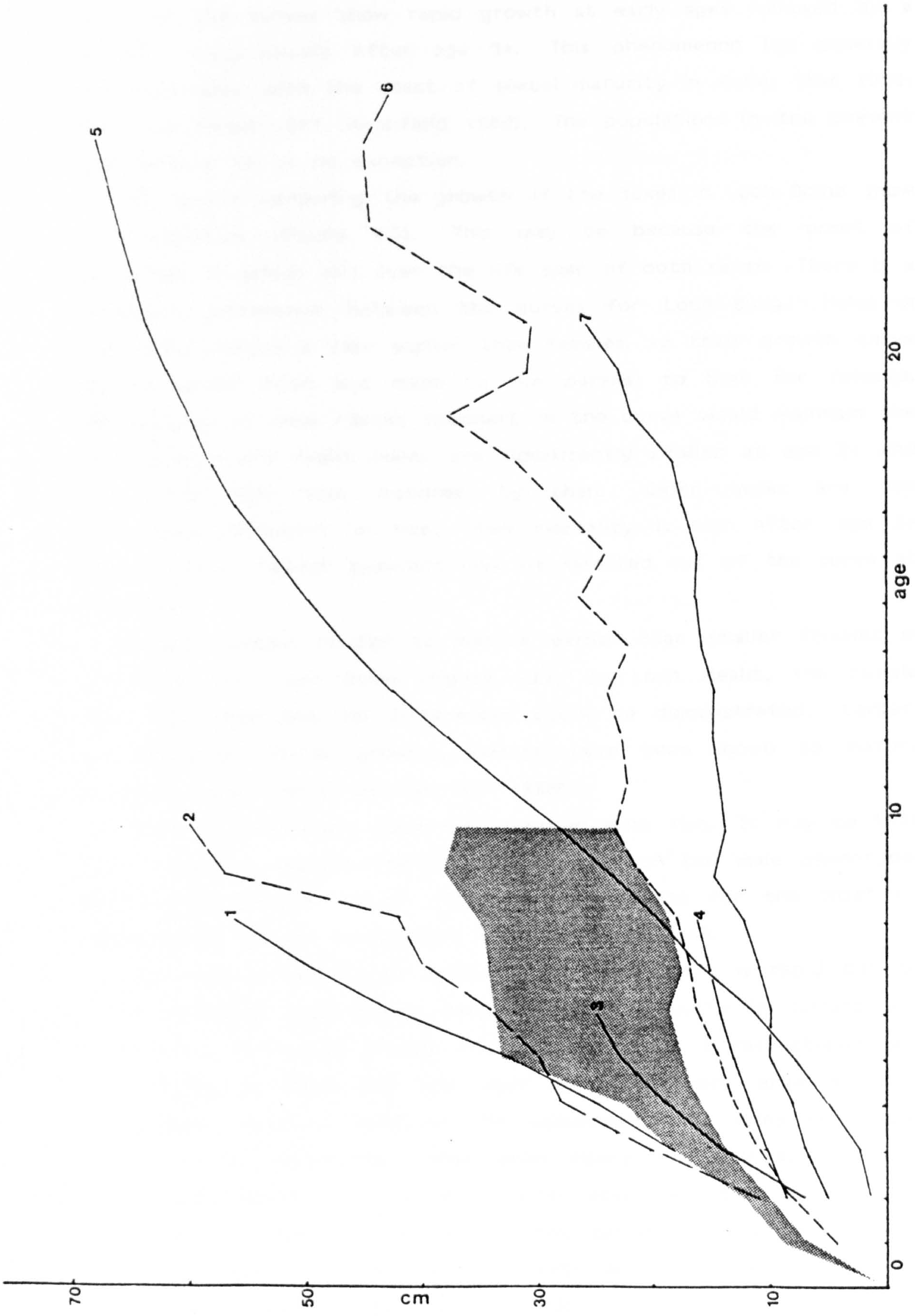


Figure 4.10 - A selection of growth curves for populations of Arctic charr from around the world. Data from Adalsteinsson 1979, Johnson 1980, and Rombough *et. al.* 1978. Stippled area corresponds to area enclosed by curves of Figure 4.9.

1-Myvatn	5-Silvia Grinnell River
2-Korsvattnet	6-Little Nauyak Lake
3-Bodensee	7-Char Lake
4-Candlestick Pond	

(*ibid*). All the curves show rapid growth at early ages followed by a gradual slowing usually after age 3+. This phenomenon has generally been associated with the onset of sexual maturity in fishes (Alm 1959; Frost and Brown 1967, Hirshfield 1980). The populations in the present study appear to be no exception.

The curves comparing the growth of the sexes in Loch Doine show no differences (Figure 4.5). This may be because the onset of maturation is spread out over the life span of both sexes. There is a significant difference between the curves for Loch Builg. Males in Loch Builg mature a year earlier than females, so their growth curve may be pulled down and made to run parallel to that for females. The inclusion of male repeat spawners in the curve would maintain the difference. Loch Meallt males are significantly smaller at age 2+ and most male fish have matured by then. Older males are not significantly different in size. Male mortality is high after age 2+ (Figure 4.1) so repeat spawners may be selected out of the curve at older ages.

Larger females tended to mature earlier than smaller females in Loch Builg and Loch Doine (Figure 4.6). In Loch Meallt, the sample sizes were small and no differences could be demonstrated. Larger, and therefore faster growing, females have been shown to mature earlier in many species of fish (Alm 1959).

No such differences could be found in male fish. It may be that size or age at reproduction is set for each of the male phenotypes described in Section 2.1.3.1. Thus the set points for the onset of reproduction may be independent of the growth rate.

The rate of growth of British charr populations is rapid but by world standards they remain relatively small. Myvatn in Iceland and Korsvattnet in Sweden (Figure 4.10, curves 1 and 2 respectively) are very productive lakes and the charr can grow very large within a short time. However, most of the populations with many very large individuals are anadromous. They grow slowly and only achieve sizes larger than British charr at much older ages (curves 5 and 6). The early stages of their growth curves show extremely slow growth. This period is spent in fresh water. Growth accelerates after the fish have emigrated to the sea (Johnson 1980).

Figure 4.8 shows the weight to age curve for the three populations of fish. Loch Doine fish put on a lot of weight during their fifth growing season. Some fish in Loch Meallt do so a year later. These fish may be exploiting a niche that opens to them upon reaching a certain size. The feeding habits of Loch Doine charr change just before this growth spurt (Section 3.1). Large Loch Meallt charr tend to eat fish rather than zoo-benthos (Section 3.1). Loch Builg charr show only a modest increase in weight gain, and it is interesting that their diet is the same throughout the life history.

Most published data on weight of charr is in the form of length-weight relationships. Those for the three lochs in the present study are given in Table 4.2. The important parameter is the slope (b).

The fish in Lochs Meallt and Doine actually become disproportionately heavier as they gain length (b>3). Those in Loch Builg add weight at a disproportionately slower rate (b<3). If one considers data from other populations one may hazard a guess as to the reasons for this.

McCart (1980) studied charr from various waters of the North Slope of Alaska and the Yukon. This area has an Arctic climate. He found that charr with an entirely freshwater life history had values of b<3 while those fish that were diadromous, and could exploit marine production, had a b value greater than 3. Johnson (1980) presents similar data for several regions of the Canadian Arctic although some of the freshwater populations have b>3, as was found in the present study. Kipling and Frost (1978) found immature charr in Windermere to be quite robust (b>3), but matures were relatively thin (b<3). Table 4.2 shows seasonal variation in "b". It would seem that the productivity of the habitat influences the amount of body mass the fish are able to produce and that this is reflected more in the weight than in the length of the fish. Proximate factors such as seasonal variation or maturation may complicate matters. Oligotrophic Loch Builg (with its thinner fish) is situated in the harshest climatic region of Britain while the other two lochs of this study (with more robust fish) have milder climates and have their production enhanced by the inputs from the agricultural activity around their shores.

4.5 SUMMARY

1. Otoliths are the best structures for ageing Scottish charr.

2. Charr are fully recruited to a gill net fishery at age 4+. This appears to be a function of behaviour rather than gear selection.

3. Charr have a relatively short life history in Britain and tend to be relatively small fish.

4. Charr growth is dependent on the richness of the habitat.

5. Changes in growth rate are associated with changes in the life history of the fish.

CHAPTER 5

RESOURCE UTILIZATION

5.1 INTRODUCTION: Resources are finite in animals and must be partitioned among growth, maintenance and reproduction. These resource allocations can be manipulated to suit various life history strategies (Calow 1981). Proximate analysis (the measurement of the four major components of animal tissue; water, protein, lipid, and ash (Love 1970)) provides a simple measure of resource allocation to soma and gonads. This chapter aims to discover the annual and life history patterns in resource utilization by various sub-groups of the populations of charr in Loch Doine and Loch Builg. These data can then be discussed in relation to the life history strategy of charr.

5.2 METHODS

5.2.1 TREATMENT OF SAMPLES: Proximate (body composition) analyses (Love 1970) were performed on 465 arctic charr collected periodically from the three lochs in 1981 and 1982. The sampling dates are given in Table 1.1. The fish were frozen as soon as possible, usually within 12 hours, after capture. The individual fish were weighed (wet weight), assigned a number and tagged with a card tag attached by string. These tags, with pencil inscriptions, were immune to the solvents used in later extractions.

On thawing, the dissection procedure started with the measurement of the fork length of the fish. Scales and the otoliths were removed for ageing. A ventral incision was made from the anus to the isthmus and the sex and state of maturity were recorded. The gonads were removed, weighed to 0.01 g and frozen in foil trays inscribed with the fishes number. Ripe ovaries were cooked (see Section 6.2), the ova counted and then frozen along with the ovarian tissue. The degree of parasitism was indexed (see Section 3.2) and the stomach contents sampled and identified. The stomach was emptied but the bowel was not. The fish was then re-frozen.

The frozen samples, both carcass and gonad, were dried to constant weight (five days for large carcasses, two days for gonads) in a model EF2 Edwards Freeze Dryer and then stored for at least several days in dessicators at room temperature. They were then weighed (dry weight) to 0.001 g on a Mettler V10 balance. Lipids were then extracted by refluxing the samples in chloroform in a Soxhlet apparatus for at least 18 hours. This was found to give a constant lean weight. The samples were oven dried overnight, stored in dessicators for at least several days and the lean weight determined to 0.001 g. The stored lean samples were badly damaged by moths before ash determination could be carried out. Ash content could only be measured for a sample of fish captured in November 1983, so that in the following analyses it has been necessary to assume that ash content is constant.

5.2.2 DATA ANALYSIS: In a comparative study of populations of animals, it is important to separate and standardize all the independent variables in order to remove autocorrelations and masking effects.

Many authors are prone to err in the former case, particularly by using proportional data (usually percents of body weight) (Barbour and Garside, 1983; Craig,1977; Elliott 1976; Farmer *et. al.* 1978; Wootton 1977). Consequently, the parameter in question is usually included in both the numerator and denominator of the calculation. In this thesis, an attempt has been made to avoid this, as explained below.

The standardization of data was discussed in detail by Le Cren (1951) for the calculation of body condition (Kn) in the perch (*Perca fluviatilis*). The idea was criticised by Weatherley (1972) on the grounds that it is usually unimportant and time consuming. Craig (1977) defended the idea as necessary for

> "scientific collation between populations in time or space...
> so that any size of fish may be compared".

The advent of modern computers now obviates the concern about excessive computational labour.

Consequently, I have followed the method of Le Cren (1951) in computing values of condition (Kn), and have adapted the method to the standardization of the other variables used in the analysis. This was done because the body length-weight relationship differs greatly between the populations (Table 5.1), and growth is allometric (b $\neq$ 3, see section 4.3.6) within the populations (Table 4.1). The omission of a correction in the first instance would mask between population

Table 5.1: Components of the regressions describing the relationship $W = aL^b$ (transformed to $\log W = a + b \log L$) for various measures of weight for the charr from Loch Builg and Loch Doine sampled after September 1 in each year.

Parameter	Loch	a	b	r	n
Wet weight	Doine	-5.386	3.194	.98	96
Lean weight	Doine	-6.015	3.154	.97	95
Wet weight	Builg	-3.893	2.533	.94	126
Lean weight	Builg	-4.262	2.367	.94	131

differences while omission of a correction for the second would mask changes over the life history of the fish. Five parameters were calculated from the proximate data, namely; condition, water, lean, lipid and energy. They were calculated for both soma and gonads.

Condition was calculated using the equation:

$$Kn = \frac{W}{aL^b} \qquad 5.1$$

where:

W is weight,

a and b are empirically derived constants from the weight to length relationship, and

L is the corrected fork length described in Section 4.2.3.

In practice, three steps were needed in the calculation. First, the constants a and b were derived by linear regression of W on L, which must be logarithmically transformed since the arithmetic relationship is a curve. Second, the expected weight ($\hat{W}$) of each fish was calculated by substituting the corresponding value for L into the equation:

$$\log W = (\log a) + (\log L \log b) \qquad 5.2$$

The constants a and b for each weight parameter are given in Table 5.1. Third since:

$$W = aL^b \qquad 5.3$$

it can be substituted into equation 5.1 producing:

$$Kn = \frac{W}{\hat{W}} \qquad 5.4$$

Since $\hat{W}$ is the weight predicted by the regression, and W is the actual measured value, Kn is an index of deviation from the population norm. Consequently, bias can creep in if sampling is concentrated in one season or sample sizes are very unequal. The former is the case in my study, so the calculation of regression 5.2 was based on fish sampled only in the last third of the year, in fact near their spawning time. Unfortunately this reduced sample sizes, so the sexes had to be pooled for the calculation of the regressions.

Condition was calculated twice, once as described above, which gave the condition of the soma with gonads, and a second time to give condition exclusive of gonads (where somatic weight was substituted for W). Both Kn values were plotted for each sex in each loch, the area between each pair of curves representing gonad development by the fish (Figure 5.3).

Condition is a measure of the plumpness of a fish, but it does not reveal much about the relative changes in body constituents. The following passages describe how I have treated the data from the proximate analysis in order to gain a true picture of what was happening in the fish.

Water content was calculated using the equation:

$$\text{Water} = 100 \; \frac{\text{carcass water (g)}}{\text{carcass weight (g)} - \text{carcass lipid (g)}} \qquad 5.5$$

This is the percent water of the lean wet weight. Lean wet weight was used in order to remove the effect of the negative correlation of percent water to percent lipid which is found in fish (Love 1970). The effect of this calculation is to reduce water to a virtual constant in relation to size (Figure 5.1c) in contrast to the relationships of water weight (Figure 5.1a) or percent water (Figure 5.1b) to wet weight . The constancy of water values (anomalies are discussed in Section 5.4.1) means that water can be dismissed as a variable and the relationship of lean and lipid can be investigated.

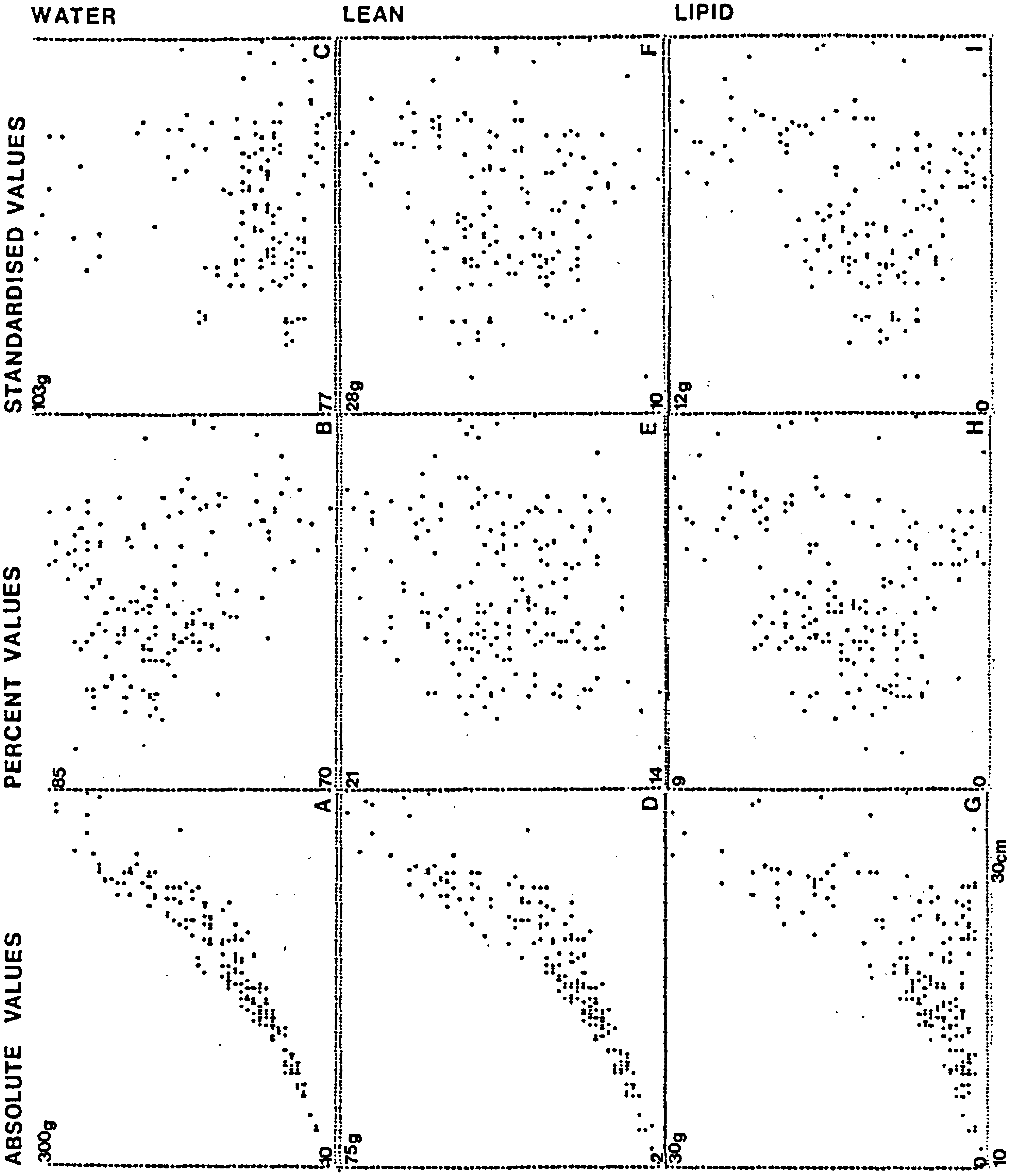


Figure 5.1 - Changes in the relationships of parameters with body size with changes in the method of their calculation. (x-axis always fork length).

Values for lean content were calculated using the equation:

$$\text{Lean} = F \frac{\text{lean weight}}{aL^b} \qquad 5.6$$

which in practice is:

$$\text{Lean} = F \frac{\text{lean weight}}{\text{expected lean weight}} \qquad 5.7$$

This gives the weight of lean in grams one would find in a fish if it were of a standard size of 214 mm fork length. As in the measure of condition, this is a measure of deviation from a norm, but the correction factor (F) allows one to assign an absolute weight to each fish. This was done to make the results more palatable to the reader.

Four steps were needed in calculating equation 5.6. First the measured values of lean weight were logarithmically transformed and regressed on the logarithmically transformed values of fork length for each fish. Second, the empirically derived values for log a and log b were substituted into the regression equation and the expected lean weights calculated (as in equation 5.2). Third, the steps through equations 5.3 and 5.4 (see equation 5.7) were followed to give a ratio value of lean. Finally, the ratio value was multiplied by the appropriate population specific correction factor (Loch Builg = 17.53; Loch Doine = 21.53) to give the lean weight of the fish as if it were of standard length.

The values for lean remain quite variable in spite of the lack of interference from other parameters (compare Figure 5.1d, e and f). Because all other parameters are removed, this variation must be taken as real. These data are analysed in Section 5.3.2.

Because the values for lean are variable, the percent method of calculation of lipid content is unreliable. This is because both variables are included in a single equation. Therefore, values for lipid content were calculated using equation 5.6 substituting lipid weight for lean weight only. Thus:

$$\text{Lipid} = F \frac{\text{lipid weight}}{aL^b} \qquad 5.8$$

which in practice is:

$$\text{Lipid} = F \quad \frac{\text{lipid weight}}{\text{expected lean weight}} \qquad 5.9$$

The steps in the calculation of equation 5.8 are the same as for equation 5.6.

The use of equation 5.9 corrects for the variation that has just been demonstrated for values of lean. This is because the denominator is the expected lean weight rather than the absolute lean weight. Examination of Figure 5.1i still shows considerable variation in lipid values (but note Figures 5.1g and h) and, again, these must be considered real.

5.2.3 ANALYSIS OF DATA FOR GONADS: The treatment of the data for gonads was similar to that for carcass values. The equations and sequences of steps in the calculations were identical except that appropriate gonad weights were substituted into the numerators of equations 5.5, 5.7 and 5.9 to produce values for grams of gonad water, lean and lipid in a fish of standard size. The use of carcass parameters in the denominators of the equations enables the comparison of somatic and reproductive investment in the fish.

5.2.4 CALCULATION OF ENERGY CONTENT: The availability of lipid and lean values allows the calculation of the energy content of the standard fish. This was done using the equation:

$$E_{kJ} = (39.3 \text{ lipid}) + (18.0 (\text{lean} - (0.11 \text{ lean}))) \qquad 5.10$$

where:

lipid is the number of grams of lipid in the standardized fish;
lean is the number of grams of lean in the standardized fish;
0.11 is the proportion of lean made up by ash; and,
39.3 and 18.0 are the approximate energy in kiloJoules per gram of lipid and lean respectively (Pond 1981).

Energy was calculated for both soma and gonad tissue. The correction for ash was omitted from the calculation for gonads since they have no bones and ash would be overestimated. It was assumed that ash free lean is equivalent to protein and that Pond's (1981) energy values are applicable to the lean and crude lipid values I have derived. Craig (1977) discussed carbohydrate content in fish and found it to be about 0.1% of wet weight in perch (*Perca fluviatilis*) and generally ignored by biologists working on the proximate analysis of fish. Here I have assumed carbohydrate to be negligible in charr.

5.3 RESULTS

5.3.1 RELATIONSHIPS OF PARAMETERS: Much of the justification for my methods of calculation is based on their effects on the relationships of the parameters of water, lean and lipid. Figure 5.2 shows how the relationships of the parameters change depending on the method of calculation.

The first column of panels in Figure 5.2 has the absolute value of the parameter on each axis. The second column of panels has on each axis the simple percent of the carcass made up by the parameters. The third column of panels has the values of the parameters calculated for the standard fish.

Figure 5.2 shows the three relationships of water content with lean content. The absolute values are directly related and strongly correlated (Figure 5.2a). This is because as a fish gets bigger, the weight of its body constituents increases. In contrast, the percent values are negatively correlated (Figure 5.2b) so that as the proportion of lean in a fish increases, the proportion of water falls. When lipid is removed from the denominators of the equations (Figure 5.2c) the relationship breaks down with water becoming very variable with respect to lean. A standard fish that has a lot of lean has slightly less water while a less robust fish tends to have more water and sometimes very much more water.

The pattern of relationships of water with lipid content is identical to that of water with lean (Figure 5.2d,e and f). When the parameters are standardized the formerly strong relationship deteriorates so that water is almost, and probably actually is, independent of lipid.

The opposite is true of the relationship of lipid to lean (Figure 5.2g,h and i). As one would expect, the absolute values are strongly correlated with size (Figure 5.2g), but the percent values, which include water in the equations, are postively, but poorly related (Figure 5.2h). When water is eliminated, the positive correlation improves greatly and shows that fish with more lean can be expected to have more lipid and vice versa (Figure 5.2i).

5.3.2 POPULATION SPECIFIC RELATIONSHIPS OF PARAMETERS WITH TIME: The figures for this section are arranged in matrices of four populations.

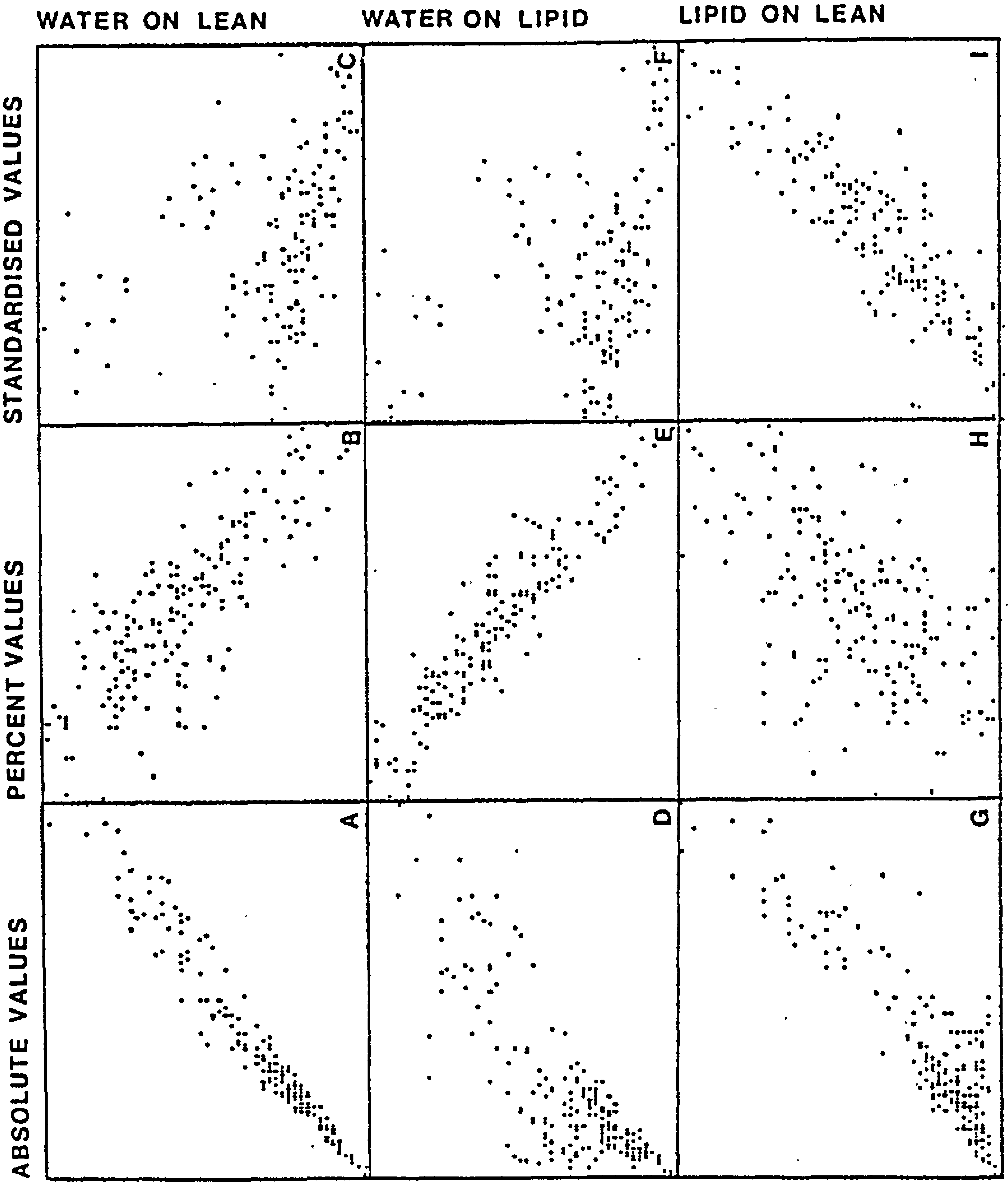


Figure 5.2 - Changes in the relationships of parameters with changes in the method of their calculation. (Parameters given as y-axis on x-axis).

The sexes are arranged in the rows and the lochs arranged in the columns. All values for males include first time and repeat spawners while these two sub-categories are kept separate in females. The results for the various maturation classes are presented separately with maturing fish in section (5.3.2), immatures in section 5.3.3, and female repeat spawners in section 5.3.4. All data for gonad development are presented in section 5.3.5.

Values for the mean of each parameter were plotted against the age of the fish in days. Age classes are assigned to the x-axis for ease of interpretation (Figures 5.3 to 5.16). Transparencies of these figures are provided to facilitate comparisons among the parameters and populations. The beginning of an age class is April 1, therefore a cycle (see below) starts in the spring and ends in winter. Two features of the plots are important. First, each graph shows a series of cycles, each cycle corresponding to an age class of fish. These I call annual cycles. Second, there are trends in the series of cycles which often show differences over the life histories of the populations. These I call the life history curves. It should be noted that these curves represent a standing age distribution, made up of several cohorts of fish (Caughley 1977). Confidence limits have not been assigned to any of the points. They were omitted because many of the samples are very small, especially at older ages, and they would make the figures cluttered and difficult to interpret. I believe that the trends in the data are real, because they are repeated consistently among the populations, and that the relative values are more important than the absolute values.

Mean values for condition are plotted against age in Figure 5.3. Two values are plotted for each sample. The lower value is always the condition of the soma and the upper is the condition of the soma with gonads. The area between the curves is an estimate of gonad investment by the fish.

The curves on all the graphs of Figure 5.3 are a series of annual cycles. Some of these are fragmentary, but are consistent with those which are complete. Each annual cycle shows the fish to be in relatively poor condition early in the year. Somatic condition improves rapidly and then declines at the end of the summer. The upper curve, representing gonad growth, increases more quickly and where the samples are more plentiful, peaks and suddenly decreases at

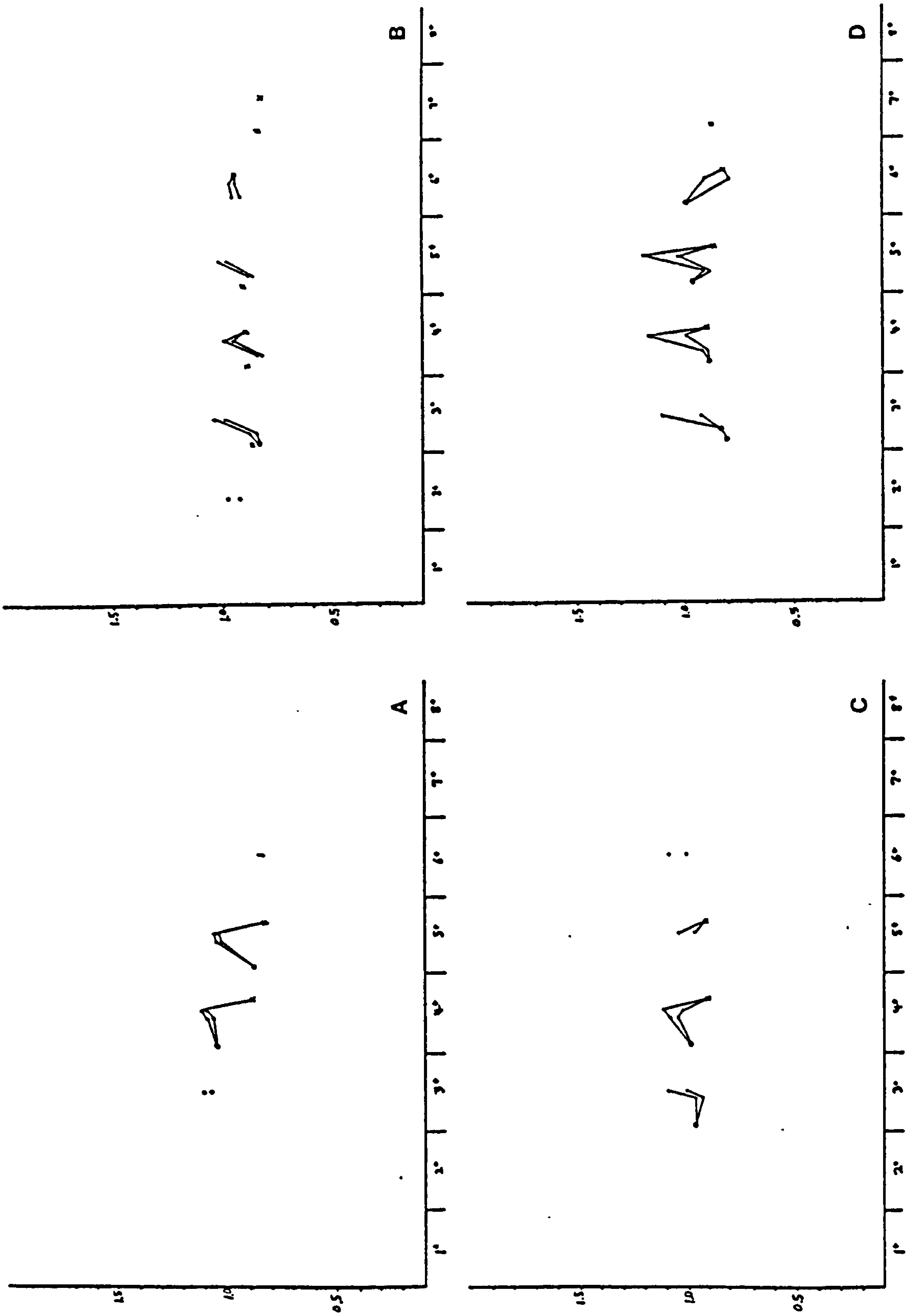


Figure 5.3 - Condition (Kn) of soma (lower curve in each panel) and soma plus gonad (upper curve) of male (upper row; A,B) and female (lower row; C,D) charr from Loch Doine (left hand column; A,C) and Loch Builg (right hand column; B,D). x-axis always age in years.

spawning time.

The life history curves for condition are variable among the populations. Males in Loch Doine show a general decrease in condition with age while males in Loch Builg remain constant. Females in Loch Doine may have a slight net increase while those from Loch Builg show a more pronounced increase up to age 5+ and then a decrease.

The apparent investment in gonads differs among the populations. It is least in Loch Doine males, slightly greater in Loch Builg males, much greater in Loch Doine females with Loch Builg females making the greatest investment by far.

Mean values for water content of "standard" fish are plotted against age in Figure 5.4. The most striking feature of these graphs is the virtual constancy of water content throughout the annual and life history curves. The only real deviation occurs in female fish where, in Loch Builg, water content soars in each annual cycle at approximately the time of ovulation and spawning (the actual time these samples were taken). Some evidence of this is also seen in the data for Loch Doine females. The remaining data appear to constitute a baseline water content.

Mean values for lean (protein ash and carbohydrate) content of sexually maturing standard fish are plotted aginst age in Figure 5.5. As was seen for condition, the plots consist of a series of annual cycles that are subsets of a trend over the life history.

The annual cycles show an increase in lean from spring samples to summer, followed by a rapid decline to low values in the autumn. The amplitude of changes over an annual cycle is much greater in the Loch Doine populations than in those from Loch Builg. Between sex differences in these changes are not apparent in Loch Doine but in Loch Builg the changes are greater in females than males.

The life history curves are variable among the populations. Males from Loch Doine show a decline after age 4+. There is a suggestion from the few points at ages 2+ and 3+ that lean increases up to age 4+. This convex curve is apparent in both female populations. Lean appears to increase slightly with age in males from Loch Builg. However, because this curve is close to being a constant, it is possible that it has been tipped upward by the bias toward autumn samples in the length-weight regression in Equation 5.6. All the other curves in Figures 5.3 to 5.16 are robust enough to prevent this bias from

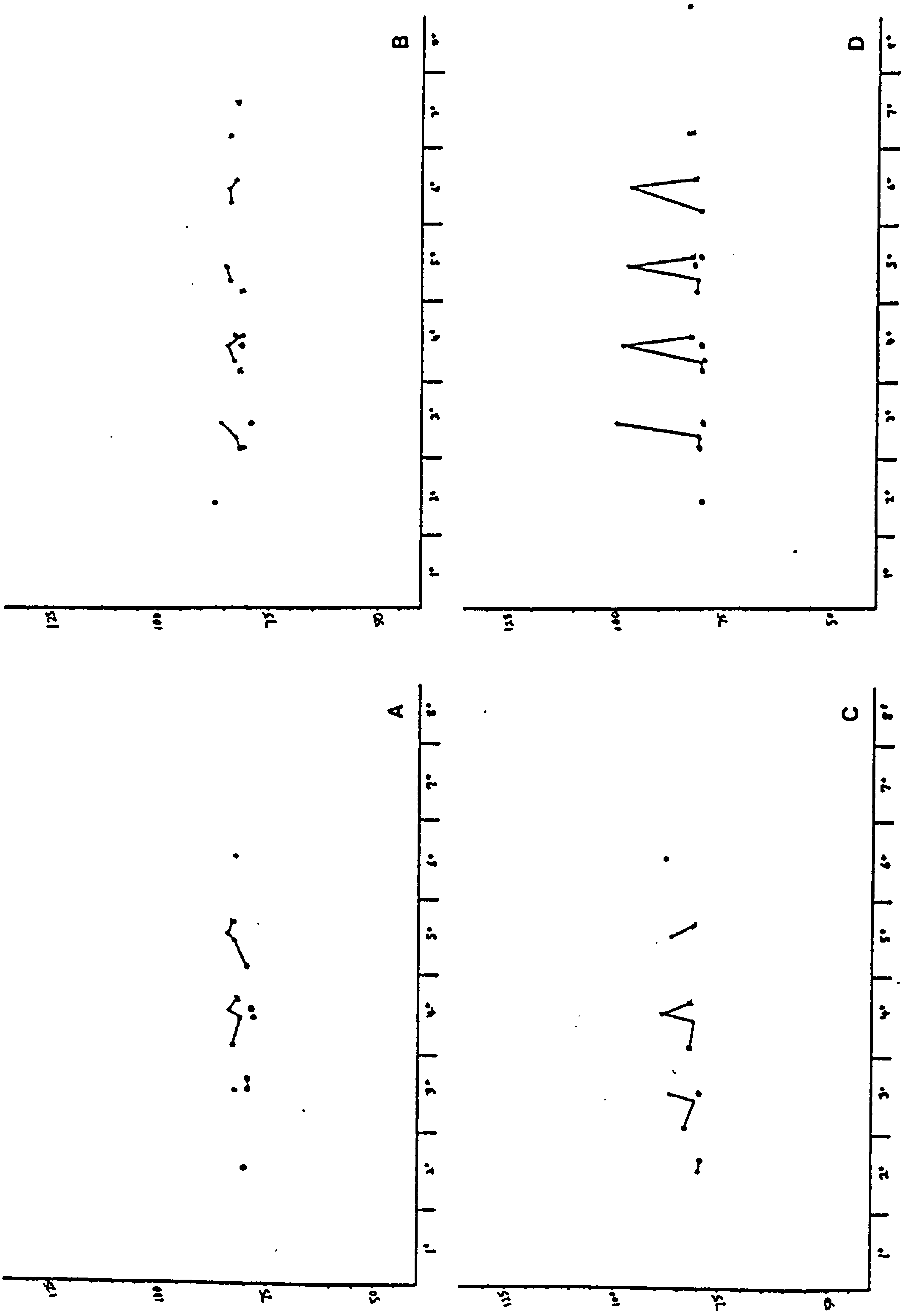


Figure 5.4 - Water content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

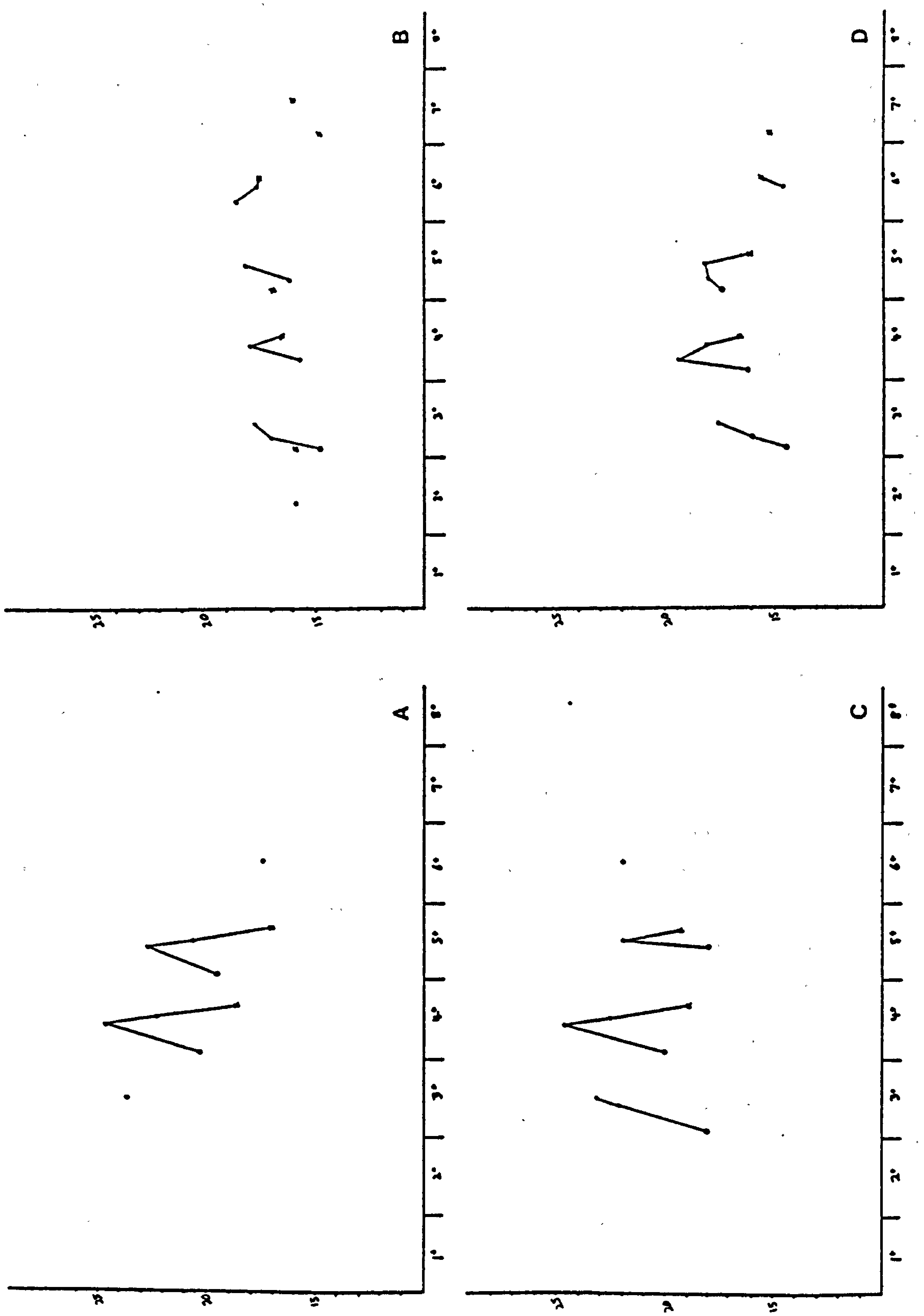


Figure 5.5 - Lean content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

affecting the results.

The life history curves of the two sexes within a loch occupy the same range of values, but the ranges are different between the lochs. Loch Doine fish are more robust (greater lean values) than Loch Builg fish.

Mean values for lipid content of sexually maturing standard fish are plotted aginst age in Figure 5.6. As was seen for lean, the plots consist of a series of annual cycles within a life history curve.

The annual cycles show an increase in lipid from spring samples (all immatures, open circles) to summer (sexually maturing fish, closed circles), followed by a rapid decline to low values in the autumn (spent fish, crosses). Again, the amplitude of the changes over an annual cycle is greater in Loch Doine than in Loch Builg. Within loch differences in the amplitude of these changes are not apparent between the sexes in either loch. Spent females in Loch Doine have higher values than immatures in the spring. The converse is true in Loch Builg females and both populations of males.

The life history curves are difficult to distinguish because of the greater amplitude of the annual cycles, but they seem to resemble those found for lean. The only departure from this pattern is the negative correlation of lipid with age found in males from Loch Builg.

The ranges of values in the life history curves are similar between the sexes within a loch, but fish from Loch Builg tend to have much less lipid than those from Loch Doine.

Mean energy values of sexually maturing standard fish are plotted aginst age in Figure 5.7. The plots consist of a series of annual cycles within a life history curve.

The annual cycles resemble those for lean and, more so, lipid. This is because energy is a function of these two quantities with lipid containing more then double the energy of lean per unit weight (Pond 1981).

The amplitudes of the annual cycles differ between the lochs, being greater in Loch Doine than in Loch Builg. There do not appear to be differences between the sexes in either loch except that females in Loch Doine may make a net energy gain over the annual cycle.

The life history curves are very similar to those found for lipid. They appear to be convex with the peak at age 4+ in all populations

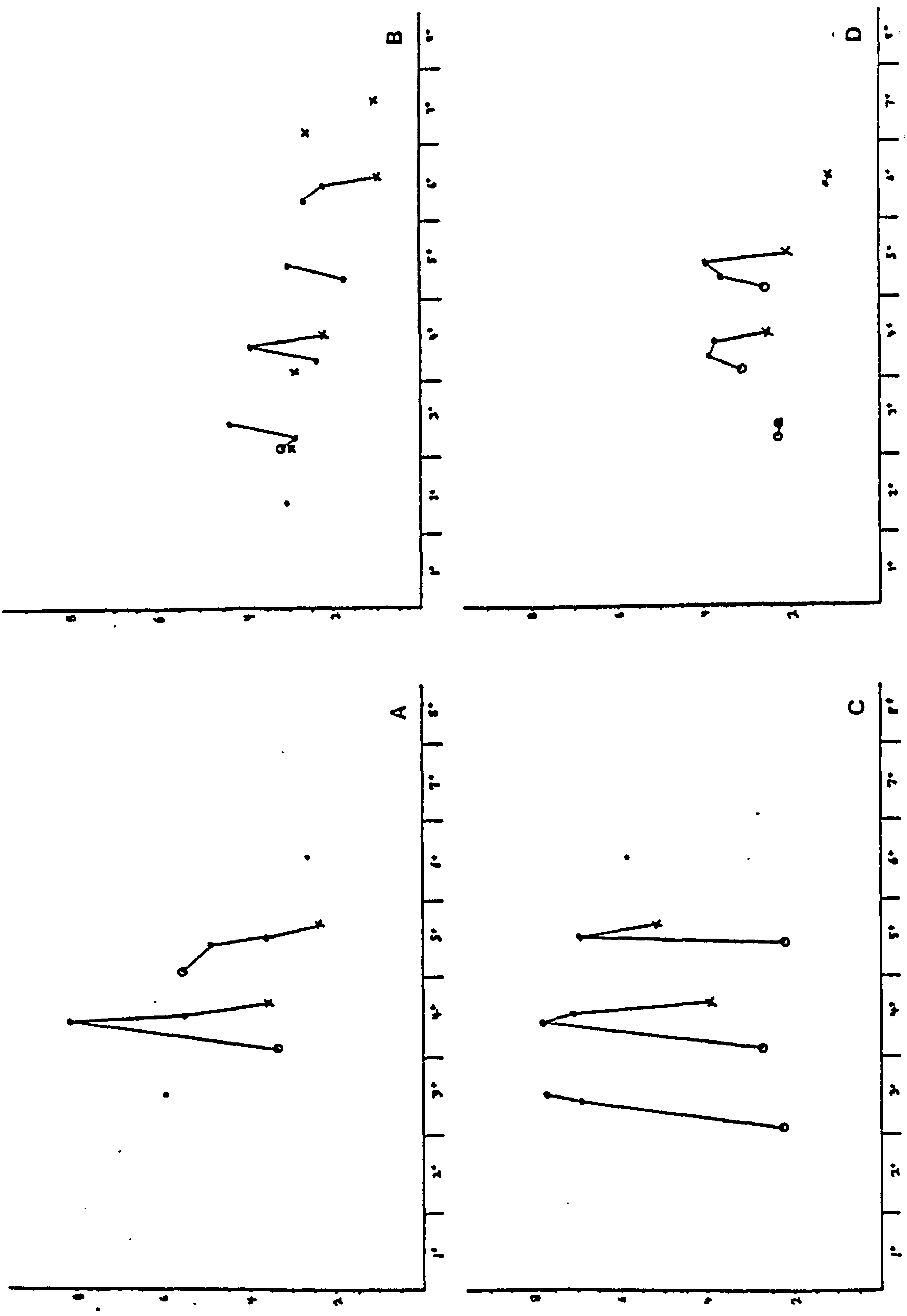


Figure 5.6 - Lipid content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

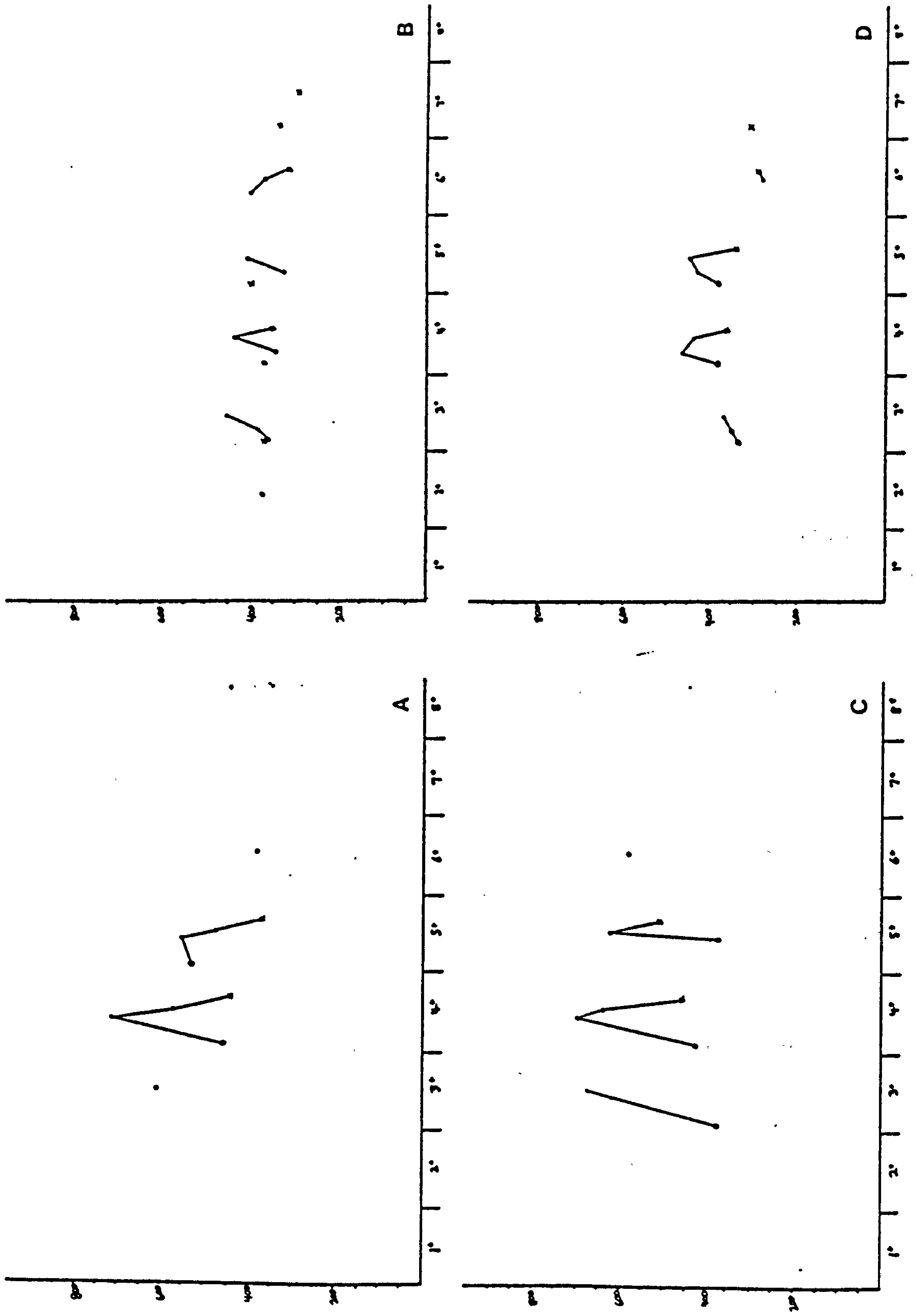


Figure 5.7 - Energy content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

except Builg males which show a steady decline in energy over the life span.

Charr from Loch Doine tend to contain more energy than those from Loch Builg.

5.3.3 IMMATURE CHARR: Mean values for body constituents of immature female charr from Loch Builg are presented in Figure 5.8. This was the only population of charr in this study to yield samples of immature charr throughout the age span of the fish.

No annual cycle is apparent in water (Figure 5.8a) which is virtually constant throughout the life history. Older fish may have a slightly greater water content.

The other parameters presented here, lean (Figure 5.8b), lipid (Figure 5.8c) and energy (Figure 5.8d) show strong annual cycles. Lean increases throughout the growing season and must be catabolized during the winter although no fish were sampled then. Lipid decreases slightly during the early summer but then increases rapidly later in the growing season. Energy increases slowly at first and then rapidly.

The life history curves are similar for all three parameters. There is a net increase in each with age (broken lines, Figure 5.8) up to age 4+, when the rate of increase in lean slows and in lipid and energy stops. The peak values after age 5+ are not comparable as they were collected earlier in the growing season. However, it appears that, even at their best, older nonmaturing fish would not exceed the peak values of younger ages.

5.3.4 REPEAT SPAWNING FEMALES: Mean values for body constituents (condition, water, lean, and lipid) of repeat spawning females from Loch Doine plotted against age are presented in Figure 5.9 while those for Loch Builg are in Figure 5.10. Energy values are given in Figure 5.11. The data are incomplete and only fragments of any annual cycles can be seen.

The life history curves are difficult to interpret since the annual data are so fragmented. Condition and water remain fairly constant over time in Loch Builg while the plots seem to show a general decline in the values in Loch Doine. Lean, lipid and energy decline with age in both lochs.

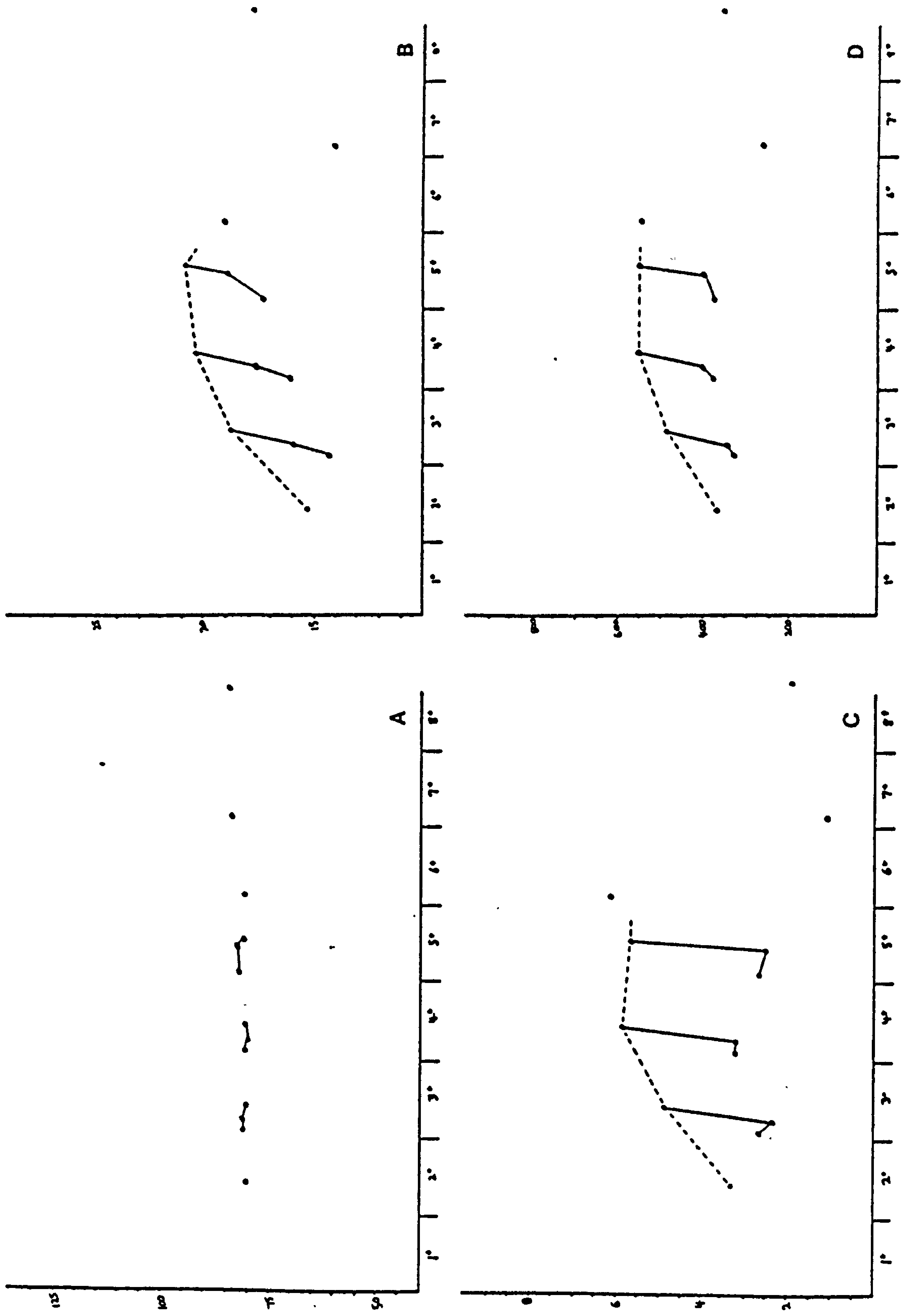


Figure 5.8 - Water (A), lean (B), lipid (C), and energy (D) content of soma of immature female charr from Loch Builg.

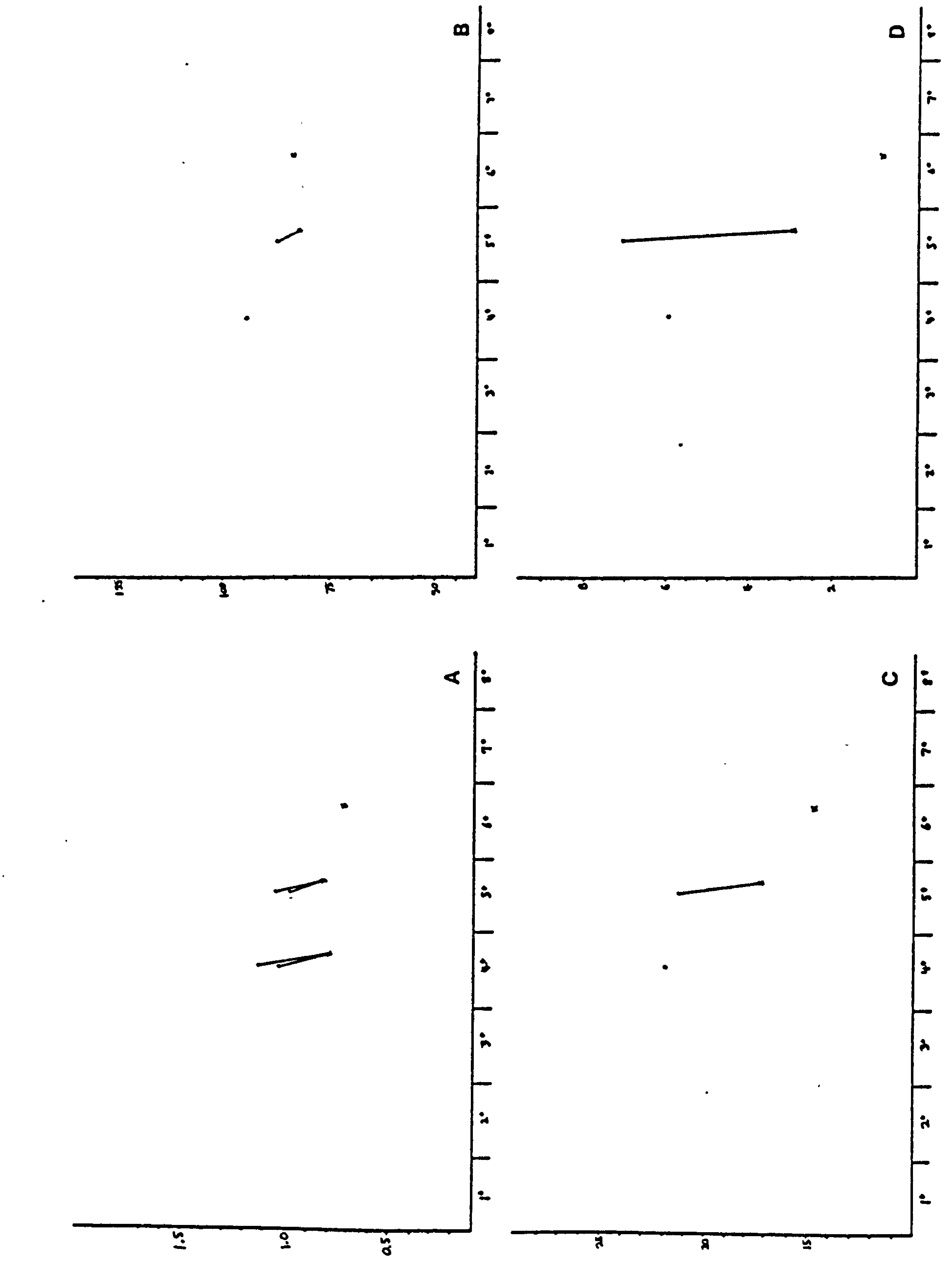


Figure 5.9 -Condition (A), water (B), lean (C), and lipid (D), content of soma of repeat spawning female charr from Loch Doine.

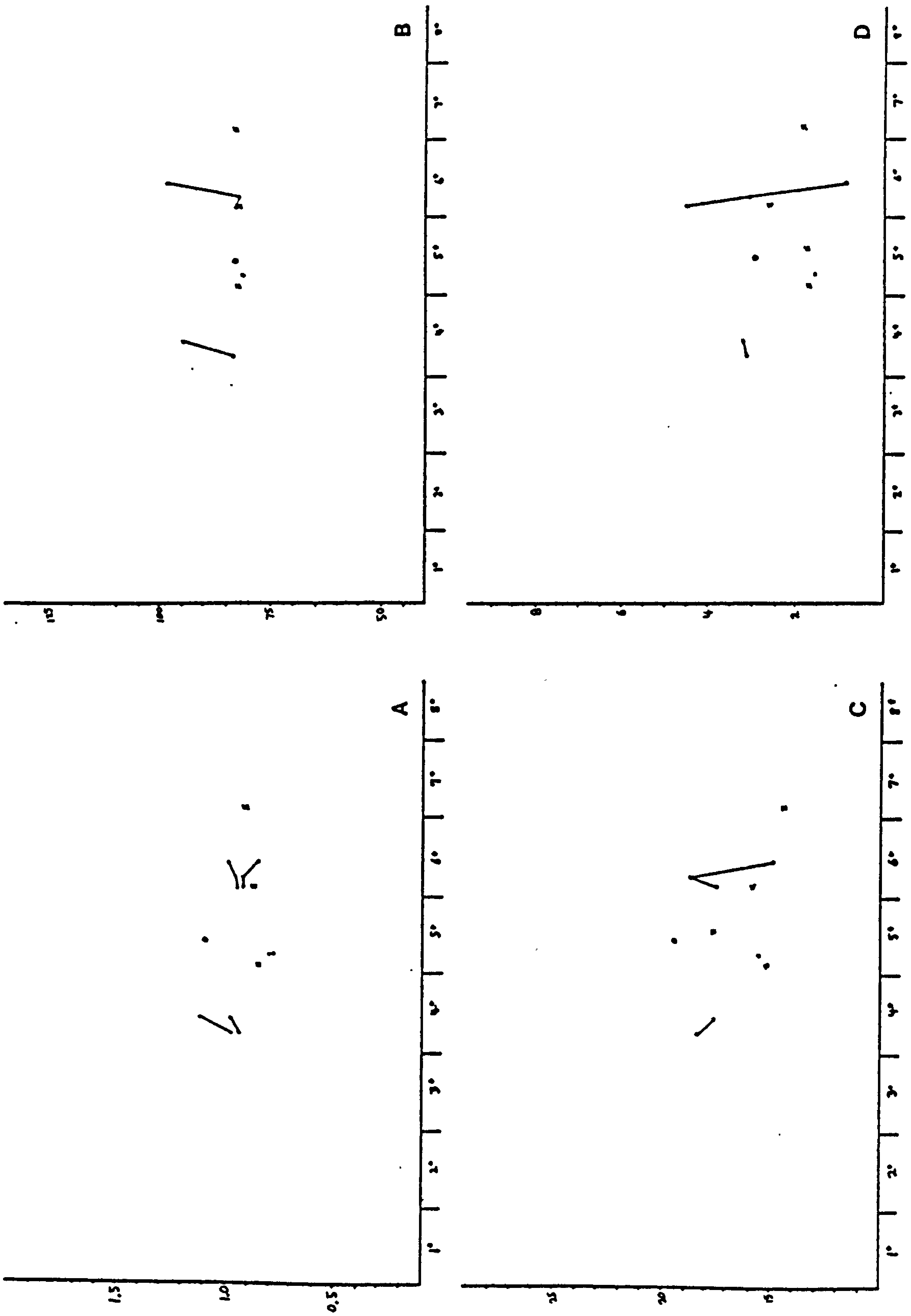


Figure 5.10 - Condition (A), water (B), lean (C), and lipid (D) content of soma of repeat spawning female charr from Loch Builg.

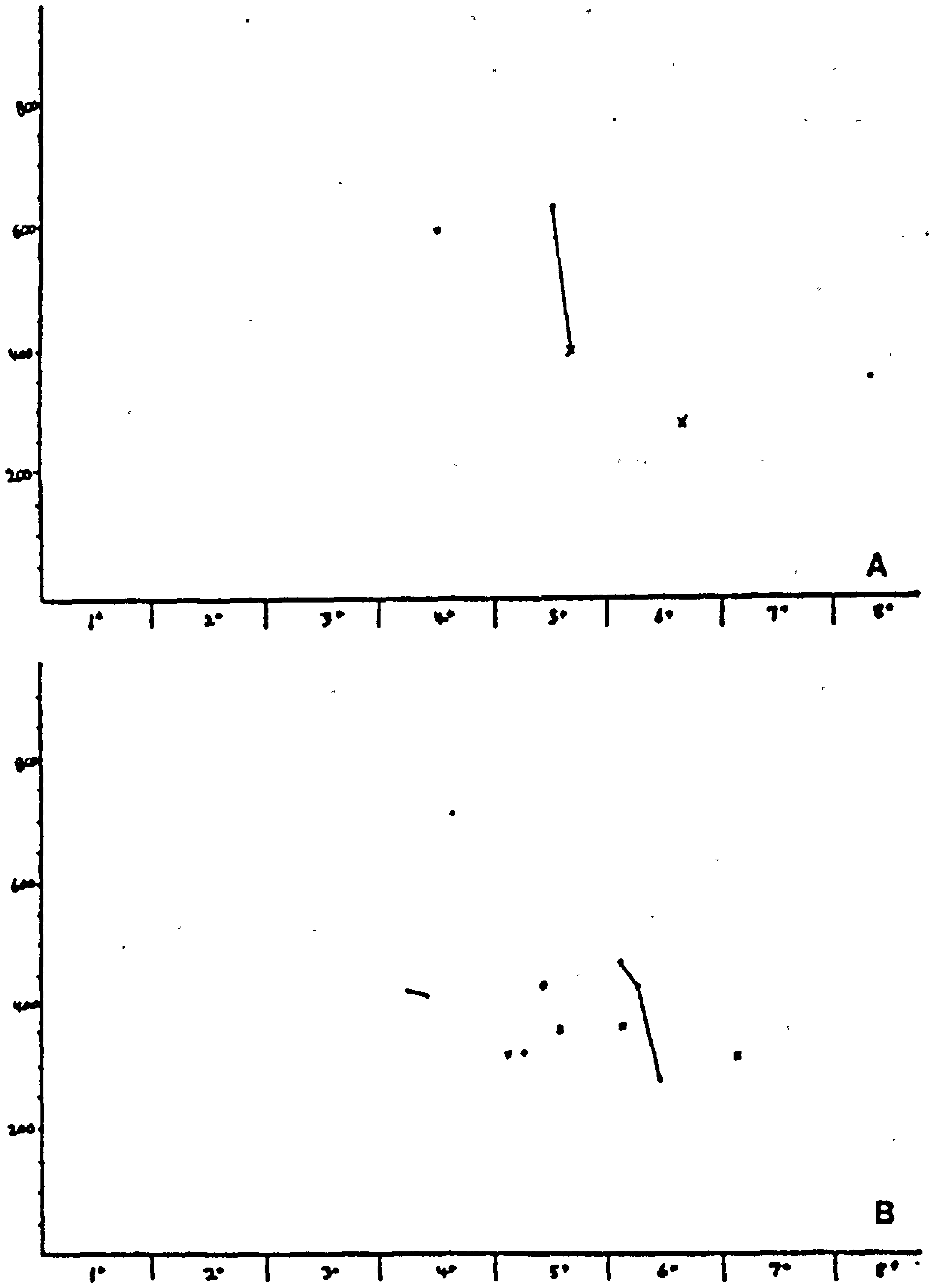


Figure 5.11 - Energy content of soma of repeat spawning female charr from Loch Doine (A) and Loch Builg (B).

These data are much more variable in comparison with the plots for female fish spawning for the first time. The general relationship of these two populations of females shows the repeat spawners to have lower values of condition, lean, lipid and energy especially at older ages. Water remains virtually constant in all fish except ripe females.

5.3.5 GONADS: The plots of proximate composition of gonads (Figures 5.12 to 5.14) closely resemble one another. This is because of the method of calculation, where gonad values are a function of carcass length-weight relationships. Thus the plotted values illustrate physical growth of the gonads rather than relative changes in composition. Thus, all the plots show a baseline near zero, where the gonads are not at all developed in immature fish. The annual cycles illustrate the investment in reproduction made by the fish.

The mean values for water content of the gonads of a standard fish are plotted against age in Figure 5.12. As was seen in the carcass analysis, the plots consist of a series of annual cycles within a life history curve.

The annual cycles of maturing gonads show that the amount of water increases dramatically in ovaries but less so in testes. As stated above, this reflects the relative size of the gonads as they mature, and are then spent. Male charr from both lochs have smaller amounts of gonad water than females, but while the male populations have similar values, the two female populations differ, with Loch Builg females having considerably more gonad water than those from Loch Doine.

The life history curves appear to be relatively constant with age. There is a suggestion of a decline in the water values of mature gonads with age in male charr. There are also differences in the values of maturing female gonads. Those from Loch Doine show a convex curve with the apex at age 4+, while those from Loch Builg show a decline over the plotted age span.

The mean values for lean content of the gonads of standard fish are plotted against age in Figure 5.13. Again, the plots consist of a series of annual cycles within a life history curve.

Apart from the differences in the actual values of the parameters, the plots of lean are virtually identical to those for

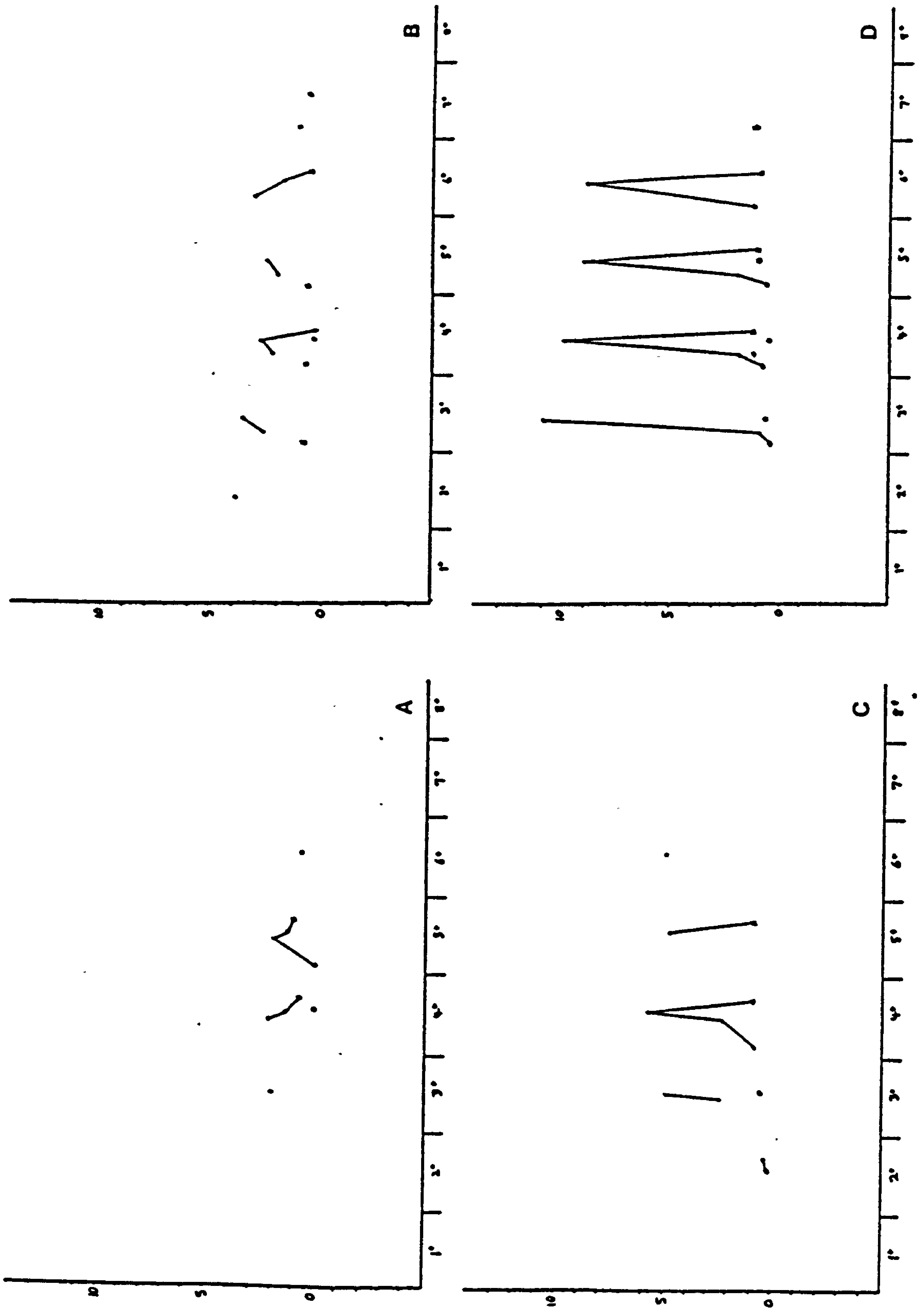


Figure 5.12 - Water content of gonads of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

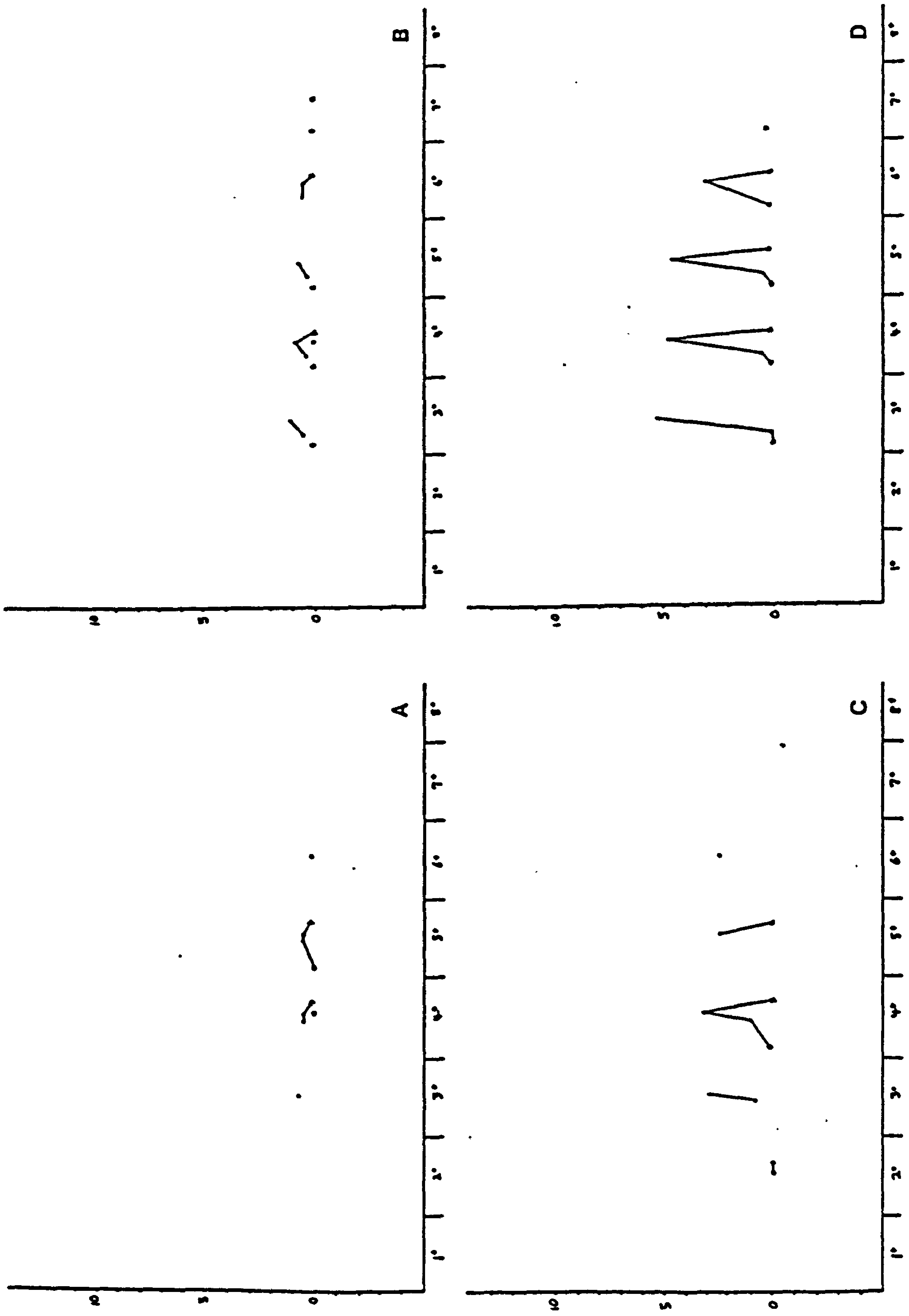


Figure 5.13 - Lean content of gonads of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

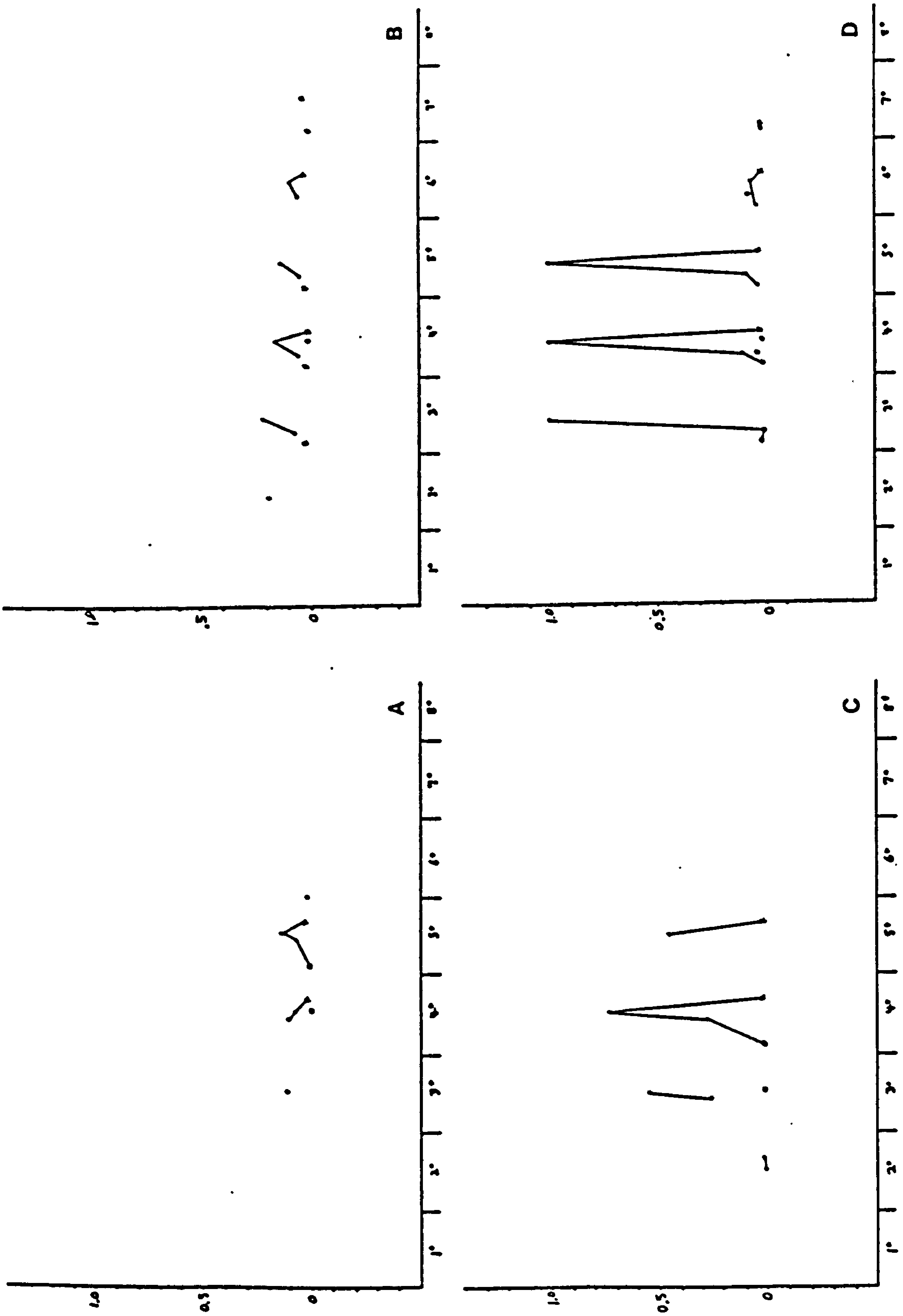


Figure 5.14 - Lipid content of gonads of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

gonad water. Maturing male charr have less gonad tissue than maturing females.

The life history curves are relatively constant with just a hint of a decline in mature gonad lean with age in all four populations.

The mean values for lipid content of the gonads of standard fish are plotted against age in Figure 5.14. As before, the plots consist of a series of annual cycles within a life history curve.

The amplitudes of the annual cycles of maturing fish vary among the populations, with male fish (similar in both lochs) showing the least change followed by much greater change in Loch Doine females with the greatest amplitudes among Loch Builg females. A startling result is the almost total lack of lipid in the ovaries of maturing females of age 6+ in Loch Builg. This result is probably real as the results for lean and water (Figs. 5.13 and 5.12) show subdued but obvious gonad growth in this sub-population. (Care was taken to ensure that the samples were consistent among the plots for all proximate components.)

The life history curves are similar to those for water and lean. Male charr from Loch Builg show a decline in lipid with age, and the fragmentary plots for Loch Doine males may be similar. Loch Doine females show a convex curve with the apex at age 4+, while Loch Builg females have constant values until age 6+, when the value of mature gonads crashes to almost nil.

The mean energy values for the gonads of standard fish are plotted against age in Figure 5.15. Again, the plots consist of a series of annual cycles within a life history curve.

The amplitudes of the annual cycles differ among the populations. They are much greater in female fish than in males and, in each sex, respectively greater in Loch Builg.

The life history curves are relatively constant, with the suggestion of a decline in older age classes in all the populations. The curve for Loch Doine females may be convex.

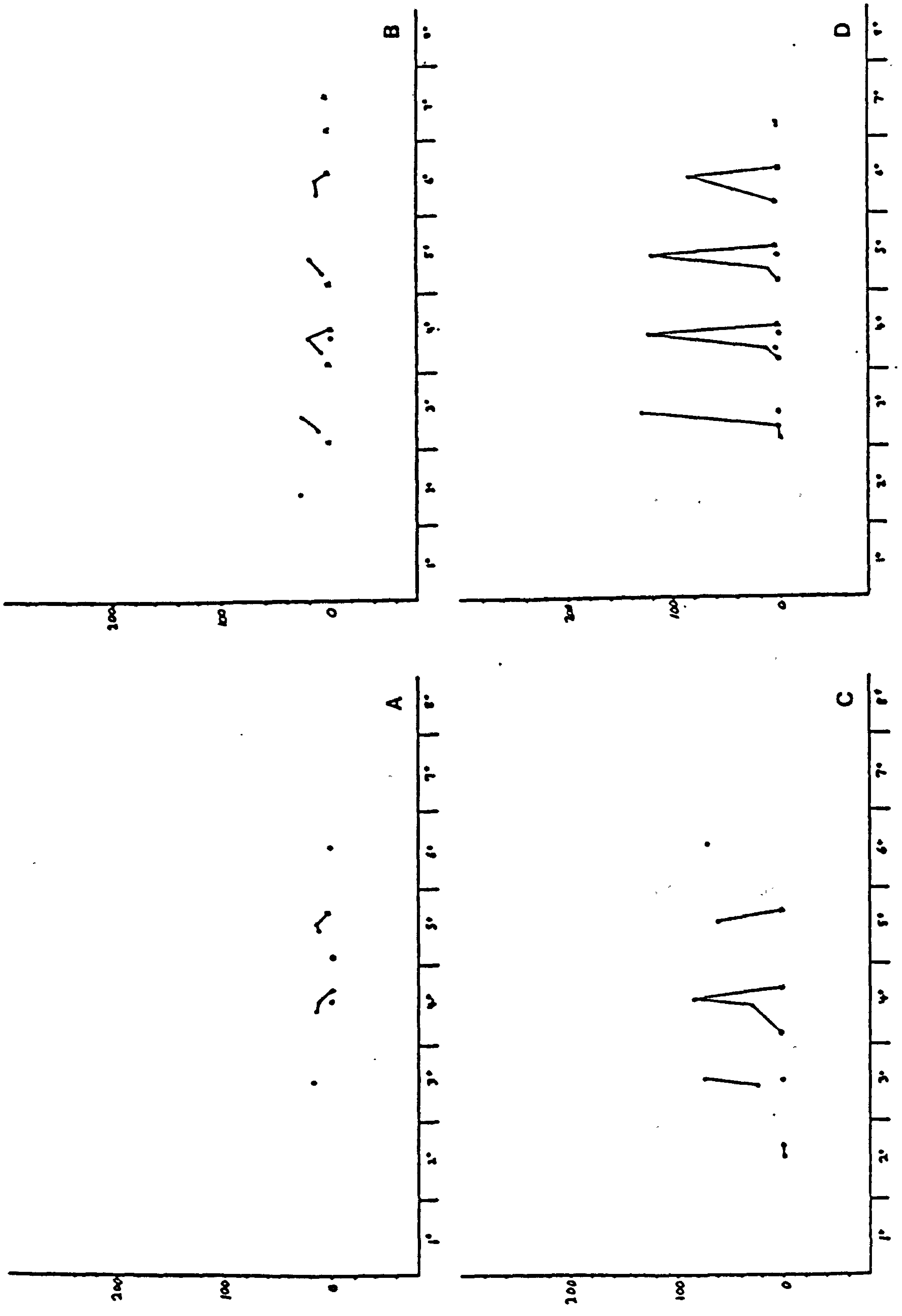


Figure 5.15 - Energy content of gonads of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

5.4 DISCUSSION

The plots of condition (Kn) over time (Figure 5.3) are interesting mostly because they illustrate the relative investment in gonads. As an index, Kn always approximates 1 and does not reflect absolute changes in proximate parameters. Also, since it measures several parameters at once it does not reveal anything about the relative dynamics of the proximate components of the fish. Therefore, Kn can only be used as a crude index of the status of a fish.

When the other parameters are regressed on Kn water again appears to be a constant (Table 5.2). Kn predicts lean quite well. However, the relationship with lipid is very poorly correlated (r^2=.28). Lipid is the major energy store of most animals (Pond 1981), so this relationship makes Kn a poor predictor of the energetic status of a fish.

I have shown in Sections 5.2.2 and 5.3.1 that with a reassessment of the methods of calculating the amounts of body constituents in a fish, the parameters can be made independent of one another, and therefore their true relationships revealed.

For instance, other authors have found by using percent calculations that water increases and decreases through the life history of a fish. My results show that water content is virtually constant throughout a fish's life history (Figures 5.1 and 5.4), but both lean and lipid vary. This is actually an artefact caused by the negative relationship of water and lipid. When the percentage of fat-free wet weight is used, water becomes a constant. This is because water is physiologically associated with lean.

In both populations of fish, and in both sexes, there is an apparent baseline at all ages of approximately 82 percent of water in the standard fish. Only in sexually maturing fish, and mostly in females, is there a departure from this baseline (Figure 5.4). It should be noted that immature fish sampled on the same date as matures having a high water level had a water level that was near the baseline (Figure 5.8). There are two possible explanations for these high water values. One is that the data are an artefact and the second is that it is a physiological phenomenon in the fish.

Table 5.2 - Components of the regressions of proximate parameters on the condition, Kn, of intact charr.

	slope	intercept	r^2	n
Water	-	-	.02	192
Lean	14.96	2.69	.71	153
Lipid	6.23	-2.77	.28	153

An examination of the data supports both of these hypotheses. A breakdown of the population of fish with expected water levels of more than 86 percent shows a preponderance of ripe female charr (Table 5.3) with a second major component of immatures. The immature fish with high water levels are a sub-sample of about twenty-five percent of a population of immature males with normal water content(Table 5.4). However, the ripe female charr with high water content represent 89% of all ripe female charr. I interpret this to mean that the immatures and the few other fish in Table 5.3 probably died or were damaged in the gill net and soaked up water when osmoregulation ceased. (It is interesting that no very low values were found in the data; the fish always gained water and never dried out. This is to be expected as fish in freshwater are hyperosmotic to the environment.) However, I know that the ripe females were collected alive and stored out of water because I was specifically fishing short-time net sets to catch brood fish. Figure 5.4 shows high water contents specifically in ripe females at all ages, but not in other groups of fish. Love (1970) shows that several species of fish greatly deplete the soma during the later stages of sexual maturation and replace the lost muscle proteins with water. He illustrates this with a figure showing a sudden rise in cod (*Gadus morhua*) somatic water content during the spawning period. Cod do not have oily flesh but the calculation of fat-free percent water content for the charr of the present study produces a similar result (Figure 5.4). It seems probable that the charr become excessively depleted at spawning time and therefore contain much more water. Charr seem to fast at spawning time (Table 3.1) and this may enhance the somatic depletion. Feeding resumes after spawning, water levels return to normal, but somatic lean continues to decline (Figure 5.5). This anomaly leads to speculation that somatic depletion may not be the only cause of high water levels. Mature females contain large amounts of coelomic fluid.

Table 5.3 - Structure of fish population with standard water value greater than 86 percent.

	Males		Females	
Maturity	Builg	Doine	Builg	Doine
immature	-	6	1	1
maturing	-	-	-	1
ripe	5	-	12	13
spent	-	-	1	1

Table 5.4 - Structure of fish population with standard water value less than or equal to 86 percent.

	Males		Females	
Maturity	Builg	Doine	Builg	Doine
immature	3	20	8	12
maturing	-	11	-	5
ripe	17	7	-	3
spent	6	7	9	13

This is evident when the fish are artificially stripped of eggs. The fluid may be a nursery medium having appropriate osmotic or dissolved gas properties for the preservation of ovulated eggs. It may also lubricate the eggs when they are expelled at spawning. The elevated water levels in mature male charr may possibly be accounted for by the seminal fluid. I have no measurements of these fluids in charr, but it would be useful to discover if indeed they do account for the extra water found in mature fish.

There is a good correlation of gonad water with body water (compare Figures 5.4 and 5.11), including the non-baseline levels. However, this relationship is spurious; the increased gonad levels being caused by an increase in gonad size, rather than water content.

The data for the amount of lean, lipid and energy in the standard fish contrast with those for water in that they vary considerably within and between populations. The annual cycles of maturing fish show an obvious build up of body tissue early in the growing season, followed by a rapid decline later in the year. Similar cycles are noticeable in non-maturing fish (Figure 5.8). It would seem that in the spring the fish are depleted after overwintering, and, since the data are corrected for length, begin to add body mass. This increase in weight continues into the summer, when gonad

Table 5.5 - Changes in somatic and gonad energy (in kJ) during the reproductive cycle in charr from the two lochs.

Loch	Sex	Soma Peak	Soma Loss	%	Gonad Gain	Gain: Loss (%)
Doine	Male	627	227	36	11	5
Builg	Male	420	87	21	21	24
Doine	Female	660	178	27	76	43
Builg	Female	454	106	23	118	111(100)

development also begins to take place in maturing fish. The rate of increase in some is reduced when gonad development accelerates (compare especially Figure 5.7d and 5.15d). In spent fish somatic values approach the overwintering low and the gonads have returned to their pre-development levels. It seems that the demands of reproduction exceed instantaneous production and the fish must catabolise somatic tissue to meet this demand. It has been shown in Chapter 4 that Loch Doine charr grow bigger than those from Loch Builg. Figures 5.5 to 5.7 show that the relationship holds for both sexes of standardised fish from these two lochs in all three parameters. In other words, the body mass, fat reserves and energy content of Loch Doine fish are always greater. However, the fluctuations of these parameters are also much greater in Loch Doine fish, so they are making a greater investment of somatic reserves in the latter part of the annual cycle (Table 5.5).

In the plots of the three parameters for gonads the opposite is true. Here, both sexes of Loch Builg fish make the greater investment, as indicated by the amplitudes of the annual cycles (Table 5.5).

In other words, the poorer fish from Loch Builg are putting the greater effort into gonad production, while the more robust fish from Loch Doine put relatively little effort into gonad production.

So, what happens to the lost energy that is not accounted for by gonad development? In Chapter 2 I described the morphology and colour of fish from these populations. It was found that charr from Loch Doine alter their body shape (lateral compression, thick, spongy skin, extended jaws with a kype) and become brightly coloured at spawning time, while the fish from Loch Builg undergo more modest changes. Captive males from Loch Doine appeared to fight more and seemed much more aggressive than captive males from Loch Builg. However, this is an impression only, as I did not make rigorous behavioural observations. The rank order of the intensity of morphological changes before spawning is, from greatest to least, Doine males, Builg males, Doine females, Builg females. This is the reverse rank order of gonad investment in these populations (Table 5.5). It seems that fish from Loch Doine invest more in reproduction than fish from Loch Builg, but the greater part of the investment is tied up in the apparatus of display and in behaviour, rather than in reproductive tissue.

It is necessary to separate the sexes while discussing changes in lean, lipid and energy content of somatic tissue with time. This is because the curves for males include repeat spawners while those for females exclude them.

The life history curves for male soma show a decline in all parameters except lean in Builg males. I can offer no good explanation for this particular result. The declines in the other curves for males may be caused by two factors. First, older fish may be poorer specimens and simply never achieve the levels of better quality fish. Second, it is likely that a greater number of previous spawners were included in the samples of older fish. Repeat spawners may have been badly depleted by their previous breeding and not be able to build up their soma to the levels of first time spawners. Therefore younger ages, with fewer repeat spawners, would have the mean values reduced less than older age classes. Either of, or a combination of, both these factors would cause a steady decline in the life history curves of these fish.

The data on investment in testes by the Loch Doine population are somewhat scanty. It appears that investment remains constant at ages 4+ and 5+, but may be reduced at age 6+. The more complete data for Loch Builg males show investment in testes declines with age. The trends in both populations may reflect the probable component of repeat spawners in each age class (based on the mean age at first reproduction (Table 7.4) whose depleted somatic reserves may affect investment by limiting the resources available to the gonads.

The life history curves for lean, lipid and energy in female soma are all convex with the apex at 4+ (5+ for lipid in Builg females). These curves represent the time taken to reach the onset of

Table 5.6 - Maximum annual energy content (kJ) of soma plus gonads of immature and mature female charr from Loch Builg

Age	Immatures	(n)	Matures	(n)
2+	378	(1)	-	-
3+	493	(2)	447	(1)
4+	559	(3)	559	(4)
5+	563	(1)	567	(2)
6+	-	-	363	(1)

reproduction by each age class of charr, as the plots are for first time spawners only.

The ascending limb of each curve represents fish that are, or have been, growing quickly and have achieved a threshold for the onset of reproduction. The descending limb of each curve represents slower growing fish, probably poorer specimens, that spawn eventually when they begin to approximate the threshold. Immature female charr from Loch Builg show strong annual cycles and well developed life history curves in somatic lean, lipid, and energy.

The annual cycles are interesting because they have a much greater amplitude than those for the soma of maturing females. However, the annual peak values are similar when the somatic and gonad values are summed in both populations (Table 5.6). This is most gratifying as it means all the female charr in Loch Builg operate on a similar energy budget.

However, the apportioning of energy is quite different between immature and maturing females. Figure 5.16 is a plot of energy values for lean, lipid and their sum, the total energy content of the soma and gonad of the two populations excluding spent fish. In every year class in each parameter the maturing females (solid lines) are building up their energy early in the annual cycle while immatures (broken lines) gain lean much more slowly and actually lose lipid reserves. The maturing females begin to direct resources to the gonads by mid-summer and rates of increase in somatic lean and lipid are slowed or reversed. Also in mid-summer the immatures begin to accumulate lean and lipid at a great rate. This may be due to the slowing of body growth. Barbour (1979) found ouananiche (*Salmo salar*) to have made a major portion of their annual growth in length by the summer solstice. These fish were not feeding and the ice-cover

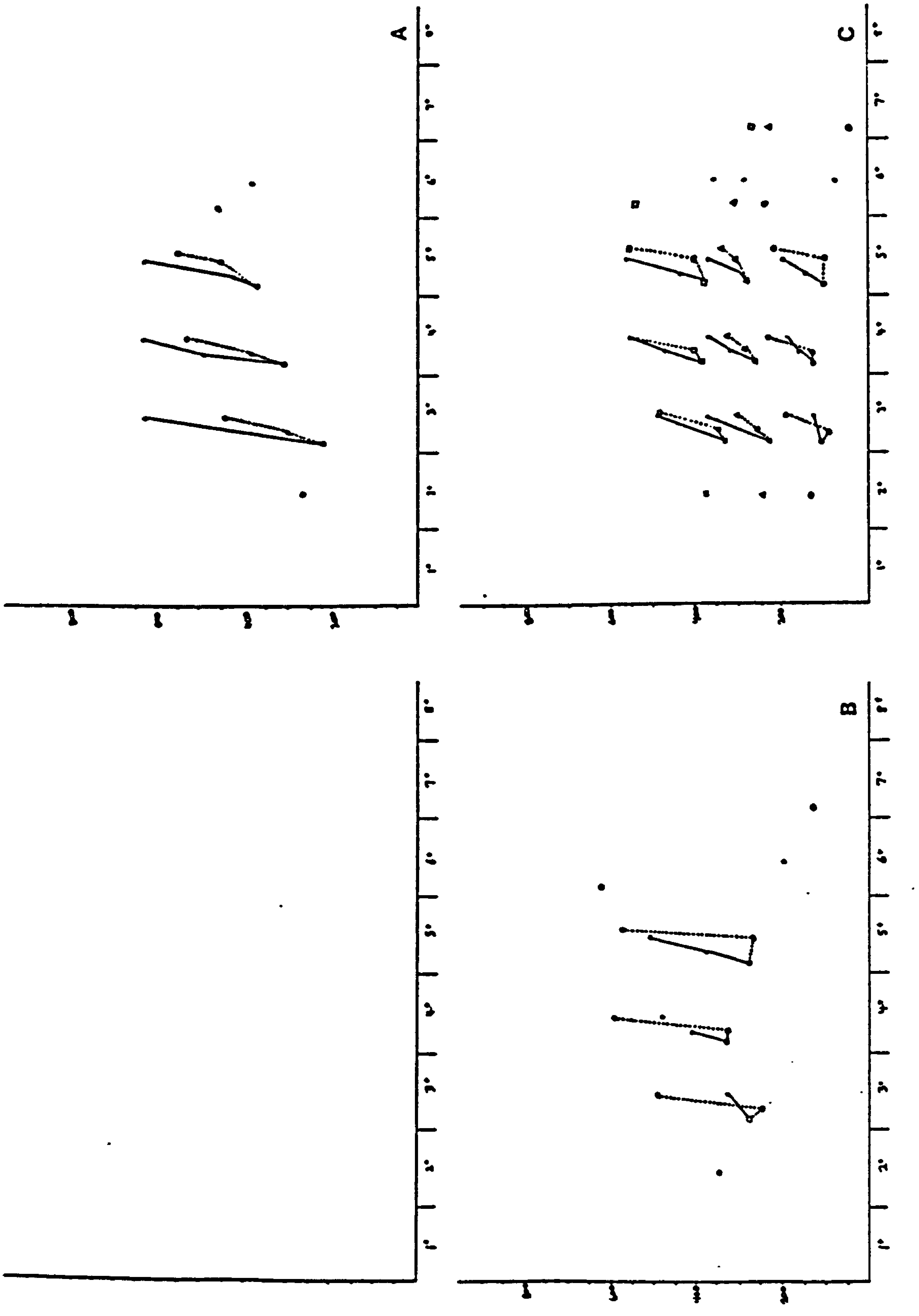


Figure 5.16 - Lean (A), lipid (B), and total, lean and lipid energy (C) content of soma plus gonad of immature (broken line) and maturing (solid line) female charr from Loch Builg.

on the lake was only just breaking up. Smolting anadromous salmon (*S.salar*) enter a fast growth phase under lengthening photoperiod (Barbour 1979). It seems that salmonids may add length early in the growing season and then recover condition later. Data on the length-weight relationship in charr in the present study and in Kipling and Frost (1978) would support this idea.

By the autumn, both populations of females have accumulated a similar amount of energy. Immatures contain a great deal of lipid and it is mostly in the soma. Matures have more lean, but less lipid. Much of the extra lean is accounted for by the gonads. Presumably lipid has been lost because it is an energy store and may have been catabolized to allow, either by direct energy transfer, or by indirect means (changes in feeding habits or behaviour) the build up of gonad material (Love 1980).

The onset of spawning may be triggered by the amount of energy the fish will have at its disposal during maturation. This is explained by Calow (1981) who showed that the relative costs of growth and maintenance increase with body size while the food gathering capacity of the animal increases at a slower rate. He describes theoretical arguments that show how organisms should reproduce when the difference in energy gained and energy expended is maximal. This occurs at an optimized body size that is determined mainly by the trophic status of the environment. In Loch Builg the peak energy level is attained at age 4+ and this corresponds to the age at which a majority of female charr spawn (Figure 6.1). Demographic considerations about spawning at age 3+ are given in section 7.1. Gross (1984) noted that theoretically one would expect a normal distribution of spawning ages around the optimum (Figure 6.1 but note Table 7.4). Also, in immature females peak annual body reserves build up with age until the fish are about age 4+ and then level off. After age 5+ reserves decline: It seems that there is a maximum energy content that the standard 214mm fish cannot exceed and this seems to be approximated by the resource optimum required for reproduction.

Table 5.7 - Springtime energy content (kJ) of soma plus gonads of immature and spent female charr from Loch Builg.

Age	Immatures	(n)	Spent Females	(n)
3	336	(17)	-	-
4	386	(9)	-	-
5	384	(1)	314	(1)
6	554	(2)	363	(4)
7	272	(1)	312	(2)
8	-	-	-	-
9	362	(1)	-	-
Mean of comparable ages:	403		330	

The fragmentary data for repeat spawning females are erratic (Figures 5.9, 5.10 and 5.11). This may be due to small sample sizes. Also, in the spring, spent female charr in Loch Builg have a lower energy content than fish that had not matured the preceeding year (Table 5.7). Mortality may be very high among the spent fish as the lake warms and they become active. It is probable that the data for survivors that are to spawn a second time (repeat spawners) are biased due to this mortality. Some very low values for lean and lipid can be seen in Figures 5.9 and 5.10. These may represent minimum values at which charr can survive. The lowest lipid values may represent structural lipids and thus be the baseline of non-catabolizable lipid in the standard fish.

5.5 SUMMARY

1. An attempt has been made to calculate unbiased values for each proximate component of charr soma and gonad. These values are set to a standard 214mm fork length fish.

2. Water was found to be almost constant when calculated as percent fat-free wet weight. This reflects the physiologically intimate association of water and protein. Anomalous high water values were found to be an artefact in immature charr but in mature fish were thought to be a symptom of excessive resource depletion. Also, they might indicate the presence of sexual fluids or osmoregulatory problems.

3. In maturing fish, somatic lean and lipid, (energy), increased in the spring and summer but were diverted to the gonads in the summer and autumn. Immature fish lost resources until summer but then stored resources in the soma throughout the summer and autumn.

4. In all populations lean and lipid, (energy), increased with age until age 4 and then began to decline.

5. Somatic energy loss was accounted for by gonad gain in Builg females. Progressively less gonad investment was made by Doine females, Builg males, and Doine males respectively. Alterations in morphology, colour, and behaviour may account for the "lost" resources.

6. In Loch Builg, immature females had the same total energy content as mature females.

7. In Loch Builg, spent female charr contained less energy than immatures in the spring following spawning. Loch Doine females may not invest as much energy in reproduction in order to enhance overwintering survival.

CHAPTER 6

REPRODUCTIVE BIOLOGY

6.1 SPAWNING

6.1.1 TIME: The Arctic charr observed in this study all spawned in the autumn or early winter. The time of spawning varied considerably among the lakes, with fish from Loch Builg breeding in September, Loch Meallt in October, Loch Doine in November-December and Loch Earn in December or January. The relevant data are summarised in Table 6.1.

The most curious point to be made from these data is that the fish from Lochs Meallt and Builg spawn at warmer temperatures than those from Loch Doine. This relative independence from temperature (Table 6.1) suggests that the timing of egg laying must be critical and therefore will take place at temperatures considered warmer than normal for the species (Johnson 1980).

6.1.2 LOCATION: The spawning sites of the charr in this study were deduced from the capture of aggregations of mature fish. In Loch Meallt, these fish were taken from a bay which had a silt free, stony substrate. The bay was exposed to very strong winds which would generate water movement and raise sediment, making the water a muddy colour, and presumably scouring the substrate. The bay was free of macrophytes in contrast to most of the remaining lake, which had a substrate of ooze. The water depth was 1-2 metres.

The presumed sites in Loch Builg were the shores parallel to the long axis of the lake. Again, this lake is windswept, but does not become muddy-coloured. The substrate is clean gravel from thumbnail to potato size interspersed by small boulders. From the shore outwards is a shelf covered by about 1 metre depth of water. This becomes a drop-off about 3-5 metres from the shore and achieves depths of more than 5 metres. Ovulated females and ripe males were captured at dusk in a drifting gill net which fished to a depth of 2 metres. Assuming the fish were near the substrate (they were caught in the lower part of the net, although it would not drift perfectly upright) they would have been quite close to the edge of the loch on

Loch	Collection Date	Day Post Summer Solstice	Day Length	Surface Water Temp.	♀ Fish Maturing	Ripe	Ovulated	Spent
Builg	10. 9.82	81	13:23'	9°		X		
	22. 9.82	93	12:15'				XX	
	25. 9.83	96	12:01'	7.5°		X	XX	X
	24.10.81	125	9:35'	-				XX
Meallt	1. 9.82	72	13:56'	12°	X	X		
	16.10.81	117	10:20'	6°			X	XX
Doine	19.10.81	120	10:11'	-	X			
	23.11.82	155	7:48'	4.5°		X		
	23.11.83	155	7:48'	6°		XX	X	
	9.12.81	171	7:07'	0°			X	XX
Earn	19.11.80	151	7:57'	-	X	X		
	6:12:83	168	7:07'	7°		X		

Table 6.1 - The state of maturity of female charr captured in the autumn and winter from four Scottish lochs.
X - some fish
XX- most fish

the shelf or at the top of the drop-off.

The presumed sites in Loch Doine are again along the long axis of the loch over apparently well scoured substrate. These fish seem to spawn in deeper water. Ovulated and spent fish that had fresh ova in their stomachs, along with small pebbles, were taken from a depth approaching 14 metres in the north east sector of the loch. A very large aggregation of ripe, and occasionally ovulated, charr was taken from a depth of about 12 metres along a talus slope that plunges down the south bank of the loch. The precipitous nature of this slope would ensure that the substrate was loose gravel. The inlet area of the loch, which is silty and weedy, had a population of mostly immature charr, thus supporting the idea that the mature fish were exploring a spawning site.

6.2 THE DYNAMICS OF THE SPAWNING POPULATION

6.2.1 AGE STRUCTURE OF THE SPAWNING POPULATION: The age frequency distributions of maturing fish for each sex of each of the charr populations are presented in Figure 6.1. All of these distributions have strong modes, usually at age 4+. Male fish from Loch Meallt have the mode at age 2+.

In Loch Doine the frequency distributions of males and females are similar. Few fish mature before age 4+, but repeat spawning females appear at this age. In Loch Builg a large number of males mature at age 3+ and repeat spawning females also appear at this age, indicating spawning at age 2+. In Loch Meallt the two distributions are quite different with most males maturing at ages 1+ and 2+ and then beginning to disappear from the population, while the females maintain the mode at 4+, with a large proportion of fish spawning at age 3+.

A comparison among the lochs shows a progression toward earlier age at maturity along the sequence Doine, Builg, Meallt. This is the reverse rank order of development of secondary sexual characters. This trend in age at maturity is evident among female fish, with increases in the relative frequency of younger spawners, but it is more obvious among the male populations, where the requirements of maturation presumably are less demanding. In males, the mode shifts two full years. This affects generation time and has profound

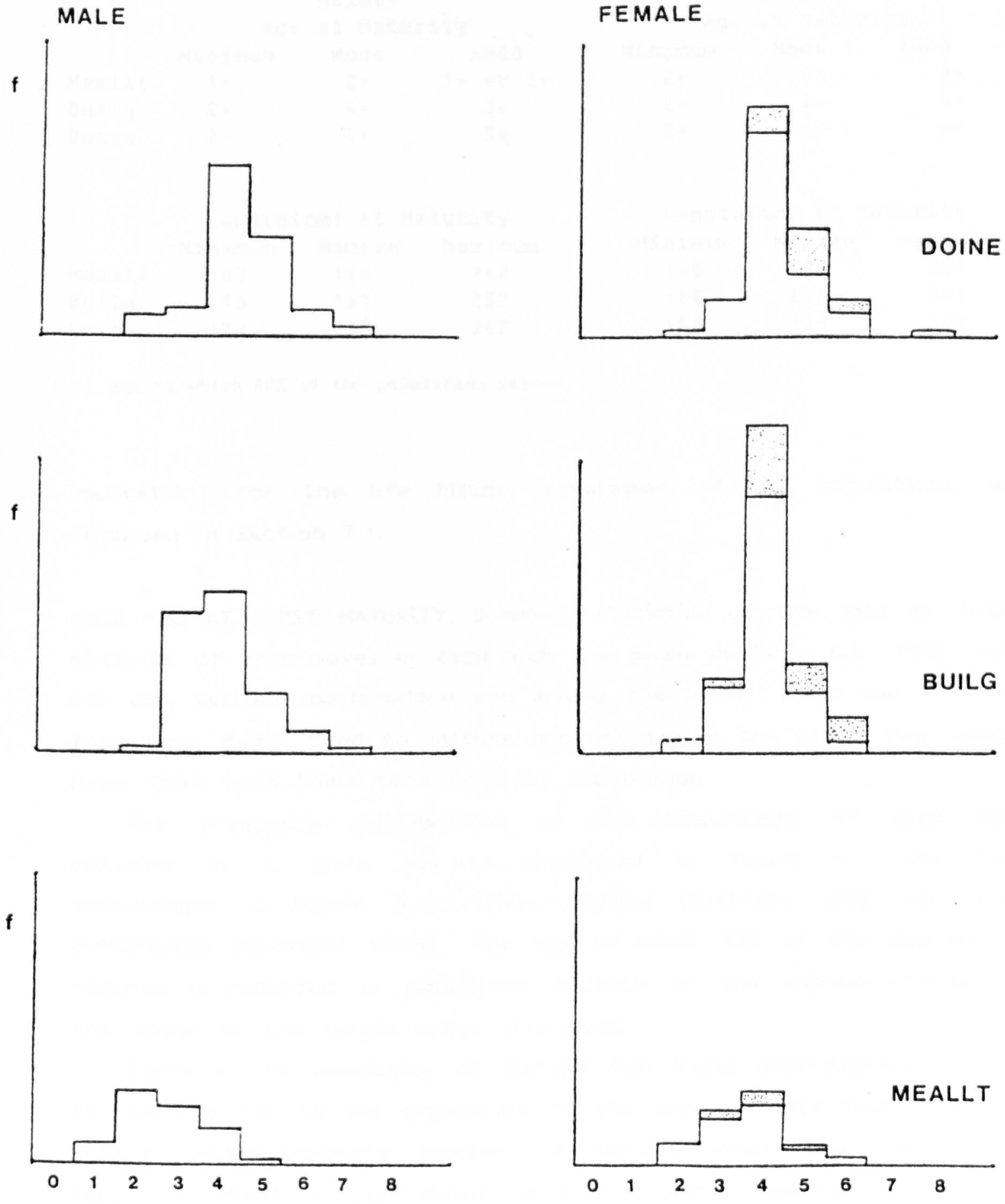


Figure 6.1 - Age composition of the spawning stocks of charr in the three lochs. All samples in all years. Stippled area represents repeat spawners.

Table 6.2 - Age and length of charr from the 3 lochs at 1st maturity.

	Males			Females		
	Age at Maturity			Age at Maturity		
	Minimum	Mode	AM80*	Minimum	Mode	AM80
Meallt	1+	2+	1+ or 2+	2+	4+	3+
Builg	2+	4+	3+	2+	4+	4+
Doine	2+	4+	5+	2+	4+	4+

	Length(mm) at Maturity			Length(mm) at Maturity		
	Minimum	Median	Maximum	Minimum	Median	Maximum
Meallt	103	169	242	148	192	304
Builg	110	197	257	169	208	264
Doine	128	233	342	166	239	304

*: age at which 80% of the population mature.

implications for the life history strategies of the populations, as discussed in Section 7.1.

6.2.2 AGE AT FIRST MATURITY: Summary statistics of the ages at first maturity of both sexes in each loch are given in Table 6.2. Male fish are very variable both within and among the lochs. Males and females from Loch Meallt tend to mature earlier than in the other two lochs. Males from Loch Doine tend to delay maturation.

The frequency distributions of the populations of each sex maturing at a given age are presented in Figure 6.1 and the percentages in Figure 6.2. These figures illustrate very well the differences described above. The age at which 80% of the population matures is regarded as significant because of the marked change in the slopes of the curves above this level.

There is the possibility of mature fish being over-represented in the samples due to the disposition of the sampling nets near spawning areas.A disproportionate number of mature males may have been caught, especially in Loch Meallt, as it is thought they may congregate to defend a breeding territory (Kipling and LeCren 1984). However, the presence of 1+ breeding males in Loch Meallt constitutes a major difference from the other lochs and moves the Loch Meallt curve on Figure 6.2 well to the left.

It is thought that females visit the spawning areas only briefly (Kipling and LeCren 1984) and thus are probably of about the same

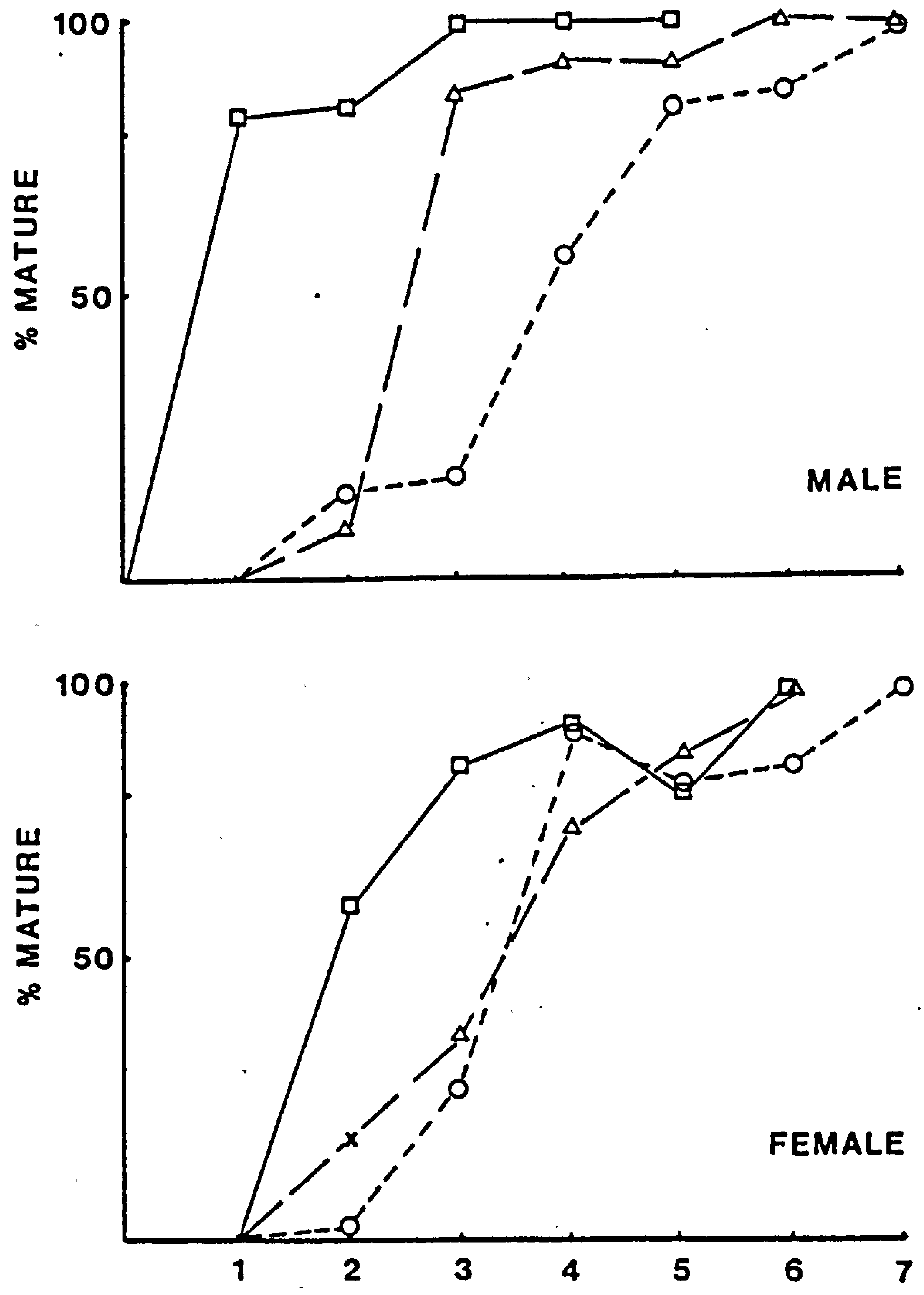


Figure 6.2 - Percent of the population of each sex maturing at a given age in each of the three lochs.
□ Meallt
△ Builg - x known only by subsequent repeat spawners
○ Doine

Table 6.3 - Percent of "n" fish mature at each age in each lake

Loch	Meallt				Builg				Doine			
Sex	M	n	F	n	M	n	F	n	M	n	F	n
Age 0	-	-	-	-	-	-	-	-	-	-	-	-
1	83	6	0	6	0	3	0	3	0		0	3
2	85	21	60	10	9	11	x*	9	15	33	2	39
3	100	14	86	14	87	38	37	43	19	36	28	32
4	100	9	94	16	93	42	74	84	59	70	91	54
5	100	1	80	5	93	15	88	16	85	27	83	18
6	-	-	100	2	100	5	100	2	88	8	86	7
7	-	-	-	-	100	1	-	-	100	2	100	1
Total Sample	92	51	74	53	69	115	60	157	48	176	53	154

* presence known only by repeat spawners at age 3.

catchability as immature females. Consistent with this, the ratio of mature to immature fish tended to be closer to unity in females than males, especially in Loch Meallt (Table 6.6).

In Figure 6.2, the population of males from Loch Meallt is shown to achieve the 80% level of maturity very abruptly at age 1+, but even if allowance is made for the possible catch bias, it is certainly achieved by age 2+. In Loch Builg, this level is achieved only by age 3+, with age 2+ fish showing little tendency to mature. The Loch Doine male population delays maturity still further, and although age 4+ is the modal age at first spawning (Table 6.3), a considerable proportion of fish do not mature until age 5+ or older, with the 80% level achieved at age 5+. In Loch Meallt, the onset of maturity can occur at any of five ages, while in Lochs Builg and Doine the fish can mature at any of six ages.

The age at maturity of cryptic and precocious males varies among the lochs (Figure 6.3 and Table 6.4). Cryptic males from Loch Builg tended to mature at a similar age to the bright males (t-test, $p=0.12$), while precocious males from Loch Doine were very much younger than the bright population (t-test, $p<0.01$). Most males from

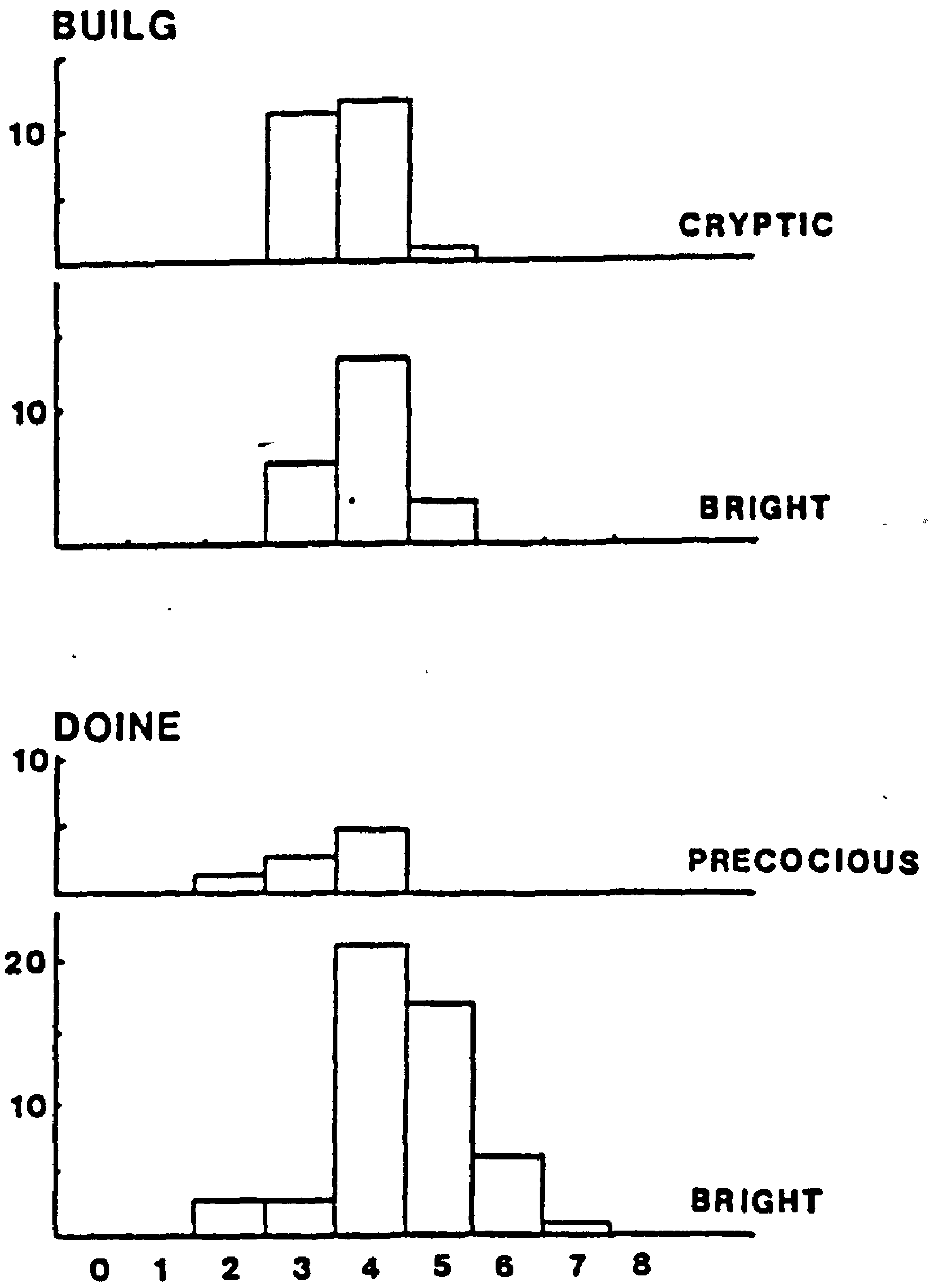


Figure 6.3 - The age frequency distribution for each reproductive phenotype among male charr from Loch Builg and Loch Doine.

Table 6.4: Mean ages and fork lengths of male phenotypes in Loch Builg and Loch Doine.

	Bright		Cryptic/Precocious	
	Age	FL	Age	FL
Builg	3.9	191	3.6	181
Doine	4.5	231	3.3	171

Loch Meallt were very young anyway so that any dimorphism of the male population is masked.

The patterns of maturation are not so distinct for the populations of females in each loch (Figure 6.2). More females mature at a younger age in Loch Meallt but there is little difference in the proportions maturing in Lochs Doine and Builg. In Lochs Meallt and Builg the onset of female maturity can occur at any of five ages while in Loch Doine it can occur at one of six ages.

6.2.3 SIZE at FIRST MATURITY: Summary statistics for size at first maturity for each sex are given for each loch in Table 6.2. Arithmetic statistics were avoided because of bias towards the most frequently captured age class. However, the median, mode and mean lengths at maturity were all similar within a loch.

Males from Loch Meallt tended to mature at a small size. Those from Loch Builg were intermediate and those from Loch Doine were quite large. The maximum size at first maturity was dramatically larger in Loch Doine.

Cryptic males from Loch Builg were slightly smaller (t-test, $p=0.03$) than bright males (Table 6.4). Precocious males from Loch Doine were very much smaller (Table 6.4, t-test, $p<0.01$) than their bright counterparts. Again, in Loch Meallt, two forms could not be distinguished.

Female charr from Loch Meallt tended to be smaller than in the other two lochs. However, in contrast to the variability amongst males, the differences among females of the three populations are not very distinct.

Table 6.5 - Percent of female spawning population (n) breeding in their second or subsequent season.

	Meallt			Builg			Doine		
Age	%	n total	n kelts	%	n total	n kelts	%	n total	n kelts
2	0	6	-	-	-	-	0	1	-
3	8	13	1	11	18	2	0	9	-
4	17	18	3	23	80	18	11	55	6
5	20	5	1	33	21	7	42	26	11
6	33	3	1	75	8	6	33	9	3
7	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	0	1	-
Total	13	45	6	26	127	33	20	101	20

6.2.4 REPEAT SPAWNING: Fifty nine of 273 (22%) mature female charr were found to be in their second or subsequent breeding season. The age specific percentage of repeat spawners is given for each loch in Table 6.5. These fish first appear at age 3+ in Lochs Meallt and Builg and at age 4+ in Loch Doine. They seem to disappear from the populations at age 6+, although this may be an artifact due to removal of the small population of old fish by sampling. One older (7+) previously spawned fish was captured in July 1981 from Loch Builg and the gonads had again begun maturation.

6.2.5 SEX RATIO: The sex was determined for 961 charr aged 1+ (2+ in Loch Doine) or more caught from the three lochs (Table 6.6). Overall 56% were female fish.

In Loch Doine the sex ratio was equal but in Lochs Meallt and Builg it was skewed toward female fish. In Loch Meallt this is probably due to differences in survival between the sexes (see section 6.5 on demography). In Loch Builg a proportion of most catches was released so that reduction of the population by sampling would be minimised. These were fish that had survived the gill net in good health. If the sexes were differentially killed by the nets (it is impossible to sex or age charr accurately in the field) then the Loch Builg data must be considered biased.

Roughly the same pattern of sex ratios is followed by the randomly caught samples.

An effort was made to catch broodstock from each lake. Standard experimental gill nets were set over shallower stony substrates and large numbers of sexually mature charr were captured. The sex ratios of these collections are heavily skewed toward males except in Loch Meallt. However, this seems to be an artifact of the life history of Loch Meallt charr as the males begin to disappear rapidly from the population after age 2+ (Figures 4.1, 4.2 and 6.1).

Table 6.6 - Sex ratios in percent of population (n) observed in each loch.

Loch	All Fish M:F	(n)	Random Collections M:F	(n)	Collected on Breeding Area M:F	(n)
Mealt	45:55	(206)	48:52	(137)	38:62*	(69)
Builg	41:59	(427)	36:64	(260)	66:34	(97)
Doine	50:50	(354)	44:56	(268)	69:31	(86)

* Meallt: Age 1+ 50:50 (10) with no females mature.
Age 2+ 75:25 (8)

Builg: These ratios are suspect because the fish killed were a subsample of the fish captured. Healthy fish were released in order to maintain the population density in the loch.

6.3 FECUNDITY

6.3.1 METHODS

MALES: Male animals produce an excess of gametes so that counting them has no practical biological meaning. However, the testes weight does give an indication of reproductive investment by males. This is the parameter that was measured in this study.

Testes were weighed from frozen samples during the gross dissection previously described. The organs were detached anteriorly by tearing the connective tissue with blunt forceps. They were torn free along the longitudinal mesentery and detached posteriorly near the vent. Therefore, the gonad weight included almost the entire genital fold. The paired testes were blotted and weighed to 0.01g on an Oertling (model V10) balance. They were then frozen for proximate analysis.

FEMALES: Ova were obtained either from dead and frozen samples of the spawning population or from live adults captured specifically for broodstock.

In dead fish, the ripe ovaries were carefully removed as described for testes, blotted on a dry surface, and weighed to 0.01g on an Oertling (model V10) balance. Repeat spawners were detected by the presence of incompletely resorbed ova in the body cavity. Often only the empty zona radiata remained.

The ovaries, plus the measured ova, were then placed in gently boiling water. This caused the boiling to cease and the samples were allowed to "poach" for a few minutes, until the ova were hard. This gentle "poaching" prevented most ova from bursting and losing material to the water. When cooked, the samples were separated from the water using a tea strainer and blotted dry. They were then "crumbled" by hand onto a clean surface, the ova breaking free from the ovarian tissue. Total counts were made of the ova in each ovary. The separated ova and ovarian tissue were then collected and frozen for proximate analysis.

Eggs were counted only from fish collected within 3 weeks prior to the time of spawning. Ova were not counted if the fish had ovulated, as egg loss occurred during the handling of the fish.

In the case of ova obtained from broodstock, I used the following procedure.

Adult charr were captured in the loch using the standard gill net previously described. The net was set on the bottom of the lake, usually in an area where spawning had previously been discovered. After an interval of no more than 30 minutes, (this period was found to cause very low mortality) the net was raised and the fish removed into a dark bucket. The net was then reset and the procedure repeated until enough fish had been taken.

The captive fish were held in buckets, with frequent water changes, until I had identified all injured fish. These were killed and retained for fecundity counts. The healthy fish were inspected for sex and ripeness (by visual assessment of secondary sex characteristics and by gentle palpation to release some gametes) and several of each sex were selected for transport to the laboratory. A summary of the broodstocks is given in Table 6.7.

The fish were transported in doubled large, black polythene bags, supported in a standard rubbish bin, and approximately one third filled with fresh lake water. No more than four pairs of adult fish were placed in each bag, which was then inflated with pure oxygen and sealed. This procedure was always the last to be done before leaving the field site so that transport time was minimised. We then drove directly to Edinburgh and released the fish into a previously prepared holding tank.

During the following days the females were tested for ripeness by gentle palpation; the males already having been selected for a ripe and running condition. If free ova appeared at the vent, the fish was stripped of ova, by antero-postero squeezing strokes, into a wetted plastic pan. Milt from more than one male was added to the ova, which were then gently stirred to expose all eggs to fertilization. After several minutes, the pan was flooded with water and drained to wash the eggs. This was repeated several times. The eggs were then poured into a previously prepared incubation tray and left undisturbed for two days. This allowed more than enough time for the ova to water harden. All ova from a female were incubated together, including batches taken on consecutive days, but each clutch (all the eggs from a female) was incubated in a separate tray.

Table 6.7 - Summary of data describing broodstock and egg collections for egg culture investigations.

Brood fish			Egg collection				
Loch	Date of capture	Maturity	Location	Date	Temperature	Number of broods	Fate
Meallt	15.10.81	ripe or ovulated	lochside	15.10.81	6°	1	killed by unusually high chlorine levels
			laboratory	16.10.81	9°	2	
	1.9.82	mature	laboratory	--	--	--	failed to spawn
Builg	22.9.82	ripe	laboratory	23.9.82	10°	2	two broods hatched, poor alevin survival, two broods infertile
			laboratory	24.9.82	11°	2	
	25.9.83	ripe or ovulated	lochside	25.9.83	7.5°	10	hatched, reared
			laboratory	27.9.83	15°	4	hatched, reared
Doine	9.12.81	ovulated or spent	lochside	9.12.81	freezing	1	infertile
	23.11.82	ripe	laboratory	9.12.82	4°	2	hatched, reared
			laboratory	11.12.82	6.6°	1	hatched, reared
	24.11.83	ripe	laboratory	5.12.83	7.7°	2	hatched, reared
			laboratory	20.12.83	5.5°	1	hatched, reared

6.3.2 RESULTS

6.3.2.1 GONAD WEIGHT

MALES: Sixty five male charr were found to be in a mature state and were used in the analysis. These were identified by the posterior enlargement of the gonad almost to the vent. Running fish may have lost some of the sex products during handling but this would not affect testes weight appreciably as most of the male organ mass consists of seminiferous tubules. Spent males were easy to detect by the reddish colour and collapsed state of the testes. These fish were rejected, as were fish collected more than three weeks before the presumed time of spawning.

Table 6.8 summarises the findings of the analyses. The rank order of mean body weight is Doine_a > Builg > Meallt. The rank order of mean gonad weight is Builg > Meallt > Doine_a. Only Lochs Builg and Doine are statistically separable (t-test, $p<.01$). The rank order of calculated gonad weight for a standard 214mm (see section 6.3.2.3) fish is similar. The rank order of gonadosomatic index (GSI), where

$$\text{GSI} = 100\,\frac{\text{gonad weight}}{\text{somatic weight}} \qquad 6.1$$

is Meallt > Builg > Doine_a. Here both Lochs Meallt and Builg have statistically greater indices than Loch Doine_a (t-test, $p<.01$). The (GSI) rank order is the reverse of that for body size.

There are two classifications for mature males from Loch Doine. Doine_a represents large adult males with well developed secondary sex characteristics. Doine_p represents small, nondescript males analogous to the precocious parr that are well known in the genus *Salmo* (see section 1.1.3.1). These precocious fish are very small, with associated small gonads (Table 6.8). However, the GSI is significantly greater than that for adult males (t-test, $p=.045$). A population of "cryptic" males has been described from Loch Builg (section 1.1.3.1), but, unfortunately, these were not recognized until after the frozen samples had been processed so the data were not kept separate.

Table 6.8 - Mean somatic and gonad weights and gonadosomatic indices(%) for male and female charr from the three lochs

		GONAD WEIGHT					
Males		observed	standard				
	SOMA(g)	weight(g)	fish	GSI	s	n	range
Meallt	67.5	3.13	4.25	4.73	1.56	13	3.0-8.6
Builg	89.5	3.56	3.68	4.13	1.12	37	2.3-6.3
Doine$_a$	129.4	2.36	2.15	1.85	0.66	7	0.7-2.8
Doine$_p$	43.9	1.00	-	2.44	0.62	8	1.3-3.6

Table 6.9 - Mean somatic and gonad weights and gonadosomatic indices for female charr from the three lochs

		GONAD WEIGHT					
		observed	standard				
Loch	SOMA	weight	fish	GSI	s	n	range
Meallt	80.0	-	-	-	-	0	-
Builg	95.0	15.1	16.98	15.9	2.93	22	11.5-22.7
Doine	153.9	19.6	16.96	13.1	3.74	34	6.8-21.2

Table 6.10 - Comparison of gonadosomatic indices of the sexes in each of the three lochs.

Loch	Male	Females	ratio
Meallt	4.73	-	
Builg	4.13	15.9	1:3.85
Doine	1.85$_a$	13.1	1:7.08
	2.44$_p$		1:5.37

FEMALES: Fifty seven fully developed pairs of ovaries were weighed. The results are summarised in Table 6.9. No weights were accepted from Loch Meallt fish as all the ova appeared very small and were tightly bound in the ovary. I could not tell if maturation had been completed.

Females from Loch Doine were found to be much heavier than those of the other two lochs (t-test, p<.01). The gonad weight of Loch Doine females is also greater than that from Loch Builg (t-test, p<.01). However, the expected gonad weight for a standard 214mm female is virtually identical in both lochs, and when the GSI is calculated, the rank order is reversed with the values significantly different (t-test, p<:01).

Table 6.11 - Observed age specific fecundity of female charr from three lochs

	Meallt						Builg						Doine					
Age	Virgin			Kelts			Virgin			Kelts			Virgin			Kelts		
	Ova	CL	n	Ova	CL	n	Ova	CL	n	Ova	CL	n	Ova	CL	n	Ova	CL	n
2	104	-	1	-	-	-	*	-	-	-	-	-	428	-	1	-	-	-
3	198	±47	11	-	-	-	207	±32	4	229	-	2	589	±154	7	-	-	-
4	252	±86	10	131	-	1	234	±30	11	227	±56	8	713	± 88	21	672	±273	3
5	196	±87	3	199	-	1	192	±45	5	218	±59	3	904	±240	6	778	± 65	6
6	321	-	1	887	-	1	219	-	2	239	±41	3	599	-	2	797	-	2
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	595	-	1	-	-	-

* indicated only by repeat spawners aged 3+.

COMPARISON OF THE SEXES: Data comparing the gonad weights of male and female charr are presented for Lochs Builg and Doine in Table 6.10. Values for Loch Meallt were omitted because no ovaries were weighed.

The GSI values show females to have much larger gonads than males. In Loch Builg investment in ovaries was nearly four times that in testes, while in Loch Doine it was seven times greater than adult males and more than five times greater than precocious males.

A comparison of values computed for standard fish of 214 mm produces similar, but slightly greater, ratios.

6.3.2.2 FECUNDITY AND AGE: The age specific fecundity for both virgin females and repeat spawners from each loch are illustrated in Figure 6.4. The data are presented in Table 6.11. Virgin female charr from Loch Doine produce many more eggs per fish at all ages than do females from the other two lochs (Anova, p<.01). The same is true for repeat spawning females (Anova, p<.01). The only exception to this is a single repeat spawner, aged 6+, from Loch Meallt that was very large with a clutch size of 887 eggs. This fish may be one of the fast growing component of the population hypothesized in section 4.4.3. The age specific fecundities of the Loch Builg and Loch Meallt virgin females are not statistically different (Anova, p=.5).

It is interesting to note that in all three populations the fecundities of virgin spawners first increase and then decrease with age. Unfortunately, except in the case of Loch Doine, I could only

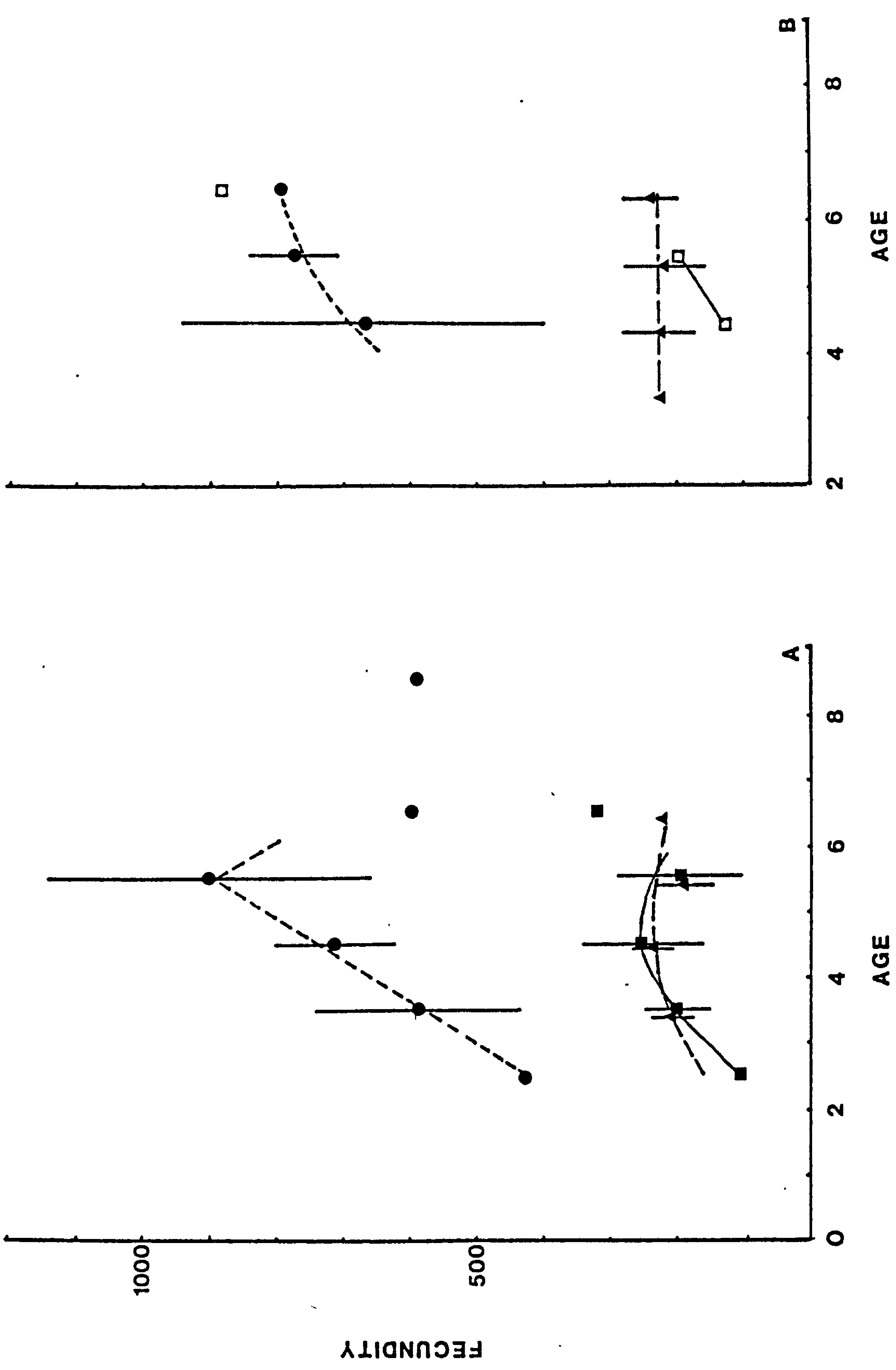


Figure 6.4 - Mean age specific fecundity of charr from three lochs. Vertical lines are 95% confidence intervals.

A-virgin females □■ Meallt

B-repeat spawners ▲ Builg

● Doine

Table 6.12 - Correlation coefficient of regressions of individual fecundity on various body measures for first time (virgin) and repeat (kelt) spawners in the three populations of charr

Independent Variable	Correlation With Individual Fecundity								
	Meallt			Builg			Doine		
(Log x)	virgin	kelt	both	virgin	kelt	both	virgin	kelt	both
Fork length	.787	.995	.861	.313	.445	.366	.797	.679	.795
Somatic weight	.798	.982	.850	.471	.190	.346	.780	.714	.780
Total weight	.810	.980	.857	.536	.407	.471	.807	.770	.804
Gonad weight	.826	.967	.849	.738	.947	.818	.759	.561	.725
Age (not logged)	.189	.951	.428	-.106	.137	.000	.203	.366	.261
n	25	3	29	22	15	37	34	11	46

illustrate these age-specific fecundity curves by ignoring the confidence intervals and fitting them by eye to the mean values. However, they could be real and an explanation of them is interesting. The increase is probably size-related while the decrease may be due to slow growing fish finally achieving maturity but being of poor fitness. The peaks of the curves coincide with the age (4+) at which most fish spawn except in Loch Doine, where it falls a year later. The implications of this are discussed in Section 6.5.

In Loch Builg, the age specific fecundity of kelts is no different to that of virgin females (Anova, p=.7). In Lochs Doine and Meallt kelts tend to have consistently fewer ova at each age than virgin females (except for the exceptional Meallt fish previously mentioned). However, this can not be demonstrated statistically. The phenomenon is explored further in Chapter 7.

6.3.2.3 FECUNDITY AND BODY SIZE: Fecundity was found to be quite well correlated with various body measurements except in Loch Builg (Table 6.12). This was probably because Loch Builg females mature at a fairly constant body size and have a variable clutch size. Therefore, the regression would be short and scattered, producing a poor correlation. In spite of the fact that somatic weight is best correlated (total and gonad weights are autocorrelated), I have chosen to use fork length as the measure of body size in this paper. This is because

Table 6.13: Components of regression $\log Ova = a + b \log X$ describing the relationship of fecundity to body size for female charr from the three lochs.

		Fork length		Total weight		Somatic weight	
Loch	Sex	a	b	a	b	a	b
Meallt	virgins	-3.994	2.767	0.614	0.893	0.630	0.898
	kelts	-6.168	3.687	-0.207	1.264	-0.198	1.280
	combined	-4.404	2.946	0.496	0.952	0.504	0.962
Builg	virgins	0.411	0.831	1.191	0.560	1.358	0.493
	kelts	-2.114	1.921	0.865	0.719	1.718	0.315
	combined	-0.381	1.174	1.096	0.607	1.465	0.440
Doine	virgins	-1.597	1.877	1.361	0.658	1.560	0.563
	kelts	-0.273	1.315	1.487	0.594	1.719	0.505
	combined	-1.337	1.765	1.500	0.595	1.633	0.546

(1) I have more data on length than weight because brood fish were often starved before they were measured,(2) length is less variable, and (3) somatic weight, which is the only weight one can use as a truly independent weight variable is not a useful predictor for fish biologists since if one gonadectomizes the fish one could easily just count the eggs.

The relationship of fecundity to fork length for the three populations is illustrated in Figure 6.5 and Table 6.13. The fecundity increases with body size in lochs Meallt and Doine but not in Loch Builg (slope, n.s.) The slopes for the three populations are statistically different (t-test for comparison of slopes, Sokal and Rohlf 1969; $p<.05$) The most important feature of these regressions is that fish from Loch Doine consistently produce more eggs than the other two populations at all sizes. Only very large fish from Loch Meallt approach the fecundity of those from Loch Doine.

A useful way to compare the fecundity of the populations is to employ the "standard" fish as in Chapter 5. This is plausible for these populations because the sizes of the fish are similar and the regressions of egg number with size overlap. The grand mean length of mature female charr in this study is 214mm so this was taken to represent the standard fish.

Table 6.14 presents the expected fecundity of a standard fish from each population. The 95% confidence limits are very small because the values are interpolated from a highly correlated

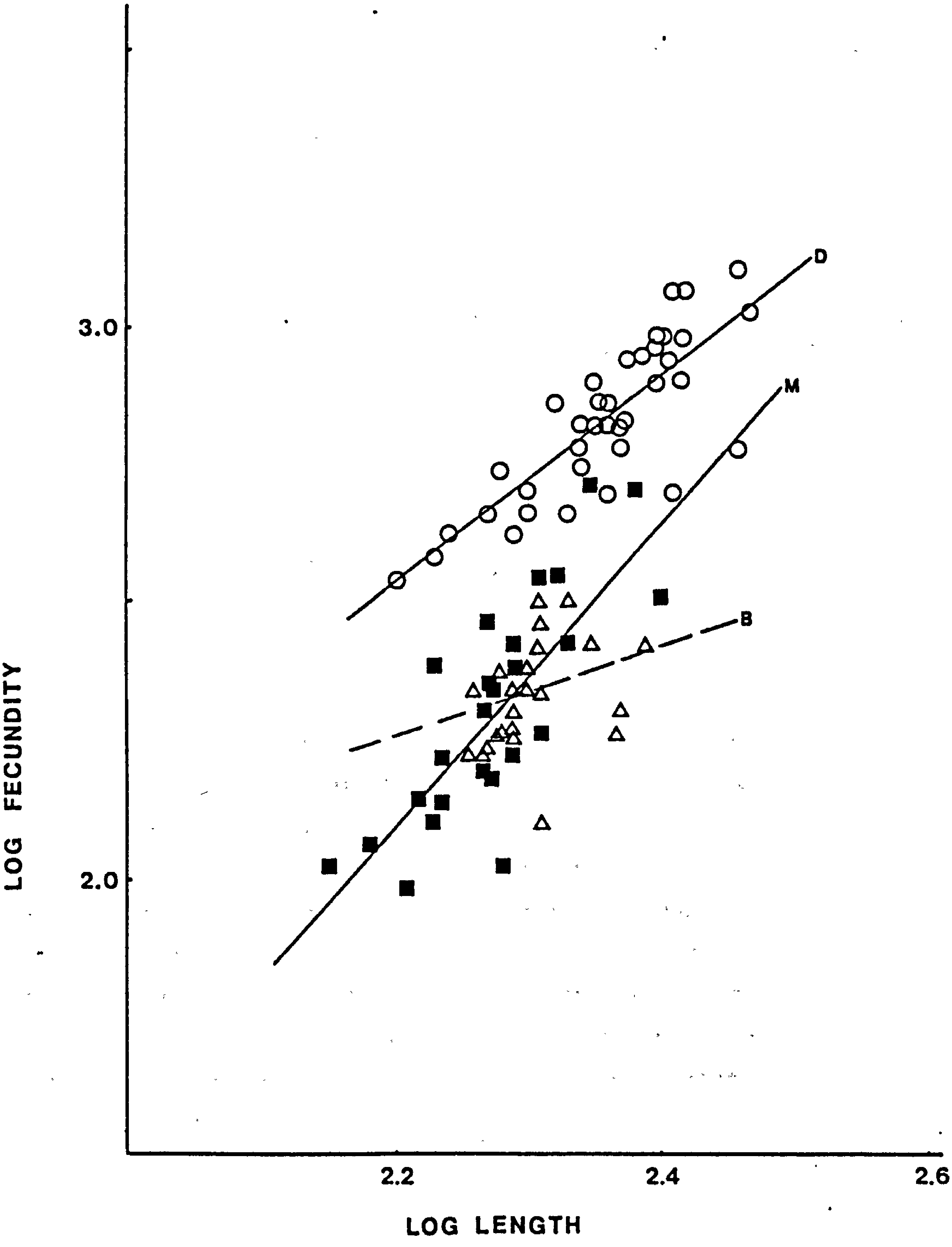


Figure 6.5 - The relationship of fecundity to fork length for three populations of charr.
■ Meallt
△ Builg
○ Doine

Table 6.14 - Expected fecundity (+95% confidence limits) of female charr set to a standard fork length of 214 mm.

	Virgin		Repeat Spawners	
Loch	F	n	F	n
Meallt	285±1.7	26	266 -	3
Builg	223±1.6	22	231±1.8	16
Doine	599±1.5	38	619±1.5	11

Table 6.15 - Number of eggs per 100 g of fish (Total Weight), based on putting the mean total weight into the appropriate regression of Table 6.12, for the female charr in this study.

	Virgin Females			Repeat Spawners		
	Mean Wet Weight	Expected Fecundity	Ova/ 100g	Mean Wet Weight	Expected Fecundity	Ova/ 100g
Meallt	93	235	253	156	367	236
Builg	101	206	204	114	221	194
Doine	177	692	391	210	735	350

regression. Analysed in this way, the data show a pattern of similar fecundities in Lochs Meallt and Builg and a very much greater fecundity in Loch Doine.

Table 6.15 presents the expected fecundity for a female of a total weight representative of its population mean. The number of eggs per 100 grams of fish was calculated from this. This parameter was calculated in order to facilitate comparison with the populations from different worldwide locations described in Johnson (1980). The pattern of relationships with weight is similar to that for the fish of standard length.

6.4 EGG STUDIES

6.4.1 INTRODUCTION: The biology of charr ova became more and more interesting as this study progressed. I first collected fertile eggs from broodstock in order to find a zero point for ageing with otoliths. However, obvious differences in egg size between populations and the constancy of size within populations suggested that the fish might be manipulating egg dimensions in an adaptive manner. Thus, I undertook to measure and culture ova from as many fish from each population as possible. This was not very successful for the Loch Meallt populations. I did better with Loch Doine ova, but my best data came from Loch Builg, where I was able to culture broods from 16 different female fish.

6.4.2 METHODS: Much effort was devoted to measuring the sizes of ova preserved in various ways. During the dissection of the dead females, a random sample of 5 ova were freed from the ovarian membrane and immersed in distilled water for a few minutes. This caused them to harden and reduced the risk of bursting. In early samples the ova were lined up on a crease in blotting paper and the overall length of the sample measured, the sample mean being the egg diameter assigned to that fish. However, because some error was caused by the ovoid shape of most of the eggs, this procedure was changed to measure the volume of the ova by first blotting dry and then taking the displacement of the sample in a pipette graduated to 1/10 of a millilitre. Again, the sample mean was the ovum volume assigned to the fish.

It was found that the only accurate measure was the volume, by displacement, of live ova that were stripped from the female, fertilized and water hardened. This measure gives the volume of egg capsule available to the embryo.

The background information for the clutches of eggs used in this study is presented in Table 6.7. Because the brood fish were captured close to spawning time, I am confident that the viable ova collected were the size they would have been if spawned naturally in the wild. However, the size of fry may have been influenced by culture conditions and I point out any suspect data throughout this section.

Table 6.16 - The size of charr from the three lochs at various stages of their early life history.

Loch	Ovum volume (cm^3)		Alevin weight (mg)		Length at first feeding (mm)*	
	mean CL	n	mean CL	n	mean	n
Meallt	.0595±.028	2	-		-	
Builg	.0715±.007	16	17.54±.002	11	23.16	4
Doine	.0433±.005	6	11.74	1	21.30	2

* calculated using equation: L = F - ((F-N)/2)

where: F = mean length of feeding fish
N = mean length of non-feeding fish
L = estimated length at first feeding

The development times and egg or embryo sizes were measured to the eyeing, hatching, and first feeding stages in each clutch. Eyeing, the appearance of eye pigmentation, is the first easily detectable ontogenetic feature in salmonid embryos. Hatching is an ontogenetic marker used by most fish biologists (but has been criticized by Balon 1980) and is the first opportunity to measure the embryo without dissecting the ovum. The onset of first feeding is crucial to the survival of young fish as the seasonal timing and size at which it occurs may influence the availability and size of food particles eaten by them.

6.4.3 RESULTS

EGG SIZE AND POPULATIONS: As mentioned above, the size of the ova differ among populations. Data on egg volumes presented in Table 6.16 support this. The populations can be placed in decreasing order of egg size as Builg, Meallt, Doine. Loch Builg ova are significantly larger than those from Loch Doine (t-test, p<.01), but Meallt ova are not significantly different in size to the other two lochs. This is probably due to the small sample (n=2) from Loch Meallt.

EGG SIZE AND THE PARENT FEMALE: Egg size appears unrelated to other parameters of the female parent fish. Figure 6.6 shows the relationships of egg volume to fork length, post-stripping weight, and

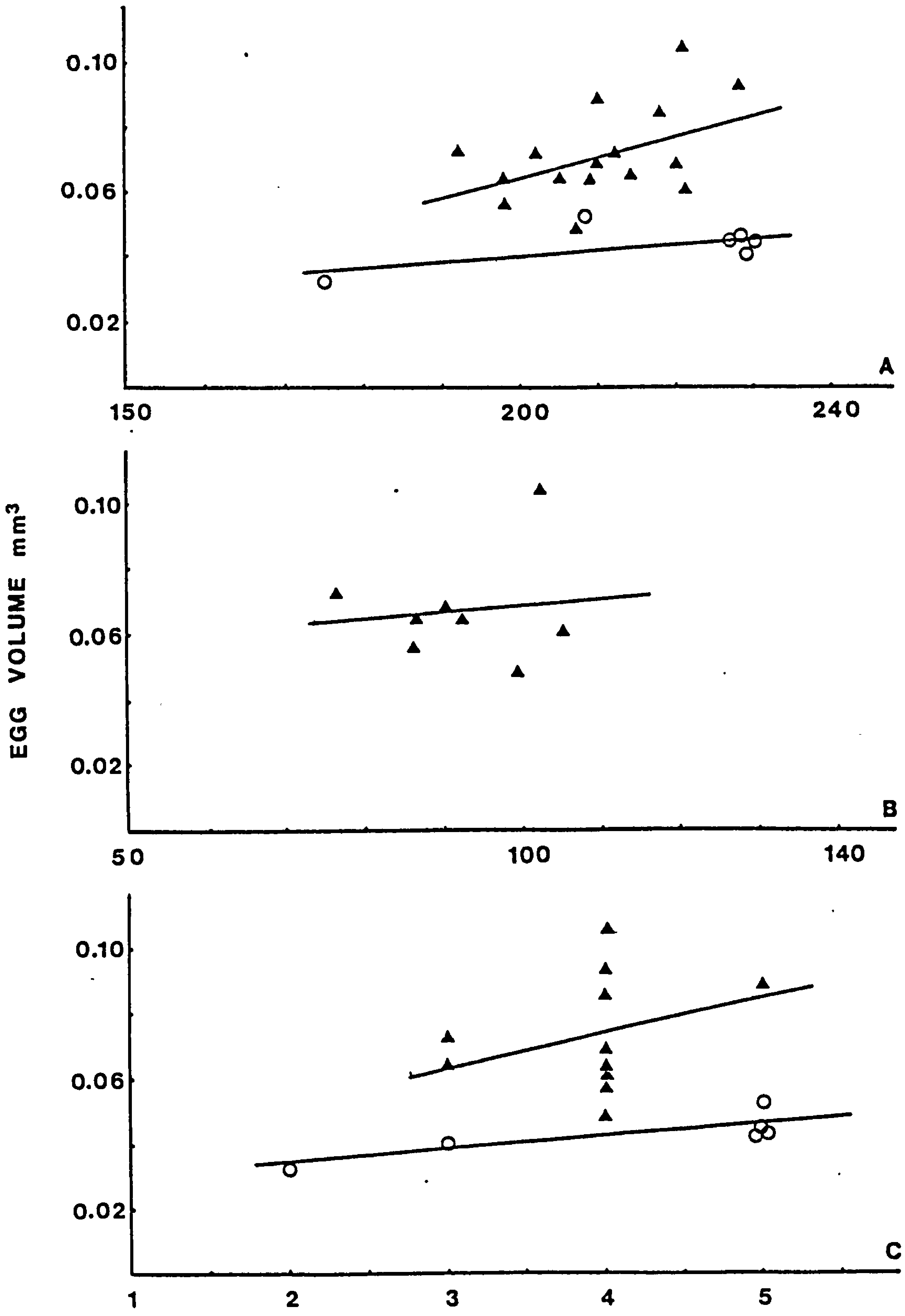


Figure 6.6 - The relationship of egg volume to fork length (A), post-stripping weight (B), and age (C), in two populations of charr.

▲ Builg

○ Doine

age, for the two lochs (Builg and Doine) where sample sizes were sufficient.

Fork length, measured immediately after each fish was stripped, is poorly correlated in Loch Builg (r^2=.2) but the slope of the regression line is significantly different from zero (p=.04). In Loch Doine, the correlation is little better (r^2=.35) and the slope of the regression is not significant (p= 0.11). One should conclude that egg size is independent of body length.

The same conclusion should be made for the relationship with post-stripping weight. I have included only data from Loch Builg in Figure 6.4, as those fish are known to have been stripped within a day of capture and thus would have a representative body weight. Again, it is found that there is a very poor correlation of egg size to the independent variables (r^2=.02), and a slope that is not significant from zero (p=.36).

The relationship with age is also doubtful, as in Loch Builg the correlation is poor (r^2=.1) and the slope of the line is not significantly different from zero (p=.18). The apparent high correlation with age for Loch Doine (r^2=.78) is suspect as the modal age at spawning, age 4+, is not represented. This was due purely to chance in the collection of broodstock.

There is no relationship between egg size and the individual fecundity of the females. There is no slope to the regression of mean ovum wet weight (determined by dividing the gonad weight by the number of ova it contains) on egg number in either loch (p=.23 in both populations) and the two parameters are not correlated (r^2=.01 in both populations).

6.4.3.3 EGG SIZE AND EARLY LIFE HISTORY: Although the size of the parent fish has little effect on egg size, the egg size appears to dictate the size of the charr at hatching and first feeding. In the case of Loch Doine, the sample size (n=2) is too small for the calculation of statistics, but it is obvious that the larger ova of one brood produce the larger alevins and fry. The relationship holds for Loch Builg although some deviation becomes apparent with increased sample size (Figure 6.7).

When one considers the two relationships with the populations combined, they are very strong (Figure 6.5a, r^2=.75; Figure 6.5b, r^2=.93)

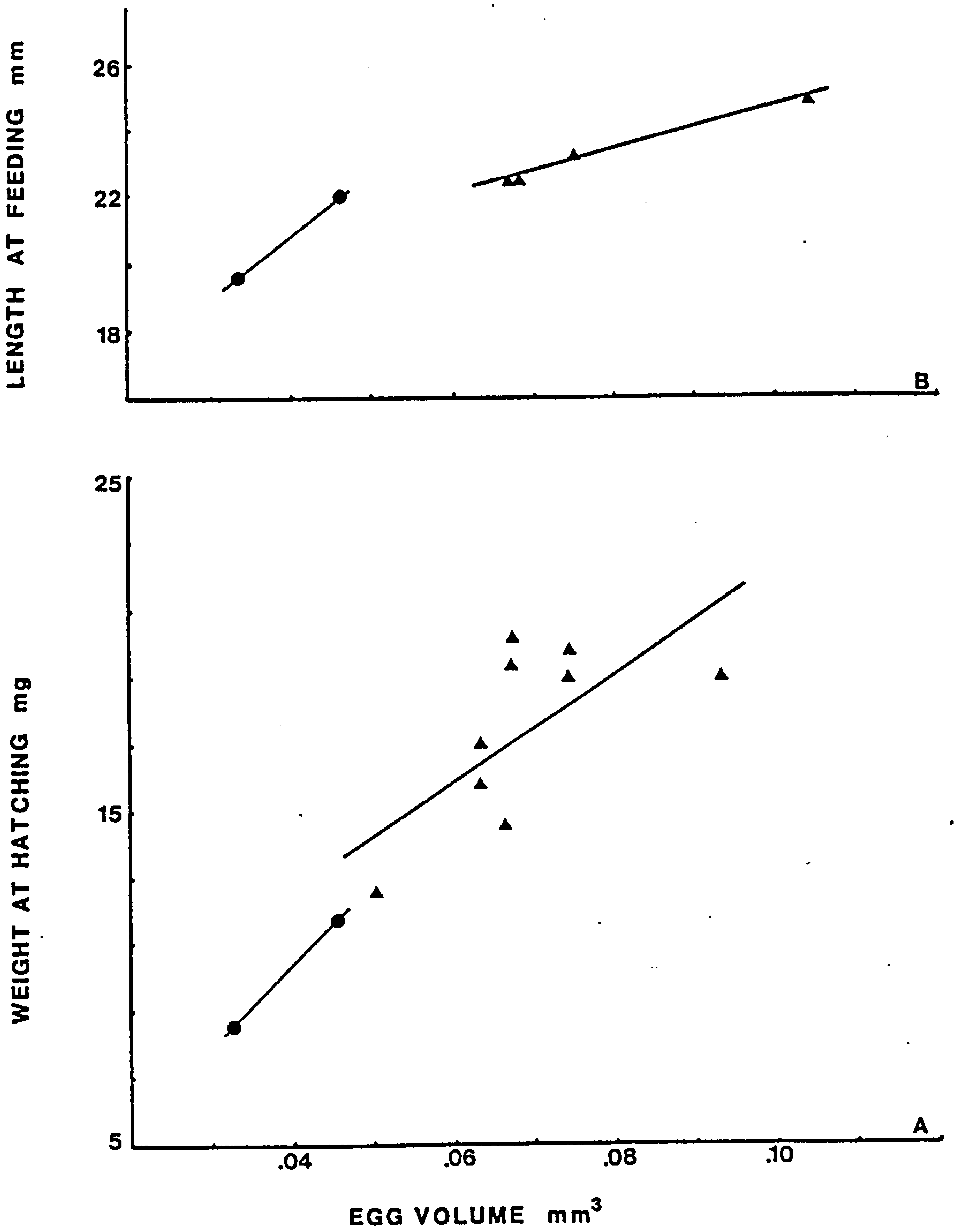


Figure 6.7 - Relationship of size of offspring to egg size in two populations of charr.
▲ Builg
● Doine

Table 6.17 - The relative size of charr from two populations at various points in their early life history.

Loch	Ovum	Alevin	First Feeding*
Builg	1.65	1.49	1.29
Doine	1	1	1

* ratio based on weight estimated using the equation:

$W = aL^b$, where:
W = weight
a = constant, assumed to be 1
L = length (table 6.16)
b = assumed to be 3.

Table 6.18 - Mean ratio of dry weights of embryo to alevin for two populations of charr

Loch	Ratio (x100)	S.D.	n	maximum	minimum
Builg	19.6	4.46	11	26.8	13.0
Doine	16.6	1.80	2	17.9	15.3

due to the differing egg size between the populations. One is obliged to conclude that egg size determines the size of charr in their subsequent early life history. To facilitate comparison between the two lochs, the arithmetic mean values of the early life history parameters are given in Table 6.16. They are expressed as relative values in Table 6.17. Loch Builg fish are consistently larger at all three stages (t-test, $p<.05$). The relative values show this quite clearly. They also show that the difference between the populations decreases with development, but it must be considered that the measurements are not strictly comparable among parameters.

The difference in egg size between the two populations raises the question of whether they achieve the same stage of development at given ages. A simple measure of development is the ratio of embryo dry weight to alevin (embryo plus yolk sack) dry weight (Marr 1966). This was measured for freeze-dried fry sampled on the day of hatching. The results are given in Table 6.18. The population means are not statistically separable (t-test, $p=.2$). The Loch Doine values are included within the range of those values for Loch Builg. The ratios were regressed on egg size to check for a trend in

Table 6.19 - Development of ova from two populations of charr incubated at 5°C.

Loch	Sp'd	Eyed	Hatch	to Eye				to 1st Hatch				to Feed		
		(dates)		T	D	TU	n	T	D	TU	n	T	D	TU
Builg	25.9	1.11	6-9.12	4.9	37	183	9	5.1	81	411	8	5.3*	143	745
1983	26.9	4.11	7.12	4.9	39	193	4	5.1	82	416	3			
Doine	5.12	11.1	5.2.84	5.4	36	195	2	5.4*	60	324	1			627
1983	21.12	23.1	2.3.84	5.2	32	167	1	5.2*	70	364	1			
Norway	18.9	31.10	14.12	4.4	40	170	-	4.4	84	370	-			680
1976$_y$														

* mean temperature includes a cold room failure where temperature rose to 12°C overnight.

T = mean temperature

D = number of days from fertilization

TU = temperature units (TxD)

n = number of clutches

y data from Balon 1980.

development, but no relationship was found (r^2=.04, slope not significant from zero). The wide variation in ratio values may be due to experimental error, but it appears that the two populations would have similar population means in any case.

DEVELOPMENT TIME: The large difference in egg size between the populations might be reflected in the duration of development. The date of spawning is markedly different between Lochs Builg and Doine, and this leads one to hypothesize that the size and thus the development time of the eggs may be adapted for producing fry at the appropriate time in spring. This idea can be tested using the information in Table 6.19 which presents data from 17 clutches of ova cultured under nearly constant conditions. The development time to eyeing is very consistent. Most remarkable is the synchrony shown by the numerous clutches from Loch Builg, regardless of variation in egg size. The data to hatching is not strictly comparable as the Loch Doine broods were temperature shocked by a cold room failure and temperature control was imprecise after that time. However, within population variation is again very low for the Loch Builg clutches. I believe that development rates are independent of egg size both between and within populations.

6.5 DISCUSSION: The time of spawning in Arctic charr can be very variable. In the present study it ranged from September to December, but was much less variable within a population. For example, in Loch Builg I caught ovulated charr moving in-shore to spawn within a three day period in September in two years. Broodstock from Loch Builg, held in the laboratory, ovulated within a four day period in September in two years while broodstock from Loch Doine ovulated within a three week period in December in three years. The peak of activity probably falls within a three week period that is specific for each population. Mills (personal communication, and in Maitland et al. in press) found charr in Loch Luichart in Scotland to spawn over a period of about three weeks.

Other populations of charr in Scotland have their spawning periods between September and November (Maitland et al. in press). Charr in the English lake district spawn from October to March (various authors in Johnson 1980). Windermere is interesting because it has two discreet spawning populations, one breeding in late autumn and the other in February and March (Frost 1965). Central European charr reproduce from November to March (Johnson 1980). The most extended spawning time I found is from the Attersee in Austria, where both sexes of charr have ripe individuals all year, but with a peak period from July to November (Brenner 1980).

In the Western Arctic of Canada and Alaska, McCart (1980) reported very variable spawning times ranging from September to December and found surprising differences in the water temperature on the spawning grounds used by the fish. Fish spawning in September (which included all the lake populations he had studied) were in habitats at about 4°C while the temperatures for December spawners in thermal springs were 14-16°C! Table 6.1 shows variation in spawning time and temperature in the current study, with Loch Builg fish spawning in September at 7°C while the charr in Loch Doine spawn in December at 4°C or less (the depths of freezing lakes are often at 4° because this is the temperature at which fresh water is most dense. A lake turns over by convection as it cools to 4°C, then cools downward from the surface because colder water floats on the 4° water).

Consideration of the development time of eggs and alevins may resolve this difference. Table 6.19 shows the development time to feeding in the laboratory (defined as the time when food particles can be seen throughout the gut) to be about 750 thermal units (TU: 1 TU = 1°C over one day) in the Loch Builg population (empirical data) and about 630 TU in Loch Doine fish (estimated from Builg data and from Balon(1980) as about 1.75 times the TU to hatching). If one assumes the incubation temperature in nature to be at about 4°C in Loch Doine, then the young fish would be ready to feed on about May 20. This date corresponds to the phase of exponential increase in the phytoplankton bloom (data from Windermere in Wetzel 1975) which is closely tracked by the zooplankton bloom (Wetzel 1975). Thus, the young charr in Loch Doine appear to develop in time to emerge when their food source is about to peak.

It is more difficult to explain the timing of spawning in Loch Builg. If the eggs were to incubate at 4°C all winter, they would emerge in the last week of March. However, the loch is situated in the harshest climatic region of Britain and may be cold enough for two or three months to slow the development of the charr ova considerably. The eggs are deposited in shallow shoreline waters, which may well cool to near 0°C for several weeks. At least eight weeks are needed to make up the difference to the last week of May, plus a few days more as development just after spawning at 7°C would be quite rapid. Data from Glenmore Lodge weather station (12 miles west-north west of Loch Builg, and at 100 metres lower altitude) show mean monthly minimum temperatures below freezing from November to March. Monthly mean temperatures are given in Table 1.4 and approach 0°C during January and February. It should be even colder at the altitude of Loch Builg. As Loch Builg freezes for at least several weeks each winter (D. Gill, gamekeeper, personal communication) I expect that the charr must spawn in September in relatively warm water in order to allow time for their offspring to develop before and after the winter freeze and to emerge to feed on the spring plankton bloom.

Arctic charr spawn in a variety of habitats that seem to meet the requirements of a silt free substrate, the continuous presence of water without freezing and cool temperatures (Johnson 1980). Charr have been found to spawn on substrates ranging from sand through gravel to boulders in either running or still waters. Cool temperatures seem to be achieved by spawning in the autumn, winter or spring or at great depth in some larger lakes (Brenner 1980; Johnson 1980). The three populations in the present study all spawned in their home lakes rather than in feeder or outlet streams. The exposed locations may have been chosen to take advantage of wind-generated water currents to irrigate the ova and prevent smothering by silt.

The characteristics of the spawning populations differ among the lochs. Loch Meallt fish tend to be younger and smaller, Loch Builg fish intermediate, and Loch Doine fish older and larger. The rate of female repeat spawning in Loch Meallt is almost double that in the other two lochs. These parameters vary greatly among various stocks of charr worldwide. Johnson (1980) summarises data from many stocks of entirely freshwater and anadromous populations. The age at maturity in both sexes ranges from two to three years in lakes in Ungava, Canada, through five to nine years in Windermere to anywhere from three to 20 years in high Arctic lakes. Males often mature at the younger ages of the ranges. Anadromous charr tend to be older at maturity, being from four to ten years old in northern Alaska and ten to 25 years old in the Canadian arctic. Fish from freshwater populations tend to be smaller than anadromous ones. Ungava females can be less than 10 cm (9.6 to 13.2), but more usual sizes are from about 17 to 33 cm. Populations from large lakes often have fish maturing at more than 40 cm, which is very large for freshwater charr. Anadromous charr tend to be larger still at maturity, and are usually over 50 cm (range 30 to 80 cm). The populations of the present study are therefore comparatively young and small at maturity.

The charr of the present study appear to spawn annually once sexual maturity is attained. The age frequency distribution of repeat spawning females is shifted one year (older) in comparison with first time spawners (Figure 6.1). Most repeat spawning females are age 4+ or 5+ with a few 3+. Since most virgin females spawn at age 3+ and 4+, only a small proportion could rest a year before a subsequent spawning. Kipling and Le Cren (1984) found tagged female charr in Windermere to spawn in consecutive years. Alm (1951 in Johnson 1980) found a similar result in Vättern in Sweden. Anadromous charr, though, regularly miss one or more years before repeat spawning but may reproduce six or more times over a period of 20 years (Johnson 1980). Many of these spawners spend two years in freshwater on a spawning cycle before returning to the sea as spent fish.

The overall sex ratio in the three lochs was 1:1.3 (56%) in favour of female fish. The preponderance of females in the total catch in each loch (Table 6.6) corresponds roughly with the random collections, which were experimental gill net sets which avoided either the time or place of spawning. The overall sex ratio of charr older than age 4 in Windermere was found to be 21:79 (1:3.8) males to females (LeCren and Kipling, 1963; Kipling and LeCren 1984). In the present study the collections made on the spawning grounds at spawning time contrast with the previous data and also contrast with sources quoted in Johnson (1980) in that males predominate in two of the lochs. He notes only one population of anadromous charr in the Canadian arctic with a sex ratio favouring males (M:F 1:0.9) and this could easily have been at unity. My results are based on single catches within a spawning period and therefore would not have sampled the turnover in the spawning population. Males tend to persist on spawning areas and hold territories while females tend to make shorter vists to lay their eggs (Johnson 1980, Kipling and Le Cren 1984). Therefore, an "instantaneous" sample would be more likely to take male fish than females. The Loch Meallt result may be explained by there being simply more females because of the higher mortality rate of males after age 2+ (Figure 6.1). It may also be that the females were older and therefore bigger and more mobile, and thus more likely to be caught in a fixed net.

The charr of Loch Doine and Loch Builg show considerable variation in the size of their gonads. In males, I have shown that gonad size is inversely related to the degree of development of secondary sexual characters. In females, this is not so, and standard length fish have gonads about the same size (note that the GSI is slightly but significantly smaller in Loch Doine females). The female charr in the present study undergo only modest changes in secondary sexual characteristics (see Chapter 2).

Reproductive investment in gonads is much greater in females than in males. In Chapter 5 I showed that most of the difference in somatic resources between mature and immature females could be generally accounted for by gonad development. I also showed a net annual loss of somatic resources in spent female charr from Loch Builg, but (recall the smaller GSI in Loch Doine) a net annual gain by Loch Doine females. It appears that the female charr are investing close to their physiological limit in reproduction, but in Loch Doine they invest slightly less. This may be because survivorship is important to them demographically (see Chapter 7) and they can "bet-hedge" (Stearns 1976) by keeping back enough resources to increase their chance of repeat spawning (Elliott 1984).

Male charr invest relatively little in gonads, but still produce an excess of gametes in comparison with females. The inverse relationship of morphology with the GSI is interesting. In Chapter 5 I found a similar inverse relationship between morphology and somatic resources. It seems that males apportion their resources between investment in sexual dimorphism and probably also behaviour and investment in gonads.

The precocious male charr in Loch Doine have relatively large gonads compared with their bright counterparts, but smaller gonads compared with males from Loch Builg or Loch Meallt. They invest in partial sexual dimorphism (Chapter 2) and are also probably still growing. These demands would limit the gonad mass they can produce but, as the demands are proportionately less than in the bigger fish, the gonads can still be relatively larger than those of Loch Doine bright males. McCart (1980) cites evidence of residual males (mean body weight 159g) in Alaska having gonads 1.5 times larger than their migratory counterparts. Similar individuals were noticed to be satellite males in spawning aggregations of large anadromous charr (McCart 1980).

The age specific fecundities of females of the three populations divide into two groups, Loch Doine with high fecundities and Loch Builg and Loch Meallt with low fecundities. Loch Meallt has the occasional fish that is very large and fecund.

The convex curves of mean age specific fecundities within a population are interesting when compared to the convex curves for somatic resources discussed in Chapter 5. It seems that the maximum fecundity is produced in fish with the greatest available resources. This is confounded in Loch Doine by the powerful influence of body size on fecundity in this population, where age 5+ females are big enough to have a greater fecundity than age 4+ even though the younger fish have better resources when standardized.

The influence of size on fecundity is poor in Loch Builg, but better in Loch Meallt and Loch Doine (Table 6.12). The correlation of fecundity with body size would probably improve in Loch Builg females if they matured over a wider range of body lengths. I feel that charr follow the general rule in fishes that fecundity is a function of body size (Wootton 1984), provided that they can grow large enough to mature over a range of sizes.

The important point to be taken from these relationships is that the Loch Doine population is always (except in the case of a single large Meallt fish) more fecund than the other two. This is not a subtle distinction, since the Loch Doine fecundities are almost always more than double those in the other two populations. This relationship also holds when somatic weight is used as the predictor instead of fork length.

Johnson (1980) gives tables of size, fecundity and relative fecundity for 18 freshwater populations of charr. The lowest number of eggs in a female fish is given as 21 in a 101 mm charr from Ungava, Canada. The greatest fecundity is in fish from Lake Umbozero in the U.S.S.R. which average 40 cm length and 2900 ova per fish. The relative fecundity though, (eggs per 100 g of fish), makes the populations comparable. The relatively least fecund are fish from Loch Garry, Scotland with 163 eggs per 100 g (Maitland et al in press) while the most fecund are from Bodensee in the European Alps at 970 ova per 100 g. The highest relative fecundity in Britain is in Windermere spring spawners at 544 ova per 100 g. (Frost 1965). Two of the populations in the present study fall in the middle of this range (Meallt and Doine) while the value for Loch Builg is quite low.

The female charr of the present study have relatively low gonadosomatic indices (GSI). The range given in Johnson (1980) is 15.4 (Lake Imandra, U.S.S.R.) to 21.8 (Faxalven, Sweden). The charr in Loch Builg have an index of 15.9, very low, and the charr from Loch Doine have a value of 13.1, the lowest I have found recorded.

Anadromous populations tend to have gonadosomatic indices and relative fecundities similar to freshwater populations. However, because they grow to much larger sizes, their absolute fecundity is much greater. Most populations have mean lengths greater then 50 cm and mean absolute fecundities of several thousand ova (range 953-5650), (Johnson 1980; McCart 1980).

The results of my studies of the biology of charr eggs are closely related to my information on fecundity. Loch Doine fish have small eggs and Loch Builg fish have eggs which are significantly larger. This is the inverse of the relationship of fecundity in the two populations. However, I have shown that egg size is independent of body size or age in the parent fish and is also independent of clutch size. This is contrary to the findings of Elliott (1984) from both empirical data and the literature on salmonids, that both egg size and clutch size increase with female size. He stated that "the reproductive strategy of brown trout is to maximize both fecundity and egg size, but neither at the expense of the other". The charr of the present study seem to be maintaining a population specific egg size, that does not vary with female size. The inverse relation of egg size to parent size between populations can best be explained as an adaptation to the requirements of their progeny at the first feeding stage. I have shown that alevin and fry sizes are directly related to egg size (Section 6.4.3.3) and this is corroborated by the literature (Elliott 1984; Wallace and Aasjord 1984). The charr in each population are probably maintaining a threshold egg size that ensures the survival of their progeny to the first feeding stage. Presumably Loch Builg fry must be relatively large, perhaps in order to handle the prey available to them, or because larger Arctic charr alevins have disproportionately larger yolk resources and survive much longer than small alevins when starved (Elliott 1984; Wallace and Aasjord 1984). This could be of great benefit to charr in the climate of Loch Builg, where seasonal variations could alter the time of the spring plankton bloom, and thus their food supply, considerably. The Loch Doine charr may have a relaxed egg size requirement because the relative constancy of their environment would make the timing of the spring bloom more reliable.

The number of eggs per female is related to size in Loch Doine, but is independent in Loch Builg. Examination of data in Johnson (1980) and McCart (1980) shows a pattern where anadromous stocks tend to have a significant relationship of egg number to size while freshwater resident charr do not. This allows speculation that the richness of the habitat may influence the ability of the fish to form an egg mass. In Loch Builg, a severe habitat, the females seem to be forced to produce a clutch of large eggs, and use approximately all of their resources (Table 5.6) in the process. The high variation in egg numbers over a small size range may therefore be a result of the fish reaching the optimal size for reproduction, the size where the difference between energy gained (food) and energy spent (maintenence and growth) is maximal (Calow 1981, p247; this thesis p76), at a small size, with the clutch size of necessarily large eggs the only factor that can vary as a function of reproductive investment. In Loch Doine, the females invest relatively less in reproduction (Table 5.6), mature at a larger size and produce small eggs. This provides the leeway for the fish to exhibit a relationship of egg number to body size, which might exist in the Loch Builg population, if a greater range of growth or egg size were possible.

6.6 SUMMARY

1. The charr of the present study spawned in the autumn or early winter on stony substrates along exposed loch shorelines. The timing appeared to be an adaptation to have fry emergence take place during the spring plankton bloom.

2. Most female charr matured at age 4+. Males tended to be younger and smaller than females at maturity except in Loch Doine, where the opposite was true.

3. Repeat spawning females occurred in all three populations studied. Subsequent spawnings seemed to occur at one year intervals after first reproduction.

4. Three male reproductive phenotypes were discovered, two each in Loch Doine (large, bright males and small precocious males) and Loch Builg, (bright males and similar sized female imitator males).

5. Male charr from Loch Doine had relatively smaller gonads than males from the other two populations as well as Loch Doine precocious males. Gonad development was inversely related to the degree of development of secondary sexual characters.

6. Female charr had relatively similar sized gonads but Loch Doine charr were always more fecund. They had significantly smaller eggs than charr from Loch Builg.

7. Fecundity was related to body size in charr from Loch Doine and Loch Meallt but not Loch Builg. Egg size was not related to any parameter of the parent female in any of the populations.

8. Egg size strongly influenced the size of offspring at hatching and at the onset of feeding. Development time was not related to egg size.

9. The reproductive characteristics of the populations can be explained as adaptations to the respective habitats.

CHAPTER 7

DISCUSSION

7.1 DEMOGRAPHIC EFFECTS OF AGE SPECIFIC REPRODUCTION

7.1.1 INTRODUCTION: It is obvious from my examination of growth and reproduction that there are considerable differences among the life histories of the three populations of charr in the present study. The Loch Doine fish stand out at reproduction because of their larger size, older age structure and greater fecundity. The consequences of these life history variations can be compared by the use of Lotka's equation:

$$\sum lxmxe^{-rx} = 1 \qquad 7.1$$

and its derivatives.

However, because of the short term of this study, one assumption is unavoidable. It is that the intrinsic rate of increase, r, is equal to zero. Stearns (1976) has pointed out that population growth rates fluctuate around zero in nature. Therefore, this assumption is not unreasonable if the populations were undisturbed before the present study. This is probably true since people do not fish for British charr, and that lake environments are fairly stable in the medium to long term (Wetzel 1975).

The assumption that the populations are not increasing or decreasing simplifies the basic equation to

$$\sum lxmx = 1 \qquad 7.2$$

which by definition is the same as

$$Ro = 1 \qquad 7.3$$

where Ro is the net reproductive rate (Krebs 1972).

Tables 7.1 and 7.2 have been constructed so that lxmx values can be calculated with Ro set to approximate 1. These values can then be compared among the populations so that the optimal life history

Table 7.1 - Static life table and age-specific fecundity schedule giving the age-specific reproductive rate for female charr in the three lochs with the net reproductive rate (Ro) set to one.

Loch	Maturation Class	Age	l_x	m_x	V_x	F_x	G_x	J_x	R_x	$\sum R_x=1$
Meallt	Virgin	0	-	0	0	-	-	-	0	0
		1	-	0	0	-	-	-	0	0
		2	.0057	139	.7920	.6	1.0	.5	.2377	.2449
		3	.0037	174	.6438	.86	.92	.5	.2547	.2642
		4	.002863	255	.7301	.94	.83	.5	.2848	.2935
		5	.000895	266	.2381	.8	.80	.5	.0762	.0785
		6	.000358	666	.2384	1.0	.67	.5	.0799	.0823
	Repeat Spawners	3	.000178	174	.0310	1.0	.08	.5	.0012	.0012
		4	.000536	255	.1367	1.0	.17	.5	.0116	.0119
		5	.000178	281	.0050	1.0	.20	.5	.0005	.0005
		6	.000178	813	.1447	1.0	.33	.5	.0239	.0246
									=.9705	
Builg	Virgin	0	-	0	0	-	-	.5	0	0
		1	-	0	0	-	-	.5	0	0
		2	.0181a	192	3.4752	.1c	1.0	.5	.1738	.1617
		3	.0106a	207	2.1942	.37	.89	.5	.3613	.3361
		4	.0056	223	1.2488	.74	.77	.5	.3558	.3309
		5	.00108	238	.2570	.88	.67	.5	.0758	.0705
		6	.000135	219b	.0296	1.0	.25	.5	.0037	.0034
	Repeat Spawners	3	.0018a	229	.4122	1.0	.11	.5	.0088	.0082
		4	.00128	228	.2918	1.0	.23	.5	.0336	.0313
		5	.00054	231	.1247	1.0	.33	.5	.0206	.0192
		6	.00041	271	.1111	1.0	.75	.5	.0417	.0388
									=1.0751	
Doine	Virgin	0	-	0	0	-	-	-	0	0
		1	-	0	0	-	-	-	0	0
		2	.0037a	428b	1.5836	.026	1.0	.5	.0206	.0237
		3	.0023a	589	1.3547	.28	1.0	.5	.1897	.2186
		4	.00145	728	1.0556	.91	.89	.5	.4275	.4926
		5	.00048	777	.3730	.83	.58	.5	.0898	.1035
		6	.000188	816	.1534	.86	.67	.5	.0442	.0509
		7	-	-	-	-	-	-	.02c	.0230
		8	.000027	595b	.0161	1.0	.5c	.5	.0080	.0092
	Repeat Spawners	4	.000164	827	.1356	1.0	.11	.5	.0075	.0086
		5	.0002997	810	.2428	1.0	.42	.5	.0510	.0588
		6	.0000817	712	.0582	1.0	.33	.5	.0096	.0111
									=.8679	

a estimated
b actual counts of entire age class
c guess

Table 7.2 - Static life table and maturation schedule giving the age specific reproductive rate for male charr in the three lochs with the net reproductive rate (Ro) set to one.

Loch	Age	l_x	m_x	F_x	J_x	R_x x100	$\sum R_x = 1$
Meallt	0	-	0	0	.5	0	0
	1	.0065 a	1	.85	.5	.2698	.8765
	2	.00376	1	.85	.5	.0160	.0520
	3	.00251	1	1.0	.5	.0126	.0409
	4	.00161	1	1.0	.5	.0085	.0276
	5	.00018	1	1.0	.5	.0009	.0029
						=.3078	
Builg	0	-	0	0	.5	0	0
	1	-	0	0	.5	0	0
	2	.0055 a	1	.09	.5	.0248	.0644
	3	.0037 a	1	.87	.5	.1610	.4183
	4	.00283	1	.93	.5	.1316	.3419
	5	.00101	1	.93	.5	.0470	.1221
	6	.00034	1	1.0	.5	.0170	.0442
	7	.00007	1	1.0	.5	.0035	.0091
						=.3849	
Doine	0	-	0	0	.5	0	0
	1	-	0	0	.5	0	0
	2	.0037 a	1	.15	.5	.0278	.1845
	3	.0026 a	1	.19	.5	.0247	.1639
	4	.00188	1	.59	.5	.0555	.3683
	5	.00072	1	.85	.5	.0306	.2031
	6	.00022	1	.88	.5	.0097	.0644
	7	.00005	1	1.0	.5	.0025	.0166
						=.1507	

a estimated

strategies can be predicted. These can be compared or contrasted with the strategies observed in the present study.

7.1.2 DEFINITIONS: Starting at the left hand column, the various parameters of the tables were calculated as follows:

Maturation Class: whether the fish is breeding for the first or a subsequent time (females only).

Age: the age of this fish at its previous birthday. As the data are based on fish captured in late summer and fall, they will have just about completed "Age + 1" growing seasons.

lx: the probablility of surviving to Age x. This was calculated by multiplying the age specific fecundity (including estimates) by the number of maturing females (including estimates) in that age class for both maturation classes (Table 7.3). Summed, this gives an estimate of total egg deposition by the sample population. Survivorship is the subsample of each sex at age x, divided by the total number of eggs. Assuming that r=o, this gives survivorship for a population that is exactly replacing itself at each generation. Due to the normal shape of the catch curve, lx values for ages to the left of the mode were estimated by extrapolation from the regression of arcsin transformed values of lx on modal and older ages for the particular maturation class.

Mx: the number of eggs produced by a female at that age (Table 7.3). These data were calculated from the regression of logarithmically transformed length specific fecundity given in section 6.3.2.3, for the mean length of the total maturing population at that age. Since males produce an excess of gametes, mx was arbitrarily set to 100, as no measure of fertilization success was available.

Vx: by definition, Vx = lxmx (Krebs,1972).

Fx: the probability that a fish will become sexually mature at that age. Calculated by dividing the number of matures by the total number of fish at that age. This accounts for the complex age structure of the breeding population.

Gx: the probability of a fish being in its maturation class. Calculated by dividing the number of females in the maturation class by the total number of females in the age class. This accounts for the

Table 7.3 - Regression predicted age specific fecundities used in the demographic analyses in the three lochs; Mean fork lengths for all maturing females in each loch; ova for these mean fork lengths; n = number of of maturing females in each sample

	Meallt			Builg			Doine		
Age	$\overline{FL}$	Ova	n	$\overline{FL}$	Ova	n	$\overline{FL}$	Ova	n
2	167	139	6	186[t]	192	6[z]	182	428	1
3	180	174	12	198	207	16	212	589	9
4	205	255	15	211	223	61	239	728	49
5	208	266	4	223	238	14	248	777	15
6	284	666	2	242	219*	2	255	816	6
7	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	298	595*	1
3	180	174	1	202	229*	2			
4	205	255	3	215	228	18	257	827	6
5	212	281	1	217	231	7	254	810	11
6	304	813	1	249	271	6	236	712	3
Egg Deposition:		11176			29642			74555	
x % female:		5588			14821			37278	

* actual data substituted for regression prediction, due to absolute counts on entire age sample

t extrapolated from older age classes

z estimated from repeat spawing survivorship age 3 to 4.

separation of repeat spawning females from those breeding for the first time. For males, Gx was assumed to be 1 as data could not be collected on frequency of spawning.

Jx: the probability of offspring being either sex. Arbitrarily set at 0.5. This accounts for each table being a demography of a single sex.

Rx: defined for this study as the product of Vx times the modifiers Fx, Gx and Jx.

Ro: the net reproductive rate; the sum of Rx.

7.1.3 RESULTS: Figure 7.1 is a plot of the Rx values from Table 7.1 and 7.2 against age for each population of females, repeat spawning females and males. Because Ro is set to one, these curves illustrate the relative importance of the age at maturation and the interaction of survivorship with age-specific fecundity. Each point therefore indicates the probable reproductive impact of a fish if it spawns at that age. This reflects a trade-off of the two components, age-specific fecundity and survivorship.

FEMALES: In Loch Builg, and for most fish in Loch Meallt, I have demonstrated that age has very little effect on clutch size (section 6.3.2.2), so that Rx is strongly directed by survivorship. Therefore, if a female can produce about the same number of ova at an early age, she should spawn at this age rather than risk dying before the next spawning season. The values of Rx for these two lochs (figure 7.1) rise at a relatively early age and so appear to support this hypothesis.

In the Loch Doine population, I have shown that clutch size is strongly size dependent (section 6.3.2.3). The size of individual fish from this loch increases dramatically after age 4 is achieved (Figures 4.4 and 4.8). This means that age-specific fecundity has a much greater impact on the values of Rx. Thus, it is very much in the fishes interest to survive as long as possible in order to grow large and fecund. The values of Rx (Figure 7.1) show relatively little reproduction at early ages but a massive effort at age 4+, the first spawning season after the growth spurt. Thus, the hypothesis and the data are in agreement.

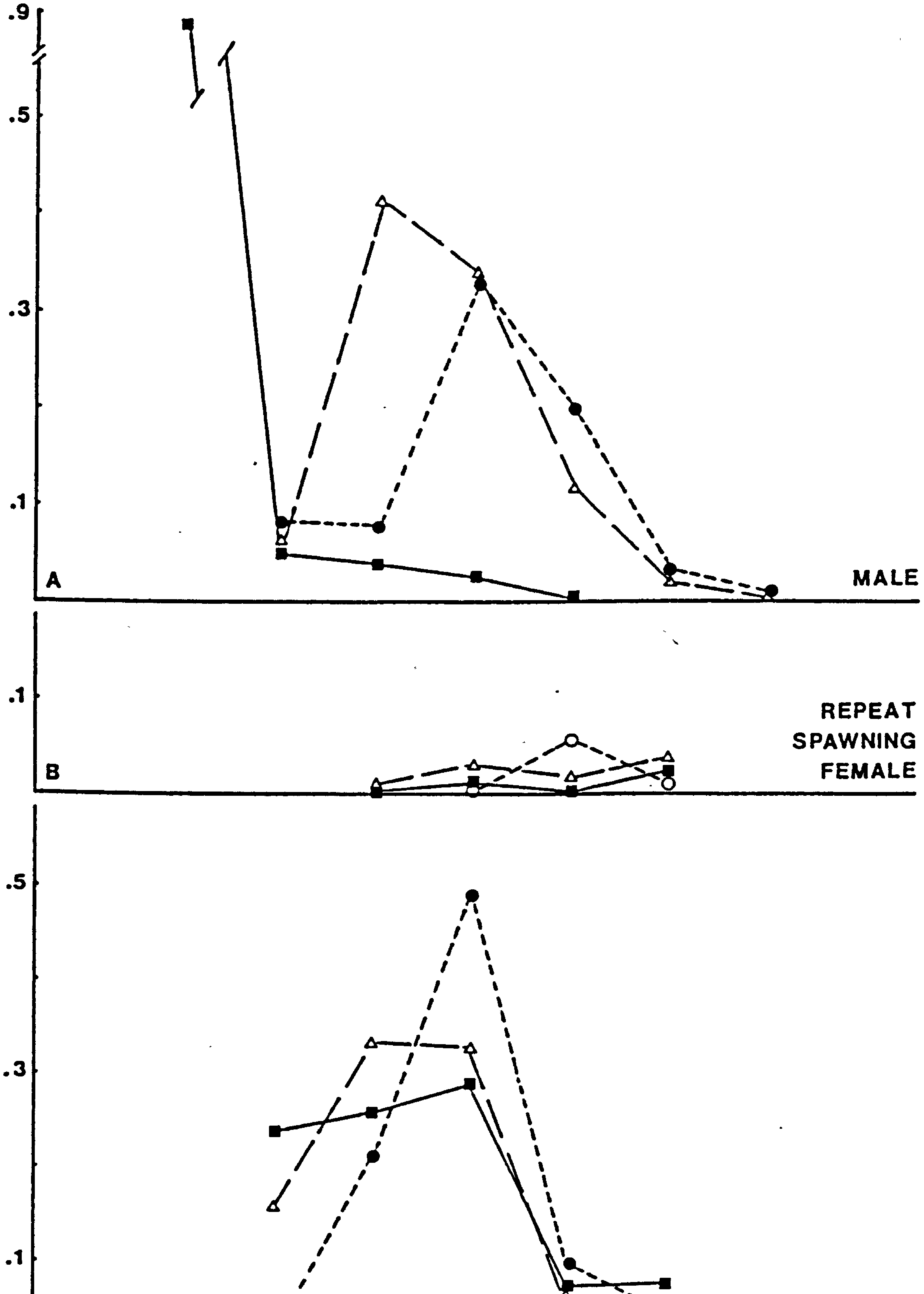


Figure 7.1 - Age specific reproduction by the charr populations of the present study.

■ Meallt
△ Builg
● or ○ Doine

FEMALE REPEAT SPAWNERS: All three populations of charr are iteroparous in that previously spawned sexually mature females were captured in the spawning populations. These fish appear one year after the age at first maturity and disappear after age 6+ (Figure 7.1b). Thus, most repeat spawners are aged 4+ in Lochs Meallt and Builg and 5+ in Loch Doine. The total contribution to reproduction by these fish is less than 10% in all the populations.

MALES: As males produce an excess of gametes, and I have no measure of fertilization success by male charr, the data for Rx in Table 7.2 and the curves of Figure 7.1 are functions of survivorship modified by the ages at reproduction. The curves are strikingly different among the three populations. Loch Meallt males reproduce at a very young age and the largest contribution (85%) is at age 1+. Older ages contribute little and are extinct by age 6. In Lochs Builg and Doine, longevity is greater (7+) but Loch Builg males achieve peak reproduction at age 3+. A component of Loch Doine males reproduces at ages 2+ and 3+ but the peak is at age 4+, with a strong component reproducing at age 5+. In short, Loch Meallt males have shortened their life history as much as possible while most Loch Doine males delay reproduction. Males from Loch Builg are intermediate.

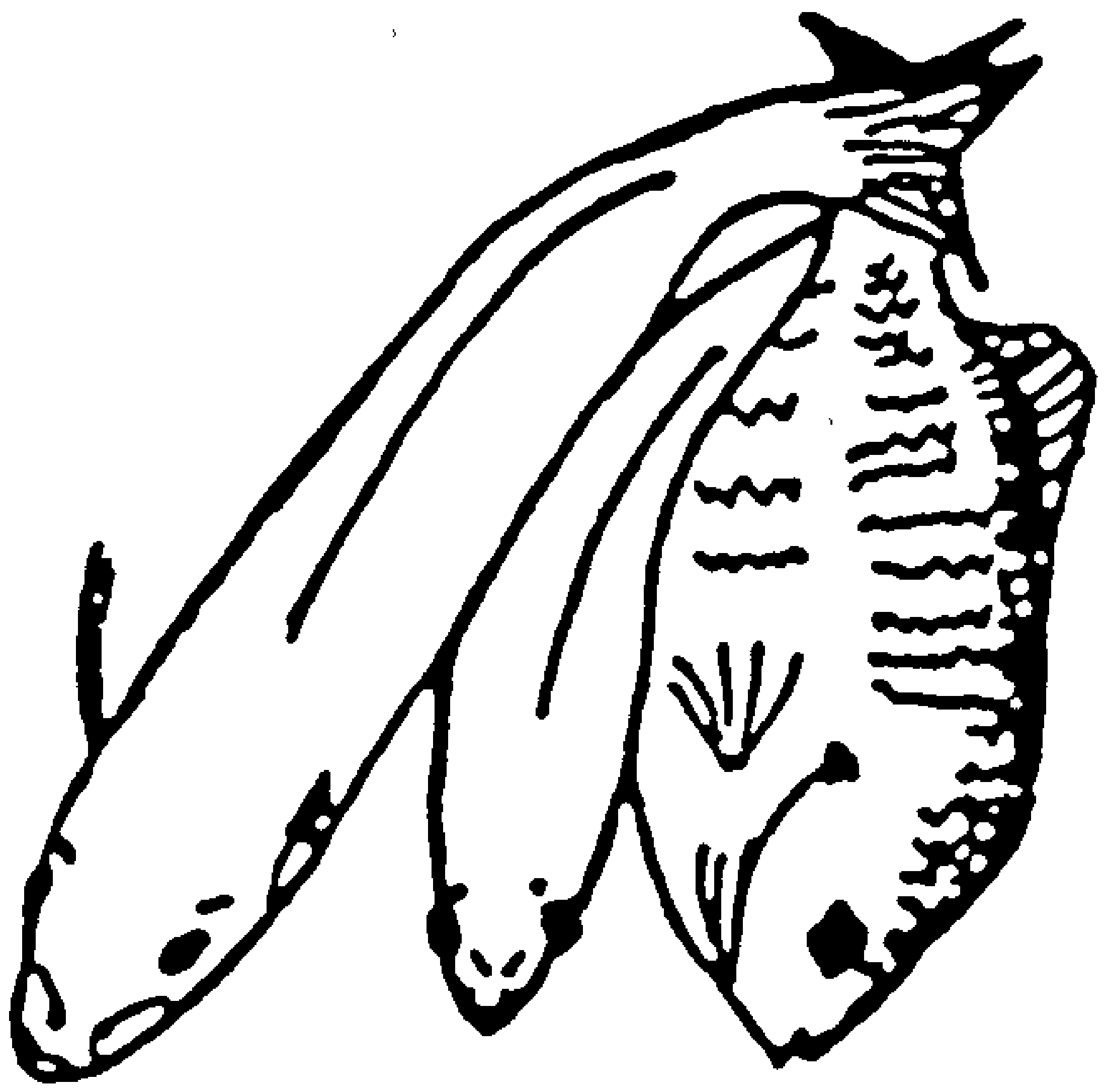
7.1.4 DISCUSSION: The demographic data and curves show considerable variation in the life histories of the three populations of charr. There is a reduction in age at maturity in Loch Meallt and to a lesser degree in Loch Builg, whereas reproduction is delayed in Loch Doine.

An interesting aspect of these curves is that most have a long tail on one side or other of the modal age of net reproduction. I believe that the maintenance in the populations of iteroparity and variation in age at first reproduction is evidence that they are operating alternate evolutionarily stable strategies (ESS's) (Charlesworth 1980; Dominey 1980; Gross and Charnov 1980; Maynard-Smith 1982). An ESS develops when a new genotype penetrates an existing gene pool, but cannot completely out-compete the original genotype. However, the original genotype cannot eliminate the new one either. In the case of the charr, other salmonids, and sunfish (Centrarchidae) (Gross 1984; Gross and Charnov 1980), it may pay to reproduce at a very young age if there is a good chance of not surviving to mate at an older age. Therefore, precocious male and also young reproducing female phenotypes become more numerous in the population. However, there is evidence (Jones 1959; Johnson 1980; McCart 1980) that these small, young males cannot court a female and induce her to spawn, presumably because the phenotype of old, bright males is behaviourally necessary to induce reproduction. The bright males, because they are dominant and territorial, fertilize a proportion of the eggs and the precocious phenotypes gain fertilizations by sneaking alongside the female at the moment of egg extrusion (Figure 7.2).

Sneaking does not seem to be a very reliable way of obtaining fertilizations. Relatively few may be needed as precocious males need only to survive half the time to sexual maturity as bright males. In certain situations, competition for mates may favour the adoption of alternative tactics. Game theory predicts that the tactics adopted by an organism depend not only on environmental constraints but also on what other members of the population are doing. The adoption of alternative tactics may reduce the individuals fitness, but it is better than not mating at all (zero fitness) and does increase (maximise) the fitness of the population as a unit (Gross 1984).

This does not explain why an ESS of early versus late maturation has not arisen in female charr. I expect the answer to this is quite simply that in Loch Meallt and Loch Builg, they do not have the resources necessary to reproduce any earlier than they do. Also, optimization theory predicts that an organism should reproduce at the level of investment which maximises the net rate of fitness return as determined by a cost-benefit function (Calow 1981; Gross 1984). The size, and therefore, age at maturity of the population should be normally distributed around this theoretical level (Gross 1984). The female charr of the present study seem to follow the predictions of optimization theory. They should have no need of alternate breeding tactics since they are the objects of competition among male charr and would always have a 100% expectation of mating.

In Loch Meallt, the males reproduce when very small and so do a large proportion of females. The small population of larger, older males in Loch Meallt is matched by a group of 5 and 6 year old females (Figure 7.1). These fish may be the component of the population that becomes piscivorous and grows to an unusually large



Bluegill sunfish

Figure 7.2 - Line drawing of nesting male (left), female (right, depositing eggs), and female mimic (between) simultaneously spawning (from Dominey 1980).

size. This loch may have a population of small spawners of both sexes and another of larger spawners of both sexes. I have no information from which I can interpret the mating strategies in this loch.

In Loch Builg the distribution of age specific reproduction is similar in both sexes. Females in this lake seem to reproduce as soon as they are able. However,. the male population consists of two similar sized phenotypes, bright males and cryptic males (see Section 2.1.3.1 and Table 6.4). These, I feel, are an ESS. The cryptic males resemble females and so do not provoke attacks from the territorial bright males. When the bright male mates, the cryptic male(s) can secure fertilizations of eggs induced by the courtship of the bright male.

In Loch Doine, the females tend to be large and somewhat colourful (Section 2.1.3.2). Their size has been demonstrated to allow a great increase in clutch size. Some young females reproduce, but they may have to be discounted since a 2+ female spawned in the laboratory produced a clutch of very small eggs that produced non-viable fry. The males in this loch delay reproduction until they are quite old and large, except for a population of precocious males. These, I think, are another ESS, where the precocious males can hide easily because of their small size (Gross 1984), and gain fertilizations by darting into the redd (nest) at the last minute.

Female mating strategy should be quite different to males, as each egg has has a better chance than a sperm of becoming a fish. She must grow large enough to produce a viable clutch of eggs, and this necessarily reduces her flexibility in the timing of the onset of maturity. Figure 7.1 shows that age at maturity can be altered, but not as much as in males. The reproductive impact of this can be quantified by calculating the mean age at first maturity using the equation (Dunham 1982):

$$\text{mean age} = \frac{xlxmx}{lxmx} \qquad 7.4$$

The mean age provides a reference point so one can examine the effect earlier or later reproduction has on the fitness of a female. The mean ages of the charr in each loch are given in Table 7.4.

Table 7.4 - The mean ages at first maturity for each sex of the charr in the three lochs.

	Male	Female
Meallt	2.07	3.54
Builg	3.69	3.51
Doine	4.87	4.13

The mean ages at first reproduction in Lochs Meallt and Builg are similar but that of Loch Doine greater. A simple model by Lewontin (1965, described in Stearns 1976) shows that a reduction of age at maturity can have a profound effect on the lifetime egg potential of an individual and on the rate of increase of a genotype. A similar model by Weatherley (1972) has been adapted to the data from the present study. This model assumes survivorship of 20% in the first year and 50% in subsequent years. Of an initial cohort of 10,000 individuals, 875 would be alive at age 3 and 375 would be alive at age 4. Fecundity values were taken from Table 7.1. The mean age at first reproduction was rounded down so that it was age 3 for Loch Builg fish and age 4 for Loch Doine fish. The number of fish surviving to breed in each population was then calculated for two generations to see if the earlier age at maturity in Loch Builg fish could account for the reduction in clutch size. In addition, the model was run with the mean ages at first reproduction reversed, i.e. assuming first reproduction at age 4 in Loch Builg and age 3 in Loch Doine. The results are plotted in Figure 7.3. These plots are of the logarithm to the base ten of the number of fish surviving to breed (Nx) on the parental generation (Px) they represent. The natural logarithm of Nx was regressed on Px to calculate the slope of the line, which is the equivalent of r in Lotka's equation. For the purposes of this exercise, r is defined as the density independent maximum rate of increase (r_{max}).

The plots show that the two populations that simulate the oberved ages at first reproduction, Loch Doine age 4 and Loch Builg age 3 have similar numbers of progeny in subsequent generations while Builg age 4 does relatively badly and Loch Doine age 3 is very successful. Obviously, when the age at maturity is similar the greater fecundity of Loch Doine fish allows them to produce many more progeny. However, the reduction of the age at

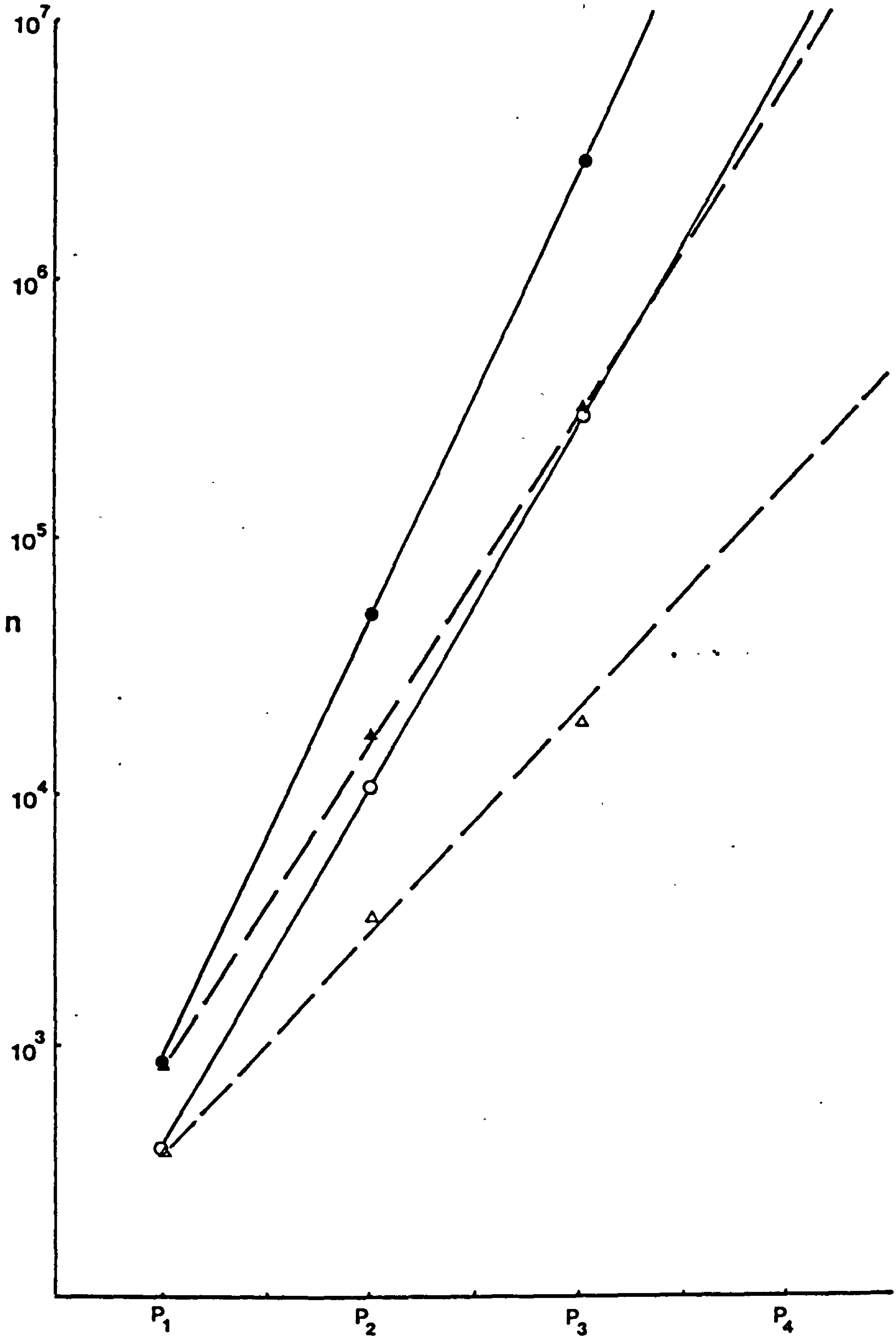


Figure 7.3 - Results from the model showing the effect of reduction of age at maturity on population increase.

△ Builg 4 ○ Doine 4

▲ Builg 3 ● Doine 3

Table 7.5 - Values for r_{max}, the maximum rate of increase, calculated for simulated populations of charr from Loch Builg and Loch Doine

Loch	Assigned Age at 1st maturity	r_{max}
Doine	3	4.05
Doine	4	3.33
Builg	3	2.94
Builg	4	2.55

maturity by Loch Builg (age 3) fish gives them a much greater number of progeny, and early on (the first 3 generations) actually more than Loch Doine. However, Loch Doine fish have a greater rate of increase (Table 7.5) and so eventually out-perform the Loch Builg populations.

The most interesting feature of this exercise is the effect age at first maturity has on r_{max}. By reducing the age by a year, the model increases r_{max} in both lochs substantially. Thus, in nature, the Loch Builg fish are doing the correct thing by reducing their age at first maturity. However, the improved r_{max} is still not as good as the value for the more fecund Loch Doine population. At first sight the model should also predict that Loch Doine fish should reduce their age at first maturity. In fact, they do not and I propose that this is a function of body size. Table 7.1 shows only 28% of the age 3 charr in Loch Doine mature. Examination of Figure 4.6 shows a great size difference between mature and immature charr in this age group. In Chapter 6 I hypothesized that egg size may be held at the minimum for alevin survival in charr because I found no relationship of egg size to any female parameter but a great difference between populations. However I did note a very small fish from Loch Doine that produced a clutch of very small ova that produced unviable fry (they starved to death (pinhead disease) before the onset of exogenous feeding). I speculate that more age 3+ females in Loch Doine do not mature because they are small and may be unable to produce viable offspring. In order to produce ova of the required minimum size they would have to reduce their clutch size, thus reducing the advantage they hold in r_{max} over the four year old spawners.

7.2 LIFE HISTORY STRATEGY IN CHARR: There has been a tremendous increase in interest in life history strategy by biologists and a vastly increased output of theories and evidence in the last fifteen years (Stearns 1976 1980). The theory that most students of the subject embraced was that of r/K selection (MacArthur and Wilson 1967) and it has stimulated many useful studies. Recent work has shown it to be unable to explain or predict all observations from nature (Stearns 1980; Sibly and Calow in press). Other processes that are independent of density or carrying capacity of the environment operate to influence the life histories of organisms (Stearns 1980).

It may now be possible to make several generalizations about current thought on life histories.

1. The habitat dictates the strategy of an organism (Southwood 1977; Dunham 1982; Sibly and Calow in press)
2. Physiological constraints may override or moderate predicted strategies (Stearns 1980).
3. Changes in relative mortality between adults and juveniles can reverse predicted life history patterns (Stearns 1976 1984; Sibly and Calow, in press).

Stearns (1976) provided a useful summary table of tactics that could be adopted by organisms evolving in fluctuating environments. His Type II environment, cyclic with a fixed period which is shorter than the lifespan of the organism, describes the environment of the charr; an environment that has a north temperate annual cycle with predictable seasonal changes. The theory predicts synchronization of the breeding time to an optimum point in the cycle, synchronization of the release of young to swamp predators, and the separation of somatic and reproductive effort in time (Janzen, 1971 in Stearns 1976).

These predictions are confirmed for the most part by the observations of the present study. The time of breeding is synchronized within a population, and I have calculated (Chapter 6) that the emergence of the young should also be synchronized. The idea of predator swamping is attractive, since it provides one explanation for the minimizing of egg size and the production of a larger clutch in the Loch Doine charr. Loch Builg charr seem to have a much larger egg size imposed on them by environmental variation (see Chapter 6). Finally, somatic growth precedes and is practically curtailed by sexual maturity in the charr.

The life histories of charr populations in Britain are probably modifications of the "normal" habit exhibited by populations that live in the central part of the species' range. This central area is more northerly than Britain, circumpolar, and usually between 60° and 80° N latitude. The charr reaches its fullest expression by dominating fresh water lakes and adapting to river habitats as well as adopting the anadromous habit. These fish, termed hypermorphic (Balon 1980), are characterized by greater (than British charr) longevity, larger size, size dependent fecundity (but variable egg size), iteroparity, and strong sexual dimorphism which develops with older age (summarized from Johnson 1980; McCart 1980). This is probably a good description of the charr that colonized British freshwaters after the last glaciation (c. 10,000 years B.P.) There is no way of knowing how many invasions by different stocks of charr took place, so the variation in the populations of charr in the present study, and the many loch-specific species described by Regan (1911), could have been inherited from their founding populations. However, this only begs the question of how the founder populations derived their life histories.

I propose that the charr from Lochs Doine and Builg, as well as Loch Earn, Windermere and other large loch populations were founded by populations similar to those described in the preceding paragraph. This is probably also the case for Loch Meallt charr, since there are good functional reasons which may have caused rapid selection for their juvenile form (see Chapter 2).

Given that Britain was colonized by the hypermorphic form of charr, the present day populations would have had to evolve from that form as the post-glacial climate of Britain moderated. Today's populations must be considered relicts as they are confined to cool lakes on the southern fringe of the charr's range. They should be descendants of lake resident populations that had arisen from and then co-existed with the founding anadromous stocks, as is still seen in the central areas of the charr's range.

The hypermorphic form of charr must represent the species "norm" with juvenilized or alternate forms derived from it. This statement is based on the evidence of the entire family Salmonidae, where hypermorphic forms comprise most, and in some species of *Onchorynchus* all, of the breeding stock in a species. Juvenilization and shortening of the life history are, I feel, characteristics secondarily evolved as responses to the environment.

The charr of Loch Doine, and probably other populations from the deeper fjord-like lochs of England and Scotland, resemble most closely the hypermorphic form. These lochs are cool, stable environments with predictable zooplankton blooms. The charr are sexually dimorphic (Chapter 2), have an older age at first reproduction and a large clutch size (Chapter 6) and may deliberately invest in iteroparity (Chapter 5). The egg size is small in Loch Doine and may be an adaptation to permit a large clutch size for swamping predators. Because the plankton bloom is predictable the fry can carry minimal reserves from the egg to last until the onset of first feeding. The adults can hedge their bets against a total failure of fry survival (Stearns 1976) by their investment in iteroparity.

I believe the charr of Lochs Builg and Meallt and probably many other hill lochs have evolved away from the hypermorphic life history as a response to their environments.

The environment in Loch Builg is colder (Chapter 1) and the fish are nutrient limited (Chapter 5), partially sexually dimorphic (Chapter 2), have a high reproductive effort (Chapter 5), reproduce when younger and smaller, but have very large ova (Chapter 6). The last point is what I think has initiated their evolution. It seems that the large ova are required to ensure the survival of fry until their first food becomes available (Chapter 6). Because the adults are nutrient limited, it is not worthwhile to grow past a certain size (Chapter 5). Thus, the clutch size has become more or less fixed (Chapter 6) and at the same time must be traded off to increase egg size. Therefore, clutch size decreases. However, the loss of clutch size can be compensated by earlier maturation (Section 7.1.4). This now precedes or interrupts the development of sexual dimorphism, so that the energy that was invested in dimorphism goes instead to the gonads, increasing reproductive effort (Chapter 5). The adults appear not to invest in iteroparity (Chapter 5) but survival may vary with the severity of the over wintering period.

Similar logic can be applied to the evolution of the charr in Loch Meallt. The habitat there is more productive (meso-eutrophic). The charr feed on benthos and may rapidly reach a threshold size where growth is no longer worthwhile (Calow 1980)(Chapter 5). The law of diminishing return may act quite quickly on this population as a large proportion of the gut contents consisted of detritus from Trichoptera cases and Gastropod shells (Chapter 3). This problem may be side-stepped by those fish that become piscivorous. As hypothesized for Loch Builg charr, the onset of reproduction would interrupt the morphological development of the fish and initiate the divergence of the population from a hypermorphic form. The direction of this evolution could have been maintained by selection for fish with characteristics more suited to "lurk and lunge" predation (Chapter 2) as their prey are cryptic and slow moving. These characteristics are, perhaps coincidentally, both juvenile and adaptive.

In conclusion, it appears that the charr is an animal that, by virtue of a sometimes spectacular phenotypic, and perhaps genotypic, plasticity, can evolve a suite of life history tactics to suit most any cool, oligotrophic aquatic habitat. This species' strategy for survival appears to be variation in all life history parameters and precise adaptation to individual habitats.

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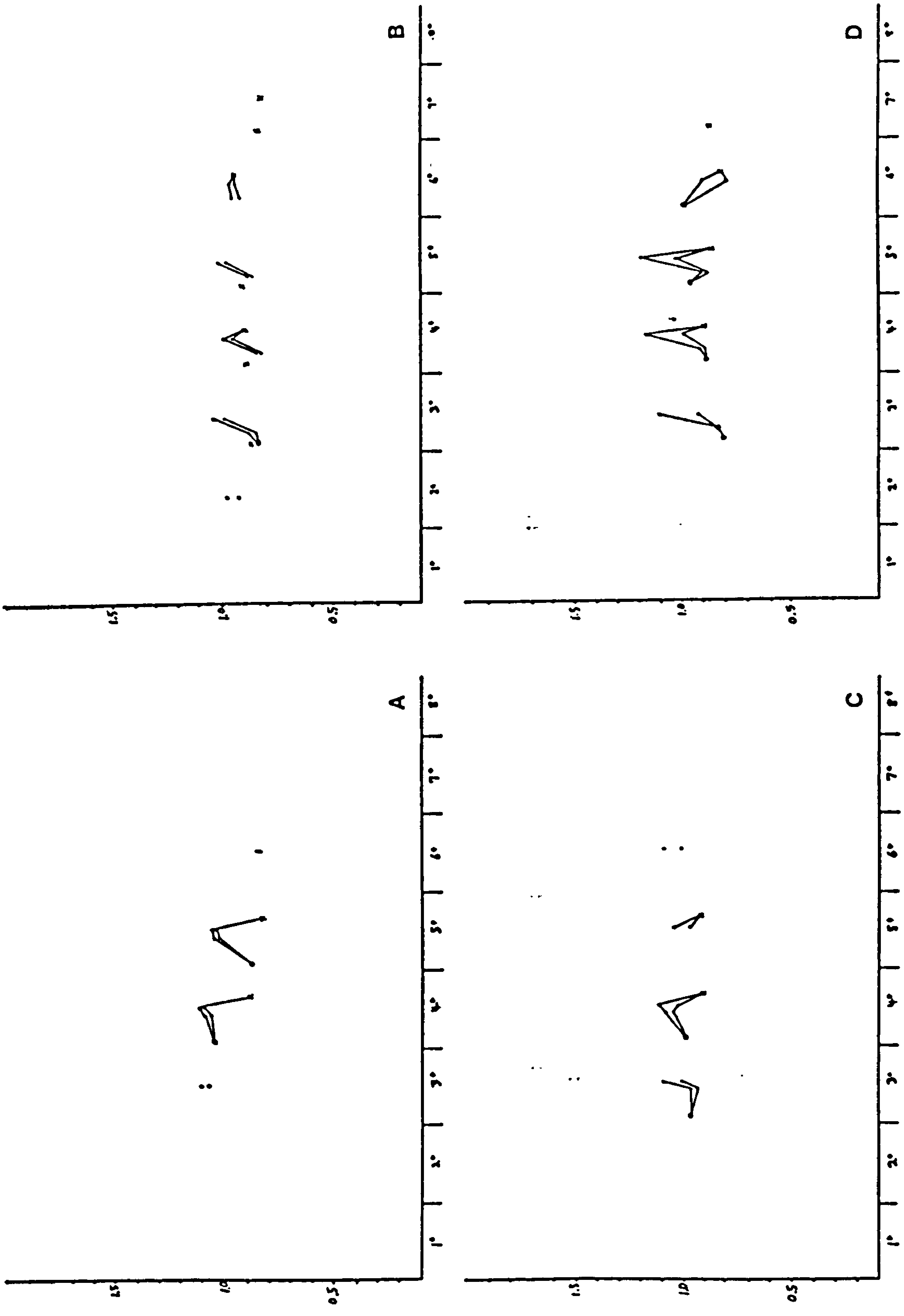

Figure 5.3 - Condition (Kn) of soma (lower curve in each panel) and soma plus gonad (upper curve) of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

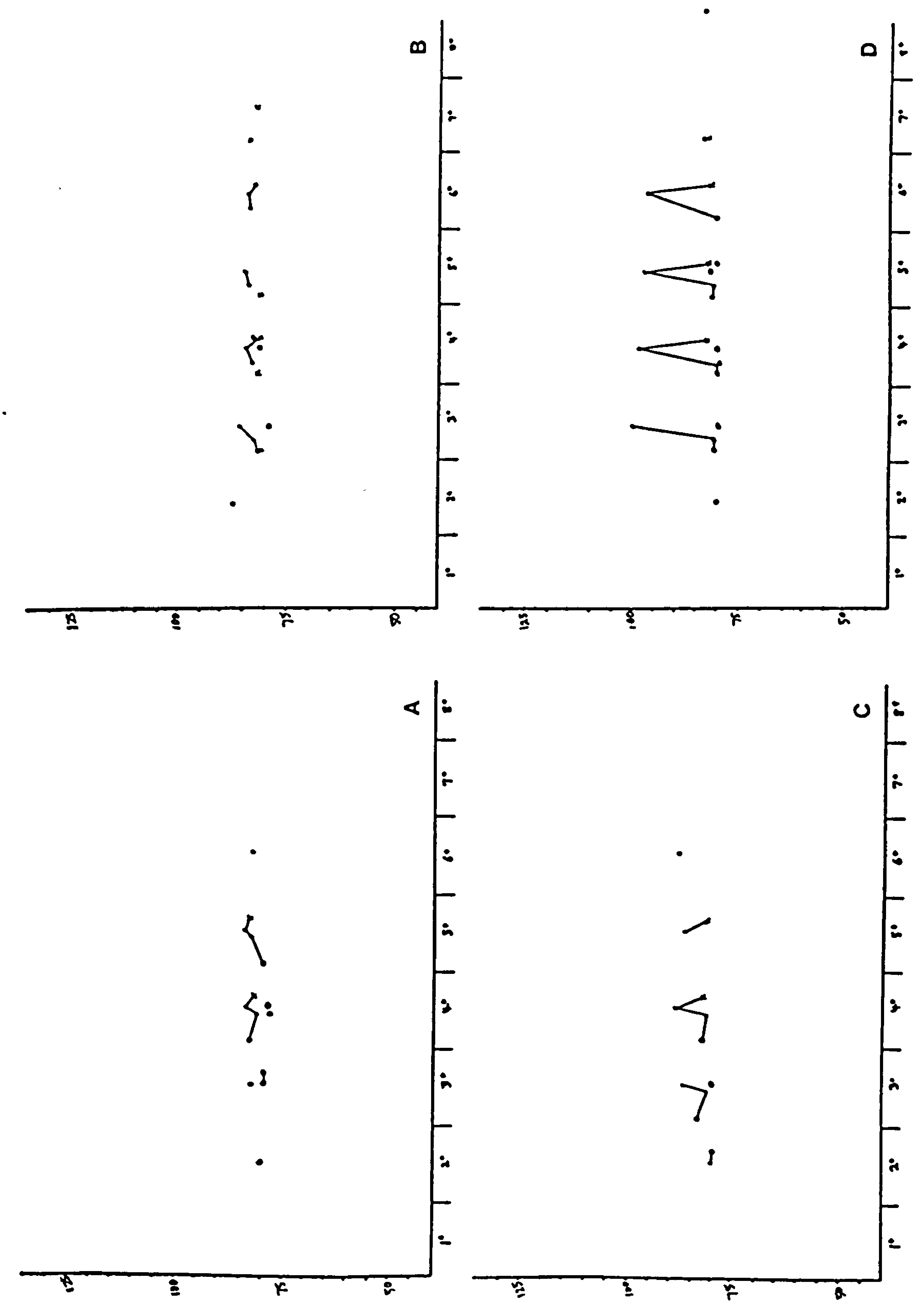

Figure 5.4 - Water content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

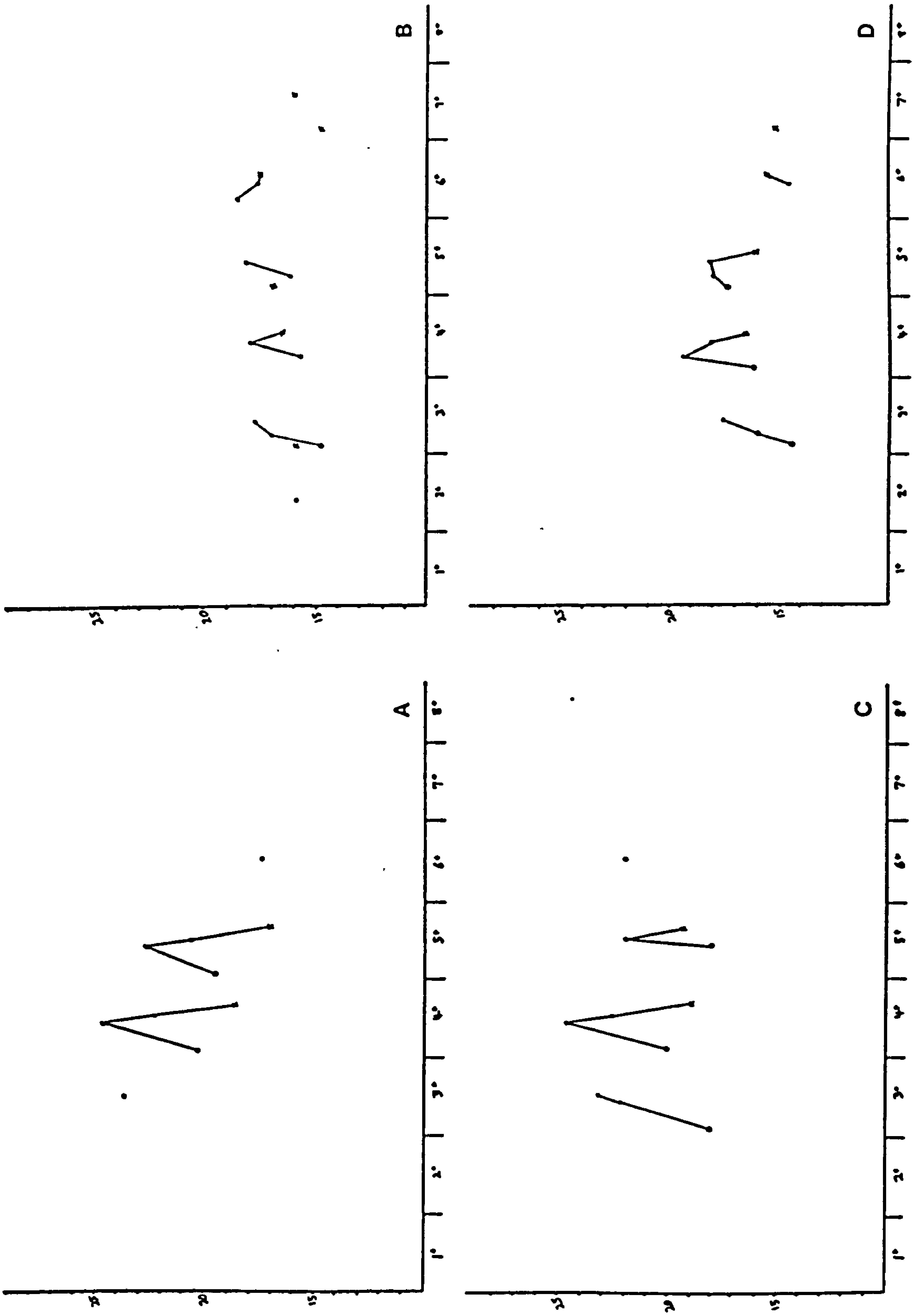

Figure 5.5 - Lean content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

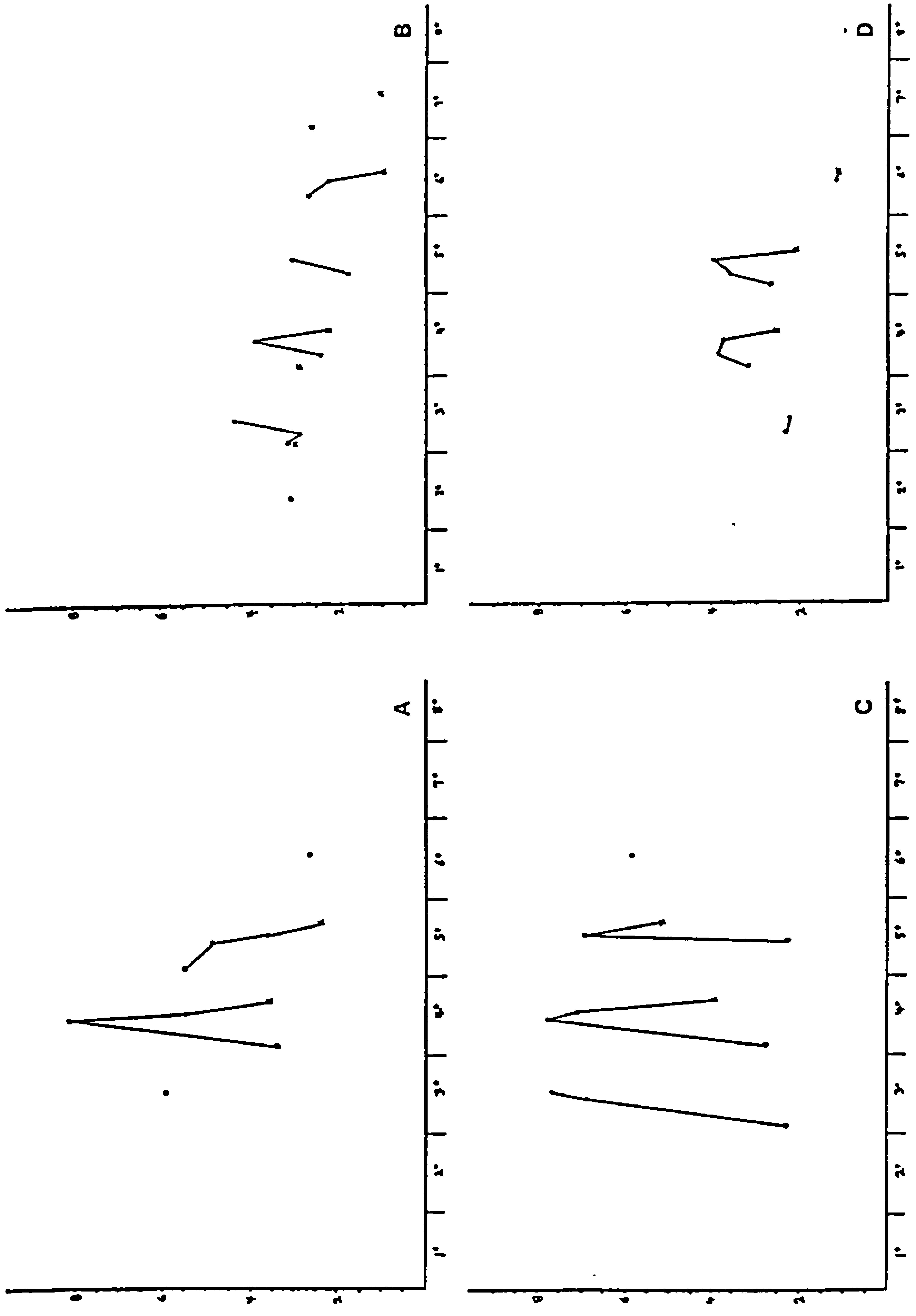

Figure 5.6 - Lipid content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).

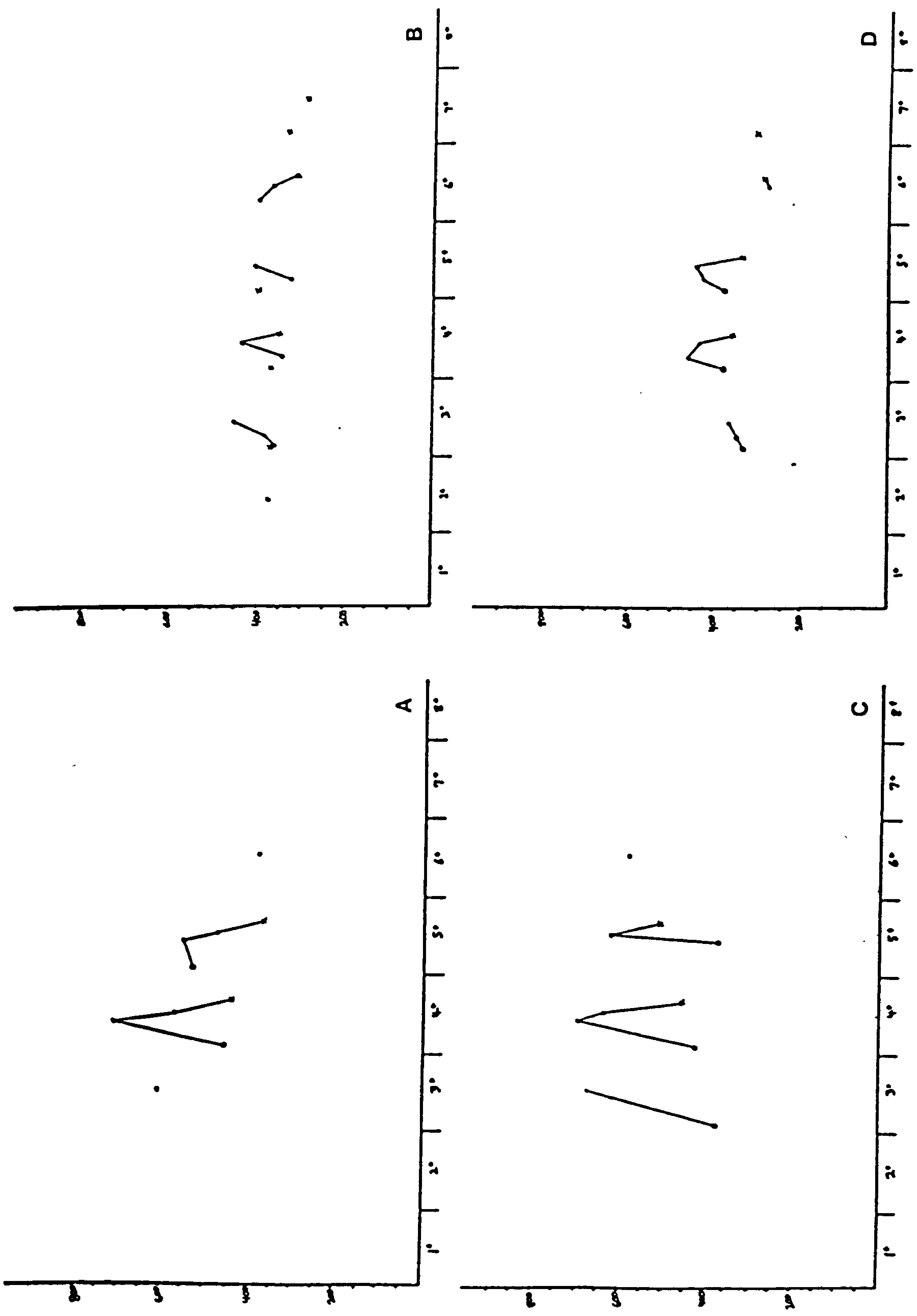

Figure 5.7 - Energy content of soma of male (upper row) and female (lower row) charr from Loch Doine (left hand column) and Loch Builg (right hand column).