GROWTH PROCESSES IN THE TWO SCOTTISH POPULATIONS OF POWAN, COREGONUS LAVARETUS (L.) (EUTELEOSTEI, SALMONIDAE) VOLUME I

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GROWTH PROCESSES IN THE TWO SCOTTISH POPULATIONS OF POWAN, *COREGONUS LAVARETUS* (L.) (EUTELEOSTEI, SALMONIDAE)

by

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A thesis submitted for the degree of Doctor of Philosophy
June 1989

CERTIFICATE

I certify that Elizabeth Allison Rachel Brown has spent nine terms engaged in research work under my supervision and that she has fulfilled the conditions of General Ordinance No. 12 (Resolution of the University Court No. 1, 1967), and that she is qualified to submit the accompanying thesis for the degree of Doctor of Philosophy.

[redacted]

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Department of Biology and Preclinical Medicine

DECLARATION

I, Elizabeth A. R. Brown hereby certify that this thesis has been composed by myself, that it is a record of my own work and that no part of it has been submitted for any other degree or professional qualification.

[redacted]

Elizabeth A. R. Brown

Thesis copyright declaration

Signature [redacted] Date 22nd August 1989.

I dedicate this thesis to the memory of my father

Allan Melville Brown

(1.5.30 - 3.1.89)

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ABSTRACT

The powan, Coregonus lavaretus (L.) is endemic to only two British waters, Loch Lomond and Loch Eck, Scotland. This thesis describes the seasonal and longer term growth processes of the two populations, concentrating on growth in length back-calculated from scales, factors affecting recruitment and mortality, reproductive cycles, and seasonal deposition and mobilisation of storage products, particularly lipid. The interrelationships of these cycles is discussed. The populations differ in their diet and duration of feeding, and it is shown that most of the inter-population differences in seasonal cycles of growth relate to these feeding differences. The Loch Eck population is the more variable. In addition to adult and immature powan, a third category is identified, termed adolescents. These are fish which are entering their first reproductive cycle. Immature and adolescent fish are analysed separately and compared with the adults. There are some differences in seasonal cycles between the juveniles and adults, mainly in relation to the presence or absence of the reproductive cycle. A preliminary histological study of the ovaries of adolescent females is carried out. Comparison of historical data with the results of the present study shows that there has been little change in the Loch Lomond powan in the past 200 years. Both lochs are coming under increasing human pressure, and conservational measures urgently need to be taken if the powan populations are to survive.

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VOLUME 2

CHAPTER 1 TELEOST GROWTH, POWAN, AND THE POWAN LOCHS

1.1 INTRODUCTION.

(a) Growth

'Growth' is an oversimplification in that it actually involves a complex of distinct, yet interrelated, processes. These processes are sometimes categorised as:

(i) somatic growth

(ii) reproductive growth

(iii) deposition and mobilisation of storage products

(Shul'man, 1974; Weatherley & Gill, 1987).

In practice, the categories are not as rigidly separable as this scheme implies; for example, although protein is essentially structural, and is therefore a component of somatic growth in teleosts, it is also drawn on as a storage product. All the growth processes are seasonal, reproductive and storage growth being characterised by cycles of accumulation and expenditure, which are often annual. The timing of the seasonal processes may be dependent on environmental cues (as in reproduction, Ch. 3.1), or by physiological triggers including feedback (as, perhaps lipid metabolism, Ch. 3.3).

In this thesis, somatic growth (Ch. 2) is defined as growth which is progressive throughout the life of a fish, although it varies seasonally in its rate, periods of rapid growth alternating with periods of slow or no growth. In teleosts somatic growth refers mainly to the long term build up of skeleton and muscle and can be measured by changes in length or weight. Length is used here as the main criterion of somatic growth because body weight is contributed to by both structural and mobilisable protein and by lipids, and the use of 'condition factors' (Le Cren, 1951; Bolger & Connolly, 1989) does not distinguish between these. Also, by the method of back-calculation from calcified tissues (Ch. 2.1), it is possible to assess the growth of fish in years other than those in which the samples were taken (Iles, 1974).

Reproductive growth (Ch. 3.1) is here defined as including gametogenesis, the development of secondary sexual characteristics, and behaviour associated with reproduction. Reproduction accounts for a very high proportion of the resources available for growth. Ovaries may account for up to 40% of the total weight in some species, and testes, though often less in bulk, may be metabolically more expensive to produce (Ursin, 1979).

Storage (Ch. 3.2, 3.3) in teleosts is mainly in the form of lipids, which may be present in very high concentrations (Shul'man, 1974). Dried specimens of candle-smelt, *Thaleichthys pacificus* (Richardson), were used as torches by Southern Alaskan Nishka Indians (Swan, 1880 cited by Miller, 1979). Protein may also be drawn upon, sometimes to a lethal extent as in Pacific salmon (Idler & Bitners, 1959; Love, 1980), but carbohydrates do not contribute significantly to storage (Elliott, 1976a; Craig, 1977). The pattern of storage and mobilisation depends on the extent to which the availability of food and metabolic requirements coincide, and varies from species to species (Shul'man, 1974) and even from population to population (Chs. 3, 5).

These growth processes depend ultimately on the food resources available, and how these resources are partitioned amongst them. Feeding, studied by Pomeroy (1987), will be discussed in this thesis as the primary factor controlling growth processes.

There have been many studies of feeding, resource partitioning, and growth in teleosts (reviewed by Weatherley & Gill, 1987), but the value of many of these studies has been limited by a variety of factors. In some cases the fish have been studied under laboratory conditions with imposed feeding regimes (e.g. Brown, 1946a,b,c; Elliott, 1975a,b, 1976,a,b,c; Weatherley & Gill, 1981, 1983,a,b). In many cases only a few of the growth processes could be simultaneously studied, for practical reasons. Shul'man (1974) wrote, "The morphological, physiological and biochemical aspects of growth may be studied, but this is practically impossible within the framework of a single investigation. It is also difficult to combine a study of growth connected with an increase of the animal's mass with a study of the growth of its reproductive tissue".

Mann *et al*. (1984) pointed out that growth processes can be profitably investigated by comparing populations of the same species in different habitats. In practice there are problems here too, as the habitats compared may differ in so many respects that it is difficult to decide which factors are important to the growth processes under study (Mann *et al*., 1984). Also the populations may not be genetically identical. To avoid this possibility, Mann et al. (loc. cit.) carried out a reciprocal transfer of sculpin, Gobio gobio, between streams in Dorset and Durham, 440km apart, but because the fish were of necessity kept in cages, the situation was artificial. The ideal would be to compare growth processes in two naturally occurring populations of genetically identical fish, living in ecologically identical habitats in the same geographical location, and differing in only a single aspect of their biology, such as feeding.

Although growth in teleosts is ultimately genetically determined (Weatherley, 1976), it is much more plastic than in birds and mammals. Teleost growth is much affected by environmental conditions. Characteristic of teleosts is the fact that the growth of individuals cannot be considered separately from the growth of their populations; the total biomass of a population may exist as many small individuals, or fewer large ones. Any long term study of individual growth should therefore be linked to a study of population growth, recruitment and mortality (Ch. 2.3). Sampling methods are a problem because of their selectivity; it is often necessary to use more than one method to sample all age groups. In addition such studies tend to be restricted to commercially valuable species, whose population dynamics are distorted by human exploitation. According to Ricker (1949), "... studies of unexploited populations are prized rarities in fishery literature". More recently, Hutchinson (1980) remarked "There seems to be no case where ... an unexploited population has been studied from egg to oldest surviving adult".

Growth in powan. The only two naturally occurring populations of powan, Coregonus lavaretus (L.), inhabit Loch Lomond and Loch Eck, Scotland. The Loch Lomond population has been studied for many years (Slack, 1955; Slack *et al.*, 1957; Maitland, 1967, 1968; Scott, 1979), but their growth has only been studied in detail since 1979. The Loch Eck population has been intensively studied only since 1984. These populations seem to present a situation close to the ideal previously outlined. They are genetically almost identical (McEwen, 1985); the lochs are ecologically similar and only 22km apart; neither population is exploited (even by anglers); and routine sampling of virtually all age groups should be feasible. The only major difference apparent between the biology of the populations is in their feeding, a fact discovered during the course of the present study and analysed by Pomeroy (1987).

Aim. The aim of this thesis is to compare the growth processes in the two populations of powan. Consideration will also be given to the status of the powan from a conservation point of view, since Loch Lomond in particular is suffering from the effects of much increased pressure from human recreational activities (Ch. 6).

(b) Powan

(i) Relationships. Powan are members of the *lavaretus* group of the Coregoninae, a subfamily whose systematics are confused by phenotypic variability, hybridisation, and introgression (Nikolsky & Reshetnikov, 1970; Svardson, 1970). There are six populations of *C. lavaretus* in Britain (Ferguson, 1974): schelly in Red Tarn, Ullswater and Haweswater in England; gwyniad in Llyn Tegid in Wales; and powan in Lochs Lomond and Eck. Electrophoretic studies have shown that the two powan populations are genetically very close; examination of 12 enzymes representing 31 or more loci showed that the populations were similar with low levels of polymorphism. The mean heterozygosity per locus ranged from 1.5% to 2.4%. Of the three polymorphic loci one, *LDH*-3 (0) was restricted to Loch Eck (McEwen, 1985). The pollan, *Coregonus autumnalis pollan* of Lough Neagh, Lough Erne, Lough Ree and Lough Derg in Ireland is more closely related to the North American ciscoes than to the other British coregonines (Ferguson *et al*., 1978). The vendace, *C. albula*, occurs in Bassenthwaite and Derwentwater in England, and until recently in Mill Loch and Castle Loch in Lochmaben, Scotland. The Scottish vendace populations are almost certainly now extinct (P.S. Maitland, pers. comm.).

(ii) Feeding (summarised from Pomeroy (1987).

In Loch Lomond, the diet from late spring to autumn was almost entirely zooplankton. Many *Chaoborus* larvae were also taken in spring and autumn but not in summer when they would have been aerial imagos. Feeding increased in intensity from May to a maximum in September, and there was considerable individual variation in the zooplanktonic organisms selected. In winter and early spring, many stomachs were empty, and the small amount of food taken was benthic, including Eurycercus, Asellus and chironomid larvae. At spawning time in January both sexes, but females in particular, "gorged themselves" on powan ova. There were virtually no non-food debris in the stomachs, except at spawning time, when there were small quantities of gravel and sand. In general, stomach contents were food material only and feeding was very seasonal.

In Loch Eck, the stomach contents throughout the year were notably consistent. They comprised mainly the benthic mollusc Pisidium and chironomid larvae in high proportions (>70%) in all samples, although in August and September the proportion of chironomids fell, with a corresponding increase in Pisidium which are a less efficient food source. Also present were Acanthocyclops viridis, ostracods, and a few Chaoborus and trichopteran larvae. Zooplankton was virtually absent. Feeding continued all the year round, except for a brief period during spawning. The stomachs of Loch Eck powan always contained a high proportion of non-food material, 60% to 80% by weight, mostly mud and plant debris.

From estimating the calorific value of prey organisms by microbomb calorimetry, and the metabolic requirements of the fish by comparison with published work (mostly on other salmonid species), Pomeroy concluded that in Loch Lomond from October to April, apart from the brief period in which powan eat their own ova, the food ingested was lower in energy value than was required for routine maintenance. From May to October, approximately twice the energy required was available with maximum ration. There was a brief interruption to this period of heavy feeding in late July to early August, when energy intake fell marginally below requirement. In Loch Eck, the energy intake exceeded the routine maintenance requirement from January to August, and only from September to November was there a significant shortfall.

Planktonic prey had a higher energetic profitability per unit dry weight than most of the prey organisms found in Eck powan stomachs, but Pomeroy calculated that the total annual input was much the same in both populations (mean of 236 KJ in Lomond, 258 KJ in Eck for three year olds; 405 KJ and 390 KJ for four year olds), and suggested that it is the rate at which food is available during the year which is the distinguishing factor between the two populations.

(c) The Powan Lochs

(i) Geology (Fig. 1.1). Both the lochs lie in a region of metamorphic rocks, the northern two-thirds of Loch Lomond and the whole of Loch Eck in quartz mica-schist and schistose grits of Dalradian origin. In Loch Lomond the schists are interrupted by a narrow band, mainly of slate, which crosses the loch from the Ross Promontory to Luss. Further south still, beyond another region of schists and grits, the rocks are sandstone. The loch is traversed by a major fault, the Highland Boundary Fault, the course of which is marked by four islands (Slack, 1957a,b; MacDonald, 1974; Anderson, 1976).

(ii) Morphology (Fig. 1.1). Like the multitude of lochs in western Scotland, Lochs Lomond and Eck were formed by glacial erosion. Prior to glaciation, earth movements about 350.10^6 years ago and subsequent erosion, resulted in a plateau sloping downwards from the west coast of Scotland to the east. The headstreams of major rivers such as the Tweed and Forth rose in the extreme west and flowed to the east coast. During the subsequent glaciation, ice moved from the granite mass north of what is now Glen Fyne, probably following the north and south running tributaries of the old rivers. The glacier overdeepened these tributary valleys into narrow, deep, steep-sided gorges which cut across the original river systems. On the basis of the distribution of erratics, the ice which gouged out Loch Lomond flowed south-south-east from the Glen Fyne granite, then trended eastward; the ice which formed Loch Eck flowed south. Arctic conditions persisted until about 13,000 years ago, when they were replaced by a milder climate (Sissons, 1983). Many of the glacier-formed valleys are now occupied by typical fjord-type sea lochs, such as Loch Long, Loch Goil and Loch Fyne. Marine influence in Loch Lomond is recorded by a band of sediment containing cysts of planktonic dinoflagellates. This marine phase lasted from about 6900 before present to 5450 before present (Dickson *et al.*, 1978). Raised beaches are recognisable at 15m above the present level (Lamond, 1931). Loch Lomond is now 8.5m above sea level, and Loch Eck is 9m above sea level, so both probably had a marine period about the same time. Remains of the old mountain ridges between the preglacial valleys are still evident. On Loch Lomond, Rudha Ban and Rudha Mor (Fig 1.2) are steep-sided prominences which constrict the loch.

The present day morphology of Loch Lomond and Loch Eck is the result of the interplay of glaciation and geology. Loch Lomond (Fig 1.2) is the largest lake in Britain in terms of surface area ($71km^2$). At 36km it is the third longest (Loch Awe 41km, Loch Ness 39km). At 189.9m it is the third deepest (Loch Morar 310m, Loch Ness 230m). At $2628m^3 .10^9$ it is second in terms of volume (Loch Ness $7452m^3.10^9$; Maitland, 1981). Loch Lomond can be divided into three main basins (Slack, 1957a). The North Basin is characteristically U-shaped in cross-section, being narrow (maximum width 1km), steep-sided and deep (maximum depth 189.9m). It extends south to a relatively shallow ridge (maximum depth 15m) between Rowardennan and Inverbeg. South of this lies the Middle Basin which is wider and shallower (maximum depth 65.5m). The Middle Basin is still in schistose rocks, but with a band of slate running across it, and contains three major islands of schistose grit at its south end: Inchlonaig, Inchconnachan and Inchtavannach. South of this lies the South Basin, wide (maximum width 8.8km) and shallow (maximum depth 24.4m though much of it is considerably less). Three islands form a group with those in the Middle Basin, but are distinguished from them by being composed of sandstone: Inchfad, Inchcruin, and Inchmoan.

Further south lies the chain of boundary fault islands: Inchcailloch, Torrinch, Creinch and Inchmurrin.

Loch Eck (Fig 1.3) by contrast is small. Its length is 10.5km, maximum depth 42.4m and the surface area is 4.58km^2. Loch Eck contains three not very clearly demarcated basins. In the north, one of 24m (maximum depth), in which all specimens used in this study were caught; one of 42.4m; and one of 25.3m at the south end (Murray and Pullar, 1910).

(iii) Climate. The regional climate of Scotland has been analysed in terms of accumulated temperature above 5.6°C and potential water deficit. All of Loch Eck and all of Loch Lomond fall into the same category of "warm wet lowland" (Birse & Dry, 1970). In terms of exposure and accumulated frost, all of Loch Eck and all of Loch Lomond except the northernmost part of the North Basin fall into the same category of "moderately exposed with fairly mild winters" (Birse & Robertson, 1970). More specifically, data are available from two Meteorological Office stations, at Benmore at the south end of Loch Eck, and Arrochymore near the south end of Loch Lomond (Table 1.1). Although such climatic information does not necessarily directly reflect physical conditions within the loch water, it is clear that both lochs are subject to much the same general climate.

(iv) Fauna. The benthic fauna of Loch Lomond has been extensively studied (Hunter, 1957; Slack, 1957c; Smith *et al*, 1981), that of Loch Eck less thoroughly (Slack, 1976). The faunae are essentially similar, though Slack (1976) states that crustaceans such as *Gammarus* and *Asellus*, and molluscs such as *Limnaea* and *Valvata* are either absent from or rare in Loch Eck. He ascribes this lack to low calcium concentrations. The zooplankton of Loch Lomond has also been more thoroughly studied than that of Loch Eck, but Pomeroy (1987) reported that the species composition in the two lochs was very similar. The standing crop and productivity of plankton is not known. In Loch Lomond, the standing crop of phytoplankton in the North Basin is very much smaller than in the South Basin, the difference possibly being associated with poorer light conditions rather than with poorer nutrient status (Tippett, 1987).

The cyclostome and teleost species present in Loch Lomond and Loch Eck are shown in Table 1.2. Although Loch Lomond contains more species than Loch Eck, several are recent introductions whose effect, if any, on the powan populations is not yet clear. Of the others, only two species are likely to have a direct impact on adult powan: river lamprey and pike. Charr are absent from Loch Lomond, though there is some evidence that they might have existed there two hundred years ago (Sinclair, 1799). Loch Eck charr are dwarfed (Friend, 1956; Maitland *et al*., 1984) and do not appear to compete with powan for food (Pomeroy, 1987).

1.2 GENERAL MATERIALS AND METHODS

(a) Sampling

All fish used during the present study (1979 to 1988) were taken by benthic gill netting. Most of the nets used were nylon multifilament with mesh sizes of 19mm, 26mm, 31mm, and 39mm bar (knot to knot) made by Norsenet, Bergen, Norway. Prior to January 1981 only 39mm bar nets were used. The length of each unit of net was 25m; usually 8 units with 2 of each mesh size, or 16 units with four of each mesh size were used. From September 26th 1985, a 36m monofilament gill net was added (Lundgrens Fiskredskaps-Fabrik A-B, Stockholm, Sweden). This net consisted of equal lengths of 12 mesh sizes ranging from 6.25mm to 40mm bar (6.25, 8, 10, 12.5, 16, 19, 22, 25, 30, 33, 38, 40). One sample of powan taken by shore-seine net in Sallochy Bay, Loch Lomond on 14th July 1969 by A.P. Scott & D.B.C. Scott is included in the present study because it is the only large catch of juvenile powan on record. Although the total and fork lengths of a subsample of 62 of these fish were recorded, they were not analysed at the time.

The gill nets were set in standard positions, wind permitting. In Loch Lomond (Fig. 1.2), this was along a relatively shallow ridge from Camas an Losgainn eastwards to the southern promontory of Sallochy Bay in the Middle Basin, in depths of 1.8m to 24m. At spawning time nets were also set between the Ross Islands on a shallow (4m to 14m) gravel bank, a confirmed powan spawning ground (Fuller *et al.*, 1976). One sample (10th January 1986) was taken in the South

Basin, near the MacDougall Bank spawning ground. In Loch Eck (Fig. 1.3), the nets were set across the loch from Rudha na Seamraig to the boathouses on the east shore. The depth on this transect ranged from 2 to 24m. During the likely spawning period (Ch. 3.1), nets were also set parallel to the shore in depths of about 1 to 4m, from the boathouses southwards. Since there are no known offshore banks in Loch Eck, as favoured for spawning by Loch Lomond powan, this shallow gravel shoreline seemed a likely alternative.

Sampling was carried out as regularly as possible but impossible weather conditions often supervened. There was also an interruption in the sampling programme on Loch Eck from May to August 1985, when the ownership of the fishing rights was sold, and permission to net had to be re-negotiated. In Loch Lomond the nets were set at about 1700 hours and raised at about 1100 hours the next day, the fish being processed within a few hours. In the case of Loch Eck, although only 22km distant "as the crow flies", a total road journey of 215km (Fig. 1.1), along with the need to launch and retrieve a boat from Dornoch Point, meant that there was a delay of about 4 or 5 hours between lifting the nets and beginning processing. The nets were set at 1300 hours, and raised about the same time the next day. Whenever possible, the fish were kept in ice during the transfer to the Yett of Ptarmigan (Fig. 1.2).

(b) Processing

(i) Field data. Processing was carried out at the Yett of Ptarmigan. The fish were laid out on trays and individually numbered using proprietary numbered self-adhesive labels ('Blick'), since these adhered well to the fish even when deep-frozen, remained legible when wet, frozen or fixed, and had negligible weight. The following were recorded (all weights wet): total length and fork length (to the nearest mm); total weight (to the nearest 2g, using a 1000g 'Piper Chemicals' electronic balance); gonad weight (to the nearest 0.01g using an 'Oertling TP 30' balance); sex and reproductive status as visually assessed; liver weight (to the nearest 0.01g); weight of viscera with intestine emptied of its contents (to the nearest 0.01g); weight of viscera with both intestine and stomach emptied (to the nearest 0.01g).

(ii) Tissues. Samples for histological study (mainly gonads, Chs. 3.1, 4), were fixed in Bouin's aqueous fixative for 24 hours, progressively dehydrated in 30%, 50%, and 70% ethanol, and stored in repeated changes of 70% ethanol to eliminate picric acid (Humason, 1972). Samples of stomach contents were preserved in 5% formalin. Gonad, liver and gut including all adherent fat, together with a sample of muscle (posterior to the cloaca), were deep-frozen in sealed polythene bags within 24 hours of catching. Selected fish were photographed using a Zeiss Contax 137 MA camera with f1.7 'Planar' lens and extension tubes, and either 'Kodacolor Gold' 100 ASA colour negative film, or 'Kodachrome 25' 25 ASA colour reversal film.

(iii) Calcified tissues. Ten scales were taken from a standard position on each fish. The standard position was on the left side, between the posterior edge of the dorsal fin and the lateral line (Plates 1 to 4). They were stored in numbered 5.5 by 5.5cm brown manilla envelopes. If no scales were available from the left side, scales were taken from the corresponding position on the right side. If this area was also denuded, scales were taken from some other area, the envelopes were labelled 'for ageing only' and they were not used for growth calculations. In the Loch Lomond sample of May 1986, in addition to scales taken from the standard position, scales were also taken from the 'shoulder' region (above the lateral line and anterior to the dorsal fin) of 62 fish for comparison. Entire heads were deep-frozen for dissection of otoliths and opercular bones at a later date.

(c) Artificial Fertilisation.

Ovulated ova were stripped from female powan and fertilised with milt from several males caught in Loch Lomond on 10th January 1985 and in Loch Eck on 26th February 1985. After a few minutes loch water was added, and the ova rinsed clear of debris. Fertilised ova adhered to the glass container in which they were fertilised. Fertile ova were maintained until hatching in trout hatchery trays in running tapwater in St. Andrews. Dates of hatching were noted and the diameter of ova measured to the nearest 0.01mm using a micrometer designed and built by Dr C. Muir. The total length of the hatchlings was measured on a microscope Vernier micrometer stage to the nearest 0.01mm. A number of individuals were reared in aquaria.

1.3 RESULTS

(a) Catches

(i) Samples 1984-1988. Table 1.3a and Table 1.4 list the dates, localities, nets used, number of fish caught and surface water temperatures in Lochs Lomond and Eck respectively. During this time, the total number of powan caught in Loch Lomond was 1458, excluding the sample of 20th October 1984, for which an exact tally was not kept. In Loch Eck, a total of 2091 powan was caught, excluding the sample of 26th September 1985, when the nets were sabotaged by anglers. On the basis of these figures, the catch of powan per unit effort, expressed as number of powan per unit of net per setting of approximately 24 hours, and taking the monofilament net as equivalent to one unit of multifilament, was 5.7 in Loch Lomond and 12.3 in Loch Eck.

(ii) Samples 1979-1984. Data from earlier Loch Lomond samples provided a rare opportunity to analyse growth processes over an extended 9 year period (Chs. 3.1, 3.2, 5). Table 1.3b gives dates and number of fish used from each sample in this series. The samples were collected by a number of people, including D.B.C. Scott, W.D. O'Connell, K.H. Rashid, A.H. Yekrangian, A.F. McCulloch, P.P. Pomeroy and several Honours students. Asterisked are samples from which scales were analysed (Brown, 1983; Ch. 2) except for 1st November 1980 for which the original data were incomplete. In Loch Eck two additional samples were taken on 12th January 1984 (118 fish) and 14th February 1984 (88 fish) by A.F. McCulloch and P.P. Pomeroy.* All these data are analysed in Chapters 3.1 and 3.2.

(iii) Sample of 17th July 1969. In this sample over 200 juvenile powan were caught (D.B.C. Scott pers. comm.). Of a subsample of 62 which were measured, the mean total length was 109mm (±22.4mm), the mean fork length was 98mm (±19.9 mm), and the range of total length was 83 to 212mm. Fig. 1.4 shows the (total) length frequency distribution of the subsample. Two distinct peaks were present, probably reflecting two age groups (Ch. 2.1, p. 48)

(b) Sex Ratios

Consideration of the overall sex ratios of all samples is not valid, since males congregate on the spawning grounds prior to the spawning season, while individual females move on to the spawning grounds as they ovulate, and leave after oviposition. Consequently males considerably outnumber females in samples taken on the spawning grounds at this time, while shoals consisting almost entirely of females may be found in deep water off the spawning grounds. Such unisexual female shoals have been found in Loch Lomond (Scott, 1979) and in Loch Eck (Fig. 1.5b, 30th January 1985). For this reason the sex ratios observed between December and February are not considered here, but in Chapter 3.1.

In Loch Lomond the sex ratios of powan caught from May 12th 1984 to June 1988 are shown in Fig. 1.5a. Outwith the spawning season, the ratio did not differ significantly from

1 male : 1 female (Chi-squared test), except in October 1984 and May 1985, when males predominated. These anomalies did not recur in later years.

In Loch Eck the sex ratios of powan caught from September 1984 to January 1987 are shown in Fig. 1.5b. Outwith the spawning season, the ratio was significantly biased in favour of males with a ratio varying from 3:1 m:f in August 1985 to close to 1:1 in April 1986 ($p < 0.05$).

(c) Artificial Fertilisation

Ova collected from Loch Lomond on 10th January 1985 began hatching on 7th March. All viable ova had hatched by 30th March. The mean diameter of 50 ova was 3.41mm (±0.15 mm). The mean total length of 40 hatchlings measured within 24 hours was 12.3mm (±0.6mm). Ova collected from Loch Eck on 26th February 1985 began hatching on 12th April, and all viable ova had hatched by the 5th May. The mean diameter of 50 ova was 3.36mm (±0.06mm). The mean total length of 40 hatchlings was 13.7mm (±0.39mm); some of these may have been up to one week old, but they were not yet feeding.

1.4 DISCUSSION

(a) Catches 1984-1988

The catch per unit effort was consistently much higher in Loch Eck than in Loch Lomond. The difference does not necessarily reflect different population densities. A net of 16 units in the standard position extended virtually from shore to shore in Loch Eck, whereas in Loch Lomond, it covered only a small part of the available water. In addition, it is known that the Loch Lomond powan inhabit different depths at particular times of year (O'Connell, 1984). In autumn they tend to be found in deeper water, and maximum catches occur in nets set southwards from Camas an Losgainn. In spring and early summer the maximum catches are in shallow inshore water. The use of a 'standard position' for nets, especially in Loch Lomond, may therefore be misleading, but since covering all possibilities was not feasible, consistency seemed the best alternative.

(b) Sex ratios

Fish display a range of mechanisms for sex determination including sex chromosomes (with either sex heterogametic), polygenic sex determination, and autosomes (Price, 1984). The expected sex ratio of populations working on the XX-XY sex chromosome system is 1 male to 1 female, as shown by the Loch Lomond population (except for October 1984 and May 1985). In earlier Loch Lomond studies, Slack *et al.* (1957) and Maitland (1969) also found male and female powan in equal proportions. In Loch Eck, the ratio was as high as

3 males to 1 female, though more recently it tended towards 1:1. The sex ratios were further analysed on the basis of year-classes (Table 1.5; Ch. 2.2). In Loch Lomond only two year-classes deviated significantly from 1:1: 1985 when males predominated, and 1984 when females predominated. In Loch Eck, all year-classes from 1976 to 1981 showed a significant male predominance. Why this should be is not clear. Possibly coincidental is that the only year in which female predominance occurred was 1984, in both lochs, although the difference in Loch Eck was not statistically significant.

Imbalance in sex ratios has been reported in some coregonine populations; in *C. kiyi* by Deason and Hile (1944), in *C. hoyi* of Lake Superior by Dryer and Beil (1964), and in *C. hoyi* of Lake Michigan where females represented an average 96% of the population during 1963-69 (Brown, 1970). Brown suggested that the imbalance resulted from poor adjustment of the fish to changing ecology, and was an early sign of a population decline. In heterogametic animals, it has been suggested that a population shifting from the 1:1 ratio will tend automatically to revert to 1:1 (Fisher 1930, cited by Ricklefs, 1980). This may be the situation in Loch Eck.

CHAPTER 2 AGE AND SOMATIC GROWTH

2.1 DETERMINATION AND VALIDATION

2.1.1 INTRODUCTION

The potential to determine the age of fish from their calcified structures was realised by a Swedish clergyman in 1759, who observed that rings on the vertebrae were related to size, small fish having fewer rings than large fish. He concluded that the number of rings expressed the age of those "inhabitants of the wet element" in years (Hederstrom, 1759). 'Osseochronometry' (Casselman, 1987) and associated growth estimations, are now widely practised techniques since a knowledge of age, growth, and also recruitment and mortality (derived from age studies), are prerequisites of any population survey. Apart from vertebrae, other hard tissues commonly utilised for ageing are fin-rays, otoliths, cleithra, opercular bones and scales (Menon, 1950; Bagenal, 1974; Bagenal & Tesch, 1978; Casselman, 1987).

Scales have been extensively employed because they are easy to remove and prepare and apparently easy to interpret. However dissension has been increasing over their reliability, particularly in old or slow growing populations, where other calcified structures have been shown to give more valid results (Aass, 1972; van Utrecht & Schenkkan, 1972; Ausen, 1976; Jonsson, 1976; MacCrimmon, 1979; Mills & Beamish, 1980; Casselman, 1983). Nevertheless, scales have been found to be valid for many coregonine populations (van Oosten, 1923; 1928; Hile, 1936; Dryer, 1963; Bagenal, 1970; Hagen, 1970), and satisfactory results were obtained using scales in a preliminary study of age and growth in Loch Lomond powan (Brown, 1983).

(a) Scale Morphology

Teleost scales are thin, flexible, transparent structures composed of protein, mainly collagen and ichthylepidin, also minerals, principally calcium phosphate and calcium carbonate. Magnesium, sodium, sulphur and iron may also be present (van Oosten, 1957). The composition and concentration of elements in scales and other calcified structures differs among species, and may also vary among populations of the same species, depending on the chemistry of the environmental water (Ihssen *et al.*, 1981). Lapi & Mulligan (1981) could assign 63% of sea-caught sockeye salmon, *Oncorhynchus nerka*, to their lake of origin by energy dispersive X-ray analysis of the part of the scale laid down while the fish was in fresh water.

Scales result from secretion between two layers of investing cells (osteoblasts or scleroblasts). A superficial mineralised 'bony' or hyalodentine layer is deposited over a deeper lamellar or fibrillar plate. Exactly how the process occurs is not understood but it is accepted (van Oosten, 1957; Simkiss, 1974) that the hyalodentine layer grows only at its edge, depositing minerals as rings or *circuli*, which radiate out concentrically from a central *focus* (Plate 5). The inner fibrous plate deposits continuous sheets below the hyalodentine layer so that the scale is thicker in the centre than at the outer margins (van Oosten, 1957).

The basis of age and growth determination from scales lies in the non-uniform pattern of the circuli. In addition to differences in the spacing between circuli, which often form distinct zones, (Plate 6), there are periodic interruptions or checks, caused by disruption in the deposition of scale material when a change in growth rate occurs.

Powan scale morphology conforms to the description of whitefish (*C. clupeaformis* Mitchill) scales given by van Oosten (1923). A common form of check in powan is where a complete circulus cuts across or unites other incomplete circuli (Plate 5). This complete circulus or check, also termed an annulus (Casselman, 1983), marks the resumption of rapid growth after a period of retarded growth. Checks frequently appear as discontinuous, anastomosed or irregular circuli (Plate 8). Checks may also be associated with gaps (Plate 5). Since retardation and acceleration of growth is an annual feature in many species including powan (Brown, 1983; McCulloch, 1984), each check or annulus represents one year. So the area between two successive checks represents one year of growth. Growth after the last check is traditionally described as '+' growth. Thus a 2+ fish denotes a fish with 2 checks and additional marginal growth on the scales (Plate 6). Plate 7 shows a 0+ fish (no checks). In the scale shown in Plate 5, a fourth check is forming on the margin and so the fish is 4 years old. When the age of a fish is known, it can be assigned to a year-class, which is the collective term for all individuals hatched in any one year.

(b) Growth Determination from Scales

In 1901, Walter (cited by van Oosten, 1928), noticed that there was a relationship between the growth zones on the scales and the "intensity" of body growth in length and height of pond carp. But it was Lea (1910) working with herring, who first attempted to estimate fish sizes at previous ages (back-calculation). He considered that the growth of the scale was directly proportional to the growth of the fish, and so the length of the fish at each annulus could be calculated from the formula:

$$ln = (Sn/S)l$$

where ln = length of the fish at annulus n

l = length of the fish when scale sample obtained

Sn = radius or diameter of annulus n

S = total scale radius or diameter

This method held for some populations (Dahl, 1910; van Oosten, 1923; Smith, 1956; Dryer, 1963). However Lee (1912), also Meek (1916) and Molander (1918) (cited by Lee, 1920; van Oosten, 1928) found that the body-scale relationship was not directly proportional; lengths calculated using Lea's equation were too low compared with measured lengths ar those ages. One suggested reason for this discrepancy was that the scale was not formed until the fish reached a certain length (Fraser, 1916). Consequently, Lea's direct proportionality formula was modified to give the Fraser-Lee equation (Fraser, 1916; Lee, 1920):

$$ln = Sn/S(l - c) + c$$

The constant, c, was originally defined as the length of the fish at the time of first scale formation (Lee, 1920) a definition soon proved to be erroneous. Among others, Monastyrsky (1930, cited by Hile, 1970) showed that the constant could not be given a morphological interpretation, but the misconception persevered for some time (e.g. van Someren, 1952; Slack et al., 1957).

Various other equations, also modifications and combinations of equations have been used (Sherriff, 1922; Fry, 1943; Carlander, 1950 (all cited by Hile, 1970); Berg, 1970; Duncan, 1980; Bartlett et al., 1984). There is no standard scale formula for back-calculation of length, as no standard body-scale relationship exists for all fish. It is also misleading to assume that a method which holds for one population of a species will automatically hold for other populations of the same species; there is no general species body-scale relationship (Hile, 1970; Casselman, 1987). Environmental conditions and genotype may vary from population to population, affecting the phenotype and growth rate (Svardson, 1950, 1970; Frost & Brown, 1967; Maitland et al., 1984). Each population therefore requires individual examination to find its body-scale relationship and the correct method of back-calculation. In other words, do whatever works. As Hile (1970) wrote, "Only one question needs to be answered, 'What length of fish matches a particular size of scale?' The investigator is free of rules in arriving at his answer. He may smooth his data by fitting a curve mathematically, he may fit his curve freehand, or he may use one method over part of his length range and another over the rest. The nature of his data must guide him."

However, the validity of the method has to be proved and validation of ageing and growth results is an aspect which has been frequently neglected (Beamish & McFarlane, 1983; Casselman, 1983, 1987). In a survey of 500 papers published between 1907 and 1980, Beamish & McFarlane (1983) found that in less than 3% had the technique been validated for all age groups. 35% of the papers did not consider age validation.

Irrefutable evidence of the validity of age estimations is if the age of the fish is known (van Oosten, 1923; Mann & Steinmetz, 1985). Alternatively the fish age may be partly known through mark-recapture methods (Ausen, 1976; Mills & Beamish, 1980). These direct methods of validation were impractical in powan: the first since natural populations were under study, the second as powan have a high mortality rate after capture, even when seine-netted (D.B.C. Scott pers. comm.). Therefore indirect methods of validation and corroboration had to be used. These include length-frequency distributions; following weak and strong year-classes; identification of a particular year-class by the presence of a physical mark on the hard structure of all members of that year-class, perhaps caused by an unusual alteration in growth rate; and measurement of the amount of marginal growth on the calcified structure to confirm the annual nature of check formation (Beamish & McFarlane, 1983; Casselman, 1983, 1987). A summary of the points indirectly corroborating use of the scale method for age and growth analysis in powan is given on pages 67-69. Another method of verification is to compare ages independently assessed from more than one calcified structure originating from the same fish (Beamish, 1981). For powan, scale readings were compared with two of the more commonly used structures, otoliths and opercular bones.

(c) Otoliths and Opercular Bones

(i) Otoliths. Teleost fish have three pairs of otoliths, dense structures contained within fluid filled chambers of the inner ear, forming receptor organs sensitive to acceleration, tilting and vibration. Of the three otoliths, the largest, the sagitta otolith, is the most frequently used in age and growth studies.

Otoliths consist of needle-shaped crystals of calcium carbonate embedded in a proteinaceous matrix. The crystals radiate out in three dimensions from a central nucleus, perpendicular to the direction of growth (Williams & Bedford, 1974; Campana & Neilson, 1985). Otoliths show a series of alternating opaque and translucent zones (Plate 11). The opaque zones represent periods of growth, while the translucent zones are relatively narrow and represent periods of reduced growth and therefore correspond to checks or annuli on scales (Casselman, 1983). Unlike scales, otoliths continue to grow under conditions of retarded body growth. However, although the organic matrix continues to be laid down, calcium deposition is disrupted, leading to the formation of visually distinct zones (Campana, 1983). In many species, otoliths grow on a daily basis and the study of otolith microzonation can show the daily age of the fish (Pannella, 1974; Campana, 1984), although use of microstructure examination for age determination to the annual level of precision is not recommended beyond the first year of life, particularly in temperate species because growth increments are often so compressed during reduced winter growth that they become indistinguishable (Campana & Neilson, 1985).

(ii) Opercular bones. Four opercular bones form the gill cover: the operculum, interoperculum, suboperculum, and preoperculum (Norden, 1961). Of these, the operculum is the largest and the most commonly used in age and growth estimations (Le Cren, 1947; Frost & Kipling, 1959; Shafi & Maitland, 1971; Blake & Blake, 1978), although Ovchynnyk (1962), comparing scales and various bones in whitefish, preferred the interoperculum. Because of their size, bones are frequently studied macroscopically, and display optical zonation as in otoliths, with narrow, translucent zones representing periods of retarded growth.

2.1.2 MATERIALS AND METHODS

A Analysis of Calcified Structures

(a) Scales

Powan scales were examined using a microfiche reader, model 'Micron 780'. The magnification was 50x, and image distortion was negligible. Dry scales could be placed in the carrier without need for further preparation unless cleaning was required. Measurements were made directly from the screen of the microfiche reader. Surprisingly few researchers have used this very convenient method (Ryan & Christie, 1975; Dauble & Gray, 1977), instead choosing preparative techniques which are considerably more time consuming, such as making cellulose-acetate impressions (Hesthagen, 1985), or mounting between glass slides (Wilson & Pitcher, 1984a) and viewing with microscopes or other projection apparatus.

Four scales from each fish were read unless only three readable scales could be found. If fewer than three scales were readable, the fish was discarded. Unreadable scales were those which were regenerated (Plate 9) or indistinct (Plate 10). After the age was assessed, measurements of the radii of each of the three or four scales were made from the focus along the anterio-median axis of the scale: (i) to its margin (total scale radius), and (ii) to each check (annulus) or, if this was indistinct, to the circulus immediately before or after the check (Plate 5). The magnified measurements were converted to actual measurements and the means of the scale readings for each fish calculated.

Scales taken from the shoulder region of powan in the Loch Lomond May 1986 sample were analysed independently and the results compared with those of the standard scales from the same fish.

(b) Otoliths

The roof of the skull was removed by a transverse cut above the eyes and the sagitta otoliths dissected out. They were cleaned by dipping in warm water and rubbing between finger and thumb. They were then dried and stored in labelled envelopes of the type used for scales.

Several methods of examination were investigated, including breaking and charring, grinding, and viewing ground or whole with transmitted or reflected light in media with different refractive indices. Powan otoliths were best examined whole in creosote (R.I. 1.538) or cedarwood oil (R.I. 1.515) against a dark background with reflected light. The translucent annular zones appeared dark against the lighter opaque growth zones. Grinding gave good results but was too time consuming (Plate 11a).

(c) Opercular Bones

The gill covers were removed and macerated in water at 100°C until the connective tissue and muscle could be rubbed off, and the four opercular bones separated. The clean bones were stored dry in labelled envelopes with the otoliths.

Examination was by polarised transmitted light. A vertical projection system was set up using an 'Aldis' 35mm projector, a 'Miranda' 28mm f2.8 lens and a rotatable polarising filter. The dry bone was placed on a slide between the filtered light source and the lens. The image, magnified 20x, was focused on to a horizontal white screen and the polarising filter rotated to give maximum contrast. The translucent annular zones appeared bright against a dark (opaque) background. The drier the bone, the clearer the image.

Of the four opercular bones, the operculum was found to be best for age determination. The suboperculum, interoperculum and preoperculum were confusing, showing varying numbers of zones.

(d) Photographic Techniques

(i) Scales. The scale was placed in water in an ultrasonic cleaner for 2 minutes, rubbed between finger and thumb to remove loosened dirt then returned to the ultrasonic cleaner. The process was repeated until the scale was clean. It was then mounted in water and flattened with a coverslip. A slide with a well was used for larger scales. Scales were photographed using a Zeiss photo-microscope with a 1x Zeiss 'Planapochromat' lens and 'Ilford' Pan F film (50 ASA).

(ii) Otolith. Both sides of the otolith were ground to the nuclear plane. The otolith was mounted in Canada Balsam (R.I. 1.532). The same photographic set-up as for scales was used, the otolith being first photographed with transmitted light (Plate 11a), then with reflected light (Plate 11b).

B Growth Calculations

(a) The Body-scale Relationship

A linear regression analysis was used to determine the relationship between total body length (dependent variable Y) and scale radius (independent variable X). This Model I or arithmetic mean regression (Ricker, 1973; Sokal & Rohlf, 1981) gives an equation of the form:

$$Y = a + bX$$

where a = the constant (y-intercept)

and b = the slope (regression coefficient).

However, an assumption of the Model I regression is that the independent variable is measured without error. Here, both variables are subject to measurement error, typifying a Model II regression. In this case Ricker (1973) recommended the use of the geometric mean (GM) regression as giving a more accurate estimate of functional relationships. Jolicoeur (1975) criticised Ricker's method, pointing out that the slope is independent of any joint function of X and Y, being only the ratio of two standard deviations. Sokal & Rohlf (1981) commented that "the subject of Model II regression is one on which research and controversy are continuing and definitive recommendations are difficult to make". Once again, it is a case of using whatever method works best.

In the regressions for each loch, the samples were selected from over a year (Table 2.1), in order to reduce any bias from possible differences in monthly body-scale relationships (Ottaway & Simkiss, 1979). The large number of fish included a wide range of fish sizes, important in a general body-scale relationship since there are allometric differences in the rate of body growth to scale growth between age groups (p. 55; Carlander, 1981). The geometric mean regression was also calculated:

$$\text{the GM slope } (v) = \pm\sqrt{\textstyle\sum y^2/\sum x^2}$$

The y-intercept (a) is obtained from $Y - vX$ by analogy with the arithmetic linear equation (Sokal & Rohlf, 1981).

(b) Back-calculation of Lengths and Growth Rates

Lengths at previous ages were back-calculated using the Fraser-Lee equation since a preliminary study indicated that it gave the best correlation with measured lengths (Brown, 1983). The constant c (y-intercept) in the equation was derived from the body-scale regression for each loch.

The growth rate in each year of life was calculated from:

$$(\ln l_2 - \ln l_1)/(t_2 - t_1)$$

where $\ln l_1$ and $\ln l_2$ are the natural logarithms of calculated lengths l_1 and l_2 at times t_1 and t_2 respectively (Ricker, 1979). The difference in time was equal to 1 year. Time 0 was taken to be the time of hatching, and the hatching length of 12.3mm was based on the mean of 40 Loch Lomond powan larvae hatched in the laboratory (Ch. 1.3c, p. 19).

This hatching length was used in growth rate calculations for both populations.

(c) Validation of Length Estimations

The mean calculated length at each age was computed for a total of 859 Loch Lomond powan from November 1980 to January 1986 inclusive; and for 1456 Loch Eck powan from September 1984 to June 1986 inclusive. To establish whether the calculated lengths were correct, they were compared with measured lengths at equivalent ages. Fish of equivalent age were those caught around their 'birthday' of April 1st (Ch. 2.2.2, p. 72). This is also the time of least growth, prior to formation of the next check (Brown, 1983; McCulloch, 1984). Mean measured lengths were calculated for the following fish:

Loch Lomond. A total of 175 fish were averaged from the samples of April 1981 and 1982, May 1984 and 1985, and June 1981 and 1982. 1 and 2 year old fish in the June samples were excluded because the youngest age groups may start growth earlier in the season than the older fish (Ch. 2.1.4, p. 61).

Loch Eck. 621 fish were averaged from the samples of February 1985 and 1986, March 1985, April 1986, and May 1985.

(d) Seasonal Growth

(i) Monthly body-scale relationships. A body-scale regression analysis (arithmetic) was carried out for each sample from 1984 to 1987.

(ii) Check formation and scale growth.

Loch Lomond: November 1980 to March 1987.

Loch Eck: September 1984 to January 1987.

The marginal scale increment was calculated as being the distance between the last check and the scale edge as a percentage of the radius from the focus to the last check. In each sample the mean and median scale increments were determined for each age group. The age was based on the number of checks present and not on the powan 'birthday'.

2.1.3 RESULTS

A Age Analysis

(a) Comparison of Scales, Otoliths, and Opercular Bones

The highest level of agreement was between scale and otolith readings (Table 2.2a). The agreement was 85% in Loch Lomond samples and 75% in Loch Eck samples. The maximum agreed age was 9 years (Loch Eck). In Loch Lomond powan, equally as many otoliths underestimated as overestimated the scale age by one year (8%). In Loch Eck, most of the otoliths which differed from scales (17%) gave a higher age, by as much as 3 years.

There was poorer agreement between opercular bones and otoliths or scales, being in the region of 60-63% for Loch Lomond powan and 56% for Loch Eck powan (Table 2.2b,c). Most of the discrepant opercular bones gave a lower age than scales or otoliths (28%-32%).

(b) Age Group Frequencies (Table 2.3)

Few 0+ and 1+ powan were caught and the numbers of the older age groups were also low. The maximum assessed age was 12+ in Loch Eck and 11+ in Loch Lomond.

(c) Comparison of Shoulder and Standard Scales (Table 2.4)

Shoulder scales were smaller and more difficult to read than standard scales. The maximum age of powan in the compared sample was 7 years. Out of 62 sets of scales, 44 (71%) were in agreement as to age, and one (2%) in disagreement (standard age 3+, shoulder age 2+). Of the remaining 17 fish, 16 (26%) had indistinct shoulder scales, but only 5 (8%) had indistinct standard scales.

B Growth Analysis

(a) Body-scale Relationships (Fig. 2.1)

Table 2.5

	Lomond	Eck
No. of fish	250	500
y-intercept (a)	106	87
Slope (b)	64.8	73.0
Correlation coefficient (r)	0.927	0.934
GM intercept	91	73
GM slope (v)	69.9	78.2

Both regressions were highly significant. Testing the slopes for equality (Sokal & Rohlf, 1981) showed a highly significant difference so proving that the body-scale relationships of the populations differ and the same intercept can not be used for back-calculation in both populations.

The smallest fish deviated below the line of best fit. The length at which this deviation occurred was estimated to be 250mm in Loch Lomond and 215mm in Loch Eck (Ch. 4 for explanation).

An unusual feature of the Loch Eck regression (Fig. 2.1b) was the non-uniform scatter. Two dense concentrations of points were separated by a relatively sparse area. The mid-point of the gap was estimated to be 284mm.

(b) Validation of Length Estimates

(i) Loch Lomond (Table 2.6a). With the exception of age 1, there was close correspondence between calculated and measured lengths.

(ii) Loch Eck (Table 2.6b). The only correspondence was at ages 5, 10 and 11. The calculated lengths were not consistent over or underestimates, but were overestimates until age 5, then became underestimates.

(c) Growth of Sexes (Table 2.7)

Comparison of measured lengths of males and females in selected year-classes showed no significant differences between the sexes in either loch. This conclusion is consistent with other observations (van Oosten, 1928; Hart, 1931; Smith, 1956; Ausen, 1976; McCulloch, 1981; Wilson & Pitcher, 1984a). Lengths and growth rates of sexes were therefore combined.

(d) Growth Rates (Table 2.8)

In both lochs the growth rate is most rapid in the first year of life (0-1) and decreases progressively with increasing age.

(e) Comparisons of Lengths Calculated from Shoulder and Standard Scales (Loch Lomond, May 1986)

Results of body-scale regressions for the 62 fish were:

Shoulder	$y = 77.3x + 129$	$r = 0.869$
Standard	$y = 62.2x + 103$	$r = 0.958$

Both regressions were significant, but the correlation coefficient (r) for shoulder scales was lower, indicating a greater variability compared with standard scales. The higher shoulder scale intercept of 129 is in accordance with their smaller size.

When back-calculating lengths from the standard scales, the intercept used was the general arithmetic 106 intercept (Table 2.5). It was likely to be the most valid because of the larger number of fish involved, and was very close to the 103 intercept calculated from these May standard scales.

The only significant difference between lengths back-calculated from the standard and the shoulder scales using the 129 intercept, was at age 1, when the calculated length from shoulder scales was 14mm higher than that calculated from standard scales (Table 2.9; $p < 0.001$). The length difference decreased to 7mm at age 2 (not significant), and continued to decrease with increasing age. If the standard 106 intercept was also used for back-calculation from shoulder scales (Table 2.9), then the lengths calculated at ages 1 and 2 from both sets of scales became very similar. Thereafter, with increasing age, the shoulder-calculated lengths became progressively lower than the standard-calculated lengths but there were no statistically significant differences.

(f) Seasonal Growth

(i) Monthly body-scale relationships. All regressions were highly significant.

Loch Lomond (Table 2.10a). The intercepts did not vary in any logical manner between months. Although a test for equality of slopes (Sokal & Rohlf, 1981) indicated highly significant differences between months ($p < 0.01$), a Tukey-Kramer multiple comparison test (Sokal & Rohlf, 1981) failed to detect any significant differences.

Loch Eck (Table 2.10b). There appeared to be a pattern in intercept variation with the months June, August and September having an intercept of over 100 in 1984, 1985 and 1986. In other months, the intercepts ranged from 68.5 to 89.7. The slopes were homogenous ($p < 0.75$).

(ii) Check formation and scale growth. Check formation was indicated by a decrease in the marginal scale increment during the year. When there were outlying individuals, the median was more useful than the mean in determining the time of check formation.

Loch Lomond.

1+ fish (Fig. 2.2a). Check formation occurred between April, the time of maximum scale increment, and June-August. Scale growth may continue over the winter months. There was notably poor growth in 1985.

2+ fish (Fig. 2.2b). In years in which samples were not taken every month, check formation occurred between April or May and August. In 1986 there was checking between May and June ($p < 0.001$). Maximum marginal scale increment was attained by November or December with little change thereafter until check formation. Growth was poor in 1985.

3+ fish (Fig. 2.2c). The time of check formation was more ambiguous than in the previous age groups. There was a decrease in mean scale increment between May and August, only significant in 1985 ($p < 0.01$). Maximum marginal increment was reached by December. Scale growth in 1985 was less than in the previous year.

4+ fish (Fig. 2.2d). In 1981 and 1982 checking occurred between the June and September samples. An apparent decrease in marginal scale increment from May to August 1984 was not statistically significant. There was a significant decrease from August to November 1985 ($p < 0.05$).

5+ fish In 5+ fish, there was a highly significant decrease between September 1985 (6.4 ± 2.8mm, 17 fish) and January 1986 (1.3 ± 3.5mm, 13 fish; $p < 0.001$). Otherwise, results of the 5+ and older age groups were inconclusive because of the few fish involved and their increased variability.

Loch Eck

1+ fish. Insufficient data.

2+ fish (Fig. 2.3a). Checking took place between April or May and June. Marginal scale increment was maximal in November or December and remained constant until check formation. Scale increment in January 30th 1987 was very significantly higher than in January 30th 1985 ($p < 0.001$).

3+ fish (Fig. 2.3b). There were no significant differences between means, but the median decreased between May and August 1985. From December 1985 to June 1986 mean and median scale increments remained constant.

4+ fish (Fig. 2.3c). Apparent decreases between May and August 1985, September and November 1985, and April and June 1986 were not statistically significant. January 1987 had a significantly higher mean than January 1985 ($p < 0.001$).

5+ fish (Fig. 2.3d). The apparent decreases in mean scale increments from September to November 1985 and April to June 1986 were not significant. The scale increment in January 1987 was very significantly higher than in January 1985 ($p < 0.001$).

6+ fish (Fig. 2.3e). There was a significant decrease in marginal increment between May and August 1985 ($p < 0.05$) and August and November 1985 ($p < 0.05$). In 1986, the median decreased between April and June. There was no significant difference between January 1987 and 1985.

2.1.4 DISCUSSION

A Age Analysis

In general, powan scales were easy to interpret. False or accessory checks have been described in some coregonines (Hile, 1936; Deason & Hile, 1944; Smith, 1956; Hogman, 1968; Wilson & Pitcher, 1984a) but were rare in powan, and readily identifiable in that they did not occur on all the scales of the fish, or were incomplete, occurring only on part of the scale. Scales from powan up to 6+, and also fast growing powan were the easiest to read. With increasing age the amount of scale growth decreased (Figs 2.2, 2.3) and checks were formed closer together (Plate 8). Consequently scales from older or slow growing fish were more difficult to age, the problem sometimes being compounded by the older scales being thickened and therefore indistinct. If old fish grow so little that they do not form checks, scales will underestimate the true age. This is the major limitation of the scale method (Casselman, 1983, 1985). In *Coregonus clupeaformis*, Mills & Beamish (1980) found that although fin-ray and scale ageing methods correponded well for fast growing populations, in slow growing populations ages derived from fin-rays were higher than ages derived from scales. Although Aass (1972) found scales of *C. albula* L. easy to read there were discrepancies from otoliths at all ages, particularly in fish over 3 years old. Otoliths mostly gave higher readings. Agreement became poorer as the age increased, with a maximum discrepancy of 7 years. Aass concluded that otoliths were more reliable. Ausen (1976) also considered otoliths to be more reliable than both scales and opercular bones; again there was good agreement to 3 years of age, but in whitefish (C. lavaretus) over 7 years, otoliths could show an extra 1 to 10 zones over scales, the deviation increasing with increasing age. According to Ovychynnyk (1962), scales were "very good" in C. clupeaformis no older than 6 years.

In powan, there was good agreement between scales and otoliths up to and including 6 years of age, with some agreement up to 9 years old (Loch Eck; Table 2.2a). When otoliths and scales disagreed, otoliths gave the higher age, by up to 3 years. However, the level of confidence in otolith reading was low compared with scales. Powan otoliths were small and dense, and reflected light was necessary to read them even when ground to thin sections (compare Plates 11a and 11b). The density increased with increasing size, and so in older fish in particular it was very difficult to read the centre of the otolith. Although grinding sometimes helped, it was very time-consuming and the brittle otolith often fractured. An additional difficulty in interpreting powan otoliths lay in distinguishing between true and false annuli, when several both narrow and broad translucent zones were present ('splits' or 'secondary' rings: Williams & Bedford, 1974).

Opercular bones were the most difficult structures to interpret. It was frequently hard to identify true annular zones. In older fish, the centre of the bone became thickened and discoloured, so obscuring earlier annuli. The opercular readings in powan therefore mostly gave lower estimates of age than scale and otolith readings (Table 2.2b,c). Frost & Kipling (1959) experienced a similar difficulty with pike (*Esox lucius* L.) operculars, as did Goldspink (1978) in roach (*Rutilus rutilus* L.)and Blake & Blake (1978) in *Labeo senegalensis* Cuvier and Valenciennes. Wilson & Pitcher (1984a) found *C. autumnalis pollan* Thompson otoliths and opercular bones too difficult to analyse.

Of the calcified tissues, otoliths frequently show the greatest number of annular zones, and have therefore been used extensively for ageing long-lived fish such as some marine species (Williams & Bedford, 1974). The usual assumption has been that the structure showing the most annuli is the one which gives the correct age, but there is now evidence to suggest that this is not the case. Otoliths can give overestimates of the true age (Lee *et al.*, 1983 cited by Casselman, 1983). The daily incremental growth of otoliths, and their sensitivity to physiological change (Campana & Neilson, 1985) could increase their propensity to form false checks (e.g. Beaumont & Mann, 1984; Berg, 1985), and multiple zonation was observed in some powan otoliths.

In conclusion, scales were preferable for age and growth analysis of powan. They were the least time consuming to collect and examine, which is advantageous when large numbers of fish are involved. The level of confidence in scale reading was higher than for otoliths and opercular bones. A comparison of ages determined from the scales of the same 400 powan by A.F. McCulloch (1981, 1984) and the author gave an average correspondence of 81% (maximum agreed age 9+). Ricker (1975) has suggested that an 80-90% agreement between sets of readings was good.

Complete validation of all ages is rarely possible in natural populations (Casselman, 1985; Casselman et al., 1985). In powan, scale results were verified for the most abundant age groups up to and including 6 years (summary 2.1.4 p. 67-69). Results from fish over 8 or 9 years of age are dubious but powan of this age are very infrequent (Table 2.3). Use of an alternative calcified structure in old powan would not necessarily be advantageous. Beside the previous criticisms, Ausen (1976) noted that annuli could also fail to form in otoliths and opercular bones of old C. lavaretus.

B Growth Analysis

(a) Validation of Length Calculations

(i) Loch Lomond. As there was close correspondence between calculated and measured lengths at all ages except age 1 (Table 2.6a) the Fraser-Lee method of back-calculation with a constant of 106 was considered valid. Use of the lower geometric mean intercept of 91 as recommended by Ricker (1973) resulted in lower calculated lengths and poorer correspondence.

The divergence of the smallest powan ($\leq$250mm) below the line of best fit in the body-scale regression (Fig 2.1a) suggests a lower intercept and so a lower calculated length. However, the cause of the mismatch at age 1 in Table 2.6a is because the calculated length underestimates the measured length. The reason for this is year to year variation in growth rate, since the measured age 1^{-} fish were members of the 1984 year-class, which had an exceptionally high first-year growth rate (Ch. 2.2). Net selection for the largest of these individuals is also a possible cause of the mismatch. Indications are that the calculated age 1 length of 149mm may generally be too high as the few other powan of this age caught have been smaller. Two 0+ powan caught in December 1983 (1983 year-class) were 78mm long (McCulloch, 1984). Even if these fish had continued growth over winter, it seems unlikely that they would have reached 149mm by the April 'birthday'. A one year old fish in April 1987 (1986 year-class) was 85mm in length. Another of the same year-class, caught in July 1987 (1+) was 103mm long. In June 1988, a 100mm 1+ powan was caught (1987 year-class). The shoal of juveniles seine-netted in July 1969 was possibly composed of two main age groups (Ch. 1, Fig. 1.4). They were either 0+ and 1+ or 1+ and 2+. The mean length of the younger supposed age group was 98 ±6.9mm. The older age group had a mean length of 132 ±4.6mm. In July, about half the growing season remains, so it is not improbable that the first age group represented exceptionally fast growing 0+ fish when the growth rate of the 1984 year-class is considered, but comparison with 0+ and 1+ fish of other year-classes suggests that the first age group was more likely to have been 1+.

Although the allometric difference in the body-scale relationship of smaller powan in Fig. 2.1 suggests a lower intercept, when a separate regression of 282 Lomond powan ≤250mm was carried out, the resulting intercept was only slightly lower than the general 106 intercept (104mm r = 0.854). Attempts to determine the body-scale relationship at smaller lengths were negated because of low numbers. If the mean length at age 1 in Loch Lomond was assumed to be 100mm, an intercept of around 43mm would be needed in the Fraser-Lee equation to give this figure. However, this is purely speculative, and using the 43mm intercept would give too low results at later ages. Pending further evidence and because of the large size of the 1984 1 year olds, the general intercept of 106 for age 1 powan was retained in this study.

(ii) Loch Eck The fact that there was no correspondence between calculated and measured lengths except at ages 5, 10 and 11 (Table 2.6b) suggests that the method of ageing and back-calculation is wrong. However, the calculated length was neither a consistent over or under-estimate, indicating that year to year variation in growth rate (Ch. 2.2) might be a cause of the discrepancies in measured lengths, particularly since the sampling period extended over only two years. So instead of combining the two years for the mean measured lengths as in Table 2.6b, the mean measured lengths were calculated for each sampling year separately: 1985 (February, March, May) and 1986 (February, April; Fig. 2.4, Table 2.11). In both years there was the same non-correspondence relative to the calculated lengths, but the change from under- to overestimation occurred one age group later in 1986 than in 1985. When year-classes were assigned to the age groups it was seen that in both sampling years measured lengths of the year-classes 1984 to 1981 fell below the overall calculated growth curve, while the 1980 to 1976 year-classes had measured lengths above the calculated curve. The mismatch could therefore have resulted from variation in growth rate between years, rather than from incorrect scale reading and back-calculation. Consequently a direct comparison was made between measured and calculated lengths of specific year-classes (Table 2.11, derived from back-calculations for individual year-classes: Appendix 3). The correspondence was improved, with no significant differences between calculated and measured lengths at age 2 and from ages 5-11 (except age 7, 1979 year-class). Ages 3 and 4 still showed a highly significant difference in both sampling years. The calculated lengths overestimated the measured lengths by 8.6mm for the 3 year olds (1982 year-class) which increased to 14.8mm at 4 years old (1982 year-class). The difference was 19.6mm for the 4 year olds of the 1981 year-class.

The lower intercept of 73mm derived from the geometric mean regression (Ricker, 1973) did not improve results since using it only decreased the average calculated lengths at ages 3 and 4 by 3mm, which is not significant (Table 2.12). Also, use of the geomtric mean intercept resulted in a significant and inappropiate decrease in calculated length at age 2.

The general body-scale regression was calculated using fish sampled throughout 1985 (Table 2.1). In 1985, the predominant year-classes were the 1982 year-class (3 year olds) and the 1981 year-class (4 year olds; Ch. 2.3,

Fig. 2.14). It is strange that although these 3 and 4 year olds were the most abundant fish in the body-scale regression, the resulting intercept of 87mm gave too high a calculated length at those ages.

Length-frequency distributions have been found useful in analysing and verifying age structures of populations (Bagenal & Tesch, 1978; Wilson & Pitcher, 1984a; Casey et al., 1985; MacDonald, 1985; Casselman, 1985). Ideally, the age groups are represented by a series of modes (peaks, or in the case of weak year-classes, troughs). In practice, usually only the smaller fish exhibit distinct modes, because the lengths of the older age groups overlap (Le Cren, 1947). Fig. 2.5 shows length-frequency distributions for Loch Eck powan (measured lengths). The class length interval is 7mm. Because seasonal changes in length over the entire sampling period would cause overlapping of the age groups, the samples were divided into half year periods:

(i) September, November and December 1984.
(ii) February, March and May 1985.
(iii) September, November and December 1985.
(iv) February and April 1986.

Between the end of one year and the beginning of the next, the lengths of the maxima (peaks) and minima (troughs) remained consistent, inferring that there was little growth from September to May. The growing season was between April-May and September, causing a temporal progression of peaks and troughs from smaller to larger. For convenience, the peaks and troughs in Fig. 2.5 were designated P1-P3 and T1-T2.

Peak 1 (P1). The mean modal length of P1 in early 1985 was 324mm. In early 1986 the mean modal length was 338mm (class 27), representing an increase of 14mm, similar to the 11mm increment between calculated lengths at ages 5 and 6 (Table 2.13). However, it could also be argued that the increment is similar to that between ages 8-9 and 9-10. P1 almost certainly represents several age groups with overlapping lengths.

Trough 1 (T1). In early 1985, the lowest class frequency in this trough occurred at a mean length of 275mm (class 17). By the start of 1985, the trough minimum had progressed to a mean 296mm (class 20), an increase of 21mm, which corresponds with the calculated increment of 23mm between age 4 and 5 (Table 2.13). On paper, T1 represents a weak year-class.

Peak 2 (P2). The mean modal length of 219mm in early 1985 (class 9), progressed to 254mm in 1986 (class 14). The 35mm increment corresponds well with the calculated increment of 38mm between ages 3 and 4 (Table 2.13).

Trough 2 (T2). T2 had a mean length of 219mm (class 9) in 1985. This trough represented the 1983 year-class which was known to be exceptionally weak (Ch. 2.3). In April 1986 the 1983 year-class was 3 years old, confirming that P2, with the same modal length the previous spring, was mainly composed of 3 year olds.

Peak 3 (P3). P3 had a mean modal length of 191mm in 1986 (class 5), and was barely present at the end of 1985. Since T2 represents the 3 year olds, P3 must represent the

2 year olds. Comparison with the mean calculated length at age 2 confirms this deduction (Table 2.6b, 193mm).

Summary of suggested ages (mean modal lengths in brackets):

P1	≥5 (324)	≥6 (338)
T1	4 (275)	5 (296)
P2	3 (219)	4 (254)
T2	-	3 (219)
P3	-	2 (191)

Although the length increments of the peaks and troughs in the length-frequency distribution appears to correlate with those back-calculated from scales, the mean lengths of the suggested age groups either did not correspond, or corresponded only approximately with measured and calculated lengths of the age groups derived from scale reading (Tables 2.6b, 2.11). One reason may be the overlapping of age groups in the length-frequency distribution. T1, the apparent weak year-class which progressed at a rate expected of the 4-5 age group, corresponds with the gap observed in the general body-scale regression (Fig. 2.1b). The mid-point of the gap was estimated to be 284mm. However, an analysis of year-class strengths based on scale ageing (Ch. 2.3) did not show a weak year-class at these suggested ages. In 1985, the age 4 fish were the 1981 year-class, which was the second most abundant that year. The 1980 year-class (5 year olds) was the third most abundant, while the dominant year-class was 1982 (3 year olds). Reference to the comparison of calculated and measured lengths in 1985 (Fig. 2.4, Table 2.11) shows that the change from calculated lengths underestimating to overestimating measured lengths occurred between the calculated lengths of 269mm (1981 year-class) and 310mm (1980 year-class). It therefore appears likely that a change in growth rate between the two year-classes was responsible for T1 and the 'gap' (Fig. 2.1b) which may have consisted mainly of smaller 1980 fish and larger 1981 fish. Hence, to deduce T1 as a weak year-class would be wrong. Length-frequency analyses should therefore be used circumspectly and with information from other sources.

The poor agreement between measured and calculated lengths at ages 3 and 4 remains at present unexplained. One possibility is the short sampling time; further sampling is required to determine whether the mismatch is restricted to the 1981 and 1982 year-classes, or if it occurs in all years. As other indications are that scale readings are reasonably valid up to 5 or 6 years of age (summary Ch. 2.1.4, p. 68) and agreement between otoliths and scales has been obtained up to 8 or 9 years, it was decided to continue working on the basis of the scale ageing and back-calculation method using the Fraser-Lee equation with 87 as constant. The length-frequency analysis suggests that the calculated annual length increment is valid, at least up to age 4. The validity of the calculated length at age 1 (130mm Table 2.6b) could not be established. The only 0+ Loch Eck powan sampled was caught in January 1987 (1986 year-class) and was 98mm in length (Plate 1).

(b) Allometric Change in the Body-scale Relationship

The deviation of the smallest powan below the line of best fit in both lochs indicates that the scale grows faster relative to the body in younger powan than it does in older powan (also noted by van Oosten, 1928). Consequently the intercept on length of young fish will be lower than that of older fish (also found by Hogman, 1970). The length of deviation in powan was estimated as $\leq$250mm in Loch Lomond and $\leq$215mm in Loch Eck. As stated earlier, a separate regression of Loch Lomond fish $\leq$250mm gave an intercept only slightly lower than 106 (104mm, 282 fish, r = 0.854). When 133 Loch Eck powan $\leq$215mm in length were separately regressed, the intercept obtained was higher than the general 89mm intercept (109mm, r = 0.765). At smaller lengths the body-scale regressions were invalid.

Comparison with calculated lengths at age (Table 2.6a,b) shows that the allometric change in the body-scale relationship occurred in powan of between 2 and 3 years of age in both lochs. It seems probable that the change is related to the attainment of sexual maturity, which occurs at this age (Ch. 4).

(c) Comparison of Growth in the Two Lochs

Loch Eck powan are significantly shorter at a given age than the Loch Lomond powan (Fig. 2.6, Table 2.14); the difference in calculated length at age ranges from 19 to 32mm. Comparison of growth rates (Table 2.8b) shows that in eight out of ten years of life, it is in fact the Loch Eck powan which have the significantly higher rate of growth.

Although Loch Lomond powan only grow faster than Loch Eck powan in their first (0-1) and third (2-3) years of life, they maintain the initial length advantage. In comparing the schelly (C. lavaretus) of Haweswater and Ullswater Bagenal (1970) found that the Ullswater fish were larger at each age because they grew much faster in their first year. Taking these two observations into account, it would seem that the amount of first year growth is critical to the final size. Brown (1946a) considered that the size reached by brown trout (Salmo trutta L.) in different waters partly depended on their growth rate in the first year. Van Oosten (1928) came to the same conclusion for Leucichthys artedi Le Sueur, observing that from the point of view of the fisheries, the growth history of first-year fish is of extreme significance. However, analysis of year to year variations in growth (Ch. 2.2) suggests that, in powan at least, it is not just the first year of growth which is of importance in determining the final relative size, but the first three years of growth. Loch Lomond powan have a higher growth rate than Loch Eck powan in two out of the three crucial years.

(d) Standard and Shoulder Scale Comparison

For growth analysis, scales must be taken from a standardised location since their size, shape and growth varies with their position on the fish (van Oosten, 1923; Dannevig & Host, 1931; McCulloch, 1981). In salmonids, scales are generally taken from an area between the lateral line and the dorsal or adipose fin (here called 'standard' scales) as these scales are the largest and least variable (van Oosten, 1928; Edsall, 1960; Kipling, 1962; Hogman, 1968; Ausen, 1976; Johnson, 1976; Mills & Beamish, 1980; Wilson & Pitcher, 1984a; Barber & Walker, 1988). A traditional position for sampling salmonid scales used to be the 'shoulder', dorsal to the lateral line and anterior to the dorsal fin (van Someren, 1952; Jones, 1953; Ball & Jones, 1960). Powan scales from the 1965-1967 samples were also taken from this shoulder area (P.S. Maitland pers. comm.; Ch. 6).

In powan, standard scales are preferable to shoulder scales. The shoulder area was more likely to be denuded of scales by the gill nets than was the standard area. While collecting the May 1986 sample of shoulder scales, 25 fish on which standard scales were present lacked shoulder scales.

Shoulder scales were generally more indistinct than standard scales. For this reason, 16 shoulder scale samples had to be discarded compared with 5 standard scale samples (from 62 fish).

Shoulder scales were more variable, as evidenced by their lower correlation coefficient in the body-scale regression compared with standard scales (p. 40). Kipling (1962) studied scales of brown trout (Salmo trutta) from different populations. All the scales were removed from below the dorsal fin near the lateral line, except for one sample which was taken from the shoulder. The shoulder sample had a greater variance around the body-scale regression line than the standard dorsal samples. Kipling suggested that the greater variance resulted from the shoulder being a rather vague and ill-defined area.

Shoulder scales were smaller than standard scales (Table 2.4). Dannevig & Host (1931) found that back-calculated lengths decreased from the posterior to the pectoral region. In powan, the higher shoulder intercept of 129mm should compensate for the smaller size of the scales. However, at age 1, a significantly higher back-calculated length was derived from shoulder scales (129 intercept) than from standard scales (106 intercept, Table 2.9). The length discrepancy decreased with increasing age and there were no further significant differences. Substitution of the 106 standard intercept into shoulder scale back-calculations resulted in similar calculated lengths at age 1, with shoulder scales then giving progressively lower lengths with increasing age compared with standard scales.

After the first appearance of scales which is at 35mm in powan (Slack _et_ _al_., 1957), scalation proceeded rapidly. In _C_. _artedi_, the first scales were noted at 34mm and the fish were fully scaled at 55mm. _C_. _kiyi_ first developed scales at 51mm (Hogman, 1970). Initially, there is little difference between standard and shoulder scale sizes in powan, but the disparity between the rate of scale growth in various positions on the fish increases with increasing fish length and allometric changes in body proportions (Plates 1 and 2). In Table 2.4, the difference in size between standard and shoulder scales increased up to 4 or 5 years of age then remained constant at 1mm, probably because of reduced growth rates. Technically, because of the size and shape difference, the intercept calculated from each scale position only should be used in back-calculations from those scales. However, the fact that there was initially little difference in scale size resulting in the shoulder intercept giving overinflated calculated lengths at the youngest ages, indicates that shoulder back-calculations using the standard intercept are more valid, particularly as it has already been suggested that calculated lengths at age 1 from standard scales using the standard 106 intercept are too high (p. 48).

(e) Seasonal Growth

(i) Monthly body-scale relationships. The variations in body-scale relationships in different months from Loch Lomond were erratic and inconclusive, while those from Loch Eck were more consistent (Table 2.10). The higher intercept in the months of June to September in Loch Eck suggests that in these months the body was growing faster relative to the scale. However, this analysis is too crude to be reliable; an improved method of analysing seasonal scale growth is to measure the uptake of ^{14}C-glycine by the scale in vitro (Ottaway & Simkiss, 1977a,b; Ottaway, 1978; Adelman, 1980; Smagula & Adelman, 1983). The rate of incorporation of labelled amino acid by the scale forming cells is related to the rate of growth of the fish at the time of sampling. McCulloch (1981, 1984) used this technique for Loch Lomond powan.

Ottaway & Simkiss (1979) working with bass, Dicentrarchus labrax, showed that there were seasonal variations between scale and body growth, so establishing that the apparent isometric relationship between scale and body length is actually the sum of a number of allometric interactions, although a long-term proportional relationship must exist or back-calculations from scales would not be possible. Casselman (1978, cited by Casselman, 1983) concluded that in northern pike (Esox lucius), isometric growth is a transitional stage that rarely and possibly never occurs. Therefore in deriving a general body-scale regression intercept for back-calculation, it is best to use samples from over the period of a year.

(ii) Check formation and scale growth. In both lochs, scale growth occurred from May to September with little or no growth from October to April (Fig. 2.2, 2.3). McCulloch (1984) found elevated ^{14}C-glycine uptake levels from May to early November. Similar times of growth have been reported in other coregonines. Van Oosten (1923) determined that scale growth in C. clupeaformis was from April to September with no growth from October to March. Growth in Lake Michigan lake herring (Leucicthys artedi) took place from May to October (Smith, 1956); and C. albula in Pluszne Lake, Poland, grew during June to October (Marciak, 1962). There may be some growth in 1 year old powan over winter (Fig. 2.2a). McCulloch (1984) showed a transitory increase in glycine uptake of powan scales in February, which was most pronounced in the 1+ age group.

Scale increments were greatest in the youngest fish and decreased with increasing age (Fig. 2.2, 2.3). ^{14}C-glycine incorporation results confirm that scales of the youngest fish are the most rapid growing (Ottaway & Simkiss, 1977a, 1979; McCulloch, 1981, 1984). Check formation marks the start of the new season's scale growth. The time of check formation was more difficult to assess in the older fish because of their reduced growth rate and the smaller sample sizes. The ambiguity may also arise from greater individual variation in the time of check formation in older fish. Consequently the annual nature of check formation, the main criterion on which age and growth estimations are based, could only be confirmed in Loch Lomond powan from ages 1+ to 4+ (Fig 2.2). The method was even more limited in the Loch Eck powan which were sampled over a shorter period of time. Check formation could only be observed as being annual in the 2+, 3+ and 4+ age groups (Fig. 2.2), but the decreases were not statistically significant. There is a hint that the younger powan form checks earlier in the year (May to July) than the older fish which may not check until August or September. McCulloch (1984) found the time of maximum ^{14}C-glycine uptake to be June and July in 2+ and 3+ Loch Lomond powan, and August and September in the 3+ to 5+ age groups. There was slight variation between years in the time of maximum glycine uptake in 3+ powan. Although this evidence is rather circumstantial, many other studies have suggested that the younger fish start growth earlier in the season (Smith, 1956; Runnstrom, 1957; Ball & Jones, 1959; Backiel, 1962; Ciepielewski, 1971; Ottaway & Simkiss, 1979; Adelman, 1980).

(iii) Factors regulating seasonal growth and check formation. Because of the complex nature of growth, the factors which regulate the initiation and cessation of seasonal growth, and consequent check formation are incompletely understood. Some possible environmental and physiological factors are the seasonally recurring ones of temperature, photoperiod, food availability and reproduction In the tropics where there is often little change in temperature and photoperiod, varying water levels have been postulated as being a seasonal cue for growth processes (Johnels, 1952; Blake & Blake, 1978).

Temperature is a major growth controlling factor through its direct effect on metabolic and digestive rates (Brett, 1979). Many species, particularly the juveniles, respond positively to increased temperature until a species specific maximum is reached. Growth rate then decreases as the energy requirements of the increased metabolism exceed the energy ingested (Brown, 1946c; Swift, 1961; McCormick *et al*., 1971; Elliott, 1975a,b, 1976c; Cui & Wootton, 1988b). Skurdal & Andersen (1985) demonstrated that an elevated temperature during the egg and alevin stage increased the number of circuli and rate of circulus formation in brown trout. Van Oosten (1923) suggested that in adult whitefish (*C. clupeaformis*), temperature was a primary factor in check formation (although only secondary in juveniles). Bhatia (1932) disagreed, claiming that variations in temperature had no direct effect on the production of annuli on rainbow trout scales. Both Hogman (1968) in coregonines and Brown (1946b) in brown trout found that check formation still occurred under experimental conditions of constant temperature. In wild sockeye salmon (*Oncorhynchus nerka*), annuli formed between November and January, a time of decreasing temperatures (Barber & Walker, 1988).

Photoperiod acts as a directive factor in growth processes, stimulating and synchronising neuroendocrine responses (Brett, 1979; Scott, 1979; Lundqvist, 1980; Skarphedinsson, 1983). Hogman (1968) found photoperiod to be more closely related to growth rate than any other variable; the annulus did not begin to form until mid-March, when the daylength was increasing. Others have also suggested photoperiod to be a factor initiating check formation (Swift, 1955; Barber & Walker, 1988). Brown (1946b) observed check formation under constant conditions of photoperiod, as well as temperature and other environmental variables, but did not reject the possibility that photoperiod was involved in seasonal growth. However, experimentally altering photoperiod did not affect feeding and growth of cod (*Gadus morhua* L.), leading Hall (1988) to suggest that this was evidence for an endogenous rhythm in growth rate, a suggestion earlier made by Brown (1946b) and Ricker (1979).

Reproduction represents a large energy investment (Ch. 3; Ursin, 1979; Wootton, 1979) and so is generally considered to be incompatible with somatic growth (Iles, 1974) and consequently perhaps a cause of check formation. Lundqvist (1980) proposed that gonadal maturation might have an inhibitory effect on photoperiod-induced growth in precocious male salmon parr, through an increase in the concentrations of androgen or gonadotropins. Other hypotheses are that the demands of gametogenesis divert energy and materials from somatic growth. Hogman (1968) suggested that high protein demand during gonadal growth diverts protein from scale formation. Van Oosten (1923), van Someren (1950) and Garrod & Newell (1958) also considered gonad maturation to be the major factor in check formation.

Food is ultimately what all growth processes depend on. When fish are starved and have no reserves to draw on, growth ceases. Circuli did not form on scales of starved salmon (Bilton, 1974). In extreme cases, notably migratory salmonids, scale reabsorption occurs (Crichton, 1935; van Someren, 1937; Bilton, 1974). A four year old powan, accidentally kept on low rations from hatching, only showed two checks on the scales. Ottaway & Simkiss (1977a) and Ottaway (1978) demonstrated biochemically that the activity of scale forming cells is greatly reduced by starvation. The spacing of circuli is affected by food availability (Bhatia, 1932; Barber & Walker, 1988). Periods of starvation can result in false or accessory check formation (Bhatia, 1932; van Oosten, 1961; Ottaway & Simkiss, 1977b; Campana, 1983). Wilson & Pitcher (1984) suggested that accessory check formation in pollan occurred when the diet changed from plankton to benthos in the autumn. However, a similar seasonal diet change occurs in Loch Lomond powan (Pomeroy, 1987) with no formation of accessory checks.

In the powan lochs, temperatures increase from March and are maximal in July or August (Table 1.1). Minimum temperatures occur in January and February. Because of the stagger in the time of check formation between age groups and individuals, somatic growth may commence during increasing, maximum, or decreasing temperatures, and so temperature does not appear to initiate growth directly. The same criticism applies to photoperiod. Both factors do have important indirect effects through their influence on the production of prey organisms. In powan, food availability and level of energy reserves appear to be most closely related to the time of growth.

In Loch Lomond, the main food intake was from May to September, during which time a positive energy balance exists (Pomeroy, 1987). Lipid reserves were built up in Loch Lomond adults from May to a maximum in August or September (Rashid, 1984). A minimum level of energy reserves may be required to be achieved before somatic growth can begin. Adults might take longer than juveniles to replenish energy reserves depleted over winter, because of their greater bulk and the greater loss occasioned by gonad growth and spawning compared with non-reproductive juveniles. If so, this could explain why adults do not start growth until later in the season. In many teleost species, reproductive effort increases with increasing body size (Love, 1970; Hislop, 1975; Craig, 1977). Consequently, the larger (and older) the fish, the greater the energy reserves which need to be restored and the longer the recuperation period before growth. The longer growing season thus available to the younger age groups would contribute to their greater somatic growth.

Retardation or cessation of somatic growth could be determined by the stage of gonad growth, a decreased level of energy reserves (Swift, 1955), or an increased concentration of growth inhibiting hormones (Lundqvist, 1980). Reduced energy intake in Loch Lomond from October to April is a possible growth inhibitory factor, but in Loch Eck feeding continues all year, except briefly when spawning (Pomeroy, 1987). At present, there is no evidence that growth in Loch Eck powan starts earlier or continues for longer than in Loch Lomond powan.

The problem with the hypothesis that gonad growth inhibits somatic growth is why the juveniles should also reduce growth in winter if they are not reproducing. Van Someren (1950) made the vague proposition that immature fish had an innate physiological rhythm foreshadowing the adult reproductive cycle, an idea also subscribed to by Iles (1974; see Ch. 4). Hogman (1968) offered no explanation. Van Oosten (1923) suggested that food was a primary factor in the formation of checks in immatures. Again, although the reduced winter feeding in Loch Lomond could be postulated as causing juvenile growth retardation, Loch Eck powan feed continually and Pomeroy (1987) noted that in both lochs, a high proportion of juveniles had material in their stomachs all year round. Seasonal variation in temperature and photoperiod therefore remain as possible factors cueing somatic growth, perhaps acting by releasing and limiting growth in both juveniles and adults rather than by directly initiating growth. Allen (1940, 1941) postulated that in young wild salmon, growth was released when water temperature exceeded 7 °C and was limited when water temperature fell below 7°C. A short day-length could reduce production of growth stimulating hormones. Dabrowski (1982a) suggested that in pollan, low temperatures, even in these cold water fish, might reduce digestive efficiency.

C Summary of Points Indirectly Verifying the Use of the Scale Method in Powan

(a) Loch Lomond

(i) Comparison of scale assessed age with ages assessed from otoliths and opercular bones (maximum sample age 5+):

Otoliths 85% agreement; maximum age 5+.
Operculars 63% agreement; maximum age 5+
(Ch. 2.1.3, p. 37; Table 2.2).

(ii) Comparison of ages assessed from standard scales and shoulder scales of the May 1986 sample:

71% agreement; maximum agreed age 7+ (Ch. 2.1.3, p. 37).

(iii) Close correspondence of back-calculated and measured lengths at ages 2-10 inclusive (Ch. 2.1.3, p. 39; Table 2.6a).

(iv) A physical mark present in scales of the 1984 year-class in the form of an exceptional amount of growth from the focus to the first check.

Observed from 0+ (Plate 7) to 2+ (rising 3, March 1987).

(v) Analysis of marginal scale increment (1981-1987) confirms annual nature of check formation for 1+ to 4+ age groups (Ch. 2.1.3 p. 41-42; Fig. 2.2).

(vi) Annual progression of strong and weak year-classes were followed up to a maximum age of 7+ (weak 1977 year-class). (Ch. 2.3.3; Fig. 2.13).

(vii) Correspondence check with A.F. McCulloch:

Average agreement 81%; maximum agreed age 9+ (Ch. 2.1.4, p. 46-47).

(b) <u>Loch Eck</u>

(i) Comparison of scale assessed age with ages assessed from otoliths and opercular bones:

Otoliths 75% agreement; maximum age 9+.

Operculars 56% agreement; maximum age 7+.

(Ch. 2.1.3, p. 37; Table 2.2).

(ii) Correspondence of back-calculated and measured lengths at all ages except for 3 and 4 year-olds. (Ch. 2.1.4 p. 50; Table 2.11).

(iii) The change from the overall calculated lengths overestimating to underestimating the measured lengths occurred one age group later in 1986 (between 5 and 6) than in 1985 (between 4 and 5). This indicates annual check formation at these ages (Ch. 2.1.4, p. 49; Fig. 2.4).

(iv) Maxima (peaks) and minima (troughs) in the length frequency distribution progressed annually at a rate corresponding to calculated growth increments (up to 4+). (Ch. 2.1.4, p. 52-53; Fig. 2.5).

(v) Analysis of marginal scale increments (September 1984-January 1987) suggested annual check formation in the 2+ to 4+ age groups (Ch. 2.1.3, p. 43; Fig. 2.3).

(vi) Annual progression of the weak 1983 year-class was followed from ages 1+ to 3+ (Ch. 2.3.3; Fig. 2.14).

2.2 GROWTH FROM YEAR TO YEAR

2.2.1 INTRODUCTION

Sampling a population over several years in order to determine whether there are alterations in growth rate is rarely practicable. If ageing and back-calculation methods are valid, calcified structures will reflect any temporal growth changes. Osseochronometry is therefore a useful technique in fisheries research, both for investigating the effects of annual variations in environmental and physiological conditions on growth, and also for monitoring the status of natural populations. Significant changes in growth rate can indicate unusual conditions, such as pollution (van Oosten, 1928), changes in water chemistry (Mills, 1985), also ill-health, variations in food availability and variations in population density (Weatherley & Gill, 1987).

Fish growth is affected by population density even when there is sufficient food (Brown, 1946c; Weatherley & Gill, 1987). A higher than optimum population density results in a decreased growth rate, frequently accompanied by loss of condition through starvation and disease. In Loch Lomond in 1968, large numbers of powan affected by fungus and an unidentified pathogen, died. Prior to this population crash, powan were very abundant, small and in poor condition. Favourable conditions leading to an accelerated growth rate may arise through a reduction in population density, as occurred after the 'crash' in Loch

Lomond (Roberts et al., 1970). Reduced population density may also result from an increased level of predation and from commercial exploitation (van Oosten, 1928; Edsall, 1960; Healey, 1980).

Significant differences in growth rate of powan from year to year has already been noted. In Loch Lomond there was little scale growth in 1985 (Fig. 2.2). In Loch Eck, a change in growth rate occurred between the 1980 and 1981 year-classes (Fig. 2.4). There was also a significantly increased amount of scale growth in January 1987 (Fig. 2.3).

2.2.2 MATERIALS AND METHODS

Loch Lomond: November 1980 to March 1987.
Loch Eck: September 1984 to January 1987.

All powan were assigned to year-classes. Assigning fish to year-classes is complicated by variation in the time of check formation (Ch. 2.1.4, p. 61) and so powan were given a standardised 'birthday'. Powan hatch in the laboratory about April (Ch. 1.3 p. 19; D.B.C. Scott pers. comm.). It is also convenient that somatic growth is minimal at this time of year, prior to formation of the next check (Figs 2.2, 2.3; McCulloch, 1984). Therefore April 1st was designated as the powan 'birthday'. If it was uncertain to which year-class a fish belonged, then that fish was omitted from this analysis.

For each year-class, the mean calculated length at age and the mean growth rate for each year of life were computed. If differences between years were shown to be significant by a preliminary ANOVA, then a Tukey-Kramer multiple comparison test (Sokal & Rohlf, 1981) was carried out to identify which year-classes differed significantly at the $p \leq 0.05$ level. The Tukey-Kramer test was selected as being the most suitable to use with the very unequal sample sizes, nevertheless it was still sensitive to year-classes which had sample numbers comparatively lower than others in the test, suggesting that those year-classes did not differ significantly.

The results were analysed in two ways:

A _Growth of year-classes_ To determine whether year-classes maintain the same fast or slow growth rate throughout their lifetime, and whether the size attained at a particular age largely determines the final size.

B _Growth of age groups_ To determine whether all age groups show similar growth trends (increased or decreased growth rate) in the same growing season.

2.2.3 RESULTS

A Growth of Year-Classes

In both lochs growth varied very significantly from year to year. Differences among years in lengths at age were statistically significant up to and including age 6 in Loch Lomond (Table 2.15a) and age 8 in Loch Eck (Table 2.15b). There were significant differences between growth rates up to and including age group 5-6 in both lochs (Table 2.16).

In the figures of lengths at age (Figs 2.7, 2.9) and growth rates (Figs 2.8, 2.10), broken lines were added to clarify age groups and fluctuations between years. This was only done up to age 5 (4-5 in growth rate figures) to avoid confusion in the figures, deriving from the decreased and more variable growth of the fewer, older fish. The data for Figs 2.7 to 2.10 are tabulated in Appendices 1 to 4.

In Tables 2.17 and 2.18, and in the text, year-classes are ordered by length or growth rate, the greatest first. The symbol >> denotes which year-classes were significantly greater or lesser than which other year-classes at the 0.05 level (results of Tukey-Kramer test, year-classes ordered as in Tables 2.17, 2.18).

(a) Loch Lomond (Figs 2.7, 2.8; Tables 2.17a, 2.18)

(i) Lengths at age 1

1984 >> all year-classes except 1985 (few fish)

1983 >> all year-classes except 1984, 1985, 1973

1981 >> 1979

Growth rates 0-1

1984 >> all year-classes except 1985

1983 >> all year-classes except 1984, 1985, 1977, 1972

Members of the 1984 year-class had the highest growth rate and were the longest at age 1, followed by the 1983 year-class.

(ii) Lengths at age 2

1983 >> 1981, 1979, 1982, 1978, 1974, 1973, 1972

1980 >> 1984, 1981, 1979, 1982, 1978, 1974, 1973, 1972

Growth rates 1-2

1980 >> 1978, 1981, 1983, 1984

1984 << all year-classes except 1974, 1973, 1972

In this age group, members of the 1984 year-class had the lowest growth rate and consequently ranked 4th in length. Powan of the 1983 year-class were the longest. Although the growth rate of the 1983 year-class was only just above average, these fish maintained the length advantage from the previous year. The year-class with the highest growth rate was 1980, which therefore ranked 2nd in length (not significantly shorter than 1983). The shortest year-classes were 1972, 1973 and 1974.

(iii) Lengths at age 3

1979 >> 1978, 1982, 1981, 1983, 1974, 1973, 1972

1980 >> 1982, 1981, 1983, 1974, 1973, 1972

1976 >> 1974, 1973, 1972

1975 >> 1973, 1972

1972 << all year-classes except 1983, 1974, 1973

Growth rates 2-3

1979 >> all year-classes except 1978, 1974, 1973, 1972

1978 >> 1980, 1981, 1983

1983 << all year-classes except 1972

Members of the 1983 year-class had the lowest growth rate of this age group, which resulted in a below average length (ranked 8th out of 11).

The 1979 year-class had the highest growth rate and consequently the longest fish, together with the 1980 year-class which ranked 2nd in length despite a below average growth rate. The lengths of fish in the 1976 year-class (3rd) and 1974 year-class (4th) were not significantly lower.

Fish of the 1978 year-class ranked second highest in growth rate (not significantly different to the 1979 year-class), and so increased its relative length ranking to 5th out of 11 (from 10th out of 13 at age 2).

(iv) Lengths at age 4

1979 >> 1981, 1982, 1973

Growth rates 3-4

1976 >> 1979, 1981, 1980

Powan in the 1979 year-class continued to be the longest, although their relative growth rate decreased to below average (ranked 7th out of 10). The 1980 year-class, had the second lowest growth rate, and moved down the length ranking to just above average (5th out of 10), although these fish were not significantly shorter than the 1979 year-class.

Although members of the 1973 year-class had the highest growth rate, it was not significant because of the small sample size. 1973 remained the second shortest year-class, as at ages 2 and 3. Fish of the 1976 year-class ranked second highest in both growth rate and length, together with 1975 fish which had an above average growth rate since 1-2. Neither year-class differed significantly in length to 1979, nor do the 1978 and 1977 year-classes. In this age group the year-class with the lowest growth rate was 1982 which consequently had fish of below average length.

(v) Lengths at age 5

1979 >> 1981, 1972

1972 << all year-classes except 1981

Growth rates 4-5

1975 >> 1977, 1976, 1978, 1980, 1979, 1981

1973 >> 1979

The 1979 year-class still had the greatest mean length although the fish were only significantly longer than the two shortest year-classes: 1972, which had remained at the bottom of the ranking since age 1; and 1981, which had the lowest growth rate of this age group. Though the 1979 year-class had the second lowest growth rate, the fish retained their size advantage. Members of the 1975 year-class had the highest growth rate and so ranked third in length.

(vi) Lengths at age 6

1972 << all year-classes except 1980

Growth rates 5-6

1972 >> 1975, 1978, 1979

Despite having the lowest growth rate, the fish of the 1979 year-class still ranked first in length, although only fish of the 1972 year-class were significantly shorter. Powan in the 1978 and 1980 year-classes also had low growth rates but were of above average length. Powan in the 1972 year-class had the highest growth rate, but remained the shortest in length. The 1976 year-class ranked second in length and growth rate, these fish having been above average in size since age 2.

(b) Loch Eck (Figs 2.9, 2.10; Tables 2.17b, 2.18b)

The 1972 year-class was excluded from the Tukey-Kramer multiple comparison test as it consisted of only a single specimen. The 1983 year-class at age 3 was excluded for the same reason.

(i) Lengths at age 1 and growth rates 0-1

1975 >> all year-classes except 1973, 1974, 1976
1973 >> 1985
1974 >> 1979, 1982, 1980, 1984
1976 >> 1981, 1979, 1982, 1980, 1984
1984, 1978, 1981 >> 1979, 1982, 1980, 1985
1977 >> 1982, 1980, 1985
1979 >> 1985

Members of the 1975 year-class had the highest first year growth rate together with members of the 1973, 1974, and 1976 year-classes. Powan of the 1985 year-class had the lowest growth rate, second lowest were the 1982 and 1980 year-classes.

(ii) <u>Lengths at age 2</u>

1974, 1976, 1977, 1975, 1978 >> 1980, 1979, 1981, 1982, 1984

1973, 1979, 1981 >> 1982, 1984

1983 >> 1984

<u>Growth rates 1-2</u>

1980 >> 1978, 1982, 1976, 1981, 1975, 1984

1979 >> 1982, 1981, 1975, 1984

1977, 1978, 1982 >> 1981, 1975, 1984

1984 << all year-classes except 1973, 1975

The lengths of the year-classes separated into two divisions, as fish of all year-classes from 1978 and earlier were significantly larger than fish of the later year-classes, except 1983 (few fish).

Members of the 1980 year-class had the highest growth rate (with 1983, 1979 and 1977 year-classes), although they only ranked just above average in length (8th out of 12), having been one of the shortest year-classes in their first year.

Fish of the 1983 year-class, with the second highest growth rate, were of similar length (7th out of 12). Fish of the 1979 year-class ranked third highest in growth rate and 9th out of 12 in length (below average).

Powan of the 1984 year-class had the lowest growth rate and the shortest length. Fish of the 1975 year-class, the longest year-class in the first year, had the second lowest growth rate of this age group and so ranked 5th in length.

(iii) Lengths at age 3

1980 >> all year-classes except 1978, 1973, 1977
1978 >> 1976, 1981, 1982, 1975
1977, 1979 >> 1981, 1982, 1975

Growth rates 2-3

1980 >> 1981, 1982, 1976, 1975
1979 >> 1976, 1975
1981 >> 1975

As a result of their high growth rate in the second and third years of life, fish of the 1980 year-class were the longest at age 3, together with fish of the 1978 (3rd highest growth rate), 1973 (growth rate ranked 7th out of 10) and 1977 (growth rate ranked 6th) year-classes.

Powan in the 1975 year-class had the lowest growth rate and so became the shortest fish, followed by powan of the 1974 year-class, which were the longest at age 2 and ranked third at age 1. Then the 1982 year-class, which with a low first year growth rate and average second and third year growth rates, continued to be relatively small.

(iv) Lengths at age 4

1980, 1979 >> all year-classes except 1982, 1973
1982 >> 1976, 1975
1975 << all year-classes except 1973, 1976, 1974

Growth rates 3-4

1979, 1980 >> all year-classes except 1982, 1973

1982 >> 1978, 1976, 1977, 1975, 1974

1981 >> 1978, 1976, 1977, 1975

With the second highest growth rate of this age group, 1980 fish continued as the longest year-class, together with fish of the 1979 year-class which had the highest growth rate. The 1982 year-class ranked third in length, having had the third highest growth rate of this age category.

Members of the 1975 year-class had the third lowest growth rate, and therefore remained the shortest year-class, folloed by the 1974 fish (2nd lowest growth rate). Fish of the 1973 year-class had the lowest growth rate of this age group and ranked 7th out of 10 in length.

(v) Lengths at age 5

1979, 1980 >> all year-classes except 1973 (few fish)

1978 >> 1976, 1974, 1975

1977 >> 1974, 1975

1981 >> 1975

Growth rates 4-5

1979 >> all other year-classes

1978 >> 1981, 1980, 1976, 1975, 1974

Powan of the 1979 and 1980 year-classes were still the longest. The 1979 fish had the highest growth rate and so moved to ranking first in length; the 1980 fish had a decreased relative growth rate (5th out of 8) but retained their size advantage.

Fish of the 1978 year-class had the second highest growth rate and ranked third in length. The smallest fish with the lowest growth rates were still the 1975, 1974 and 1973 year-classes.

(vi) Lengths at age 6

1979 >> all year-classes except 1978, 1980

1978, 1980, 1977 >> 1976, 1974, 1975

Growth rates 5-6

1978 >> all year-classes except 1977, 1973

1977 >> 1976, 1975, 1980

Powan of the 1979, 1978 and 1980 year-classes continued to be the longest although the 1980 year-class had the lowest growth rate, and the relative growth rate of the 1979 year-class also decreased slightly (3rd out of 7). Fish of the 1978 year-class had the highest growth rate in this age group. The smallest fish were in the 1975, 1974 and 1973 year-classes.

(vii) Lengths at age 7

1979 >> 1976, 1973, 1974, 1975

1978, 1977 >> 1976, 1974, 1975

1976 >> 1975

Although there were no further significant differences in growth rates (Table 2.16b), members of the 1979 year-class continued to be the longest, followed by members of the 1978 and 1977 year-classes. 1975, 1974 and 1973 were still the three shortest year-classes.

(viii) Lengths at age 8

1977 >> 1974, 1975

1976 >> 1975

Powan of the 1977 and 1976 year-classes were the longest, powan of the 1974 and 1975 year-classes were the smallest.

The single member of the excluded 1972 year-class remained the smallest throughout (Fig. 2.9).

B Growth of Age Groups

(a) Variability of Year to Year Growth

(i) Loch Lomond (Figs 2.7, 2.8; Tables 2.15a, 2.16a). Growth in the first year was very consistent, with the exception of the fast growing 1983 and 1984 year-classes. If they were excluded, the between-year length range (Table 2.15a) decreased from 31mm to 13mm, and the coefficient of variation decreased from 5.07 to 2.62, lower than at the older ages. The first year growth rates, even without the exclusion of the 1983 and 1984 year-classes, were also considerably less variable than in older fish (Table 2.16a). Growth rates were most variable at 4-5, 5-6 and 6-7. Between-year variation in length was greatest at ages 10 and 3, then 2 and 7.

(ii) Loch Eck (Figs 2.9, 2.10; Tables 2.15b, 2.16b). As in Loch Lomond, growth was most consistent in the first year. Growth rates then increased in variability to a maximum at 4-5. There was most variation in length at age 11, then at ages 4, 5 and 6.

(b) Comparison of Growth in Individual Years

Growth rates are the most useful criterion when comparing growth in individual years, since they show immediate changes which may not be reflected by corresponding changes in lengths. The calendar years of growth were examined in chronological order from 1976 in Loch Lomond and 1975 in Loch Eck, extending from April 1st to March 31st. In the following analysis the year of life (age category) is given first, then the year-class in brackets. ↑ or ↓ represents the change in growth rate relative to the previous year-class, irrespective of statistical significance. A plus sign indicates average or above average growth rate. A minus sign indicates below average growth rate. A fraction, e.g. 5/12, indicates the relative ranking of the growth rate of that year-class compared with the other year-classes, in this case 5th out of 12.

(i) Loch Lomond (Fig. 2.8; Table 2.18a; Appendix 2)

1976-1977 (Loch Lomond)

0-1	(1976)	↓	-	(6/13)
1-2	(1975)	↑	+	(5/12)
2-3	(1974)	↓	+	(3/12)
3-4	(1973)	↑	+	(1/10)
4-5	(1972)		+	(2/10)

1977-1978 (Loch Lomond)

0-1	(1977)	↑	-	(5/13)
1-2	(1976)	↑	+	(4/12)
2-3	(1975)	↓	+	(5/12)
3-4	(1974)	↓	+	(3/10)
4-5	(1973)	↓	+	(3/10)
5-6	(1972)		+	(1/10)

1978-1979 (Loch Lomond)

0-1	(1978)	↓	-	(8/13)
1-2	(1977)	↓	+	(7/12)
2-3	(1976)	↓	-	(8/12)
3-4	(1975)	↓	-	(6/10)
4-5	(1974)	↓	+	(4/10)
5-6	(1973)	↓	+	(3/9)

1979-1980 (Loch Lomond)

0-1	(1979)	↓	-	(10/13)
1-2	(1978)	↑	+	(6/12)
2-3	(1977)	↓	+	(7/12)
3-4	(1976)	↑	+	(2/10)
4-5	(1975)	↑	+	(1/10)
5-6	(1974)	↓	-	(5/9)

1980-1981 (Loch Lomond)

0-1	(1980)	↑	-	(9/13)
1-2	(1979)	↑	+	(2/13)
2-3	(1978)	↑	+	(2/13)

3-4	(1977)	↓	+	(4/10)
4-5	(1976)	↓	-	(6/10)
5-6	(1975)	↓	-	(6/9)

1981-1982 (Loch Lomond)

0-1	(1981)	↑	+	(4/13)
1-2	(1980)	↑	+	(1/12)
2-3	(1979)	↑	+	(1/12)
3-4	(1978)	=	+	(4/12)
4-5	(1977)	↑	-	(5/10)
5-6	(1976)	↑	+	(2/9)

1982-1983 (Loch Lomond)

0-1	(1982)	↓	-	(7/13)
1-2	(1981)	↓	+	(8/12)
2-3	(1980)	↓	-	(9/12)
3-4	(1979)	↓	-	(7/10)
4-5	(1978)	↓	-	(7/10)
5-6	(1977)	↓	-	(5/10)

1983-1984 (Loch Lomond)

0-1	(1983)	↑	+	(2/13)
1-2	(1982)	↑	+	(3/13)
2-3	(1981)	↓	-	(10/12)
3-4	(1980)	↓	-	(9/10)
4-5	(1979)	↓	-	(9/10)
5-6	(1978)	↓	-	(7/10)

1984-1985 (Loch Lomond)

0-1	(1984)	↑	+	(1/13)
1-2	(1983)	↓	+	(8/12)
2-3	(1982)	↑	+	(4/12)
3-4	(1981)	↑	-	(8/10)
4-5	(1980)	↑	-	(8/10)
5-6	(1979)	↓	-	(9/9)

1985-1986 (Loch Lomond)

0-1	(1985)	↓	+	(3/13)
1-2	(1984)	↓	-	(12/12)
2-3	(1983)	↓	-	(12/12)
3-4	(1982)	↓	-	(10/10)
4-5	(1981)	↓	-	(10/10)
5-6	(1980)	↑	-	(8/9)

(ii) Loch Eck (Fig. 2.10; Table 2.18b)

1975-1976 (Loch Eck)

0-1	(1975)	↑	+	(1/12)
1-2	(1974)	↑	+	(6/12)
2-3	(1973)	↑	+	(7/11)

1976-1977 (Loch Eck)

0-1	(1976)	↓	+	(4/12)
1-2	(1975)	↓	-	(11/12)
2-3	(1974)	↓	-	(10/11)
3-4	(1973)	↓	-	(10/10)

1977-1978 (Loch Eck)

0-1	(1977)	↓	+	(7/12)
1-2	(1976)	↑	+	(8/12)
2-3	(1975)	↓	-	(11/11)
3-4	(1974)	↑	-	(9/10)
4-5	(1973)	↑	-	(8/8)

1978-1979 (Loch Eck)

0-1	(1978)	↑	+	(6/12)
1-2	(1977)	↑	+	(4/12)
2-3	(1976)	↑	-	(9/11)
3-4	(1975)	↑	-	(8/10)
4-5	(1974)	↑	-	(7/8)
5-6	(1973)	↑	-	(6/7)

1979-1980 (Loch Eck)

0-1	(1979)	↓	-	(10/12)
1-2	(1978)	↓	+	(3/12)
2-3	(1977)	↑	+	(6/11)
3-4	(1976)	↑	-	(6/10)
4-5	(1975)	↑	-	(6/8)
5-6	(1974)	↑	-	(5/7)

1980-1981 (Loch Eck)

0-1	(1980)	↓	-	(2/12)
1-2	(1979)	↑	+	(3/12)
2-3	(1978)	↑	+	(3/12)
3-4	(1977)	↓	-	(7/10)

4-5	(1976)	↓	-	(5/8)
5-6	(1975)	↑	-	(4/7)

1981-1982 (Loch Eck)

0-1	(1981)	↑	+	(8/12)
1-2	(1980)	↑	+	(1/12)
2-3	(1979)	↑	+	(2/11)
3-4	(1978)	↑	-	(5/10)
4-5	(1977)	↑	+	(3/8)
5-6	(1976)	=	-	(4/7)

1982-1983 (Loch Eck)

0-1	(1982)	↓	-	(11/12)
1-2	(1981)	↓	-	(10/12)
2-3	(1980)	↑	+	(1/11)
3-4	(1979)	↑	+	(1/10)
4-5	(1978)	↑	+	(2/8)
5-6	(1977)	↑	+	(2/7)

1983-1984 (Loch Eck)

0-1	(1983)	↑	-	(9/12)
1-2	(1982)	↑	+	(7/12)
2-3	(1981)	↓	+	(4/11)
3-4	(1980)	↓	+	(2/10)
4-5	(1979)	↑	+	(1/8)
5-6	(1978)	↑	+	(1/7)

1984-1985 (Loch Eck)

0-1	(1984)	↑	+	(5/12)
1-2	(1983)	↑	+	(2/12)
2-3	(1982)	↓	+	(5/11)
3-4	(1981)	↓	+	(4/10)
4-5	(1980)	↓	-	(5/8)
5-6	(1979)	↓	+	(3/7)

1985-1986 (Loch Eck)

0-1	(1985)	↓	-	(12/12)
1-2	(1984)	↓	-	(12/12)
2-3	(1983)	↓	-	(8/11)
3-4	(1982)	↑	+	(3/10)
4-5	(1981)	↑	+	(4/8)
5-6	(1980)	↓	-	(7/7)

2.2.4 DISCUSSION

A Growth of Year-Classes

No year-class had a consistently high or low growth rate throughout its life. The relative size reached at the end of a growing year (except the first year) depended not only on the growth rate in that year, but also on the size attained in the previous year. The effect of variations in growth rate decreased with increasing age and size.

In lake herring, Leucichthys artedi Le Sueur, the largest fish at 3 and 4 years of age were generally the fastest growing in their first year (van Oosten, 1928). Brown (1946a) also commented that the amount of first year growth was important in determining the final size of brown trout. In powan, the fastest growing year-classes in the first year of life were not the largest when adult, as exemplified by the fate of the three top ranking year-classes at age 1 in Loch Lomond (Table 2.17a). Powan of the 1984 year-class were exceptionally fast growing in their first year. Due to their large size, six 0+ fish of this year-class were caught, an unusual occurrence. However, in their second year, the 1984 fish had the lowest growth rate of all the year-classes (Table 2.18a), and so slipped to ranking 4th in length. Powan of the 1983 year-class, also notably large in their first two years, underwent a progressive decrease in relative growth rate. Consequently by age 3, their mean length was below average, their growth rate being the lowest of any other year-classes in the third year. The fish of the 1981 year-class finished as the second smallest at age 5. Similar observations can be made in Loch Eck for the five longest year-classes at age 1; 1975, 1973, 1974 and 1984 (Tables 2.17b, 2.18b). The growth rate in the second year of life does not decide final length either, as was shown in Loch Lomond by the 1983 year-class, and also by the 1980 year-class. Fish of the 1980 year-class had the highest growth rate in the second year and so moved up in length ranking from 8th out of 12 at age 1 to being 2nd at age 2. Despite a below average growth rate in their third year, 1980 fish still ranked 2nd at age 3, but because the growth rate remained below average, their relative length decreased to just above average in later years. The same situation was also seen in Loch Eck; the three year-classes with the longest fish at age 2 (1974, 1973 and 1976) had below average lengths from ages 3 and 4.

The year-classes which eventually produced the longest fish, originally had the smallest fish in the first year. In Loch Lomond, powan of both the 1979 and 1976 year-classes were below average length at age 1 and top ranking at age 3 (Table 2.17a). In Loch Eck, fish of the 1979 year-class were below average length at ages 1 and 2, just above average length at age 3, and top ranking thereafter (Table 2.17b). 1980 fish, ranking second smallest at age 1, had just above average length at age 2 and were longest at ages 3 and 4, 2nd longest at age 5 and 3rd longest at age 6. Fish of the 1978 year-class were of above average length throughout their life, ranking 2nd at age 3, and thereafter remaining in the top four in length. It therefore appears that in powan it is the size attained by the third (or fourth) year of life which largely determines the final relative length. There are exceptions, for example the 1980 year-class in Loch Lomond, and alterations in the relative size rankings of the intermediate year-classes in both lochs.

The majority of powan become sexually mature at 3 years of age, with a corresponding decrease in growth rate (Ch. 4). The reduction in growth rate at the time of maturation and with increasing size, means that fluctuations in growth rate will tend to be progressively less apparent (van Oosten, 1928; van Oosten & Hile, 1947), unless they are extreme, or positively or negatively accumulative; for example the 1980 year-class in Lomond which had a consistently below average growth rate from 2-3. In the comparison of growth in Lochs Lomond and Eck (Ch. 2.1.4, p. 55-56; Fig. 2.6; Tables 2.8, 2.14), the question arose as to why Loch Eck powan should be consistently smaller at age when their growth rates were generally significantly higher. It was suggested that because Loch Lomond powan had the higher growth rate in their first and third years of life (before maturity), they maintained the size advantage thereafter.

Law of compensatory growth. The fact that the powan which were longest in their first year might end up smallest in their later years and vice versa appears to conform to the 'law of compensatory growth' originated by Gilbert (1914, cited by van Oosten, 1928). Gilbert observed that sockeye salmon, O. nerka, which were large at the end of their second year generally grew more slowly in succeeding years than did the salmon which were small at the end of their second year, so that at maturity all individuals were of a uniform size. In powan however, fish of different year-classes were not of uniform size at maturity. Despite conflicting evidence that large juveniles became large adults, van Oosten (1928) concluded that compensation in growth occurred in the lake herring, since the smallest yearlings became the fastest growing fish and the largest yearlings the slowest.

Lee's phenomenon. Another aspect of long-term growth analysis often remarked on is 'Lee's phenomenon of apparent change in growth rate', where lengths back-calculated from older fish are lower than those back-calculated from younger fish (Lee, 1912). Although lengths back-calculated from older and younger members of the same year-class have not been compared in powan, the earliest year-classes did tend to be the shortest in length. In Loch Lomond, the year-classes 1972, 1973, and 1974 were consistently small (Fig. 2.7, Table 2.17a), as was the single 1972 fish from Loch Eck (Fig. 2.9). On the other hand, fish of the Loch Eck 1973, 1974 and 1975 year-classes were in fact the longest at ages 1 and 2, and did not move down to the bottom of the length ranking table until age 3 (age 4 for 1973; Table 2.17b). Lee (1912) put forward seven possible explanations for her 'phenomenon', which included net selectivity, change in the scales through shrinkage or reabsorption, actual change in growth rate, and change in the size composition with age through selective elimination by death. Van Oosten (1928) reviewed these possibilities in detail and concluded that only the last idea (size-selective elimination by death) was acceptable. The selective effect of mortality is also the most likely explanation for 'Lee's phenomenon' in powan. The faster growing members of a year-class may die earlier than slower growing fish and so only the slowest growers survive to be the oldest (Craig, 1974, 1979, 1982). Experiments with zebra danios, Brachydanio rerio (Hamilton Buchanan), demonstrated that with a few exceptions, fast growing fish did have higher mortality rates than slower growing fish, so suggesting that growth rate and mortality rate are linked through some kind of physiological ageing process (Craig & Fletcher, 1984).

Difference in growth rates of Loch Eck year-classes observed in Ch. 2.1.4. The change from calculated lengths overestimating to underestimating measured lengths (Fig. 2.4, Table 2.11) was traced to a disproportionate increase in measured lengths of the 1976-80 year-classes compared with the 1981-85 year-classes (p. 49-50). These back-calculated results verified that Loch Eck powan of the 1980 year-class were significantly longer than fish of the 1981 year-class at ages 3, 4, and 5 (Table 2.17a). At age 3, the 1977, 1978 and 1979 fish were also significantly longer than the 1981 and 1982 fish. At age 4, fish of the 1979 year-class were significantly longer than fish of all other year-classes except 1982 (and 1973). At age 6, fish of the 1979, 1978, and 1977 year-classes were larger than fish of the 1981 year-class although only the 1979 fish were statistically significantly larger.

B Growth of Age Groups

That powan growth is affected by environmental conditions is evidenced in Loch Lomond by the abrupt decrease in growth rate of more than one age group in 1985-1986 (Fig. 2.8). There have been relatively few studies investigating causes of variation in the year to year growth of natural populations (van Oosten & Hile, 1947; Runnstrom, 1957; Le Cren, 1958), and generally they were inconclusive. Because of the interactive complexity of growth processes, it is difficult, if not impossible, in natural populations to correlate year to year fluctuations in growth rate with specific environmental changes. Often the environmental variations are incompletely known. In the powan lochs, there are no continuous records of environmental conditions over several years. No long-term monitoring of food organisms has been carried out. Maitland *et al*. (1981a) found zooplankton abundance in Loch Lomond in 1977 to be minimal in April and maximal in June. In 1983, Pomeroy (1987) also found zooplankton numbers to be lowest in April; the maximum was in July. Pomeroy observed considerable variation in plankton abundance in Loch Lomond. The density of zooplankton in May 1985 was particularly low compared with May of the previous two years, an observation which tallies with the poor growth in Loch Lomond in 1985. Three Loch Eck plankton hauls were taken but were not analysed quantitatively. Qualitatively they were similar to Loch Lomond zooplankton (Pomeroy, 1987). There is some information on the numbers of benthic fauna in Loch Lomond (Smith et al., 1981a,b), but none on Loch Eck.

Temperature variations have been correlated with changes in growth rates (Lindstrom, 1962; Berg, 1970). Le Cren (1958) found a strong positive correlation between the growth of Lake Windermere perch of all age groups and the number of degree days over 14°C (surface water temperature was routinely measured). Runnstrom (1957) observed some correlation of growth with June and July temperatures in 1 year old brown trout. Svardson (1951) suggested that hot summers caused improved growth in whitefish in northern Sweden. No relationships were found between temperatures and growth of lake herring (van Oosten, 1928), or lake whitefish Coregonus clupeaformis (van Oosten & Hile, 1947).

High summer temperatures can have an adverse effect on growth. According to Pokrovskii (1962), when water temperatures reach 18-20°C, whitefish begin to fast. In the autumn of 1976, fish deaths were reported in excess of 20°C and the lough became deoxygenated (Wilson, 1983). Lough Neagh is shallow with a maximum depth of 17m. Deeper lakes like Loch Lomond stratify in summer, although in the shallow southern basin stratification is only temporary in midsummer (Slack, 1957b). Powan can potentially avoid the upper warm strata. Loch Lomond powan migrate seasonally, tending to frequent deep water in autumn and shallow water in spring and early summer. Shoals of Loch Lomond powan have been seen in shallow water around the islands on dull, calm, warm days (Lamond, 1931; D.B.C. Scott pers. comm.) and so Loch Lomond powan do not appear to be adversely affected by high summer water temperatures, which in any case seldom exceed 20 °C. Higher temperatures are in fact liable to be favourable, since in addition to its direct effect on growth, temperature acts indirectly through its influence on the life cycles of the prey organisms. In general, increased temperature and light results in an increase in the abundance of plankton, with zooplankton reaching a maximum about a month after the phytoplankton (Macan & Worthington, 1951). Pokrovskii (1962) noted that in deep lakes where whitefish can find suitable temperature conditions lower down, growth was intensified in years with hot summers, which encouraged the growth of plankton. Pisidium feeds on detritus; Chironomus feeds on plankton (Jonasson & Mathiesen, 1959), so that increased temperatures may indirectly affect the growth and abundance of these benthic animals through increased plankton numbers. Svardson (1951) cites Vallin (unpublished) who found a greater production of chironomid larvae in the littoral zone of Lake Suorva (Sweden) in August of a hot year. Below the thermocline, at a depth of 10-21m the number of bottom animals was fairly constant during the five years studied.

Although no regular water temperature records were available, climatological summaries were obtained from the Meteorological Office. They were recorded at Arrochymore, Loch Lomond (Fig. 1.2) from 1972-87 and at Benmore, Loch Eck (Fig. 1.3) from 1982-87. Monthly means of air temperatures, precipitation and daily mean sunshine were available. Surface water temperatures are generally related to air temperatures (Table 2.19), and air and water temperatures are related to the amount of sunshine (van Oosten & Hile, 1947), which is itself important in the production of plankton. Growth rates were therefore compared with sunshine levels (Fig. 2.11). Overall means were calculated for the months of April to September inclusive, (Table 2.20a) since these are the months of the main growing season (Ch. 2.1.4, p. 60).

Daily mean sunshine was only recorded at Arrochymore. The amount of solar radiation reaching the loch varies in Loch Lomond, the steep mountainous northern basin being more shaded than the open southern basin. Tippett (1987) suggested that the lower phytoplankton productivity in the northern basin resulted from the lower light levels. Since Loch Lomond and Loch Eck air and surface water temperature were very similar (Table 1.1, 2.19), Arrochymore sunshine levels were also considered in relation to the growth rates of Loch Eck powan.

In general, the same growth trends were not observed in all age groups in any one year with the following exceptions:

In both lochs 1981-82 was a year of high growth rate (Figs 2.8, 2.10). The mean daily sunshine from April to September 1981 was average (Table 2.20a); only April had a notably high sunshine level (Fig. 2.11).

In Loch Lomond in 1982-83, growth rates were below average (Fig. 2.8). The sunshine in 1982 was also below average, particularly in August and September. Growth in 1985-86 was very low (except in the 0-1 age group). The 1985 April-September sunshine was the lowest of the 15 years, particularly in July, August and September, so there would seem to be a correlation with growth, and also with the low plankton density in May 1985 (Pomeroy, 1987).

In Loch Eck growth in 1984-85 was above average (Fig. 2.10). Overall sunshine in 1984 was also above average, particularly in May and July (Fig. 2.11). In 1986-87 a high growth rate in 2+, 3+ and 4+ powan (Fig. 2.3a,b,c) was not matched by below average sunshine, low in May and July, and only notably high in September.

The conclusion for both lochs is that there is only partial correlation of growth rate with sunshine. Although sunshine is probably a major factor affecting growth, there are many other contributory factors.

Differential growth trends. The youngest ages often showed a different growth trend to the older fish. In Loch Lomond, growth of 0-1 powan frequently differed from the 1-3 age groups, which in turn differed from the 4-6 age groups. Examples are the years 1979-80, 1980-81, 1983-84 and 1984-85. A similar pattern was observed in Loch Eck, in the years 1976-77, 1980-81, and 1982-83. In some years in Loch Eck, growth trends in the 0-1 and 1-2 age groups differed from the older fish (1977-78, 1978-79 and 1982-83; also 1983-84 in Loch Lomond). The different growth of the 0-1 age group may be connected with the relative consistency of first year growth (Figs 2.7 to 2.10, Table 2.16). Coregonines are notoriously difficult to catch in their first year (van Oosten 1928; Hart, 1930; Pritchard, 1930; Smith, 1956; Hogman, 1973), and the habitat of 0+ and early

1+ powan has yet to be discovered (Slack *et al*., 1957). If they shoal separately, they may experience differing or more uniform environmental conditions from the main shoals. Reckahn (1970) studying *C. clupeaformis* and Valtonen (1970) studying *C. nasus* Pallas have reported that different age groups had different temperature preferences. Separate shoaling may mean that competition for food is reduced.

Differential growth trends among age groups has been described in other species. Growth was relatively constant in the first two years of life of Windermere perch, *Perca fluviatilis*, despite fluctuations in population density. Le Cren (1958) suggested that this was because for their first year and part of their second, perch fed on plankton and bottom fauna and were not generally short of food. The growth of 1-3 year old lake herring (*Leucicthys artedi*) in Lake Erie differed from that of older fish (van Oosten, 1928). For their first and part of their second year, lake herring were thought to shoal separately in Saginaw Bay, a region favourable to their growth. Runnstrom (1957) noted that growth of 1 year old brown trout differed from that of older age groups. The only large catch of juvenile Loch Lomond powan in July 1969 was mainly composed of two age groups with a few larger individuals (Fig. 1.4), reinforcing the suggestion that powan juveniles shoal together, with the older juveniles gradually drifting into the main shoals. In Loch Eck, the youngest powan caught were eating benthos. Since the universal first food of coregonines is plankton (Jacobsen, 1974, 1982), it is likely that Loch Eck juveniles initially consume plankton and so could be expected to exhibit year to year growth trends differing from older fish, depending on the availability of plankton relative to benthos. However, there was only one 0+ and few 1+ Loch Eck fish caught (Table 2.3) which were with the main shoal and may have been unrepresentative. If they tend to shoal separately until their second year, they could be planktivorous for at least part of that year, which might explain the similarity of 0-1 and 1-2 growth in some years.

The change in growth trends after the age of 3 could correspond to sexual maturity (Ch. 4). The suggested difference in the time of seasonal growth between the youngest and oldest powan relative to size and reproductive effort (Ch. 2.1.4, p. 65) might partly explain the difference in growth trends above and below 3 years of age. Favourable conditions early in the year (i.e. April-June or July) might promote growth in the juvenile fish, but if conditions are unfavourable at the time of adult growth (July-September), poor adult growth will result, and vice versa. To test this hypothesis, mean hours of daily sunshine were calculated for April-June and July-September in each year (Table 2.20b).

(i) Loch Lomond (Fig. 2.8, p. 84-87)

1979-1980. The 3-4 and 4-5 age groups had high growth rates, while younger age groups had average or below average growth rates. Sunshine levels in April-June 1979 were slightly below average, so there could be a correlation with the average growth of the youngest powan. Unfortunately, there were no climatic records for July, so no conclusions could be drawn for the latter half of the growing season. Mean sunshine was average in August and high in September (Fig. 2.11).

<u>1980-81</u>. Age groups 1-2 and 2-3 had high growth rates; the 3-6 age groups had decreased growth. April-June 1980 had high mean sunshine, particularly in April and May. Mean sunshine in July-September ranked second lowest (out of 15 years). Therefore there appears to be a correlation.

<u>1983-84</u>. The 0-1 and 1-2 age groups had high growth rates, with older fish having below average growth. 1983 had the lowest mean sunshine in April-June particularly in May, and slightly above average sunshine during July-September. So although there may be a correlation with the older fish, there was no correlation between sunshine and growth of the two youngest ages.

<u>1984-85</u>. In this year, 0-1 powan had the highest growth rate of their age group. Growth rates in age groups 1-3 were average or above average. 1984 had above average sunshine in April-June (highest in May), which might correlate with good growth of the youngest powan, but sunshine levels were also above average from July-September, particularly in July, which does not seem to correlate with the below average adult growth rate.

(ii) <u>Loch Eck</u>. In Loch Eck, there was no correlation between mean sunshine and growth rates of the age groups in the years listed except (as in Lomond), in 1980-81, when growth was above average in age groups 1-3 (sunshine was above average during April-June and below average during July-September). There may also be some correlation in 1977-78 when 0-2 fish showed above average growth rates possibly correlating with high April-June sunshine in 1977. Sunshine levels were also high in July-September 1977, which does not correlate with low adult growth.

An obvious argument against the hypothesis is why, if the growing season of young fish extends from May to September, should they not also respond to favourable late season conditions? During the increased ^{14}C-glycine uptake by the scale-forming cells from May to November, there were two maxima in 2 and 3 year olds, in June or July and September (also in 4 year olds in 1982). The June-July maximum was the highest, suggesting that this is when most growth occurs (McCulloch, 1984) and so perhaps conditons early in the season are the most important, while conditions later in the season would have less effect on somatic growth in these age groups. A further objection to the hypothesis is that if early season conditions are good, would adults not replenish energy reserves more quickly and so start somatic growth earlier, resulting in increased growth rates as in the younger fish?

In lake herring, van Oosten (1928) also suggested that the earlier seasonal growth of 2 and 3 year olds (which have moved to shoal with the adults) might result in their differing growth to the adults. However, his hypothesis was that with their longer growing season and higher growth rates, the 2 and 3 year olds would be more affected by year to year variation in environmental conditions. Van Oosten's hypothesis is feasible but does not explain why in some years (e.g. Lomond 1979-80) older fish should have a high growth rate, and younger fish a low growth rate, unless it is because most growth in young fish occurs in the first part of the growing season and if that is poor then overall growth is reduced.

Comparison of year to year growth in Loch Lomond and Loch Eck. Neither population had consistently greater variability in year to year growth (Tables 2.15, 2.16). Loch Eck appears more variable in year to year growth from ages 4 to 7.

There were some *similarities* in growth trends in the two lochs (Table 2.18):

1980-81

0-1 (1980)	below average growth rates; ranks lower in Eck than in Lomond.
1-2 (1979)	above average; ranks 2nd in Lomond, 3rd in Eck.
2-3 (1978)	above average; ranks 2nd in Lomond, 3rd in Eck.
3-4 (1977)	decreased growth rate compared with previous year class.
4-5 (1976)	below average.
5-6 (1975)	below average.

1981-82

0-1 (1981)	above average. Ranks higher in Lomond.
1-2 (1980)	highest growth rate in both lochs.
3-4 (1979)	highest growth rate in Lomond, ranks 2nd in Eck.

1985-86

1-2 (1984) lowest growth rate in both lochs.

2-3 (1983) below average; lowest growth rate in Lomond.

5-6 (1980) 2nd lowest growth rate in Lomond, lowest in Eck.

Main dissimilarities:

1975-76

0-1 (1975) below average growth in Lomond, highest growth rate in Eck.

1981-82

3-4 (1978) above average growth in Lomond (4th), below average growth rate in Eck.

5-6 (1976) second highest in Lomond, below average in Eck.

1982-83

1-2 (1981) above average growth in Lomond, 3rd lowest in Eck.

2-3 (1980) below average growth in Lomond, highest growth rate in Eck.

3-4 (1979) below average growth in Lomond, highest growth rate in Eck.

4-5 (1978) below average in Lomond, 2nd highest in Eck.

5-6 (1977) just above average in Lomond, 2nd highest in Eck.

1983-84

0-1 (1983) 2nd highest growth rate in Lomond, below average in Eck.

3-4 (1980) 2nd lowest in Lomond, 2nd highest in Eck.

4-5 (1979) 2nd lowest in Lomond, highest in Eck.

5-6 (1978) below average in Lomond, highest growth rate in Eck.

1984-85

0-1	(1984)	highest growth rate in Lomond, above average in Eck.
1-2	(1983)	average in Lomond, 2nd highest in Eck.

1985-86

3-4	(1982)	lowest in Lomond, 3rd highest growth rate in Eck.
4-5	(1981)	lowest in Lomond, average in Eck.

The similarities in growth trends that exist between powan in the two lochs seem to be more than coincidental. They suggest a common meteorological factor affecting growth, but only a vague correlation has been found between sunshine (and thus temperatures) and growth rates. The benthic feeding habits of Loch Eck powan may account for much of the dissimilarity in growth between the populations, because of the differing life cycles of the planktonic and benthic prey organisms. A greater similarity might be expected between year to year growth of the first year fish in both lochs if they both fed on plankton, but this is not the case. Despite the general ecological similarities of Loch Lomond and Loch Eck (Ch. 1.1), local conditions will vary, for example nutrients (affecting plankton production) and population densities. Van Oosten & Hile (1947) found differences in growth rates of lake whitefish (*C. clupeaformis*) taken from different parts of Lake Erie. They did not find any correlation between growth and sunshine and temperatures, but only between growth, precipitation and turbidity, a correlation which they could not explain.

The inconclusiveness of whether variations in sunshine and temperatures relate to variations in growth rate is understandable since there are many other environmental and physiological variables affecting growth rates. A further complication is that they interrelate. The effect of one variable will vary depending on the degree of influence of other variables. For examples, the effect of temperature on growth depends to some extent on the nutritional state of the fish (Elliott, 1975a,b; Cui & Wootton, 1988b).

In Loch Lomond in 1984-85, it was not only first year powan which had a high growth rate. 1 and 2 year old ruffe, Gymnocephalus cernua (L.) also had a high growth rate (Murphy, 1988). Young ruffe feed on plankton (Fedorova & Vetkasov, 1974), so the above average temperatures of 1984 together with a surfeit of plankton might benefit the young stages of both species.

2.3 RECRUITMENT AND MORTALITY

2.3.1 INTRODUCTION

It is not known how many powan there are. The inaccessibility of wild stocks of fish presents problems in the analysis of population size (Robson & Regier, 1968). In very few cases, numbers may be directly counted, as by fish counters in fish passes, but usually numbers have to be estimated from samples, by observing fluctuations in sample sizes (catch per unit effort) and by mark-recapture methods (Ricker, 1978; Youngs & Robson, 1978). Mark-recapture has not been feasible in powan, mainly because of their sensitivity to capture (D.B.C. Scott pers. comm.), although the method has been used for other coregonine populations with limited success (Lindroth, 1957; Ausen, 1976). Using echo-sounding, Jurvelius *et al.* (1988), estimated the size of a vendace (*C. albula*) stock.

The problem with these techniques is that they are approximations with no direct verification (Weatherley & Gill, 1987). With hydroacoustical methods, it cannot always be certain which species are being observed. For this reason, Jurvelius *et al.* (1988) collected data at night during summer when adult vendace remained in the hypolimnion, and most other schooling fish migrated to the epilimnion.

The age structure of samples can provide information on year-class strengths and mortality rates. A major determinant of population size is the number of young fish recruited into the population each year (Le Cren, 1961; Bagenal & Braum, 1978). Recruitment is not constant, fluctuations in year-class strengths having been observed in many species, including coregonines (Christie, 1963; Dryer, 1963; Aass, 1972; Ausen, 1976; Wilson, 1983), and possible causative factors have been discussed (van Oosten & Hile, 1947; Pokrovskii, 1962; Lawler, 1965). The mortality rate in the first year of life is often exceedingly high (Gulland, 1965; Salojarvi, 1982). Estimates of egg mortality have been set as high as 97% for the Baikal omul *C. autumnalis migratorius* (Georgi), (Shumilov, 1971) and 95% for Loch Lomond powan (Slack *et al.*, 1957).

2.3.2 MATERIALS AND METHODS

The samples used were those from Loch Lomond, January 1981 to March 1987; and Loch Eck, September 1984 to January 1987. The Loch Lomond November 1980 sample was omitted since a single mesh size of 39mm was used, and consequently the net was highly selective for fish over 3 years of age.

A Year-class Strengths

The total number of powan in each year-class was determined (a) for the entire sampling period, and (b) for each sampling year (1st April to 31st March). Year-class indices (YCI) were calculated using the method of Mills & Mann (1985). The percentage frequency of a particular year-class in any one sampling year was divided by the average frequency of fish of that age taken over several years' samples. The mean of these year-class indices was then calculated (Table 2.21). 0+ and 1+ fish were omitted because few were caught (Table 2.3). Fish of 9+ and over were also excluded from calculations since they were rare and the validity of their ageing dubious (Ch. 2.1.4).

B Mortality and Survivorship

Unmodified catch statistics cannot be used to assess the numbers of fish of each age group present in the population because of such factors as net selectivity and differing habitat preferences (Ricker, 1949). Relatively few powan of the younger, smaller age groups were caught

(Table 2.3). The ascending limb of the catch statistics has therefore to be ignored. In Loch Lomond, only powan 2+ and over could be used, and in Loch Eck, those aged 4+ and over. It is therefore necessary to devise some way of making a count of the numbers of young fish in the population without actually catching any.

In order to reduce the effect of net selectivity and year-class variations, a static life table was compiled (Begon & Mortimer, 1986), using a variation of the method employed by Lowe (1969) in his study of red deer on the Scottish island of Rhum. By ageing deer found dead over a six year period (from their teeth), Lowe was able to reconstruct the age structure of the population in a particular year (at the beginning of the sampling period). Ageing powan from scales allows a similar reconstruction. For example, a 4+ powan caught in 1984 (1980 year-class) would have been alive and 1+ in 1981, 2+ in 1982 and so on (Table 2.22, derived from Appendices 1, 3). However, strengths of year-classes in powan varied to the extent that there was no year in which there was a consistent decline in numbers from yongest to oldest. Lowe smoothed such year-class variations out statistically. To smooth these variations out in powan, the number of fish in each age group was summed for the years in which samples were taken. In Loch Lomond, the years summed were 1981-1986. In Loch Eck, the years 1984-1986 were summed.

The means of numbers of fish in each age group was determined over the six years in Loch Lomond and three years in Loch Eck (Table 2.23). Mortality rates and survivorship calculated from means did not differ significantly from those calculated using totals, up to age 6. From age 7 onwards, using means resulted in a higher survivorship than using totals, because of the paucity of older fish. Consequently total numbers decreased more rapidly from age 7 than did the means (compare Table 2.22 with 2.23). It was decided that the lower mortality for older fish derived from means was likely to be the more realistic, since a slight reduction in mortality in the last years of life has been observed in several freshwater salmonid populations (Weatherley & Gill, 1987).

Calculations for Table 2.23 after Lowe, 1969; Begon & Mortimer, 1986:

x = number in each age group, in this case the mean number

lx = standardised number in each age group, taking 1000 as the starting density,
e.g. Lomond l_2 = (138 x 1000)/149

dx = standardised number dying in each year,
e.g. Lomond d_2 = 926-624

qx = mortality rate. Relates dx proportionally to lx,
e.g. Lomond q_2 = 302/926

$\log_{10} x$ = survivorship. Log_{10} of the standardised number.

Using this method of smoothing, the numbers of powan in Loch Lomond are highest at age 1 and decrease thereafter, but the method was only partially successful with Loch Eck samples, where the numbers in age groups, though improved compared with the age group frequencies (Table 2.3), still increase from age 1 to a maximum at age 3 before declining. This occurred because of the large year-class strength variations which were not completely smoothed out by the short 3 year sampling period (Table 2.2). Therefore ages 1 and 2 were omitted and the mortality analysis started from age 3 (Table 2.23b).

2.3.3 RESULTS

A Year-Class Strengths

(a) Loch Lomond

In terms of the year-class index, 1975 was the strongest year-class, then 1973, then 1974 and 1984 (Tables 2.21a). The 1975 year-class appeared relatively numerous in the sampling year of January 1981 to September 1981 (Fig. 2.13) but whether the 1973 and 1974 year-classes were genuinely strong is unsubstantiated, particularly as the ages of older fish are of dubious validity.

In terms of number of fish, 1984, ranking third in year-class index, was exceptionally strong (Figs 2.12a, 2.13). In the sampling year 1986-87, the 1984 year-class accounted for 51% of the total catch. In addition six 0+ fish of this year-class were caught in 1984-85. 1980 was numerically the second strongest year-class, then 1981, which is in general agreement with the year-class index.

The weakest year-classes were 1977 and 1983 in that order. Very few 1985 powan were caught. Although they were still in the scarce 1+ age group by completion of sampling, a larger number of 1+ fish had been caught in previous years (Fig. 2.13) and so 1985 may also be a weak year-class.

(b) Loch Eck

The strongest year-class was 1982. The year-class index then ranked 1976 second and 1981 third (Tables 2.21b, 2.24). Numerically, 1981 was second, then 1980 (Fig. 2.12b, 2.14).

The weakest year-classes were 1983 and 1977, 1983 being an almost complete failure. It is not possible to be conclusive about the abundance of the 1985 year-class, which compared with catches of the 1984 year-class (Fig. 2.14), may be weak. However, there were only three samples taken in 1986-87, compared with six in 1985-86.

B Mortality and Survivorship

Despite some smoothing of net selectivity, its effect was still apparent. Since relatively few 1+ fish were caught, the difference between the number of 1+ and 2+ fish was lower than it should be, and so the mortality rate calculated for 1 year olds will be rather low (Table 2.23a).

(a) Loch Lomond

Survivorship declined with increasing age (Fig. 2.15a). The rate of decline increased from ages 3 to 5 (compared with age 1 to 3), and again from ages 5 to 7, during which period the rate of decline in survivorship was greatest. The decline continued from ages 7 to 10, but at a reduced rate. The mortality rate (Fig. 2.15b), increased from age 1 to 3, appeared to remain constant or decrease slightly from 3 to 4, before increasing once more to a maximum at ages 5 and 6. A decreased mortality rate at 7 was followed by a reincrease to age 10.

(b) Loch Eck

The decline in survivorship was less from ages 3 to 4 than from 5 to 7 (Fig. 2.15a). Between 7 and 10 years of age, the decline was reduced, before accelerating once more from age 10. There was a rapid increase in the mortality rate (Fig 2.15b) from 3 to 4, followed by a further increase to a high level at age 6. The mortality rate decreased at age 7, then reincreased to age 10.

2.3.4 DISCUSSION

A Recruitment

The year-class index method (Mills & Mann, 1985), although useful in quantifying year-class strengths, has drawbacks. As in mortality rates, the mean percentage occurrence of age groups needs to be calculated over several years, otherwise there is a greater effect of weak and strong year-classes. For example, the exceptionally strong 1984 year-class in Loch Lomond (Fig. 2.13) results in an increased average for the percentage frequency of 2 year olds, consequently depressing the year-class index for other year-classes at age 2. This type of effect would be more pronounced in Loch Eck, where sampling was only over three years. In order to improve reliability, Mann & Mills (1986) obtained data for a particular year-class for three successive years before including it in their analysis. Even so, they found that after a sequence of weak year-classes, an average year-class appeared initially to be very strong.

Although in terms of year-class index, Loch Lomond powan had stronger year-classes than Loch Eck powan (Table 2.24), the year-class strengths in Loch Lomond were less variable, the year-class index over twelve year-classes varying by a factor of 5.3 compared with 27.2 over nine year-classes in Loch Eck. The strongest year-class in each loch in the period 1979-85 differed, being 1984 in Loch Lomond and 1982 in Loch Eck. However, in both lochs, the ranking in year-class index of the remaining year-classes was very similar, with the weakest year-classes being 1983 and 1977, and possibly 1985. These similarities are strongly indicative of a common factor affecting year-class survival. As discussed in Chapter 2.2.4, meteorological conditions are the most likely candidates. It is interesting that 1977 was also a poor recruitment year in Lough Neagh pollan (Wilson, 1983). Other studies have noted similar year-class abundances in different water systems and species in the same years, and suggested that there may have been a climatic factor in common (Goldspink, 1978; Mills & Mann, 1985). However, local conditions modify year-class strengths (Hile, 1936), as exemplified by the most abundant year-class being 1982 in Loch Eck, but 1984 in Loch Lomond.

Statistical correlation of year-class strengths with possible causative factors is of limited use. Gulland (1965) warned against the risk of correlations arising by chance, also pointing out that estimates of year-class strengths and probably of environmental factors are liable to contain considerable variance. A further disadvantage is the number of pairs of observations needed for the analysis to be statistically valid, when there is only one pair of observations per year. In Loch Lomond there are twelve possible pairs, in Loch Eck, only nine. An additional complication is that as in growth (Ch. 2.2.4), more than one factor is involved in regulating recruitment, since not every year-class fits the expected results of a single hypothetical cause (van Oosten & Hile, 1947; Lawler, 1965; Aass, 1972).

(a) Factors Affecting Egg Survival

(i) Environmental

Wind-induced turbulence. High winds cause turbulence and strong currents, particularly over shallow areas such as the powan spawning grounds. These grounds were possibly selected because the water currents keep them silt free (Slack, 1955). However, the effects of wind-induced currents are potentially adverse. No observations on powan spawning behaviour have been made, but spawning in captive Swedish *C. lavaretus* involved a pair swimming towards the surface of the water to shed ova and milt which then drifted down (Fabricius & Lindroth, 1954). Turbulence could reduce the percentage of eggs fertilised if ova and milt are separated during their descent, and could sweep the drifting eggs off the spawning ground to less favourable areas. Translocation by currents remains a risk if eggs do not become lodged in crevices between small stones or among plants (Slack, 1955; Lindroth, 1957). There are no wind data available, but waves 1.5m high have been experienced over the spawning ground between the Ross Islands (Fig. 1.2) at spawning time (D.B.C. Scott pers. comm.). Wind-induced turbulence at spawning time has been shown to reduce whitefish recruitment in Lake Pereslavkoe, Russia (Pokrovskii, 1962). Miller (1956) suggested that the cause of weak year-classes of whitefish in Pigeon Lake, Alberta, was the destruction of eggs by strong wind-induced currents. Loch Eck powan spawn along parts of the shoreline. Eck is an elongated loch running north to south (Fig. 1.3), and winds in those directions tend to funnel down the length of the loch. All spawning grounds in Loch Eck could therefore be exposed to similar currents, in contrast to Loch Lomond, where a particular wind direction and strength would not affect all spawning grounds in the same way, because of the various islands and bays. This might explain why the 1983 year-class, while weak in Loch Lomond, was an almost complete failure in Loch Eck.

Temperature. The incubation period of coregonine eggs has been experimentally shown to be affected by temperature (Price, 1940; Maitland, 1967; Colby & Brooke, 1970, 1973). However, the temperature on the spawning grounds during winter incubation (4°C) is not likely to vary significantly from year to year and so is unlikely to affect powan recruitment.

Oxygen concentration. Deoxygenation during winter has been identified as causing mortality of whitefish eggs in a eutrophic lake (Ausen, 1976), but it is unlikely to occur in the oligotrophic lochs of Lomond and Eck. Smith *et al.* (1981c) found Loch Lomond water to be consistently over 80% oxygen saturated.

(ii) Predation

By invertebrates. In Loch Lomond, powan eggs are preyed on by the larva of the trichopteran *Phrygania* (Slack, 1955). Slack estimated that *Phrygania* destroyed about 65% of live eggs on the McDougall Bank (Fig. 1.2) in 1953. Offshore banks are surrounded by areas uninhabited by *Phrygania*, but the first instar larvae are partially planktonic and may be carried to the spawning banks by water currents (Weerekoon, 1957). Since the numbers of *Phrygania* on the spawning ground would depend upon the frequency, strength and direction of the wind generated currents during their planktonic stage, the extent of their predation on the powan eggs would be expected to vary fom year to year (Slack, 1955). It is not known if a similar situation exists in Loch Eck. Shumilov (1971) estimated that in the Baikal omul (*Coregonus autumnalis migratorius*), 29% of egg mortality was caused by invertebrates.

By fish. Powan eat their own eggs. The extent of the cannibalism is not known, but Pomeroy (1987) found many powan eggs in the stomachs of Loch Lomond powan, particularly the females, from January to March. Fewer Loch Eck powan stomachs contained eggs. While watching spawning *C. lavaretus*, Fabricius & Lindroth (1954) noticed that eggs sinking after being spawned were eaten by the whitefish before they reached the bottom. Eggs which lay on the surface of the gravel were also eaten, but those that fell into crevices escaped predation. Other reports of coregonid cannibalism include Hart (1931b, *C. clupeaformis*), Smith (1956, *Leucicthys artedi*), Shumilov (1971), Jacobsen (1974, *C. lavaretus*), Wilson (1984, *C. autumnalis pollan*). Shumilov (1971) estimated that the omul was responsible for a major part of the 7% egg mortality resulting from fish predation, the other minor egg predators being grayling and lenok (*Brachymystax lenox*). Hart (1930) suggested that perch (*Perca flavescens* Mitchill) were a significant predator on *C. clupeaformis* eggs. Powan eggs have been found in trout stomachs (Maitland, 1969).

A major egg predator is the ruffe, _Gymnocephalus cernua_, a recent introduction into Loch Lomond (Ch. 6). Pokrovskii (1962) cites Balagurova (1958) who estimated that ruffe predated on coregonine eggs to the extent of 80-90% in Lake Syamozero, Karelia. In two other Russian lakes, yields of whitefish increased when the numbers of ruffe were reduced. Murphy (1988) found evidence of ruffe feeding on powan eggs in Loch Lomond between February and April. Since the 1984 year-class in Loch Lomond was strong, and the 1983 and 1985 year-classes, though weak, were also weak in Loch Eck, there is no evidence of ruffe having any adverse effect on powan numbers as yet.

(b) _Factors Affecting Survival of Larvae and Fry_

(i) _Environmental_

Currents. Wind-induced currents may transport larvae to other areas, though whether this has an effect on mortality or is a natural mechanism for dispersal of larvae from the spawning grounds is not known.

Temperature. Most effect upon powan larvae and fry survival is probably indirect, through its influence on plankton production, but the effect may also be a direct one, with increased temperature increasing the rate of growth (McCormick _et al._, 1971) and so reducing the period of vulnerability to predation.

(ii) _Predation_. Nothing is known about the extent of predation upon larvae and fry by invertebrates, birds or fish. Potential piscine predators in Loch Lomond are trout, eels, perch and pike, of which the first two occur in Loch Eck. Ruffe also take fry (Fedorova & Vetkasov, 1974; C. Adams pers. comm.).

(iii) Food availability. In common with other whitefish species, the first food of both Loch Lomond and Loch Eck powan is almost certainly zooplankton (Lindroth, 1957; Teska & Behmer, 1981; Jacobsen, 1982) though there is no verification of this in Loch Eck. Powan hatch around April (under laboratory conditions); zooplankton numbers increase from a minimum in April (Pomeroy, 1987). For two or three weeks after hatching, the larva absorbs its yolk sac (Slack *et al*., 1957), which may sustain it during the time of low plankton abundance, although larvae do begin to feed before the yolk sac is completely absorbed (Taylor & Freeberg, 1984). Gulland (1965) considered the most critical time after hatching to be during the change from endogenous to exogenous feeding when heavy mortalities occur. Taylor & Freeberg (1984), in experiments on laboratory reared *C. clupeaformis*, found that when all larvae had absorbed their yolk sac, there was total mortality, except for the three highest feeding levels. Only when the larvae were fed to excess were there no deaths. The availability of plankton is therefore a major factor affecting year-class strengths (Gulland, 1965; Salojarvi, 1982).

Plankton abundance varies from year to year (Pomeroy, 1987). The similarity of environmental conditions in the two areas (Table 2.19) may mean that plankton production in both lochs will be similarily affected by year to year variations in meteorological conditions such as sunlight and temperature. This may explain the similarity in recruitment in the lochs (Table 2.24), particularly with regard to the weakest year-classes. In Loch Lomond, May 1985 had less plankton than the previous two years (Pomeroy, 1987), which correlates with the apparent weak 1985 year-class in Loch Lomond.

If the crucial time for survival is the time of first feeding, and as the plankton numbers increase from April to July, then favourable conditions for plankton production during these months will be important in determining the level of recruitment (Taylor & Freeberg, 1984). If the daily mean sunshine levels for the months of April to June (Table 2.20b) are compared with the year-class indices (Table 2.24) some correlation is apparent. In Loch Lomond, five of the six years with above average sunshine had high year-class indices. In Loch Eck, if sunshine means in the years preceding 1976 are excluded, the overall average April-June sunshine becomes 5.07 hours, and of the five year-classes with the highest year-class indices, four are in years with above average sunshine (1982, 1981, 1980, and 1984). 1983 had the lowest April-June sunshine and was a weak year-class in both lochs. 1985 also had low April-June sunshine.

Some exceptions related to both lochs. 1977 had a high level of early sunshine, yet that year-class was the weakest in Loch Lomond and second weakest in Loch Eck. 1976, with the second lowest April-June sunshine was a strong year-class, ranking fourth in Loch Lomond and second in Loch Eck.

A year-class which clearly differed in relative abundance in the two lochs was 1982, the strongest in Loch Eck but the third weakest in Loch Lomond. 1982 was a year with below average April-June sunshine, though if the years 1972-1975 were excluded (Loch Eck) the sunshine ranked just above average.

Comparing year-class strengths with July-September sunshine (Table 2.20b) demonstrates that 1976 had the highest mean July-September sunshine of the years studied, and so there may be some correlation between year-class strength and sunshine in the latter half of the feeding season. However 1977, third ranking in July-September sunshine, was a weak year-class; 1984, also third ranking in late sunshine and a strong year-class, also had above average sunshine in April-June. Of the years with the lowest July-September sunshine, 1985, a suspected weak year-class, also had a low April-June sunshine. 1980 had a fairly high year-class index (above average April-June sunshine). 1978 was quite a weak year-class in both lochs. 1982 was the strongest year-class in Loch Eck. There seems to be more correlation between year-class strengths and sunshine levels in the early part of the season, as was suggested by Taylor & Freeberg (1984).

Svardson (1951) related hot summers to rich year-classes of whitefish in Sweden. Aass (1972) observed a relationship between warm Junes and strong year-classes of cisco (C. albula) in some years. Van Oosten & Hile (1947) found that in 1926 in Lake Erie, not only whitefish, but fry of six other species had strong year-classes. They could find no correlation between meteorological-limnological conditions and year-class strengths, although they pointed out that the apparent lack of correlation could not be taken as proof that weather does not influence year-class strengths, because of the complex interrelationships of factors which affect recruitment.

(iv) Growth. Growth rate is a more subtle, yet important factor affecting the mortality of fry and is related to feeding and temperature. The smaller the fry, the more vulnerable they are to predation (Lindstrom, 1962; Gulland, 1965; Mann & Mills, 1986). Smaller fry may be less able to compete for food and catch fast moving prey (Svardson, 1951; Gulland, 1965; Mills & Mann, 1985). In Loch Lomond, the 1984 year-class was both very strong and exceptionally fast-growing in its first year (Ch. 2.2.4). This is contrary to the theory of density-dependent growth, since it indicates that population density does not affect first year growth (Runnstrom, 1957; Le Cren, 1958). Le Cren (loc. cit.) suggested that growth of first year perch were not affected by population density because there was always a sufficiency of food (plankton and benthos). However, the weak 1983 year-class in Loch Lomond had a high first year growth rate despite below average sunshine in that year. It is possible that the reduced number of 1983 powan fry in Lomond meant that there was an abundance of food available, even if plankton production was low (growth rates of Loch Lomond adults were below average). This was not the case in Loch Eck where the first year growth of the 1983 year-class was low. The strong 1982 year-class in Loch Eck had the second lowest first year growth rate (Table 2.18b), the high numbers of fry perhaps causing a scarcity of food in a year of average or low plankton production. So the possibility of density-dependent growth cannot be discounted. In 0 group (first year) dace, the availability of food was not a limiting factor in productive chalk streams as no density-dependent growth was observed. However, density-dependent growth did occur when extremely high densities of larvae were maintained in cages (Mann & Mills, 1986).

(c) Estimation of First Year Mortality

It is possible to estimate very approximately the extent of first year mortality in Lomond powan from the life table (Table 2.23a), knowing: the age-specific fecundity; the percentage of females which mature at each age (Ch. 4, Table 4.7a); and the sex ratio (Ch. 1, Fig. 1.5a). Finnigan (1983) showed that 20.7 ripe ova are produced per 1mm fork length of female powan in Loch Lomond. The sex ratio does not deviate significantly from 1:1. Table 2.25 shows the number of ova produced on this basis.

If 95% egg mortality is assumed (Slack *et al.*, 1957), then out of the total 527,767 eggs oviposited (Table 2.25), 26,388 will hatch. If 149 of those 26,388 hatchlings survive to be 1 year olds (total number of powan from Table 2.23a), this represents a 99.43% mortality. The mortality occurring between the ova produced and the end of the first year equals an extremely high 99.97%. Salojarvi (1982) estimated a 99% mortality in the first growing season of Polish C. lavaretus.

B Mortality and Survivorship (Post-yearling)

From age 3, powan in Loch Eck had a consistently higher survivorship than in Loch Lomond (Fig. 2.15a). The mortality rate in Loch Lomond was higher than in Loch Eck at ages 3, 5 and 6 (Fig. 2.15b).

The mortality pattern was very similar in both populations. Both showed slightly reduced mortality around age 4 with a one year difference, between age 3 and 4 in Loch Lomond and 4 and 5 in Loch Eck, though this may be coincidental. Both populations had high mortality at 6 years, followed by significantly reduced mortality at 7 years of age. Mortality increased again at older ages. Maitland (1969) described powan over 6 years as being infrequent in Lomond.

(a) Food Availability

In the first year of life, food availability is a major factor affecting mortality. Older fish have built up reserves which they can draw on in times of starvation, a seasonally routine event in many species (Ch. 3). Compared with most terrestrial animals a major feature of fish is their ability to withstand long periods of starvation. Love (1970) cites examples, including 78-100 days for cod (Gadus morhua) and 3 years for eels (Anguilla anguilla). Therefore food depletion in adult powan may not be a direct cause of mortality unless over an extended period. Starvation may be an indirect cause of death by lowering resistance to disease and predation.

(b) Disease

In the summer and autumn of 1968, large numbers of dead and moribund powan were found around Loch Lomond. These fish had severe fungal infections, also a circular discoloured area on the head. They were small and of poor quality. The pathogen could not be identified. Recovery was quick and complete, no cases being found in the summer of 1969, when the fish were much larger and in better condition (Roberts *et al*., 1970). 'Bald spot disease' has not been observed since. Prior to this population crash the powan were very numerous (D.B.C. Scott pers. comm.), and it is possible that overcrowding led to starvation, poor growth and lowered resistance to the disease. No such 'crash' has been reported for Loch Eck powan.

Fungus infection (*Saprolegnia* spp.) is endemic to both populations (Plates 3, 4). The effect on mortality is unknown. Fungus is probably secondary to wounding and stress (Richards, 1978) and may not be lethal unless disabling. The incidence of fungal infection is particularly high after spawning and affects twice as many male as female powan (Pomeroy, 1982). It is usually the fins which are affected.

(c) Parasites

Powan in Loch Eck were notably free of parasites compared with powan in Loch Lomond. In Loch Lomond even small 1+ fish were heavily parasitised. Cysts on the heart and liver (Plates 17, 19) and to a lesser extent on the swimbladder, gonad and kidney, of Loch Lomond powan have been identified as being caused by the fluke *Cotylurus erraticus* (Copland, 1957; Roberts *et al.*, 1970). *Cotylurus* has not been observed in Loch Eck powan. Cysts on the gut (Plate 12) are caused by the tapeworm (*Diphyllobothrium* spp.). Similar cysts have occasionally been seen in Eck powan (Plate 24). Tapeworms are frequently found in the intestine of powan from both lochs. Copland (1957) identified the cestode *Protocephalus fallax* in the intestine of Loch Lomond powan.

The difference in parasite load between the two populations could be a reason for the lower mortality rate of Loch Eck powan. The protocephalid tapeworms are not thought to harm fish (Needham & Wootten, 1978), but in America, *Diphyllobothrium* plerocercoids are known to kill coregonines and brown trout (Hoffman & Dunbar, 1961, cited by Needham & Wootten, 1978). The effect of the *Cotylurus* trematode on the mortality rate of Loch Lomond powan is not known.

(d) Predation

In Loch Lomond, the river lamprey *Lampetra fluviatilis*, preys preferentially on powan (Maitland, 1980). Small powan under 250mm were rarely scarred, but larger fish frequently were. Fresh wounds occurred only in summer, especially in July and August. Maitland (1980) found little evidence that the attacks affected the growth or condition of the powan, but wounding can be severe. The river lamprey does not occur in Loch Eck. In the Great Lakes, the sea lamprey, *Petromyzon marinus* (L.) is commonly considered to be a significant source of coregonine mortality (Reckahn, 1970; Spangler, 1970).

Other potential predators are pike in Loch Lomond, and eels in both lochs, although eels may only attack moribund or dead fish. Various bird species take fish, and otters have been observed in Loch Lomond.

(v) Senescence

In August 1984, a herring gull was found eating a powan on the shore outside the Yett of Ptarmigan. This male fish was 375mm in length. The scales were indistinct, but the age was over 8+. The caudal fin was badly affected by fungus. Very rarely are dead powan found, generally being eaten by scavengers and predators (with the exception of the 'crash' in 1968). Woodhead (1979) commented that death from senescence was rare in the wild. The little which is known of fish senescence derives largely from experimental studies. Symptoms of senescence have been observed in the gonads of old powan (Plates 15, 16), the oocytes and spermatocytes degenerating and the gonads being invaded by connective tissue, which corresponds with observations on aquarium fish (Woodhead, 1979). Reproductive senescence frequently correlates with an increase in fat stores. An apparently contradictory theory is the one of reproductive effort increasing with increasing size and age, until the level of the energy reserves expended are such that the fish dies of exhaustion (Love, 1970,; Mann et al., 1979). Dabrowski (1982b) suggested that a continual increase in cholesterol levels in males could eventually lead to death. There is no evidence that 'reproductive exhaustion' causes the high mortality rate of 5 and 6 year old powan in both lochs (Fig. 2.15b). Reproductive senescence was only observed in the oldest powan.

Growth rate may also have an effect on mortality. In Ch. 2.2 it was suggested that faster growing fish aged more rapidly than slower growing fish, which therefore lived longer (Craig, 1974, 1979, 1982). A rich food supply could also accelerate physiological ageing (Svardson, 1951; Craig & Fletcher, 1984).

CHAPTER 3 REPRODUCTIVE AND STORAGE GROWTH PROCESSES

3.1 REPRODUCTION

3.1.1 INTRODUCTION

Reproduction is a major growth process in teleost fish, making considerable inroads on available resources. Beside the energy involved in gametogenesis itself, a great deal must be expended in behaviour associated with reproduction: migration (sometimes with osmotic complications), social behaviour, courtship and spawning, and in some cases parental care. Estimates of the energy involved in gametogenesis are relatively easy to make (Ch. 3.2, 3.3; Wootton & Evans, 1976; Craig, 1977; Wootton, 1979), but are more problematic for the associated behavioural activities. Investment in reproduction may be so high as to be lethal, as in semelparous species, but in less extreme cases the form the investment takes varies. Teleosts range from typically r-selected species such as the cod, Gadus morhua (L.), in which the average fecundity for modal females is 1,620,000 ova (Hislop, 1984), with enormous juvenile mortality, to extreme k-selected species such as kelesa, Scleropages formosus (Muller & Schlegel), in which an average female produces only 25 ova each 1.9 cm in diameter which are orally incubated by the male until the yolk sac is absorbed (Scott & Fuller, 1976).

A characteristic of reproduction is that it is cyclical, with the cycles seasonally timed, though with varying degrees of accuracy. It is often said that the cycle is timed in such a way that the young are produced at the most favourable time of year for their survival (Cohen, 1977; Bye, 1984), but as Scott (1979) pointed out, it is equally likely that other stages of the cycle besides the last may also be timed for maximum efficiency; for example food availability for the adults during phases of intense gametogenesis, either directly or via the 'buffering' effect of storage products (Iles, 1974; Wootton, 1979; Allen & Wootton, 1982). Some stages of the reproductive cycle are triggered by environmental 'cues', the best recognised of which is change in photoperiod, though any regularly recurring environmental event which a species could detect might equally well be effective (Scott, 1979; Bye, 1984; Scott, in press). Gametogenesis of powan in Loch Lomond has been studied in general terms by Slack et al. (1957); in terms of gonadosomatic index by Maitland (1969); in terms of light microscope histology by Fuller et al. (1976) and Scott (1979); and in terms of histology and electron microscopy by Rashid (1984). Gametogenesis has not yet been studied in Loch Eck powan.

Powan in Loch Lomond spawn on shallow offshore gravel banks (Scott, 1979) and possibly also in shallow water around the shoreline (Maitland, 1969). Two well established spawning sites are the McDougall Bank in the South Basin and between the Ross Islands in the Middle Basin (Fig. 1.2). Males gather on the spawning grounds some time prior to spawning and remain there until spawning is over. Individual females move on to the grounds as they ovulate, and leave after oviposition which occurs soon afterwards (Fuller _et al._, 1976). In consequence spawning grounds can be recognised by the preponderance of males while samples taken in deep water at the same time consist mostly, and sometimes entirely, of females which have not yet spawned or are spent.

Spawning in Loch Lomond usually begins about the winter solstice, and lasts for 3 to 4 weeks. In some years it may begin up to two weeks earlier or later, but the duration remains the same (Scott, 1979). Prior to this study, nothing was known of the location and timing of powan spawning in Loch Eck.

3.1.2. MATERIALS AND METHODS

(a) Assessment of Reproductive Status

(i) By inspection. Ovaries and testes were examined visually when the specimen was dissected. Visual inspection of adult gonads was most useful at spawning time, when the proportions of the various stages gave a useful indication of when spawning began and ended. In females there were clear differences between fish which had not yet begun final maturation, with their oocytes compact, yellow-orange in colour, and opaque (Plate 17); those in which the maturation divisions were in progress, the oocytes being deep orange in colour and translucent (Plate 18); ovulating fish in which the coelom contained many free ova (Plate 19); and spent fish, in which only a few free ova remained (Plate 20). These four stages were respectively termed 'preovulating', 'barely ovulating', 'ovulating' and 'spent' by Fuller (1974). In males the changes were less abrupt, but ripe or 'running' males were identifiable by the milky consistency of the testes (Plate 24), and spent males by the increased vascularisation of the testes (Plate 25).

Immature fish of both sexes could be readily identified by their minute gonads, those of males being generally too small to weigh under field conditions. A further category also identifiable visually were fish entering their first reproductive cycle as they do not conform to the normal adult cycle. These 'adolescent' (Hickling, 1930) and immature individuals are dealt with separately in Chapter 4.

(ii) By gonadosomatic index. Both gonadosomatic index (gonad weight*100 / total weight) and somatic gonadosomatic index (gonad weight*100 / somatic weight) were calculated. It was decided to use gonadosomatic index rather than somatic gonadosomatic index in this study since it is the index most commonly used in other studies (Wootton, 1979). Gonadosomatic indices have been criticised as being poor indices of gonad activity, mainly on the grounds that the relationship of ovarian weight to body size changes with the stage of oocyte development (Delahunty & de Vlaming, 1980; de Vlaming *et al.*, 1982). Scott (1979) made a similar criticism, though from a less statistical viewpoint. Rashid (1984) studied gametogenesis in Loch Lomond powan, using gonadosomatic index, light microscopy and electron microscopy. From his results it is evident that although some stages of gametogenesis are not reflected in the gonadosomatic index, certain others are (e.g. exogenous vitellogenesis, spermiogenesis). To avoid the risk of confusing different stages of gametogenesis, comparison between gonadosomatic indices in different years were only made if samples were taken within 2 weeks of each other (in the first fortnight or the last fortnight of each month). Ovulated ova were not included in ovarian weight, only the residual stroma being weighed, since the weight of ova lost during oviposition and expressed during catching could not be assessed.

(b) Biochemical Analysis

Gonads of Loch Eck powan were deep-frozen for the analysis of lipid, water and protein content. They are considered in Chapter 3.3.

3.1.3 RESULTS

No attempt was made to measure fecundity in this study. However, to determine whether gonad size was related to age, the mean gonadosomatic indices of preovulating adult females from both lochs were calculated for each age group (Table 3.1). The low numbers of fish in some age groups meant that statistical significance was doubtful, but the youngest females (2+ in Loch Eck, 2+ and 3+ in Loch Lomond) tended to have lower gonadosomatic indices than the older females. Gonadosomatic indices of females from 3 to 6 years of age were very similar. In Loch Eck, there is a hint that gonadosomatic index may decrease in females over 6 or 7+. In a very few old powan (8+ and over) gonads were absent or atretic (Plates 15, 16), but such fish showed no sign of somatic decrepitude, and often had large lipid reserves. Apart from these geriatric individuals, few fish departed from the normal adult reproductive cycle. There were a few adult individuals which appeared to be out of phase with the rest of the population (see Ch. 4), two hermaphrodites out of 17,500 powan examined (Scott, 1975; Brown & Scott, 1988), and one 5+ fish lacking gonads (Plate 14).

(a) Gametogenesis

(i) Loch Lomond.

Females. The mean gonadosomatic indices of females in samples from January 1979 to February 1987 are shown in Fig. 3.1a. The general pattern of change in gonadosomatic index corresponded with that described by Rashid (1984).

During spawning the gonadosomatic index decreased rapidly to a February value of about 2%. At this stage the spent ovary consisted of dividing oogonia, previtellogenic oocytes, follicular calyces, and some unovulated vitellogenic oocytes (Plate 20). A further decrease in gonadosomatic index to 1% by April or May was indicative of the resorption of calyces and oocytes. Endogenous vitellogenesis began in early April to May (Plate 21), but this was not reflected by the gonadosomatic index, which did not increase significantly until June, when exogenous vitellogenesis began. Until then the oocytes remained small, and bright orange in colour (Plate 22). As exogenous vitellogenesis progressed, the gonadosomatic index increased exponentially from June to a maximum in December with a corresponding increase in size of oocytes (Plate 17). The final stages of maturation and ovulation occur in quick succession, probably in 24 to 48 hours (Hickling, 1930; Scott, 1979; Plates 18, 19). At this stage females moved on to the spawning grounds. Aberrations occurred in April 1980, June 1981, and April 1982, when higher than expected gonadosomatic indices were accompanied by large standard deviations (Fig. 3.1a). There were highly significant differences between years in the maximum gonadosomatic index reached (Table 3.2a). High prespawning gonadosomatic indices occurred in 1980, 1981 and 1984. In 1985, the gonadosomatic index was notably low.

Males (Plates 23 to 27). The mean gonadosomatic indices of males in samples from January 1979 to February 1987 are shown in Fig. 3.1b. The general gonadosomatic index pattern over the entire period corresponded to that described by Rashid (1984). After spawning, the gonadosomatic index remained low until June or July before increasing rapidly to a maximum in September or October. Between October and December the gonadosomatic index decreased as spermiogenesis occurred. There was a transient increase before spawning, so transient as to be missed in some sampling years. There were significant differences between years (Table 3.2a). The maximum gonadosomatic index in 1981 was relatively high; in 1985 it was low.

(ii) Loch Eck

Females. The mean gonadosomatic indices of females in samples from January 1984 to January 1987 are shown in Fig. 3.2a. The seasonal cycle of gonadosomatic index in Loch Eck females was virtually the same as that in Loch Lomond. Maximum gonadosomatic index immediately preceded the sudden decrease at spawning, with a period of further gradual decrease until March or April. A rapid increase accompanied exogenous vitellogenesis in late summer and autumn. There were significant differences in the gonadosomatic indices between years (Table 3.2b); on the 12th January 1984 it was significantly higher than on the 9th January 1985, and on the 30th January in 1985 it was much higher than on the 30th January 1987. These differences may relate to the differences in the time of spawning (see p. 143), rather than to differences in gonad size. There was no difference between the maximum gonadosomatic indices in 1985 and 1986. Occasional histological samples confirmed the similarity of oogenesis in the two lochs.

Males. The mean gonadosomatic indices of males in samples from January 1984 to January 1987 are shown in Fig. 3.2b. The pattern differed slightly from that in Loch Lomond. In Loch Eck males, the maximum gonadosomatic index occurred in November (there was no October sample). A transitory prespawning increase was apparent in January 1985, but not in 1986 when the widely spaced samples would have missed it. Minimum gonadosomatic index was reached in April or May, and was followed by an increase to the maximum late in the year.

(b) Location and Timing of Spawning

(ii) Loch Lomond. A sample taken on the Ross Islands spawning ground on 10th January 1985 showed a sex ratio typically dominated by males, as did the sample of 9th January 1986 in Sallochy (Fig. 1.5a). On the 9th January the net was set partly inshore on a shallow gravel substrate. Without taking samples at closely timed intervals throughout the spawning period, it is difficult to determine exactly when spawning begins and ends. However, the proportions of preovulating, maturing and spent fish in a sample gives some indication of the progress of spawning. Between 1979 and 1987, the earliest estimated start of spawning was 15th December 1981 and the latest estimated start of spawning was in 1980, when spawning began in the first week of January (Fig. 3.3). All spawning periods which could be reliably timed lasted for about 4 weeks.

(ii) Loch Eck. Since there are no offshore shallow banks in Loch Eck, nets were set on a gravel substrate inshore; parallel to the shore in depths of 1 to 4m, at right angles to the standard offshore netting position. On 26th February 1985, the ratio of males to females in the inshore net was 6.6:1 (Fig. 1.5b). A net in the offshore position on the same date produced 0.6:1 m:f. Nets in the offshore position on the 9th January 1985 and the 30th January 1985 gave ratios of 0.6:1 and 0.13:1 respectively. Earlier, on 17th December 1984, the ratio was 1.2:1 (as compared to a ratio of 1.9:1 in September 1984). These figures strongly suggest that there is a spawning ground inshore, with males gathering there as much as two months prior to spawning (Fig. 1.5b). A similar situation was apparent in 1985-86 with a m:f ratio of 13:1 inshore on 5th February 1986, and 0.8:1 offshore. It is clear that males were moving to the spawning ground as early as 19th December 1985, when the offshore ratio was 0.7:1. In the spawning period of 1987, the offshore net gave the usual low ratio of males to females, but unfortunately the inshore net drifted in gale force winds and its catch was atypical.

The timing of spawning in Loch Eck varied more from year to year than in Loch Lomond, though the spawning period had the same duration of 4 weeks (Fig. 3.3). The first Loch Eck sample in the present series was taken in the standard offshore position on 12th January 1984 by A.F. McCulloch and P.P. Pomeroy. 79% of the catch was female, and none had yet ovulated. A second sample in the same location on 14th February 1984 was 82% female, all but one of which were spent. Spawning can therefore be reliably identified as having taken place in the 4 week period between these samples. In 1985 spawning did not begin until 30th January and ended on 26th February. In 1986 spawning was estimated to have begun about the first week of January, and was definitely complete by 5th February. In 1987, spawning was complete by 30th January, and therefore probably started at the beginning of that month.

3.1.4 DISCUSSION

(a) Fecundity

Maitland (1969) and Finnigan (1983) related the number of ova immediately prior to spawning to the fork length of female Loch Lomond powan. Twelve of Maitland's fish were caught in December 1964, 88 in December 1966. There was no significant difference between years. He calculated that the average fork length of spawning females was 272mm, and that such a fish would contain 5,750 ova. The largest specimen he caught was "almost 8 years old" with a fork length of 369mm and total weight of 695g. It contained 23,467 ova. Finnigan analysed 74 fish caught from October 1982 to January 1983 and found that 20.7 ova were produced per 1mm of fork length. The number of ova for a fish of fork length 272mm was therefore 5,629, which is very similar to the value obtained by Maitland (1969).

In many species reproductive effort increases with increasing age and size (Love, 1970; Mann & Mills, 1979; Wootton, 1979). The limited data obtained from comparing gonadosomatic indices (Table 3.1) would suggest that this is not true of older powan. From 3+ to 6+, the gonadosomatic index remains much the same. In powan 7+ or 8+ and over, gonadosomatic index may decrease. Therefore, high reproductive effort is unlikely to be a major cause of increased mortality in 5 and 6 year old powan (Ch. 2.3, Fig. 2.15b). Gonadosomatic index is a very crude way of analysing reproductive effort, especially when such low numbers are involved, but similar results were found for vendace, C.

albula (Kamler & Zuromska, 1979; Kamler et al., 1982). The heaviest eggs were produced by vendace of medium age (3+, 4+). Older females produced smaller, poorer quality eggs, as did the youngest females (2+). Young female powan (2+ in Eck, 2+ and 3+ in Lomond) had a lower gonadosomatic index than older females. Hislop (1988) found that young 2+ haddock, Melanogrammus aeglefinus, had significantly smaller and lighter eggs than older haddock. Because eggs from first time spawners are often of inferior quality, the recommendation in aquaculture is that female broodstock are not used until after their first spawning (Bye, 1984).

When the number of ova produced by the various age groups of Loch Lomond females was calculated in Table 2.25 (for estimation of mortality in Chapter 2.3.4), the greatest contribution in numbers of ova was from the 3+, 4+ and 5+ age groups in that order, suggesting that these age groups are the most important to the spawning population.

Environmental conditions certainly affect fecundity, in terms of both the quantity and the quality of oocytes (Wootton, 1973b; Kamler & Zuromska, 1979; Zawisza & Backiel, 1979; Kamler et al., 1982). In view of the high energy cost of oocyte production (Ursin, 1979; Dabrowski, 1982b), it seems likely that food availability is a major factor affecting gonad growth (Wootton, 1979). In the multiple spawning stickleback, Gasterosteus aculeatus L., the rate of the final stage of maturation and the number of spawnings were related to the food supply (Wootton, 1973a, 1977). In haddock, egg production and feeding level were positively correlated (Hislop et al., 1978). In Loch Lomond, 1985 was a poor year both in terms of plankton production (Pomeroy, 1987) and in growth rate (Ch. 2.2). The gonadosomatic indices of both sexes was also low (Fig. 3.1), indicating a similar correlation of feeding and fecundity.

(b) Gametogenesis

The pattern of gametogenesis was similar in females of Lochs Lomond and Eck but differed in the males. Recrudescence of the testis began earlier in Loch Eck males but their maximum gonadosomatic index was not reached until later, suggesting a long period of moderate spermatogenetic growth, as compared to a short rapid period of growth in Loch Lomond males (Fig. 3.2b). This difference might be associated with the feeding differences in the two populations (Ch. 5).

(c) Location and Timing of Spawning

The timing of spawning appears to be determined by when the females ovulate, since males are present on the spawning grounds up to 2 months previously, and are 'running' for at least a month after spawning is over. The presence of ripe males in autumn may explain early statements that powan spawn at that time (Lamond, 1922, 1931). The spawning time of females is limited to 4 weeks.

Spawning time is partly under genetic control (Fabricius, 1950; Svardson, 1970; Scott, in press). Photoperiod is considered to be an important cue in the environmental timing of the reproductive cycle of salmonids (Bye, 1984; Scott, in press). In his review of environmental control of salmonid reproductive cycl~~es~~, Scott (loc. cit.) does not refer to coregonines, but includes charr (Salvelininae). In summary, long daylength initiates a 41-week cycle of gametogenesis and short daylength accelerates it, resulting in spawning. The definition of 'long' and 'short' is disputable and there are exceptions. Autumn spawning trout (October-November) have a cycle of less than 41 weeks; the explanation offered is that they are particularly sensitive to the accelerating effect of short daylength. Trout which spawn in late winter (February-March) have a cycle of more than 41 weeks; the explanation offered is that these stocks are uncommon and are almost exclusively domesticated rainbow trout strains. Spring and summer spawners (June-September) have a much longer cycle, explained by low temperatures in winter retarding gonadal development in their more northerly habitats. In all cases spawning time is apparently determined by a photoperiod months in advance and it is suggested that ovulation occurs automatically at the end of the reproductive cycle. However, Scott (in press) points out that "most of the experimental work on photoperiodic control of spawning in salmonids has been carried out on domesticated strains of rainbow trout and brook charr".

Maitland (1969) suggested that increasing daylength after the winter solstice, in association with low water temperature and high water levels, might cue spawning in powan. Fabricius (1950), and Svardson (1970) have also postulated temperature as being important in the timing of spawning of whitefish. Scott (1979) argued that since photoperiod and temperature changes are minimal at this time of year, they are unlikely to be involved. He postulated that powan became entrained to lunar cycles, and that a particular moon phase (unspecified) might trigger ovulation in a female which had reached a state of physiological readiness. Since moon phases fluctuate from year to year, but never by more than two weeks, Loch Lomond powan might therefore be expected to spawn within a period delimited by the stagger from year to year in moon phases, during December or January. If for any reason fish reached readiness in time to be triggered by the moon phase before the normal one, spawning might take place a month early. If they were slow in reaching readiness, spawning might not be triggered until the moon phase after the normal one. O'Connell (1984) estimated the beginning of spawning times of powan in Loch Lomond over a period of various years until 1981, and found that they approximated to the date of the full moon. Although it is not realistic to define exactly when spawning begins and ends to much closer than one week, there appears to be a correlation.

Fig. 3.3 shows the estimated spawning times in Loch Lomond from 1979-80 to 1986-87, as well as O'Connell's data for earlier years. Spawning times in Loch Eck from 1983-84 to 1986-87 are also shown, as are the dates on which the moon was full in December, January and February in each year. The pattern in Loch Lomond from 1981-82 follows that of previous years. The start of spawning appears to be associated with moon phase. The earliest start was in the first week of December (in 1976) and the latest start was in the first week of January (in 1979). The correlation could well be circumstantial, given the difficulty of defining the spawning period. In Loch Eck, however, not only were the spawning periods in 1983-84 and 1985-86 four weeks later than in Loch Lomond, but their timing corresponded with the difference in moon phases in those years. In 1983-84 spawning began in mid to late December in Loch Lomond but not until mid to late January in Loch Eck. In 1984-85 spawning started at the end of December in Loch Lomond compared with the beginning of February in Loch Eck. In 1985-86 and 1986-87, the time of spawning was the same in both lochs.

It is postulated that because Loch Eck is so much smaller than Loch Lomond, year to year differences in enviromental characteristics, particularly food availability might be more extreme in Loch Eck than in Loch Lomond (Ch. 5). Consequently, the time taken to achieve spawning 'readiness' in Loch Eck could be more variable than in Loch Lomond. It is therefore likely that Loch Eck powan might respond to a wider range of moon phases.

The spawning time of other British coregonines differs. In gwyniad in Llyn Tegid it is cited as beginning at the end of January (Maitland, 1967). Maitland (loc. cit.) described problems in cross-fertilising Loch Lomond powan with gwyniad in two years (1964, 1966) because of this difference in timing. Bagenal (1970) describes schelly in Ullswater and Haweswater as spawning between mid-January and mid-February (1965 to 1967). These observations were based on only a few years, and in these relatively small lakes there may well be year to year variations in spawning time as in Loch Eck. Pollan (*C. autumnalis pollan*) in Lough Neagh spawn in mid-December (Dabrowski, 1982a; Wilson & Pitcher, 1984b). Wilson & Pitcher (loc. cit.) cite Lough Neagh fishermen as believing that the spawning of pollan is related to the phase of the moon.

3.2 WEIGHT CHANGES RELATIVE TO DEPOSITION AND MOBILISATION OF STORAGE PRODUCTS

3.2.1 INTRODUCTION

When ingested energy is surplus to immediate needs, it is stored in reserves, mainly of lipid, but also of protein and glycogen (Shul'man, 1974). Consequently weight increases until a 'negative energy balance' occurs, when the energetic needs exceed that supplied by the assimilated food. Then the reserves are mobilized and weight decreases. "Storage growth" is therefore closely related to the quantity and quality of feeding, and to the requirements of metabolism and growth processes such as somatic growth and reproduction. According to Shul'man (1974), the very strict time limits of reproduction call for especially intensive energy expenditure. Northern temperate species which spawn in winter or spring concentrate gonad growth in autumn or winter, times when food may be scarce. They are therefore particularly dependent on stored energy for gametogenesis and spawning (Reshetnikov _et al._, 1970; Mackinnon, 1972; Rashid, 1984; Pomeroy, 1987).

Seasonal deposition and mobilisation of storage products can be assessed by analysing changes in weight: of the whole fish, and of individual tissues and organs. The problem with comparing overall fish weights is that weight is related to size, and every sample contains a differing range of fish sizes. One method is to compare fish of a 'standard' length throughout the time of study (Idler &

Bitners, 1959; Mackinnon, 1972; Craig, 1977; Medford & MacKay, 1978; Dawson & Grimm, 1980). Dawson & Grimm (1980) analysed female plaice, Pleuronectes platessa L., of approximately 35cm in length. The other authors calculated a 'standard length' by averaging all fish lengths. In each sample, the measurement of interest (e.g. body weight) was regressed against the fish lengths, and from the regression, the body weight of the 'standard' fish could be estimated. To reduce size-dependent variability, Medford & Mackay (1978) only used pike (Esox lucius), of 45-55cm in length. The spawning run of sockeye salmon (Oncorhynchus nerka), is very uniform in size (Idler & Bitners, 1959). Craig (1977), working on energy changes in perch (Perca fluviatilis), opted to use fish which were large enough to show little somatic growth. This approach is of no use in a study where young, rapidly growing fish are of interest. An alternative method is to relate the weight to the size of the fish, either as a ratio of the length, or in the case of organs and tissues (such as the gonads, Ch. 3.1), as a ratio of the somatic or total weight of the fish.

Condition factors. The relationship of weight to length can be described by the formula:

$$W = aL^b$$

where W = weight, L = length, and a is a constant. The exponent, b, equals 3 for an 'ideal' fish which maintains the same shape with increasing size. This relationship is the basis of the condition factor, (Le Cren, 1951):

$$K = W/L^3 \times 10^5$$

Some salmonids are close in form to the 'ideal' (Tesch, 1968). Pomeroy (1987) verified that when log length was plotted against log weight, the exponent b was always around 3 for powan in both lochs (Loch Lomond, 2.608 to 3.441; Loch Eck, 2.512 to 3.305), although there was significant variation between sexes. Le Cren (1951) calculated b for specific categories of perch, categorised by age, sex and maturity, and used the calculated exponent for each category instead of the standardised 3, so obtaining a 'relative condition factor'. This method was also used by Craig (1977) for perch and Wilson & Pitcher (1983) for pollan (_C. autumnalis pollan_). It was decided to use the standard exponent of 3 in calculating condition factors for powan in both lochs, because differences between the two populations and seasonal changes in condition factors would be apparent, even if not strictly accurate (Elliott 1976a; Wootton _et al._, 1978; Bolger & Connolly 1989). Calculation of relative condition factors is an involved method and in view of the large amount of heterogeneity between powan samples (Pomeroy, 1987), might not be any more accurate. Bolger & Connolly (1989) reached a similar conclusion in their review of condition indices.

Total fish weight is affected by seasonal variations in gonad weight, particularly in females (Ch. 3.1). Subtracting gonad weight from the total weight (somatic weight) results in the somatic condition factor (SCF), which is useful in removing some of the 'blanketing' effect of gonad changes (Scott, 1963, 1979; Wootton, 1979).

Liver. Although the liver of powan is negligible in weight compared with the total body weight, the liver has several important functions including glycogen storage (Valtonen, 1974), and the synthesis of yolk precursors during ovarian development (Shackley & King, 1978). The livers of Loch Eck powan were generally larger and paler in colour than those of Loch Lomond powan, except during the spawning season when Loch Eck powan livers ranged in colour from dark red to pale brown (Plate 13).

Liver weight was studied as a percentage of somatic weight (hepatosomatic index). Delahunty & de Vlaming (1980) concluded that since hepatosomatic index did not change over the range of body weights examined, it was an appropriate expression of liver size.

Viscera. In many species, including powan, a major site of lipid deposition is around the viscera (Shul'man, 1974; Rashid, 1984). Changes in visceral weight may therefore conveniently reflect changes in the amount of visceral lipid. The visceral weight was calculated as a percentage of somatic weight (viscerosomatic or gut-somatic index).

Indices are not entirely satisfactory, since they derive from two variables, and a change in either will alter the index. However, they have the advantage that results from fish of differing sizes and age groups may be averaged, and also that Loch Lomond and Loch Eck populations may be compared, irrespective of size differences. Indices are an approximation, but useful.

3.2.2 MATERIALS AND METHODS

The Loch Lomond powan analysed were from the samples of January 1979 to March 1987 (Table 1.3). For Loch Eck, fish from January 1984 to January 1987 were analysed (Table 1.4). In the earlier 1979-84 Lomond samples (Tables 1.3b), total length, total weight, sex and gonad weight were routinely recorded, and so the gonadosomatic index (Ch. 3.1) and somatic condition factor could be calculated for all samples even if liver and visceral weights were not recorded.

The following indices were calculated:

(i) <u>(Somatic) Hepatosomatic index</u> (HSI)

= Liver weight/Somatic weight x 100

(ii) <u>(Somatic) Gut-somatic index</u> (GtSI)

= Emptied visceral weight/Somatic weight x 100

(iii) <u>Condition factor</u>

= Total weight/(Total length)^3 x 10^5

(iv) <u>Somatic condition factor</u>

= Somatic weight/(Total length)^3 x 10^5

Only reproductively normal adults are analysed in this chapter; immature and adolescent powan are considered separately in Chapter 4. Somatic condition factor is analysed, the condition factor is only used in relation to total lipid content (Ch. 3.3) and in the Chapter 5 figures. Although the term 'viscerosomatic' index (VSI) is the more correct, the term 'gut-somatic' index (GtSI) is used to reduce possible confusion between VSI and VLSI, the visceroliposomatic index (Ch. 3.3, 5).

3.2.3 RESULTS

(a) Loch Lomond

(i) Hepatosomatic Index (HSI) Fig. 3.4

Females. From a minimum in April or May, the hepatosomatic index of females increased until July and remained constant until August or September, before increasing once more to a maximum in October. The hepatosomatic index then decreased, gradually at first until December or early January, then more rapidly during spawning. The decrease continued until April or May.

There were significant differences from year to year, with the exception of April and late May samples, when hepatosomatic index was at a minimum (Table 3.3a). In 1984 and 1985, the hepatosomatic indices were low and reached a maximum later (November or December).

Males. From a minimum in April or May, the hepatosomatic index of males increased rapidly to a maximum in July. The hepatosomatic index then decreased until October, and remained at a low level until April.

There was significant variation in the hepatosomatic index from year to year, except in late May and early July (only two samples, Table 3.3a). In May 1984, male hepatosomatic index was higher than in previous years, although later 1984 samples were average. As in the females, the hepatosomatic indices in 1985 were low.

(ii) Gut-somatic Index (GtSI) Fig. 3.6

Females. The gut-somatic index was highest in July or August 1985 before decreasing, rapidly at first till September, then more gradually to a minimum in January or February. There was a slight increase in gut-somatic index between January and May 1985 ($p < 0.05$), then a more rapid rate of increase from May to August 1985, and June to July in 1986.

There were no significant differences between years.

Males

Male gut-somatic index followed a similar seasonal pattern to the females, except that the January to May 1985 increase ($p < 0.05$) was not as pronounced.

There were no significant differences between January samples, but the gut-somatic index in May 1985 was significantly higher than in May 1986 ($p < 0.02$).

(iii) Somatic Condition Factor (SCF) Fig. 3.5

Females. From a maximum in July, August or September, the somatic condition factor decreased till January or February, with the greatest rate of decrease occurring from September to October. In the years 1980 to 1983, there was a transient increase in somatic condition factor in March or April. Minimum somatic condition factor occurred in May in all years. In several years, the most rapid rate of increase was between May and June.

There were highly significant differences between corresponding months in different years (Table 3.3b), although minimum and maximum somatic condition factors did not differ significantly between years. The significant monthly differences therefore resulted from variations in the timing of somatic condition factor changes between years.

Males. Male somatic condition factor decreased from a maximum in July, August or September until January. The initial decrease (September to October) was often the most rapid. From January, the somatic condition factor remained constant, before a further slight decrease to a minimum in April or May. The somatic condition factor then increased rapidly to its maximum.

Differences between years were very highly significant (Table 3.3b).

(b) Loch Eck

(i) Hepatosomatic Index (HSI) Fig. 3.7

Females. The hepatosomatic index was maximal in November or December, after which it decreased rapidly until February. Between February and April 1986, there was a rapid increase in hepatosomatic index, which then remained constant until June. From May or June to August, the hepatosomatic index decreased to a minimum, but by September, was increasing rapidly again to the November-December maximum.

There was a difference in timing in the two years. The 1984-85 maximum was reached in December or early January, but the 1985-86 maximum was reached in November (there was no October sample). The magnitude of the hepatosomatic index also varied between years (Table 3.4a); September, November and December in 1984 were significantly lower than in 1985. The April (1st) 1986 hepatosomatic index was significantly higher than in March (27th) 1985. The hepatosomatic index in January 12th 1984 was significantly lower than in January 9th 1985.

Males. From a maximum in June (no July sample), the male hepatosomatic index decreased to a low level in August, and remained low until September. The hepatosomatic index then increased until January. Over spawning there was a pronounced decrease to February, followed by a rapid recovery to the pre-spawning level in March. The hepatosomatic index then remained high until June.

The hepatosomatic index was significantly lower in 1984-85 than in 1985-86 (Table 3.4a).

(ii) Gut-somatic Index (GtSI) Fig. 3.6

Females. The gut-somatic index was at a maximum in June and August, then decreased to a minimum in January or February, with the greatest rate of decrease being between August and September (November-December in 1984). From February, the gut-somatic index increased to the June-August maximum. The greatest rate of increase occurred from March to May in 1985, and between April and June in 1986.

There was significant variation between years (Table 3.4b). Although there was no significant difference between December gut-somatic indices in the two years, the gut-somatic index in February 1985 was significantly higher than in February 1986, and April 1986 was significantly higher than March 1985.

Males. Maximum gut-somatic index occurred in June, July or August, followed by a highly significant decrease from August to September ($p < 0.001$). Between September and November the gut-somatic index increased again, and remained constant until December. The gut-somatic index then decreased to a minimum in February, before increasing gradually from March to June.

There was no significant difference between December samples. As in females, the gut-somatic index in February 1985 was significantly lower than in February 1986, and the gut-somatic index of April 1st 1986 was significantly higher than March 27th 1985 (Table 3.4b).

(iii) Somatic Condition Factor (SCF) Fig. 3.8

Females. The somatic condition factor was maximal from June to August. From August to September it decreased, thereafter remaining constant until December or early January, when there was a further decrease during spawning to a minimum in February.

With the exception of the September and early January samples, differences between years were very highly significant, with the somatic condition factor increasing from 1984 to 1987 (Table 3.4c).

Males. The somatic condition factor was at a maximum in June (no July sample) before decreasing slightly until September. There was a significant decrease from November to December 1985 ($p < 0.02$), the decrease continuing to a minimum in February. The somatic condition factor increased from March to its maximum.

There were no significant year to year differences between the January and September samples, but differences in other months were highly significant (Table 3.4c), indicating an increase in somatic condition factor from 1984 to 1987, as in the females.

3.2.4 DISCUSSION

Hepatosomatic indices, gut-somatic indices, and somatic condition factors are discussed individually in this section. How they interrelate to each other and to other growth proceses, will be further discussed in Chapter 5.1.

(a) Hepatosomatic Index

(i) Loch Lomond (Fig. 3.4).

Female hepatosomatic index was significantly higher than male hepatosomatic index with the exception of February to May in most years, when both sexes were at a minimum, also June 16th 1981, June 29th and July 26th 1986.

The low April-May liver weights reflect depletion of reserves during spawning and early spring when feeding has virtually ceased. Finnish *C. nasus* (Pallas) were found to have very low levels of liver lipid and glycogen at this time (Valtonen, 1974).

The hepatosomatic index increase from May to July coincides with the increase in feeding intensity. From July to August, when the rate of feeding is constant (Pomeroy, 1987), the hepatosomatic index in both sexes was either constant or declined slightly. Male hepatosomatic index declined from August to October, despite the fact that feeding intensity was highest in September, perhaps in relation to rapid testis growth from August to a September or October maximum (Ch. 3.1, Fig. 3.1b).

Despite a significant reduction in feeding after September, the hepatosomatic index of females increased from

August to a maximum in October. The greatest rate of hepatosomatic index increase coincided with the time of rapid gonadosomatic index increase (September-October, Fig. 3.1a). This increase in liver weight therefore reflects the increased activity of the liver in synthesing yolk precursors for deposition in the developing oocytes (Reshetnikov et al., 1970; Chechenkov, 1973; Shackley & King, 1978). The gradual decline in hepatosomatic index from October to December presumably results from a reduction in exogenous vitellogenic activity.

(ii) Loch Eck (Fig. 3.7).

Female hepatosomatic index was significantly higher than male hepatosomatic index with the exception of January 30th 1985 and 1987.

The hepatosomatic index in both sexes was at a minimum directly after spawning. When spawning had been completed, feeding recommenced and the hepatosomatic index returned to the pre-spawning level by March 1985. In males and females, the hepatosomatic index remained constant until June (no July sample), but an increase in somatic condition factor (Fig. 3.8) indicates that body weight was increasing, and so liver weight must have been increasing in proportion. The hepatosomatic index of both sexes then decreased to August. Pomeroy (1987) found that although Loch Eck powan were feeding most heavily in August, the diet was mainly Pisidium which has a low calorific value compared with chironomids. The inferior nutritional value of Pisidium could be a reason for the low hepatosomatic index in August.

Vitellogenesis accounts for the increase in the female hepatosomatic index from August to a November-December maximum. During spawning, the hepatosomatic index decreased in both sexes. Prior to the spawning decrease, male hepatosomatic index increased from September, possibly because Loch Eck fish were still feeding, and the energy requirements for testis development may have decreased (the gonadosomatic index was high, Fig. 3.2).

(iii) Comparison of the hepatosomatic indices of Loch Lomond and Loch Eck powan.

Loch Eck powan had significantly higher hepatosomatic indices than Loch Lomond powan (Table 3.5). There were also differences in their seasonal cycles. Loch Lomond female hepatosomatic index increased continuously from a minimum in April or May to a maximum in October. Loch Eck female hepatosomatic index increased at a more rapid rate from a minimum in February until March or April, remained constant until June, then decreased for a second time to August before the vitellogenic increase to a November or December maximum. Although the hepatosomatic index of females in both populations decreased during spawning, Loch Lomond female hepatosomatic index continued to decrease until May, while Loch Eck female hepatosomatic index increased after spawning.

In males of both lochs, the hepatosomatic index was highest in June-July. Loch Eck male hepatosomatic index then decreased to a low level in August and September. Loch Lomond male hepatosomatic index also decreased, but from August to October, remaining low until November. By November

Loch Eck male hepatosomatic index was increasing, and continued to increase until spawning in December or January. There is a hint that Loch Lomond male hepatosomatic index may also increase before spawning, but the increase was later, from November to December. The hepatosomatic indices of males in both populations decreased over spawning, but Loch Eck males recovered rapidly to a high level in March-April, while the hepatosomatic index of Loch Lomond males remained low until May.

The seasonal fluctuations in hepatosomatic index in both lochs were therefore closely related to feeding. Spawning is a time of fasting and extra energetic requirements (Ch. 3.1), and so hepatosomatic index decreased in both sexes in both populations. Resumption of feeding after spawning is marked by an increase in hepatosomatic index. Loch Eck powan resume feeding just after spawning, and consequently the hepatosomatic index reincreases rapidly. Loch Lomond powan do not resume intensive feeding until April or May, and therefore the hepatosomatic index remains low until May. A relationship between food availability and liver weight has also been noted by Valtonen (1974), Heidinger & Crawford (1977), Allen & Wootton (1982), Adams & McLean (1985), and Cui & Wootton (1988a).

Since liver weight reflects nutritional state, it is likely that the year to year variations observed result from variations in food availability. In Loch Lomond, plankton abundance was low in 1985 (Pomeroy, 1987); hepatosomatic index in both sexes was also low (Fig. 3.4). In Loch Eck in

1984, hepatosomatic index was low in males and females. Feeding intensity was low in September 1984, but as this was the only September sample analysed by Pomeroy, it is not known whether feeding is always poor in September, or if 1984 was unusual.

(b) Gut-somatic Index (Lomond and Eck, Fig. 3.6)

The gut-somatic index results were of limited use in assessing changes in visceral fat levels. Lack of samples meant erratic and inconsistent results, particularly in Loch Lomond powan, where visceral weight was affected by varying degrees of parasitic infection (Plate 12). For this reason Jensen (1980) avoided using charr, (Salvelinus alpinus) infected with Diphyllobothrium, in calculations of 'gut indices'.

In most of the Loch Lomond samples, females had a higher gut-somatic index than males, significantly so in May, August and November 1985, and also in January and May 1986. However, Loch Lomond males had a higher gut-somatic index in October and December 1984, June and July 1986 and February 1987. The results were therefore inconclusive as to whether one sex had a consistently higher gut-somatic index.

In Loch Eck, male gut somatic index was higher than females in most months, significantly so in December 1984, November and December 1985, February 1986 and January 1987. Although females had the higher gut-somatic index from February to September 1985, the difference was only significant in February.

Loch Eck powan generally had significantly higher gut-somatic indices than Loch Lomond powan (Table 3.5). There were some similarities in seasonal gut-somatic index variations in the two lochs. During feeding, the gut-somatic index increased to a maximum, which was in August in Loch Lomond, and from June to August in Loch Eck. From August to September, the gut-somatic index decreased as visceral fat was mobilised, perhaps for gonad growth. In Loch Lomond, the gut-somatic index in both sexes continued to decline until spawning in January, since feeding virtually ceases after September. After spawning, the Loch Lomond gut-somatic index remained low until feeding recommenced in May.

Despite continued feeding, the gut-somatic index of Loch Eck females also decreased from September until after spawning, signifying that visceral fat is utilised for ovarian growth. However, Loch Eck male gut-somatic index increased from September to November and remained high until spawning.

During spawning, the male gut-somatic index decreased to a greater extent than the female gut-somatic index, possibly because males are involved in spawning activities over a longer period of time (Ch. 3.1). Plates 24 and 25 show the lack of visceral fat in spawning and spent males. After spawning, the gut-somatic index of Loch Eck powan increased earlier and more rapidly than in Loch Lomond, because of the earlier resumption of feeding in Loch Eck.

In Loch Lomond, there were no significant differences between years in the female gut-somatic index, though in males the gut-somatic index in May 1985 was significantly higher than in May 1986. As feeding was poor in 1985 (May-September), males may have overwintered 1985-86 with a lower level of visceral fat, compared with 1984-85.

In Loch Eck the later spawning in 1985 may account for the gut-somatic index in both sexes being lower on March 27th 1985 than on April 1st 1986. In 1986, a longer feeding period would have elapsed since spawning compared with 1985.

(c) Somatic Condition Factor (Lomond and Eck, Fig. 3.8).

Somatic condition factor is the ratio of somatic weight to the cube of length. As length cannot decrease to any significant extent, an increasing condition factor indicates that weight is increasing relative to length. However, a decreasing condition factor can mean either decreasing weight or increasing length or a combination of the two. An increase in gonad weight may cause an apparent decrease in somatic condition factor, even though there is no overall decrease in weight, since somatic weight equals total weight less gonad weight. Condition factor (CF) has been included in the overall figures in Chapter 5 to help determine the influence of changes in gonad weight on the somatic condition factor. Most of the somatic weight of a fish derives from the muscle mass, and so changes in somatic condition factor will generally reflect changes in the weight of muscle relative to the length.

At all times, powan in Loch Eck had a very significantly higher somatic condition factor than in Loch Lomond (Table 3.5). Plates 3 and 4 show Loch Eck and Loch

Lomond adult males caught within two days of each other. The Loch Lomond male obviously had the lower condition.

In both lochs, males generally had higher somatic condition factors than females, except during the period when somatic condition factor was increasing to a maximum. In Loch Lomond, male somatic condition factor was significantly higher than the females, except in July, August and September. In Loch Eck, although males had a consistently higher somatic condition factor, the differences were only significant in September, November and December 1984, and in January 30th, February and November 1985.

Seasonal variation. The increase in somatic condition factor after spawning indicates an increase in weight. In Loch Eck, feeding resumes soon after spawning, and so the somatic condition factor increased from February or March to June. Since Loch Lomond powan did not start intensive feeding until April or May, the somatic condition factor did not increase until then. The month in which Loch Lomond somatic condition factor was maximal varied from July to September (Fig. 3.5), although the maximum occurred most often in August. In Loch Lomond, feeding intensity decreased from September and there was a decline in somatic condition factor in both sexes until spawning. In Loch Lomond males, the rate of somatic condition factor decrease was greatest from September to October and December to January, the first rapid decrease possibly being connected with gametogenesis, the second with spawning activities. In Loch Lomond females, the most rapid rate of decrease in somatic condition factor occurred between September and December, coinciding with a rapid increase in gonad weight (Fig. 3.1).

In Loch Eck, both sexes showed a decrease in somatic condition factor (and condition factor, Fig. 5.2) from June to August or September. The cause could be reproductive growth, somatic growth, decrease in weight, an increased metabolic rate through increased water temperature, or some combination of these factors (Ch. 5). From September to November in Loch Eck, male somatic condition factor may increase slightly because of the continued feeding. For the same reason, the somatic condition factor of Loch Eck females remained constant from September to December, although ovarian weight was increasing.

During spawning, feeding ceased and weight decreased. In both lochs there was a greater spawning decrease in male somatic condition factor than in female somatic condition factor. Female somatic condition factor decreased to a greater extent earlier, presumably because more stores were utilised in ovarian growth.

Year to year variations

In Loch Lomond (Fig. 3.5). Though the month when the somatic condition factor reached a maximum varied between years, it was the same for both sexes. In 1980, there was a rapid early increase to a maximum in July. In 1981, the maximum was not reached until September. In other years maximum somatic condition factor occurred in August. As both sexes responded similarly, the timing variations are likely to have been the result of environmental variations, particularly food availability. In 1985, when plankton production was low (Pomeroy, 1987), the somatic condition factor was also low.

In the Loch Lomond 1980-1983 samples, the transient increase in female somatic condition factor, in March and April (also observed in gonadosomatic index, Fig. 3.1), was possibly due to the mistaken inclusion of adolescents in the results.

In Loch Eck (Fig. 3.7) there was an increase in the somatic condition factor of both sexes from 1984-87. The low condition in 1984-85 may have related to the late 1985 spawning (Ch. 3.1), with spawning occurring earlier as condition improved.

3.3 LIPID ANALYSIS, WATER AND PROTEIN CONTENTS

3.3.1 INTRODUCTION

Indices of weight show gross changes of tissues over time, but do not define what is actually changing. The major components of the fish body were generalised by Love (1970) as being water (70-80%), protein (20-30%), lipid (2-12%) and much smaller amounts of carbohydrates and minerals. The major source of energy in most fish is lipid, since it is "the most caloric, most conveniently deposited, stable and economical source of energy in the organism" (Shul'man, 1974). Brett & Groves (1979) estimated the amount of energy physiologically available to the fish from synthesised lipid, protein and carbohydrate to be 9.45, 4.80 and 4.10 kcal/g respectively.

The name 'lipid' encompasses several classes of compounds, including triglycerides, phospholipids, sterols, wax esters and free fatty acids. In many fish, triglycerides form the main energy reserves. They may account for up to 75% of all reserve fat and are preferentially mobilised (Shul'man, 1974). In these fish, the phospholipids, free fatty acids and sterols are structural lipids, and form a relatively stable component, not being mobilised unless tissue is broken down and protein mobilised (Love, 1970, 1980; Lizenko _et_ _al_., 1975; Caulton & Bursell, 1977).

The lipids ingested depend on the food eaten. For instance, many zooplanktivores, mainly marine fish, consume large numbers of calanoid copepods in which wax esters comprise two-thirds of the dry weight (Lee & Hirota, 1973). In freshwater organisms, wax esters are not found in great quantity and are not generally consumed by freshwater fish. Instead, triacylglycerols are the main component of the ingested lipid (Cowey & Sargent, 1979).

The sites of fat deposition vary in different species of fish. Shul'man (1974), listed the main sites as being:

(i) subcutaneous connective tissue (tunas, eels, carp, certain herrings).

(ii) muscle (mackerels, horsemackerels, anchovies, certain Clupeidae, Salmonidae, Acipenseridae).

(iii) abdominal cavity, mesentery (Cyprinidae, certain Clupeidae, Percidae, whitefishes, pike).

(iv) liver (Gadidae).

(v) in the bones and at the base of fins (Pleuronectidae)

Each species frequently has more than one fat store; in coregonines, including powan, muscle and viscera are the main site of lipid deposition (Reshetnikov *et al.*, 1970; Dabrowski, 1982a,b; Rashid, 1984). The gonads, although also a major site of lipid deposition in females, cannot be considered to be a reserve, since the lipid is not mobilised for energy, but is spawned and so is lost to the fish. Reabsorption from the gonad has been reported in times of starvation in rainbow trout (*Salmo gairdneri*; Scott, 1962), though the process of reabsorption itself requires energy, and may be an effect of starvation rather than a response to starvation. Gonadal resorption also occurs in atretic fish.

The changes in lipid content resulting from seasonal variation in feeding intensity and energetic requirements occur not only in recognised fat stores, but throughout the body. Lizenko et al., (1975) found corresponding fluctuations in lipid levels in gills, swimbladder and nervous tissues of Coregonus albula.

In this study, lipid extraction was based on the 'rapid' method of Bligh & Dyer (1959), homogenising the tissue with a mixture of chloroform and methanol. The final homogenate separates into two layers, with the chloroform layer containing the lipids and the methanolic layer the non-lipids. Despite the relative crudity of this method, it is still time consuming, and in the time available, it was only possible to analyse tissues from Loch Eck powan, and compare them with previous lipid analyses of Loch Lomond powan carried out by Reid (1982) and Rashid (1984). The tissues analysed from Loch Eck powan were gonad, liver, viscera and muscle, in all of the reproductive categories.

The concentration of lipid in muscle varies with its type (white or red) and position in the fish, most reports indicating that lipid content increases towards the tail region (Love, 1970, 1980; Wills & Hopkirk, 1976). Therefore muscle samples should be taken from a standardised position, which in this and the Lomond study (Reid, 1982), was defined as being posterior to the dorsal fin and anterior to the cloaca.

Water content was estimated from the dried residue remaining from the lipid analysis. An estimate of 'protein' was then derived, based on the assumption that the remaining fraction after removal of lipid and water is substantially proteinaceous, the amount of carbohydrates and minerals (ash) being negligible (Weatherley & Gill, 1987). The glycogen content of brown trout was found to average 0.3% of the body weight (Elliott, 1976a). Craig (1977) determined an average carbohydrate content of 0.13% in perch. Both authors subsequently excluded carbohydrate from their analyses. There is little seasonal variation in ash content in perch (Craig, 1977) or in brown trout, in which the ash content only ranged from 2.4-2.8% of the wet body weight (Elliott, 1976a).

Close correlations have been observed between each of the components of the fish body and their size (review Weatherley & Gill, 1987). Consequently, estimates of body or tissue composition (proximate analyses), have been made from an easily measured parameter such as length, weight, water content and condition factor, a method considered useful in view of the tedious nature of biochemical analyses (Iles & Wood, 1965; McComish et al., 1974; Elliott, 1976a; Jensen, 1980; Dabrowski, 1982a; Weatherley & Gill, 1983b; Gill & Weatherley, 1984).

3.3.2 MATERIALS AND METHODS

The powan analysed were from the following Loch Eck samples:

Sample date	No. analysed
1985	
27th March	31
17th May	21
4th August	23
24th November	46
19th December	30
1986	
5th February	28
1st April	69
26th June	34
1987	
30th January	53

(a) Lipid Analysis

(i) The tissues were defrosted, weighed and placed in individually marked 'Colworth stomacher' bags. The entire liver and viscera were used. The entire gonad was used unless it was large, when a subsample of 2-5g in weight was taken. The sample of muscle analysed weighed from 4-6g and bones, skin and scales were removed. The tissues were refrigerated at 1 °C until required (about 15 hours).

(ii) Chloroform, methanol and water were added so that the initial volume was in the ratio of 1 part chloroform to 2 parts methanol to 0.8 parts water. Allowance was made for the amount of water already present in the tissue [see (b)]. The amount of chloroform added was in approximate proportion to the weight of the tissue. For example, if the tissue weighed 7.56g, an initial 8ml of chloroform was added. To 3.4g of tissue, 3ml of chloroform was added. To tissues weighing under 2g, a minimum of 2ml of chloroform was added.

Example:

A 2.93g liver with 73% water content. Initial volumes of solutions:

Chloroform - 3ml
Methanol - 6ml
Water - 0.26ml

(iii) The bag containing tissue and solutions was placed in a 'Colworth 80' stomacher and as much air expressed as possible. The tissue was homogenised for 3 minutes.

(iv) More chloroform was added, enough to double its proportion in the mixture [the same amount as in (ii)] and the mixture was homogenised for 2 minutes.

(v) The same amount of water as chloroform in (iv) was added, and the mixture was homogenised for a further 30-45 seconds.

(vi) The homogenised mixture was decanted into a Buchner funnel, 7cm or 9cm in diameter with 'Whatman No. 1' filter paper and filtered under suction. As water content was being estimated from the residue, care was taken to remove as much tissue residue as possible from the stomacher bag. When filtration was complete, the residue was pressed to ensure extraction of all liquid.

(vii) The filtrate was transferred to a 50 or 100ml burette and allowed to stand at room temperature until the layers had separated. The lower layer was the chloroform-lipid layer, the methanol and non-lipid constituted the upper layer. Complete separation took from 10 to 45 minutes.

(viii) The choroform-lipid layer was tapped off, and the volume measured with a pipette. A 5ml aliquot was then placed in a weighed 25ml conical flask. If the total chloroform-lipid volume was less than 5ml, all of it was used.

(ix) The flask was placed in a water bath at 40°C and the aliquot evaporated to near dryness under a stream of oxygen-free N_2. The flask was then transferred to a vacuum oven at 60 °C for 30 minutes, before being cooled in a dessicator and weighed.

(x) The percentage of lipid in the tissue sample was calculated as:

(residue wt.(g) x total vol. chloroform layer(ml)/
aliquot (ml) x sample wt.(g)) x 100

(b) Estimation of Water Content

Because optimum extraction of lipid is obtained when the final mixture contains chloroform, methanol and water in the ratio of 2:2:1.8, it was necessary to predetermine the moisture content of the tissues so that the amount of water added could be adjusted to achieve the correct ratio. The water content of tissues varies seasonally (Weatherley & Gill, 1987), but because of lack of samples, tissues from only a few fish could be released for moisture determination

These were from the samples of 24th November 1985 (1 female, 8 males), and 1st April 1986 (3 females, 5 males). The weighed tissues were dried in weighed dishes in a vacuum oven at 60 °C until a constant weight was reached (usually overnight). As the difference between wet and dried weights was assumed to be the weight of water lost, the percentage water content could be calculated. Water is lost during freezing and thawing, so in the case of viscera and liver, where the entire tissue sample was analysed, the wet weight used in calculations was the field weight (before freezing). In the case of large gonads and muscle, there was sufficient tissue to allow a portion to be removed for water determination by oven drying, in parallel with the lipid analysis of that tissue sample.

The water content was estimated from the lipid analysis residue as follows:

(wet wt. of tissue sample^{+} - dry wt. of total residue / wet wt. of tissue sample^{+})100

+ field wet weight for viscera and liver.

dry weight of total residue = the dried filtered residue plus the dried lipid residue.

After filtration, the filter paper (of known weight) containing the tissue residue was dried in a vacuum oven at 60 °C for an hour, then weighed. The dry weight of the filtered residue could then be calculated. The dried lipid residue was the dried weight of lipid in the 25ml conical flask after evaporation of the chloroform [(a), (ix)], adjusting proportionally if the aliquot used was less than the total volume of the chloroform-lipid layer.

(c) Estimation of Protein Content

Since the lipid content was known, and the amount of water estimated from the residue, the amount of protein could be deduced on the assumption that almost all of the remaining weight after subtraction of lipid and water was protein (Ch. 3.3.1).

(d) Calculations

Weights and percentages of lipid, water and protein in each tissue were calculated, also the total weights of lipid, water and protein in the whole fish. Because weight is related to size (Ch. 3.2.1), the weight of lipid in each tissue was related to the somatic weight of the fish:

(i) Gonadoliposomatic index (GONLSI)
= (Total weight of lipid in gonad/somatic weight)100

(ii) Hepatoliposomatic index (HPLSI)
= (Total weight of lipid in liver/somatic weight)100

(iii) Visceroliposomatic index (VLSI)
= (Total weight of lipid in viscera/somatic weight)100

(iv) Musculoliposomatic index (MLSI)
= (Total weight of lipid in carcase*/somatic weight)100

* carcase remains after removal of gonad, liver and viscera.

The total weight of each body constituent was related to the total weight of the fish:

(v) Total percentage of lipid in the body (Total Liposomatic index)

= (Total weight of lipid/Total fish weight)100

(vi) Total percentage of water in the body

[(Total weight of water/Total fish weight)100] - 3%

(vii) Total percentage of protein in the body

= (Total weight of protein/Total fish weight) + 3%

In (vi) and (vii), 3% was subtracted (water) or added (protein) to adjust for overestimation of water content from the residue [Ch. 3.3.3 (a)].

In the spawning samples of February 1986 and January 1987, the females and males were further categorised by gonad state (Ch. 3.1):

Females	Males
(i) Preovulating	(i) Pre-spawning
(ii) 'Barely ovulating'	(ii) Spawning
(iii) Spent	(iii) Spent

and by liver colour for each sex:

(i) Pale
(ii) Mid
(iii) Dark

Results from immature and adolescent powan are analysed in Chapter 4.

(e) Relationships

(i) Lipid and Water. The total percentage of lipid in the body (LSI) was regressed against the total percentage of adjusted water in the body. The percentage of lipid in the gonad was regressed against the percentage of water in the gonad, calculated from oven drying. All sexes and reproductive categories were combined.

(ii) Lipid and Condition. The condition factor (CF) was regressed against the total percentage of lipid in the body (LSI).

(iii) Lipid, water and protein relative to length. The total weight of each constituent was regressed against the total length of the fish, arithmetically (except water) and as a log-log transformation.

(iv) Lipid relative to weight. The total weight of lipid was regressed against the total weight of the fish (log-log).

3.3.3 RESULTS

(a) Estimation of Water and Protein Content

Table 3.6 shows the mean percentage water content of gonad, liver, viscera and muscle, estimated from: (i) the residue remaining after lipid analysis, and (ii) oven drying. The two estimates for ovary, testis and muscle were from the same fish in all samples. The two liver and visceral water estimates could not be from the same fish since the entire tissue had to be used in lipid analysis; because of the small size of the liver, and because of the non-uniform distribution of lipid around the viscera. However, the oven derived estimates were only compared with residue derived estimates from the same samples (November 1985 and April 1986), because of the possibility of seasonal variation in water content.

In all tissues, water content assessed from the residue overestimated that assessed from oven drying since any residue lost during the lipid analysis was counted as water loss. The greatest discrepancy was in the liver (13%). Although some of the discrepancy could result from the comparison of different individuals, the liver homogenised into fine particles and consequently a greater residue wastage occurred compared with other tissue samples. The least observed loss was from visceral and muscle samples. In muscle, the discrepancy between estimates from the lipid residue and from oven drying was 3%. The 6% discrepancy in the visceral estimates may have mostly arisen through the comparison of different fish.

The discrepancy in water estimate affects the protein estimate. It was decided not to investigate seasonal fluctuations in water and protein in individual tissues, particularly because the estimated 'protein' content (which includes a small percentage of ash and carbohydrates), has not been verified by biochemical analysis. Therefore water and protein content were only assessed for the whole fish. As estimates were based on residue values, the water and protein estimates were adjusted by 3%, which was the overall mean discrepancy between oven and residue estimates. This value is reasonable since muscle, with an average 3% discrepancy, comprises the bulk of the fish. Liver, despite the large 13% discrepancy, is negligible in weight.

<u>The general body composition of adult powan</u> was estimated as being 2-4% lipid, 18-20% 'protein', and 75-79% water (Table 3.7). Ash constitutes 1-3% of body weight in most species (Shul'man, 1974). This being so, the values for powan were very similar to those given by Elliott (1976a) for brown trout (2-7.7% lipid, 16.2-17.5% protein, 72-81% water, 2.4-2.8% ash).

(b) Lipid Analysis

The lowest percentage of lipid (per weight of tissue) was in the muscle (2-3%), the highest percentage was in the male viscera (8-22%). Female visceral lipid ranged from 4-11%. The mean percentage of lipid in the liver of both sexes ranged from 1.5-9%; and in the testis from 3-7%. These percentages (Table 3.7) relate to the concentration of lipid within a tissue, and not to the total weight of lipid in the whole tissue mass. Although muscle had the lowest concentration of lipid, it forms the bulk of the fish and so generally accounted for most of the lipid within the body (Fig. 3.14). The large seasonal changes in mass (and so lipid content Fig. 3.14a) of the ovaries is also not shown by these percentages. Total weights of lipid alone are of little use because of the somatic aspect (Ch. 3.2.1, p. 153), therefore the total weight of the lipid was related to the somatic weight of the fish (liposomatic indices). Assessing changes in liposomatic indices is complicated by the two variables, yet it is still a convenient method.

(i) Gonadoliposomatic Index (GONLSI) Fig. 3.9

Females. The gonadoliposomatic index was minimal just after spawning, remaining constant until April. Between April and June, the gonadoliposomatic index increased ($p < 0.01$). The increase from June to August was not significant. The gonadoliposomatic index then increased very rapidly to a pre-spawning maximum in November or December.

Males. Male gonadoliposomatic index was minimal in March and April, before an increase (not statistically significant) to May. The increase continued at a constant rate until August. There was no significant change between August and November. The increase from November to December was not significant. The gonadoliposomatic index decreased over spawning.

(ii) Hepatoliposomatic Index (HPLSI) Fig. 3.10

Females. From a post-spawning minimum, the hepatoliposomatic index increased until February or March (January 1987 to March 1985 $p < 0.02$), remained constant until April, then continued increasing to a maximum in June (April-June $p < 0.05$). There was a highly significant decrease between June and August ($p < 0.01$). The hepatoliposomatic index increased between August and December, but the increase was not statistically significant.

Males. The hepatoliposomatic index was low after spawning (February 1986, March 1985) then increased to a maximum in June (only May 1985 to June 1986 was statistically significant, $p < 0.05$). There was a decrease in hepatoliposomatic index from June to August which was highly significant ($p < 0.001$). The hepatoliposomatic index then increased again, gradually from August to November ($p < 0.05$), then more rapidly from November to December ($p < 0.02$). There was year to year variation, which caused the apparent zig-zag in the figure from February to June. Hepatoliposomatic indices were lower in 1985 than in 1986.

(iii) Visceroliposomatic Index (VLSI) Fig. 3.11

Females. Visceroliposomatic index was low from January to March, then increased to a maximum in June and August (March 1985 to May 1985, $p < 0.02$; April 1986 to June 1985, $p < 0.05$). From August till November, the visceroliposomatic index decreased, but the decrease was not statistically significant (few fish). The visceroliposomatic index then remained low until March.

Males. Male visceroliposomatic index was at a minimum after spawning in March 1985 and increased to a maximum in August 1985 (March to May 1985, $p < 0.02$; May to August 1985, $p < 0.01$). In 1986, the visceroliposomatic index was constant from April to June. Between August and November, the visceroliposomatic index decreased significantly ($p < 0.001$). There was a significant increase from November to December ($p < 0.05$). Although the visceroliposomatic index in January (1987) was higher than in December (1985), the difference was not significant.

There was variation between years. In both sexes the visceroliposomatic index in March 1985 was lower than in February and April 1986.

(vi) Musculoliposomatic Index (MLSI) Fig. 3.12

Females. Maximum musculoliposomatic index was in June, followed by a very highly significant decrease to August ($p < 0.002$). The slight decrease from August to November was not significant. Only one female was analysed in December. The musculoliposomatic index in January 1987 was significantly higher than in November 1985 ($p < 0.02$). It remained low from January until March or April, before increasing till June ($p < 0.001$).

Males. Statistically, no significant differences were detected. Male musculoliposomatic index was maximal in June, before decreasing to August. The musculoliposomatic index then increased slightly from August to November, otherwise remaining low until April.

(v) Total Liposomatic Index (LSI) Fig. 3.13

Females. The total liposomatic index increased from April to a maximum in June ($p < 0.002$). This was followed by a significant decrease from June till August ($p < 0.001$). There were no further statistically significant differences, although the total liposomatic index increased from August to November. The total liposomatic indices in January 1987 and December 1985 (1 fish) were lower than in November 1985.

Males. There were no statistically significant differences. Total liposomatic index was maximal in June then decreased rapidly till August. Between August and December was a slight increase in total liposomatic index which continued until spawning (February 1986). From February to April (1986), the total liposomatic index either decreased or remained constant, before increasing to the June maximum.

(vi) Changes in Lipid Content over Spawning Table 3.8

Females. There was a decrease in all liposomatic indices between preovulating and spent stages, but as there were few preovulating females, the only significant decreases were in the gonadoliposomatic index ($p < 0.05$) and the visceroliposomatic index ($p < 0.001$). All preovulating fish had pale coloured livers. Spent and ovulating females had 'mid' and dark livers. Pale livered females had a higher overall lipid content than 'mid' and dark livered females, although the only significant differences between pale and dark livered fish were in the gonadoliposomatic index ($p < 0.05$) and visceroliposomatic index ($p < 0.01$).

Males. In the sample of February 1986, only one pre-spawning and one spent male were analysed. However, there was a decrease in lipid content over spawning, repeated in the January 1987 sample, where the decreases in hepatoliposomatic index and visceroliposomatic index were significant (Hepatoliposomatic index running - spent, $p < 0.05$; visceroliposomatic index pre-spawning - spent, $p < 0.02$; running - spent, $p < 0.05$). Males with pale livers generally had a higher lipid content than dark livered males, although the only significant differences were in the total liposomatic index of February 1986 ($p < 0.001$) and the musculoliposomatic index of January 1987 ($p < 0.05$).

(vii) Distribution of body lipid. Fig. 3.14 shows the proportion of the total body lipid contained in each tissue (calculated from the liposomatic indices).

Females (Fig. 3.14a). Most of the body lipid was contained in the muscle, except in the pre-spawning December female when most of the total lipid was in the ovaries, and the muscle only accounted for 35% of the remaining lipid. The liver contained the smallest proportion of the total lipid (1-4%). The viscera varied from 5% after spawning, to containing a maximum 17% of the total body lipid in August. The percentage of body lipid in the ovaries was negligible after spawning (1%), but increased from April to June (4%). Between August and November, the ovarian proportion of the total lipid increased rapidly, from 7% to 43%, and by December, the ovaries accounted for 53% of all the body lipid.

Males (Fig. 3.14b). Muscle accounted for the greatest proportion of the total body lipid (72-91%), then the viscera, which ranged from 8% after spawning to 25% before spawning. The liver contained a negligible 0.9-3% of the body lipid, minimal after spawning, maximal in August. The proportion of lipid in the testes was also negligible, ranging from 0.6% in April to 2% from August until spawning.

(c) Relationships

(i) Lipid and water

Total liposomatic index (LSI) to total percentage water (adjusted). 222 observations, March 1985 - January 1987.

Regression coefficient	(b)	-1.023
Constant	(a)	79.98
Correlation coefficient	(r)	-0.605

Percentage of lipid (concentration) to percentage of water in gonad (sexes combined). Water estimated from oven drying. 162 observations.

Regression coefficent	(b)	-1.696
Constant	(a)	83.34
Correlation coefficient	(r)	-0.723

Lipid and water content were inversely related. The relationship based on water estimated from oven drying had only a slightly higher correlation than that based on the adjusted estimate from the lipid analysis residue.

(ii) Lipid (LSI) and condition factor (CF)

235 observations

Regression coefficent	(b)	4.825
Constant	(a)	-1.849
Correlation coefficient	(r)	0.391

There was a weak positive correlation between total liposomatic index and condition factor.

(iii) Total fish length and total weights of lipid, protein and water. The weights of the body constituents increased allometrically with increasing length (Fig. 3.15 lipid; Fig. 3.16, protein). Transformation of the data gave the following relationships:

$\log Y_{lipid} = -7.54 + 3.396 \log X_{length}$ $r = 0.854$ (236 observations)

$\log Y_{protein} = -6.88 + 3.47 \log X_{length}$ $r = 0.984$ (234 observations)

$\log Y_{water} = -5.52 + 3.169 \log X_{length}$ $r = 0.993$ (234 observations)

Strong positive correlations existed between the weight of lipid, protein or water and fish length, with water having the highest correlation, then lipid.

(iv) Lipid weight and total fish weight

$\log Y_{lipid} = -1.758 + 1.083 \log X_{weight}$ $r = 0.882$ (234 observations)

The correlation between total fish weight and lipid was slightly lower than between fish length and lipid.

3.3.4 DISCUSSION

(a) Lipid Content Relative to Weight Changes

(i) Gonad

Females (Figs 3.2a, 3.9). After the decrease in gonadoliposomatic index and gonadosomatic index at spawning, the gonadosomatic index continued to decrease slightly until April, as post-spawning reabsorption occurred (Rashid, 1984) However, gonadoliposomatic index appeared to reach a minimum directly after spawning (February), and remained at that level until April before increasing, two months before any significant increase in gonadosomatic index (June). Endogenous vitellogenesis commenced in March in Loch Lomond females (Rashid, 1984). After August, both ovarian lipid and ovarian weight increased rapidly, during the stage of exogenous vitellogenesis. By December, the ovaries represented an average 12.5% of the body weight, and 53% of the total body lipid (Fig. 3.13a). A similar proportion of body lipid was found in the ovaries of pre-spawning pollan, *C. autumnalis pollan* (52%; Dabrowski, 1982a), vendace, *C. albula* (50.8%; Dabrowski, 1982b) and Lake Chun whitefish, *C. lavaretus* (69%; Reshetnikov *et al.*, 1970).

Males (Figs 3.2b, 3.9.). As in females, the lipid content of the gonad reached its minimum in March, before the gonadosomatic index which continued to decrease until May as the testes regressed. Although the gonadoliposomatic index increased from April to May, the increase was not statistically significant and so it is inconclusive as to whether testis lipid increases before testis weight. The percentage concentration of lipid in the testes reached a maximum in May (6.61%) and June (5.18%, Table 3.7b), before the gonadoliposomatic index which was maximal in August, and remained constant until spawning. Gonad weight (GSI) reached a maximum in October or November.

The highest percentage proportion of total body lipid in powan testes was 2% (Fig. 3.14b), which is considerably lower than the 7% estimated for vendace (Dabrowski, 1982b) and the 10% estimated for Lake Chun whitefish (Reshetnikov et al., 1970). Considering the negligible weight of testes (maximum gonadosomatic index 1.72%), the estimated 2% seems not unreasonable.

(ii) Liver (Figs 3.7, 3.10). In most months, females had the higher hepatoliposomatic index, although the difference was only significant in March 1985 ($p < 0.02$). Males and females had equal hepatoliposomatic indices in August, and males were significantly higher in January 1987 ($p < 0.05$). With the exception of January, the sexes showed a similar pattern of hepatoliposomatic index variation.

Liver lipid (HPLSI) and liver weight (HSI) were low after spawning, but increased rapidly when feeding was resumed. In June, both the hepatoliposomatic index and hepatosomatic index were at a maximum, before decreasing significantly from June to August. Between August and December, hepatoliposomatic index increased in both sexes, possibly as a result of improved feeding quality after August. In males, the hepatosomatic index showed a similar increase, so suggesting that male hepatosomatic index directly reflects the nutritional and energetic state throughout the year. In females, hepatosomatic index and hepatoliposomatic index fluctuated similarily from after spawning until August. Female hepatosomatic index then increased significantly from August to a maximum in November or December. This increase in weight was likely to be a result of the liver's vitellogenic role since the corresponding liver lipid increase was not significant.

(iii) Viscera (Figs 3.6, 3.11). In most months males had a higher visceral lipid content than females, significantly so in January ($p < 0.02$), April ($p < 0.001$) and November ($p < 0.001$). In June, females had the higher visceroliposomatic index, although the difference was not significant.

In both sexes, changes in visceroliposomatic index and gut-somatic index corresponded. Both indices increased after spawning to a maximum in June and August, and decreased between August and November. Kissack (1986) analysed the September 1985 sample and found a visceroliposomatic index value of 0.28 in females and 0.26 in males, indicating that the greatest rate of visceroliposomatic index decrease was from August to September (as in the gut-somatic index). Male visceroliposomatic index then increased from August to November, again corresponding with the gut-somatic index. Female gut-somatic index and visceroliposomatic index continued to decrease from September to spawning. Therefore seasonal changes in gut-somatic index do reflect deposition and mobilisation of visceral fat.

(iv) Muscle (Figs 3.8, 3.12). The musculoliposomatic index in males was consistently higher than in females although the difference was only significant in November 1985 (p <0.001). Males and females showed similar seasonal variations in musculoliposomatic index, except from August to November. The September results of Kissack (1986) suggest a further decrease in musculoliposomatic index from August to September, the musculoliposomatic index then remaining constant or increasing until November.

Because changes in somatic condition factor mainly reflect changes in muscle and associated lipid weight relative to length, the seasonal variations of somatic condition factor were very similar to those of the musculoliposomatic index. Both were minimal after spawning, increased to a maximum in June, and decreased until August or September. Somatic condition factor and musculoliposomatic index then either remained constant or continued to decrease until spawning (in females) or increased slightly until November or December (in males).

(v) Total lipid. The total liposomatic index (LSI, Fig. 3.13) also showed very similar seasonal fluctuations to the musculoliposomatic index and somatic condition factor, because most of the fish is muscle. The only difference may have been from August to November, when the female total liposomatic index did not decrease with the decrease in musculoliposomatic index. Instead it increased, and to a greater extent than the male liposomatic index. If the difference is genuine, the explanation might be that the total liposomatic index includes the large amount of lipid deposited in the ovaries at that time. Males could be depositing more lipid in the muscle, which in females is being mobilised for ovarian growth (Dabrowski, 1982a,b).

As with the musculoliposomatic index, males had a consistently higher total liposomatic index than females, although the difference was only significant in April 1986 ($p < 0.02$).

(b) Comparison of the Lipid Content of Loch Eck and Loch Lomond Powan

Rashid (1984) analysed the visceral lipid of adults from the Loch Lomond samples of December 1978 to February 1980. There were two January and February samples (1979 and 1980) which were combined for the comparison with Loch Eck (Table 3.9c, Fig. 3.17). Reid (1982) analysed gonad, liver, muscle and total lipid for Loch Lomond powan from September 1981 to March 1982 (Table 3.9a,b,d,e). Reid's sample sizes were very small, with a maximum of 5 fish in each category, too few for valid statistical analysis.

Caution is necessary when comparing results from different years because of year to year variation. Therefore somatic condition factors for Loch Lomond samples from January 1979 to February 1980 were compared with the somatic condition factors for the Loch Eck 1984-1987 samples. Also compared with the equivalent Loch Eck samples were the gonadosomatic indices, hepatosomatic indices and somatic condition factors for Loch Lomond from September 1981 to March 1982. The results were consistent with the comparison of Loch Eck and Loch Lomond indices for 1984-87 as the hepatosomatic indices and somatic condition factors of the Loch Eck powan were significantly higher than the Loch Lomond powan.

(i) <u>Gonadoliposomatic index</u> (Table 3.9a). There were no significant differences between the gonadosomatic indices or the gonadoliposomatic indices of Loch Lomond and Loch Eck males. Loch Eck females had a higher gonadoliposomatic index in early February and March ($p < 0.05$). Loch Eck female gonadosomatic indices were also significantly higher in January, February and March, the reason being the later Loch Eck spawning. Loch Lomond female gonadoliposomatic index was very significantly higher in November, possibly also related to the difference in spawning time.

(ii) <u>Hepatoliposomatic index</u> (Table 3.9b). As in the hepatosomatic index comparison, Loch Eck powan had higher hepatoliposomatic indices than Loch Lomond powan, with the exception of females in January. The only statistically significant differences were in January in males, and in March in males and females. The hepatoliposomatic index in Loch Lomond males and females decreased from September until spawning, as did the hepatoliposomatic index of Loch Eck females. During spawning, the hepatoliposomatic index decreased in both sexes in both populations, then while the Loch Lomond hepatoliposomatic index remained low (little feeding) the Loch Eck hepatoliposomatic index increased with resumption of intensive feeding.

(iii) <u>Visceroliposomatic index</u> (Table 3.9c, Fig. 3.17) In general, seasonal changes in Loch Lomond 1978-1980 visceroliposomatic indices corresponded with the seasonal fluctuations in Loch Lomond gut-somatic indices during 1984-1987 (Fig. 3.6). As in Loch Eck, Loch Lomond males tended to have more visceral fat than females. There was a hiatus in the Loch Lomond visceroliposomatic index increase from July to August. Further investigation is required to determine if this hiatus occurs in all years or is peculiar to 1979, but Pomeroy (1987) found that feeding remained at a constant rate from June to August (1983) before increasing again until September.

The differences in visceroliposomatic index between the two populations relate to the feeding differences. The continuously feeding Loch Eck powan have the higher visceroliposomatic index from winter to early summer, significantly higher from December to May in males, and from January to May in females. The Loch Lomond powan achieved a later but significantly higher maximum visceroliposomatic index (females $p < 0.01$; males, $p < 0.001$), possibly because the planktonic diet of the Loch Lomond powan has a higher calorific value than the benthic diet of the Loch Eck powan (Pomeroy, 1987). Virtual cessation of feeding in Loch Lomond after September results in a decrease in the visceroliposomatic index until spawning as visceral lipid is mobilised. Loch Eck visceral lipid decreased from August to September; then in males, either reincreased or remained constant until spawning. The visceroliposomatic index of Loch Eck females continued to decrease, and by November or

December, Loch Lomond and Loch Eck females had similar levels of visceral fat. Because the Loch Eck powan return to intensive feeding directly after spawning, there was an earlier increase in visceroliposomatic index (and an earlier maximum) compared with the Loch Lomond powan which do not recommence planktonic feeding until May. After May, Loch Lomond visceroliposomatic index increased rapidly to the September maximum.

(iv) Musculoliposomatic index (Table 3.9d). Loch Lomond musculoliposomatic index decreased from September in females and October in males to February, the greatest rate of decrease in Loch Lomond males being from November to January. The musculoliposomatic index of Loch Eck females also decreased slightly from August. The Loch Eck male musculoliposomatic index remained fairly constant from August until spawning, with perhaps a slight increase. The highest musculoliposomatic indices obtained for Loch Eck powan in June were lower than the highest musculoliposomatic indices recorded for Loch Lomond powan (females, $p < 0.02$, males not significant). In November, Loch Lomond musculoliposomatic indices were still significantly higher than Loch Eck musculoliposomatic indices, although in February and March, Loch Lomond musculoliposomatic indices were significantly lower than Loch Eck musculoliposomatic indices.

(v) Total liposomatic index (Table 3.9e). In Loch Lomond, the total liposomatic index decreased from a high level in September (females) and October (males) until late

February, with most of the decrease occurring between November and January. The total liposomatic index in Loch Eck remained constant or increased slightly from August or September until spawning, therefore Loch Eck powan had a significantly higher total liposomatic index from January until March.

The high September mean for Loch Lomond females was 5.57, compared with the Loch Eck female June maximum of 3.37 ($p < 0.001$). Loch Lomond males had a high total liposomatic index of 4.43 in October, the Loch Eck male maximum in June was 4.32. In November, the Loch Lomond total liposomatic index was significantly higher than in Loch Eck.

In summary, powan in Loch Lomond may achieve a higher maximum lipid content than in Loch Eck because of the higher calorific value of the Loch Lomond diet. After September, feeding in Loch Lomond is greatly reduced, and so the Loch Lomond powan utilise their fat stores. Loch Eck powan continue feeding and so have a higher lipid content over winter and until early summer. The exception is the liver, which in Loch Eck powan has a consistently higher lipid content.

(c) Proximate Analysis

An inverse relationship between water and lipid has been shown in many species (reviews Love, 1970; Shul'man, 1974; Weatherley & Gill, 1987). In herring, *Clupea harengus*, the lipid-water relationship varied little in conditions of good and poor growth and was independent of physiological conditions (Iles & Wood, 1965). Iles & Wood concluded that the relationship was close enough to derive lipid estimates if the water content was known (r = 0.99). A lipid-water correlation of 0.98 was calculated for brown trout (Elliott, 1976a) and 0.818 for perch (Craig, 1977). These correlations are higher than those calculated for powan (0.605 and 0.723, p. 192). Weatherley & Gill (1983b) considered that in immature rainbow trout the lipid-water correlations and protein-water correlations were not as satisfactory as the correlation between lipid or protein and body weight. Caulton & Bursell (1977) found that although the lipid-water correlation in Tilapia rendalli was high (r = 0.887), estimations from this relationship were not acceptable, being prone to gross errors. The fat content of fish in high condition was underestimated, while the fat content of fish in low condition was greatly overestimated.

Lipid is considered to be the main determinant of condition (Groves, 1970 cited by Weatherley & Gill, 1987), but the correlation between condition factor and lipid in powan was unsatisfactory (r = 0.391) and so lipid content cannot be reliably estimated from the condition factor. Elliott (1976a) obtained a good correlation between lipid and condition in brown trout (r = 0.862), but Weatherley & Gill (1983b) obtained a poor correlation in rainbow trout (r = 0.50).

Potentially the best basis for proximate analysis in powan is from the relationships of fish length or weight to each body constituent (r values on p. 193). Estimations from length do not allow for seasonal or year to year variations in condition. For this reason, weight is the better criterion (Weatherley & Gill, 1983b), but the conservatism of relationships on which the proximate analysis method is based has a drawback, in that during starvation any lipid lost will be replaced to some extent by water, and so the lipid content may be overestimated.

Table 3.10 compares some weights of lipid, protein and water estimated from the relationships to these derived by analysis. Estimates from the lipid-body weight relationship did tend to be closest to the analysis values. The estimates were accurate in small and average powan (179mm to 296mm) but there were discrepancies. Adolescents (Ch. 4) which have a particularly high lipid content (Fig. 3.15), were considerably underestimated. Estimates for the larger fish range from being accurate, to being over or underestimates.

The assumption of proximate analysis is that all fish fit a general relationship. This is true of the majority of 'average' fish, but fish are not all average. Adolescents obviously have a different lipid-length or lipid-weight relationship. There is greater individual variation in the larger powan (Fig. 3.15, 3.16), and so they do not necessarily fit the calculated relationship. Aberrant fish are not identified. Proximate analysis may be time saving and is an interesting exercise, but is of little practical use.

(d) Protein Growth

In comparison with total lipid content, the total protein content (% of total body weight) varied little during the season (Table 3.8). As Shul'man (1974) observed, "unlike the fat content dynamics the dynamics of protein content in fish is extremely featureless". Protein growth can be shown by the absolute increase in total protein weight with fish size (Fig. 3.16). Because total protein content does not vary much seasonally, the relationship of total protein weight to fish length (Fig. 3.16, $r = 0.984$) is closer than the relationship of lipid weight to fish weight (Fig. 3.15, $r = 0.854$).

CHAPTER 4 JUVENILES

4.1 INTRODUCTION

In all previous studies of powan (e.g. O'Connell, 1984; Rashid, 1984; Yekrangian, 1984; Pomeroy, 1987), the fish were categorised as being either 'immature' (not reproductive) or 'mature' (undergoing the normal adult reproductive cycle). The same distinction has been generally made in studies of many other teleost species. It became apparent during the present study that there were two distinct categories of pre-adult fish. These juvenile powan might be either (i) immature, with minute gonads showing little or no gametogenetic activity during the year, or (ii) adolescent, in which some gametogenesis occurred, but it was not completed, was often out of phase with the normal adult cycle, and did not appear to culminate in spawning.

The aim of this chapter is to investigate how the seasonal cycles of juvenile powan compare in the two lochs, and to discover what factors might determine the transition from immaturity to adolescence, and from adolescence to being fully adult. With the exception of gametogenesis, seasonal cycles of juveniles and adults will not be compared until Chapter 5.1.

4.2 MATERIALS AND METHODS

Immature and adolescent powan were caught during routine sampling, but their numbers were low compared to adults (Ch. 2.2, 2.3), a factor which frequently made statistical analysis unreliable. Standard measurements were taken (Ch. 1.2, p. 15), and weight indices were calculated as described in Chapters 3.1 and 3.2. Lipid, protein and water content were analysed in Loch Eck juveniles as described in Chapter 3.3. As there were no significant differences between weight and lipid indices of immature males and females the sexes were combined, except for the gonadosomatic index of immature females. Gonads of females which could be clearly identified as being adolescent on dissection were fixed for histological examination as described in Chapter 1.2. It was often difficult to distinguish macroscopically between adolescent and adult males, but whenever possible presumed adolescent testes were also fixed for histological examination.

The histological sections were stained with Masson's trichrome stain and photographed with a Zeiss photomicroscope using Zeiss 'Planapochromat' objective lenses and 'Kodachrome 25' colour reversal film.

4.3 RESULTS

(a) Gametogenesis

(i) Immature The ovary of immature females was arranged in distinct lamellae. It contained only oogonia and small previtellogenic oocytes less than 100 µm in diameter, with densely staining cytoplasm. Balbiani bodies appeared in the cytoplasm later. The gonadosomatic index was negligible. The immature testis (negligible in weight) consisted only of spermatogonia in various stages of mitotic division.

(ii) Adolescent The ovary of adolescent females was categorised in five stages:

Initial. The first stage of adolescence was defined by the appearance of bright orange granulation in the colourless matrix of the small immature ovary (as at the extreme posterior end of the ovary in Plate 29). Histologically, the lamellar structure persisted, but the Balbiani bodies progressively disappeared, the cytoplasm became uniformly pale staining, and the number of nucleoli increased (Plate 35). The gonadosomatic index remained low.

Early. Macroscopically the ovary consisted of a compact mass of uniformly bright orange oocytes up to 370 um in diameter, and was not more than one third of the length of the body cavity (Plate 29). In microscopical sections, the lamellar structure of the immature ovary was lost. Lipid vesicles appeared close to the nucleus (Plate 36). At this stage the mean gonadosomatic index in Loch Eck was 0.46 ±0.36 (Table 4.9).

Intermediate. The ovary consisted of bright orange oocytes up to 560 µm in diameter, and it occupied up to two-thirds of the length of the body cavity (Plate 30). Histologically, endogenous vitellogenesis was in progress, and there was a conspicuous oolemma (Plate 37). The mean gonadosomatic index in Loch Eck was 1.03 ±0.40 (Table 4.9).

Late. The ovary occupied the full length of the body cavity, with bright orange oocytes up to 720 um in diameter (Plates 32, 33). The mean gonadosomatic index in Loch Eck was 3.12 ±1.77 (Table 4.9). Exogenous yolk granules were present in the cytoplasm (Plates 38, 39), but even the maximum number of exogenous granules observed (Plate 40) were much fewer than in adults. In a number of oocytes undergoing exogenous vitellogenesis the cytoplasm stained more densely than usual and the oocytes had a very irregular outline (Plate 39). It is possible that an atretic change from the normal processes of exogenous vitellogenesis was occurring at this stage, but further investigation is required.

Atretic. Several late stage adolescent ovaries became atretic (Plate 34). They were highly vascularised and contained degenerating vitellogenic ooytes often with a hypertrophied oolemma and granulosa (Plate 41).

The various adolescent stages did not occur at specific times of the year, the initial stage being found throughout the year (Table 4.1). The most advanced late stage usually occurred from the normal adult spawning season to April or May, at which time atretics were also most frequent.

Adolescent males were much more difficult to distinguish macroscopically from adults than were the females, except when they were at an early stage (Plate 28), but like the females they seemed to differ to the adults in timing. Plate 42 shows the testis of an adolescent male from Loch Eck, caught on 5th February 1986, when normal adult males would have seminiferous tubules packed with spermatozoa, and little spermatogonial mitotic activity (Rashid, 1984). The adolescent testis consisted of spermatogonia in various stages of division, together with later stages of spermatogenesis even including spermatids, which would not normally occur before late summer in the adult.

(b) Gonadosomatic Index

(i) Loch Lomond. Table 4.2a shows the mean gonadosomatic index of immature female powan from 1981 to 1987. It ranged from 0.1 to 0.36, and showed no significant seasonal variation.

The gonadosomatic index of adolescent females from 1981 to 1987 is shown in Fig. 3.1a (together with that of the adult females). There was a hint of an annual cycle though it was not statistically verifiable, partly because of low numbers, but mainly because the stages of adolescence were not distinctly seasonal, so that there were varying numbers of early, intermediate and late adolescents in any one sample. The gonadosomatic index of adolescents was at a maximum between April and May each year (see also Table 4.2b), at which time the gonadosomatic index of adult females was minimal. At this time it could be difficult to distinguish macroscopically between the ovaries of adult and adolescent females.

Because of the small size of the testis in immature powan, and the uncertainty in identifying adolescents, comparable data for males are not available.

(ii) Loch Eck. As in Loch Lomond, there was no significant seasonal variation in the gonadosomatic index of immature females (Table 4.3a).

The gonadosomatic index of adolescent females from 1984 to 1987 is shown in Table 4.4 together with that of the adult females. Apparent maxima occurred in December and April, but they could not be statistically confirmed for the same reasons as explained for the Loch Lomond adolescents.

(c) Hepatosomatic Index

(i) Loch Lomond. Fig. 4.1a shows the mean values of the hepatosomatic index of immature powan over the period 1981-1987. There was little seasonal variation, but the hepatosomatic index was minimal in March, increased to a maximum in July, and then decreased until October or November, thereafter remaining constant until January or February.

Fig. 4.1a also shows the corresponding mean values of the hepatosomatic index for adolescent females. The seasonal cycle was very similar to that of the immatures, although the maximum was in August (perhaps coincidental).

Immatures tended to have higher hepatosomatic indices than adolescent females, but the difference was only significant in June ($p < 0.001$). Adolescent females had significantly higher hepatosomatic indices in March ($p < 0.002$), May ($p < 0.05$) and August ($p < 0.001$).

(ii) Loch Eck. Fig. 4.1b shows the mean hepatosomatic indices for 1984-87. In immatures there was a marked seasonal cycle, with maximum values in February and April, and minimum values in May and June.

Adolescent females also had a clearly defined seasonal cycle which closely resembled that of immature fish. The maximum hepatosomatic index was in January and February; it then declined to June. Unfortunately, between June and November only one adolescent and no immatures were caught.

The adolescent females generally had higher hepatosomatic indices than the immatures, although only significantly so in January ($p < 0.02$), and December ($p < 0.05$).

(iii) Loch Lomond and Loch Eck compared (Fig. 4.4). Juveniles in Loch Eck had consistently higher hepatosomatic indices than those in Loch Lomond. The differences were statistically significant in most months (Table 4.5). Hepatosomatic indices in Loch Eck juveniles were also more seasonally variable, even when compared with the Loch Lomond combined data for 1981 to 1987 (Fig. 4.1a, b). The seasonal cycles differed in timing as the maximum hepatosomatic index in Loch Lomond juveniles occurred in summer, in July or August (Fig. 4.1a), while in Loch Eck juveniles the maximum occurred about February (Figs. 4.1b; 4.4a,b). Minimum hepatosomatic index occurred about March in Loch Lomond juveniles, but in May and June in the juveniles of Loch Eck.

(d) Gut-Somatic Index

(i) Loch Lomond (Fig. 4.2a). Information was particularly scanty, extending only from October 1984 to February 1987 (see also Fig. 4.5). In immatures, maximum values probably occurred in September or October, with little change from November until May or June. The adolescent female cycle was essentially similar, with a maximum in October.

With the exception of December, adolescent females had higher gut-somatic indices than the immatures, although the only statistically significant difference was in May ($p < 0.02$).

(ii) Loch Eck (Fig. 4.2b). Immature gut-somatic index increased from December to a maximum in April or May, then decreased to a minimum in June. The cycle in adolescent females was similar; the gut somatic index was high in April and low from May to September. It then reincreased from September and remained high from November to January.

With the exception of June, adolescent females had higher gut-somatic indices than immatures. The differences were only statistically significant in February ($p < 0.001$), and December ($p < 0.001$).

(iii) Loch Lomond and Loch Eck compared (Fig. 4.5a,b). With the exception of the end of 1984 and beginning of 1985, juveniles in Loch Eck had higher gut-somatic indices than in Loch Lomond. The only differences which were statistically significant were between the immatures in February 1986, and between the adolescent females in June 1986 (Table 4.5). The timing of the seasonal cycle differed, since in Loch Lomond the gut-somatic index was maximal in September or October, while in Loch Eck, the maximum occurred from February to April.

(e) Somatic Condition Factor

(i) Loch Lomond (Fig. 4.3a). In immatures, the somatic condition factor decreased from September to February, remained constant until April or May, then increased to a maximum from July to September. The somatic condition factor cycle of adolescent females was similar, with a maximum in August, followed by a fairly rapid decrease until November. The somatic condition factor was minimal in March, and remained low until April-May or June.

The somatic condition factor of adolescent females was consistently higher than the immatures, very significantly so in most months ($p < 0.001$); only in March, April and November was there no significant difference. In June, the somatic condition factors of immature and adolescent females were the same.

(ii) Loch Eck (Fig. 4.3b). In immature powan, the somatic condition factor was probably minimal in December, thereafter increasing to a high level in the months of April to June. The somatic condition factor of adolescent females was highest in December, January and May and lowest in March.

As in Loch Lomond, Loch Eck adolescent females had a higher somatic condition factor than immatures in all months. The difference was significant in January ($p < 0.001$), February ($p < 0.001$), November ($p < 0.05$), and December ($p < 0.001$).

(iii) Loch Lomond and Loch Eck compared (Fig. 4.6a,b). Loch Eck juveniles had consistently higher somatic condition factors than Loch Lomond juveniles, very significantly so in some months (Table 4.5). The timing of the seasonal cycle in the two lochs differed; maximum somatic condition factor occurred in summer (July to September) in Loch Lomond juveniles, but at the start of the year in Loch Eck juveniles (April-June in immatures; January to May in adolescent females).

The higher weight indices of Loch Eck juveniles compared with Loch Lomond juveniles reflected the situation in the adults of the two lochs (Ch. 3.2.4). The difference in the timing of the seasonal weight cycles in juveniles of the two populations must relate to the difference in feeding in the two lochs (Ch. 5).

(f) Tissue Composition (Loch Eck fish only)

Tables 4.6a,b,c show lipid percentages and indices, and also total weights of lipid, protein and water as as percentage of the total body weight. The total weight of lipid and the total weight of protein relative to the length of the fish are shown in Figs. 3.15 and 3.16 respectively.

(i) Lipids. Adolescent powan were readily distinguished macroscopically by their large visceral fat bodies and pale coloured livers (Plates 29 to 34). Although immature powan did not have so much visceral fat, their livers were even paler in colour, being almost white.

Distribution. The percentage distribution of total body lipid in the gonads, liver, viscera and muscle is shown in Fig. 3.14 for (c) immatures, (d) adolescent females, and (e) adolescent males. In immature powan, the percentage of total body lipid in the gonads was negligible; the liver contained from 3 to 7%; the viscera contained 10 to 21%; and the muscle contained from 73 to 84% of the total body lipid.

In adolescent females, the gonad contained a significant proportion of the body lipid, 3 to 10%; the liver contained from 2 to 4%; the viscera contained from 22 to 31%; and the muscle contained from 50 to 71% of the total lipid.

In adolescent males the gonad lipid was not measurable. The liver contained from 1 to 10%; the viscera from 2 to 9%; and the muscle from 63 to 90% of the total body lipid.

Seasonal lipid cycles.

Gonadoliposomatic index. In adolescent females the gonadoliposomatic index was high in December, January and April (Fig. 3.9), and so was similar to the gonadosomatic index (Table 4.3b). Adolescent gonadoliposomatic index was low in February and November. The erratic results were possibly due to the varying numbers of early, intermediate and late adolescents caught in each sample.

Hepatoliposomatic index (Fig. 3.10). In immatures, the hepatoliposomatic index was maximal in January and February and decreased to a minimum in June.

The cycle of the hepatoliposomatic index in adolescent females was similar, being high in January and February and decreasing to a low level in June. The hepatoliposomatic index of adolescent males also decreased between April and June (Table 4.6c). The seasonal changes in hepatoliposomatic index therefore corroborated the changes in hepatosomatic index.

Immatures had higher hepatoliposomatic indices than adolescent females in January, February and April although the difference was only significant in April ($p < 0.05$).

Visceroliposomatic index (Fig. 3.11). In immature powan the maximum visceroliposomatic index was in

February. The lowest levels were from November to January. Allowing for the fact that fewer fish were used in the lipid analysis, there is some similarity with the gut-somatic index cycle (Fig. 4.2b).

In adolescent females the visceroliposomatic index was high in December and January and decreased until June. The April to June decrease also occurred in adolescent males (Table 4.6c) and was statistically significant in both sexes ($p < 0.05$). The seasonal changes in gut-somatic index were very similar (Fig. 4.2b).

With the exception of June, adolescent females had higher visceroliposomatic indices than immatures, significantly so in December ($p < 0.02$).

Musculoliposomatic index (Fig. 3.12). In immatures the musculoliposomatic index was highest from January to April and was followed by a decrease from April to June. The musculoliposomatic index was low in November and increased to January. The increase from December 1985 to February 1986 was statistically significant ($p < 0.01$).

The cycle in adolescent females was similar; the musculoliposomatic index was highest in January and declined to June. Adolescent males also showed a decrease from April to June (Table 4.6c), the decrease being significant in both sexes ($p < 0.01$). Adolescent females also had a high musculoliposomatic index in November.

Adolescent females generally had higher musculoliposomatic indices than immatures, except in June. However, none of the differences were statistically significant.

Total Liposomatic Index (Fig. 3.13). In immatures, the total liposomatic index was high in January and decreased until June. Total liposomatic indices were low in November and December.

In adolescent females the total liposomatic index was highest in February, decreasing to April. The total liposomatic index was lowest in December.

Adolescent female total liposomatic indices were very much higher than in the immatures, the differences being statistically significant in April ($p < 0.002$), and December ($p < 0.05$).

The seasonal cycles of immature and adolescent musculoliposomatic and total liposomatic indices were not entirely similar to the somatic condition factors (Fig 4.3b), possibly because fewer fish were used in the lipid analyses.

(ii) Protein. As in adults (Ch. 3.3.4, p. 204) there was little seasonal variation in total protein content of juveniles (Table 4.6). There was an distinct allometric change in the relationship of protein to fish length (Fig. 3.16), with the immatures and early stage adolescents having a higher rate of protein growth than the adults and later stage adolescents (Chs. 4.4, 5.1).

4.4 DISCUSSION

(a) Reproductive Maturity

The factors which determine the change from immaturity to maturity in teleosts have been the subject of much debate (Alm, 1959; Iles, 1974; Stearns & Crandall, 1984). To a certain extent the onset of reproductive maturation is under genetic control (e.g. Thorpe *et. al.*, 1980), which modifies or is modified by other factors, such as age, growth rate and the amount of body reserves. In powan, two distinct stages are involved in the attainment of reproductive maturity, the first being the change from immaturity to adolescence, the second the change from adolescence to full maturity.

(i) Age. Sund (1911, cited by Iles, 1974) first pointed out that members of the same year class, hatched at much the same time, might mature at quite different ages. Table 4.7a shows the percentage of powan in each age group which were immature, adolescent or adult. Both sexes are shown, though adolescent males were less reliably identifiable than females. All of the (few) 0+ powan caught were immature.

Most females were still immature at 1+ (83-86%) and the remainder were adolescent (14-17%). At 2+ all three categories were represented, but the majority were adolescent (46-57%). At 3+ the majority of females were adult (72-85%), and at 4+ virtually all females were adult (95-97%). Maturity in the two populations evidently occurred at much the same age, though the proportion of females becoming mature at 2+ and 3+ was slightly higher in Loch Eck than in Loch Lomond.

Almost all male powan were fully mature at 3+ (95-98%). As in females, a higher proportion of Loch Eck males matured at 2+ (68%), compared with the Loch Lomond males (37%).

There were year to year variations in the age at which powan became mature. Table 4.7b shows the proportions of immatures, adolescents and adults in the 1+ to 3+ age groups caught in the sampling years 1984 to 1987 (April 1st to March 31st), separated into year-classes. In Loch Lomond all 1+ fish of both sexes of the 1983 and 1985 year-classes were immature. However, in the 1984 year-class 15% of 1+ females were adolescent and 24% of 1+ males were fully mature. This initial acceleration of maturity was not maintained into the second year, only 22% of females of the 1984 year-class being adult at 2+, compared to 18% of the 1982 and 63% of the 1983 year-class. In males too, the figure stabilised.

(ii) Growth rate. In Lough Neagh pollan, Wilson & Pitcher (1984b) described year to year variations in the age of maturity related to growth rate, and a number of other studies have related early maturity to fast growth (Alm, 1954, 1959; Bergel'son & Nikanorov, 1969; Berg, 1970; Craig, 1982). The early maturing 1984 year-class of Loch Lomond powan had the highest first year growth rate observed in this study, but a very low growth rate in their second year, when the 1983 year-class had a higher growth rate (Ch. 2.2). There were no corresponding variations in Loch Eck where the 1984 year-class showed only average growth.

Table 4.8 shows the mean total length of powan relative (a) to reproductive status and (b) to reproductive status and age. The adolescents were very significantly longer than the immatures in both sexes in each loch (Table 4.8a; p <0.001), and the adults were very significantly longer than the adolescents (Table 4.8b).

There was no difference between the lengths of immature females and males in either loch, but adolescent females tended to be longer than the adolescent males, suggesting that males mature at a smaller size, an observation which is consistent with their becoming mature a year earlier than females.

Comparing the two populations, both immature and adolescent females in Loch Lomond were very significantly longer than in Loch Eck (p <0.001 for each category; Table 4.8a). Immature males in Loch Lomond were also longer than in Loch Eck. Though there was no difference between the lengths of the adolescent males shown in Table 4.8a (all age groups combined), Loch Lomond adolescent males were very significantly longer than Loch Eck adolescent males at 1+ (p <0.001; Table 4.8b). Loch Eck powan therefore mature at a shorter length than Loch Lomond powan.

Change in growth rate related to maturity. In the general body-scale relationships (Fig. 2.1) the small fish deviated below the line of best fit. The length at which the deviation occurred was estimated to be 250mm for Loch Lomond powan and 215mm for Loch Eck powan, and it was postulated that the allometric change might be related to reproductive maturation (p. 55). Comparison with length at maturation

(Table 4.8) confirms this hypothesis. In Loch Lomond, 2+ adolescent females had an average length of 235mm and 3+ adolescent females an average length of 250mm. Adult 2+ and 3+ females averaged 264 and 285mm respectively. The mean lengths of adult males were also over 250mm with juveniles below this length. In Loch Eck, 2+ adolescent females had a mean length of 219mm, adult 2+ females averaged 230mm in length. While 2+ adolescent males were about 211mm long, adult 2+ males had a mean length of 225mm.

Reproductive maturation has been correlated with a reduction in growth rate in many species (Brown, 1957), although Shul'man (1974) considered that " the notion common among ichthyologists of a slowing down in the growth of fish in relation to the onset of sexual maturity appears to be inadequately substantiated". According to Alm (1959), growth does not depend on maturity, instead, maturity depends on growth; while Iles (1974) could observe no sharp change in growth relative to maturation in herring. However, it does seem conclusive that in powan there is a distinct change in growth related to some stage of maturity, as scale growth decreases relative to body growth.

(iii) Level of body reserves. A distinctive feature of adolescent powan was their large fat reserves (Plates 29 to 33; Figs. 3.13, 3.15). High levels of fat have also been reported in juvenile Lake Chun and Lake Sevan C. lavaretus (Reshetnikov et al.,1970; Reshetnikov & Yermokhin, 1975) and in juvenile C. lavaretus ludoga (Bolotova, 1976). Reshetnikov et al. (loc. cit.), suggested that a certain amount of fat had to be accumulated before reproductive maturation could occur. Iles (1974) made a similar suggestion with regard to protein. He pointed out that teleosts mobilise somatic protein during gonad growth, and hypothesised that in juvenile fish, protein is primarily used for somatic growth and is therefore not available for gametogenesis. As the growth increments decrease with increasing age, progressively more protein is held in reserves until enough has been accumulated to support maturation. In powan, adolescents have higher somatic condition factors (which partly reflect protein level) than immatures (Fig. 4.3; p. 214-215). The fact that Loch Eck powan have higher somatic condition factors than Loch Lomond powan (Fig. 4.6) means that they would have the potential to reach a critical protein level sooner, so explaining their more rapid rate of maturation.

These results indicate that maturity in powan may be induced by a build-up of a certain level of lipid and/or protein reserves. However, separate examination of the stages of adolescence suggest otherwise [see (b) below].

(b) Adolescence

There are surprisingly few accounts of adolescence as observed in powan (Hickling, 1930; Reshetnikov *et. al.*, 1970). It may be that a discrete adolescent stage occurs in only a few teleost species. The only detailed paper on adolescents so far found is that of Hickling (1930) who categorised hake, *Merluccius merluccius*, as 'immature', 'adolescent', and 'mature' and subdivided the 'adolescent' category into 'commencing', 'intermediate' and 'advanced' based on criteria closely matching those used for powan in this thesis. He found that many adolescent ovaries never developed beyond the 'commencing' stage, others no further than the 'intermediate' stage. Hickling described the adolescent phase as a "tentative pre-spawning maturation, which closely reflects the spawning rhythm in adult hake, but does not lead to spawning".

(i) Inception of adolescence. The change from immaturity to the first stage of adolescence in powan is not seasonally determined. Immatures and early stage adolescents were found throughout the year (Table 4.1), suggesting that reproductive maturity may be initiated at any time of year, so that photoperiod or other environmental cues are not likely to be involved. Late stage and atretic adolescents were more frequent about spawning time and until April or May, at which time the gonadosomatic index of the adolescents was maximal. In April and May, the gonadosomatic index of adult females was at a minimum and so adult and adolescent gonadosomatic indices coincided (Fig. 3.1a, Table 4.4).

The change from immaturity to adolescence cannot be directly dependent on the level of lipid and/or protein reserves, since both immatures and early stage adolescent powan have similar lipid and protein weights (Figs 3.15, 3.16). However, there is a significant difference in lipid and protein indices between the early adolescents and the intermediate and late stage adolescents. In Loch Eck, early adolescents had a mean length of 211mm, while intermediate and late adolescents were over 215mm in length (242 and 246mm respectively). Therefore in Loch Eck, 215mm marked not only an allometric change in the body-scale relationship (Ch. 2.1.4, p. 55; Fig. 2.1b), but also a change in lipid and protein weights relative to length (Figs 3.15, 3.16).

(ii) Progress of adolescence. The adolescent reproductive cycle is incomplete compared to that of adults. Endogenous vitellogenesis occurs normally, with oocytes reaching the usual adult size (c.f. Rashid, 1984), but exogenous vitellogenesis is much reduced, and the maximum oocyte diameter attained is less than half the normal adult diameter. This reduction in exogenous vitellogenesis is reflected in the absence of the accompanying rise in hepatosomatic index seen in adult females (Fig. 4.1; Ch. 5.1.2). Exogenous vitellogenesis in adults involves the mobilisation of a great deal of lipid (Ch. 5.1.2), but the failure of exogenous vitellogenesis in adolescents cannot be due to a lack of lipid since lipid stores are characteristically high at this stage (Figs 3.13, 3.15). The musculoliposomatic and total liposomatic indices increased after early adolescence (Table 4.9), and ovarian lipogenesis was apparently normal in histological sections (Plate 37).

There are three possible reasons for the failure of exogenous vitellogenesis:

(1) A timing cue which switches adults from an advanced stage of endogenous vitellogenesis into exogenous vitellogenesis about midsummer is missed by adolescents,

because they are out of phase with the adult cycle. However, there is no evidence of such a cue.

(2) The endocrine machinery for exogenous vitellogenesis has not yet been established in adolescents. It has been suggested that steroidogenic cells in teleost ovaries are formed from theca cells in the follicles of atretic oocytes (Guraya, 1986). It is possible that if atretics do not yet exist in adolescents, then neither do steroidogenic cells or oestrogens which stimulate vitellogenin production in the liver (Yekrangian, 1984). The adolescent 'dummy run' might therefore be to establish steroidogenic tissue. However, it is difficult to visualise how species lacking an adolescent phase would achieve this.

(3) Insufficient protein reserves are available to permit the production of exogenous yolk. This possibility accords with the concept of Iles (1974) that as annual growth increments decrease with increasing age, progressively more excess material is deposited in reserves instead of being used for somatic growth, until enough is available for gametogenesis. This would explain the large lipid reserves in intermediate and late stage adolescents; also the fact that the large amounts of lipid mobilised during adult exogenous vitellogenesis are not utilised by adolescents. It follows that immatures and early stage adolescents do not have such a high lipid content because of their rapid somatic growth. In his review, Shul'man (1974) concluded that in young of the year fish, protein growth is very rapid and predominates over fat accumulation, but at

maturity and in old age, fat accumulation predominates over protein growth.

(iii) Transition from adolescence to adulthood. It is not known how the ovaries of late stage adolescents make the transition into full reproductive maturity. Three possibilities are:

(1) Adolescents which reach maximum ovarian development at the normal adult spawning time spawn, but produce smaller than normal ova. The production of undersized ova by first time spawners has been described in other species (Ch. 3.1.4, p. 147). These fish would presumably enter their first adult cycle immediately afterwards, at the usual time. However, apart from the possibly lower gonadosomatic indices of young powan (Ch. 3.1.4, p. 147), there is no evidence of powan spawning abnormally small ova. Plate 15 shows an atretic female with small ova apparently ovulated into the body cavity, but this was an old and abnormal specimen.

(2) The ovaries of adolescents reaching their maximum development might undergo atresia and reabsorption of oocytes. Atretic late stage adolescents were common in spring and early summer (Table 4.1). Such fish (with considerable stores of lipid) would then begin their first adult cycle.

(3) The ovaries of adolescents reaching their maximum development at an inappropiate time of year for spawning might remain at that stage until the time of year when adults coincide at a similar stage in their cycle, and then the adolescents enter a normal adult cycle. Between April

and May the gonadosomatic indices of adult and adolescent females were similar (Fig. 3.1; Table 4.4), and it was often difficult to distinguish the ovaries visually.

(iv) Older adolescents. Some powan identified as late phase and atretic adolescent females were found to be older than the majority of adolescents (Plate 33; Table 4.7a). They may have been genuinely late maturing specimens or (perhaps more likely) adults which for some reason had missed one reproductive cycle and had begun the next at an adolescent level out of phase with the normal adults. Reshetnikov et. al. (1970) observed "resting" whitefish females to be at the same gametogenetic stage as fish which had not previously spawned.

(c) Conclusion

It is unfortunate that few juvenile powan were caught, and so proper statistical analysis of the results was generally not possible. In the case of Loch Eck fish, which were the only ones in which the body composition was analysed, information was even more limited than in Loch Lomond, since between June and November no immatures and only one adolescent female were caught. To continue the study will require the development of new catching methods specifically for the young fish, also knowledge of their whereabouts.

Although the results are fragmented and the conclusions speculative, they are presented here since adolescence in teleosts seems to be poorly documented. A proper analysis of adolescence could throw light on the factors influencing the onset of reproductive maturity and on the physiological mechanisms involved.

CHAPTER 5 GENERAL DISCUSSION

5.1 INTERRELATIONSHIPS OF SEASONAL GROWTH PROCESSES

5.1.1 FEEDING

(a) Loch Lomond (Figs 5.1a,b)

From April or May, Loch Lomond powan begin feeding on zooplankton which increases in abundance from April to a maximum in July (Pomeroy, 1987). During this time their energy intake exceeds their energy expenditure (positive energy balance) and the excess is deposited as reserves. This deposition is evidenced by a general weight increase in the liver, viscera and muscle from May. Fig. 3.17 shows the parallel increase in visceral lipid (from Rashid, 1984). After July, total zooplankton numbers decline, but powan feed most intensively in September, after a hiatus in the feeding intensity increase from July to August (Pomeroy, 1987). Maximum condition is reached in August in both sexes (Fig. 5.1). However, there is slight year to year variation in the time of maximum condition (Fig. 3.5); in 1979 the visceroliposomatic index was highest in early September (Fig. 3.17), as was the somatic condition factor (August and September; Fig. 3.5). The time of most rapid increase in condition is earlier in females (May to June) than in males (June to July), an observation which was also made in pollan by Dabrowski (1982a).

The hepatosomatic index in males is maximal in July, followed by a decrease to August in most years (Fig. 3.4).

Despite the increase in feeding intensity from August to September, the gut-somatic index and somatic condition factor also decrease in both sexes, signifying an increased energy demand, either for metabolic maintenance or growth processes. This decrease occurs a month before the estimated time of negative energy balance calculated by Pomeroy (1987) on the basis of his feeding results.

After September feeding virtually ceases in Loch Lomond and stored reserves are the main source of energy. Weight and lipid indices (Fig. 3.17) therefore continue to decline over autumn and winter, reaching a minimum in April or May (Plates 21, 26). In both sexes, the gut-somatic and viscero-liposomatic index may increase transiently after spawning since a high proportion of fish feed, mainly on benthos and powan eggs (Pomeroy, 1987). Otherwise feeding intensity remains low until the increase in plankton in spring.

(b) Loch Eck (Fig. 5.1c,d)

Loch Eck powan feed throughout the year on benthos, except for a brief period of starvation during spawning. As a result of the spawning fast and the energetic requirements of reproduction, energy reserves and consequently weight indices are minimal after spawning. Feeding resumes soon after spawning. The weight and lipid content of the liver increase very rapidly; the hepatosomatic index is at a high level by March or April and remains high until June, while the hepatoliposomatic index continues to increase from spawning to a maximum in June (Fig. 3.10). Visceral lipid (Fig. 3.17) and visceral weight also increase from February-

March (Plates 20, 25) to a maximum in June to August (Plate 22). The total liposomatic index (Fig. 3.13) does not increase significantly until after March or April, largely because it reflects the muscle lipid which does not increase until after April (Fig. 3.12). Therefore visceral lipid is deposited before muscle lipid, a state of affairs also found by Reshetnikov & Yermokin (1975). Muscle lipid and total lipid are maximal in June, as is the somatic condition factor.

From June to August, a significant decrease in lipid content occurs. Muscle lipid (Fig. 3.12), somatic condition factor and condition factor decrease, as does the liver weight and liver lipid (Fig. 3.10). The gut-somatic index and visceral lipid do not decrease until later (August to September), so although visceral lipid is deposited first it is depleted last; alternatively, visceral lipid is preferentially replenished. Vendace (C. albula) had a maximum energy value in July, which thereafter decreased, but the "remains" (which included viscera) had a maximum energy value in September (Dabrowski, 1983).

The question is why, when Loch Eck adults feed continuously, do they lose condition? Pomeroy (1987) found that although Loch Eck powan were feeding most heavily in August, their August diet was comprised mainly of the mollusc Pisidium which has a lower ash-free calorific value than the chironomids which normally form the bulk of their diet. This factor, in conjunction with increased energetic requirements could account for the negative energy balance. The quality of the diet improves after September, which may explain why the somatic condition factor remains constant from September to December and lipid content also remains constant or increases slightly, despite the energy demands of gametogenesis. The exceptions are the female visceral lipid (Fig. 3.11) and muscle lipid (Fig. 3.12) which decrease until spawning. Pomeroy (1987) calculated that a negative energy balance in Loch Eck powan occurred from September to November which is not consistent with these results.

5.1.2 REPRODUCTION

(a) <u>Females</u> (Fig. 5.1a,c)

After the rapid decrease during ovulation (Plates 18, 19, 20), the gonadosomatic index decreases more gradually until March or April as the ovaries regress (Plate 21). The lipid content of the spent ovaries is negligible (Fig. 3.9) and is minimal directly after spawning, thereafter remaining constant until April. When feeding resumes, weight and lipid reserves increase, to an August maximum in Loch Lomond and a June maximum in Loch Eck, but the gonadosomatic index does not alter significantly in either population until June (Plate 22). Therefore the gonadosomatic index fails to indicate the occurrence of endogenous vitellogenesis which commences in March, in Loch Lomond at least (Rashid, 1984). Ovarian lipid (Loch Eck) increases before the gonadosomatic index does, from April (1% of total body lipid) to June (4% of total body lipid; Figs 3.9, 3.14a), which presumably relates to the appearance of lipid vesicles in the cytoplasm during endogenous vitellogenesis (Plate 37). But since the visceral and muscle lipid are also increasing at this time (Figs 3.11, 3.12) more lipid is being deposited than utilised.

Exogenous growth phase oocytes first appear in late June to early July (Rashid, 1984). This is reflected by the gonadosomatic index which increases gradually from June until August. The liver produces yolk precursors (vitellogenin) which are transported in the blood and sequestered by the ovaries (Reshetnikov et al., 1970; Shackley & King, 1978). In females of both lochs, the involvement of the liver in exogenous vitellogenesis first becomes apparent from August when ovarian weight starts increasing rapidly. In Loch Eck females, the hepatosomatic index increases from a low level in August. This increase is particularly significant because the hepatosomatic index of the Loch Eck males remains low until September and the female hepatoliposomatic index increases only slightly (Fig. 3.10). In Loch Lomond females the rate of increase in the hepatosomatic index from August to September is greater than in previous months, although the rate of hepatosomatic index increase accelerates from September to October, when the gonadosomatic index increase is also at its most rapid. The highest rate of increase in Loch Eck female hepatosomatic index is the initial August to September increase, with the gonadosomatic index and gonad lipid (Fig. 3.9) increasing at a constant high rate from August to November, but it is not possible to be conclusive as the sampling period in Loch Eck was short and variations in spawning time confuse the issue.

Although gonad weight increases until spawning in Loch Lomond females, liver weight is maximal in October. It then declines slightly until spawning starts, indicating a decrease in liver vitellogenic activity before spawning. This observation correlates with ovarian development since Rashid (1984) found a maximum 71.2% of oocytes to be at the exogenous vitellogenic stage by early November, with the proportion decreasing significantly thereafter as final maturation took place (61% at the end of November, 5% at spawning). In the combined figure 5.1c, the hepatosomatic index of Loch Eck females appears to reach its maximum at the same time as the gonadosomatic index (December), but reference to Figures 3.2a and 3.10 indicate that in Loch Eck the hepatosomatic index may also maximise before the time of maximal gonadosomatic index.

A decrease in lipid content and increase in water content of the ovaries just prior to spawning has been described in pollan by Dabrowski (1982a) and in vendace by Lizenko et al. (1975), but although the December gonadoliposomatic index appears to be lower than in November (Fig. 3.9), a single powan hardly constitutes valid evidence.

Oogenesis requires a high expenditure of energy and deposition of large amounts of protein and lipid in the oocytes to sustain the embryo. Therefore when the rate of ovarian growth increases substantially from August, there is a decrease in stored reserves; somatic condition factor and muscle lipid decrease (Fig. 3.12), as do the gut-somatic index and visceroliposomatic index (Fig. 3.17a). The visceral fat reserves appear to be important to ovarian build-up (Fig. 3.14a; Reshetnikov et al., 1970; Bolotova, 1976). In females of both populations the initial decrease in visceral weight coincides with the rapid increase in gonadosomatic index (August to September). This visceral weight decrease is despite the continuation of feeding in both lochs; until September in Loch Lomond females and until spawning in Loch Eck females. The decrease in gut-somatic and visceroliposomatic indices in Loch Lomond females continues at a rapid rate until October (the month of maximum hepatosomatic index). Although the gut-somatic index (in 1985) then remains constant until spawning, the visceroliposomatic index (in 1979), the more valid measurement of visceral lipid in Loch Lomond powan (Ch. 3.2.4, p. 168), continues to decrease until November (Fig. 3.17a). In contrast, the gut-somatic index of Loch Eck females, after the initial rapid August to September decrease, decreases little from September to November. There is then a more rapid decrease in gut-somatic index from November until January or February. In Loch Lomond females, somatic condition factor decreases from August until spawning. In Loch Eck females, after the June to September decrease, the somatic condition factor remains constant until December, despite the increasing gonad weight. These differences must result from the different duration of feeding in the two lochs. Loch Lomond females are almost entirely dependent upon body reserves for exogenous vitellogenesis. Loch Eck females either do not use the reserves as extensively, or are able to replenish them to a certain extent.

During spawning there is a decrease in weight and lipid content of all tissues. Most of the lipid loss is from the ovaries, since over 50% of the total body lipid is ovulated (Fig. 3.14a; Reshetnikov *et al.*, 1970). Both Loch Lomond and Loch Eck powan starve during spawning and energy reserves are utilised for basic metabolic maintenance and spawning activities. However, the spawning decrease in somatic condition factor and visceral lipid (shown by gut-somatic index and visceroliposomatic index, Fig 3.17a) is not as great as during oogenesis, which is when most of the reserves are mobilised.

Since exogenous vitellogenesis is such a drain on body reserves, it is possibly the stage when oogenesis is retarded or aborted if reserves are insuffecent. Late stage adolescent females appear not to progress beyond the stage of early exogenous vitellogenesis, and older females have been found which were at the same stage (Ch. 4.4, p. 229). Under starvation conditions rainbow trout (*Salmo gairdneri*) resorbed vitellogenic oocytes (Scott, 1962). De Vlaming (1971, cited by Wootton,1979) found that starvation for 40 and 80 days did not affect the initial increase in the size of the ovaries of the goby, *Gillichthys mirabilis* Cooper, but during active vitellogenesis, 23 days of starvation resulted in ovarian regression. The winter flounder, *Pseudopleuronectes americanus*, reacted to food shortage by reducing the recruitment of vitellogenic oocytes, rather than by resorbing them (Tyler & Dunn, 1976). In sticklebacks

(Gasterosteus aculeatus), ration size had no effect on ovary size during the relatively slow autumn to winter increase. When ovaries increased rapidly in size in the spring, females on higher rations matured more quickly (Wootton, 1979) and the number of spawnings were highly correlated with ration size (Wootton, 1973a, 1977). When there was little food available, the number of spawnings were limited to one or two (Wootton et al.,1978), since inter-spawning intervals became extended and the ovaries regressed (Wootton, 1979). This effect of ration size on maturation time in sticklebacks may be a clue to the delayed spawning of Loch Eck powan in 1985, which could have been related to their relatively low condition in 1984 (Fig. 3.8a).

The principal signs of reproductive senescence in females are failure of vitellogenesis and atresia of ripe oocytes (Plate 15; Woodhead, 1979).

(b) Males (Fig. 5.1b,d)

The gonadosomatic index decreases during spawning (Plates 24, 25) and until April or May as the testes regress (Plate 26). As in females, the gonadoliposomatic index appears to reach a minimum (March, Fig. 3.9) before the gonadosomatic index (April or May). Directly after spawning, mitotic division of spermatogonia begins, and primary spermatocytes are abundant by the end of June in Loch Lomond. By August, secondary spermatocytes and spermatids are present (Rashid, 1984). The gonadosomatic index of Loch Eck males increases more rapidly earlier (May to June) than that of the Loch Lomond males, where the initial June to

July increase is more gradual. This difference might relate to the higher condition of Loch Eck males, allowing them to undergo spermatogenesis more rapidly at an earlier stage; or the reason could be that the Loch Eck males start feeding again immediately after spawning. After June the condition of Loch Eck males decreases, which could account for the reduced rate of increase in gonadosomatic index from June. The suggestion by Ursin (1979) that spermatozoa, consisting almost exclusively of RNA, DNA and lipids, were likely to be the most expensive substance in the fish body, may at least partly explain the decrease in hepatosomatic index in Loch Lomond males from August to October, although they are still feeding well in September. From August to September is the time when the gonadosomatic index increases most rapidly in Loch Lomond males. In both populations, the somatic condition factor declines from August, the highest rate of decrease in Loch Lomond males being from September to October. There is also a rapid decrease in Loch Lomond male gut-somatic index from August to September, the rate of decrease being much reduced from September to October as the gonadosomatic index reaches its maximum. Loch Eck male hepatosomatic index is low from August to September, and the gut-somatic index decreases from August to September, although this last decrease also occurs in females, and so other factors may be responsible. However, the August-September decrease in visceral lipid was greater in males than in females (Fig. 3.17). A decrease in energy reserves during spermatogenesis has been observed in pike, <u>Esox lucius</u> (Medford & Mackay, 1978) and in perch, <u>Perca</u>

fluviatilis (Craig, 1977). Data for pollan showed a decrease in male condition from July to August (Wilson & Pitcher, 1983). Valtonen (1974) observed a decrease in the liver weight of male C. nasus Pallas in August.

In Loch Eck, male condition (SCF and CF), gut-somatic index, visceroliposomatic index (Fig. 3.11) and musculo-liposomatic index (Fig. 3.12) reincrease from September to November or December, unlike the Loch Lomond males where the body reserves decrease, consistent with the reduced feeding in Loch Lomond after September. An increase in liver weight in males of both lochs before spawning may be connected with the high liver glycogen levels reported in spawning C. nasus Pallas males (Valtonen, 1974). There may also be an increase in liver lipid content, at least in Loch Eck males (Fig. 3.10).

During spermiogenesis, the gonadosomatic index decreases gradually from the maximum until spawning, possibly because of the reduction in cell size (spermatocytes to spermatozoa) and the withdrawal of water. Immediately before spawning there is a transient increase in testes weight, due to hydration of the testes (Plate 24).

During spawning, a significant general decrease in weight indices occurs, reflecting the spawning fast and increased activity in spawning behaviour. Since a negligible proportion of body lipid is contained in the testes (Fig. 3.14b), shedding of milt directly accounts for a lipid loss of only about 1% of the total lipid, but more lipid is expended from the viscera and muscle than in females (Figs 3.11, 3.12), probably because male spawning is of longer duration. Males have a higher incidence of fungal infection after spawning than females, possibly indicative of higher levels of stress (Pomeroy, 1982; Plates 3, 4).

(c) Comparison of energy expenditure of males and females (Fig. 5.1a,b,c,d)

Males undergo their main reproductive losses possibly during spermatogenesis (August to October) and certainly during active spawning from January to February (Chechenkov, 1973; Dabrowski, 1982a). Females utilise most of their body reserves during exogenous vitellogenesis (August to December; Reshetnikov *et al.*, 1970). By December, the gut-somatic index of females had decreased by 99% in Loch Lomond and 82% in Loch Eck, compared with a male decrease of 67% in Loch Lomond and 52% in Loch Eck (compare Plate 17 with Plate 23). Although female powan suffer greater body depletion than males (e.g. Figs 3.5, 4.3; also observed in perch by Craig (1977) and in vendace by Dabrowski (1982b)), they may compensate by increasing their reserves more rapidly. After spawning, Loch Eck adults resume intensive feeding, and a large number of Loch Lomond adults feed on benthos and powan ova. Pomeroy (1987) found that Loch Lomond females in January, February and April feed more heavily than the males. In both populations, female gut-somatic index may initially increase more than the males after spawning, but the visceroliposomatic index does not (Fig. 3.17) so no conclusions can be drawn. In fact, the stomachs of Loch Eck females contained proportionately less food than the males in the March and May samples (Pomeroy, 1987). It has already been noted however, that the somatic condition factor of females does increase more rapidly earlier than the males (Fig. 3.5). Dabrowski (1982b) cites Szypula (1965) who reported that the feeding intensity of female vendace was 130% higher than the males from February to May. Female *C. lavaretus ludoga* accumulated fat far more intensively than males during the foraging season (Bolotova, 1976).

(d) Seasonal cycles of juveniles compared with adults

In his comparison of seasonal cycles in immature, adolescent and adult hake, *Merluccius merluccius*, Hickling (1930) found that although the amplitude increased from immature to adolescent and adolescent to adult, the timing of the seasonal cycles was very similar. This was also found by Le Cren (1951) when comparing seasonal condition in 3 year old immature and mature female perch, and by Iles (1974) in herring. Iles commented that this seems to be something of a paradox, given the apparent antagonism of reproductive and somatic growth processes. Why should the juveniles which are not affected by the presumed antagonism, have similarly timed cycles to the adults? In powan, do juvenile growth processes "foreshadow" (Hickling, 1930) adult growth processes?

(i) Gonad. Adolescent powan are not in phase with the adult gametogenetic cycle; in adolescent females the cycle is incomplete as it does not appear to progress beyond early exogenous vitellogenesis; while male adolescents show spermatogenic stages which are not present in adult males at the same time of year (Ch. 4).

(ii) Liver.

Loch Lomond (Fig. 4.1a). The hepatosomatic indices of juveniles and adult males are very similar in their seasonal timing. They are all at a maximum from July to August, decrease to October, and thereafter remain constant until April or May before increasing to the summer maximum. The hepatosomatic index of adult females also increases from a low level in April or May but after July or August adult female liver weight continues to increase to an October maximum and so the cycle diverges from that of the adult males and juveniles.

Immatures tend to have higher hepatosomatic indices than adult males, significantly so in January ($p < 0.01$), May ($p < 0.05$), July ($p < 0.001$), September ($p < 0.01$), October and November ($p < 0.001$). Adolescent females had very significantly higher hepatosomatic indices than adult males in May, August and October ($p < 0.001$). However, overall the hepatosomatic indices of the juveniles are closer to the adult males than to the adult females which had consistently higher hepatosomatic indices than the other reproductive categories, although the differences were not generally significant in March, April and May (or in July in immatures).

Similarities in the hepatosomatic index cycles of adults and juveniles are clearly related to feeding, such as the increase from April to May, during the period of intensive feeding, the summer maximum in adult males and juveniles, which is followed by a decrease when feeding ceases. The increase in adult female hepatosomatic index from August is related to the reproductive cycle. As it is not matched by the adolescents it would appear that the liver of adolescent females is not involved in exogenous vitellogenesis to any significant extent.

Loch Eck (Fig. 4.1b). The seasonal cycles of hepatosomatic and hepatoliposomatic indices (Fig. 3.10) differ in juveniles and adults. From April to June the hepatosomatic indices of juveniles decrease while those of adult males and females remain fairly constant. The adult decrease is later, from June to August. From January to August the adult and juvenile hepatoliposomatic indices show similar differences (Fig. 3.10). Juvenile hepatosomatic index increases from November to February; adult hepatosomatic index decreases over spawning to a low level in February.

Juveniles (especially adolescent females) tend to have higher hepatosomatic indices than adult males though the differences were only significant in January ($p < 0.01$), February ($p < 0.001$) and April ($p < 0.002$) in immatures; and January ($p < 0.001$), February ($p < 0.001$) and December ($p < 0.02$) in adolescent females. In June, the hepatosomatic index of adult males was significantly higher than the adolescent females ($p < 0.001$). Compared with adult females, the hepatosomatic index of immatures was significantly higher in March ($p < 0.001$), and of adolescent females from

January to March (significant in February $p < 0.001$). In all other months adult females had the higher hepatosomatic index. With the exception of June, the hepatoliposomatic index of juveniles was considerably higher than adults (Fig. 3.10).

Therefore the seasonal cycles in juvenile and adult liver weight and lipid are not the same. In adults of both sexes there are variations related to reproduction which are not observed in the juveniles. The decrease in February (spawning), and the increase in hepatosomatic index of adult females from August, are not reflected by the adolescent females. Juvenile livers generally contain more lipid than adult livers (hence their paler colour, Plate 13), which may account for the hepatosomatic indices of Loch Lomond juveniles tending to be higher than those of the adult males. An interesting question is why the hepatosomatic indices of juveniles and adult males in Loch Lomond appear to be generally closer than in Loch Eck, where the hepatosomatic indices of juveniles approach those of the adult females (Fig. 4.1a,b). It may be that juveniles in Loch Eck have proportionally more liver lipid than juveniles in Loch Lomond.

(iii) Viscera

Loch Lomond (Fig. 4.2a). Juveniles tend to have the higher gut-somatic index which reaches a maximum later (October) compared with the adults (August). Similarities between adult and juvenile cycles are: (a) possibly the increase from June, related to feeding, and (b) the autumn decrease, also related to feeding.

Loch Eck (Fig. 4.2b). As in Loch Lomond, Loch Eck juveniles generally have higher gut-somatic indices than the adults. The seasonal timing of the gut-somatic index cycles is evidently very different. Juvenile gut-somatic index is high from January to April, when adult gut-somatic index is low, and when juvenile gut-somatic index is low in June, adult gut-somatic index is high. The seasonal cycles of adult and juvenile visceroliposomatic index also differ (Fig. 3.11). Adolescent females have a higher level of visceral lipid than the other categories, except in June, when juvenile visceral lipid is minimal (see Fig. 4.2b for immatures) and adult visceral lipid is at a high level.

(iv) Muscle (SCF, MLSI)

Loch Lomond (Fig. 4.3a). In general, the seasonal pattern of somatic condition factor is similar in all groups; a minimum from March to May, increasing to a maximum in July or August, before decreasing once more.

Immature powan have the lowest somatic condition factor and adult males the highest. The somatic condition factor of adult males was very significantly higher than that of immatures at all times ($p < 0.001$), and was higher than that of adolescent females in most months, significantly so in March ($p < 0.001$), June ($p < 0.05$), August ($p < 0.05$), November ($p < 0.001$) and December ($p < 0.05$). In July there was no difference, and in August the adolescents were significantly higher ($p < 0.05$). Adolescent females did not have consistently higher somatic condition factors than adult females.

In amplitude, immatures varied less over the season than did the other categories. The most seasonally variable were adult females, then adolescent females.

Loch Eck (Fig. 4.3b). The seasonal timing of changes in juvenile somatic condition factor differs from the adults. In June adult somatic condition factor is at a maximum while juveniles have low somatic condition factors. From December to January, juvenile somatic condition factor may increase while adult somatic condition factor decreases or remains constant, but there is too little information to be conclusive.

Immatures have the lowest somatic condition factor, and adult males the highest, with the exception of January, February, May and December when adolescent females were the highest. From September to February and also in May, adolescent females had higher somatic condition factors than adult females, statistically significantly so in December ($p < 0.05$), January ($p < 0.001$), February ($p < 0.002$) and May ($p < 0.05$).

There was a difference in the seasonal timing of the musculoliposomatic index of juveniles and adults (Fig. 3.12), in June, the adult musculoliposomatic index was at a maximum, while the juvenile musculoliposomatic index was minimal. Adolescent females tended to have the highest musculoliposomatic indices with the exception of June when adults were significantly higher, and December when males might be higher (not significant). After adolescent females, adult males had the highest musculoliposomatic index.

In terms of the Loch Lomond somatic condition factor cycle, immatures have the lowest amplitude, as was found in other species by Hickling (1930), Le Cren (1951) and Iles (1974). However, unlike the findings of these authors, adult and adolescent powan seemed to have much the same seasonal amplitude in somatic condition factor, and in the other weight and lipid indices there was no consistent difference in amplitude from immature to adult. Adolescent females had a considerably higher lipid content than the other categories (Fig. 3.13), particularly in the muscle (Fig. 3.12) and around the viscera (Figs 3.11, 4.2a,b). Immatures have a high liver lipid content (Figs 3.10, 3.14c, 4.1), also a lot of visceral lipid (Figs 3.11, 4.2a,b), but a lower level of muscle lipid (Fig. 3.12). In consequence immatures have a lower somatic condition factor than adults and adolescents (Figs 4.3a,b) and a lower total liposomatic index than adolescents (Fig. 3.13).

In powan the timing of juvenile seasonal cycles does not always match that of the adults. Unlike the findings of Hickling (1930), Le Cren (1951) and Iles (1974), there are differences which are related to the reproductive cycle, particularly in adult females.

In Loch Lomond, feeding is very seasonal (Pomeroy, 1987) and the similarities between juveniles and adults are almost certainly related to feeding cycles. When intensive feeding resumes in spring, there is a general weight increase in all categories from a low winter level to a high midsummer level (July-August). When feeding is reduced, weights decrease. In this respect, adult Loch Lomond males match the juveniles more closely than do the adult females, because of the greater effect of oogenesis on the weight and condition of the adult females.

In Loch Eck, there is even less similarity between juveniles and adults. The seasonal cycles of immatures and adolescents are more similar to each other than they are to the adults and it is difficult to relate similarities and differences to feeding and reproduction, probably because feeding in Loch Eck is continuous and aseasonal. The decrease in juvenile lipid and weight indices in June when adult lipid and weight indices increase to a maximum is puzzling, unless it has to do with somatic growth (see next section).

To conclude, the timing of the seasonal cycles of juvenile powan do not foreshadow those of the adults.

5.1.3 SOMATIC GROWTH

In both lochs, growth in length occurs from May to October or November, with the younger, smaller fish generally commencing growth earlier in the season than older, larger fish. Weight and lipid content increase before length, an observation also made by Lizenko *et al.* (1975) and Iles (1984). It seems probable that a critical level of body reserves, or according to Dabrowski (1982a) "a normal physiololgical state", has to be achieved before linear growth can be initiated. It was suggested (Ch. 2.1.4) that the reason for the later growth of older and larger fish is because they take longer to recuperate after spawning. Although reproductive effort is known to increase with age and size in some species (Love, 1970; Mackinnon, 1972; Hislop, 1975; Craig, 1977), there is no evidence that this is the case in powan, indeed, the gonadosomatic index suggests that it is not (Ch. 3.1.4, p. 147). Increasing physiological size may be the cause of the shorter growing season and decelerating growth rate. Environmental stimuli such as photoperiod and temperature cue and regulate some seasonal physiological processes (Swift, 1955; Hogman, 1968; Delahunty et al., 1978; Brett, 1979; Scott, 1979; Bye, 1984; Scott, in press), but because of the non-synchronised time of growth between age groups, it is possible that temperature and photoperiod release and limit linear growth rather than directly initate it. Allen (1940, 1941) suggested that the growth of brown trout was released by a temperature of 7°C in spring and limited when the temperature fell to 7°C in autumn.

If Loch Lomond powan do most of their growing in July and August-September (McCulloch, 1984) then growth in length coincides with the time of maximum condition, which is in August in most years (Fig. 5.1a,b). A disproportionate increase in length over weight will cause a decrease in somatic condition factor, but the the Loch Lomond somatic condition factor decrease could also result from weight loss through mobilisation of lipid and protein stores for gametogenesis and for routine maintenance, particularly since feeding virtually ceases after September. So many different things may be happening at the same time that it is difficult to distinguish their effects.

Somatic growth is an energy consuming process (Shul'man, 1974). Growth hormone enhances fish growth by increasing food consumption and food conversion efficiency, and also promotes lipolysis (Donaldson et al., 1979; Weatherley & Gill, 1983b, 1987). In Loch Eck adults, a general decrease in lipid content (Figs. 3.9, 3.10, 3.12, 3.13) and condition (Fig. 5.1c,d) occurs from June (maximum) until August. Since this decrease occurs in both sexes, and precedes rapid ovarian growth it indicates that gametogenesis is not responsible; somatic growth might be. The reduced food quality in August (Pomeroy, 1987) and higher summer temperatures could mean increased metabolic energy demands, though fluctuations in temperature might have little effect on the bottom feeding Loch Eck powan. Both these factors could contribute to the reduction of lipid reserves during somatic growth. Loch Eck juveniles also show a decrease in lipid reserves but the decrease occurs earlier in the year, from an April maximum until June (Figs 3.10 to 3.13). If this earlier decrease is caused by somatic growth, it is consistent with the theory of an earlier start to the growing season for younger fish. From April to June, photoperiod and temperature increase (Table 2.19) and feeding is good, Pomeroy (1987) found the diet in May to have the highest calorific value of the samples analysed. Somatic growth therefore seems a strong possibility for the lipid decrease. The question arises as to why Loch Lomond juveniles do not show a similar early decrease. Perhaps because they reduce feeding in winter, Loch Lomond juveniles do not have the high lipid content of the continually feeding Loch Eck juveniles early in the year. When Loch Lomond juveniles do start intensive feeding in spring, their energy intake from the plankton could be sufficient to support both somatic growth and deposition of energy reserves, which may not be the case for benthic feeding Loch Eck juveniles, with a lower calorific intake (Pomeroy,1987).

In Loch Eck adults, the decrease in muscle and liver lipid (June-August) occurs before the decrease in visceral lipid (August-September, Fig. 3.11). In somatic growth, it could be the muscle lipid which is preferentially utilised. This suggestion is also made in view of the fact that the somatic condition factor (Fig 4.3a,b) and muscle lipid (Fig. 3.12) of the rapidly growing immature powan is lower than in adolescents and adults, although there is little difference in visceral lipid content (Figs 3.11). In pollan, Dabrowski (1982a) correlated decreasing muscle fat with increasing gonadosomatic index. On this basis, Wilson & Pitcher (1983) attributed the decrease in somatic condition factor to the gonadosomatic index increase in female pollan. However, their figure shows that the somatic condition factor in female pollan initially decreased rapidly from June to August, before the ovary commenced its rapid increase in size (August-November). Therefore gonad growth does not seem to be responsible for the initial somatic condition factor decrease; somatic growth might be. However, a complication in Lough Neagh is the absence of thermal stratification and high summer temperatures (Wilson, 1983; Dabrowski, 1985). The energy requirements of an increased metabolic rate could also account for the somatic condition factor decrease in pollan. Dabrowski (1985) estimated that in summer, respiratory energy used 51-66% of the energy consumed by female Lough Neagh pollan compared with 41-49% in Polish vendace.

Why, particularly in younger Loch Eck powan, if somatic growth continues throughout the season (May to October), do the weight and lipid indices decrease early in the year with a build-up thereafter? McCulloch (1984) showed that the initial period of growth may be the time of most rapid growth, as the rate of ^{14}C-glycine incorporation into the scales of Loch Lomond powan was higher in June-July than it was later. He suggested that there were two growth rate maxima in the season, one in June or July, and a second, smaller maximum in August or September. However, the bimodal pattern of seasonal growth did not occur in all age groups in all years, with the oldest (5+) age group in 1983 showing a single August growth rate maximum (McCulloch, 1984). Swift (1955) observed two seasonal growth rate maxima in 3 year old brown trout.

Iles (1974) suggested that rapid somatic growth and ovarian development were likely to be temporally separate, but in powan, somatic growth in August-September coincides with the start of rapid gonad build-up, so the two growth processes are not mutually exclusive, at least not initially. At some stage, defined by the level of energy reserves (Swift, 1955), photoperiod or temperature, somatic growth ceases and reserves are mobilised for gametogenesis and metabolic maintenance. The growing season of juveniles (non-reproductive) is possibly limited by photoperiod or temperature rather than by food availability, since Loch Eck juveniles feed all year round.

Protein growth reflects somatic growth (Fig. 3.16), which in first year fish is very rapid and predominates over fat accumulation (Shul'man, 1974). Fast growth is advantageous in reducing the period of vulnerability to predation and increasing feeding competitiveness (Ch. 2.3). In this period of intensive growth, lipid may not be being accumulated because it is being preferentially catabolised. Growth hormone may cause preferential mobilisation of lipid so protein can be deposited (Markert et al., 1977, cited by Weatherley & Gill, 1987). With the onset of reproductive maturity lipid accumulation increases, and the rate of somatic growth decreases. That there is an allometric change in growth at the time of maturity (around a length of 250mm in Loch Lomond and 215mm in Loch Eck), is shown in the body-scale relationships (Fig. 2.1) and in the relationship of length to lipid weight (Fig. 3.15) and length to protein weight (Fig. 3.16). Fat accumulation continues to increase with increasing age in some species (Shul'man, 1974; Delahunty & de Vlaming, 1980), although in female perch Craig (1977) found fat content to decrease with age.

5.2 VARIATIONS IN GROWTH PROCESSES FROM YEAR TO YEAR

There are variations in amplitude of growth processes between years (Ch. 2.2, 3.2) but an attempt to correlate variations in all the the various growth processes was negated because evidence for correlations were so circumstantial and fluctuations in individual growth processes could not be consistently correlated. It was impossible to establish definite causes of the variations because of the lack of information on long-term environmental conditions within the lochs, and also because of the complexity of factors affecting growth (Brett, 1979). The more noteworthy year to year variations are given below.

(a) Loch Lomond

(i) 1979-80. Maximum somatic condition factor (Fig. 3.5) although lower than average, remained constant for an extended period, from July to early November, before decreasing during November. Visceral lipid (Fig. 3.17) was at a maximum in September 1979, later than the gut-somatic index maximum in 1985 (August, Fig. 3.10). Gonadosomatic index (Fig. 3.1) and hepatosomatic index (Fig. 3.4) were average, but growth rates in the 3-4 and 4-5 age groups (adults) were above average. There may have been a longer feeding and growing season in this year. Mean September sunshine was high (Fig. 2.11b).

(ii) 1980-81. There was a rapid early increase in somatic condition factor to a July maximum (Fig. 3.5) which may correlate with a high female gonadosomatic index (Fig. 3.1a). There was no October sample so it is not known whether maximum female hepatosomatic index (Fig. 3.4) was also higher than average. 1980 was notable for high April and May sunshine, but had low June, July and August levels (Fig. 2.11, Table 2.20). There may have been a rapid early increase in plankton abundance, favouring early deposition of body reserves which were utilised in ovarian growth.

(iii) <u>1984-85</u>. Female gonadosomatic index reached a high maximum (Fig. 3.1a), but there was no September sample to determine whether the somatic condition factor reached a higher level than in August. Male gonadosomatic index was average. 1984 was particularly notable for the high growth rate of the first year fish (1984 year-class) although growth rates of the adults (3-4 and 4-5 age groups) were low (Fig. 2.8, Ch. 2.2.3 p. 87). 1984 had high sunshine levels in May and July (Fig. 2.11).

(iv) <u>1985-86</u>. Gonadosomatic indices (Fig. 3.1), hepatosomatic indices (Fig. 3.4), somatic condition factors (Fig. 3.5) and growth rates (Fig. 2.8) were universally low, in both sexes and all age groups (except the growth rate of the 0-1 age group). Sunshine levels were average from April to June but were particularly low in the summer months (July to September, Table 2.20). 1985 was also a year of high summer rainfall. Plankton in May 1985 was known to be scarce compared with the previous two years (Pomeroy, 1987) and so lack of food was almost certainly responsible for limiting growth in this year.

(b) Loch Eck

(i) 1984-85. Hepatosomatic indices and somatic condition factors were low in both sexes (Figs 3.7, 3.8). Female hepatosomatic index maximised later (December) than in the following years. Spawning in 1985 was late (Fig. 3.3) as was spawning in 1984 (Pomeroy, 1987). Growth rates were low (Fig. 2.10). Pomeroy (1987) found a low feeding intensity in September 1984 but because this was the only September sample analysed, it is not known whether feeding in September is usually low or was peculiar to that year.

(ii) 1985-86. Hepatosomatic indices (Fig. 3.7) and somatic condition factors (Fig. 3.8) were higher than in the previous year with the female hepatosomatic index maximising earlier (November). Spawning was also earlier than in the previous two years (Fig. 3.3). The growth rates of the 3-4 and 4-5 age groups were higher than the previous year (Fig. 2.10).

(iii) 1986-87. Hepatosomatic indices (Fig. 3.7), gut-somatic indices (Fig. 3.6) and somatic condition factors (Fig. 3.8) were all higher than the previous two years and spawning was earlier, coinciding with the time of the Loch Lomond spawning (Fig. 3.3). Growth rates were considerably higher in all age groups (shown by marginal scale increments, Fig. 2.3).

Therefore in Loch Eck from 1984-87 there was a progressive increase in growth rates and weight indices, and also in lipid reserves. The lipid content of liver (Fig. 3.10) and male viscera (Fig. 3.11) were lower in March and May 1985 than in February, April and June 1986. The lipid content in January 1987 was also high (male hepatoliposomatic index, Fig. 3.10; visceroliposomatic index, Fig. 3.11; total liposomatic index, Fig. 3.13). The increase in growth rate and condition over 1984-87 also occurred in Loch Eck juveniles (Figs 4.4, 4.5, 4.6).

A correlation seems to exist between the time of spawning and condition, since earlier spawning paralleled the increase in condition. The maximum female gonadosomatic index in Loch Eck did not differ between 1984-85 and 1985-86. Since spawning time in Loch Lomond did not vary significantly in these years (Fig. 3.3) and climatic conditions in the two regions are similar (Tables 1.1, 2.19), it is unlikely that fluctuations in temperature or photoperiod caused the change in Loch Eck spawning time. It was more likely to have been a physiological factor, such as an insufficiency of, or delay in, the build up of body reserves, so retarding the process of exogenous vitellogenesis which may be dependent on stored reserves. Why Loch Eck females should delay spawning rather than spawn at a consistent time but with a lower gonadosomatic index as occurred in Loch Lomond 1985-86 (Fig. 3.1a) is not known.

5.3 THE TWO POPULATIONS COMPARED

5.3.1 SUMMARY

(a) Genetics and Morphology (Chapter 1)

The populations probably originated from the same stock some 10,000 years ago. They are genetically similar with low levels of polymorphism. Of the polymorphic loci, one allele is restricted to Loch Eck (McEwen, 1985). Gill rakers are a criterion frequently used in identifying populations, stocks and species since they are under genetic rather than environmental control (Svardson, 1970). Loch Eck powan have a significantly higher number of gill rakers per gill arch than Loch Lomond powan (Miller, 1984).

Supernumerary pelvic fins have been found occasionally in Loch Lomond powan (Gervers, 1954; Slack *et al.*,1957) and in schelly (Bagenal, 1970). Supernumerary pelvic fins have also been observed in Loch Eck powan, and in addition, fused pelvic fins, an abnormality not discovered in the Loch Lomond population (Brown & Scott, 1987).

In the past thirty years, Loch Lomond powan have not deviated significantly from a 1:1 sex ratio (Slack *et al.*,1957; Maitland, 1969), but the Loch Eck population was predominantly male at the start of the sampling period in 1984 with the balance shifting towards a 1:1 ratio by 1986.

(b) Somatic Growth (Chapters 2.1, 2.2)

(i) Despite their higher growth rate in most years, powan in Loch Eck were significantly shorter at each age than in Loch Lomond, since Loch Lomond powan had higher growth rates in two of their first three years.

(ii) There were both similarities and dissimilarities in growth trends of the two populations in the same years. Year to year growth in Loch Eck may be more variable, but results were not conclusive.

(c) Recruitment (Chapter 2.3)

The most abundant year-class in each loch differed, being 1984 in Loch Lomond and 1982 in Loch Eck. Apart from these, year-class strengths were similar in relative magnitude. The same year-classes were weak in both lochs (1983, 1977 and possibly 1985). The 1983 year-class, weak in Loch Lomond was an almost complete failure in Loch Eck. Over the period 1976-85, year-class strengths were more variable in Loch Eck than in Loch Lomond.

(d) Mortality (Chapter 2.3)

Powan in Loch Eck had a higher survivorship than in Loch Lomond. The pattern of mortality in the two lochs was very similar. Loch Eck powan were notably parasite-free.

(e) Reproduction (Chapter 3.1)

Both populations spawn in shallow areas with a gravel substrate. The spawning grounds in Loch Lomond are off headlands and on shallow offshore banks; in Loch Eck, powan spawn along suitable parts of the shoreline.

The time of spawning in Loch Lomond was very consistent (end of December to the first two weeks in January), in Loch Eck it was more variable (January to February or March). Apart from differences resulting from the later Loch Eck spawning, gonadosomatic indices in the two lochs were of similar magnitude. The gonadosomatic index of Loch Eck males increased rapidly earlier than that of Loch Lomond males.

(f) Weight Indices (Chapter 3.2)

Loch Eck powan were heavier for length than Loch Lomond powan. They had a very significantly higher liver weight and somatic condition factor. Their visceral weight was also generally higher than the Loch Lomond powan.

After spawning, the weight indices of powan in Loch Eck increase earlier and initially more rapidly than in Loch Lomond. The condition of Loch Eck powan was maximal in June, whereas the maximum condition of Loch Lomond powan was from July to September (August in most years). Loch Eck powan show a decrease in weight and condition from June to August, not observed in Loch Lomond powan.

(g) Seasonal Lipid Content (Chapter 3.3)

Loch Eck powan had a consistently higher liver lipid content. In muscle and around the viscera, Loch Eck powan had a higher lipid content than Loch Lomond powan over winter and early summer. After spawning, the lipid content of Loch Eck powan increased before Loch Lomond powan.

Although the lipid increase was later in Loch Lomond powan, it was more rapid, and reached a maximum value which was significantly higher than in Loch Eck.

(h) Juveniles (Chapter 4)

Juveniles in Loch Eck were heavier for length than juveniles in Loch Lomond, having significantly higher hepatosomatic indices, gut-somatic indices and somatic condition factors. The hepatosomatic indices of Loch Eck juveniles were more seasonally variable, and all weight indices followed a differently timed seasonal cycle from those in Loch Lomond juveniles.

Powan matured at the same age in both lochs, but because of the difference in length, Loch Eck powan were smaller at maturity than Loch Lomond powan. Reproductive maturation may be completed more rapidly in Loch Eck than in Loch Lomond, possibly because of the higher condition of the Loch Eck powan.

5.3.2 FEEDING

All growth processes ultimately depend on the energy intake, and in both powan populations, the total energy intake for the year is much the same. The difference between the populations is in the rate at which the energy is ingested, determined by the duration of feeding and the calorific value of the prey (Pomeroy, 1987). Loch Lomond powan feed intensively on plankton from May to September, Loch Eck powan feed on benthos throughout the year, except during spawning. The higher calorific value of the Loch Lomond planktonic diet (Pomeroy, 1987) is presumably the reason why the Loch Lomond powan achieve a higher maximum lipid content than the Loch Eck powan despite the difference in feeding duration. Shul'man (1974) observed that in general, fish which are supplied with food throughout the year store much less fat than fish which interrupt feeding for a long time. The higher level of reserves in Loch Lomond powan compensates for the reduced feeding period from October to April, when they have to rely almost entirely on stored energy reserves to meet their needs, unlike the continously feeding Loch Eck powan. When the female visceral weights (Fig. 5.1a,c) and lipid contents (Fig. 3.17a) are compared, the decrease in Loch Eck female gut-somatic index and visceroliposomatic index from August-September until spawning is slight compared with the rapid decrease in the Loch Lomond females over the same period. Similarly, while Loch Lomond female somatic condition factor decreases from August until spawning (Fig. 5.1a), Loch Eck female somatic condition factor remains constant from September until December before decreasing (Fig. 5.1c). Loch Lomond male visceroliposomatic index decreases from September until spawning, while after an initial August to September decrease, Loch Eck male visceroliposomatic index reincreases until spawning (Fig. 3.17b). It was estimated that by December, the gut-somatic index of Loch Lomond females and males had decreased from the maximum by 99% and 67% respectively, compared with a Loch Eck gut-somatic index decrease of 82% for females and 52% for males. The continuously feeding Loch Eck powan either do not mobilise as much of their body reserves, or can replace them to some extent. Consequently powan in Loch Eck have the higher lipid content from winter to early summer. Dabrowski (1985) compared the energy budgets of vendace and pollan. He found that body depletion in vendace during intensive ovary growth (October and November) was much greater than in pollan, probably because vendace reduce their feeding earlier.

A previous sample of Loch Eck powan were found to be feeding on zooplankton (Slack et al., 1957). It seems likely that this was a genuine Loch Eck sample since their low level of parasite infestation was commented on (Copland, 1957). The sample was small (17 powan) and may not have been representative of the population; or there could be sub-populations with differing feeding habits. This last suggestion seems unlikely because of the small size of Loch Eck but is worth investigating. Otherwise there has apparently been a complete change in diet in the past 30 years, as out of the few hundred Loch Eck powan in this study whose gut contents were analysed, only one fish included zooplankton in its diet (Pomeroy, 1987). The summer diet of the gwyniad comprised both benthos and zooplankton (Haram & Jones, 1971). They concluded that the gwyniad were opportunistic feeders, the composition of their diet reflecting the availability of food items. However, plankton is available in Loch Eck, and is similar in species composition to that in Loch Lomond.

Why should the Loch Lomond and Loch Eck powan diets differ? It is possible that the smaller volume of water in Loch Eck is more affected by enviromental variation than in Loch Lomond, and so the plankton productivity in Loch Eck could vary more between years than in Loch Lomond. The benthos, which feeds on dead plankton and detritus (Macan & Worthington, 1951) could be a more reliable source of food and buffer the Loch Eck powan to some extent from immediate changes in plankton abundance. Loch Eck powan feed throughout the year either because of the lower calorific value of the benthos, or because the benthos is available all year. The significantly higher condition of powan in Loch Eck compared with Loch Lomond would suggest that year-round benthic feeding is a favourable strategy.

Shul'man (1974) suggested that the forage status of planktivorous fish was on the whole inferior to that of benthophages, since the planktivores were "graspers" and required more energy to catch their smaller prey and so could not grow and increase their fat reserves simultaneously, but this is not true of Loch Lomond powan. It appears that in Loch Lomond juveniles at least, the energy intake fom plankton feeding is sufficient to support rapid growth and fat deposition, while Loch Eck juveniles and adults show a significant decrease in feeding (possibly related to rapid somatic growth), suggesting that the energy intake is not sufficent to support rapid somatic growth and deposition of energy reserves. The benthic feeding Loch Eck powan may well expend as much, if not more energy foraging around in the mud than Loch Lomond powan do, especially when plankton is abundant. It is possible that when zooplankton becomes more scarce after July, Loch Lomond powan expend progressively more energy in foraging. The decrease in lipid stores and condition from August to September, despite intensive feeding, could in part relate to foraging becoming energetically uneconomical. At some point (after September) plankton numbers reach such a low level that starvation becomes the better option and so Loch Lomond powan discontinue feeding.

5.3.3 LIVER

In powan, the liver is negligible in weight and lipid content (1-4% of total lipid), and so is not a significant lipid reserve compared with for example, cod (Gadus morhua) in which the liver may contain 15-75% lipid (Jangaard et al., 1967). However, there is significant seasonal variation in liver weight and lipid content, particularly in Loch Eck powan which had larger livers than Loch Lomond powan (Figs 3.7, 4.4). In addition, interest was engendered by the differences in their colour, as Loch Eck powan livers ranged from very pale brown to dark red, particularly over the spawning season (Plate 13). The liver colour appeared to be related to the amount of visceral fat, since powan with a lot of visceral fat had pale livers (Plate 23) while powan with little fat, for example spent fish, had dark livers (Plate 13). 'Mid' coloured livers were found in spawning and post-spawning fish which had resumed feeding. Analysis of the lipid content of powan categorised by liver colour

(Table 3.9) confirmed that liver colour was generally related to the level of lipid reserves, not only in the liver, but in other tissues, though low numbers, individual variation and subjectivity of the colour assessment reduced the statistical validity. Adolescents with their very high lipid content (Ch. 4, Fig. 3.13) had particularly pale livers (Plates 29 to 31). The livers of immature Loch Eck powan were almost white. Lipid analysis demonstrated that despite their small size, the proportion of total body lipid in immature livers was high compared with adults and adolescents (Fig. 3.14).

A similar variation in liver colour relative to lipid content has been observed in marine species. In cod, a large creamy liver indicated a good state of nutrition, while a small reddish or brownish liver signified depletion (Love, 1980). Hickling (1930) noticed differences in liver colours of hake. Wessels & Spark (1973, cited by Love, 1980) classified two species of hake (Merluccius capensis, M. paradoxus) as well fed or starving on the basis of liver colour (creamy or red). Love also cites the Reverend Samuel Ward (1776) who wrote "the liver of a ling is extremely white so long as the fish continues in season and abounds with a fine flavoured oil, but as soon as it goes out of season, the liver becomes very red and affords no oil. this is, in some degree, the case with cod and other fish, but the difference is not so very remarkable".

There were no discernible differences in the liver colour of Loch Lomond powan which were universally mid-brown (Plates 21, 27). This may be because they contain less lipid than Loch Eck powan livers (Table 3.10b), or because the type of lipids differs because of the difference in diet (Ch. 3.3.1). The difference in liver size between populations (even in the immatures) also presumably reflects the difference in feeding. Wootton _et al._ (1978) compared females of upland and lowland populations of sticklebacks (_Gasterosteus aculeatus_). The lowland population had larger livers and a higher condition for much of the year compared with the upland population, the difference in liver size becoming manifest as early as 2 or 3 months of age. It was suggested that the lowland population had the better food supply.

The rapidity with which the liver weight and lipid content alters during starvation and after resuming feeding (e.g. Loch Eck males over spawning, Fig. 3.7b) confirms that the liver is a sensitive monitor of nutritional and energetic status, being faster in its response than visceral indices or condition factors (Valtonen, 1974; Tyler & Dunn, 1976; Heidinger & Crawford, 1977; Allen & Wootton, 1982; Cui & Wootton, 1988a). The liver has been shown to be sensitive to temperature, decreasing in weight at higher temperatures, probably because of increased maintenance energy requirements (Heidinger & Crawford, 1977; Adams & McLean, 1985). This may be partly why hepatosomatic and hepatoliposomatic indices decreased in Loch Eck powan from June to August, the months with highest temperatures. Adams & McLean (1985) suggested that the liver was a useful index of somatic growth in young largemouth bass (_Micropterus salmoides_); Cui & Wootton (1988a) made a similar suggestion for minnows (Phoxinus phoxinus). Changes in the liver weight are also a useful indicator of toxicant stress (Heidinger & Crawford, 1977; Adams & McLean, 1985). However, the liver has many functions and so can alter for reasons other than the nutritional state; as during its vitellogenic role in the female reproductive cycle (Shackley & King, 1978), which in powan causes a significant increase in liver weight from August to October (Loch Lomond) or November (Loch Eck). Livers of female sticklebacks were sensitive to ration, but the degree of sensitivity varied in different phases of the energetic cycle (Allen & Wootton, 1982). Fluctuations in liver weight have therefore to be studied in relation to the reproductive cycle (Allen & Wootton, 1982; Adams & McLean, 1985; Cui & Wootton, 1988a).

CHAPTER 6 THE POWAN, PAST, PRESENT AND PROSPECTS

The uniqueness of the Scottish powan was early recognised. Sibbald (1684) simply recorded its presence; "Poana, Anguillae species in Lacu Leimonio", but an earlier reference to Loch Lomond was more informative; "This Loch beside abundance of other fishes hath a kind of fish of the owne, named powan, very pleasant to eate" (Monipenny, 1612). An early reference to Loch Eck reads, "The most remarkable thing with regard to Loch Eck is, its abounding with fresh water herring. They are a dry insipid fish and are not discovered in any other lake on the west coast, excepting this and Loch Lomond" (Sinclair, 1799). According to Lamond (1911, 1931), the Loch Lomond powan has a curiously distinctive flavour of its own, faintly suggestive of cucumber. In Yarrell (1859), also with reference to the Loch Lomond powan: "From the estimation these fish are held in by the local inhabitants, they are seldom sent far before they meet with a ready sale and are entirely unknown in the markets of Glasgow." Powan were caught by drag-nets between March and September (Yarrell loc. cit.). At this time the powan fishery must have been on a small scale and localized (Sinclair, 1799). A commercial fishery on a larger scale existed during the war years when there was a food shortage. From May to September in 1917 to 1926, catches in Loch Lomond by the pollan fishermen from Lough Neagh ranged from approximately 51,500 fish in 1918 to 10,000 fish in 1926 (Lamond, 1922, 1931). Powan were popular in the English Midlands where they were sold as "pollen" and sometimes as "grayling". In 1926 demand declined, the price fell and powan fishing was abandoned midway through the season (Lamond, 1931). Large numbers of powan were once again caught during the 1939-46 war (Maitland, 1972a). Since then there has been no demand for them and Loch Lomond powan remain commercially unexploited. No documented records have been found of a powan fishery in Loch Eck, although there was one organised by the Youngers of Benmore during the First or the Second World War (P.S. Maitland pers. comm.). A licence from the Nature Conservancy Council is now required in order to catch powan.

The time of optimum condition of Loch Lomond powan has not changed in two hundred years. Then, powan were considered to be best to eat in July and August (Sinclair, 1799). Yarrell (1859) recorded that best condition was in August and September, the powan remaining out of condition from spawning until March.

The Statistical Account of Buchanan (Sinclair, 1799) referred to the Loch Lomond powan ("pollac") as being the size of a large herring. Parnell (1838, cited by Yarrell 1859) gave a detailed morphological description from a specimen 14 inches (356mm) in length and stated that powan occasionally grew to 16 inches (406mm). Lamond (1911) recorded a specimen of 17 inches (432mm) and 1 pound 3 ounces (539g) in weight. Individuals of 2 pounds (907g) were "not uncommon" (Lamond, 1931). Comparison of these fish with the largest powan caught during the present sampling programme (Table 6.1) suggests that the maximum size has altered little.

An opportunity to compare present growth rates with those of earlier Loch Lomond powan was provided by Dr P.S. Maitland, who generously lent scales which had not been previously analysed. The scales originated from a ring-netted sample taken at Inchfad in July 1952 by the late F.W.K. Gervers (39 fish), and from samples taken at spawning time (December to January) by P.S. Maitland in 1965-66 and 1966-67. The 1965-66 fish were collected from various localities: Arrochymore (45), McDougall Bank (40), Tarbet (41), and Rudha Ban (48). The 1966-67 fish were caught at the Ross Islands (72; Fig. 1.2). Benthic gill nets with mesh size ranging from 19-40mm were used in both years (Maitland, 1967). In addition to weight and sex, total length was recorded for the 1952 sample; fork lengths for the 1965-67 samples. These were converted to total lengths on the basis of a regression analysis of total length to fork length of 300 Loch Lomond powan caught from May 1984 to May 1985:

$$\text{Fork length (mm)} = 0.877 \times \text{total length} + 1.873$$

$$r = 0.998$$

The methods of back-calculation and validation were as described in Ch. 2.1. Regression analyses of body length to scale radius gave the following results:

Sample	Number	y-intercept (a)	Slope (b)	Correlation coefficent (r)
1952	39	223	29.9	0.57
1965-67	246	121	63.4	0.83

1952 sample. It is not known from what region of the body these scales were removed, but their variability in size and shape suggests that they did not come from any standardized position. The body-scale regression intercept was unacceptably high, and the correlation coefficient was low. It was decided to use the 106mm intercept derived from the standard scales of 1980-86 (Ch. 2.1) for back-calculation, and this resulted in a surprisingly close correspondence between the back-calculated lengths and measured lengths of the same fish (Table 6.2a). Only at age 3 was there a significant difference, which could be because the sample was taken in July, by which time the young fish in particular have already begun their season's growth (Ch. 2.1.4). However, it would be unrealistic to ascribe much validity to results from these fish.

1965-67 samples. These scales were taken from the shoulder region and the 121 intercept obtained from the body-scale relationship was similar to that derived for shoulder scales of 62 fish in the May 1986 sample (129; Ch. 2.1). Back-calculation of lengths was carried out using both the 121 intercept and the 106 intercept derived from the standard scales. When compared with measured lengths at age, there were significant differences in the 2, 3 and 6 year old fish and also in the 4 year olds when the 121 intercept was used (Table 6.2b,c). Since the 106 intercept gave marginally better correlation with measured length it was used in comparisons and growth rate calculations.

Because of the poor correlation, samples for 1965-66 and 1966-67 were analysed separately and the calculated lengths at age from the 1966-67 sample compared with the measured lengths at that age of the same year-classes in the previous year (1965-1966; Table 6.3). The correspondence was improved, except (inexplicably) in the 6 year olds, so indicating that the initial poor correlation when compared overall (Table 6.2b) was due to a change (decrease) in growth rate in the two years.

Growth from 1952-1986. Both the measured and calculated lengths of the 1980-86 fish were significantly higher than the 1965-67 and 1952 fish (Fig. 6.1, Table 6.4). Comparison of the growth rates (Table 6.5) showed that growth rates of the 1965-67 powan were significantly lower than those of the 1980-86 powan in the first three years of life, but that there were no significant differences in later years (apart from 5 year olds). The growth rates of the 1952 fish were significantly lower than the 1980-86 fish in their second and third years only. There were no significant differences in growth rates between the 1952 and 1965-67 powan.

The 1965-1967 samples were collected prior to the population crash of 1968 associated with fungal infection and 'bald spot disease' (Ch. 2.3). Before the crash, powan were very abundant (D.B.C. Scott pers. comm.) and during the crash were described as being small and of poor quality (Roberts *et al.*, 1970). Therefore the small size and decreased growth rate noted from the growth calculations are consistent with these observations, and so are part of year to year variability (Ch. 2.2), and not a permanent long term change.

So the growth characteristics of Loch Lomond powan appear to have remained remarkably constant over a long period of time. This is despite increasing human influence (Maitland, 1972a; Maitland et al., 1981b; Hamilton, 1988). In the past twenty years, recreational use of Loch Lomond has increased considerably, particularly water use (Plate 43). Loch Lomond is within easy reach of Glasgow and its suburbs (Fig. 1.1). The eastern side of the loch from Balmaha to Rowardennan is the most frequented by long stay tourists and day-trippers since it has more amenities in the form of beaches, boat-launching sites, camping areas, car parks and walks (Tivy, 1979). On busy days, overspill from car parks park on beaches and along one or both road verges, causing blockages on an already narrow road. Increasing tourist pressures on the east side are illustrated by the fact that in 1973 there were four peak days when parking was at or over capacity; in the poorer 1978 season, there were eleven (Tivy, 1979). More recently, on at least two occasions in the past two years, the eastern road was so crowded that it had to be closed to non-residents (R. McMath pers. comm.).

Intensive tourist pressure brings attendant problems of damage, erosion of beaches and paths by wheels and feet, conflict between recreational pastimes, and pollution of land and water. The west coast road (A82) is a main road to the north-west of Scotland, and is extensively used by through traffic. It has fewer recreational amenities, and tourists are generally "in transit" (Tivy, 1979). For some distance, the busy A82 closely follows the loch shoreline

(Fig. 1.1). Consequently it is narrow and twisting with sharp bends round rocky outcrops and with inadequate lochside crash barriers, and so is a slow and dangerous road to use. Major improvements to the route are now underway, involving extensive and environmentally disfiguring blasting of the outcrops (Plate 44) and dumping of large amounts of rubble along the lochside to widen sections of the existing road. Rubble and debris are also being dumped in the loch itself (Plate 45), a procedure causing concern (Hamilton, 1988). At present, dumping is not near known powan spawning areas, but increased silt levels may be a risk.

Perhaps the greatest threat to the future of the Loch Lomond powan at present comes from the recent introduction of the ruffe, Gymnocephalus cernua (L). Previously its most northerly habitat was Teeside, England (Maitland, 1972b). Loch Lomond is renowned for large pike and it is likely that ruffe were introduced as live bait by pike fishermen. Incidentally, ruffe were not recommended as pike live bait by Gay (1975) as he failed to catch pike with them despite extensive use. The first specimens of ruffe were discovered in the loch in 1982 (Maitland et al., 1983). Since then numbers have increased drastically. Table 6.6 (on next page) shows (a) numbers of ruffe caught on trash screens of the water supply intake works at Ross Priory (from Maitland & East, 1989) also (b) catches in routine gill net samples during the present study.

Table 6.6

(a)	1982	1983	1984	1985	1986	1987
No. ruffe	17	47	406	2021	795	1286
% of total fish catch	8	19	56	76	63	92

(b)	1984	1985	1986	1987	1988
Total no. ruffe for year	2	64	109	99	3 (June)
No. during April/May (spawning)	2 (May)	52 (May)	57 (May)	67 (April)	

Murphy (1988) found that 92% of the ruffe in the Sallochy area (Table 6.6b) were hatched in 1983 and 1984. 62% of the ruffe were members of the 1983 year-class, signifying a population explosion in that year. Also present were the 1982 (1%) and 1985 (6%) year-classes. Ruffe are major predators on eggs (Fedorova and Vetkasov, 1974) and large depredations on whitefish eggs in Russia have been noted by Pokrovskii (1962; Ch. 2.3, p. 123). Although ruffe in Loch Lomond are known to feed extensively on powan eggs (Murphy, 1988; C. Adams pers. comm.), there is no evidence as yet that the abundance of powan is being reduced by ruffe. 1984 was a strong powan year-class, and 1985 appeared weak (Ch. 2.3), but all growth processes in 1985 were reduced, almost certainly because of scarcity of food (Ch. 5.2). Nevertheless, there is real cause for concern.

Loch Eck, although smaller, less well known and less scenic than Loch Lomond, was rated among the top ten Scottish lochs in terms of proximity of shore line to a major road (Fig. 1.1), and the number of recreational facilities relative to loch size (Tivy, 1980). Being smaller, its capacity to withstand the effects of tourism is less. Results of this study indicate that Loch Eck is the less stable of the two populations, shown by their changing sex-ratio, greater variations in year-class strengths, spawning times, and (possibly), growth rates compared with the Loch Lomond powan. Therefore the Loch Eck population is potentially at greater risk from adverse influences. P.S. Maitland and A. Lyle (Fish Conservation Centre, Stirling), are currently attempting to introduce powan into other waters as an insurance against total extinction, as has occurred to the other Scottish whitefish, the Lochmaben vendace C. albula (Maitland, 1966; P.S. Maitland pers. comm.).

Regular monitoring of powan growth processes may warn of adverse influences, but in most cases, by the time the effect is noted, the damage will have been done. The ruffe is a case in point. Although movement of fish species between different water bodies is prohibited in England and Wales, it is not yet illegal in Scotland. There is a real need to control and minimize the increasing human impact on the lochs if the original two populations of this rare Scottish fish are to be conserved.

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