THE BIOLOGY OF THE ARCTIC CHAR, *SALVELINUS ALPINUS* L., OF LLYNNAU PERIS AND PADARN; WITH SPECIAL REFERENCE TO THE DINORWIC RESERVOIR SCHEME.

Thesis submitted in accordance with the requirements of the University of Liverpool for the Degree of Doctor of Philosophy

by

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September 1980

Frontispiece. Arctic char from Llyn Padarn in spawning colouration. Female above, male below.

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CHAPTER ONE INTRODUCTION

1. Description of Char*

The arctic char, Salvelinus alpinus (Linnaeus 1758), is a member of the genus Salvelinus (Richardson 1836), which is one of the nine genera comprising the family Salmonidae, which includes the trout, salmon, grayling and whitefish. Salvelinids may be separated from members of the genera Salmo and Oncorhynchus by the arrangement of the teeth on the vomer, the bone in the middle of the roof of the mouth; the teeth are restricted to the head of the vomer in Salvelinus, but in the other two genera they are on the shaft as well during early life. The body shape of char is typically troutlike, but they can easily be distinguished from trout by their smaller and greater number of scales, and they typically have a pattern of light markings against a dark background as opposed to dark markings against a lighter background in trout.

The colouration of arctic char is extremely variable, depending on age, sex, locality and mode of life, but throughout most of the year they are a drab silvery colour with white flecks laterally and dorsally. At the approach of spawning, in some populations, most of the males and some of the females assume a brilliant colouration, becoming dark green or blue-green dorsally and bright orange-red ventrally. The anterior edges of the pectoral, pelvic and anal fins may also be delineated with a bright white strip. This colour change is most spectacular in anadromous

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* It is debatable which spelling 'char' or 'charr' is correct; the latter apparently being original. I have used 'char', which is the most common usage.

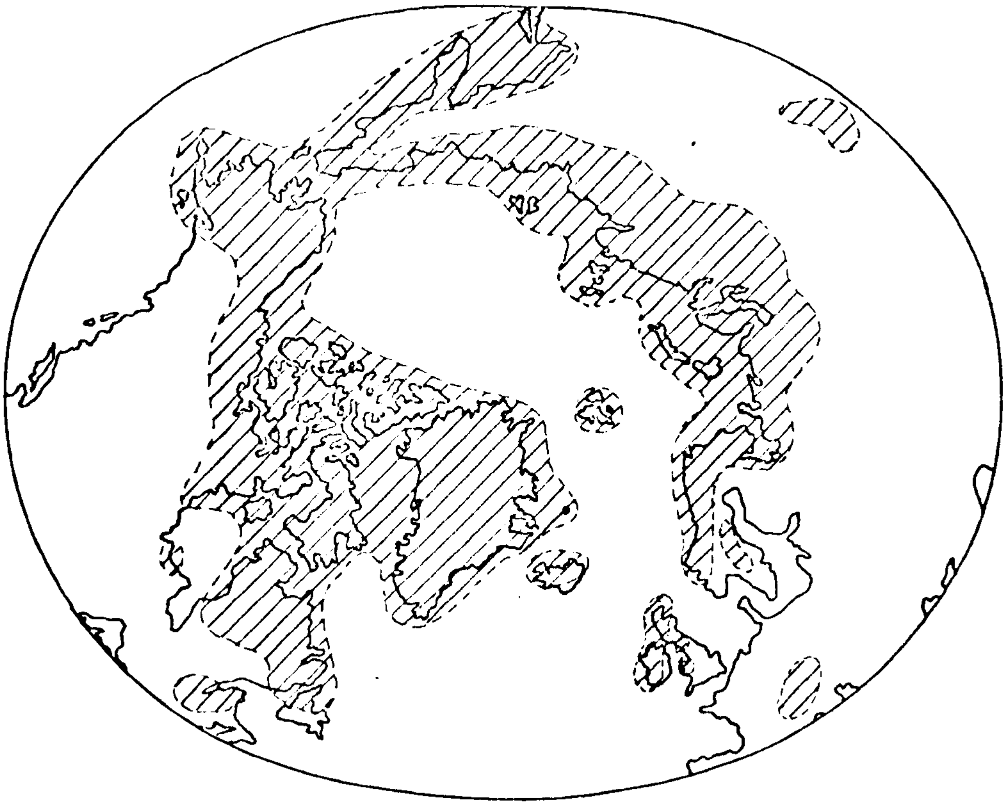
populations,but often occurs,perhaps to a lesser extent, in some non-anadromous forms, e.g.Llyn Padarn (see frontispiece), but there may be little or no colour change in others, e.g. Llyn Peris.

1.2 Distribution of Char

The arctic char has a virtually circumpolar distribution in the Northern Hemisphere (Fig.1.1) and ranges further North than any other freshwater fish, to the limit of land (Scott & Crossman, 1973). Anadromous populations occur in Alaska, northern Canada, Greenland, Iceland, northern Scandinavia and northern USSR, as well as numerous arctic islands. Non-anadromous populations are also common in this area, and often found existing sympatrically with the migratory form. The southerly limit of the anadromous habit corresponds roughly with the 45°F average sea surface isotherm. Below this range, isolated freshwater populations occur; principally in northeastern America, Sweden, the British Isles, the Alpine region of Europe and central USSR. They remain as relicts from when the anadromous populations ranged much further South during the last ice-age.

The British Isles, especially Scotland and Ireland, have probably the biggest concentration of arctic char populations in the world (Friend, 1959). They have been recorded from over 100 lochs in Scotland (Friend, 1959), being found predominantly in the Highlands, but also in the Southern Uplands and the Western and Northern Isles. In a more recent study, Campbell (1979) noted their presence in 88 lochs, but this was by no means exhaustive. Went (1946) reported them from up to 45 loughs in Ireland, mainly in the western maritime counties. They are present

Fig.1.1 The World distribution of arctic char.



in about 12 lakes in the English Lake District; principally Coniston, Windermere, Bassenthwaite, Wastwater, Ennerdale, Crummockwater, Haweswater, Buttermere, Loweswater and Goatswater; and four, Llynnau Bodlyn, Cwellyn, Peris and Padarn, in Wales (Figs. 1.2 and 1.3). The full distribution in the British Isles is still uncertain. Two new localities were found in Scotland during the 1950's, Loch Eck and Loch Luichart, (Friend, 1959), and a number of populations have become extinct in recent times (see page 154).

Populations of char in the British Isles are typically found in large, deep oligotrophic lakes, often together with other salmonids, but they have been occasionally recorded from small or shallow lakes. Typical extremes of depth are such as Loch Morar (maximum depth 314.5m) and Loch Borallan (maximum depth 7m). Factors which affect whether or not char are present in a particular lake are not known; there being perhaps no char in an apparently suitable lake although they may be present in others nearby. Toivonen (1972) considers that shallowness and brown colouration of the water, due to humic colloids, together with the presence of large numbers of other fish species, are contributing factors to the absence of char in otherwise suitable Fenno-scandian lakes, but this is apparently not true for the British Isles. A more complete knowledge of the watersheds during the last ice-age would perhaps help to explain the present distribution of char.

Anadromous arctic char are of commercial importance in many parts of its range, such as northern Canada, Greenland and northern USSR, and in certain areas they may be suffering from overfishing (Dempson and Best, 1976; Dempson, 1978). Non-anadromous populations are only of significant importance in Sweden and some lakes in the European Alps.

Fig. 1.2 The distribution of char in the British Isles.

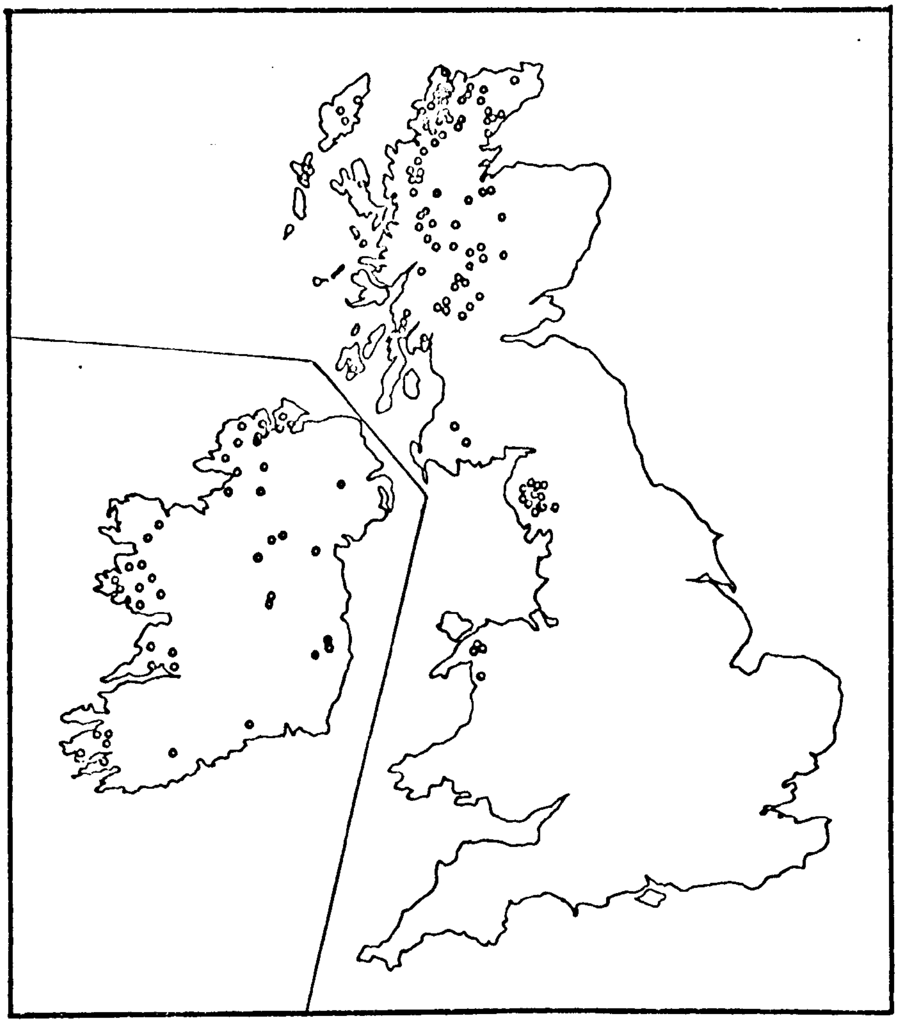
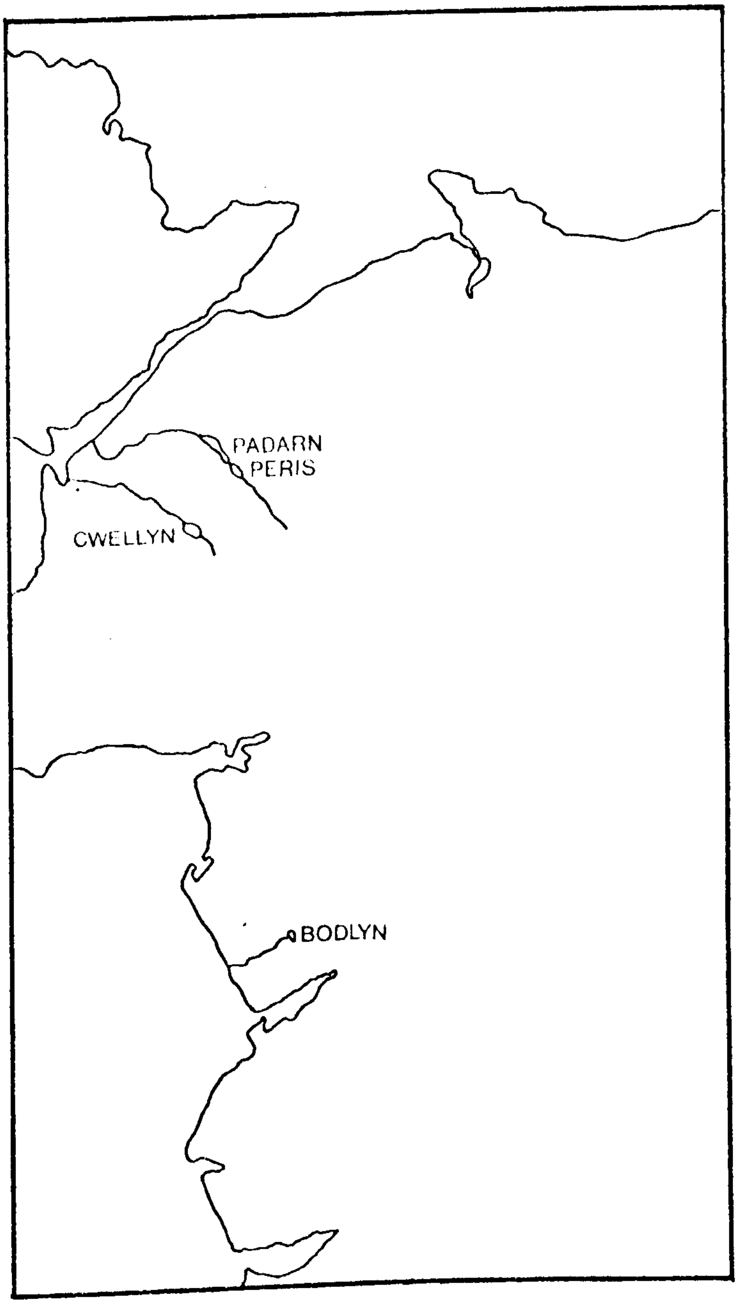


Fig. 1.3 The distribution of Welsh char populations.



In the latter area char have been planted in many lakes to increase the stocks (Steiner and Pechlaner, 1974). There are no commercial fisheries other than of very local importance in the British Isles, although, until the Salmon Acts of 1873, char were netted in large numbers from the spawning beds of Windermere (Kipling, 1972) and Llyn Peris. It is a popular sport fish in many parts of the world, but because of its relatively small size and the specialised techniques required to catch it on rod and line, it is not greatly prized in most parts of the British Isles.

1.3 Aims of the Study and the Dinorwic Pumped Storage Scheme

Despite the large number of arctic char populations in the British Isles, little is known of its biology. Only the Windermere (Frost, 1945a;1951; 1952; 1955; 1963; 1965; 1977; 1978; Frost and Kipling, 1980; Kipling, 1957; Kipling and Frost, 1978; LeCren and Kipling, 1963; LeCren et al., 1972) and Welsh populations (Powell, 1966; Sullivan, 1975) have been studied in any detail; other works have dealt mainly with its taxonomy (e.g. Gunther, 1862; Day, 1887; Regan, 1908; 1909a; 1909b; 1911; 1914; Friend, 1959) or its relationship with ferox trout (Hardie, 1940; Campbell, 1979). This present study was undertaken to supplement the work carried out by Powell (1966) on the Llanberis char and, in particular, to assess the effects of a pumped storage reservoir scheme on the populations. The scheme was changed during the early stages of this study, which also caused alteration in the aims of the study. These are described below.

Llyn Peris was chosen as the lower reservoir of the Dinorwic hydro-electric pumped storage scheme. Marchlyn Mawr, a smaller lake to the northeast of Llyn Peris and 503m higher, will be the upper lake. Water will be pumped from the lower to the upper reservoir when demand for electricity is low and returned to the lower reservoir, driving water turbines and generating electricity, when demand is high. On completion, the scheme will be able to replace 1320MW within 11s of demand (Anon., 1976). A system of tunnels will connect the two lakes (Fig. 1.4) and the turbines themselves will be underground. Llyn Peris will be isolated from the present water system, except during conditions of high flow; the inflowing stream, Afon Nant Peris, being diverted directly into the outflowing stream, Afon-y-Bala, by an underground tunnel 2.2km in length (Fig. 1.5). Rogers and Cane (1979) provide details of the construction and dimensions of the tunnel.

The original scheme involved raising the water level of Llyn Peris by constructing dams 11.5m in height and enlarging the lake by removing slate and rock waste. The water level would fluctuate between 97.5m O.D. and 111.0m O.D. The effects on char of lake regulation is well documented from studies in Scandinavia (Runnstrom, 1951; 1964; Nilsson, 1961; 1964; and others). These are mainly the loss of spawning beds and a reduction of the littoral, benthic and planktonic fauna, resulting in increased competition with brown trout for the remaining food. Therefore the study was originally aimed at distinguishing the spawning sites and examining the available food to try and assess its probable alteration.

However, due to local representation, the plans for the scheme were altered, the main change being a lowering of the dams from a height of 114.5m O.D. to 107m O.D. This would reduce the minimum water level to

Fig. 1.4 Diagram of the relationship between Marchlyn Mawr and Llyn Peris, and their interconnecting tunnel.

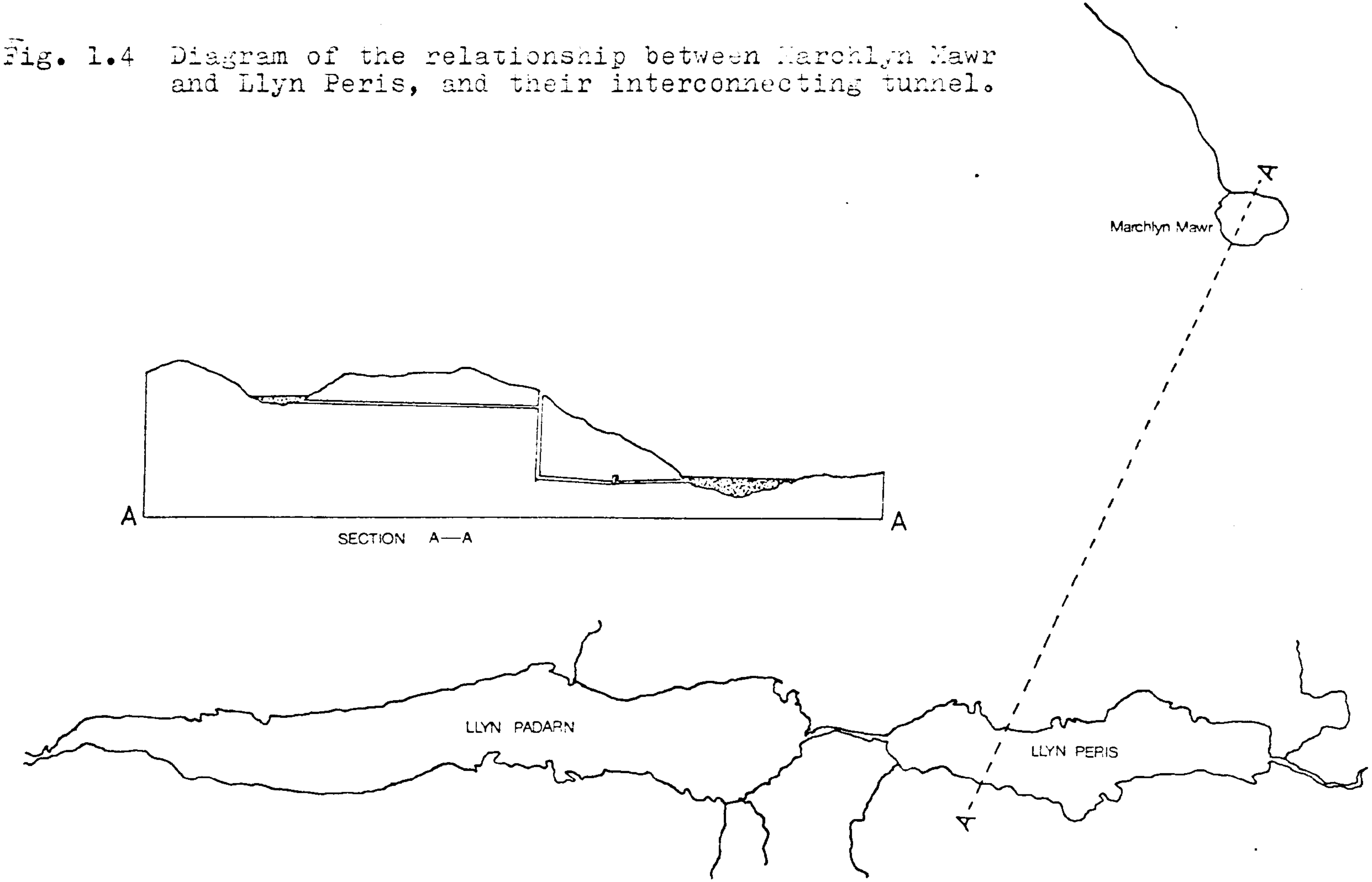
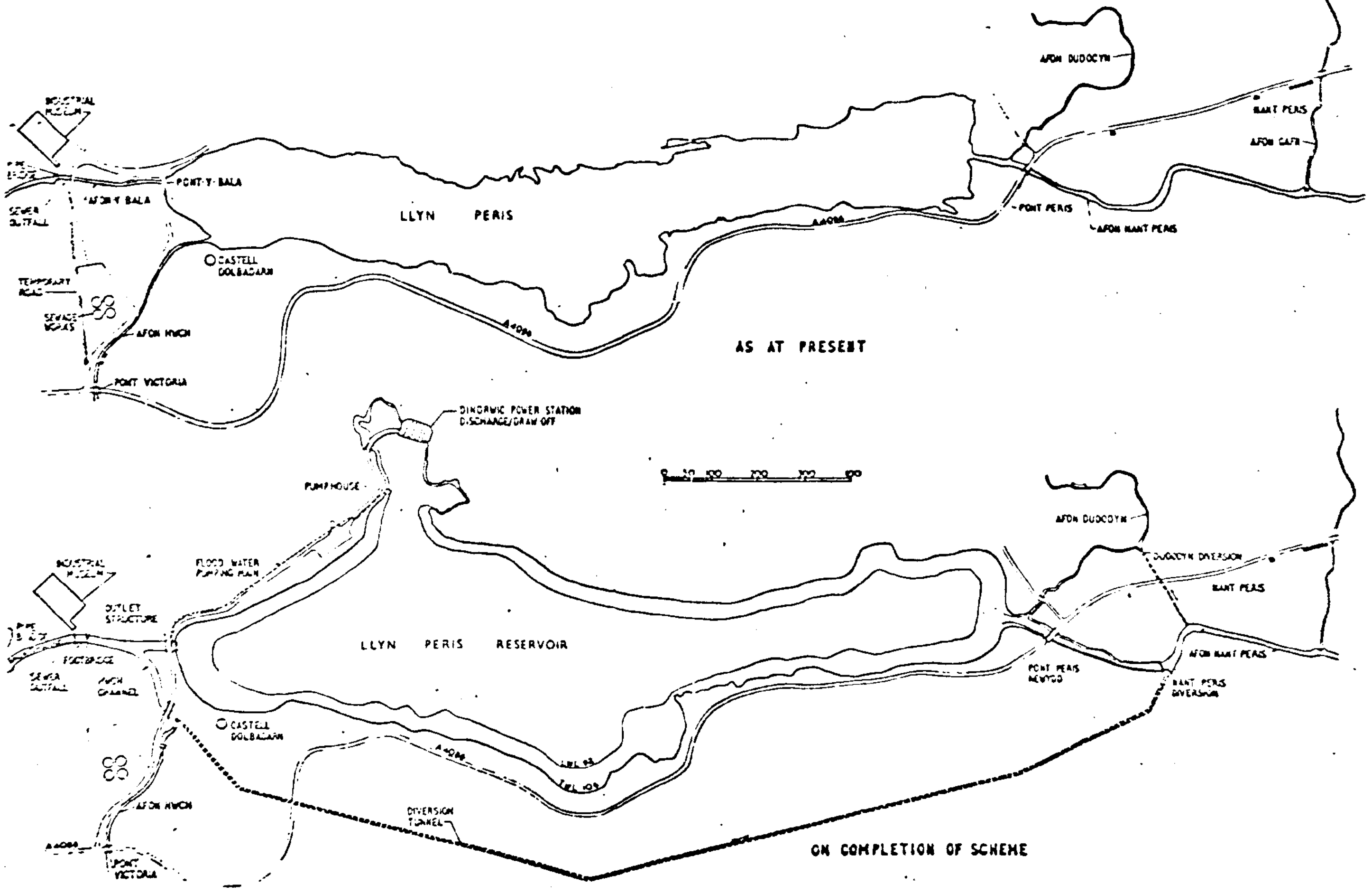


Fig. 1.5 Plans of Llyn Peris before and after completion of the scheme.



92m O.D. which was calculated to be below the height at which silt would be sucked into the pumps from the bed of the lake. It was therefore decided that it was necessary to drain Llyn Peris and to infil it to a depth of 90m O.D. using 2.5 x $10^6 m^3$ of slate waste. The lake would further be enlarged to 57ha (Fig. 1.5). The minimum water level would then be only 2m in depth. This drastic fluctuation in water level, with the resultant loss of littoral, benthic and planktonic fauna, the loss and continued exposure of spawning beds and a rise in the water temperature by 10^oC above ambient, would certainly result in the extinction of the char population, even if attempts were made to restock on completion of the scheme.

It was originally thought that the scheme would have no effect on the char population of Llyn Padarn, which connects with Llyn Peris via a short stream (see Chapter 2). However, preliminary results from gill net catches in Llyn Peris indicated that there may have been a migration of char from Llyn Padarn into Peris for spawning. Such a movement was described by Day (1880-1884), and Powell (1966), although she was unable to confirm it, thought it possible. The aims of this study were therefore altered, and it was decided to concentrate on aspects of the biology of Llyn Peris char not examined in detail by Powell (1966), particularly the reproductive biology, and to determine whether the migration existed, and if so, what proportion of the Llyn Padarn char were involved. The meristic and morphometric characters of both populations were also examined, together with those of Llyn Cwellyn char, to study their relationship.

CHAPTER 2 DESCRIPTION OF THE STUDY AREA AND FIELD METHODS

2.1 The Study Area

Llynnau Peris and Padarn are interconnected lakes lying at the bottom of the Llanberis pass, 13km east of Caernarvon, Gwynedd. They are situated in a deep pre-glacial basin, running approximately south-east to north-west, containing Pre-Cambrian lavas and Ordovician states. The valley has been extensively modified and scoured by glacial action.

Llyn Peris is the upper of the two lakes and is a typical cold, deep oligotrophic lake. It has a maximum length of 1.76km and a maximum width of 0.34km and the height of the water surface is 103.5m O.D. A hydrographic survey carried out for the Central Electricity Generating Board in 1970 (Fig. 2.1) differs from that published in 1886 (Fig. 2.2) in that a thick ridge of silt has been deposited across the middle of the lake. This effectively separates the lake into two basins; a relatively shallow one, maximum depth about 24m, at the southeast, and a deeper one, maximum depth 34m, at the northwest (Fig. 2.3).

The northeastern shoreline of Peris is artificial, consisting of waste slate from the Dinorwic quarry which has encroached into the lake, considerably reducing its area. The southwest shore is of steep cliffs, falling rapidly into deep water , except for a relatively shallow bay towards the south-eastern end. The extreme ends of the lake have the only large areas of natural stony substrata. Samples of the lake bottom taken by grab showed it to be composed predominantly of slate flour.

Fig. 2.1 LLYN PERIS HYDROGRAPHIC SURVEY

BATHYMETRIC CONTOUR PLAN

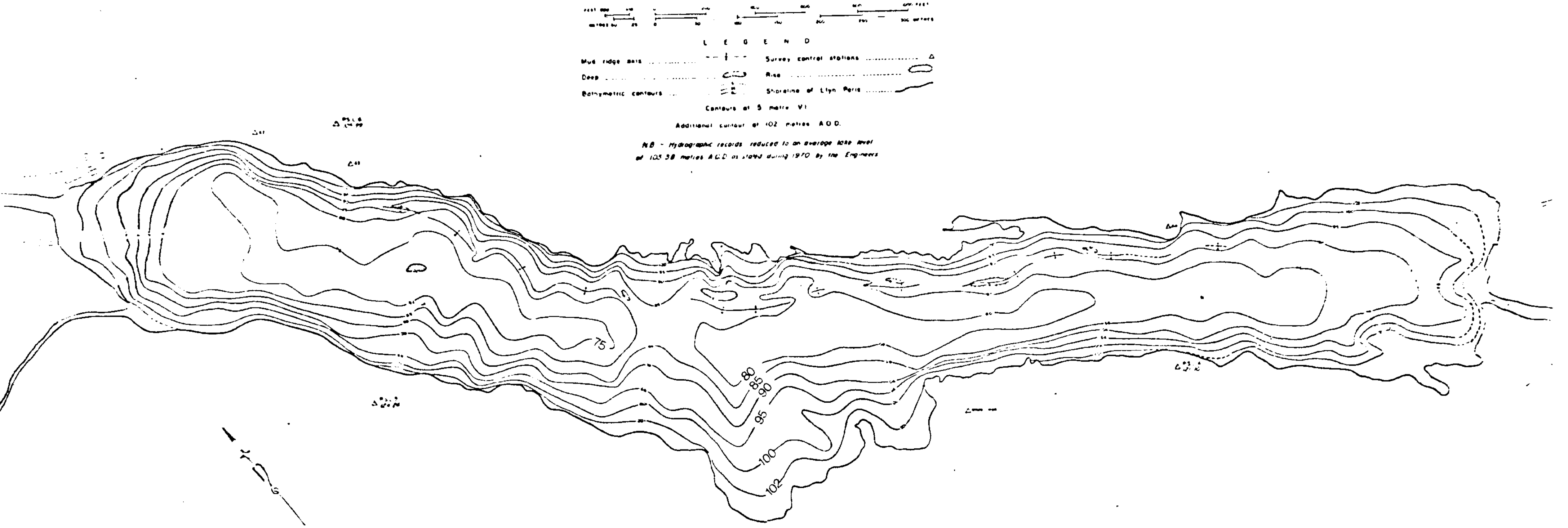


Fig. 2.2 Bathymetric survey of Llyn Peris and Llyn Padarn, 1886. Depths in feet below normal surface level.

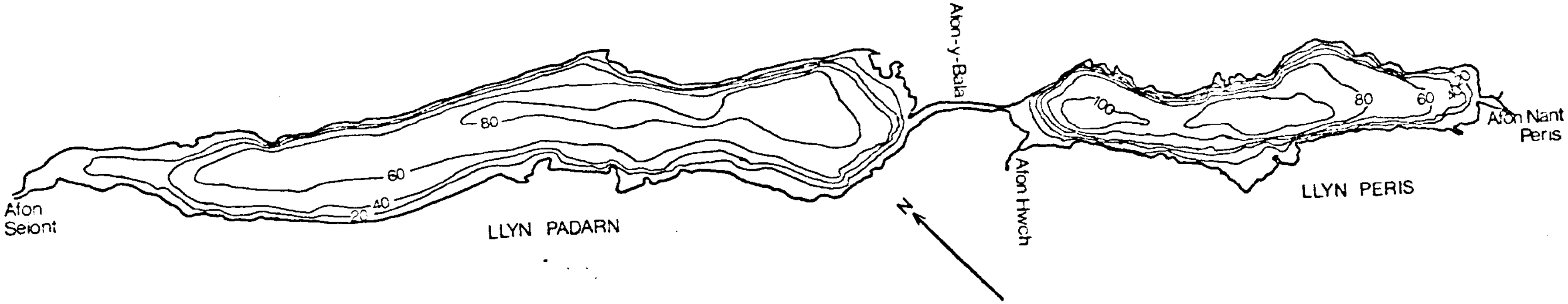
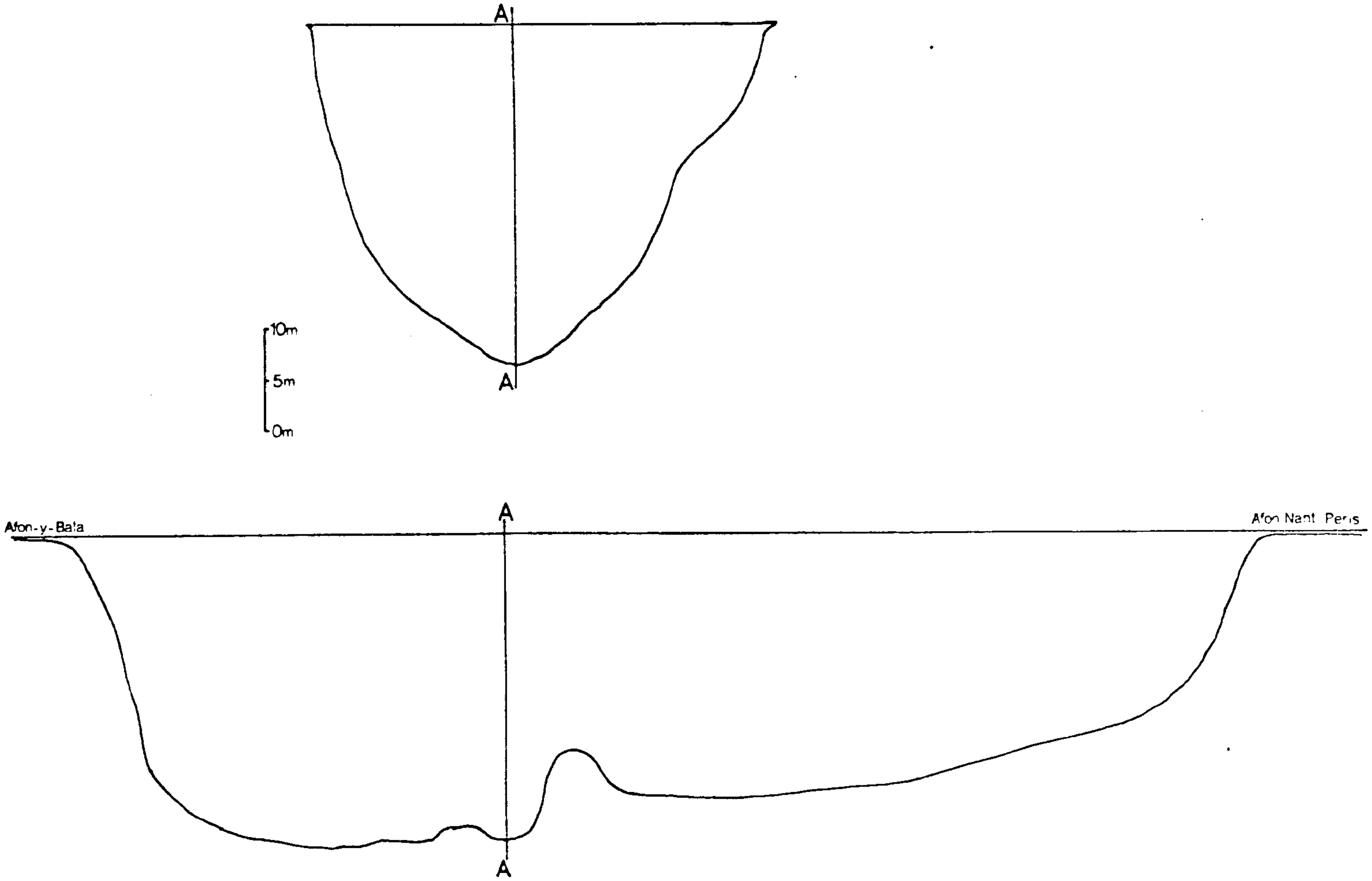


Fig. 2.3 Longitudinal and cross-sectional diagram of Llyn Peris



Llyn Padarn is a larger, shallower lake with a length of 3.2km and a maximum width of 0.53km, and a water surface level of 103.4m O.D. It is mesotrophic in character, mainly due to the effects of treated sewage, which is discharged into the lake via the interconnecting stream, the Afon-y-Bala, and a greater incident light intensity, which is due to the greater amount of mountain shading suffered by Llyn Peris (Pentecost and Happey-Wood, 1978). No recent hydrographic survey has been carried out on Llyn Padarn, but that of 1886 (Fig. 2.2) was shown to be substantially correct by echo-sounding during the present study and by Powell (1966). The maximum depth of the lake is approximately 29m. The northeast and southwest shorelines are almost completely artificial, having been walled up into railway embankments. There is a long stretch of gently shelving shoreline extending from the mouth of the Afon-y-Bala to the Afon Goch, as there is near the outflowing stream, the Afon Seiont, which eventually enters the Menai Strait at Carnarvon.

The two lakes drain a watershed of about 48km^2, and they are the remnants of a much larger body of water which originally extended from Gwastadnant in the southeast to Cwm-y-Glo in the northwest, a distance of about 5.94km. The lakes became separated in recent times by the deposition of sediments brought down by the Afon Hwch, which now enters Llyn Peris at its northeast corner.

The lakes are fed by four main streams. The Afon Nant Peris drains the Llanberis pass and enters Llyn Peris at the extreme southeast end. A major tributary, the Afon Dudodyn, drains from the east and enters the Nant Peris near its estuary. The Afon Arddu rises on the northern slopes of Snowdon and joins with the Afon Huch, which drains Llyn Dwythwch and enters the bottom end of Llyn Peris. The Afon Goch and Afon Fachwen enter

Llyn Padarn from the southwest and northeast respectively.

Despite their interconnection and close proximity, the two lakes differ markedly in their primary productivity; Llyn Padarn having a 3.4 times faster production rate than Llyn Peris (Pentecost and Happey-Wood, 1978). As has been mentioned, this is mainly a result of the treated sewage effluent, which raises the phosphorus content, but the higher incident light intensity and temperature is also contributory. The higher primary productivity in Llyn Padarn is also reflected, as might be expected, in the greater quantity of the zooplankton, particularly the larger species such as Diaptomus gracilis and Leptodora kindti. The benthic fauna also differs, with Pisidium and chironomids being dominant in Llyn Peris and oligochaetes in Llyn Padarn, although the biomasses are similar (Pugh-Thomas, 1975). This difference in the bottom fauna is possibly related to the nature of the lake beds; that of Llyn Peris being composed primarily of slate flour.

Rooted plants are sparse in both lakes, being restricted to stands of Isoetes, Glyceria and Littorella. The artificial and steeply-shelving shorelines are completely devoid of rooted vegetation; it being restricted to the extreme ends of both lakes and to some relatively shallow bays.

The fish populations of both lakes is the same, comprising arctic char, brown trout and sea trout (Salmo trutta L.), salmon (Salmo salar L.), minnow (Phoxinus phoxinus L.), three-spined stickleback (Gasterosteus aculeatus L.) and the eel (Anguilla anguilla L.).

2.2. Field Methods

2.2.1 Fishing Techniques

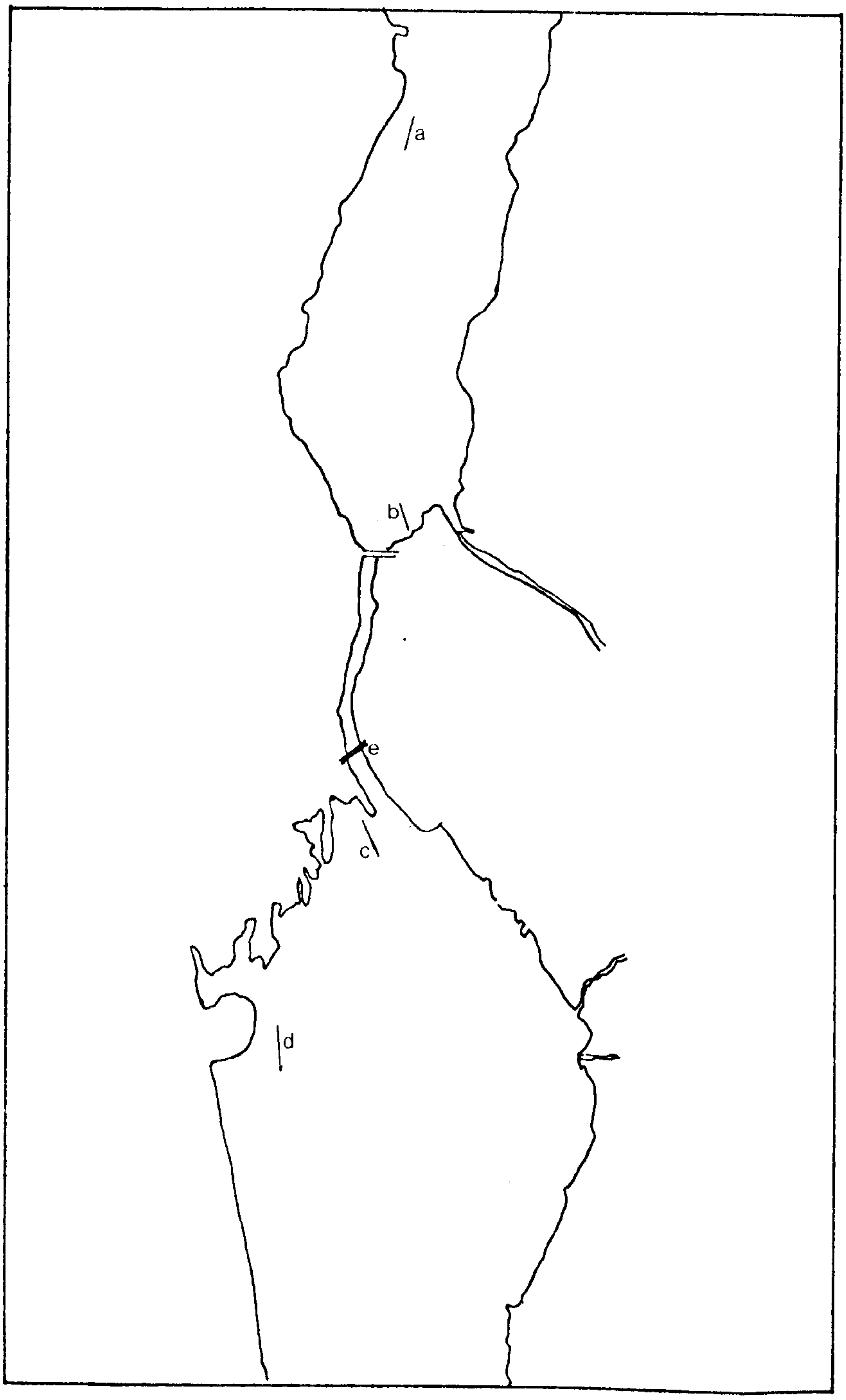
A variety of fishing techniques were tried in an attempt to catch representative samples of char throughout the year.

Bottom set gill nets. Gill nets were set to fish near the bottom at weekly or fortnightly intervals between October and January, and monthly at other times of the year from November 1973 until January 1976 in Llyn Peris, and from September 1974 until January 1976 in Llyn Padarn.

Gill nets are highly selective for size of fish (e.g. Olsen, 1959; McCombie and Fry, 1960; Von Brandt, 1974). Accordingly, a large range of gill nets were tried, varying from 9mm to 29mm mesh, knot to knot. Small mesh nets are inefficient and highly selective (Heard, 1962), and it was found that nets of less than 19mm mesh rarely caught fish in any quantity. 24mm mesh nets caught the largest size range of char, larger mesh nets catching very few even though many larger trout were captured. It was therefore decided to use nets of 19mm, 21mm and 24mm mesh, each 30m in length by 2m deep, as combined "standard" units. These were set at two fixed sites in each lake throughout the year to enable comparisons of catch per unit effort to be made. The location of these sites is shown in Fig. 2.4. Site B and C were in shallow water (less than 5m in depth) and sites A and D were in deep water (greater than 20m). Site B (shallow water; Llyn Peris) was discontinued in January 1975, but site A sampling continued primarily to obtain information on the gonad development of the char, but the data were also used for growth studies.

The "standard" units were supplemented by others of the same mesh, and

Fig. 2.4 The fixed gill netting sites of Llyn Peris and Llyn Padarn. a; deep water, Peris, b; shallow water, Peris, c; shallow water, Padarn, d; deep water, Padarn. Site e is the fyke net site.



by smaller mesh nets, principally 9mm and 12mm mesh, to obtain sufficient samples and to examine the distribution of char throughout both the lakes. In the summer months, May to September, char were difficult to catch in bottom set gill nets, and many had to be set to catch a representative sample of char.

The gill nets were normally fished overnight, for periods between 12 and 18 hours.

Surface and Midwater Gill Nets

Gill nets were occasionally set to fish on the surface, using larger floats on the top line, but they rarely caught char in significant quantities.

To try and assess the vertical distribution of the char, two methods of setting gill nets in midwater were attempted. The first used nets set to fish horizontally, the depth set by using a series of buoyed lines attached at intervals along the float line of a sinking gill net. The variable winds caused these nets to twist badly, and they never caught char. The other method was to set the nets vertically. The technique used was similar to that described by Lackey (1968), with the nets supported by large buoys on the surface and heavily weighted at the bottom for stability. To stop the nets from collapsing inwards, spreaders of cane were attached at the top and bottom and at 5m intervals between. They were only set at irregular intervals, but they never caught sufficient char to allow meaningful analysis.

Seine Nets

The precipitous and artificial nature of the shoreline rendered the majority of both lakes unsuitable for seine netting. The only suitable areas were those shown in Fig. 2.5, at the extreme ends of each lake. A straight walled net 55m in length, 4m deep, with a mesh of 30mm (knot to knot) in the arms and 10mm in the centre, was used.

Many attempts were made throughout the year to capture char from the shore during daylight. None were captured, although large numbers of trout were taken. LeCren and Kipling (1963) described the capture of large numbers of char from Lake Windermere by seine netting the spawning grounds in late Autumn, during the dark. This was tried at station 1 in Llyn Peris and station 3 in Llyn Padarn at irregular intervals during November and December. A number of char were caught at station 3, which were presumably about to ascend the Afon-y-Bala (see Chapter 5), but few were caught at station 1.

Electric Fishing

A 240v, 300 watt, A.C. generator, with semi-rectified output, was used to sample the Afon-y-Bala from November to January, and occasionally in the Afon Nant Peris and Afon Hwch. No char were ever caught, although brown trout, sea trout and salmon were taken regularly.

Fyke Nets

Standard eel fyke nets were set in the Afon-y-Bala from November 1974 to January 1975. They were laid at an oblique angle across the river to

Fig. 2.5 The seine netting sites of Llyn Peris and Llyn Padarn (stippled areas)

minimise the effects of the water current on them, and, despite being washed out by heavy floods on a number of occasions, large numbers of char were captured. The catch was enumerated, measured, the state of maturity noted (whether ripe, running ripe or spent), tagged and released above or below the trap depending on the direction they were travelling. Those caught in an upstream pot (the mouth of the fyke directed downstream) were assumed to be moving upstream and vice versa. This assumption, which is one used in the design of fixed traps (e.g. Shetter, 1938), was tested by marking a number of fish that were assumed to be moving upstream and releasing them downstream of the fykes. On recapture, they were invariably in an upstream pot. Small samples of fish were also taken for more detailed examination.

The original fyke nets were constructed with knotted mesh, and it was noted that the snout of char became badly abraded by the netting after even a short period of confinement. Knotless netting is known to be much less harmful to fish (Coles and Butterworth, 1976), and new nets were constructed using this material. These were fished during November and December 1975, but, although they cured the abrasion problem, they were unfortunately badly damaged during a heavy flood in mid-December.

Midwater Trawl

A midwater trawl was developed from a design by Ruppe and deRoche (1960), but constructed of knotless netting. This was used successfully in Llyn Tegid (Butterworth and Coles, 1977), capturing large numbers of 0+ and 1+ gwyniad, which had not been previously sampled. Unfortunately, a boat of suitable size to use it in Llyn Peris and Llyn Padarn was not available in time to allow long term sampling, but on the one occasion it was used (February 1976) it did capture 2 one year and 1 two year old char from a depth of 20m, together with large numbers of sticklebacks.

Angling

During the summer and early autumn when char were difficult to catch by gill net, sampling was supplemented by rod and line catches. The method used in the Llanberis lakes differs from that of Windermere (Frost,1977) in that baited hooks are used rather than artificial lures. Char can be caught by fishing from the bank, but it is more efficient from a boat. A weight of about 28g is attached to the bottom of the line, and four side lines are attached at about 1m intervals above it. The hooks are generally baited with maggots, and the tackle is lowered to the bottom of the lake and then slowly raised until a shoal of char is found. Echo-sounding aided the location of the fish, and a large number of fish could be captured in a short time.

2.2.2 Tagging

With the exception of a small number of fish retained for detailed gonad and age examination, all char captured by fyke and seine net were measured and tagged using small, individually numbered, green plastic tags. These were attached by nylon monofilament wire through the hypaxonic muscles beneath the dorsal fin, the fish normally having been narcotized with MS 222 (Sandoz, Switzerland).

Char captured by gill net **were** also occasionally used for tagging. The nets were always retrieved slowly to minimise the effects of pressure changes on the fish. Any char that were relatively undamaged after removal from the nets were immediately transferred to containers of fresh water, and later placed in large knotless keepnets. Those that showed no signs of distress were tagged and replaced in the holding nets. Only those that still exhibited no signs of distress were later released. Char tagged after capture in gill nets have been used for distribution studies (e.g. Alm, 1951), and have also been used for population estimation (Steiner and Pechlaner, 1974). However, Fagerstrom et al. (1969) found tag losses from char to be high and because of this, and the uncertainties over the survival of the char, population estimates were not attempted for the Llanberis population.

On recapture, the tag number, length and place of recapture were noted. Anglers were encouraged to report any recaptures by the offer of a 50 pence reward for the return of any tag with details of capture.

2.2.3 Preservation of Samples

30 Char captured from Llyn Peris in each month from October 1973 until May 1974 were preserved in 10% formalin immediately upon capture. The abdomen was slit to aid penetration of the preservative. Various authors have reported the shrinkage of fish preserved in formalin, including Shetter (1936) and Parker (1963). Powell (1966) found that char shrank to a minimum of 97.3% of their original length after 14 days in formalin. To confirm this, 30 char, of as wide a length range as possible, were measured upon capture and after 14 days in preservative.It was found that they had shrunk by an average of 2.9%. Therefore all char so preserved have had a correction factor of 1.03 added to their length.

All other char captured in Llyn Peris, and all those taken from Llyn Padarn, were immediately transferred to a cool-box and placed in a deep freeze on return to the laboratory, usually within eight hours of capture.

2.2.4 Substrate Sampling

During January 1976, all possible spawning sites of the char, in both lakes and some afferent streams (see Chapter 5) were sampled for deposited eggs. A suction sampler was used, connected to a hand pump. The device consisted of an outer box, 45cm square and 25cm in height, inside which was a flat plate, with holes 0.6cm in diameter around the periphery. The plate was attached to a central tube, 4cm in internal diameter, which was, in turn, connected to the pump. The plate was held off the substrate by bolts at each corner, and the height off the bottom could be adjusted by altering the lengths of the bolts, the plate being free to slide up the outer box. The sampler was placed on the bottom in the desired place, and the pumped water, together with any eggs, was strained through a 2mm mesh sieve. The suction was powerful enough to displace quite large stones. The contents were preserved in 5% formalin for later examination. The sampler had been used successfully for gwyniad (Coregonus lavaretus) ova deposited in the shallows of Llyn Tegid (Coles pers. comm.), and although it was possibly not powerful enough to sample deeply buried eggs, it was sufficient for shallowly buried char eggs.

The names used to describe the substrate sizes of the possible char spawning grounds in Chapter 5 were taken from Welch (1948) and are shown in Table 2.1.

Table 2.1 Classification of Substrate Particles

Diameter of particle in mm.	Name applied to particle
More than 256	Boulder
256-64	Cobble
64-4	Pebble
4-2	Granule
2-1	Very coarse sand
1-0.5	Coarse sand
0.5-0.25	Medium sand
0.25-0.125	Fine sand

The laboratory methods, and some minor field techniques are described in the individual chapters.

CHAPTER THREE THE AGE AND GROWTH OF LLANBERIS CHAR

3.1 Introduction

Nordeng (1961) commented that "correct conclusions regarding a number of biological phenomena in fish are wholly dependent upon a correct age determination. The age determination of the char has hitherto presented considerable difficulty and this may, to a certain extent, be the reason why the biology of this fish is so little known, notwithstanding its wide distribution".

The age determination of salmonids is most often estimated from their scales; the wide bands of the summer rings and the narrow bands of winter rings being, with practice, easily distinguished. No such convention exists with arctic char, and many methods have been employed by workers in an attempt to determine a valid and reliable technique.

Scales have been used by a number of authors, including Dahl (1926); Slastnikov (1935); Dussart (1952); Sprules (1952); Swan (1954); Martin (1955a); Nordeng (1961); Gullestad (1974); Powell (1966); Frost (1978); Frost and Kipling (1980). However, Slastnikov (1935); Nielsen (1961); Nordeng (1961); and Gullestad (1974) did not regard them as suitable indicators of age. Nordeng (1961) compared scale annuli with otolith zonation and found that frequently the first year was missing from the scales. He also found that correspondence between scale annuli and otolith zonation broke down completely after maturation. Gullestad (1974), also comparing scales and otoliths, estimated that the first winter zone was not present on the scales of all char, and that the second zone was not present on 85% of them. Frost (1978), in her study of

Windermere char, found that the first year annulus was missing in some spring spawned char, and for older fish annuli could be missing due to erosion at the edge of the scale or the slow growth rate. Swan (1954) also describes difficulties in reading char scales from various locations. Nielsen (1961) was unable to differentiate any annuli whatsoever on scales from Greenland char. Furthermore, measurements between individual rings, plotted graphically, failed to demonstrate any system for determining annuli which correspond to the zonation found in otoliths.

Because of these anomalies, many workers have used otoliths for ageing arctic char, including Hansen (1940); Sprules (1952); Grainger (1953); Andrews and Lear (1956); Thomson (1957); Nielsen (1961); Nordeng (1961); Powell (1966); LeJeune (1967); Saunders and Power (1969); Hunter (1970); McCart and Craig (1973); Skreslet (1973a); Moore and Moore (1974); McCart and Bain (1974); Craig (1978); Rombough et al. (1978). The validity of the technique has been demonstrated by Grainger (1953); Nielsen (1961); Nordeng (1961); Powell (1966).

In her definitive work on Llanberis char, Powell (1966) considered that, whereas both the scales and otoliths of Llyn Peris char were suitable indicators of age, only the scales of the faster growing Llyn Padarn char were usable.

Most of the detailed work concerning the growth of char has been on anadromous populations, and relatively little on non-anadromous ones. Accounts that have been published on the latter include populations from Scandinavia (Runnstrom, 1951 ; Nilsson and Filipsson, 1971; Klemetsen et al., 1972; Power, 1973), North America (Sprules, 1952; Everhart and Waters, 1965; Saunders and Power, 1969; Hunter, 1970; McCart and Craig, 1973, McCart and Bain, 1974; Craig, 1978; Rombough et al., 1978), France (Dussart, 1952; 1954), Jan Mayen Island (Skreslet, 1973a) and Kamchatka (Savvaitova, 1976a). The only studies relating to British populations are those of the Llanberis lakes (Powell, 1966)and Lake Windermere (Frost, 1951; 1978; Frost and Kipling, 1980).

In this study, the scales and otoliths of Llyn Peris and Llyn Padarn char were examined as to their suitability for age determination and the otoliths were used to determine the annual and seasonal growth of the char.

3.2 Laboratory Methods

Fish examined in the laboratory were measured, to the nearest mm, from the tip of the nose to the fork of the tail and weighed to the nearest gram. A sample of scales was removed from the shoulder of the fish, using a blunt scalpel, cleaned, and mounted dry on a glass side. They were examined under transmitted light using a binocular microscope.

The top of the skull of each fish was removed with an horizontal section to expose the sacculus of the inner ear. The largest of the three otoliths on each side, the sagitta, was removed, wiped clean, and stored dry. Nordeng (1961) found that the otoliths of char became more opaque and difficult to interpret after prolonged periods of dry storage. This was probably due to the penetration of air into the lamellae and can be remedied by heating while immersed in glycerine (Lawler and McCrae, 1961).

For age determination, each otolith was immersed under cresol contained in a black watch glass for 5 minutes and examined with a low power binocular microscope, using reflected light. Thicker otoliths, from older char, required grinding before an accurate age could be assigned, and this was carried out either directly on a 600 grade carborundum stone, or after the otolith had been embedded in methyl methacrylate (Saunders and Power, 1969). If the otolith was still not clear, the other otolith of the pair was burnt in a low flame, broken in half, the broken edge ground to the nucleus and examined (Christensen, 1964).

Measurements of the otoliths for back calculations of growth were made, using a graduated eyepiece, from the nucleus of the otolith along the longest, anterior, axis (Fig. 3.1). Measurements were made to each winter band and to the edge.

3.3 Age Determination

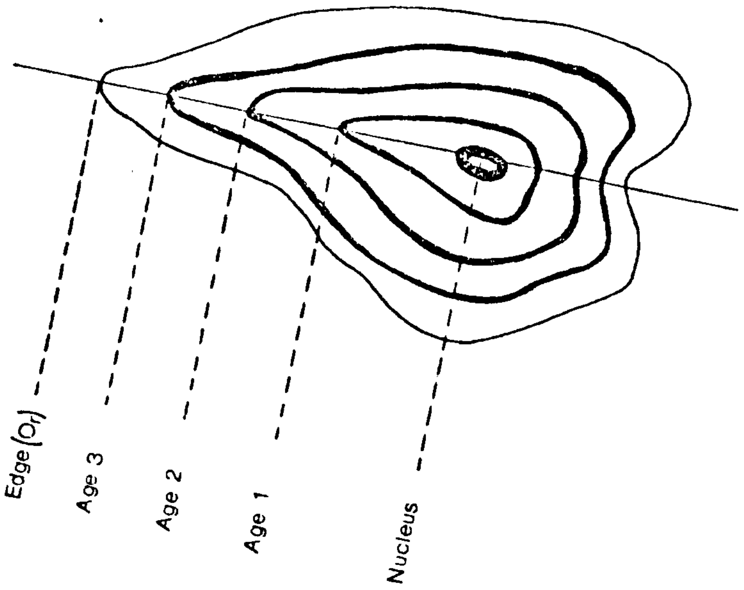
3.3.1 Description of Scales and Otoliths

The scales of char are fragile and about half the size of those from a trout of the same length. Compared to trout scales, the circuli are fewer and more crowded, and more uniform in texture so that the winter and summer bands are not in such clear contrast, and the checks not so obvious.

The validity of the use of scales from Llyn Peris and Llyn Padarn char for age determination has been shown by Powell (1966). She described the following criteria for identifying winter bands:

(1) Winter rings, where present, are closer together than the summer rings.

Fig. 3.1 Diagram of a typical char otolith (sagitta) with three annual rings, showing the measurements taken for back-calculation.



(2) Winter rings look generally less robust than summer rings.

(3) Winter rings are irregular and broken, and the number of rings of this type formed in any one year may be as low as one or two.

(4) Winter rings only rarely extend round the scale margin as do the summer rings. Consequently, the first ring of a summer band usually 'cuts over' the outer ends of the incomplete rings of the previous year's band.

In the present study, extreme difficulty was found in establishing the identity of winter rings, especially on the scales of Padarn char. This is discussed in section 3.3.2.

Compared with marine fish, the otoliths of char are very small in relation to the length of the fish. The shape of a typical one is shown in Figure 3.1. The right and left otoliths are alike as a mirrored reflection, but occasionally one was deformed and unreadable. The lateral surface is smooth and slightly convex, and it is this surface that is viewed for age determination.

Otoliths have been used to estimate the age of marine fish since the beginning of the century. Rollefsen (1933) found that the otoliths of old cod often had more zones than the corresponding scales, since which otoliths are now used almost universally for ageing marine fish. With a few exceptions, they are not in common use for freshwater fish, and the only salmonid for which they are in reasonably common use is the arctic char (Nordeng, 1961).

Otoliths are used for ageing on the assumption that the bands of opaque material (appearing white under reflected light) are laid down during the period of rapid growth in late spring, summer and early autumn, and that hyaline material (appearing dark under reflected light) is laid down mainly during the winter. This assumption has been shown to be valid for most teleosts in the Northern Hemisphere, and demonstrated for Llanberis char by Powell (1966). The histochemistry of this process of the laying down of the zones is not fully understood, but Dannevig (1956) describes the chemical composition of the zones of cod otoliths.

3.3.2 Accuracy of Age Determination

To determine the apparent accuracy of the two methods used for age determination, a total of 250 scales and 250 otoliths from char of both Llyn Peris and Llyn Padarn were read twice and compared. The results are shown in Table 3.1.

For char from Llyn Peris, 92.8% of the scales and 94.8% of the otoliths gave duplicate readings. For Llyn Padarn char, whereas 85.0% of the otoliths gave duplicate readings, only 59.2% of the scales did so. In addition, the age determined from the scales of Padarn char could differ by as much as two years; the otolith estimates only differed by one year.

These results compare to those found by Powell (1966) for Llyn Peris, but differ markedly from her estimates for Llyn Padarn char. She found agreement in her scale readings of 66.4%, but only classified 34% of the otoliths as certain.

Prior to further preparation by grinding or burning, only 34% of otoliths

Table 3.1 Age at First Reading vs. Age at Second Reading of Scales and Otoliths

Llyn Peris scales

		Age at 2nd reading						
		2	3	4	5	6	7	8
Age at 1st reading	2	9						
	3		41					
	4		3	104	1			
	5			4	41	1		
	6				4	20	2	
	7					1	12	1
	8						1	5

92.8% agreement

Llyn Peris otoliths

		Age at 2nd reading						
		2	3	4	5	6	7	8
Age at 1st reading	2	9						
	3		41					
	4		2	107				
	5			2	42	2		
	6				2	23	1	
	7					1	12	
	8						2	5

94.8% agreement

Llyn Padarn scales

		Age at 2nd reading						
		2	3	4	5	6	7	8
Age at 1st reading	2	12	1					
	3	8	34	7				
	4		21	64	9			
	5		4	14	22	8		
	6			4	9	8	2	
	7				2	7	6	1
	8					1	4	2

59.2% agreement

Llyn Padarn otoliths

		Age at 2nd reading						
		2	3	4	5	6	7	8
Age at 1st reading	2	13						
	3		44					
	4		8	84	7			
	5			9	41			
	6				5	16	3	
	7				4	10	1	
	8					3	5	

85.0% agreement

from Padarn char were readable.

In this study, only the ages determined from otoliths are considered. All otoliths were read at least twice. If agreement was reached after the second reading, that age was considered valid. If agreement was not reached, the otolith was read a third time and the two similar readings were considered the true age. In no instance were all three readings different.

3.3.3 Time of Check Formation

Powell (1966) demonstrated that the annual check (the deposition of the hyaline zone) was formed on the otoliths of Llanberis char during January and February. The percentage of otoliths examined from each lake in each month which had white (opaque) edges is shown in Fig. 3.2. In both lakes, only otoliths with hyaline edges were found during January, and by June all otoliths had white (opaque) edges. This indicates the cyclical nature of otolith zone formation, validating the age estimation technique.

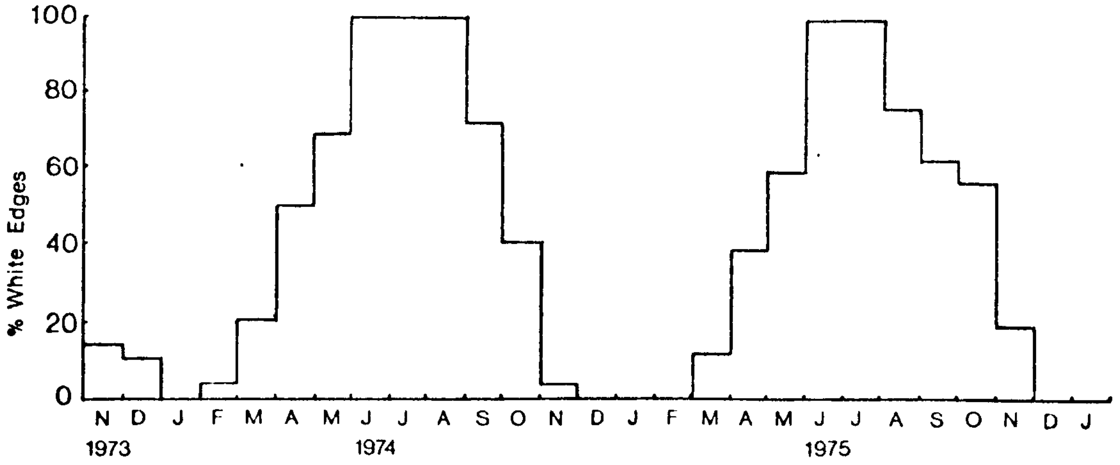
January 1st was used as the birth date for char in agreement with the convention used by Powell (1966), although data provided by Swift (1965) and observation of char hatched artificially indicate that the true birth date is nearer March 1st.

3.3.4 Age Structure of the Samples

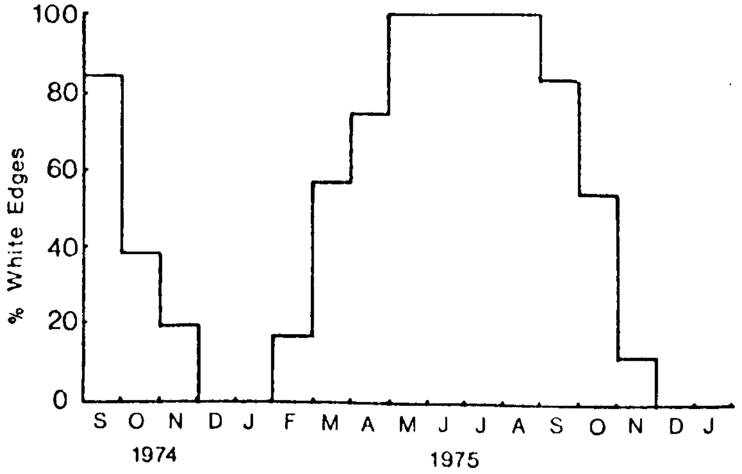
The age distribution of the samples from November 1973 to January 1976

Fig. 3.2 The percentage of char otoliths with white (opaque) edges in each monthly sample.

Llyn Peris



Llyn Padarn



from Llyn Peris and from September 1974 to January 1976 from Llyn Padarn are shown in Table 3.2.

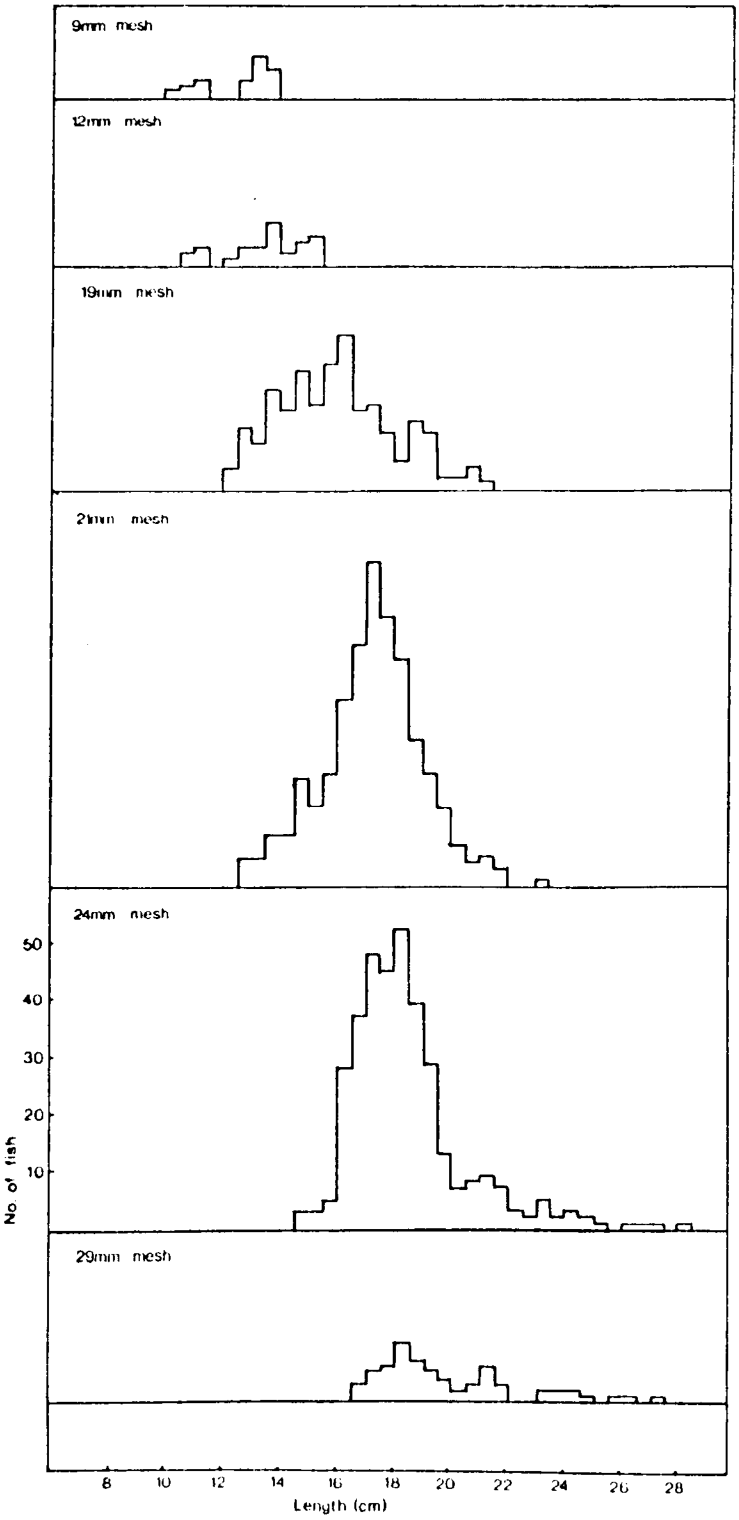
Johnson (1976) and Power (1978) described fish populations in arctic lakes which are dominated by older fish and show an age structure similar to those found in Peris and Padarn, but in these waters the lack of representation of the 0+-1 and 1+-2 age groups, and the poor representation of the 2+-3 and 3+-4 age groups, is indicative of the inefficiency of the sampling methods. Small char are extremely difficult to catch in lakes (Frost, 1965) and the age structures for Llyn Peris and Llyn Padarn char were almost certainly due to the highly selective nature of the sampling technique, that of gill nets.

Table 3.2 Age Distribution of Llyn Peris and Llyn Padarn Char Samples

	Numbers of Fish	
Age Group	Llyn Peris	Llyn Padarn
2+-3	30 (3.46%)	37 (4.79%)
3+-4	185 (21.34%)	184 (23.80%)
4+-5	352 (40.60%)	301 (38.94%)
5+-6	150 (17.30%)	120 (15.52%)
6+-7	86 (9.92%)	72 (9.31%)
7+-8	46 (5.31%)	40 (5.17%)
8+	18 (2.08%)	19 (2.46%)
Total	867	773

Figure 3.3 shows the length-frequency distribution of 1027 char captured from both lakes in various gill nets. Small mesh nets are highly

Fig. 3.3 The length-frequency distribution of char captured in the various sizes of gill nets.



inefficient at capturing small fish (Heard, 1962), which is reflected in the low numbers of char taken in the 9mm and 12mm mesh nets. Kipling (1957) suggested that a range of gill nets should be used for sampling a fish population as representatively as possible. The length-frequency diagrams justify this, and show the validity of choosing the 19mm, 21mm, and 24mm nets for most of the sampling. Char of four years of age and older were probably sampled representatively in both lakes.

The oldest char found in both lakes was in its eighth year of life. This is a similar lifespan to the char sampled by Powell (1966) from Llanberis and for Windermere char (Frost, 1951; 1978). In arctic regions, a lifespan of 14 years is not uncommon in landlocked populations (Sprules, 1952; Hunter, 1970; Savvaitova, 1976a) and Skreslet (1973a) recorded an age of 28 years for non-anadromous char from Nordlaguna, Jan Mayen Island.

During the winter, and especially in November and December, large numbers of char of length greater than about 21cm were found in Llyn Peris, mainly in nets set in shallow water. Despite intensive fishing, no char of this length were found at other times of the year. They were easily distinguished from the resident Peris fish by their colouration, faster growth rate and better condition. They can be shown to be char which have migrated from Llyn Padarn for spawning, and their significance is discussed in Chapter 5.

3.4 The Growth of Llanberis Char

3.4.1 Seasonal Growth in Length

The mean lengths of char from Llyn Peris and Llyn Padarn were calculated for the 1967 to 1973 year classes in each monthly sample.The means were plotted against time to show the seasonal variation in growth (Figs. 3.4 and 3.5). The small sample sizes in some months, especially the summer when char can be difficult to catch, can cause anomalies, but a smoothed seasonal curve can be drawn by eye for each year class, taking into account the sample size and standard deviation. The analysis of seasonal growth data can provide a more accurate assessment of when growth occurs within the year than does annual growth data. In both lakes, the main period of growth was from early summer (May/June) to autumn (September/October), which corresponds to the period of maximum feeding found by Powell (1966) and to the period of greatest primary production (Pentecost and Happey-Wood, 1978) and presumably to the corresponding peak in plankton and benthos, the dominant food of char (Powell, 1966). There was little or no growth during the winter months, corresponding to the minimum feeding and primary production. This cessation of growth also corresponds to the laying down of the hyaline 'winter' band on the otoliths.

The rate of growth was greatest for the younger fish, and decreased with increasing age, demonstrated by the flattening of the growth curves. For fish of the same year class, there was a greater increase in length shown by the Padarn fish than those from Peris. This will be discussed later.

There has been, apparently, no other study of the seasonal growth of arctic char, but Cooper (1953) found a similar sigmoidal seasonal growth pattern for brook trout, <u>Salvelinus fontinalis</u>, from three Michigan streams.

Fig. 3.4 The seasonal growth in length of Llyn Peris char; 1967 - 1973 year classes. The number of observations is shown, but the standard deviations have been omitted for clarity.

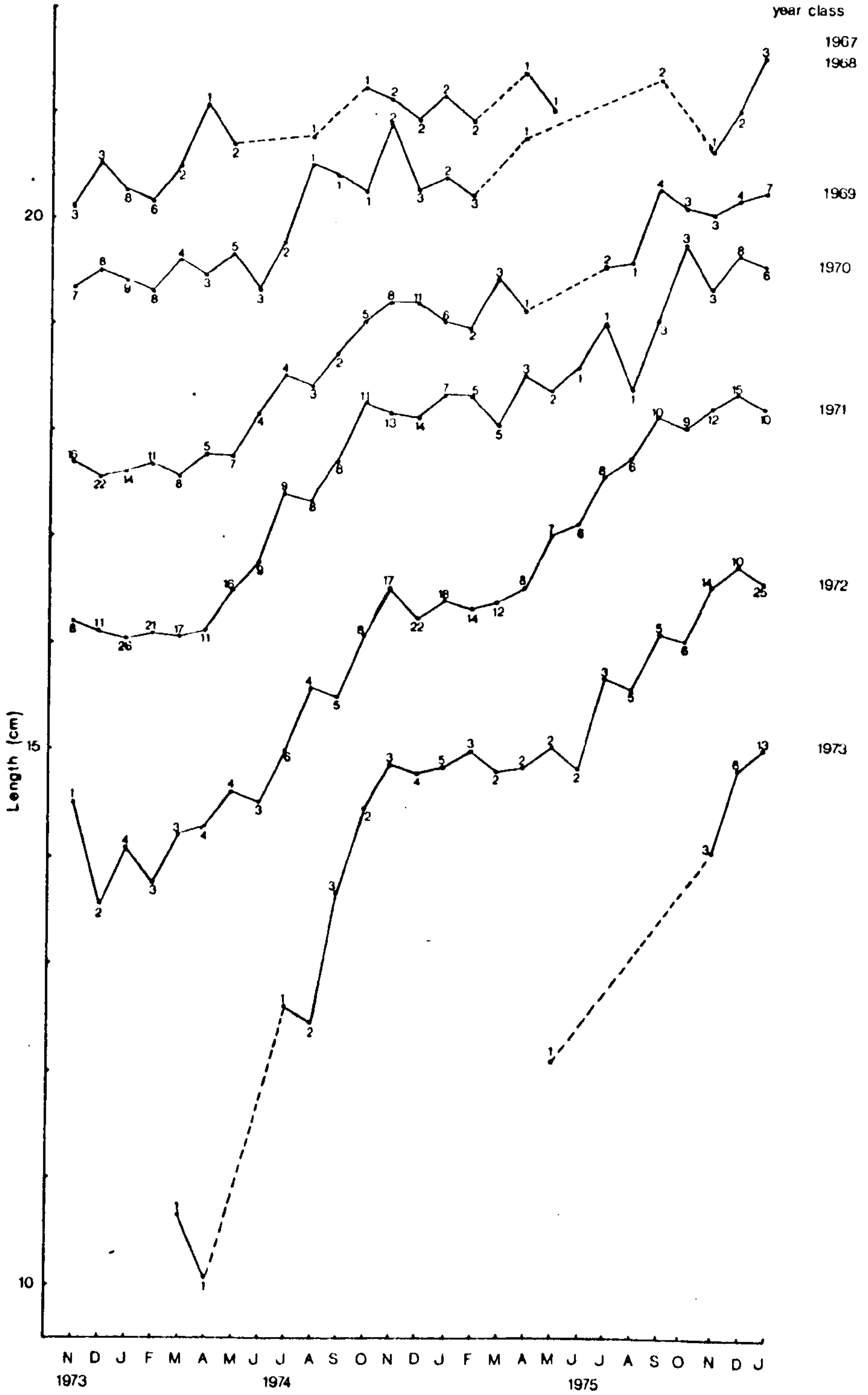
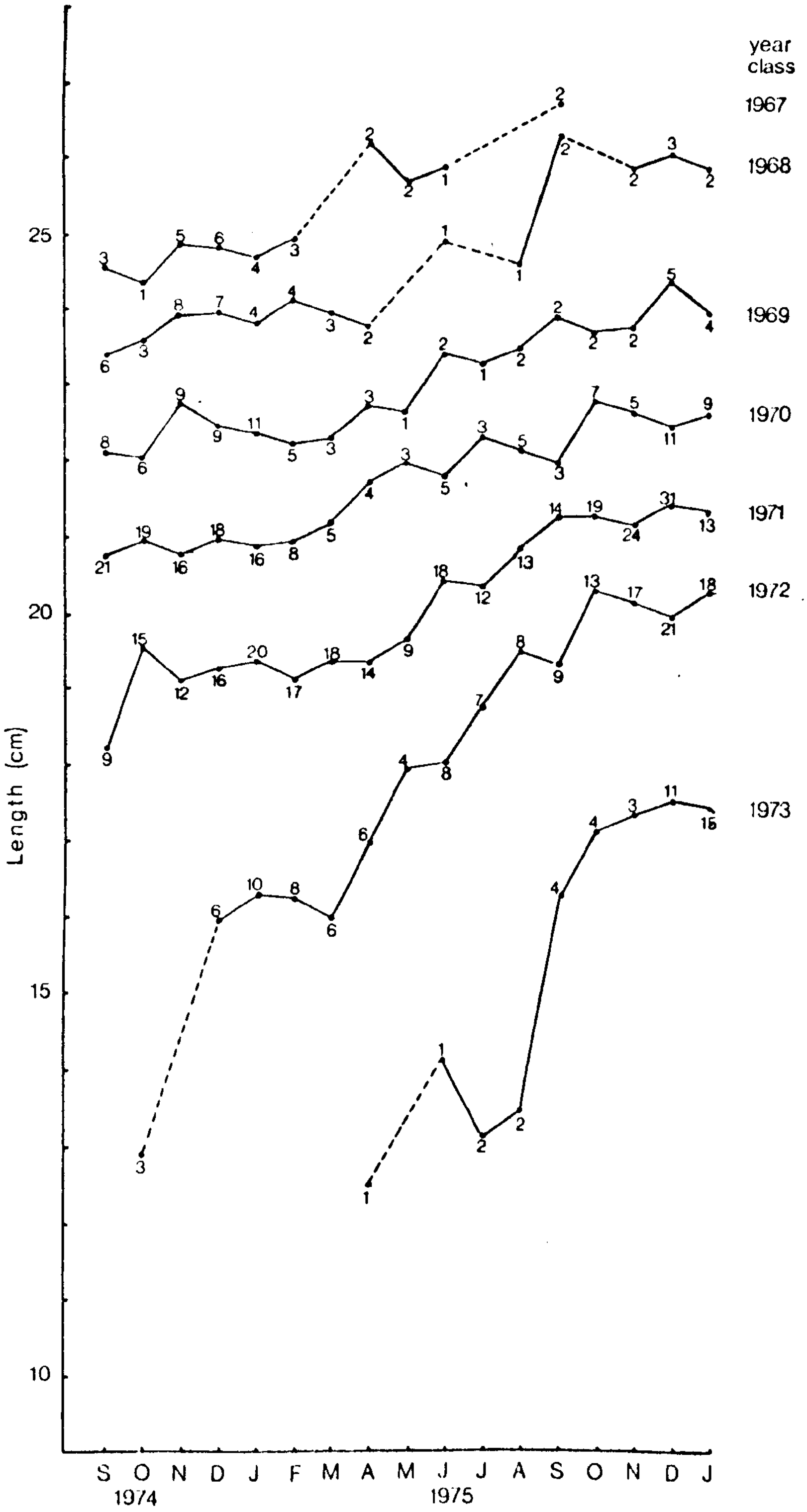


Fig. 3.5 The seasonal growth in length of Llyn Padarn char; 1967 - 1973 year classes. The number of observations is shown, but the standard deviations have been omitted for clarity.



3.4.2 Seasonal Growth in Weight

The seasonal growth in weight, shown as the mean monthly weight of each year class, of char from both lakes is shown in Figs. 3.6 and 3.7. The weight of fish is more variable than the length, but the growth curves show a basically similar pattern to those of length. There was a marked depression in the average weights of the older year classes between December and March, due to the shedding of gonadal products and loss of condition following spawning (see Chapters 4 and 5) and the paucity of available food.

3.4.3 Annual Growth in Length

Calculations of the average length of char at each age for each year class were made by determining the relationship between the annual checks on the otoliths and the total length of the char. Calculations of this type have been most often made from scales, and Hile (1970) reviews the methods. Otoliths have only occasionally been used, mainly for marine fish (e.g. Templeman and Squires, 1956; Reay, 1972; Warburton, 1978).

The method relies on there being a proportional relationship between the growth of the fish and the structure used for ageing the otoliths. A regression of fish length against otolith radius showed this relationship to be valid for char from both lakes ($r = 0.976$ for Llyn Peris and 0.964 for Llyn Padarn; $p < 0.001$), and gave the following results:

$$O_r = 0.36 + 0.11L \text{ for Llyn Peris}$$

$$O_r = 0.28 + 0.12L \text{ for Llyn Padarn}$$

Fig. 3.6 The seasonal growth in weight of Llyn Peris char; 1967 - 1973 year classes. The number of observations is shown, but the standard deviations have been omitted for clarity.

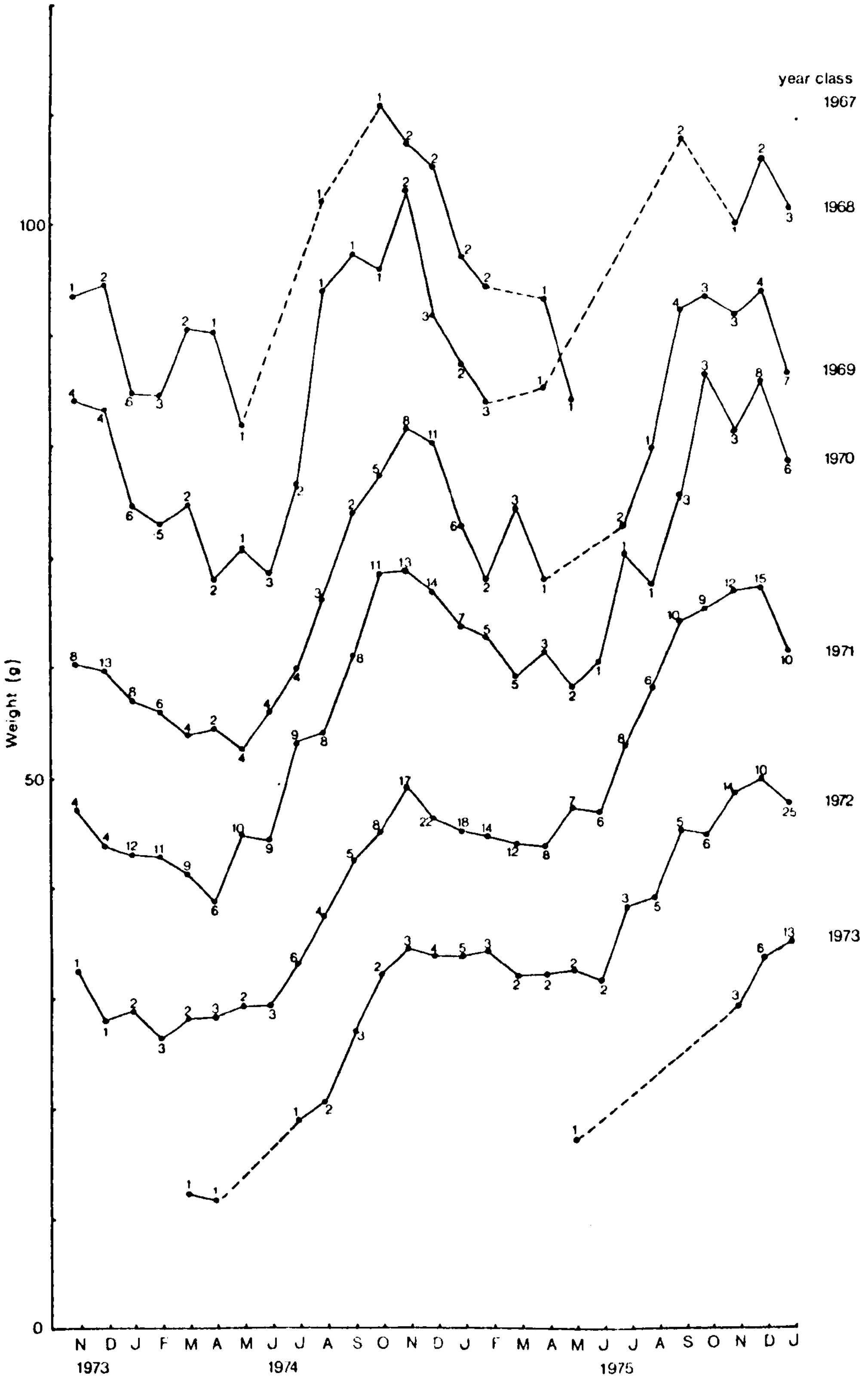
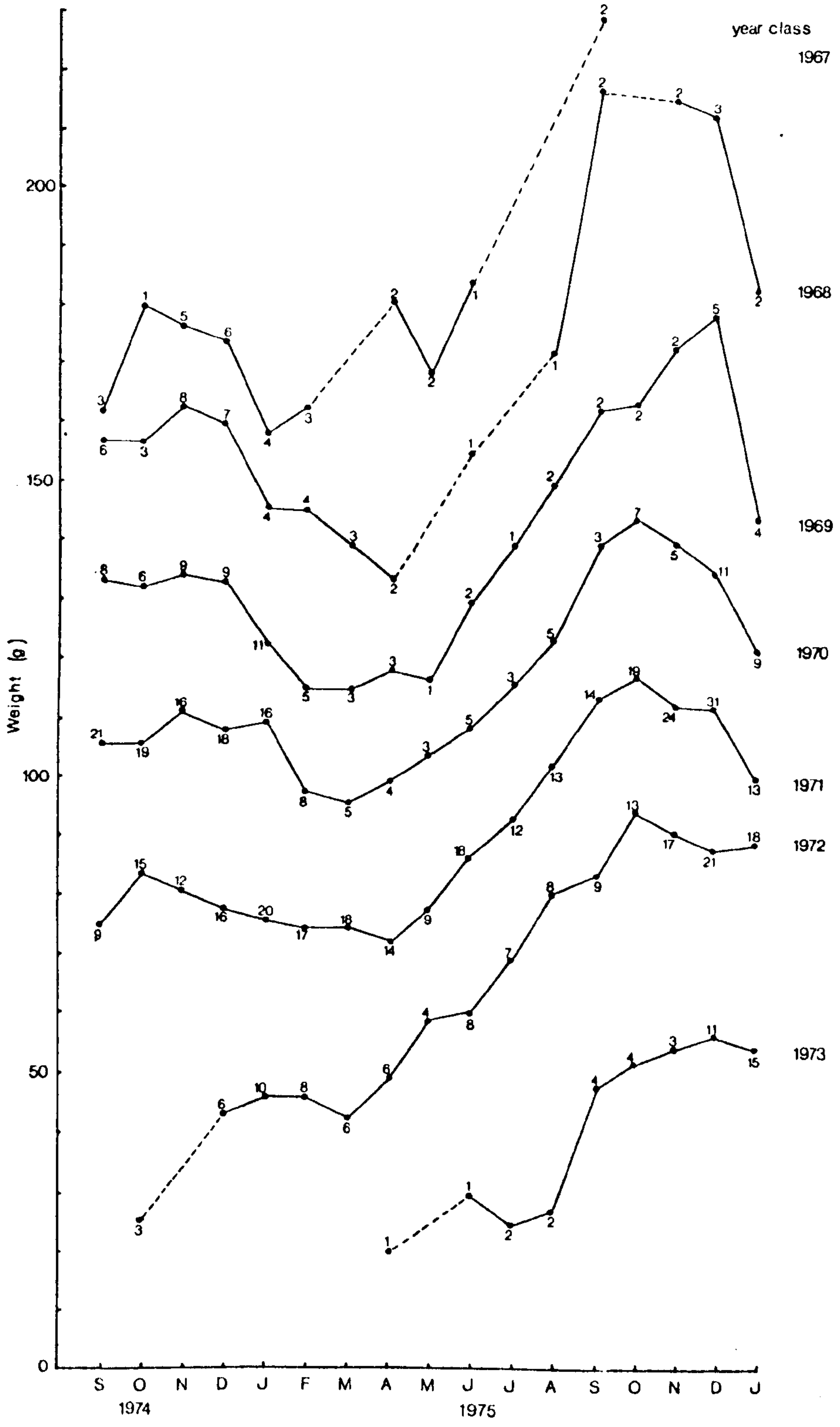


Fig. 3.7 The seasonal growth in weight of Llyn Padarn char; 1967 - 1973 year classes. The number of observations is shown, but the standard deviations have been omitted for clarity.



where O_r = otolith radius in units

L = fork length of char in cm

The intercept when $O_r = 0$ was -34mm for Llyn Peris and -26mm for Llyn Padarn char. These estimates were used to replace the constant C in the formula;

$$L_n - C = \frac{O_n}{O_r} (L-C)$$

where L_n = length of fish at age n

O_n = otolith radius at check n

O_r = total otolith radius

L = length of fish at capture

Nordeng (1961) also demonstrated a linear relationship between otolith radius and fish length for char, which differed widely for different populations. Grainger (1953), however, for char from Baffin Island, found there to be a logarithmic relationship. The reason for these differences is not known, but similar different relationships occur when using scales for the same species from different localities (Hile, 1970). Powell (1966) assumed a linear relationship for both scale and otolith radii against fish length in her earlier study of Llanberis char, but did not use a correction factor. Examination of the above formula shows that this would result in an overestimation of the lengths when calculated from otoliths (C being -ve), and an underestimation when calculated from scales (C usually being +ve).

The calculated mean lengths for both sexes for each lake at each age were calculated separately and compared using a 'd' or 't' test (Table 3.3).

Table 3.3 Mean, standard deviation and number of observations for the length of each age group of male and female char, back-calculated to that age from all year classes. The value of probability for 'd' or 't' tests between means at each age is given

Llyn Peris

	Age	1	2	3	4	5	6	7	8
Females	length (cm)	7.09	11.16	14.31	16.19	18.03	19.52	20.73	21.28
	S.D.	0.73	1.02	0.79	1.24	1.24	1.08	1.05	1.64
	n	430	430	414	313	163	82	29	11
Males	length (cm)	7.19	11.24	14.23	16.36	17.94	19.43	20.64	21.13
	S.D.	0.82	1.05	0.93	1.28	1.31	1.16	1.08	1.42
	n	437	437	423	339	137	68	37	7
	p	>0.05	>0.1	>0.1	>0.05	>0.1	>0.1	>0.1	>0.1

Llyn Padarn

	Age	1	2	3	4	5	6	7	8
Females	length (cm)	7.01	12.38	16.23	19.54	21.42	22.94	23.97	25.02
	S.D.	0.83	0.93	0.92	1.01	1.09	1.18	1.13	0.94
	n	387	387	372	288	126	70	32	10
Males	length (cm)	6.91	12.32	16.15	19.67	21.54	22.85	24.45	25.36
	S.D.	0.94	1.12	0.99	0.86	1.18	1.24	1.06	1.03
	n	386	386	364	264	125	61	27	9
	p	>0.1	>0.1	>0.1	>0.05	>0.1	>0.1	>0.05	>0.1

There was no significant difference between the lengths at any age, and therefore the data for males and females were combined. Table 3.4 shows the back-calculated mean lengths for the combined data at each age for the 1966 to 1973 year classes for both lakes. Lee's phenomenon (Lee, 1920), which causes the computed lengths at a given age to be smaller the older the fish from which they are computed, is not apparent in the results from either lake.

Table 3.4 The mean back-calculated lengths in cm at each age for the 1966 to 1973 year classes of char from Llyn Peris and Llyn Padarn. The combined means, and standard deviations, for each age group is shown, and the probability value for 'd' or 't' tests between the mean lengths at each age from both lakes is given.

Llyn Peris

	Age	1	2	3	4	5	6	7	8
Year Class	n								
1966	11	7.61	11.42	14.22	16.02	18.18	19.78	20.98	21.24
1967	37	6.58	10.98	14.09	16.58	18.01	19.61	20.76	21.08
1968	72	7.21	11.54	14.63	16.42	18.22	19.59	20.68	21.06
1969	156	6.63	10.61	13.68	15.81	17.63	19.07	20.18	
1970	234	7.13	11.20	14.36	16.38	18.38	19.58		
1971	222	7.68	11.31	14.21	16.35	18.22			
1972	111	6.84	11.38	14.58	16.61				
1973	24	7.57	11.63	15.55					
Mean		7.14	11.20	14.27	16.28	17.99	19.48	20.63	21.22
S.D.		0.86	1.08	0.82	1.28	1.32	1.19	1.06	0.89
n		867	867	837	652	300	150	64	18

Llyn Padarn

	Age								
Year Class	n								
1966	3	7.53	12.99	16.81	19.32	22.58	23.38	24.12	25.82
1967	29	7.44	12.03	16.42	19.83	21.42	22.97	24.15	24.98
1968	47	6.61	12.22	16.68	20.07	21.39	23.24	24.38	25.63
1969	75	7.03	13.01	15.12	18.86	21.98	22.56	23.84	
1970	158	7.24	11.48	15.53	19.38	21.24	22.65		
1971	274	6.38	12.68	16.22	19.80	21.40			
1972	144	7.26	12.14	16.71	20.11				
1973	65	7.76	13.18	17.58					
Mean		6.96	12.35	16.19	19.60	2.53	22.90	24.19	25.18
S.D.		0.92	1.13	1.06	0.94	1.26	1.24	1.14	0.98

cont/

n	773	773	736	552	251	131	59	19
p	<0.001 Pe>Pa	<0.001 Pa>Pe	<0.001 Pa>Pe	<0.001 Pa>Pe	<0.001 Pa>Pe	<0.001 Pa>Pe	<0.001 Pa>Pe	<0.001 Pa>Pe

The mean length at each age for the 1967 to 1973 year classes were also plotted graphically for both populations, and are shown in Figs. 3.8 and 3.9.

Some variation in the growth rates of different year classes is apparent. This may be a result of the relative abundances of the particular classes, which has been shown to depend on the temperature (LeCren, 1958; Kipling and Frost, 1970), but the uncertainties with the sampling techniques did not allow any estimates of relative year class strengths to be made. There was no overall trend for the growth rates to be increasing or decreasing in younger year classes, and therefore both populations could be considered to be reasonably stable. Hunter (1970) found that there was a tendancy for the average lengths at a given age to increase in successive sampling years during his study of the char population of Keyhole Lake, which he concluded as being due to the effects of the removal of fish during sampling. As has been mentioned above, this was not evident for the Llanberis lakes.

Because the variation in the growth of the year classes was relatively little, the data from the individual year classes were combined to provide an average growth rate for both lakes (Table 3.4; Fig.3.10). The lengths at each age from both lakes were compared using 'd' or 't' tests. The Peris char grew significantly faster than those from Padarn ($p < 0.001$) in their first year of life, but the Padarn char grew faster ($p < 0.001$) at all subsequent ages. Whether the faster growth during the first year by Peris char was real, or whether it was due to errors

Fig. 3.8 The back-calculated lengths of Llyn Peris char; 1966 - 1973 year classes.

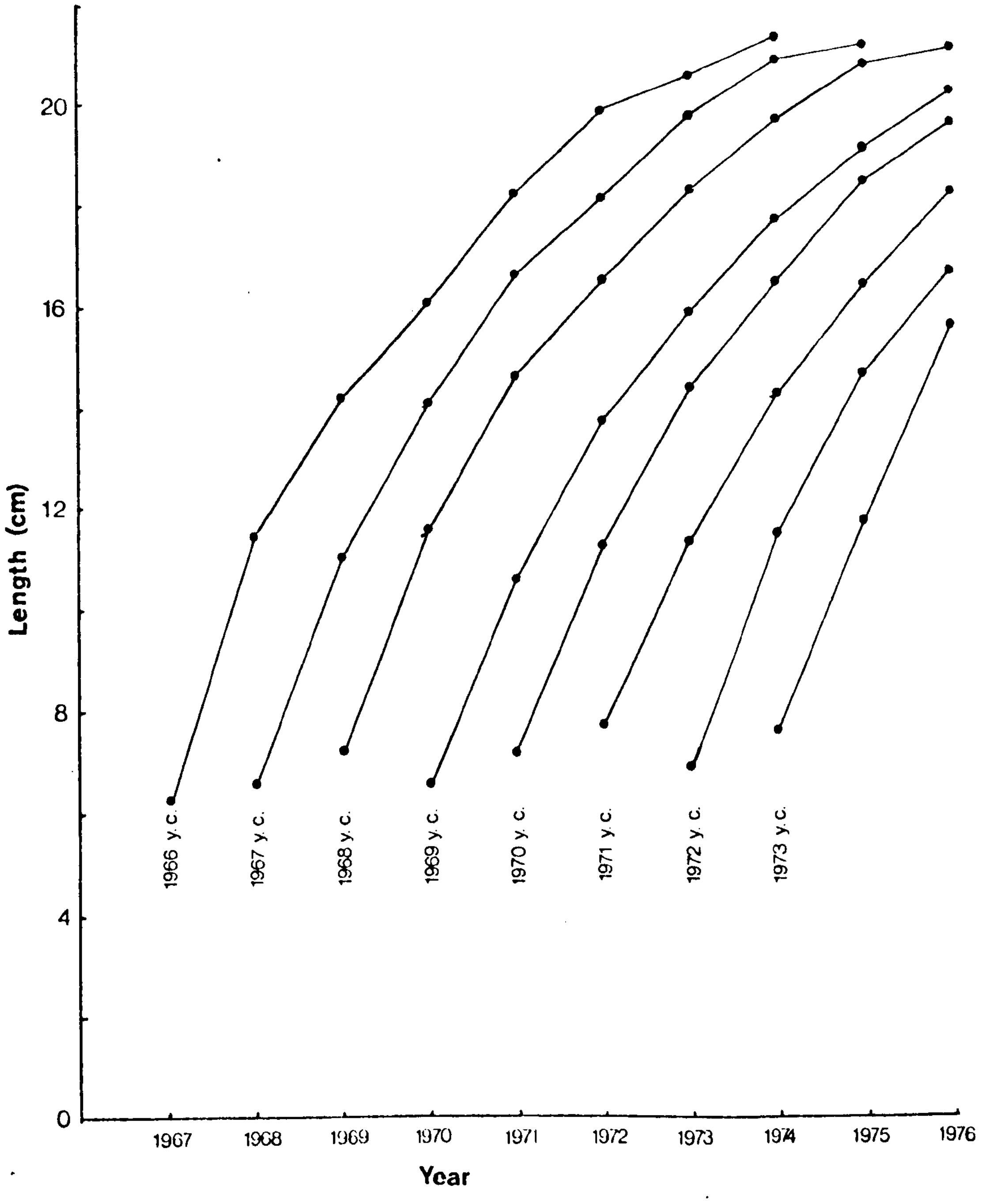


Fig. 3.9 The back-calculated lengths of Llyn Padarn char; 1966 - 1973 year classes.

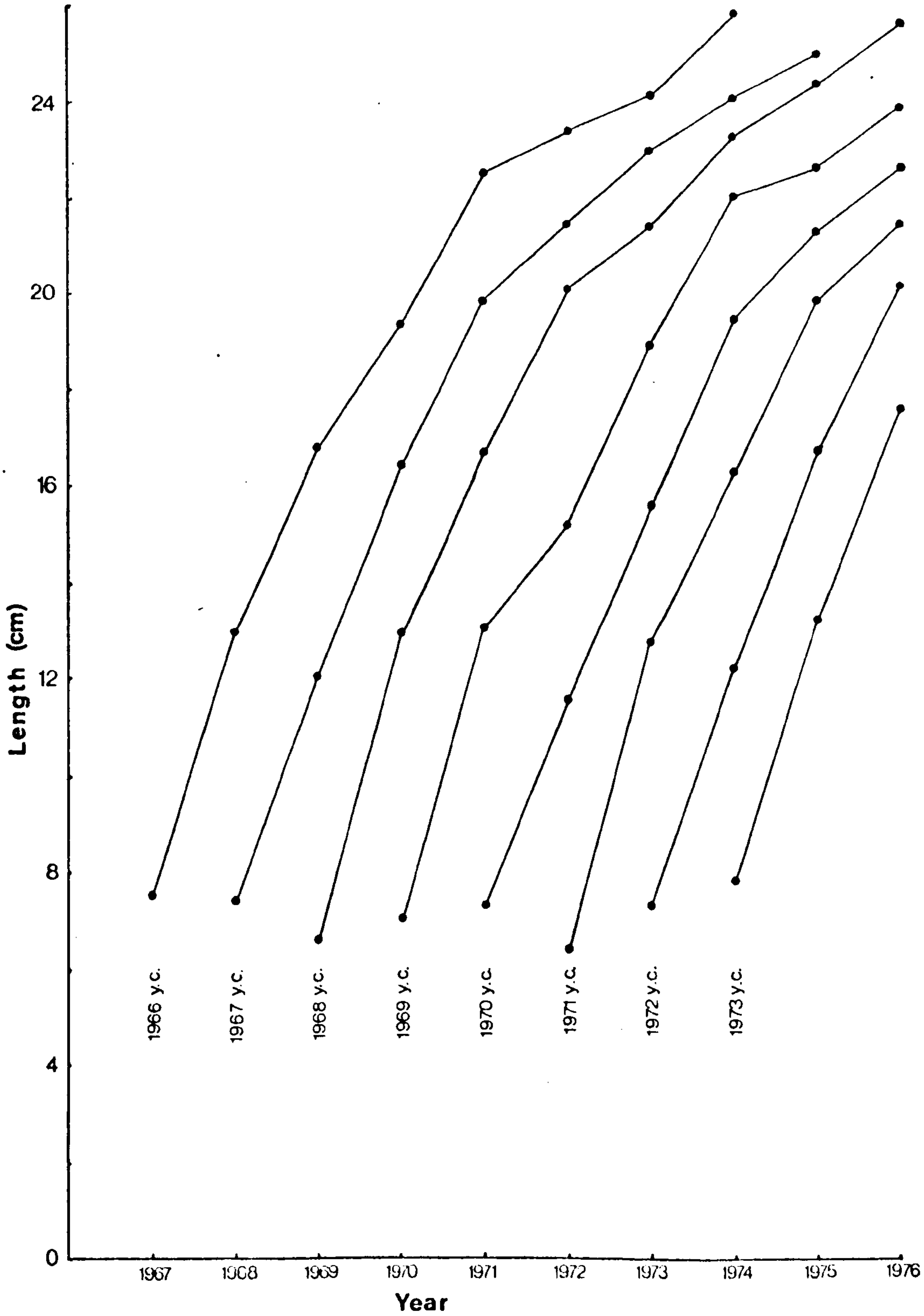
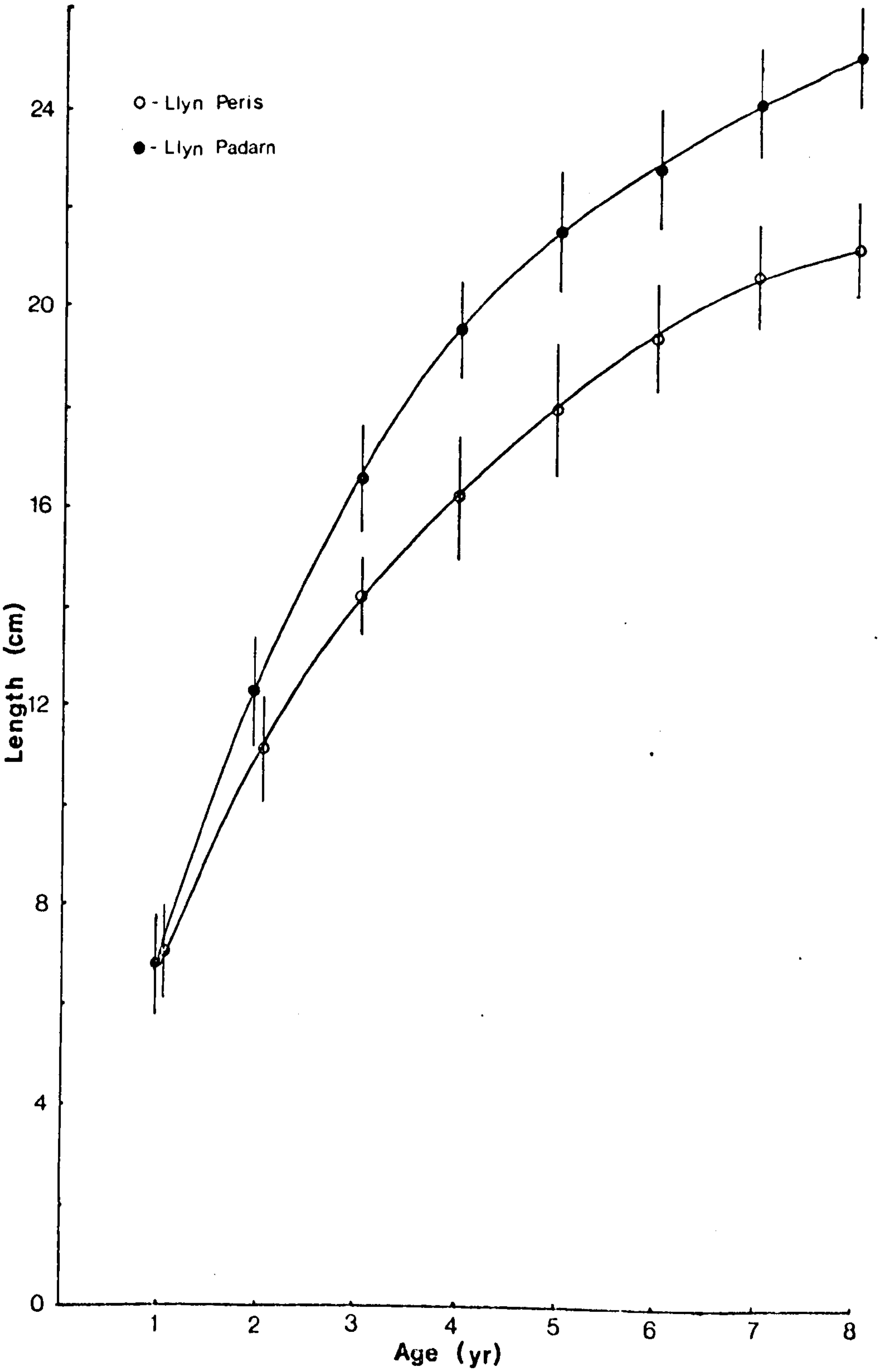


Fig. 3.10 The mean back-calculated lengths of char from Llyn Peris and Llyn Padarn.



in back-calculation, is not known, because no yearling char were sampled from either lake to provide a comparison. A possible explanation for this difference is provided in Chapter 5. However, the fact that the Padarn char grew faster thereafter and reached a greater ultimate size was real, and could be confirmed, at least for the older age groups, from the observed lengths. Various factors can affect the growth rate of a fish population, such as density, temperature and available food. Stoklowsowa (1968) demonstrated that the optimum temperature for the growth of Windermere char was between 12 and 16^{o}C. Depth-time diagrams presented by Pentecost and Happey-Wood (1978), and irregular measurements taken during this study, indicates that the water temperature at mid-depth, where char normally frequent, was between 12 and 16^{o}C for a slightly longer period in Llyn Padarn than Llyn Peris. Pentecost and Happey-Wood (1978) also found that there was a 5.5 times greater standing crop of phytoplankton and a 3.4 times faster rate of primary production in Llyn Padarn. This was, apparently, not due to the lower water temperature of Peris, which is a result of a greater degree of mountain shading, but to the higher concentration of phosphorus in Llyn Padarn caused by treated sewage effluent, which is discharged into the Afon-y-Bala. Preliminary studies of the zooplankton (Whitehouse and Lewis, 1975), showed that the species composition was different in the two lakes and that Llyn Padarn supported a much bigger population, especially of the larger species, such as Diaptomus gracilis and Leptodora kindti, as may be expected from its greater primary production. The benthic fauna also differed between the two lakes (Pugh-Thomas, 1975); chironomids and Pisidium being dominant in Llyn Peris, and oligochaetes in Llyn Padarn. The difference was possibly due to the nature of the substrate, particularly the greater amount of slate flour in Llyn Peris. Unlike the zooplankton, the density of bottom fauna was similar in both lakes. It was not possible to make any population estimates of the char population in either lake, but it is considered that overcrowding was not the limiting factor for growth, and that the differences in the growth rate between the two populations is due to the greater amount of available food in Llyn Padarn and possibly to the prolonged higher temperatures in the lake.

Table 3.5 shows the calculated mean lengths at each age from the present study compared to those of Powell (1966), which were determined from scale data.

Table 3.5 The mean length in cm of char at each age from Llyn Padarn and Llyn Peris in 1966 and 1976

		AGE							
		1	2	3	4	5	6	7	8
Llyn Peris	1966	4.2	8.8	13.2	15.7	18.4	19.4	21.0	21.2
	1976	7.14	11.20	14.27	16.28	17.99	19.48	20.68	21.22
Llyn Padarn	1966	5.52	9.62	14.36	19.55	21.60	23.0	24.0	
	1976	6.92	12.35	16.19	19.60	21.53	22.90	24.19	25.18

At ages 1 to 4, for both lakes, the calculated lengths from the present study were consistently higher. As noted earlier, this was probably caused because Powell (1966) did not use a correction factor for her calculations, resulting in an underestimate of the lengths of the younger age groups. However, the similarity of the estimated lengths in later years indicates that the growth rate of the char had not changed markedly in the intervening years, confirming the relative stability of the populations.

Gulland (1965); Dickie (1968) and Ricker (1975) have all commented on the desirability of fitting mathematical expressions to growth curves. These are of value in computing yield and production and can lead to a better understanding of the mechanisms underlying the growth process. The most important practical application is that they show a generalised description, free from minor variations in the original observations (Dickie, 1968).

The best known model is that ascribed to Von Bertalanffy (1938; 1957), for which methods of fitting have been described by Beverton and Holt (1957); Gulland (1964) and Ricker (1975).

The Von Bertalanffy expression for length (l_t) at age t as a function of t is usually written as;

$$l_t = l_\infty(1-\exp^{-k(t-t_0)})$$

where l_∞ = the mathematical asymptote of the curve

k = a measure at which the growth curve approaches the asymptote

t_0 = a time scale equivalent to the hypothetical time at which the fish would have been zero length if it has always grown in the manner described by the equation

The parameters in this equation were estimated using the graphical methods described by Beverton and Holt (1957), Gulland (1964) and Ricker (1975). The mean length at each age was obtained by taking the average of all lengths back-calculated to that age from all year classes of char from each lake. Mean lengths at age t were then plotted against those of age t+1 (Walford, 1946) for both populations (Figs. 3.11 and 3.12).

Fig. 3.11 (A) Walford graph for length of char from Llyn Peris. (B) $\mathrm{Log}_e(L_\infty - l_t)$ plotted against age for trial values of L_∞ = 23·0cm and 23·7cm.

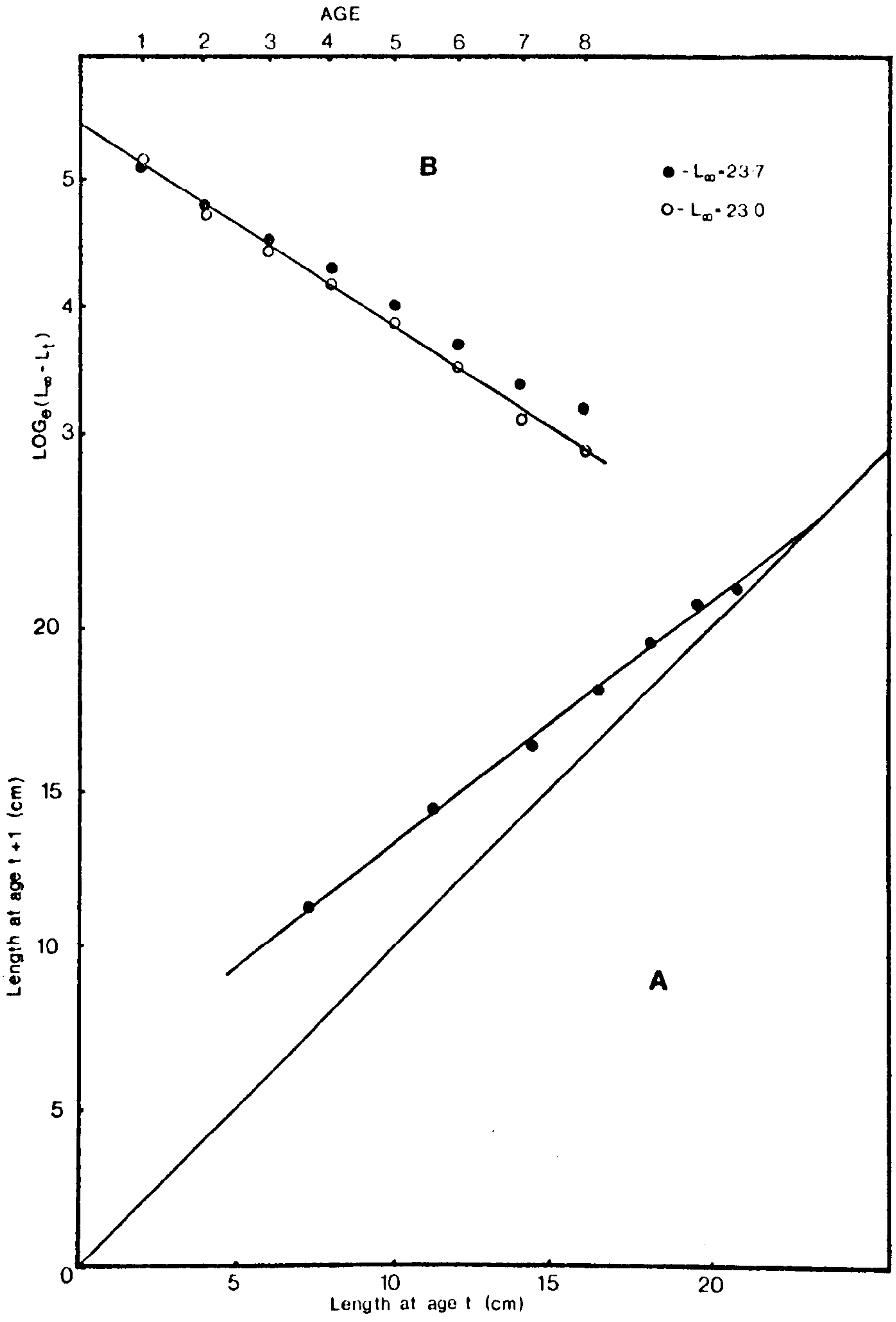
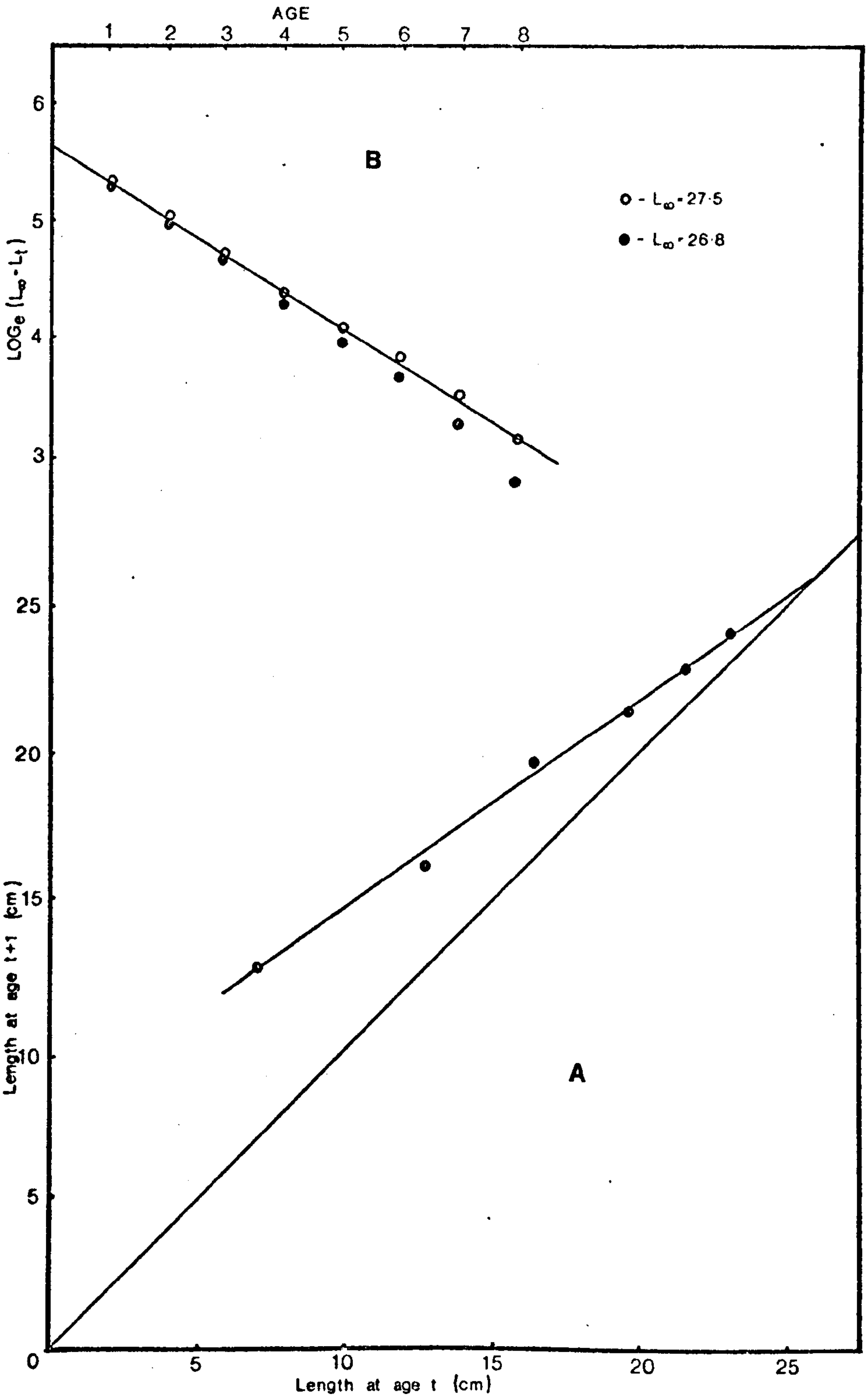


Fig. 3.12 (A) Walford graph for length of char from Llyn Padarn. (B) $\text{Log}_e(L_\infty - l_t)$ plotted against age for trial values of L_∞ = 26·8cm and 27·5cm.



A line was fitted to these points by eye, as the use of the least squares regression analysis was inappropriate (Ricker, 1975). The intersection of this line with a line 45^0 diagonally from the origin provided an estimate of l_∞, the average 'maximum' length. This was used as the first trial value for l_∞; graphs of $\log_e(l_\infty - l_t)$ against t were plotted, and the value of l_∞ altered until that which gave the best straight line was found (Figs. 3.11 and 3.12). The slope of this line was k, and its Y axis intercept was equated to $\log_e l_\infty + l_t$, from which the value of t_0 was found. The substitution of these values into the Von Bertalanffy equation for t = 1......n gave the theoretical length of char at each age. These theoretical lengths are compared with the back-calculated lengths in Table 3.6

These results indicate that the growth of char in Llyn Peris and Llyn Padarn was quite well described by the Von Bertalanffy model.

Table 3.6 Comparison of back-calculated lengths (l_c) and lengths fitted by the Von Bertalanffy model (l_b) in cm, for char from Llyn Peris and Llyn Padarn

		AGE							
		1	2	3	4	5	6	7	8
Llyn Peris	l_c	7.14	11.20	14.27	16.28	17.99	19.48	20.69	21.22
	l_b	5.52	10.35	13.34	16.10	17.40	19.32	20.24	20.93
Llyn Padarn	l_c	6.96	12.35	16.19	19.60	21.53	22.90	24.19	25.18
	l_b	6.96	12.57	16.67	19.64	21.78	23.35	24.41	25.30

Minor deviations occurred from the model in the younger age groups in Llyn Peris. In particular, the length at the end of the first year as described by the Von Bertalanffy model was smaller than that of Llyn Padarn, not larger as with the calculated data. This can either be ascribed to inaccuracies in back-calculation or that the Peris char were growing unusually quickly during their first year. Unfortunately,as has been mentioned, younger char were not vulnerable to the fishing techniques used and this phenomenon cannot be checked.

Calculated length for age data can also be compared in terms of instantaneous growth rates (G) using the equation;

$$G = (\log_e l(t+1) - \log_e l(t)) \times 100 \qquad \text{(Ricker, 1975)}$$

where l(t) = length at time t

and l(t+1) = length at time t + 1

G is expressed as percentage length increase per annum. The values of G for char from Llyn Peris and Llyn Padarn are shown in Table 3.7.

Table 3.7 The specific annual growth rates of Llyn Peris and Llyn Padarn char, expressed as percentage length increase per annum

	YEAR							
Llyn	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
Llyn Peris	137.8	45.0	24.2	13.2	10.0	8.0	6.0	2.5
Llyn Padarn	135.0	57.4	27.1	19.1	9.4	6.2	5.5	4.0

The values of G in the first year of life were calculated using an initial length of 1.80 cm, which was the length that char hatched artificially began to feed.

Frost and Brown (1967) considered that one advantage of using the specific growth rate over other methods is that it takes into account both the initial and final sizes of the fish, and therefore gives a much more accurate comparison of the growth rate of fish of different sizes than does any other method. Various authors have emphasised the influence of the specific growth rate during the first year of life on the overall growth pattern of salmonids (Frost, 1945; Ball and Jones, 1960; Thomas, 1964). Thomas (1964) found that trout with the highest G in the first year always attained greater lengths at the end of each subsequent year. This is apparently not true for Llanberis char; the specific growth rates of both populations were similar in the first year, but the Padarn char maintained a higher growth rate in their second, third and fourth years of life, thus achieving greater size. A rapid decline in the specific growth rate has also been associated with the onset of maturity (Frost and Brown, 1967). A small number of male char spawn at the end of their second year, and most are mature at the end of their fourth year (see Chapter 4). This corresponds to the rapid decline in specific growth rate of Padarn char, but the decline in Peris char is more gradual. It was suspected that Peris char matured slightly earlier than those of Padarn, but, because of the small number of samples, it could not be shown conclusively.

3.4.4 Annual Growth in Weight

The calculated length of Llyn Peris and Llyn Padarn char at the end of each year were converted to weights using length/weight relationships. The relationships chosen were calculated from char captured during January, the end of the growth year, although the maximum weight per unit length is actually in October/November, immediately prior to spawning. Tesch (1968) showed that the relationship between length and weight can usually be represented by;

$w = a\ell^b$ where w = weight

ℓ = length

a = a constant

b = an exponent, usually a value between 2 and 4

This equation can be transformed to;

$$\log w = \log a + b(\log \ell)$$

The 'regression coefficient' is b, and log a is the intercept of the line with the y axis. The equations for Llyn Peris and Llyn Padarn during January were:

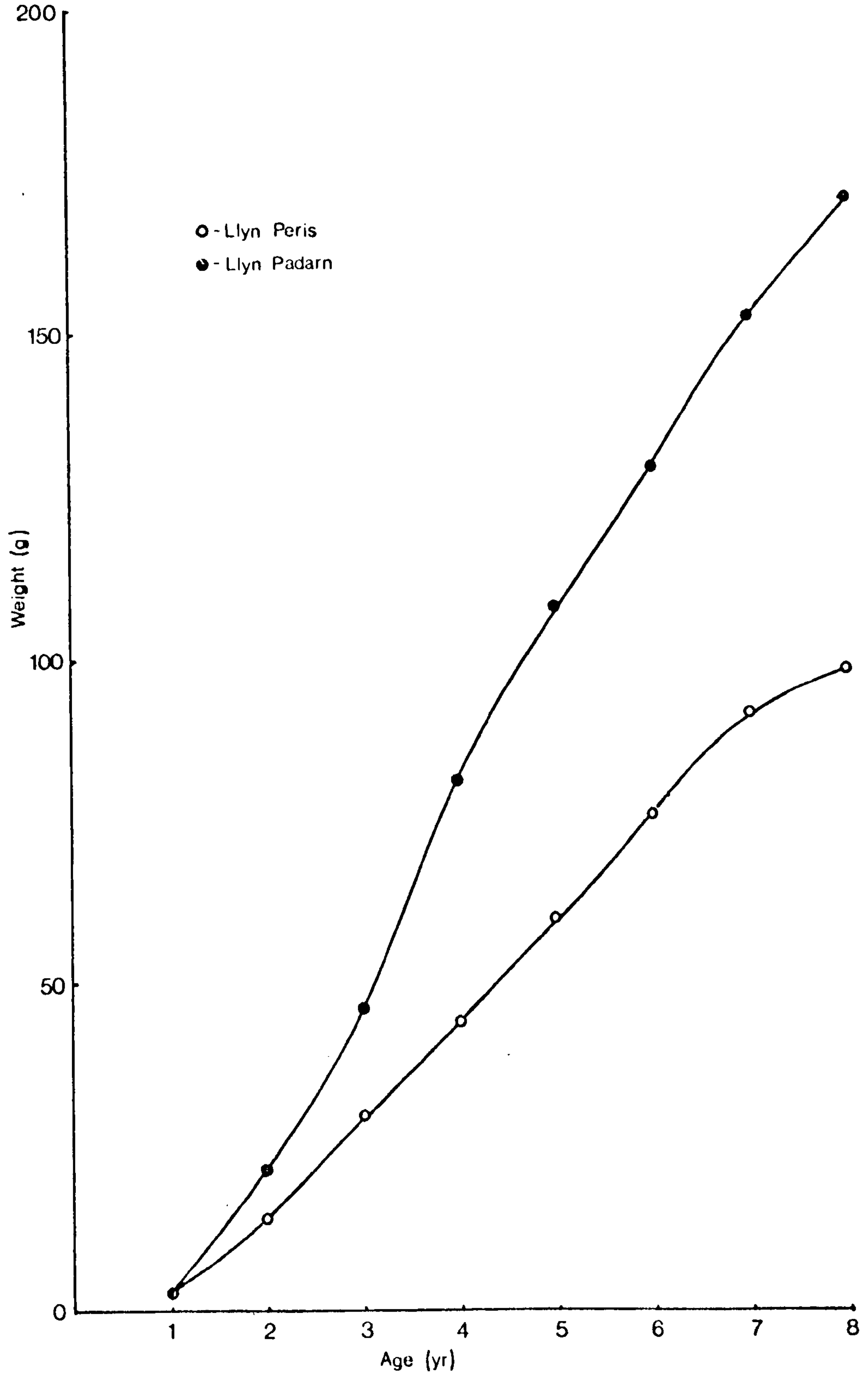
$\log w = 3.0044 (\log \ell) - \log 1.9974$ for Llyn Peris

$\log w = 3.0014 (\log \ell) - \log 1.9713$ for Llyn Padarn

There was a significant correlation ($p < 0.001$) for both relationships, proving their validity ($r = 0.9848$ and 0.9064 respectively).

The resultant annual rates of growth in weight are shown in Fig. 3.13. These differ from the rates of growth in length in that they show a steady increase in weight throughout the life of the fish, whereas the increase in length progressively slows. The results may not be strictly accurate bacause the length/weight relationships were calculated using predominantly fish that were mature. Tesch (1968) showed that the relationship can alter during the development of the fish when they may pass through several 'stanzas'. No small char were captured and the validity of the relationship at younger ages cannot be verified. Also, the sampling technique, gill-nets, may be very biased and the smallest fish of those actually sampled were probably not typical of others of the same age (Kipling, 1957).

Fig. 3.13 The estimated annual growth in weight of Llyn Peris and Llyn Padarn char.



As with the length data, the rate of growth in weight was greater for Llyn Padarn than Llyn Peris, char in their eighth year of life being almost twice as heavy.

The calculated weight for age may, as with length, also be compared in terms of instantaneous growth rates (G) by substituting weight at time t and weight at time t + 1 in the equation on page 60 . These are shown in Table 3.8.

Table 3.8 The specific annual growth rates of Llyn Peris and Llyn Padarn char, expressed as percentage weight increase per annum

	YEAR							
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
Llyn Peris	130.6	135.0	72.8	39.6	30.4	23.9	18.0	7.8
Llyn Padarn	128.4	172.2	81.3	57.4	28.2	18.5	16.5	12.0

The results confirm the observations made from the calculated weight for age data, that the relative rate of increase in weight remained at a higher level throughout the life of the fish than did the weight.

3.4.5 Comparisons of the Growth of Llanberis Char with Other Populations

Table 3.9 compares the mean annual lengths of some non-anadromous char populations from various localities. As may be expected from the circumpolar distribution of the char, there are large differences in growth reported from the different environments. The growth of the Llanberis populations are slightly slower than the autumn and spring spawning Windermere char, but are similar to the dwarf populations found in that lake. From Europe, the population from L. Geneva is notable for its much faster growth rate, especially in view of its shorter lifespan. Some of the riverine, but non-migratory, populations in Alaska, and the lacustrine char from Maine, have generally similar growth rates to the British populations, but other Alaskan riverine char, and those from Candlestick Pond, Newfoundland, grew more slowly. Those from Metamek Lake, Quebec, Keyhole Lake, Alaska, Little Fish Lake, Alaska and Lake Nachikin, Kamchatka have a comparable growth rate to the Llanberis char in their first eight years of life, but reach a greater ultimate size by virtue of their much longer lifespan. All these populations, with the possible exception of L. Geneva, are benthophagic or planktivorous, but it has been reported that piscivorous char from L. Onega, USSR, reach a length of 74cm, and those from the Kara Sea - Taimyr peninsula area of the USSR, which are also predacious, have a lifespan of 20-26 years and attain a weight of 10-15 kg (Behnke, 1972). Skreslet (1973a) also reported that predacious char from Nordlaguna, Jan Mayen Island, had a lifespan of up to 28 years and reached a length of 63.6 cm.

Table 3.9 The mean annual length (cm) of non-anadromous arctic char from various waters

A G E

Locality	Source	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Llyn Peris	present study	7.14	11.20	14.27	16.28	17.99	19.48	20.69	21.22							
Llyn Padarn	present study	6.96	12.35	16.19	19.60	21.53	22.90	24.19	25.18							
L.Windermere,Autumn spawners	Frost & Kipling, 1980	6.3	11.6	18.2	24.0	27.0	28.0	28.2								
L.Windermere,Spring spawners	Frost & Kipling, 1980	5.3	10.2	17.4	25.3	29.5	31.7	33.0	33.1							
L.Windermere dwarf Autumn "	Frost & Kipling, 1980	6.3	10.2	14.8	18.1	20.9	22.8									
L.Windermere dwarf Spring "	Frost & Kipling, 1980	5.3	8.5	12.1	15.5	18.6	19.5									
L. Geneva, France	Dussart, 1952		24.6	30.0	35.3	40.9	56.4									
L. Janet, France	Dussart, 1954			16.3	18.3	22.9										
L. Ovre Bjorkvattnett,Sweden	Nilsson&Filipsson,1971			18.15	21.62	23.93	25.29	26.66	26.97	28.23						
L.Torron,Sweden;Pre-impoundment	Runnstrom, 1951	9.1	15.5	24.1	30.0	34.5										
L.Torron,Sweden, Post "	Runnstrom 1951	7.7	13.0	18.4	23.6	26.8										
L. Nachikin, Kamchatka	Savvaitova, 1976a						35.2	37.0	40.3	42.5	41.5	46.0	38.5			50.5
Candlestick Pond,Newfoundland	Rombough et al, 1978	8.58	10.20	11.86	13.28	14.40		16.40								
Metamek Lake, Quebec	Saunders&Power, 1969			12.0	16.3	17.6	18.7	24.0	27.6	30.9	36.6	39.5	40.6	42.3	41.7	40.5
Six Lakes, Maine	Everhart&Waters, 1965	11.7	17.0	23.4	26.9	29.0	27.2									
Keyhole Lake, Alaska	Hunter,1970		12.3	15.9	19.3	21.3	22.7	24.6	27.4	29.9	30.6	31.6	32.6	33.3	34.4	
Little Fish Lake, Alaska	Sprules, 1952		16.3	16.5	18.8	19.0	23.1	25.9	27.4	28.4	31.0	30.7	35.1	34.5	35.1	37.8
Cache Creek Spring, Alaska	McCart & Bain, 1974		10.29	13.22	16.21	17.08	20.61	22.39	25.03	23.70	24.10					
Unnamed Spring, Alaska	McCart & Craig, 1973	5.38	8.57	11.30	12.17	13.33	14.88	15.67	14.85							
Shublik Springs, Alaska	McCart & Craig, 1973	5.01	7.50	10.28	12.89	15.17	16.51	16.47	19.33	20.25						
Canning River, Alaska	Craig, 1978	8.8	11.2	14.6	18.0	20.1	24.5	24.2	28.1	27.4	31.5					

CHAPTER 4 THE GONAD DEVELOPMENT AND FECUNDITY OF THE LLANBERIS CHAR

4.1 Introduction

The reproductive cycle of most teleosts is reflected by large seasonal changes in the size of the gonads. Although these changes have been well documented for many freshwater fish, for example perch, Perca fluviatilis (L.), (LeCren, 1951),chub, Squalius cephalus (L.), (Hellawell, 1971; Mann, 1976a), roach, Rutilus rutilis (L.), (Bray, 1971; Mann, 1973; Hellawell, 1972), pike, Esox lucius (L.), (Mann, 1976b), little is known of the cycle in arctic char. Hunter (1970) provides some detailed information from his study of an arctic lake, and Powell (1966) made a limited study of the Llanberis populations. The Dolly Varden, Salvelinus malma (Walbaum), a species closely related to the arctic char, was examined by Blackett (1968), and Vladykov (1956) investigated the development of the ova in brook trout, Salvelinus fontinalis (Mitchill).

The fecundity of the arctic char has been well documented, both for anadromous (Sprules, 1952; Grainger, 1953; Thompson, 1959; Moore, 1975) and non-anadromous populations (Maar, 1949; 1950; Dunbar and Hildebrand, 1952; Martin 1955a; Frost, 1965; Saunders and Power, 1969; Savvaitova, 1973; McCart and Craig, 1973; Doerfel, 1974; Rombough et al., 1978).

In this chapter, data are represented on the annual changes in condition and development of the gonads in the Llanberis char. The fecundity was also studied and related to various body **variables**.

4.2 Laboratory Methods

Char collected from Llyn Peris and Llyn Padarn between September 1974 and January 1976 were measured, to the nearest mm, from the tip of the snout to the fork of the tail and weighed to the nearest gram. The gonads were sexed macroscopically, excised from the body cavity, and weighed to the nearest 0.01g on an electric balance.

The condition factor of each fish was estimated from the nomograms devised by Cuinat (1971) which uses the formula of Hile (1936);

$$K = 100wl^{-3} \qquad \text{where } w = \text{weight in g}$$
$$l = \text{length in cm}$$

This was determined both for the total weight of each fish (K) and for the weight without the gonads (K_0).

The maturity index was calculated using the formula;

$$M.I. = \frac{\text{Gonad weight}}{\text{total weight - Gonad weight}} \times 100$$

The excised ovaries were preserved in modified Gilson's fluid (Simpson, 1951), the ovarian tissue having been split to aid penetration of the preservative. The samples were occasionally agitated by hand to help the breakdown of the ovarian tissue, and the samples remained in the preservative for periods varying between 6 months and 4 years. Prior to further examination, the remaining ovarian tissue was removed and the ova washed repeatedly in water. To allow for any deformity due to preservation, the mean ova diameter for each fish was determined by measuring the length of 20 ova arranged in a row and then dividing by 20.

Various authors (e.g. Vladykov, 1956; Thompson, 1959; Rombough et al., 1978) have reported differences between the weights of the left and right ovaries in arctic char, which may result in a variation of egg diameter between the ovaries. No attempt was made to analyse this difference in the present study, although it was noticed, and, to safeguard against any variation in diameter, the ova were well mixed before picking out 20 to measure.

The distribution of ova sizes within the ovaries was assessed by drawing 100 ova at random from each of the ovaries of 5 fish captured from Llyn Peris and measuring their diameter with an ocular micrometer. The diameters were recorded in 0.20mm size classes, and the exercise was undertaken for samples taken in April, August and December only.

Because of the relatively small number of ova contained in the ovaries, the fecundity of the char was estimated by direct counting rather than volumetrically or gravimetrically.

The term 'mature' is applied to those fish which would have probably spawned that year and 'immature' to those which would not.

4.3 The Annual Cycle of Condition

Bagenal (1957) remarked that it is desirable to consider the condition of the fish prior to analysing data on their breeding and fecundity; many breeding phenomena might be associated with the well-being of the particular individuals.

The commonest estimation of the condition factor in fishery studies is that of Fulton (1911), modified by Hile (1936);

$$K = \frac{100w}{l^3} \quad \text{where w is in cm and l in gm}$$

The heavier a fish is at a given length, then the larger the value of 'K' and therefore the 'better' its condition. This formula is only strictly valid when the growth of fish is isometric; having an unchanging body form with increased length, confirmed by the regression coefficient (b) in the length/weight relationship ($w = al^b$) being equal to 3. For allometric growth, where b does not equal 3, LeCren (1951) considered that the relative condition factor, K_n, derived from the formula;

$$K_n = \frac{100w}{l^b}$$

is more suitable, the value of b being determined from the length/weight relationship under 'standard' conditions or from pooled monthly data. As it is usually difficult to decide what conditions are standard and as there is normally considerable error in the estimates of b, the relative condition factor has been much less used than Fultons (Ricker, 1975).

Although the values of b for Padarn and Peris char varied between 2.52 and 3.49, significantly different from 3, for most of the year, it was decided, in this study, to use the formula of Hile (1936) to enable comparisons to be made with what little information is available from other workers.

Figs. 4.1 and 4.2 show the mean monthly condition factors, with standard deviation, for male, female and immature char from Llyn Peris and Llyn Padarn. Smoothed curves were fitted by eye. The condition factor is shown both for the weight with gonads (K) and without (K_0), although there was negligible difference in these parameters when the gonads were

Fig. 4.1 The mean condition of mature male, mature female and immature Llyn Peris char in each month.

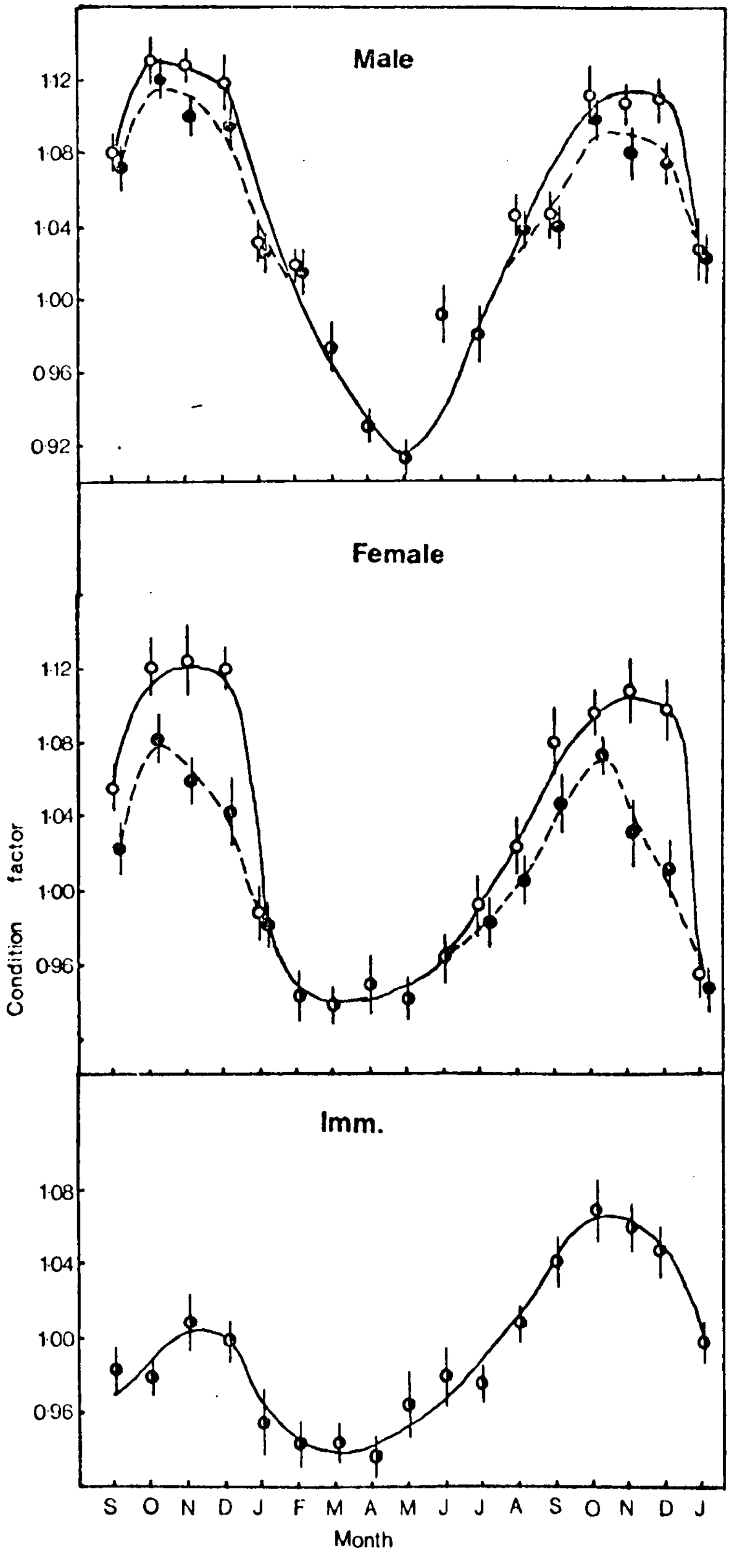
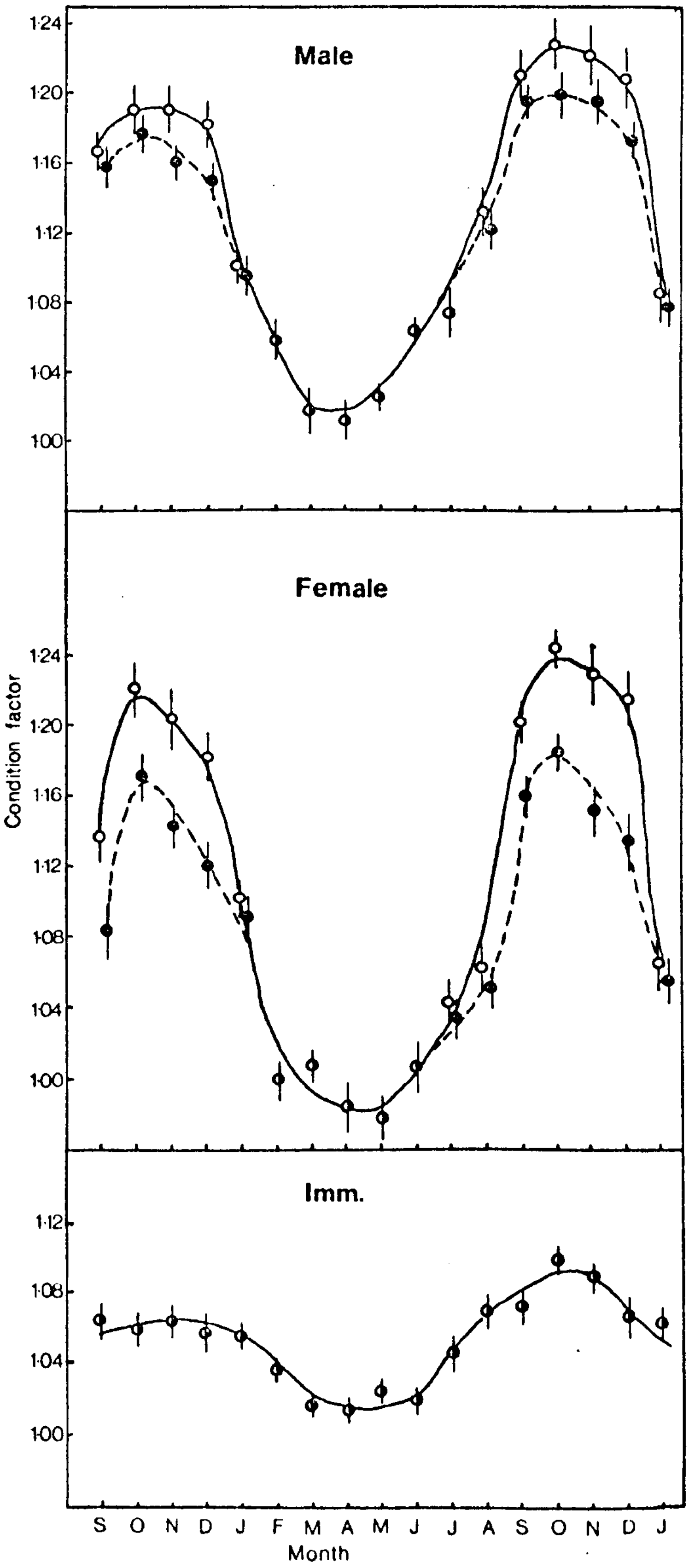


Fig. 4.2 The mean condition of mature male, mature female and immature Llyn Padarn char in each month.



very small; for the immature fish all year and the mature males and females in spring and early summer. An annual cycle of the condition of the fish is evident for all three groups; it being highest, that is a greater weight per unit length, around October, and lowest during April and May. With the mature fish, the peak of total condition, with gonads, was maintained from October to December, the spawning period, but there was a decline in the condition without gonads over this period, indicating that food reserves were being used during the rapid development stage of the gonads (section 4.4). A similar pattern has been observed in other fish species, for example the perch (LeCren, 1951), the long rough dab, Hippoglossoides platessoides (Fabr.), (Bagenal, 1957) and dab, Limanda limanda (L.), (Htun-Htan, 1978). Greene (1926) found that king salmon, Onchorhynchus tschawytscha, lost 51.6% of their total muscle mass; the fat content of the muscle fell from 15.2 to 2.2% and the protein content fell from 17 to 13.7% at spawning. Similar changes have been recorded in other fish, for example the herring, Clupea harengus, (Wood,1958) and the mackerel, Scomber scombrus, (Luhmann, 1956). This fall in condition of the char also corresponds to a decline in feeding (Powell, 1966), either due to the paucity of available food or to the behaviour associated with spawning. Because a fall was also observed in the condition of immature fish over this period, the decline was probably due to the lack of available food. The decline was more pronounced in the mature females than the mature males, indicative of the larger gonads produced by the females, and a correspondingly greater depletion of the food reserves.

Following spawning, there was a rapid loss in condition throughout the rest of the winter and spring, reaching a minimum in April and May.

There was then a rapid increase through the summer, attaining a maximum, as discussed, in October and November. These changes corresponded approximately with the cycle of feeding intensity observed by Powell (1966) in her earlier study. The condition cycle without gonads was similar in both mature males and females and the values were approximately equal at the same time of year; the females reaching a greater condition with gonads in the winter by virtue of their greater gonad weight. In general, the condition of the Padarn char was greater than those from Peris at corresponding times of the year (K = 0.98 - 1.24 for Llyn Padarn; 0.95 - 1.14 for Llyn Peris). There was also an annual cycle in the condition of the immature char, but of a reduced intensity than the mature fish; the condition of those from Padarn again being greater than Llyn Peris char.

There has been, as far as can be ascertained, no other study of the annual cycle of condition of the arctic char, but Cooper (1953) demonstrated a similar one to those found for Llanberis char for brook trout, Salvelinus fontinalis, in three Michigan streams. Saunders and Power (1969) calculated condition factors of between 1.02 and 1.32 for arctic char from Metamek Lake, Quebec, and Skreslet (1973a) for char from Jan Mayen Island, found that 'large' char had condition factors between 1.0 and 1.5, similar to the values found for Llanberis char, but that mature 'small' char had very low condition factors of between 0.4 and 0.9.

4.4 Development of Gonads

The gonad structure of female arctic char is similar to that of other salmonids. There are two ovaries, usually unequal in size, which are attached by connective tissue to the body cavity anteriorly and are free posteriorly. As in other salmonids, the oviducts are lacking and the mature ova are released from the ovary and collect in a trough formed by the extension of the peritoneal membrane surrounding the ovary. The two troughs unite posteriorly on the upperside of the intestine to form a single 'oviducal channel' which guides the ova to the genital pore (Kendall, 1921).

Ova are always present in the ovaries of char, and three types can normally be distinguished in the ovaries of mature females, and are similar to those described by Vladykov (1956) for brook trout:

Class a, recruitment stock: these are small, yolkless (appearing white in preserved samples) ova less than 1mm in diameter. These eggs develop in clusters that are intermingled with the maturing ova throughout the ovary. After the mature ova are spawned, the recruitment eggs remain in a loose string of ovarian tissue. A portion of these eggs will provide the future spawning stock.

Class b, maturing ova: these are the largest ova in the ovary which are usually yellow in the immature stages of development and orange at the attainment of maturity. The ova diameter increases from about 1mm in the early stages to 3-4mm at spawning. During development they gradually decrease in number but increase in size. All maturing eggs which stop developing become atretic.

Class c, atretic ova: these are the originally maturing ova which become degenerate while the remaining ova continue to develop into maturity. They gradually lose shape, become white and are reduced in size as degeneration proceeds. Vladykov (1956) compared their existence to that of a 'safety valve'. If all the original ova in the ovary develop to maturity, they would possibly burst from the ovary prior to spawning. He concluded that from 39 to 44% of the maturing ova in brook trout could be expected to become atretic. Henderson (1963), working with hatchery-reared brook trout, showed that when an adjustment was calculated for the changing length of the female during the secondary growth of the ova, the extent of atresia was less than 5%. Wydoski and Cooper (1966), studying wild populations of brook trout, considered that the extent of atresia was primarily related to conditions of food growth, and they found that under favourable growth conditions, as in a hatchery, atresia may reduce egg numbers by only about 5%, but under less favourable conditions, as in a natural population, reduction in egg number may be over 50%.

Atretic ova were obvious in the ovaries of Llanberis char, but no attempts were made to estimate their numbers. Atresia occurs mainly in the first stages of ova maturation, and all estimates of fecundity in the present study were made from females captured in November and December only, when atresia should have been completed (Vladykov, 1956; Henderson, 1963).

The testes of the male arctic char are, as with the ovaries, also paired and lie below the swim bladder, against the wall of the body cavity and extend along its whole length. In immature fish they are narrow white tubular structure, slightly thickened anteriorly. In maturing fish, the anterior, and later the middle portions of the testes expand and become creamy coloured. The final size of the testes never fills the body cavity to the same extent as the ovaries. The maximum width of each testis varies from about 1mm in immature char to a maximum of 11-12mm immediately prior to spawning.

Plots of gonad weight against body weight in each month showed there to be a linear relationship for both sexes. Examples are shown in Figs. 4.3 to 4.5 for male and female char caught in September and December. The linear relationships were confirmed by plotting the logarithm of the gonad: body weight ratio against body weight (LeCren, 1951). The data for September and December, males and females (Fig. 4.6) each gave horizontal bands of points on the graphs for each sex in each month. Although there is some individual variation, there was, therefore, a constant gonad weight: body weight ratio for all sizes of char of the same sex at the same state of maturity in each lake.

A similar constant ratio has been reported for many fish populations including perch (LeCren, 1951), roach (Hellawell, 1972), dace (Mann, 1974) and pike (Mann, 1976b), but the relationship may be linear or non-linear for the same species from different localities, or between sexes. For instance, Hellawell (1971) found there to be an increase in relative gonad weight with increasing body weight for female chub, but a constant relationship for males; whereas Mann (1976a) found there to be a constant relationship for both sexes of the same species from a different locality. Hunter (1970) demonstrated a constant relationship in char from an arctic lake as did Frost (1965) for mature autumn and spring spawning char in Windermere. Blackett (1968) also found there to be a constant relationship for anadromous Dolly Varden and used the variation in the slope of the regressions between ovary weight and body weight to illustrate the seasonal changes in maturity.

Fig. 4.3 The relationship between gonad weight and body weight of male and female mature char from Llyn Peris and Llyn Padarn for September.

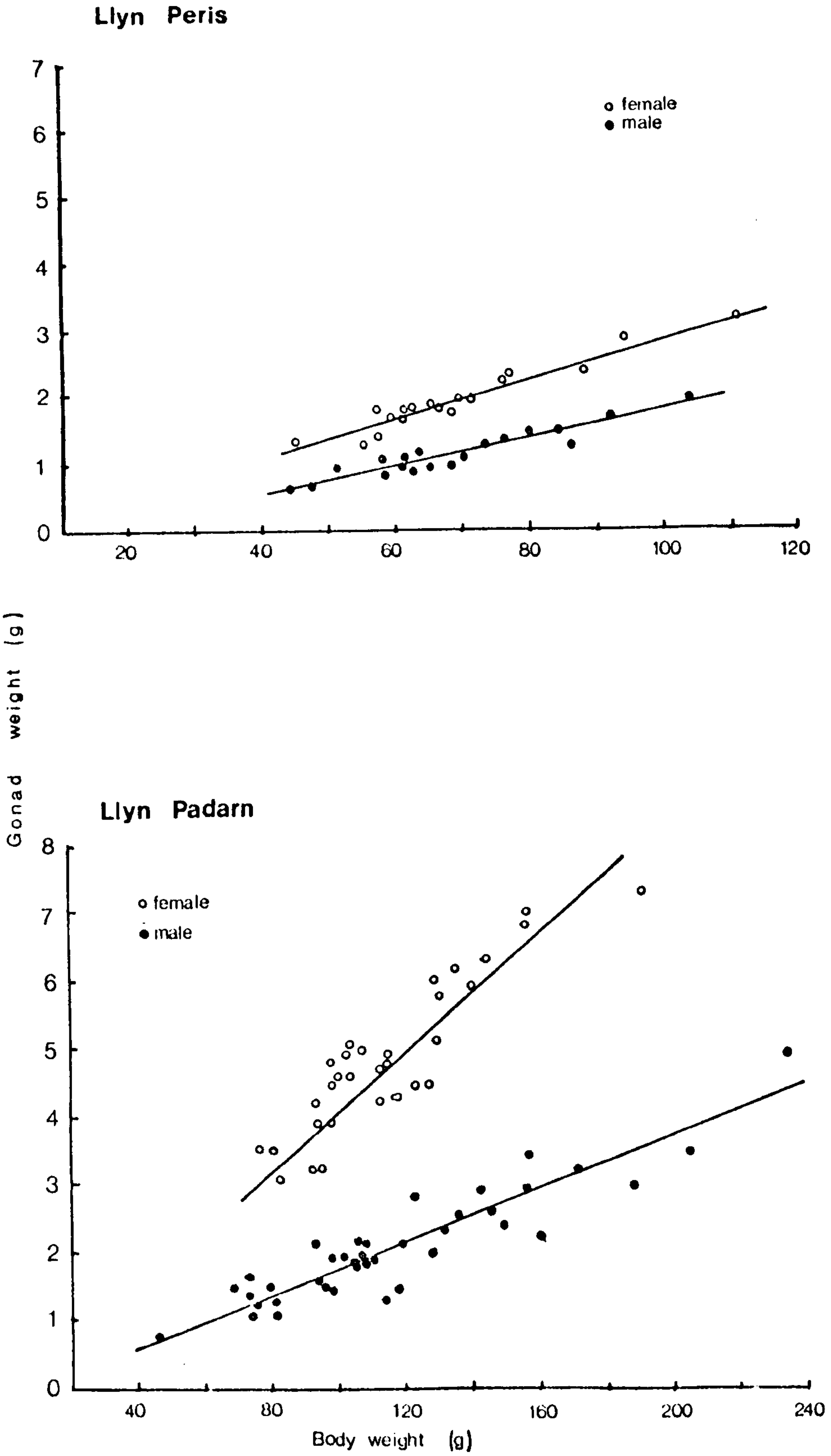


Fig. 4.4 The relationship between gonad weight and body weight of male and female mature char from Llyn Peris for December.

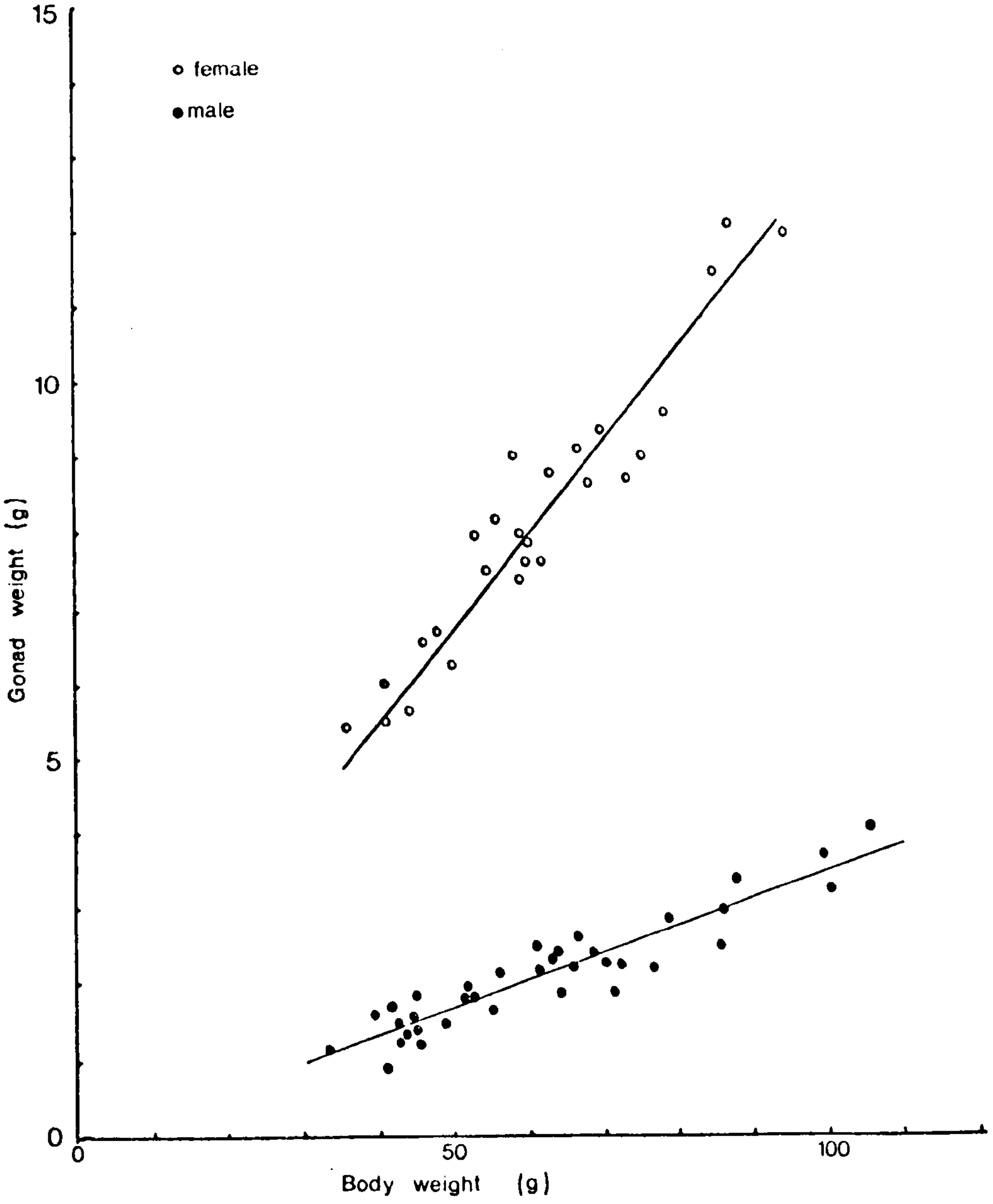


Fig. 4.5 The relationship between gonad weight and body weight of male and female mature char from Llyn Pararn for December.

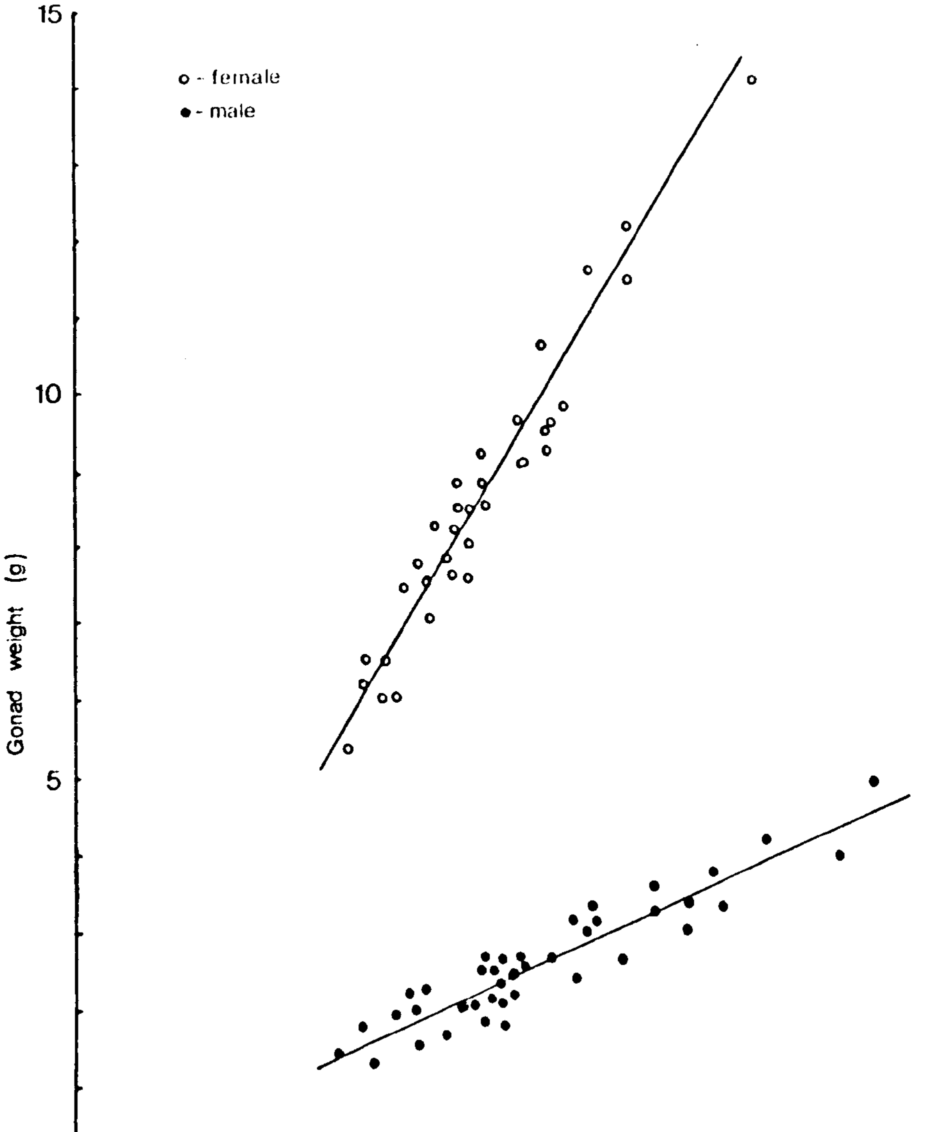
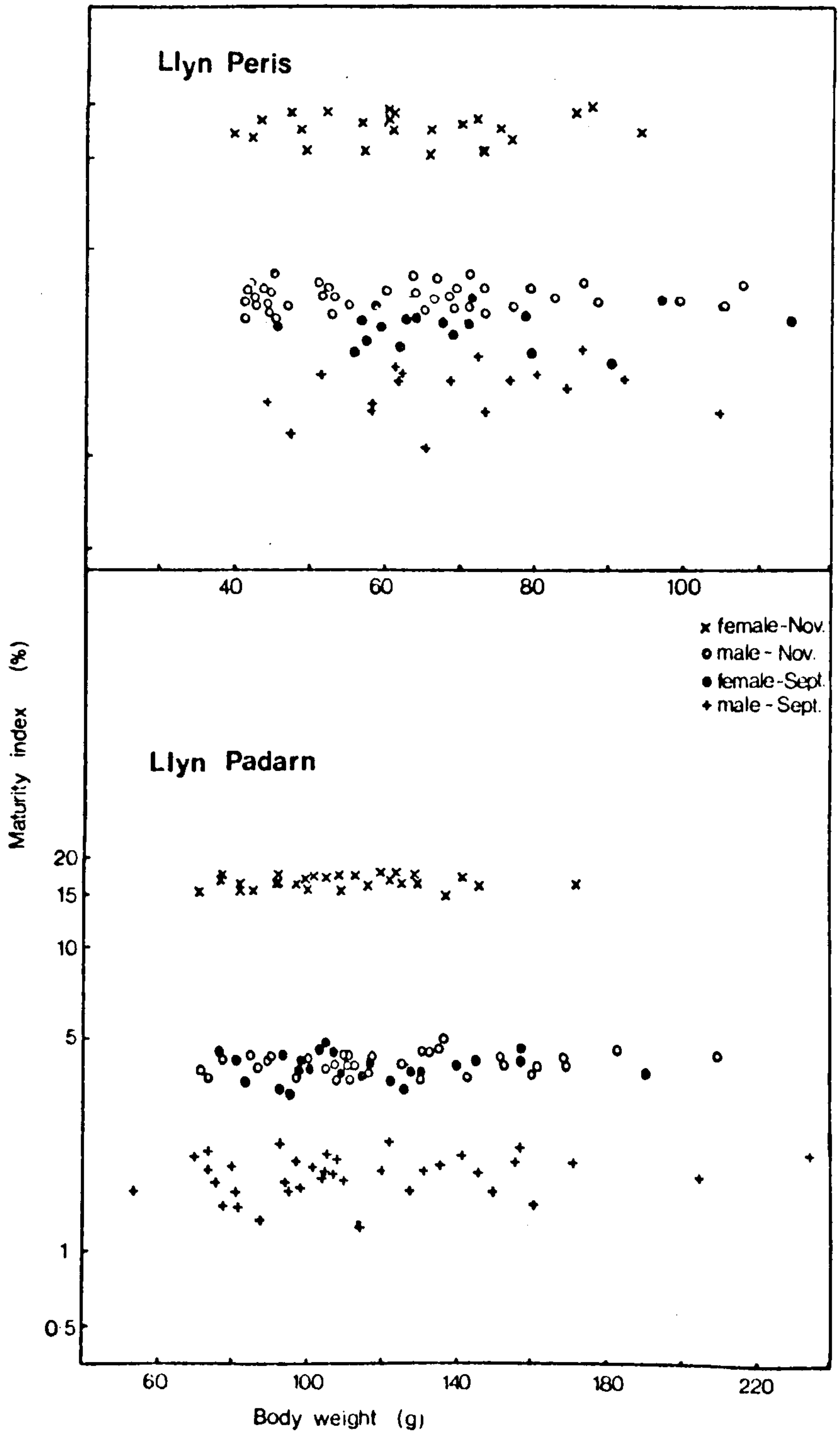


Fig. 4.6 The relationship between Maturity Index (log. scale) and body weight of mature male and female char from Llyn Peris and Llyn Padarn for September and December.



The constant gonad weight: body weight relationship for Llyn Peris and Llyn Padarn char enabled plots of the mean ratio, expressed as a percentage, for each month to show the seasonal changes of gonad development. These are shown in Figs. 4.7 and 4.8, smoothed lines having been drawn by eye. The ovaries of mature females were of minimum size, approximately 1% of body weight, between February and June. They increased slightly in weight during July and August, and rapidly in September, October and November, attaining their maximum size in early December, immediately prior to spawning. The ultimate size of the ovaries was greater for Padarn char, 17-18% of body weight, than for Llyn Peris, 13-14%. Freshly spent females had empty ovaries of about 3% body weight. Frost (1965) found that autumn spawning char of Lake Windermere had ovaries of about 20.6% body weight at maturity, and the spring spawners about 19.7%. There is,therefore,variation in the gonad weight: body weight ratio even between populations from the same lake, and so the difference between the Llanberis char is not surprising. It is possible that this is due to the growth and condition of the fish; Windermere char grow appreciably faster than those from Padarn which in turn grow faster than Peris char. Moore (1975) also found great variation in the mature ovary weights of migratory char from nearby rivers in the Cumberland sound area of Canada.

The mature males showed a similar seasonal variation to that of the females. The minimum size of the gonads, between February and June, was about 0.5% of body weight, and they began increasing in size in July, at about the same time as the females, but attained their maximum, or near maximum, size, about 3.5% of body weight for Llyn Peris and 5% for Llyn Padarn char, in November, slightly earlier than the females. By being ready to spawn throughout the spawning period, the males are

Fig. 4.7 The seasonal variation in the Maturity Index for mature male, mature female and immature char from Llyn Peris.

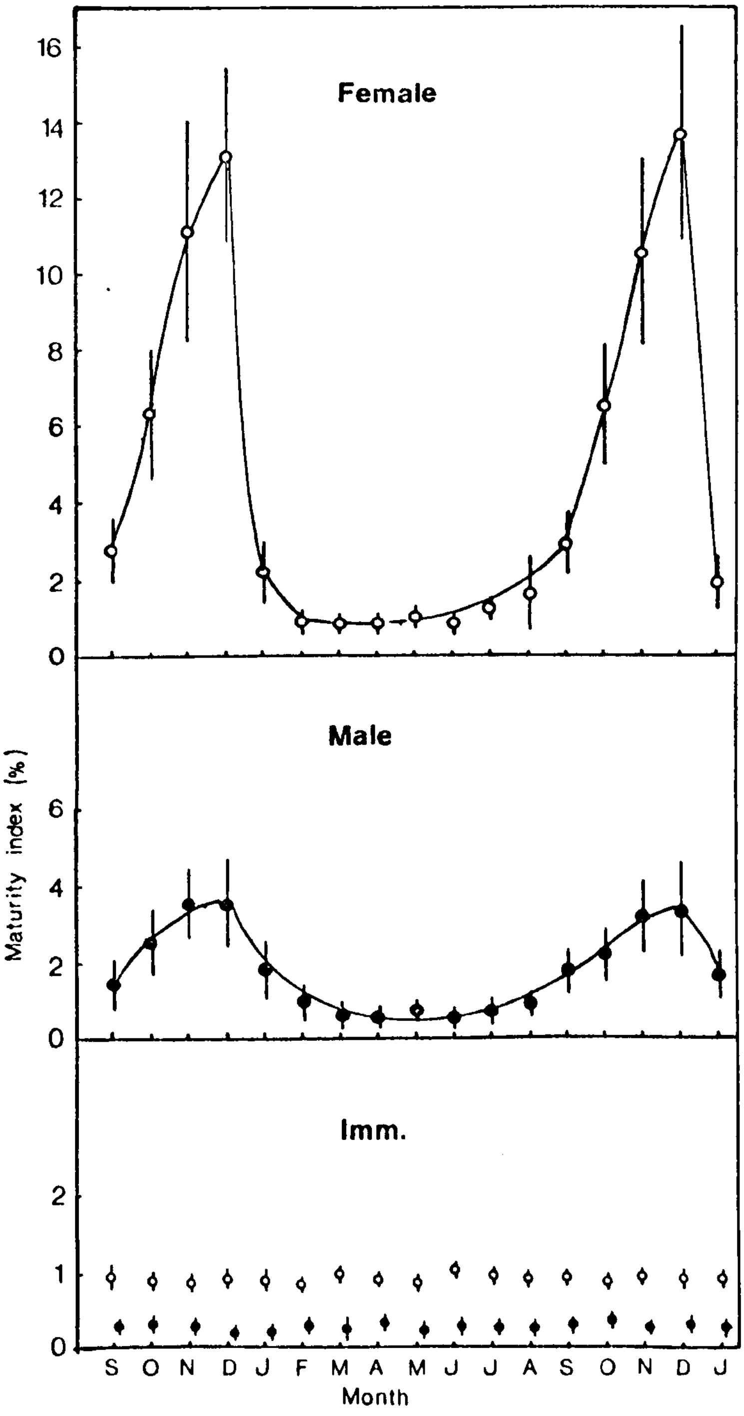
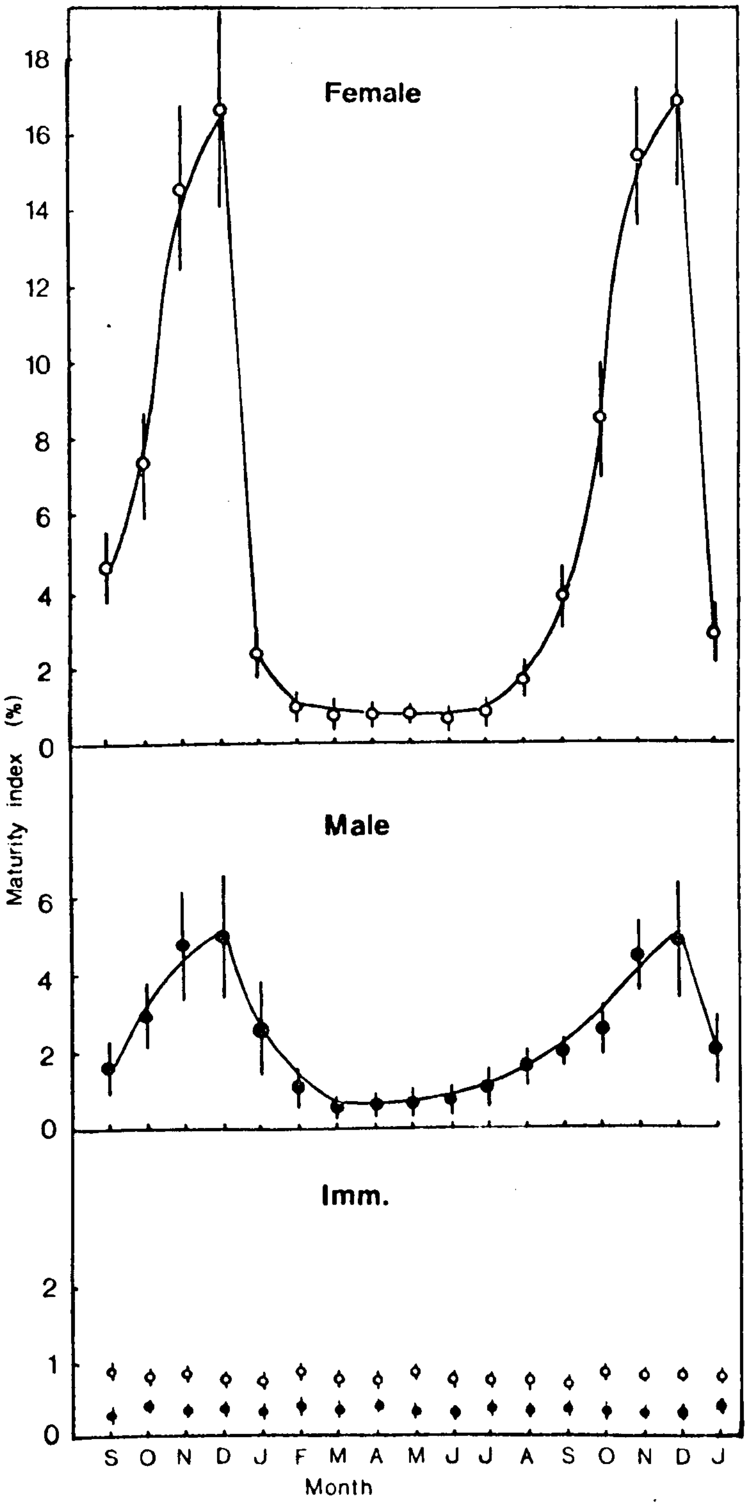


Fig. 4.8 The seasonal variation in the Maturity Index for mature male, mature female and immature char from Llyn Padarn.



presumably able to maximise their reproductive opportunities. The comparatively high weight of the testes in January (about 2% of body weight), after the spawning has been completed, indicates that most of the males do not use all the contents of their testes during spawning. The maturity index for immature fish remained reasonably constant, with no discernible seasonal variation, throughout the year and their gonads were of about the same proportional size as the quiescant gonads of the mature fish; about 1% of body weight for females and 0.5% for males.

The rapid increase in the weight of the ovaries prior to spawning is due to the uptake of fluid by the oocytes, which results in them swelling and becoming hyaline (Fulton, 1898). The seasonal variation in size of the class b (maturing) oocytes is shown in Fig. 4.9 for Llyn Peris and Llyn Padarn char. The average diameter of the quiescant ova, between January and July, is about the same for both lakes, between 0.8 and 1mm, and increases rapidly from August to December, reaching a maximum size of 3.96mm (s.d. = 0.18) for Llyn Padarn char and 3.55mm (s.d. = 0.16) for Llyn Peris (significantly different, $p < 0.001$). A similar seasonal variation was demonstrated for a population of non-anadromous riverine char in Alaska by McCart and Craig (1973).

The relationship of the class a and class b oocytes in the ovary is shown by the length/frequency histograms of oocyte diameter for April, August and December (Fig. 4.10). There was a group of class a, recruitment stock, oocytes, diameter about 0.3mm, present throughout the year. The class b, developing ova, were approximately 0.9mm in diameter in April, increasing to about 1.5mm in August and 3.5mm in December, prior to spawning. In December, there were indications that the class b oocytes that would be spawned in the following year were beginning to develop

Fig. 4.9 The seasonal changes in egg diameter of mature arctic char from Llyn Peris and Llyn Padarn.

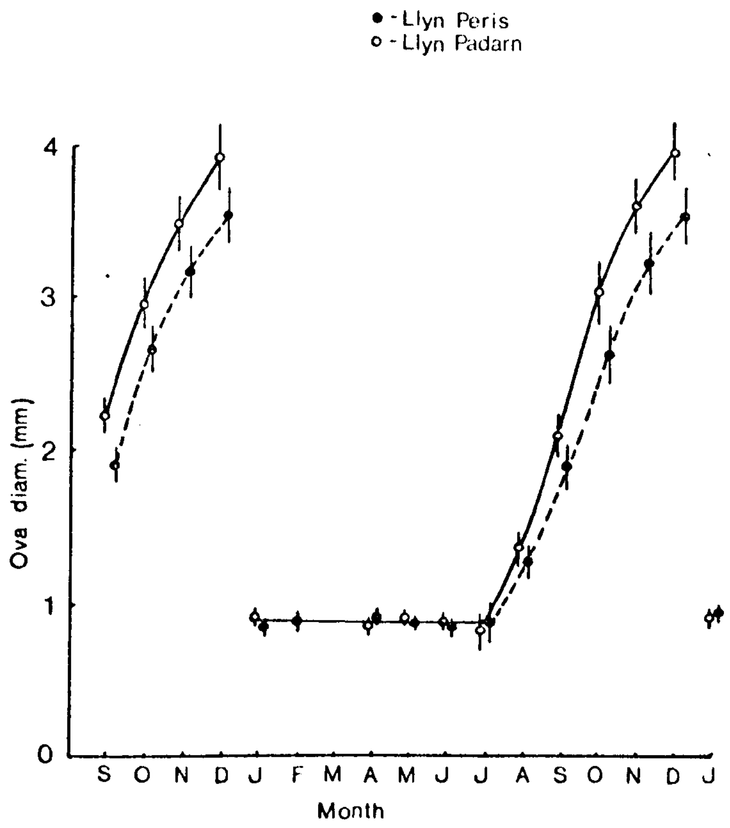
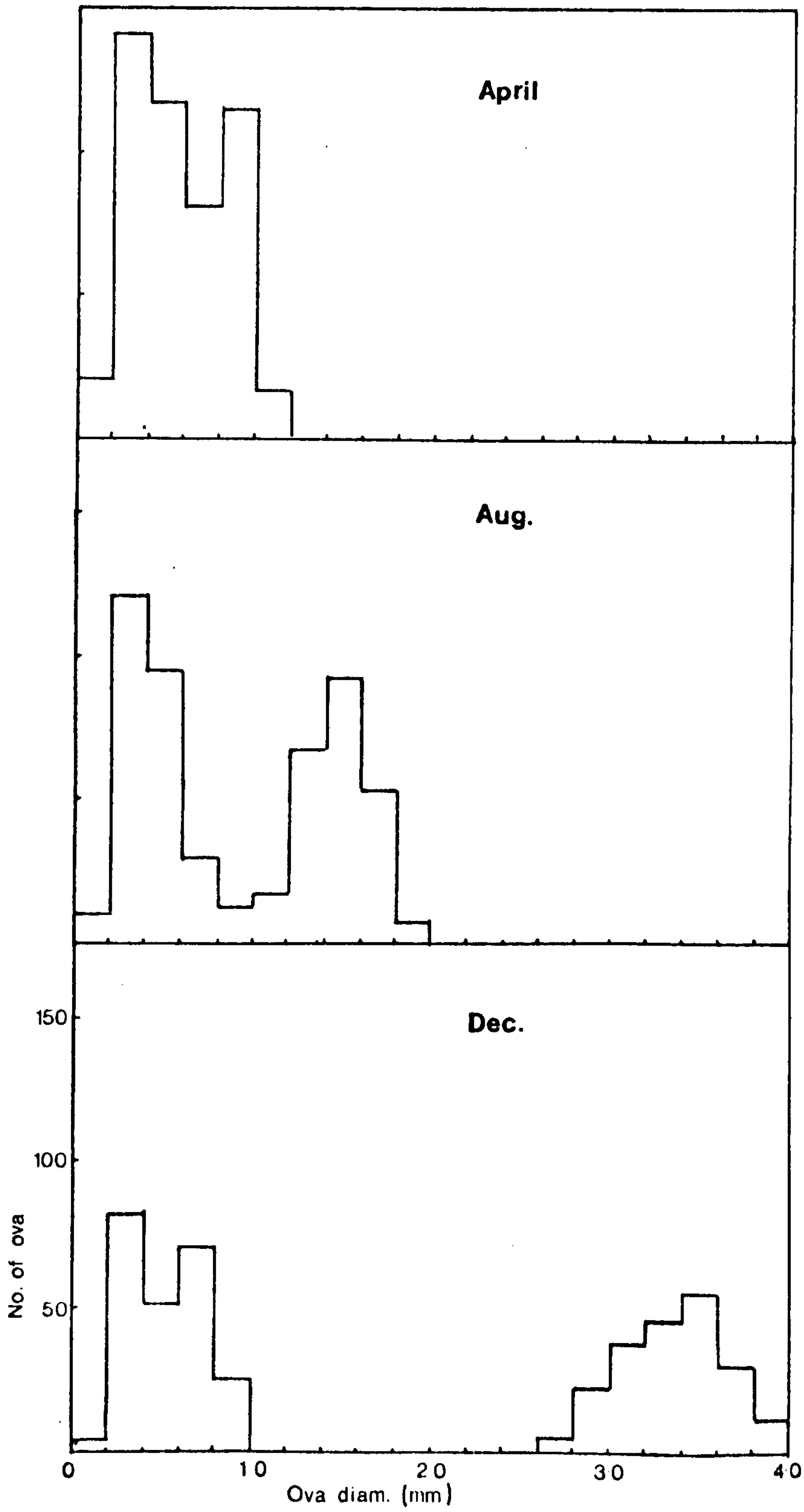


Fig. 4.10 The length-frequency distribution of oocytes in the ovaries of char in April, August and December.



from the class a oocytes. This cycle of development has also been shown for brook trout (Vladykov, 1956) and for the bloater, Coregonus hoyi, of Lake Michigan (Emery and Brown, 1978), but has apparently not been demonstrated for arctic char previously. Stuart (1953) reported that the ova of brown trout, Salmo trutta, increased from 0.3mm to 6mm in a single season, development of similar magnitude taking two years to complete in salvelinids and coregonids.

The ultimate size of mature ova reported from other populations is extremely varied. Saunders and Power (1969) found that ova diameters varied between 3.2 and 4.4mm; Rombough et al.(1978) diameters between 2.5 and 3.4mm; McCart and Craig (1973) diameters between 3.7 and 4mm; and Hunter (1970) reported an average ova diameter of 4.78mm, all for North American populations of non-migratory char, while Moore (1975) reported that the ova diameter from four anadromous populations varied between 3.2 and 4.3mm.

Maar (1950) reported ova sizes varying between 3.9 and 4.8mm for some Scandinavian populations and Frost (1965) between 3.9 and 5.1mm for Lake Windermere char, but these were the diameters of fertilised ova which are larger than unspawned ones. The relationships between ova size and fecundity, fork lengths and ovary weight is discussed in section 4.6

4.5 Attainment of Sexual Maturity

Table 4.1 shows the percentage of mature male and female char found at different ages in each lake.

Table 4.1 The number of mature char, expressed as a percentage, found at each age from Llyn Peris and Llyn Padarn

		AGE NEXT BIRTHDAY						
		3	4	5	6	7	8	9
Llyn Peris	Males	30	77	100	100	100	100	100
	Females	0	51	92	100	100	100	100
Llyn Padarn	Males	21	58	100	100	100	100	100
	Females	0	23	90	100	100	100	100

This indicates that there was precocious maturity of the male char in both lakes, some individuals being mature at the end of their second year. All the males were mature by the end of their fourth year. No females were found mature at the end of their second year in either lake, but some matured during their third year and all were mature at the end of their fifth year of life.

It was suspected, from the data in Table 4.1, that there might have been a slight difference in the average age of maturity between the two populations because of the lower percentage of mature char in the second and third age groups (age 3 and 4 next birthday) in Llyn Padarn. The samples were too small for analysis of the second age group, but the actual numbers of mature and immature male and female char in the third age group were tested for differences by X^2 analyses (Table 4.2).

Table 4.2 Contingency tables to compare the numbers of mature char of each sex from both lakes

Males	Mature	Immature	Total	
Llyn Peris	37	11	48	
Llyn Padarn	21	15	36	χ^2 (with Yates' correction) = 2.56
Total	58	26	84	$0.05 < p < 0.10$

Females	Mature	Immature	Total	
Llyn Peris	23	32	45	
Llyn Padarn	8	27	35	χ^2 (with Yates' correction) = 2.68
Total	50	40	80	$0.05 < p < 0.10$

Although the χ^2 values for both males and females are approaching significance ($0.05 < p < 0.10$), the slight indication that the Llyn Peris char mature slightly earlier than those of Llyn Padarn has to be rejected at the 95% confidence level. Larger samples, or a method of sampling that was unbiased for fish of younger age groups, may have shown the suggested difference.

Alm (1959) showed that in fish of the same age maturity was reached earlier by larger fish. To analyse for this in the Llanberis char, Students' 't' tests were performed on the average size of mature and immature male and female fish from each lake. Again the samples were too low for meaningful analysis of the fish in their second year, so computations were only carried out on the data for fish in their third year (4 next birthday). The results are shown in Table 4.3.

Table 4.3 Comparisons of the average lengths of 3 year old mature and immature char from both lakes

	N	Mean length	s.d.	Significant differences between means
Llyn Peris				
Females, immature	23	16.11	0.73	yes, 0.001 < p < 0.002
Females, mature	32	17.12	0.94	
Males, immature	11	16.06	0.61	no, 0.10 < p < 0.25
Males, mature	37	16.48	0.77	
Llyn Padarn				
Females, immature	27	19.42	0.94	yes, 0.001 < p < P.002
Females, mature	8	20.46	1.03	
Males, immature	15	19.28	1.02	yes, 0.01 < p < 0.02
Males, mature	21	20.19	0.98	

Except for the Llyn Peris male char, the mature fish were significantly larger than the immature ones at the same age, which supports the findings of Alm (1959). As mentioned previously, a larger or less biased sample, may have detected a significant difference between the Llyn Peris males.

Maturity at an early age and relatively small size is typical of many non-anadromous arctic char populations (Sprules, 1952; Frabricius, 1953; Frost, 1965; Saunders and Power, 1969; McCart and Craig, 1973; Rombough et al., 1978). However, not all populations exhibit precocious male maturity; in some lakes both the males and females mature at an early age and small size. Dunbar and Hildebrand (1952) reported catches of mature males of 5.3cm in length and mature females of 6.4cm, in their first year of life, and Martin (1955a) caught male and female char as small as 7.6 and 8.9cm which were also mature, both from populations in the Ungava bay area of Quebec.

Most non-migratory char spawn every year after maturity, but Hunter (1970) and Savvaitova (1976a) reported that spawning was irregular in some long living, but slow growing, populations. Migratory char do not generally mature until their 10th or 12th year and spawn every second or third year thereafter (Yessipov, 1935; Grainger, 1953; Moore, 1975), although Nordeng (1961) reported annual spawning by migratory char from northern Norway.

4.6 Fecundity of the Llanberis Char

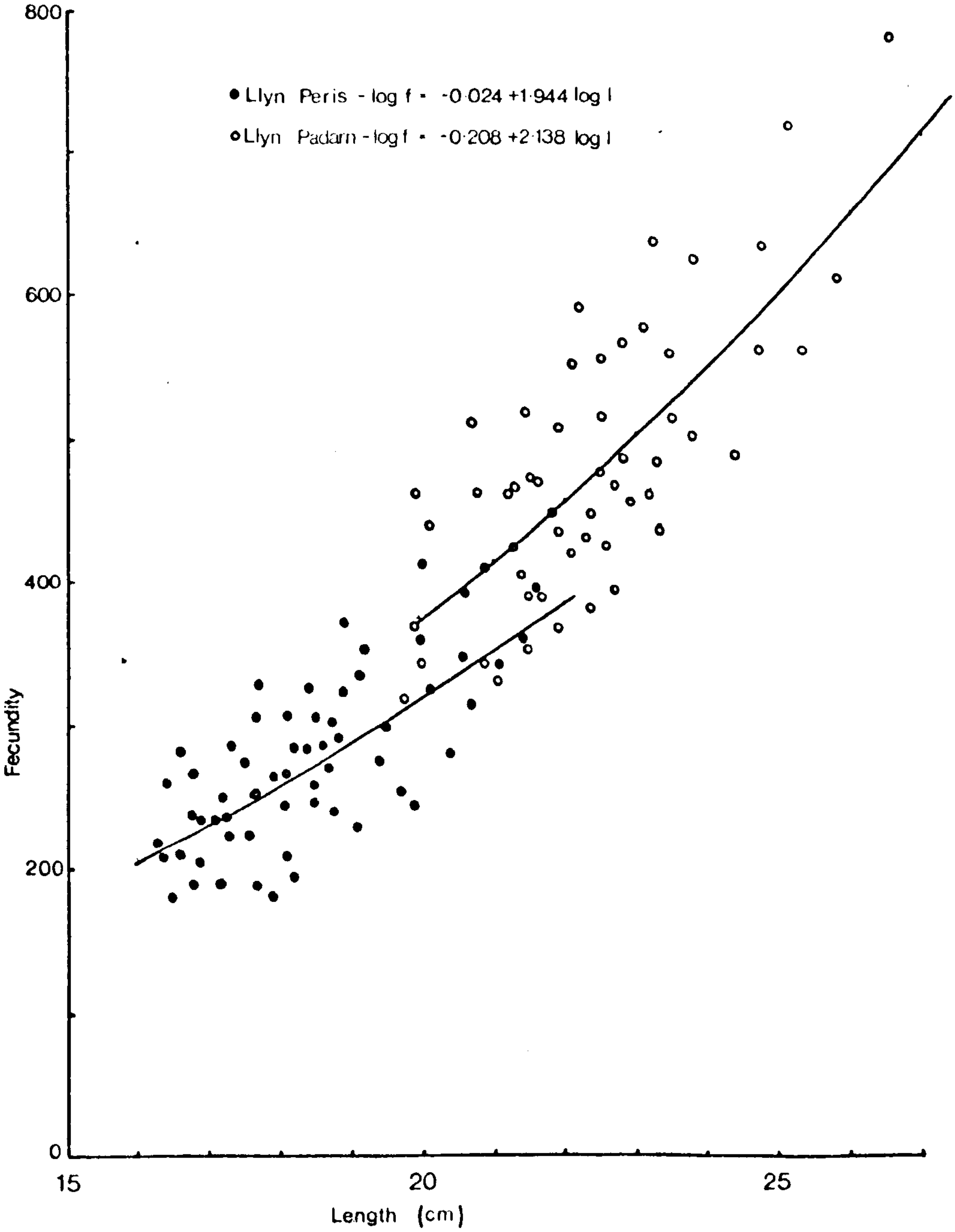
The fecundity of a fish may be defined as the potential number of ova that a female is capable of depositing upon spawning (Blackett, 1968). It is not the number of ova in the ovaries at any one time, because the number decreases during the early stages of maturation due to atresia (Vladykov, 1956; Henderson, 1963; Wydoski and Cooper, 1966), an observation apparently unknown to Maar (1949) and Grainger (1953). As has been mentioned, counts of the number of ova were therefore only made from char caught in November and early December, when atresia has been completed (Vladykov, 1956), but before the ovaries were running ripe, which may have caused an underestimation due to losses. At this time, the length and body weight of the char were relatively unchanging (Chapter 3). Data concerning mature ova diameter or ovary weight were only taken during December, as there was growth in both of these parameters during November.

The fecundity varied between 190 (fish length 16.8cm) and 415 (fish length 20.0cm) for Llyn Peris char, and 320 (fish length 19.7cm) and 780 (fish length 26.5cm) for Llyn Padarn char. Regression curves and scatter diagrams for the relationship between fecundity and the fork length of the fish are shown for both lakes in Fig. 4.11.

The regression equations were calculated from logarithmically transformed data and they are indicated, together with their correlation coefficients, for each population. Although the data for both lakes were very scattered, both correlation coefficients were significant, indicative of a positive relationship between fecundity and fork length. Grainger (1953); Thompson (1959) and Moore (1975) showed similar logarithmic relationships, but Maar (1949) and Hunter (1970) found linear relationships, although their data were very scattered. Some very slow growing populations of char showed no relationship whatsoever between fecundity and length (Dunbar and Hildebrand, 1952; Saunders and Power, 1969; McCart and Craig, 1973; Rombough et al., 1978). Blackett (1968; 1973) found there to be a logarithmic relationship for both anadromous and non-anadromous populations of Dolly Varden.

The curves showing the relationship between fecundity and length are plotted from antilogarithm values for convenience of interpretation. Logarithmic transformation tends to give the data homoscedasticity, destroying the relationship of increasing variance in fecundity with increased length. Conversion of the logarithmic value to natural numbers for graphical purposes may not provide a regression curve that will fit the upper parts of the data as well as the straight line fit of the transformed data (Blackett, 1968).

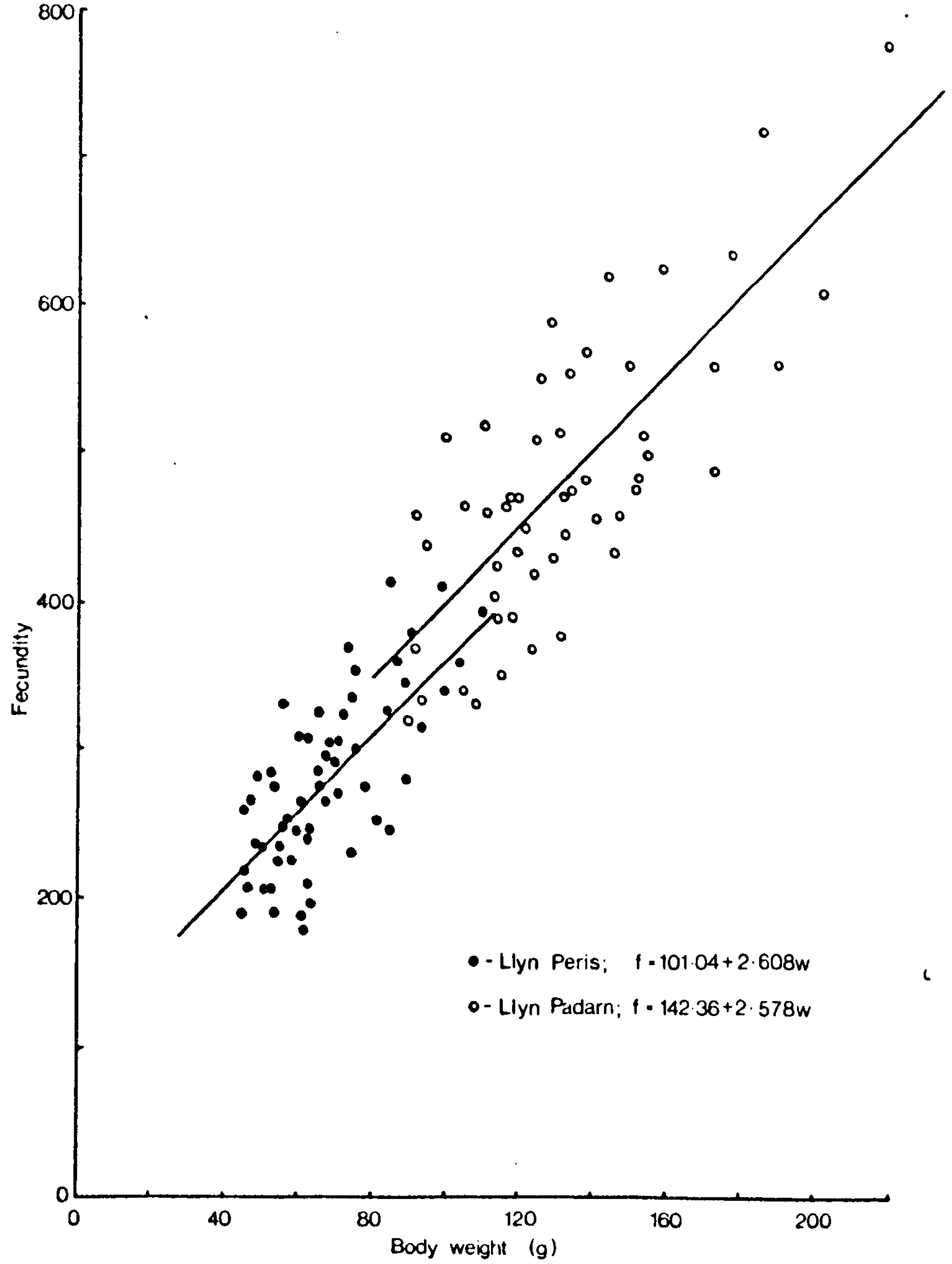
Fig. 4.11 The relationship of fecundity to fork length for Llyn Peris and Llyn Padarn char.



Analyses of covariance indicated that there was no significant difference ($p < 0.1$) in the slopes (relative rate of increase in fecundity), but there was ($p < 0.001$) in the elevations (average logarithm of fecundity adjusted to a common logarithm of body length). On average, a small Padarn char of 20.0cm would produce approximately 65 more eggs than a Peris char of the same length. Scott (1962), for rainbow trout, Salmo gardneri, and **Ba**genal (1969), for brown trout, found that better fed fish were more fecund. This may be due to the greater amount of atresia in less well fed populations, as shown by Wydoski and Cooper (1966). The greater condition of the Padarn char may indicate that they enjoy better feeding, which may explain the difference in fecundity.

There was a better correlation for untransformed data relating body weight to fecundity ($r = 0.715$ for Llyn Peris char and $r = 0.727$ for Llyn Padarn), which may be expected since the relationship of weight to length is similar to that of fecundity to length. The scatter diagrams and regression equations for the relationship of fecundity to weight are shown in Fig. 4.12. Again, there was no significant difference in the slopes of the regression ($p < 0.1$), but there was ($p < 0.01$) in the elevations. Bagenal (1957), during his study of the long rough dab, showed that a better estimate of fecundity could be obtained from body weight data than length. Blackett (1968) suggested that preference should be given to fecundity:length relationships because greater variance can usually be expected from weight measurements due to the variable stomach contents of the sampled fish and that the total weight is influenced by fecundity and is, therefore, not a completely independent variable. Char, and especially those which have been in gill nets for a period of time, do not have heavy stomach contents (Powell, 1966), and the

Fig. 4.12 The relationship between fecundity and body weight of Llyn Peris and Llyn Padarn char.



weights used in this present study were of total weight less ovary weight. The correlation coefficients of length and body weight against fecundity for Llanberis char would indicate that body weight is the better estimator, but both would be subject to a good deal of error when used separately.

Bagenal (1957) also suggested that gonad weight was a good estimator of fecundity. Scatter diagrams and regression equations of this parameter for Llanberis char are shown in Fig. 4.13. The correlation coefficients ($r = 0.764$ for Llyn Peris; $r = 0.761$ for Llyn Padarn) are slightly better than the body weight:fecundity and length:fecundity relationships, but only marginally so. There was a significant difference in both the elevations ($p < 0.001$) and the slopes ($p < 0.001$) of the regression; Peris char having a greater number of ova per unit weight of ovary than Padarn char, which is accounted for by the difference in ova diameter shown in section 4.4

There was no significant correlation between ova diameter and fecundity ($r = 0.253$ for Llyn Padarn, $p < 0.10$; $r = 0.072$ for Llyn Peris, $p < 0.10$), but there was for the relationships between ova diameter and length, although the data were very scattered. The relationships between ova diameter and length are shown in Fig. 4.14, the logarithmically transformed data giving a slightly better correlation than the untransformed data. There was, therefore, a tendency for the average diameter of the ova to increase with increased length of the fish. Maar (1950); Grainger (1953) and Moore (1975) have all shown similar relationships in other populations of arctic char. Svardson (1949a), however, reported that there was normally a negative relationship between the size of the ova and fecundity, suggesting that there must be a balance, brought about by natural selection, in which the greater potential survival inherent

Fig. 4.13 The relationship of fecundity to ovary weight for Llyn Peris and Llyn Padarn char.

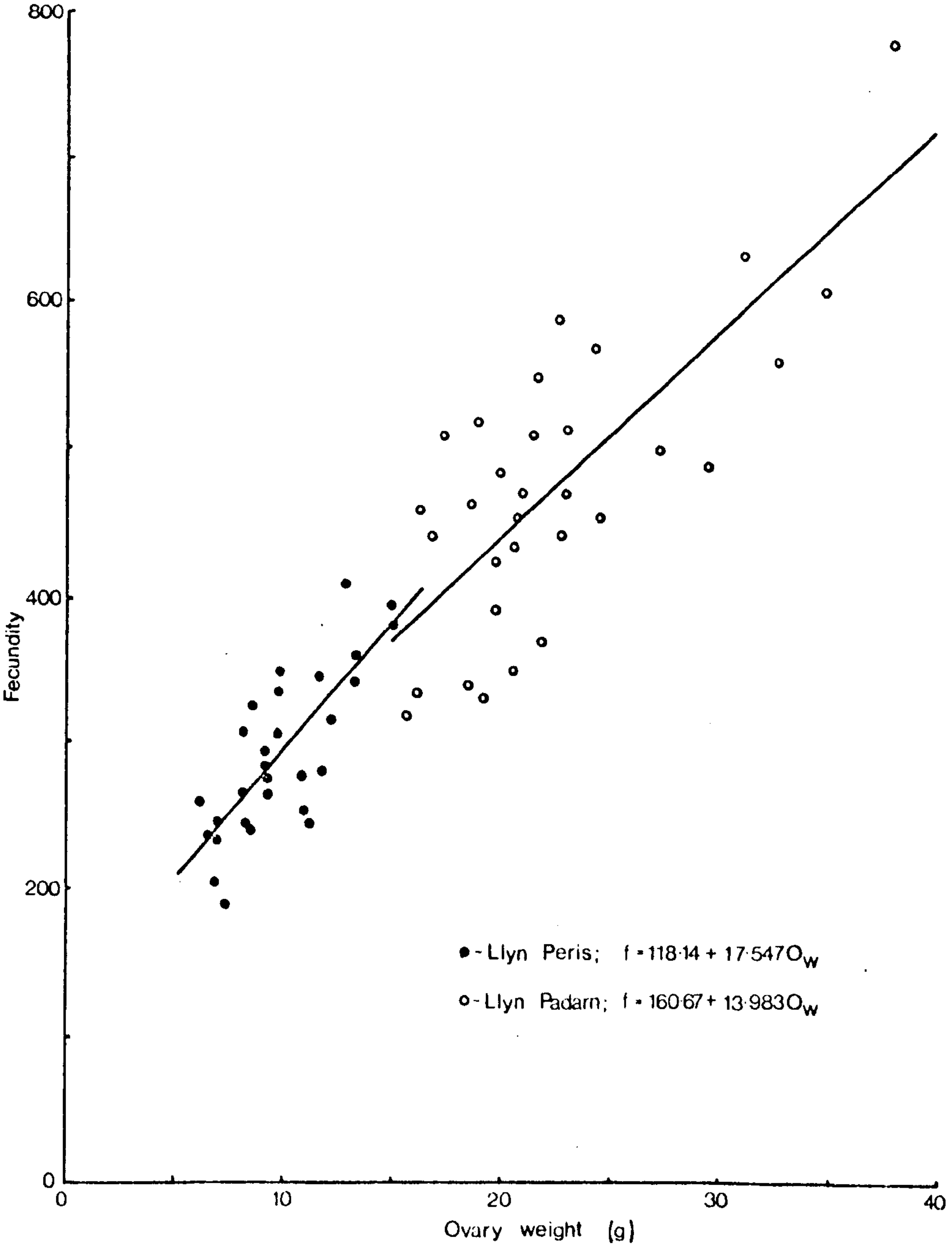
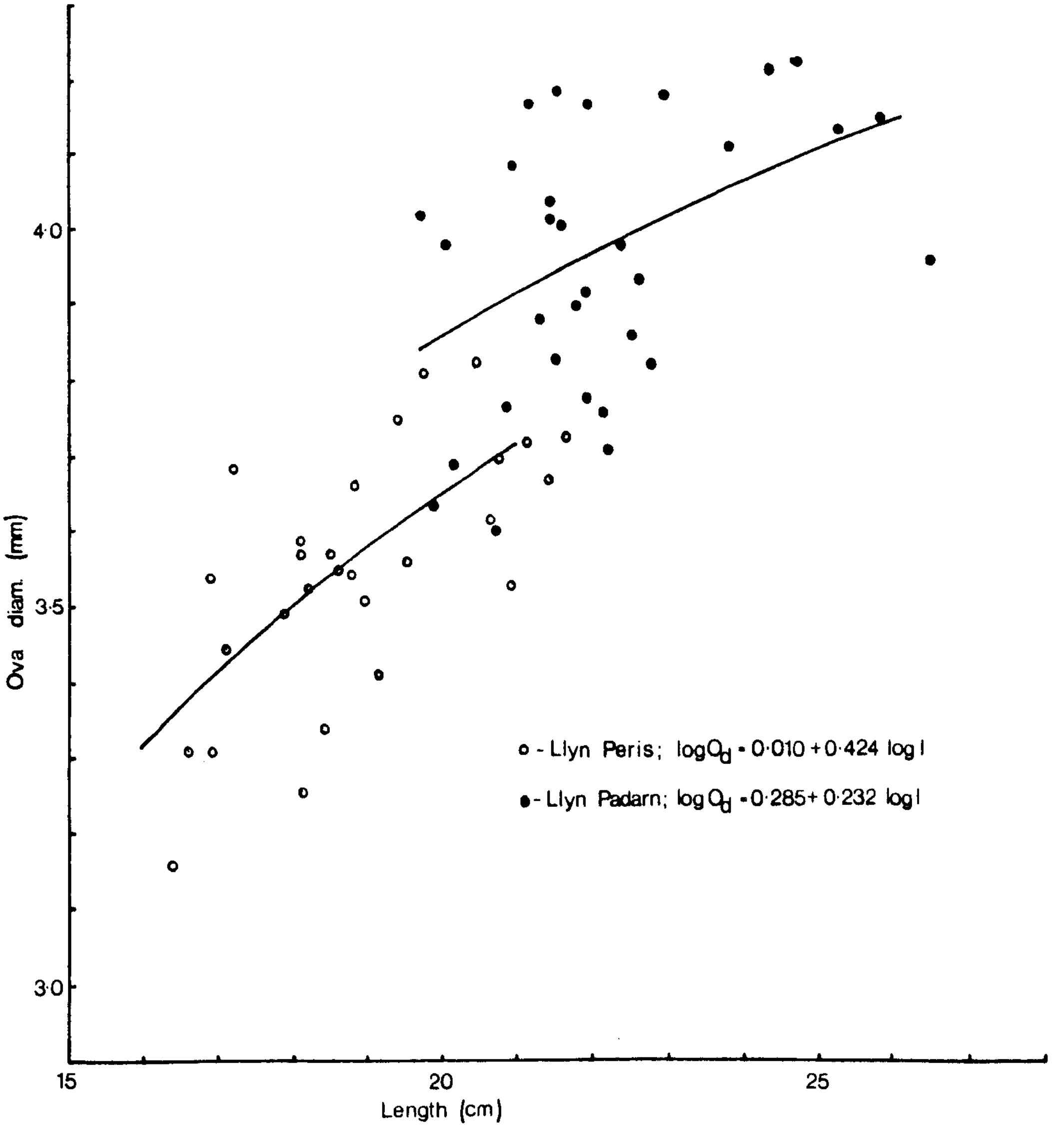


Fig. 4.14 The relationship of ova diameter and fork length of char from Llyn Peris and Llyn Padarn.



in the deposition of large numbers of eggs would be offset by the possibly lesser survival of smaller eggs. Bagenal (1957) also concluded that larger and better fed brown trout produced more, but smaller, eggs than poorly fed fish. Southern (1932) found, with brown trout, that there was a positive correlation between ova diameter and fish length within the same population, but that in general there was a tendency for slow growing populations to produce fewer, but larger, eggs than faster growing ones; thereby ensuring that the larger fry produced from the larger eggs would have a good start in an environment unfavourable to growth. Llyn Peris char produce fewer and smaller eggs than those of Llyn Padarn, not larger as may be expected from Southern's (1932) data. This possibly supports the evidence that the two Llanberis char populations are genetically similar, as discussed in Chapter 6.

Vladykov (1956) found there to be a highly significant negative correlation between ova diameter and the number of ova per gram of ovary. The data for this relationship for Llyn Peris and Llyn Padarn char is shown in Fig. 4.15. There was a highly significant correlation ($r = 0.987$ for Llyn Padarn, $p < 0.001$; $r = 0.969$ for Llyn Peris, $p < 0.001$) for the logarithmically transformed data. The two regression equations were similar in both slope and elevation ($p > 0.1$), and the curve for the pooled data, plotted from antilogarithm values, is shown. Because the weight of ovarian tissue is very small compared to the total weight of the ovary, Vladykov (1956) considered that a knowledge of ova diameter and the total weight of the ovary would provide a very accurate estimate of fecundity in brook trout. This is also true for arctic char from the Llanberis lakes, and the data would be particularly valuable if the relationship were constant between years and for other arctic char populations.

Fig. 4.15 The relationship between the number of eggs per gram of ovary and the egg diameter for Llyn Peris and Llyn Padarn char.

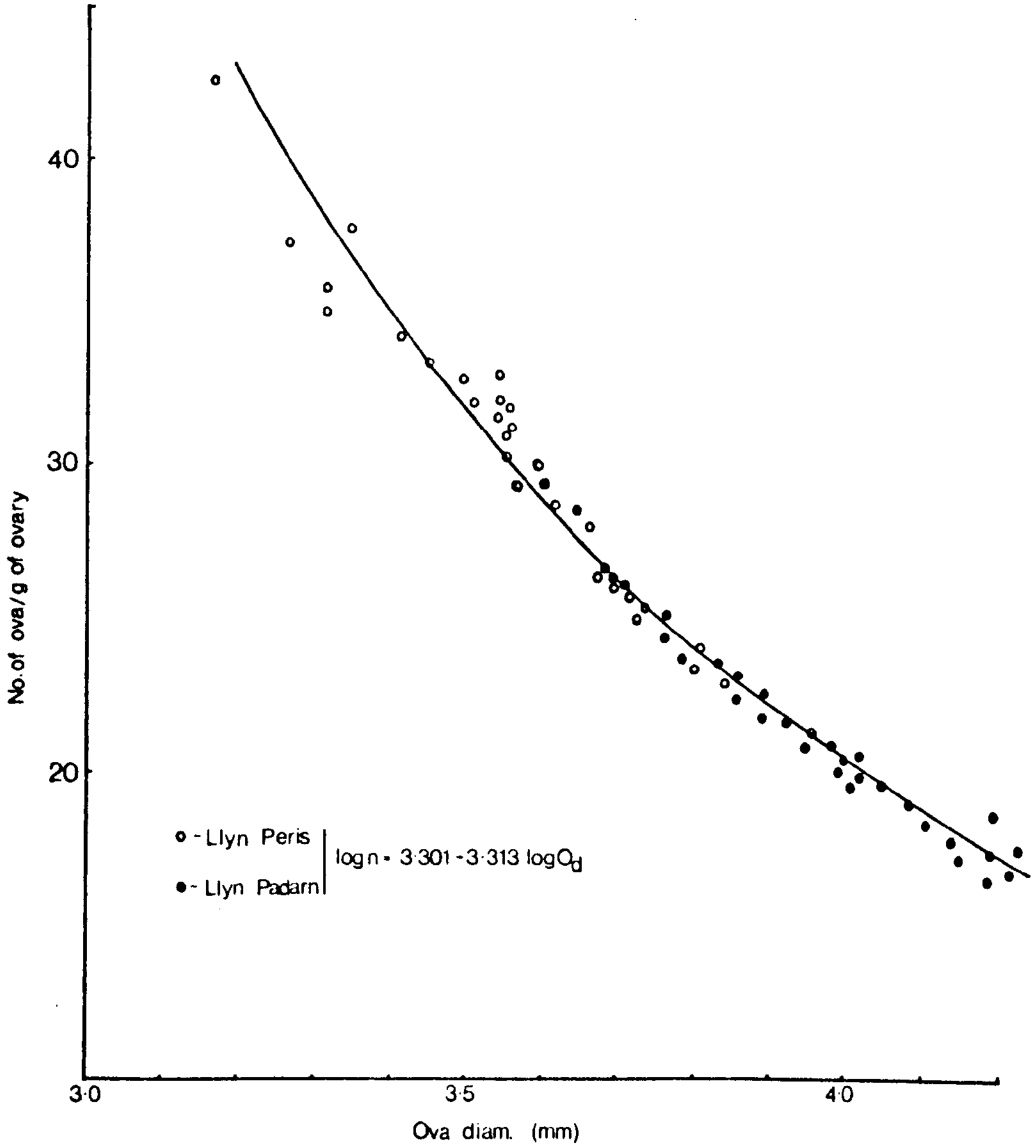


Table 4.4 shows the fecundity of arctic char from various locations. As with the growth rate (Chapter 3), large variations have been recorded from different populations. In general, the fecundity of arctic char is related to the growth of the fish. Therefore the anadromous and the faster growing non-anadromous populations, such as those from L. Azabach'ye and Metamek Lake, are the most fecund, with up to 7,000 eggs per female recorded from Baffin Island and Ungava Bay. By contrast, very slow growing populations have extremely low fecundities, with as few as 17 eggs being recorded from a female of length 8.1cm in the Ungava peninsula area. The fecundity of the only other British populations on record, those of L. Windermere, are higher than those from Llanberis, almost certainly due to the greater size of the fish, and are similar to many Swedish populations of about the same length range. The Llanberis char are similar in fecundity to other populations of similar size range; Blasjon IV, Jormsjon, and the brook char of Kamchatka.

Table 4.4 The Fecundity of arctic char from various locations.

Locality	Source	length range (cm)	fecundity	anadromous or non-anadrom
Llyn Peris	Present study	16.3 - 21.4	190 - 416	non-anad.
Llyn Padarn	Present study	19.7 - 26.5	320 - 780	non-anad.
L. Windermere autumn spawners	Frost, 1965	Av. 29.0	Av. 1220	non-anad.
L. Windermere spring spawners	Frost, 1965	Av. 31.0	Av. 1720	non-anad.
Leipikvattnet I (Sweden)	Maar, 1949	33 - 40	1519 - 3176	non-anad.
Leipikvattnet II (Sweden)	Maar, 1950	31 - 43	1425 - 3471	non-anad.
Blasjon I (Sweden)	Maar, 1949	26 - 39	540 - 1746	non-anad.

Locality	Source	length range (cm)	fecundity	anadromous or non-anadro
Blasjon II (Sweden)	Maar, 1949	26 - 37	600 - 1260	non-anad.
Blasjon IV (Sweden)	Maar, 1949	23 - 28	325 - 620	non-anad.
Jormsjon (Sweden)	Maar, 1949	24 - 31	380 - 803	non-anad.
Candlestick Pond (Newfoundland)	Rombough et al,1978	11.1 - 14.5	61 - 104	non-anad.
Ungava Peninsula (Quebec)	Dunbar & Hildebrand, 1952	8.1 - 9.4	17 - 24	non-anad.
Metamek Lake (Quebec)	Saunders & Power, 1969	29.9 - 48.0	358 - 3661	non-anad.
Shublik Springs (Alaska)	McCart & Craig,1973	11.7 - 18.3	84 - 199	non-anad.
Unnamed Spring (Alaska)	McCart & Craig,1973	12.3 - 15.8	42 - 187	non-anad.
Baffin Island	Moore, 1975	40 - 80	2000 - 7000	anad.
Baffin Island	Grainger, 1953	37 - 43	2300 - 3000	anad.
Ungava Bay, Quebec	Grainger, 1953	46 - 66	2000 - 7000	anad.
Wood River Lakes (Alaska)	Thompson, 1959	37.6 - 54.6	1182 - 4038	anad.
L.Azabach'ye, (Kamchatka) predatory char	Savvaitova, 1973	30 - 75	900 - 1324	non-anad.
L.Azabach'ye Benthophages	Savvaitova, 1973	30 - 55	1514 - 2782	non-anad.
L.Dal'neye, (Kamchatka)	Savvaitova, 1973	30 - 60	685 - 2400	non-anad.
Stone Char (Kamchatka)	Savvaitova, 1973	40 - 60	1600 - 2624	non-anad.
Brook Char (Kamchatka)	Savvaitova, 1973	9.5 - 23.9	165 - 346	non-anad.

CHAPTER 5 THE REPRODUCTIVE BEHAVIOUR AND MOVEMENT OF THE LLANBERIS CHAR

5.1 Introduction

One of the first records of the spawning behaviour of the Llanberis char was made by Day (1880-1884), in which he describes a migration from Llyn Padarn into Llyn Peris during November and December and the subsequent spawning of the char on the shallows at the northern end of the lake. Powell (1966) was unable to confirm these observations but considered them likely and described a spawning site at the northern end of the lake. She also thought it probable that if both populations did spawn in Llyn Peris they did so on separate spawning grounds, the Llyn Peris char spawning in deeper water than the Padarn population.

The study made by Frost (1965) of the Windermere char is the most detailed concerning the spawning habits of arctic char on record. She found there to be three distinct spawning groups; one spawning in the shallows of the lake in autumn; another spawning in an afferent stream also in the autumn; and a third in deep water during the spring. Other observations on the breeding habits of non-anadromous char have been made by Andre (1922); Maar (1949); Alm (1951); Runnstrom (1951); Sprules (1952); Savvaitova (1973); Doerfel (1974); Kimura (1977) and others. The actual spawning act of the char has been described by Facricius (1953); Fabricius and Gustafson (1954) and Frost (1965), and they also discussed the choice of spawning substrate.

In this chapter, the time of spawning, movements both within and outside the spawning season and the choice of spawning sites of the Llanberis char are described.

5.2 Laboratory Methods

Most of the data used in this chapter were obtained from field observations, which have been described, and from previous chapters. Small samples of fish caught by fyke net were also brought back to the laboratory for examination; their fork lengths and weight were measured, and their age and maturity index estimated.

The maturity state of the gonads of all fish examined was also assessed using the method of Orton et al. (1938);

Stage I : gonadial tube visible as thin, light coloured strands in the males. In the females the gonadial tube differs in being slightly wider at the anterior end. This corresponds to a maturity index of about 0.5% for males and 1.0% for females.

Stage II : increased width of the gonadial tube at the anterior end.

Stage III : gonads fill out about half the body cavity. The testes are creamy-white and the oocytes are visible in the ovary.

Stage IV : gonads fill more than half the body cavity.

Stage V : gonads fill the body cavity.

Stages II to V represent the maturation stage of the gonads, from August to November, and the equivalent maturity indices are from 1 to 3-4% for males and 1.5 to 12-16% for females.

Stage VI : gonads ripe. Gonadial products ooze from the vent when the flanks are gently squeezed.

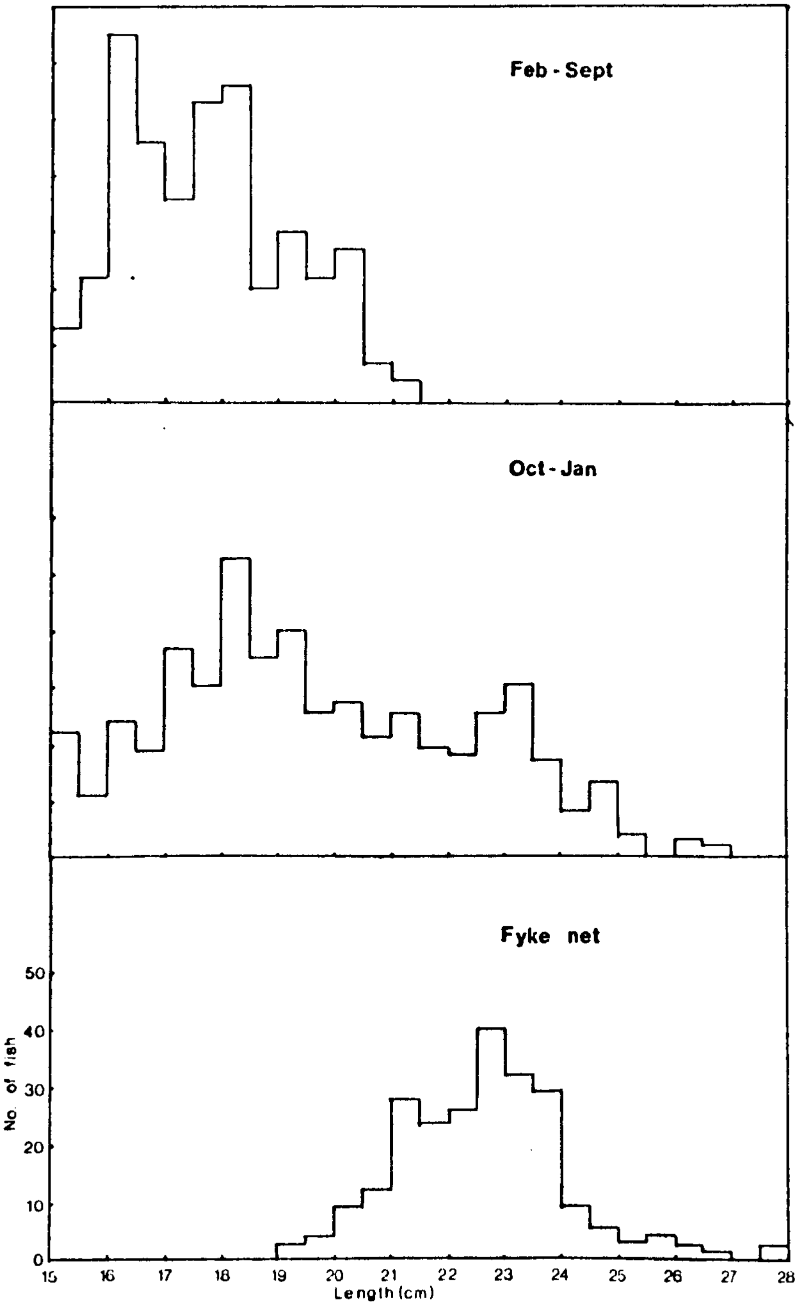
Stage VII : gonads spent.

Estimates of the maturity of the fish from these stages give a better numerical indication of when the char were running ripe or recently spent than does the maturity index.

5.3 Movement of Char during the Spawning Period

In the first year of study of the char population of Llyn Peris it was found that large numbers of char of length greater than 21cm were only caught between October and January, mainly in November and December. Although char of all sizes were more difficult to catch during the summer, intensive efforts failed to catch fish greater than this length (Fig. 5.1). These "large" char, of length between 19.3 and 26.8cm were easily distinguished from the "normal" Peris char by their greater growth rate and condition factor. Frost (1965) and Frost and Kipling (1980) concluded that there were up to 4 different races of char in Lake Windermere, differing in growth rate and spawning time, and workers in other countries have also found two or more races in one lake (Berg, 1948; Reisinger, 1953; Nilsson, 1955; Schindler, 1957; Svardson, 1961; Nordeng, 1961; Klemetsen and Ostbye, 1967; Nilsson and Filipsson, 1971; Nyman, 1972; Savvaitova, 1973; Skreslet, 1973a; Doerfel, 1974; Brennet, 1976). However, it was considered that the "large" char of Llyn Peris, because they were only evident at certain times of the year, were more likely to have been emigrants from Llyn Padarn, for spawning, as had been recorded, though not proven, earlier.(Day 1880-1884; Powell, 1966).

Fig. 5.1 The length-frequency distribution of char caught by gill net between February and September and October and January in Llyn Peris and by fyke net in the Afon-y-Bala.



These findings prompted work on the Padarn char population, and Table 5.1 compares the mean length at each age of mature Peris, Padarn, and "large" Peris char, all captured in November and December 1974.

Table 5.1 Mean lengths, with standard deviation (in parentheses) of 'normal' and 'large' Llyn Peris char and Llyn Padarn char, at each age. The means were compared by means of 'd' or 't' tests, and the results are shown

		Age next birthday			
	4	5	6	7	8
Llyn Peris 'normal'	16.64 (1.05) n=22	18.12 (0.94) n=27	19.26 (0.99) n=19	20.48 (1.21) n=5	20.94 (1.51 n=4
Llyn Peris 'large'	20.84 (1.18) n=9	21.24 (0.96) n=14	22.48 (1.06) n=18	24.15 (1.24) n=9	24.51 (1.98 n=5
Llyn Padarn	20.21 (1.09) n=12	20.86 (0.79) n=31	22.61 (0.86) n=18	23.90 (1.04) n=15	24.82 (1.08 n=11
Difference 'large' Peris vs 'normal Peris	yes $p < 0.001$	yes $p < 0.001$	yes $p < 0.001$	yes $p < 0.001$	yes $p < 0.001$
Difference 'large' Peris vs Padarn	no $p > 0.1$	no $p > 0.05$	no $p > 0.1$	no $p > 0.1$	no $p > 0.1$

The mean lengths at each age were significantly different between the 'normal' Peris and 'large' Peris char, but not between the Padarn and 'large' Peris char. Therefore, as was thought likely, the 'large' Peris char originated from Llyn Padarn.

To monitor this migration, it was decided to try and trap migrating char in the interconnecting stream, the Afon-y-Bala, commencing in November 1974 and continuing through the spawning periods (November to January) in

1974/75 and 1975/76. It was, unfortunately, not possible to instal a permanent fixed trap in the stream, so fyke nets were used. These are not generally suitable for fast flowing waters,tending to wash away, so they were set at the lower end of the Afon-y-Bala where the stream widens and deepens, slowing the flow (Platel). To minimise the effects of the water current, a chain of nets was set at an acute downstream angle. Despite these precautions, the nets were still regularly washed out during floods. They were fished for 14 nights between November 26th and January 5th, 1974-1975. Trapping was recommenced on November 5th 1975, and were fished for 12 nights until December 11th,when a series of heavy floods brought down some trees and badly damaged the nets. They were checked at first light and again in late afternoon. No char were caught during daylight, and none were seen during electrofishing operations, and it was considered that char only moved through the river in darkness. Because the nets were only set irregularly, it was not possible to correlate char catches with water flow or other physical parameters.

The length-frequency of char caught in the fyke nets is also shown in Fig. 5.1. This corresponds closely with the length-frequency of the 'large' char caught in Llyn Peris, again confirming that the latter fish originated in Llyn Padarn. Table 5.2 shows the number of ascending and decending char captured in the fyke nets.

Acsending fish were always ripe (Stage V), although some of the males were running ripe (Stage VI). The few descending fish captured were always spent. It was thought that the male chars began ascending before the females, but because secondary sexual characters are not always apparent, this could not be proven.

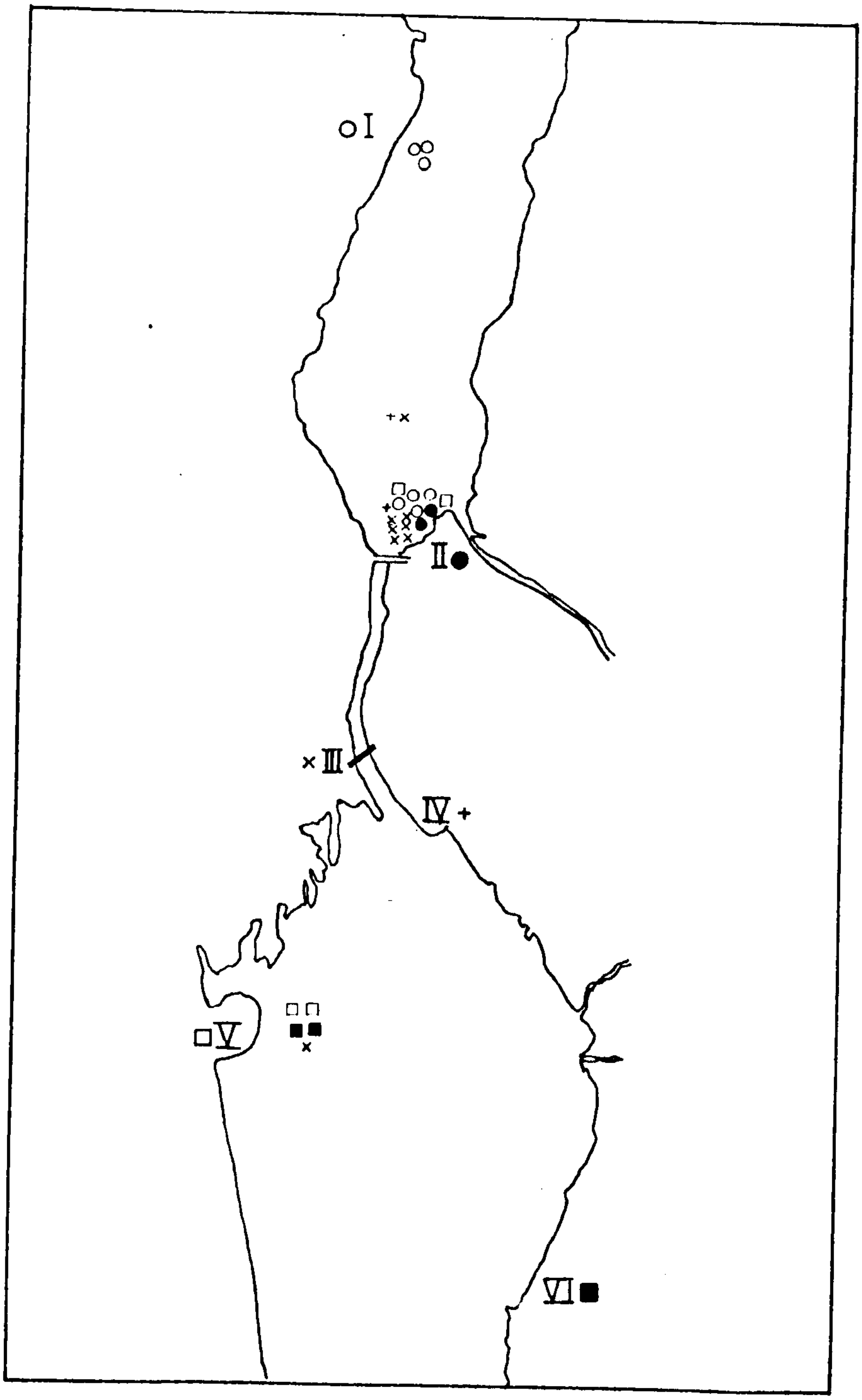
Plate 1. The lower section of the Afon-y-Bala with Llyn Padarn in the background. This is the point at which the fyke nets were installed.

Table 5.2 The number of char captured by fyke net in the Afon-y-Bala in 1974/1975 and 1975/1976

Date	Ascending	Descending	Date	Ascending	Descending
Nov. 26	8		Nov. 5	0	
27	6		6	1	
28	12 (broken)		19	3	
Dec. 3	10		20	2	
4	15 (broken)		26	4 (broken)	
5	26		27	6	
10	53		28	4	
11	48	6 (broken)	Dec. 2	11	
16	21	12	3	13	
17	11	9 (broken)	4	8 (broken)	
Jan. 8	-	3	9	39	4
9	-	1	10	13	7 (broken and removed)
14	-	-			
15	-	- (removed)			
Total	210	21	Total	104	11

Apart from the char retained for age estimation and gonad examination, all were tagged as described in Chapter 2. Fig. 5.2 shows the site of recapture of char from October to January which were originally tagged in the Afon-y-Bala and at other sites. 7 Char, tagged after capture in the fyke nets, were subsequently recaptured in Llyn Peris, six in the shallows at the northwest end and one in deeper water. 3 Char tagged in Llyn Padarn itself were also recaptured in Llyn Peris, and a further 10

Fig. 5.2 The point of recapture of marked char between October and January. The symbols represent the site of original capture; the sites are shown by Roman numerals with their corresponding symbols alongside.



char tagged in Llyn Padarn were recaptured in the fyke nets. 4 Char tagged in Llyn Peris were recaptured on the shallows at the northwest end of the lake.

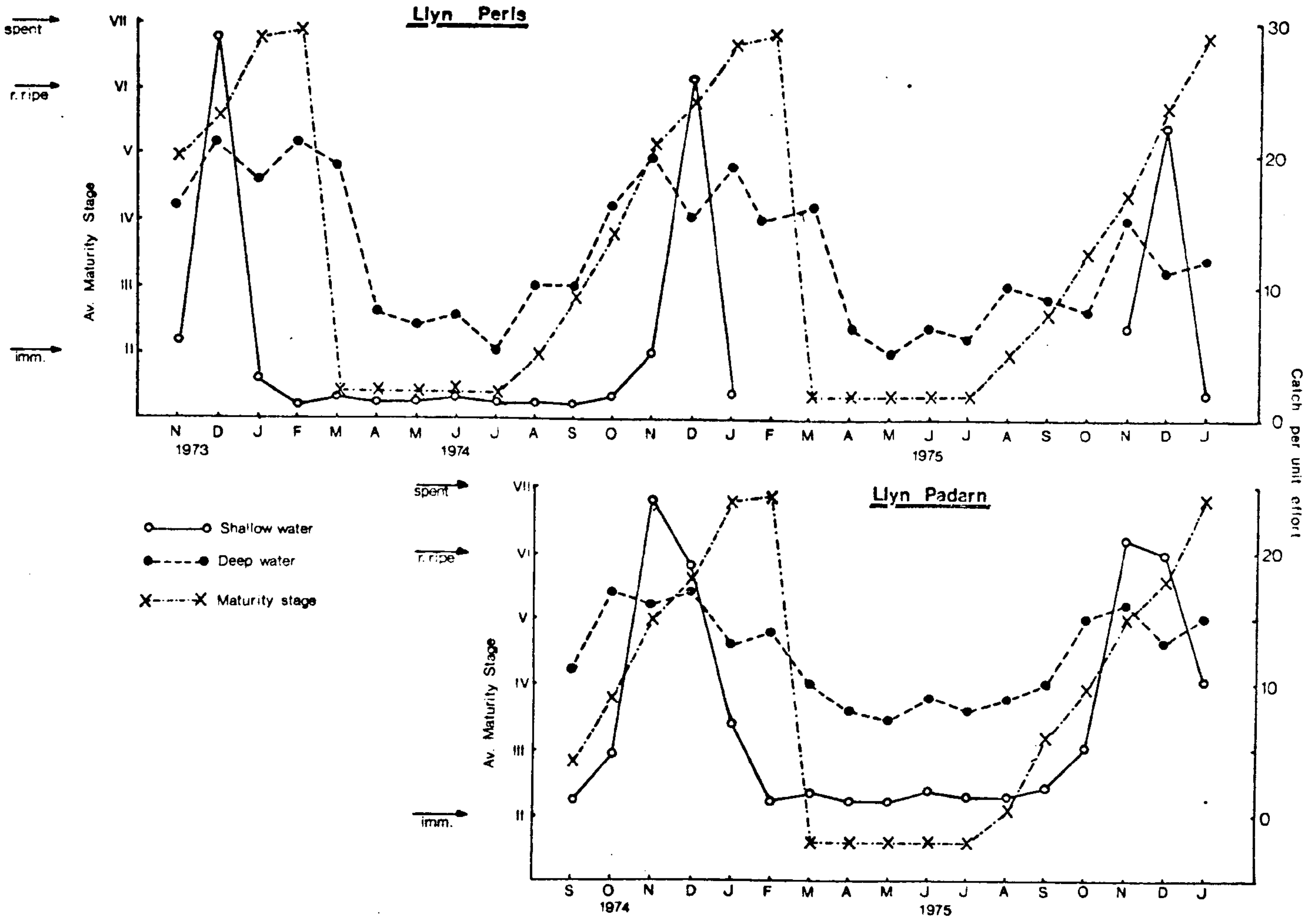
There is, therefore, definite confirmation of the char migration from Llyn Padarn into Llyn Peris for spawning. Such migrations are not unknown in char populations. Frost (1965) describes a movement out of Lake Windermere into the River Brathay, and also from Ennerdale into the River Liza. Char in Loch Insh move 7 miles up a stream for spawning, and similar examples have been found in Sweden (Fabricius, 1950) and USSR (Savvaitova, 1976a). However, these are all migrations into and spawning within the stream itself. Movements from one lake into another for spawning have, apparently, not been described previously, although Dunbar and Hildebrand (1952) thought that it might occur between two small lakes in the Ungava peninsula area.

The origin of this movement between Llyn Padarn and Llyn Peris is obscure, but is possibly a relict behaviour from when the lakes were undivided. If all the char in the original one lake spawned in the same place, then presumably they continued to do so after the lake was divided by deposition of silt from the Afon Hwch. This behaviour obviously carries serious implications on the survival of Llyn Padarn char after the completion of the reservoir scheme, when access to Llyn Peris will be denied. This is discussed in Chapter 7.

5.4 The Site of Spawning

Fig. 5.3 shows the catch per unit effort of char taken in the standard series of gill nets from deep and shallow water in both lakes compared

Fig. 5.3 The catch per unit effort of char in the 'standard' gill nets set in deep and shallow water and their average stage of maturity.



with the maturity of the fish. The maturity in this instance was taken as the average of the maturity stage assigned to each individual (mature fish only considered). This follows the annual cycle described from the maturity indices, discussed in the previous chapter, but it gives a better numerical estimate of when the char were running ripe or freshly spent. Jensen (1979) demonstrated that catch per unit effort of char in standard gill nets gave a reasonable estimate of abundance at particular times of the year, although there were large seasonal variations in catches, as was found with the Llanberis populations. The catch rate at the shallow water sites was very low in both lakes between January and November. In Llyn Peris, it increased rapidly in November, reaching a peak in December, declining again in January. There was a similar pattern in Llyn Padarn, but the peak in catch rate was marginally earlier than in Llyn Peris, and extended at quite a high rate into January. The catch rate from deep water was also at its lowest during the summer, but never as low as that from shallow water. Throughout this period, the char are apparently dispersed over all the lake, and this is discussed in section 5.6. The fixed deep water sites in each lake were chosen because they were thought by local fishermen to be places at which char aggregate before spawning, and this is supported by the increase in catch rate in autumn.

The char caught at the deep water sites of both lakes and the shallow water site in Llyn Padarn during November and December were predominantly at Stage V of maturity, although some of the males and a very small number of females were at stage VI, running ripe. The char caught in shallow water in Llyn Peris at this time were invariably running ripe, semi-spent or completely spent. Large numbers of trout were also caught at the shallow water site in Llyn Peris at this time and examination of their stomach contents showed them to have been feeding heavily on ova.

It was therefore considered that this was a spawning site, and was the same place that Powell (1966) has described. It was,apparently, well known by local villagers and was thought to be the same site from which char were netted during spawning prior to its prohibition.

The substrate at this site was a mixture of large pieces of slate, together with granules, pebbles and cobbles (the classification of substrate is given in Chapter 2). There was no weed growth and little encrusted algae. Char have been shown to spawn invariably on substrates of gravel or small stones (Maar, 1949; Alm, 1951; Runnstrom, 1951; Sprules, 1952; Fabricius, 1953; Fabricius and Gustafson, 1954; Frost, 1965; Savvaitova, 1973; Kimura, 1977), and they will not use fine sand or silt (Fabricius and Gustafson, 1954). Runnstrom (1951) reported spawning on Isoetes covered areas of the bottom of Lake Torron, but this involved construction of the redds within the gravelly substrate rather than on or among the plants themselves. Fabricius and Gustafson (1954) found that char would not spawn on fine sand with Isoetes.

The spawning act of the char is very similar to that of the brown trout described by Jones and Ball (1954), and has been reported by Fabricius and Gustafson (1954) and Frost (1965). A bed, or depression, is cut into the substrate, effected by suction caused by vigorous vertical flapping of the tail; the female, who does the cutting, being on her side.
After the spawning has been completed, the fertilised eggs falling into the bottom of the pit, the female then 'cuts to cover'. Unlike the trout where this cutting is vigorous and the majority of eggs are buried in the substrate, this action by the char is relatively feeble and large numbers of uncovered eggs remain; most being washed into the interstices of the substrate rather then being actually buried (Fabricius, 1953;

Fabricius and Gustafson, 1954; Frost, 1965).

To determine the extent of the suspected spawning site at the northwest end of Llyn Peris, and to try and find other sites in both Llyn Peris and Llyn Padarn, it was decided to investigate the deposition of ova, using a suction sampler, during January 1976. This sampler had been used successfully for gwyniad, Coregonus lavaretus, eggs in Llyn Tegid (Coles pers. comm.).

The sites chosen for investigation were the suspected site and other areas where the substrate appeared suitable. The bottom of both lakes in deep-water areas is composed of silt; Powell (1966) found there to be no stony areas in this region, which was confirmed during the present study by grab samples and echo-sounding. The suitable areas in the littoral zone were also limited by the precipitous and artificial nature of the shorelines. The sites actually chosen for investigation, Fig. 5.4, had the following characteristics:

Llyn Peris

Site A: the suspected spawning site (Plate 2). The nature of the substrate has already been described, and it extended to a depth of about 2.5m. It extended from the mouth of the Afon Hwch to the outflow of the Afon-y-Bala.

Site B: this is a relatively shallow bay, the substrate being composed predominantly of fine silt, but was chosen because of its good growth of Isoetes. Pebbles and cobbles were confined to the extreme edge. Depth up to 4m.

Fig. 5.4 The sites examined for deposited ova.

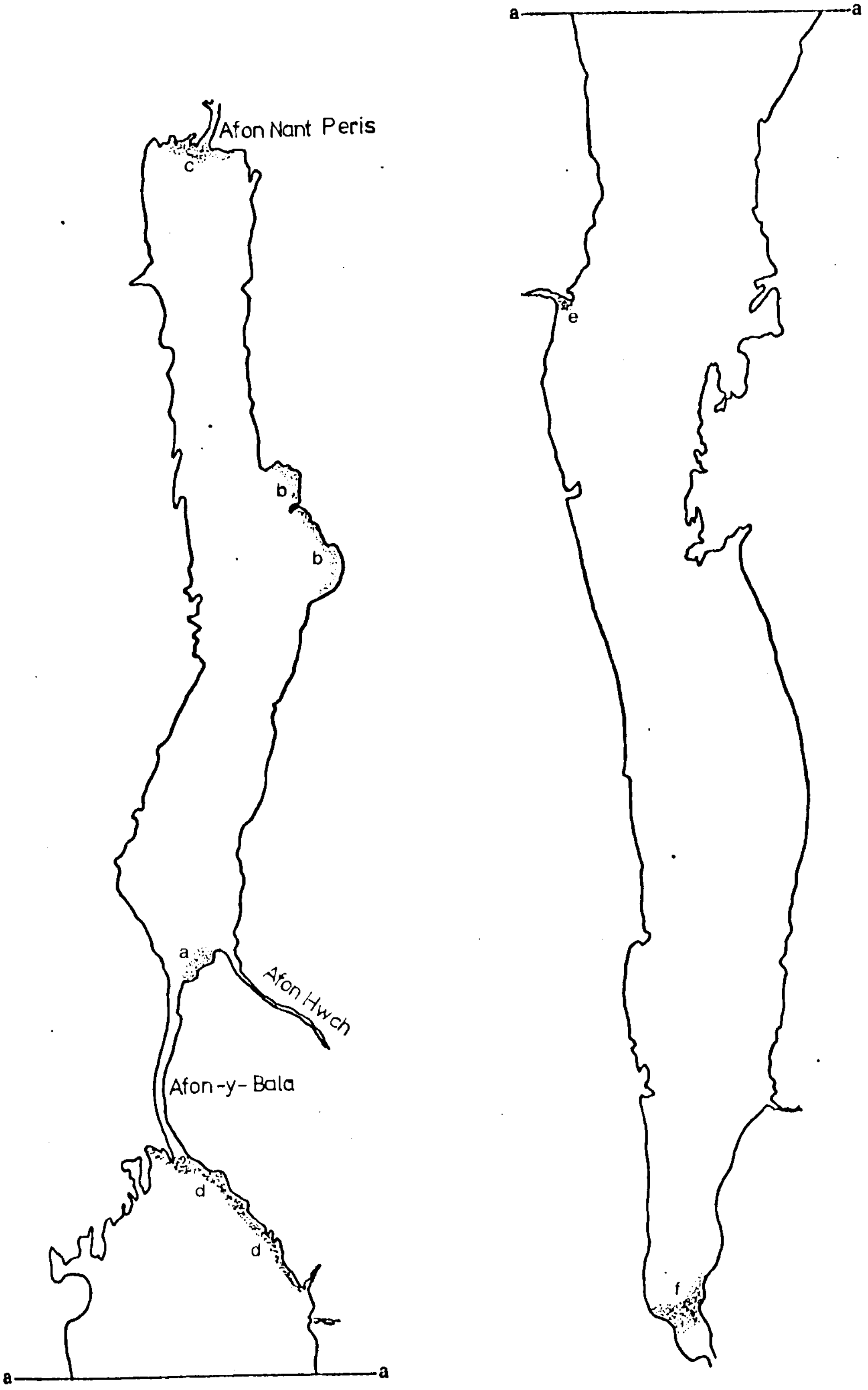


Plate 2. The spawning site in Llyn Peris, which extends from the estuary of the Afon Hwch (right foreground) to the mouth of the Afon-y-Bala. This photograph was taken after the construction of the dam had started, and the area in the foreground has been stripped of the dense woodland that covered it down to the water edge. The Afon Hwch has been diverted, but the old bed may be seen in the left foreground.

Site C: the mouth of the Afon Nant Peris and adjoining banks. (Plates 3 and 4). The substrate ranged from medium sand to pebbles, but over much of the area the stony substrate overlaid silt. Depth to 1.5m.

Llyn Padarn

Site D: extended from the mouth of the Afon-y-Bala to the mouth of the Afon Goch (Plate 5). The substrate was predominantly stony with sizes varying form fine grit to boulders. There was a good deal of algal growth on the substrate, which was quite compacted. Depth to 2m.

Site E: this was a very restricted site near the mouth of the Afon Fachwen on the eastern shore. It was a clean, uncompacted substrate composed predominantly of granules and pebbles. Depth to 1.5m.

Site F: this was an extensive site at either side of the outflowing river, the Afon Seiont (Plate 6). The substrate varied in size from silt to boulders, but was predominantly of pebbles and cobbles. Depth to 3m.

Irregularly spaced transects, between 5 and 20m apart, were sampled at each site by wading or from a boat, to the limit of the suitable substrate. Non-anadromous char have been reported to spawn in streams (Fabricius, 1950; Runnstrom, 1951; Frost, 1965; Savvaitova, 1973; and others), and so the Afon-y-Bala, Afon Hwch and Afon Nant Peris were occasionally electrofished in the spawning season, during daylight. No char were captured, even in the Afon-y-Bala, and none were ever observed.
These streams and others, such as the Afon Goch and Afon Fachwen, were

Plates 3 & 4. The estuary of the Afon Nant Peris and adjoining shore to the west. The precipitous and artificial nature of much of the shoreline of Llyn Peris is apparent.

Plate 5 (above) The southeastern shore of Llyn Padarn. Apparently suitable spawning gravel extended from the jetty in the right centre to the estuary of the Afon-y-Bala.

Plate 6 (below) The lower end of Llyn Padarn. The Afon Seiont flows out beneath the bridge.

also fished by other workers from Liverpool University but no char were ever found. Electrofishing at night was not attempted, but Frost (1965) reported that char remained in the River Brathay during the day. However, the beds of the Afon Hwch and Afon Nant Peris were sampled for distances up to 300m for their confluence with the lake, as was all the Afon-y-Bala.

To differentiate between brown trout and char eggs which might be sampled, ova were stripped from ten trout, ranging in length from 20.5 to 28.7cm, captured from the Afon Hwch in November. The eggs were mixed and allowed to stand in water for two hours to swell to their maximum size, and then preserved in 5% formalin. 200 were measured and their average diameter was 4.81mm, standard deviation 0.19mm. The mean diameter of fertilised char eggs, estimated by measuring 200 of a sample taken for artificial rearing, and also preserved in 5% formalin, was 4.28mm, s.d. 0.24mm. There was a significant difference ('d' = 24.98, $p < 0.001$) between the diameters of trout and char eggs. The trout eggs could also be distinguished by being a deeper orange colour than those of char in their unpreserved state.

Table 5.3 shows the number and mean diameter of eggs sampled from each site.

Ova of the same diameter to those of char were only found at Site A, between the Afon-y-Bala and Afon Hwch, the suspected spawning area. The approximate limit of deposited ova is shown in Fig. 5.5, the majority being found in depths of water between 75 and 200cm, similar depths to those reported by Frost (1965) for autumn spawning Windermere char. No efforts were made to sample quantitatively, but Coles (pers. comm.) showed this to be possible for coregonid eggs using this method.

Fig. 5.5 The approximate limits of the spawning site at northwest end of Llyn Peris (stippled area).

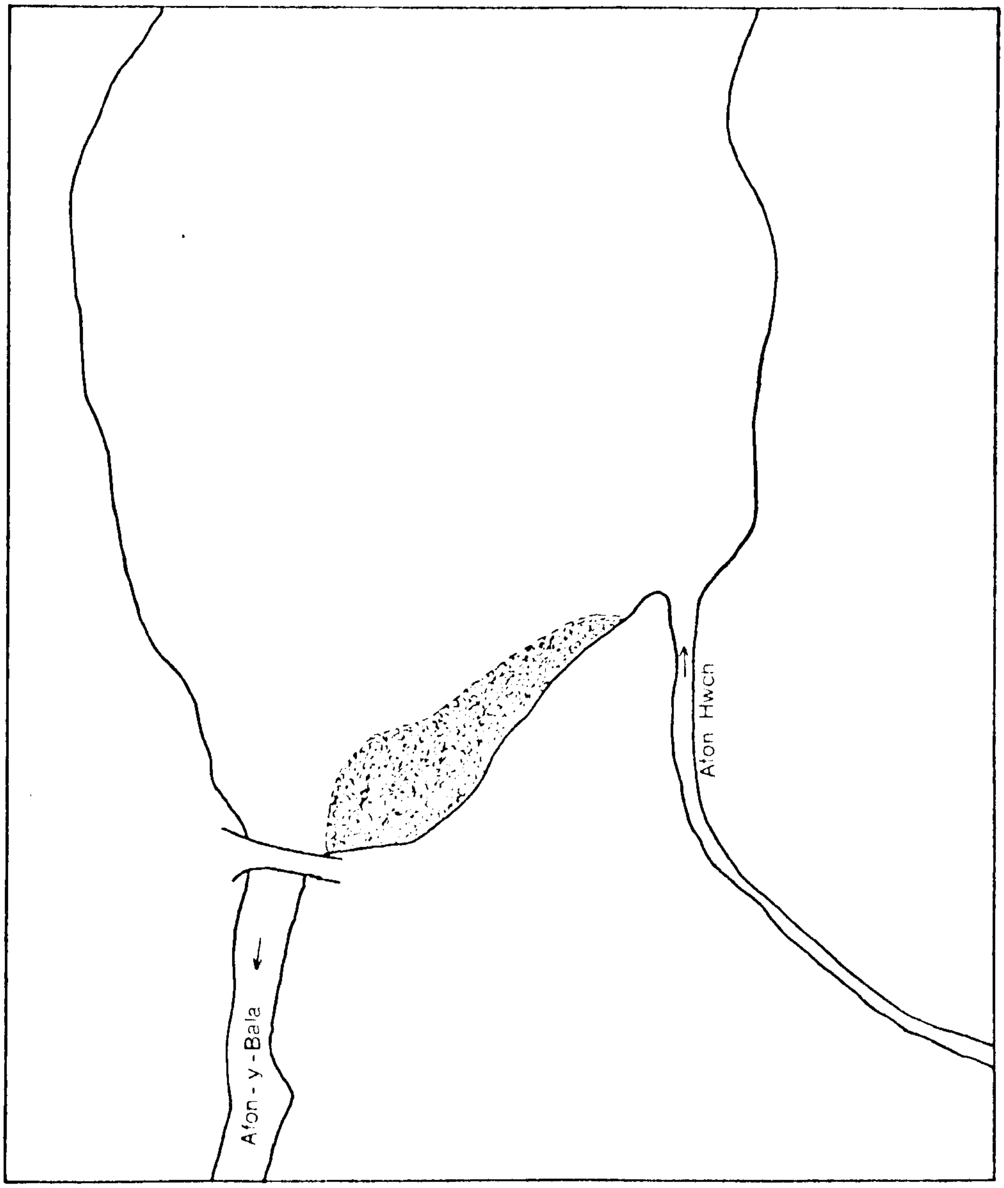


Table 5.3 The number and mean diameter, with standard deviation, of eggs sampled from sites A to F and the Afon-y-Bala, Afon Hwch and Afon Nant Peris. The diameters were compared with the 'standard' char and trout eggs by means of 'd' or 't' tests and the results are shown

Site	A	B	C	D	E	F	Afon y Bala	Afon Hwyh	Afon Nant Peris
No.	436	0	32	0	6	125	134	238	296
Dia(mm)	4.21	-	4.74	-	4.87	5.03	4.84	4.79	4.83
s.d.	0.26	-	0.20	-	0.16	0.36	0.19	0.21	0.20
compared w. standard char ova	n.s. $p>0.1$	-	s $p<0.001$	-	s $p<0.001$	s $p<0.001$	s $p<0.001$	s $p<0.001$	s $p<0.001$
compared w. standard trout ova	s $p<0.001$	-	n.s. $p>0.05$	-	n.s. $p>0.05$	s $p<0.001$	n.s. $p>0.1$	n.s. $p>0.1$	n.s. $p>0.1$

The small number of larger eggs, similar in size to trout eggs, found at site C in Llyn Peris and Site E in Llyn Padarn were thought to be trout eggs washed from the nearby streams, and all of them were opaque and obviously dead. Most of the eggs found at site F were very near the mouth of the outflowing river. They were significantly larger than the 'standard' trout eggs, and the samples probably contained salmon eggs, salmon having been observed spawning in this area.

It seems probable, therefore, that all of the char of the Llanberis system spawn at the one site. Powell (1966) considered that if Padarn char did actually spawn in Llyn Peris, then they probably did so at a different site; the Peris fish, because of their lighter colouration, possibly in deeper water. As has been discussed, no suitable spawning areas have been found in deep water in Llyn Peris. The colouration of char is very variable, with slowly growing char often paler in colour.

Frost (1965) commented that the autumn (shallow water) spawning char of Lake Windermere were less intensively coloured than the spring (deep water) spawning fish. She attributed the difference to the larger size of the spring spawners. The same is probably true for Llanberis char; the larger Padarn char being more deeply coloured than the smaller ones of Llyn Peris.

Whether there was any segregation between Padarn and Peris char on the spawning grounds was not determined. The average diameter of unspawned mature ova was greater for Padarn char (Chapter 4), but no comparisons were made for fertilised ova, nor were the samples from each transect kept separate, but no difference in egg diameter was noticed during sampling. Data presented in Chapter 6 and the study carried out by Child (1977) indicated that Padarn and Peris char were genetically the same, implying no segregation on the spawning grounds; the two populations mixing freely at spawning. What mechanism, if any, that determines whether char remain in Llyn Peris or migrate to Llyn Padarn is not known. Volabuev (1977) described two groups of *Salvelinus neiva* from Lake Korral , different in growth rate and several other factors, which spawned on the same grounds at the same time, also with no apparent segregation.

Swift (1965) showed that the hatching time for char eggs from Lake Windermere was closely correlated with temperature. Conversion of his data indicated that the eggs took about 422 degree days to incubate (Hunter, 1970). Frost (1965) found that autumn (mid-November) spawned eggs from about the second week in February to mid-March, 64 to 80 days from spawning. This would put the time of hatching of Llanberis char, which spawn in mid-December (section 5.5), between mid-March and mid-

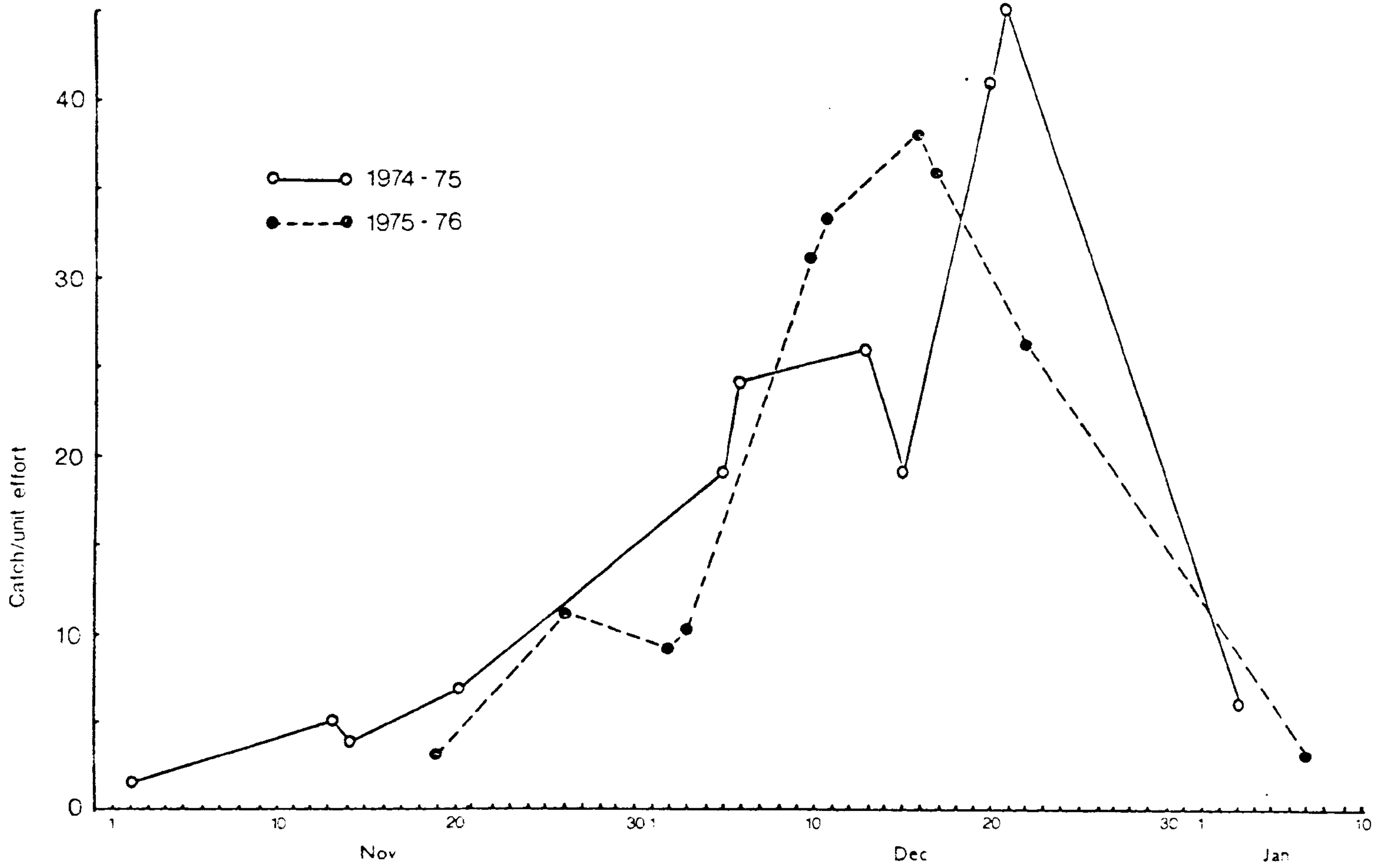
April. Plastic traps (Breder, 1960) were placed on the spawning site over this period in 1975, but no char alevins were captured. Frost (1965) showed that char alevins remain in the gravel until the yolk-sac is absorbed, and then immediately migrate into deeper water. This may explain why the traps were unsuccessful.

The time and size at which the younger char emigrate to Llyn Padarn was also not determined. Frost (1965) found that char hatched in the River Brathay almost immediately migrated downstream to the lake. The growth of Peris and Padarn char was significantly different at all ages, which implies that segregation occurs early in life. The Llyn Peris char were shown to grow faster only in their first year. If this anomaly was true and not due to errors in back-calculation, it could be a result of the extra stress placed on the Padarn char during this short migration.

5.5 Time of Spawning

The development of the gonads and ova of the char described in Chapter 4 indicate that spawning occurred during December, both in 1974 and 1975. Frost (1965) demonstrated that the spawning period of the autumn, shallow spawning, char of Lake Windermere could be correlated with the catches of the gill nets set on the spawning grounds. Gill nets set on the spawning grounds in Llyn Peris were not fished with such regularity as in Windermere, but the catch per unit effort in the nets (Fig. 5.6) suggested that spawning took place over a period of about 4 weeks from the beginning of December, with the period of maximum activity in the third week. This is later, and a much shorter duration, than for the autumn spawning Windermere char which may begin in late October and carry on until mid-December, a period of 10 to 12 weeks (Frost,1965). The water temperature in Llyn Peris during the

Fig. 5.6 The daily catch per unit effort from November to January for the shallow water site of Llyn Peris.



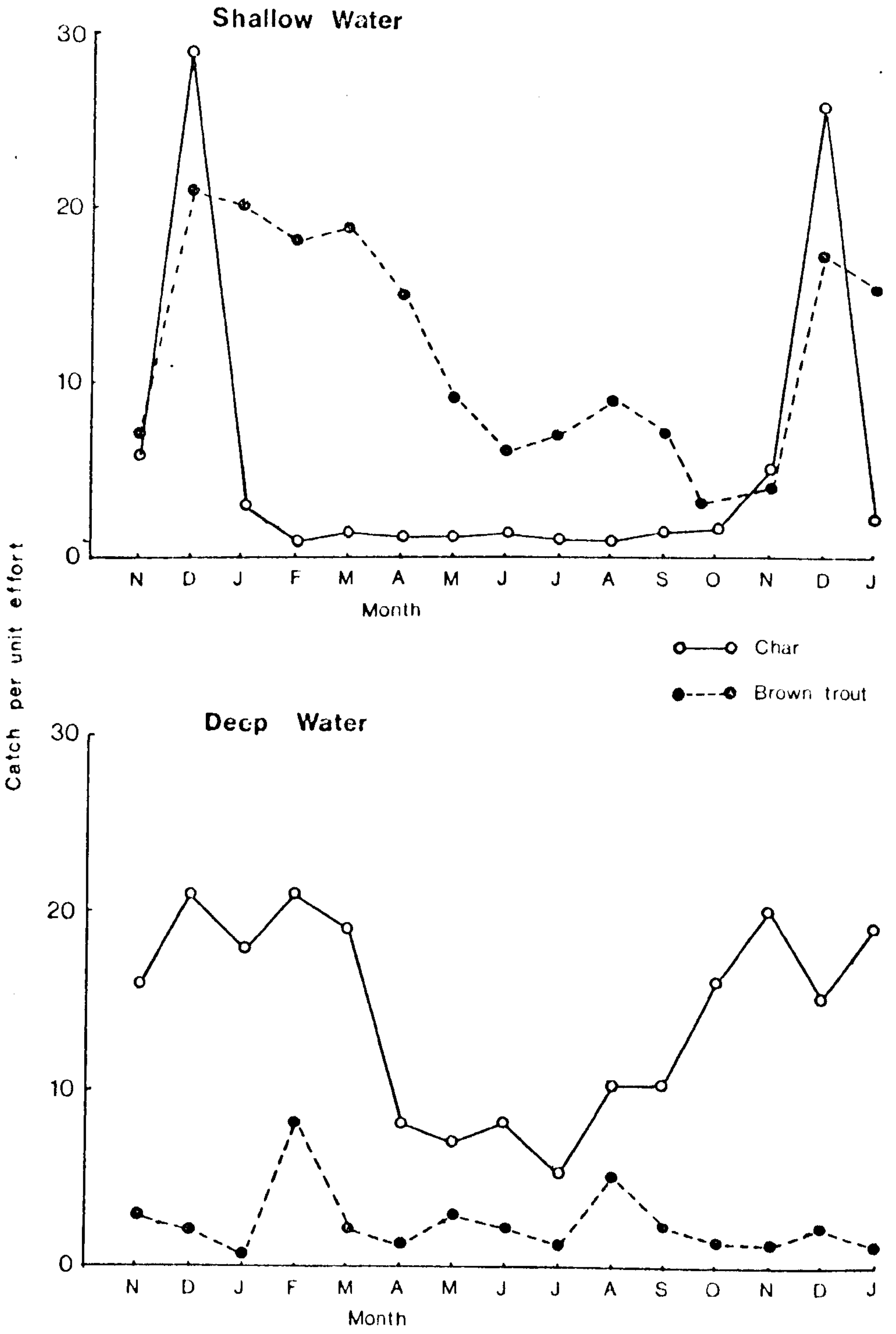
spawning period was about $8^{O}C$, about the same as for the Windermere autumn spawners. Frost (1965) reviews the possible stimuli, for example day-length and/or temperature, which govern the onset of spawning.

5.6 Depth Distribution

Attempts to analyse the diurnal vertical movement of the char quantitatively were unsuccessful. Very few fish were caught in the vertically set gill nets, mainly because of twisting; although they have been used satisfactorily by other workers (Hartmann, 1962; Horak and Tanner, 1964; Lackey, 1968; Bartoo et al., 1973; and others). Fig. 5.7 shows the catch per unit effort of char and trout in the standard deep and shallow set gill nets from Llyn Peris. Brown trout were rarely caught in deep water, but were commonly caught in the shallow water nets, the opposite to that found for char. This would indicate a segregation between the two species as has been demonstrated for other sympatric trout and char populations. When found living allopatrically, char and brown trout tend to have very similar feeding habits, and char tend to inhabit the littoral zones of lakes (Nilsson, 1955). When existing sympatrically with trout, the char alter their feeding habits, probably because of the greater aggressiveness of trout (Svardson, 1949b), and become more dependant on plankton (Nilsson, 1960; 1963). Trout then tend to inhabit the littoral zone almost exclusively and char the deeper waters. Similar observations have been made for populations of cutthroat trout, Salmo clarki, and Dolly Varden, Salvelinus malma,(Andrusak and Northcote, 1971) and for landlocked salmon, Salmo salar, and brook trout, Salvelinus fontinalis,(Lackey, 1970).

Echo-sounding and catches by rod and line during the summer showed there

Fig. 5.7 The catch per unit effort of char and brown trout in the shallow and deep water gill nets in Llyn Peris.



to be a movement towards the surface by the char at dusk, as was noticed by Powell (1966). Dembinski (1971) demonstrated a similar movement by vendace, Coregonus albula, which was associated with a corresponding upward migration by plankton, which is also the major food of Llanberis char (Powell, 1966).

Hunter (1970) found that male char were more commonly caught in the littoral areas than were females, whereas Skreslet (1973a) found females more often in the littoral. The catches of char from the littoral zones of Llyn Peris and Llyn Padarn were too rare, except during spawning, for any conclusions to be made.

5.7 Shoaling Behaviour

Hunter (1970), during his study of an arctic lake, commented that numbers of char were frequently caught within a restricted radius in the gill nets. Although his findings were not analysed, he considered this to indicate that the char were travelling about the lake in small schools, or aggregates. Similar observations were made during the present study, and shoaling behaviour was inferred from echo-sounding and catches by angling. Analysis of these data was made difficult by the low catches of char at certain times of the year, but was carried out for char caught from Llyn Padarn in a standard set of gill nets, which had been divided into sections (1m x 1.5m), during August and November. The results are shown in Table 5.4 which shows the number of char captured in each section of gill net, the frequency of such capture, the expected frequency if the catches followed a Poisson distribution and χ^2 values. The combined χ^2 values for both months was significantly different from that expected for random distribution ($p << 0.001$). The variances were greater than 1, and therefore the distributions were contagious (Zar, 1974).

Table 5.4 The observed and expected frequencies of the number of char captured in each section of the gill nets during August and November. The combined χ^2 values are shown.

	No. of char per section (x)	frequency of observation f	expected probability PX	expected frequency $F_1 = \lvert p(x) \rvert_n$		χ^2
AUGUST	0	25	0.406570	14.64		7.34
	1	4	0.365913	13.17		6.39
	2	2	0.164661	5.93		2.60
	3	0	0.049398	1.78		1.78
	4	2	0.011115	0.40		6.40
	5	2	0.002001	0.07		51.63
	6	1	0.000300	0.01		88.92
					Total	165.06
						$p < 0.001$
DECEMBER	0	24	0.301194	10.84		15.96
	1	3	0.361433	13.01		7.70
	2	0	0.216860	7.81		7.81
	3	2	0.086744	3.13		0.40
	4	3	0.026023	0.94		4.54
	5	1	0.006246	0.23		2.67
	6	2)	0.001249	0.045)		
	7	0) 3	0.000214	0.008)	0.054	160.72
	8	1)	0.000032	0.001)		
					Total	199.80
						$p < 0.001$

Berst and McCombie (1963) considered that when there was a relatively small catch in a gill net it is reasonable to assume that the spatial distribution of fish in the net corresponded to their distribution on approach. This implies that the char were moving round the lake in small schools as suggested by Hunter (1970), and also for Dolly Varden by Andrusak and Northcote (1971). The effects of avoidance or attraction due to fish already captured cannot be assessed, but it was noticed that when large numbers of trout were captured in shallow-water gill nets their distribution was much more scattered than the char, although this was not analysed quantitatively. Although again it could not be determined accurately, echo-sounding suggested there to be an increase in the shoal size of char at the approach of spawning, and Powell (1966) thought that the shoals might be of individual sexes.

5.8 Seasonal Movement

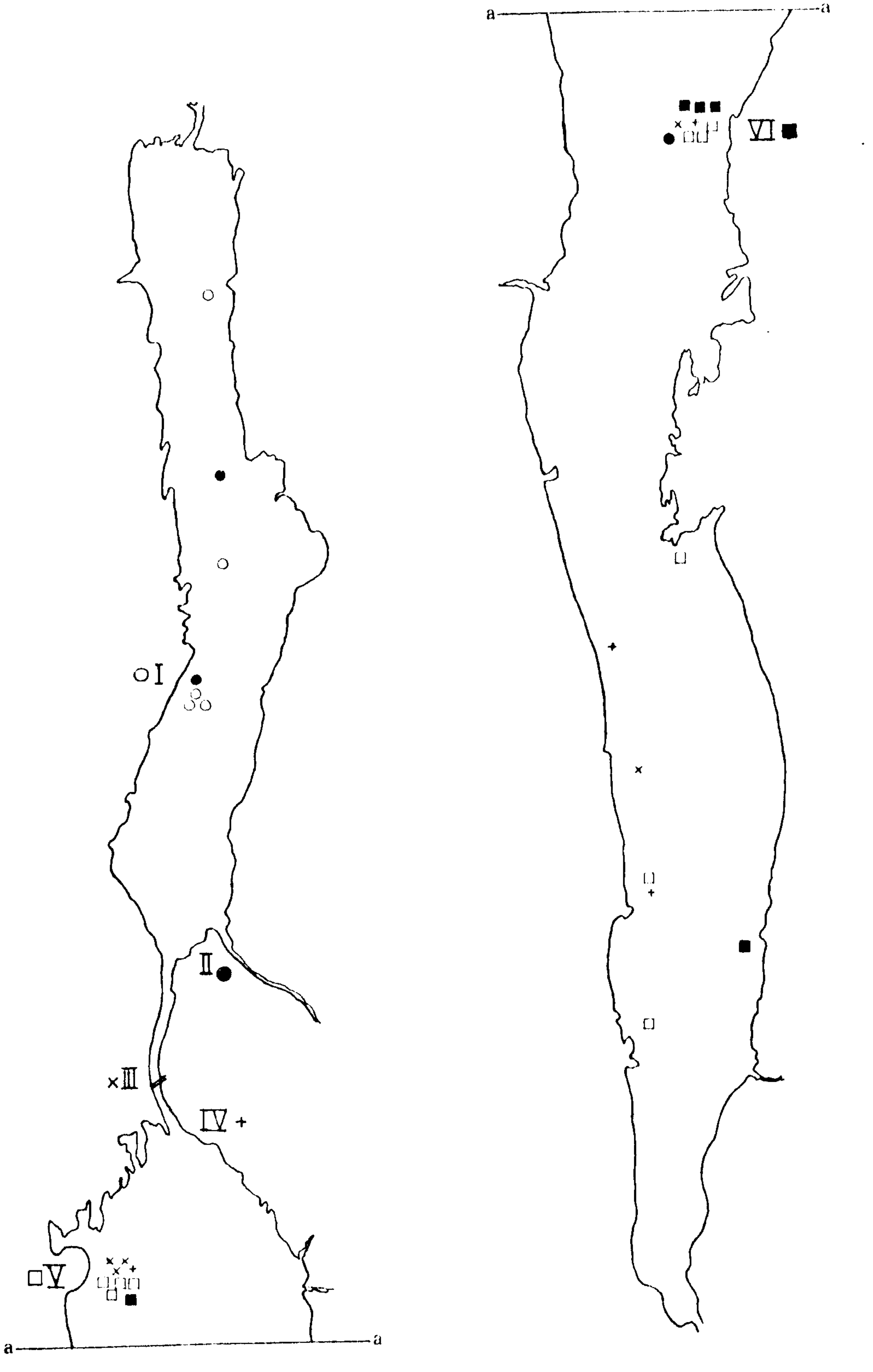
Aass(1971) reported post-spawning and winter movements of char into the littoral zone for feeding in reservoirs in Norway, and Hunter (1970) and Skreslet (1973a) also found that char were quite commonly caught in the littoral zone at certain times of the year. Fig. 5.3 showed that char were only rarely caught in the littoral zones of Llyn Peris and Llyn Padarn outside of the spawning season. It also demonstrated that the catch per unit effort in deep water declined in the summer, as was noticed by Powell (1966). This was possibly due to dispersal of the fish throughout the lake following spawning, similar to that found for Lake Vattern (Alm, 1951), and to a reduction in the shoaling behaviour. Echo-sounding and angling indicated that the char spent much of their time in mid-water throughout the summer and would not be vulnerable to bottom-set gill nets. At these times, a mid-water trawl would have been a most useful sampling tool, as demonstrated for gwyniad, another pelagic salmonid, in Llyn Tegid (Butterworth and Coles, 1977). Unfortunately, a suitable trawl was developed too late for sampling for this study, but on the one occasion it was used, in February 1976, it did catch a number of char from mid-water including, most significantly, two one year old and one two year old char of a size not vulnerable to other techniques.

The recaptures of tagged fish outside the spawning season are shown in Fig. 5.8. Although the majority of recaptures were in the fixed net positions at sites I, V and VI (sites II and IV caught few char and no tagged ones outside the spawning season, and site III, the fyke nets, was only used between November and January), catches from irregularly set nets and by angling indicated that the char were distributed over the whole of both lakes during the summer and did not occupy discrete territories. There was no evidence that fish moved between the lakes outside the spawning season.

From observations made during this study, and from information supplied by local anglers, it is possible to hypothesise on the movements of the char in both lakes during the year. In Llyn Peris, during the summer, char swim in small schools throughout the lake, mainly in mid-water (depth 10-15m), perhaps rising nearer the surface during darkness. During late October and early November they congregate in the vicinity of site I, mainly on or near the bottom. During spawning, in December, they move onto the spawning shallows during the night, returning offshore into deeper water during the day. LeCren and Kipling (1963) and Frost (1965) showed that the males remain on the spawning beds for a longer period than the females in Lake Windermere, but it was not possible to demonstrate this for Llanberis char. After spawning, the char disperse, although they may congregate briefly at site I until about mid-January.

In Llyn Padarn, the char are also dispersed over all the lake, in small schools in mid-water,during the summer. They appear to congregate in the vicinity of site VI in September and October, and move across to site V during November. They then ascend the Afon-y-Bala during the hours of

Fig. 5.8 The point of recapture of marked char between February and September. The symbols represent the site of original capture; the sites are shown by Roman numerals with their corresponding symbols alongside.



darkness, the males possibly starting to do so before the females. They spawn in the same place as the Llyn Peris char, and also move offshore during the day. The spent char descend the river immediately after the completion of spawning and disperse throughout the lake. It is not known when the fry emigrate to Llyn Padarn, but it is presumably soon after feeding has commenced.

CHAPTER 6 TAXONOMIC CHARACTERISTICS OF WELSH CHAR

6.1 Introduction

Behnke (1972) remarked that "the diverse array of ecological and behavioural adaptations found in the salmonid fishes of recently glaciated lakes, often resulting in sympatric, morphologically similar "sibling species", raises several profound questions on the speciation process and rate of evolutionary change .....".
This is especially true of the arctic char and different populations have been given large numbers of specific or subspecific names which bear little significance to evolutionary reality.

Two species within the genus *Salvelinus* are considered to have well defined limits. They are; *Salvelinus (Christivomer) namaycush*, the North American lake char, indigenous to the Great Lakes region, and *Salvelinus (Baione) fontinalis*, the American brook char (trout), indigenous to north-eastern North America but which has been introduced to most continents. MacCrimmon and Campbell (1969) give an excellent review of its present distribution. The other species within the genus are often referred to as the *'Salvelinus alpinus complex'*, and includes *S. alpinus*, *S.malma*, the Dolly Varden of western North America and north east Asia and their many derivatives.

S.malma was originally described by Walbaum from Kamchatka, but from this region it is often difficult to distinguish from *S. alpinus* (Savvaitova, 1961). In North America, McPhail (1961) considered there to be obvious differences between the two, although Behnke (1972) commented that further studies could find there to be less differentiation than originally thought. Morrow (1973) described a new species, S.anaktuvukensis, from the Brooks range area of Alaska which Frohne (1973) showed to have closer affinities to S. malma than S. alpinus. A further species, S. confluentus, the bull trout, was recently described by Cavender (1978) which is also similar to, and may be sympatric with, S. malma.

Salvelinus alpinus was originally described as Salmo alpinus by Linnaeus from Scandinavia, but great confusion has arisen because of the habit of giving new specific or subspecific names to specimens from different geographical areas. Regan (1911) recognised 15 full species of Salvelinus from the British Isles, Berg (1948) 11 species from the Soviet Union, Jordon et al. (1930) 12 species from North America and Nilsson (1832), quoted by Nilsson and Filippson (1971), 6 species from Scandinavia. Ladiges and Vogt (1965) described 24 subspecies from Europe.

Behnke (1972) considered there to be only one European char which should be treated as a separate species because of its marked dissimilarity from other forms of S. alpinus; that is the 'tiefseesaibling', named as S. profundus by Berg (1932), which inhabits some Alpine lakes. Martin (1939) concluded that all North American arctic char were one species and that they were similar to non-anadromous Norwegian char, but he could not show that anadromous North American and Norwegian char were the same. McPhail (1961), in his study of the 'Salvelinus alpinus complex' of North America, considered that the arctic char previously described from the eastern Canadian arctic as S. rossii (Richardson); S. alipes (Richardson); S. nitidus (Richardson); S. arcturus (Gunther) and S. naressii (Gunther) were all conspecific with S. alpinus. He also concluded that the isolated non-migratory populations of eastern North America, S. marstoni (Garmen) in Quebec, S. aureolus (Bean) in New

Hampsshire and Maine and *S. oquassa* (Girard) in western Maine should be considered as synonyms of *S. alpinus*. Qadri (1974) also showed that all three species were conspecific with S. alpinus, but should be given subspecific status, *S.a.oquassa*, because of their geographical isolation. Vladykov (1954) had thought that *S. aureolus* and *S. marstoni* were distinct species, with the latter being conspecific with *S. oquassa*. Vladykov (1957) further divided *S. marstoni* into three subspecies, *S.m.marstoni*, *S.m.intermedius*, and *S.m.canvanaghi*, but this was based on characters which he had previously (Vladykov, 1954) dismissed as being of little use in char taxonomy. McPhail (1961) and McCart and Craig (1971) concluded that there are two distinct forms of *S. alpinus* in North America which may warrant subspecific status, which were referred to as the eastern Arctic form and the western Arctic-Bering Sea form.

The Bering Sea region of Asia must claim the distinction of possessing the most confusing array of char populations which defy any logical scheme of classification. Savvaitova (1961; 1969; 1973; 1976a; 1976b) overcame this by regarding the various forms of *S. alpinus* from this region, and also from Siberia, as biological forms of a single, polymorphic, species. She considered that the morphological diversity amongst chars are due to unstable environmental conditions and the great variability of adaptive changes which the chars manifest to compensate for them. Some may possibly have reached species level, but there is no evidence of irreversibility. She also included *S. malma* as a synonym of *S. alpinus*, unlike McPhail (1961) for North American populations.

The systematics of chars is further confused by the existence of many examples of two or more populations living sympatrically. They may be of similar form and habit differeing, for instance, only in the time or place of spawning, or they may differ markedly in appearance and mode of life as well. In Alpine lakes three 'types' of char are described; the tiefseesaibling, the wildfangsaibling and the normal saibling. They may be present in a variety of combinations, or singly, in different lakes (Reisinger, 1953; Schindler, 1957; Doerfel, 1974). Brennet (1976) considered that it was impossible to estimate how many populations of char there are in Attersee. Sympatric populations have also been recorded from Scandinavia (Maar, 1949; 1950; Nilsson, 1955; Svardson, 1961; Nordeng, 1961; Klemetsen and Ostbye, 1967; Nilsson and Filipsson, 1971; Nyman, 1972), Jan Mayen Island (Skreslet, 1973a) and the Soviet Union (Berg, 1948; Savvaitova, 1961; 1973). The only possible example of sympatric population of arctic char recorded in North America is that of Metamek Lake, Quebec (Saunders and Power, 1969), but the differences between the two populations could be a result of irregular spawning; the 'silver' char having spawned in the previous year and the 'red' char were approaching spawning. Behnke (1972) opined that sympatric populations with ecological and life history distinctions should be treated as distinct species, especially from a fishery management point of view. Because of scientific nomenclature problems, taxonomists will have to accept a classification permitting two reproductively isolated populations of Salvelinus alpinus to occur in some lakes.

Compared to the rest of the range of Salvelinus, the British Isles, especially Scotland, has a greater concentration of char populations than recorded elsewhere (Friend, 1959). However, from what little is known of them, they are apparently less diverse, in form and habit, than in other areas, possibly because they are normally found in competitive situations with other species, principally brown trout, which reduces the ecological niches available to them (Skreslet, 1973b). They are planktivorous or benthophagic, never principally piscivorous, of a relatively small size, rarely over 600g, and always lacustrine, although, as mentioned previously, some ascend rivers to spawn. By contrast, up to six different types of non-anadromous char have been described from Kamchatka (Savvaitova, 1973; 1976b) ranging from benthopagic brook char, of maximum length 24cm, to the piscivorous stone char which reaches a length of 60cm. The char of the British Isles are slightly differentiated from those of the European mainland, suggesting that they originated in postglacial times from an ancestral anadromous char somewhat divergent from those settling in the Alpine lakes and Baltic Basin (Behnke, 1972). Only one sympatric population has been described, from Lake Windermere (Frost, 1955; 1965), where there are two varieties differing in spawning time and place, growth rate and some meristic characters. Dwarf populations of both types may also exist (Frost, 1965; Frost and Kipling, 1980). Differences between the two major populations may disappear when they are reared under identical conditions (Frost, 1965).

Gunther (1866) listed six species of char from the British Isles separable by vertebrae and pyloric caeca numbers. They were S. alpinus (59-62 vertebrae; 36-42 pyloric caeca); S. killinensis (62 vertebrae; 44-52pyloric caeca); S. willughbii (59-62 vertebrae; 32-44 pyloric caeca); S. perisii (61 vertebrae; 36 pyloric caeca); S. grayi (60 vertebrae; 37 pyloric caeca) and S. colii (63 vertebrae; 42 pyloric caeca). However, Day (1880-1884; 1887) regarded them all as varieties of the same species.

Regan (1911) concluded that there were 15 species of char in the British

Isles; *S. willughbii*; *S. lonsdalii*; *S. maxillaris*; *S. perisii*; *S. mallochi*; *S. killinensis*; *S. inframundus*; *S. struanensis*; *S. gracillimus*; *S. colii*; *S. grayii*; *S. trevelyani*; *S. fimbriatus*; *S. scharffi* and *S. obtusus*; although he later (Regan, 1914) thought them all to be synonymous with *S. alpinus*,and Friend (1959) considered that populations with obviously differing characters that are geographically isolated should be considered as subspecies. Behnke (1972) was of the opinion that only one char from the British Isles was obviously different from the rest and that is *S.fimbriatus* of Lough Coomarsaharn in Co. Kerry, which, because of its high numbers of gillrakers, may represent a relict population of a distinct stock which shares closer affinities with the char of the European mainland and the Kara Sea - Taimyr peninsula area. Ferguson (1977) examined specimens of char from Lough Finn, Co. Donegal, originally described as *S. trevelyani*, and showed them to be *S. alpinus*.

One of the many problems in char taxonomy is the great variety of morphometric measurements that have been used to differentiate char populations, making comparisons difficult. This has, to some degree, been resolved in more recent studies, and the measurements devised by Vladykov (1954) and Hubbs and Lagler (1958) are most often used. A further problem is that body proportions and meristic characters may change with the length of the fish, and also that body proportions may alter markedly over a relatively short period of time. Vladykov (1954) contended that the number of gillrakers of char varied with length, and Nilsson and Filipsson (1971) showed there to be a slight increase in gillraker and pyloric caeca with length for char from Lake Ovre Bjorkvattnet, although McPhail (1961) found no correlation between the numbers of gillrakers, pyloric caeca and lateral line pores with length. Friend (1959) estimated that the head shape of Llanberis char had altered between 1865 and 1954 and that male char netted from Girlsta Loch (Shetland Isles) in 1965 had shorter heads and fins than specimens in the British Museum. Taning (1952) and Wilder (1952) also showed that meristic characters could be influenced by temperature during the development of the embryo.

Because of the uncertainties when using morphometric and meristic characters and to try and define true relationships between arctic char populations, both sympatric and allopatric, there has been an increased use in the application of gel electrophoresis to systematics. Tsuyuki et al. (1966) made comparisons of zone electropherograms of muscle myogens of *S. namaycush*, *S. alpinus* and *S. malma* and found obvious similarities, the patterns for *S. alpinus* and *S. malma* being virtually superimposable and consistent with subspecies characterisation. Saunders and McKenzie (1971) examined the muscle protein pattern of *S. alpinus*, *S. aureolus* and *S. oquassa* and found there to be no inter-specific variations, although there were interpopulation variations in eyelens proteins, liver LDH and liver esterase, verifying the conclusions reached by morphometric and meristic examinations. Zakharova et al. (1971) concluded that all the different populations of *S. alpinus* they studied were closely related. Nyman (1972) analysed the esterase polymorphism in 31 populations of arctic char from North America, Greenland and Scandinavia and 2 specimens of Dolly Varden. He concluded that there were 3 sibling species of char within the *S. alpinus* complex in Scandinavia, one of which was conspecific with North America and Greenland populations. Unlike Tsuyuki et al. (1966) and Zakharova et al. (1971) he considered that *S. malma* was a distinct species. In conjunction with the present study, Child (1977) studied the biochemical polymorphisms in char from the four Welsh populations and found the Llyn Peris and Llyn Padarn populations to be genetically similar, but that there were interpopulation variations between Peris/Padarn, Llyn Cwellyn and Llyn Bodlyn. The Llyn Bodlyn char were more closely related to Peris/Padarn than those of Llyn Cwellyn.

In this chapter data are presented to describe and compare some morphometric and meristic characters of the two Llanberis char populations and that of Llyn Cwellyn. Llyn Cwellyn is a deep, oligotrophic lake of about 9ha in area, situated in a valley running parallel to that of Llanberis and about 6km to the southwest. It discharges via the Afon Gwyrfai into the Menai Straits near to the mouth of the Afon Seiont, the efferent river of Llyn Padarn. In the previous chapter, it was considered that the Llyn Peris and Llyn Padarn char spawn in the same place and at the same time. If the two populations are morphologically similar, but dissimilar to that of Llyn Cwellyn, which possibly arose from the same anadromous stock, it would support this hypothesis and also indicate, as suggested, that there is no segregation during spawning.

6.2 Laboratory Methods

30 Mature char from each of Llyn Peris, Llyn Padarn and Llyn Cwellyn, captured by gill net during October and November 1974, were examined. Their fork length was measured to the nearest mm and eight body measurements were taken which were adopted from Vladykov (1954) and Hubbs and Lagler (1958) and had been shown by Oulette and Qadri (1966) and Qadri (1974) to be of most use in differentiating char populations. They were; Bdl - body length from anterior upper end of the opercle to fork of tail; pDF - distance from insertion of dorsal fin to fork of tail; pA - distance between origin of pectoral fin to origin of anal fin; DaD - distance from insertion of dorsal fin to origin of adipose

fin; SP - anterior tip of snout to origin of pectoral fin; Ma - length of maxilla; H - head length; I - interorbital width. The interorbital width and length of maxilla were transformed into percentages of the head length and the other measurements into percentages of the fork length.

6 Meristic counts were made as follows; LL - number of pored lateral line scales; PC - number of pyloric caeca, counted as each caecum was detached from the main mass; GR - number of gillrakers (total count and number on lower arch only) on the first left gill arch; V - total number of vertebral centra, not including the urostyle; E - number of epineurals; R - number of ribs. The number of vertebrae, epineurals and ribs were estimated after the fish had been boiled in dilute KOH and the flesh carefully teased away.

Percentages or proportions form a binomial, rather than a normal, distribution; the deviation from normal being greater at small or large values (0 to 30% and 70 to 100%). Therefore the data from morphometric measurements were transformed to their arcsine (Zar, 1974), which results in it having an underlying distribution that is nearly normal. It is not, therefore, possible to statistically compare untransformed data from other studies. The data on meristic and transformed morphometric characters were subjected to two-factor analyses of variance to assess the effects of groups of fish, their sex and their interactions. Only the effects of groups, not the sex, showed some significant differences at a 0.5% level. Whenever the F values were found to be significant, the means for the character were compared using the Newman-Keuls multiple range test (Zar, 1974). The coefficients of difference;

$$\mathrm{CD} = \frac{\text{mean for pop}^{\underline{n}}\text{ b} - \text{mean for pop}^{n}\text{ a}}{\text{s.d. pop}^{\underline{n}}\text{ b} + \text{s.d. pop}^{\underline{n}}\text{ a}}$$

were also calculated (Mayr et al., 1953), values of 1.28 and higher being considered as indicating subspecific status. At this value, 90% of the fish in each of the two groups differed from one another.

6.3 Results and Discussion

The details of the fish studied are shown in Table 6.1.

Table 6.1 Details of fish studied for morphometric and meristic; comparison. The lengths, in cm, are shown as range (numerator) and mean (denominator).

Locality	Males		Females	
	n	fork length	n	fork length
Llyn Padarn	16	$\frac{19.7\text{-}25.2}{22.3}$	14	$\frac{20.8\text{-}24.2}{22.7}$
Llyn Peris	14	$\frac{16.5\text{-}21.3}{18.3}$	16	$\frac{16.5\text{-}22.1}{19.0}$
Llyn Cwellyn	17	$\frac{15.8\text{-}21.7}{19.2}$	13	$\frac{17.2\text{-}21.4}{18.7}$

The ranges and mean lengths of char for both Llyn Cwellyn and Llyn Peris were similar, but were smaller than those from Llyn Padarn. The small number of Llyn Cwellyn fish studied made detailed growth analysis impossible, but their growth rate was of the same order of magnitude as Llyn Peris char and their longevity was similar to both Llanberis char populations.

The state of gonad maturation indicated that the Cwellyn char would spawn at about the same time of year as those of Llanberis (December) and therefore probably do so in shallow water, as discussed in Chapter 6. A notable difference was that of colouration. At the approach of spawning, the Padarn char undergo a spectacular colour change; most of the males,and some of the females, assume a brilliant deep orange colour ventrally and the anterior edge of the pectoral, pelvic and anal fins become white. This change is not as apparent in the Peris char and most of the fish remain pale. The reason for this is obscure, but it is probably due to the smaller size of the Peris char, but not, as Powell (1966) suggested, to them spawning in deeper water. However, the Cwellyn char, of similar size to those of Peris, also assume this deep colouration, as intense, if not more so, than those of Padarn.

The details of morphometric and meristic measurements are shown in Table 6.2.

Of the morphometric measurements, all those of Llyn Peris and Llyn Padarn were of no significant difference, but three of the measurements from Llyn Cwellyn were different; the positions of the dorsal fin, pectoral fin and the relationship of the interorbital width to head length. However, the coefficients of difference (CD) values were all below 1.28 (subspecific value), confirming the considerable overlap in observations.

It is difficult to make detailed comparisons with morphometric data from other populations; in the majority of cases the data are not equivalent, often fragmentary and not suited for statistical comparisons because of the non-normal distribution of proportional data. Doerfel

Table 6.2 Morphometric and meristic measurements of the three char populations. Whenever the F values were significant at 0.5%, samples were compared by the Newman-Keuls multiple range test. Underlined samples are not significantly different. The mean and standard deviation (in parentheses) are given for each population. The morphometric measurements were compared after arcsin transformation, and the values are shown transformed back to proportions.

Character	Llyn Cwellyn	Llyn Peris	Llyn Padarn
H/FL %	21.00 (1.03)	21.32 (1.10)	21.37 (1.06)
BdL/FL %	86.10 (1.54)	85.09 (1.97)	85.23 (1.59)
pDF/FL %	60.02 (1.24)	59.15 (1.03)	59.47 (1.16)
PA/FL %	50.21 (1.84)	49.51 (2.07)	49.48 (2.06)
DaD/FL %	33.97 (1.37)	33.96 (1.20)	33.95 (1.22)
SP/FL %	19.61 (0.99)	20.73 (1.18)	21.12 (1.16)
I/H %	31.61 (3.21)	29.50 (3.11)	29.63 (3.16)
Ma/H %	48.85 (2.90)	49.90 (2.80)	49.03 (3.12)
No. of vertebrae	60.68 (0.99)	61.21 (0.85)	61.42 (0.99)
No. of ribs	33.24 (1.19)	34.40 (1.03)	34.42 (1.11)
No. of epineurals	27.84 (1.11)	29.07 (1.12)	28.72 (1.10)
Total no. of gillrakers	21.27 (1.11)	21.71 (1.41)	21.64 (1.30)
No. of gillrakers, lower arch	13.73 (0.78)	13.36 (0.91)	13.69 (0.88)
No. of lateral line pores	130.60 (3.84)	131.32 (2.94)	131.88 (3.26)
No. of pyluric caeca	35.89 (3.06)	37.40 (2.90)	36.98 (3.16)

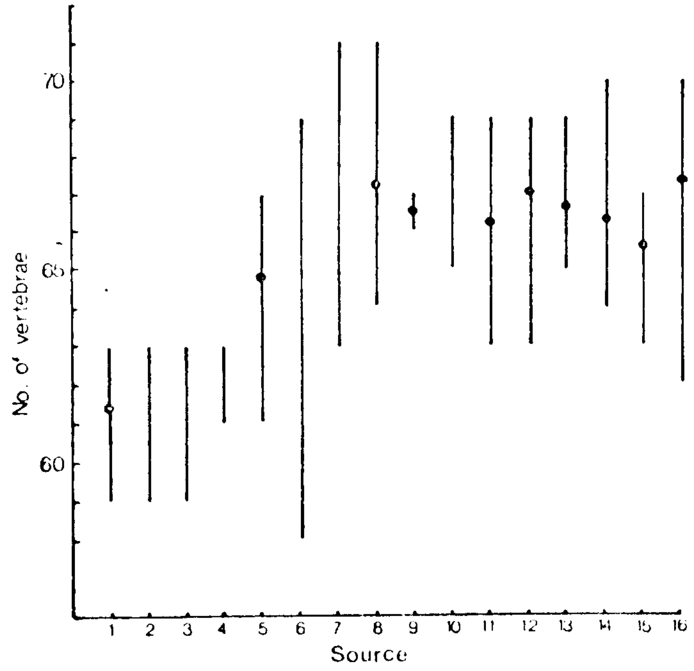
(1974), Qadri (1974) and Rombough et al. (1978) all used some measurements the same as those used in this study. The body proportions were similar for all populations except that the head length of the Candlestick Pond, Newfoundland, char (Rombough et al., 1978) was greater than the others (23% for Candlestick Pond, 21% for Welsh char; 20% for eastern North America char; 18.3-19.2% for Alpine char), and the dorsal fin was further forward in the Welsh char (60% of fork length for Welsh char; 48% for Newfoundland and eastern North America). The latter difference is also shown by the distance between the dorsal and adipose fins being least in the Welsh char. Where comparisons are possible, there are only minor differences in body proportions between Welsh char and those from Loch Girlsta and Loch Eck (Friend, 1959), L. Nachikin, USSR, (Savvaitova, 1976a) and North America (Vladykov, 1954).

As with the morphometric data, there were no significant differences in any of the meristic counts between the Llyn Peris and Llyn Padarn populations, but there were for the number of vertebrae, ribs and epineurals between Llanberis char and those of Llyn Cwellyn. Again, no coefficient of difference values were approaching 1.28. Because of the lower number of ribs and epineurals, it was probably the precaudal vertebrae that were fewer in number in Llyn Cwellyn char; Vladykov (1954) showing them to be more variable. Taning (1952) demonstrated that the number of vertebrae could be influenced by temperature during embryo development, so, if the two Llanberis char populations do spawn at the same time and at the same place, as hypothesised, it is not surprising that their vertebral counts were similar. Some authors (Vladykov, 1954; Reshetnikov, 1961; Nilsson and Filipsson, 1961) have shown that the number of gillrakers and pyloric caeca varies with length, whereas McPhail (1961) found that they did not. No correlation ($p > 0.10$) was found between the number of gillrakers or pyloric caeca and length for any of the three char populations studied, possibly because only mature char were examined.

The number of vertebrae recorded for arctic char populations is extremely variable (McPhail and Lindsey, 1970). In general, the counts recorded for Welsh and other British Isles populations are lower than elsewhere (Fig. 6.1). The reason for this is unknown. A low vertebral count is often associated with low temperatures during embryo development (Taning, 1952), but, from the paucity of available information, the temperature is higher for British char than for more northerly populations. If the cause is genetic, then this would support the view of Behnke (1972) that the ancestral anadromous char settling in British lakes was divergent from those settling elsewhere. The low vertebral count possibly also accounts for the lower numbers of pored lateral line scales found for British populations (125-180 vs 160-210 for Alpine char).

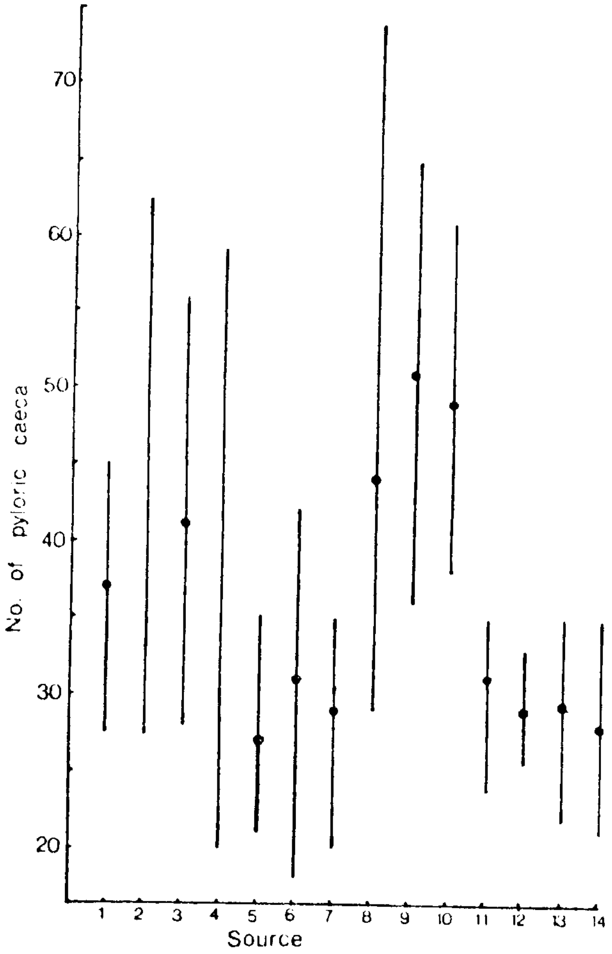
The number of pyloric caeca found in arctic char populations is, even more than the vertebrae, extraordinarily variable. Vladykov (1954) considered them one of the most important taxonomic characters for differentiating char populations, but found that the number varied with length, whereas McPhail (1961), and also the present study ($p > 0.10$), found no correlation between the number of caeca and length. He also considered them as a highly valuable character for comparing char populations, although Oulette and Qadri (1966) and Qadri (1974) did not. Fig. 6.2 shows the number of pyloric caeca found for various populations. The British and Swedish populations are intermediate in their number of caeca, and are possibly nearer McPhail's (1961) eastern Arctic classification than the western Arctic-Bering Sea one. Reshetnikov (1961) demonstrated that a greater number of pyloric caeca is associated with predatory feeding and a smaller number with the consumption of benthos. There is little to support this contention from Fig. 6.2; the predatory Kamchatka River and stone char have relatively few caeca, and those with the most caeca, the eastern Arctic populations, are benthophagic (McPhail, 1961).

Fig. 6.1 The range, with means where given, of the number of vertebrae of arctic char from various locations.



1) Welsh lakes (present study). 2) Lake Windermere (Frost, 1965). 3) Other British populations (Gunther, 1866; Regan, 1909a). 4) Ireland (Regan, 1908). 5) Eastern North America (Vladykov, 1954). 6) Cache Creek, Alaska (McCart & Bain, 1974). 7) Northern Labrador (Andrews & Lear, 1956). 8) Eastern Arctic (McPhail, 1961). 9) Western Arctic-Bering Sea (McPhail, 1961). 10) Karluk Lake, Alaska (DeLacy & Martin, 1943). 11) Lake Dal'neye, Kamchatka (Savvaitova, 1976a). 12) Lake Nachikin, Kamchatka (Savvaitova, 1976a). 13) Kamchatka River benthophages (Savvaitova, 1973). 14) Kamchatka River predators (Savvaitova, 1973). 15) Stone char, Kamchatka (Savvaitova, 1973). 16) Brook char, Kamchatka (Savvaitova, 1973).

Fig. 6.2 The range, with means where given, of the number of pyloric caeca in arctic char from various locations.

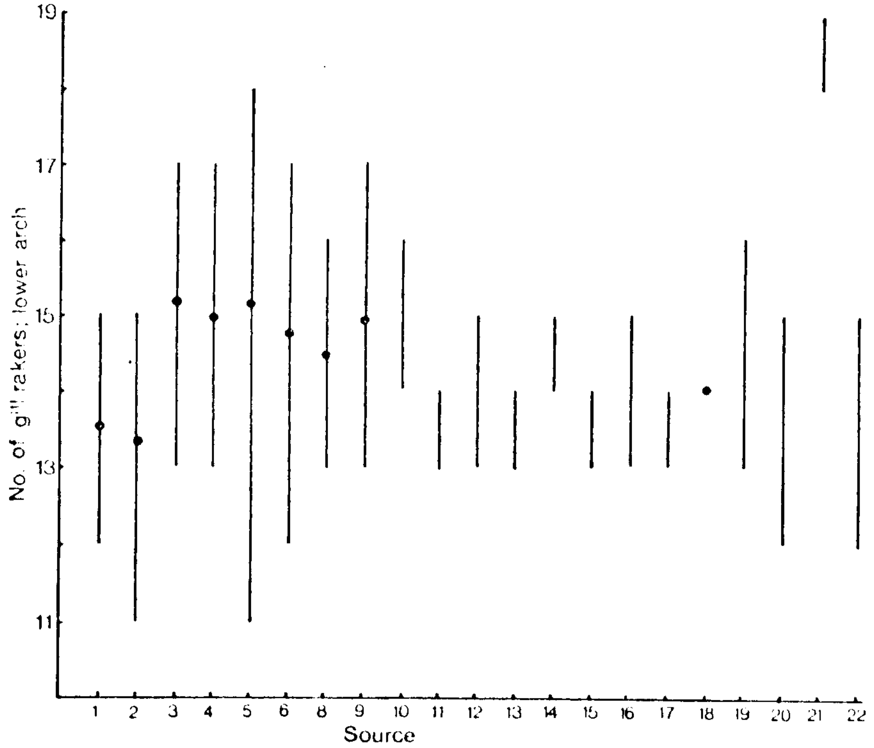


1) Welsh lakes (present study). 2) Other British waters (Regan, 1908; 1909a). 3) Lake Ovre Bjorkvattnet, Sweden (Nilsson & Filippson, 1971). 4) Eastern North America (Vladykov, 1954). 5) Cache Creek, Alaska (McCart & Bain, 1974). 6) Canning River, Alaska (Craig, 1978). 7) Western Arctic-Bering Sea (McPhail, 1961). 8) Eastern Arctic (McPhail, 1961). 9) Lake Nachikin (Savvaitova, 1976a). 10) Lake Dal'neye (Savvaitova, 1976a). 11) Kamchatka River benthophages (Savvaitova, 1973). 12) Kamchatka River predators (Savvaitova, 1973). 13) Stone char, Kamchatka (Savvaitova, 1973). 14) Brook char, Kamchatka (Savvaitova, 1973).

The number of gillrakers is often used in char taxonomy, and is a highly regarded character by many authors (McPhail, 1961; Savvaitova, 1973; 1976a; Qadri, 1974), but was considered by Vladykov (1954) to be of little use, mainly because the number tended to increase with age, an observation also made by Nilsson and Filipsson (1971). However, McPhail (1961) and the present study ($p > 0.10$) found no correlation between gillraker number and length for mature char. Fig. 6.3 shows the number of gillrakers found on the lower arch for arctic char populations from various British waters. The number found for the three Welsh populations is very similar to the Lake Windermere autumn spawners and the Scottish and most Irish populations. The char from the rest of the Lake District, including the Lake Windermere spring spawners, generally have a slightly higher count, although the overlap is considerable. As Behnke (1972) pointed out, the char from Lough Coomarsaharn, Co. Kerry, described as S. fimbriatus by Regan (1908), is the only population that really stands out from the other British char because of their high number of gillrakers, indicating that they may have arisen from different ancestral stock. However, Frost (1965) showed that when the two populations of Windermere char are artificially reared, their gillraker counts were similar, about the same as found for the wild autumn spawners. She also reported that wild Ennerdale char have a mean gillraker count of 15.1, but only 13.9 when reared artificially, and suggested that the number of gillrakers may be influenced by the environment. This may account for the high gillraker count in S. fimbriatus.

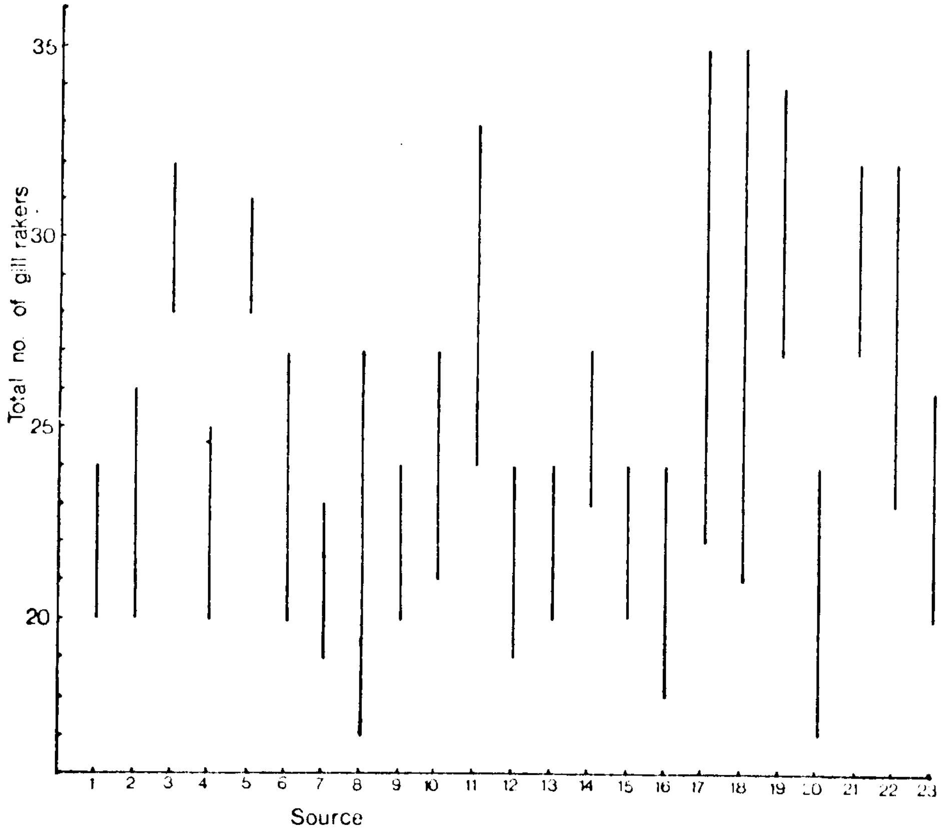
Fig. 6.4 shows the total number of gillrakers found in other populations of char throughout the world. With the exception of S. fimbriatus, the number of gillrakers found for British char populations is similar to the 'tiefseesaibling' of Alpine lakes and both the 'normal' and

Fig. 6.3 The range, with means were given, of the number of gill rakers on the lower arch in arctic char from various populations in the British Isles.



1) Welsh lakes (present study). 2) *S. willughbii*, Lake Windermere, autumn spawners (Frost, 1965). 3) *S. willughbii*, Lake Windermere, spring spawners (Frost, 1965). 4) *S. willughbii*, Coniston (Frost, 1965). 5) *S. willughbii*, Ennerdale (Frost, 1965). 6) *S. lonsdalii*, Haweswater (Frost, 1965) 7) *S. willughbii*, Buttermere (Frost, 1965). 8) *S. willughbii* , Crummockwater (Frost, 1965). 9) *S. killinensis*, Loch Killin (Regan, 1909a). 10) *S. struanensis*, Loch Rannoch (Regan, 1909a). 11) *S. gracillimus*, Loch Girlsta (Regan, 1909a; Friend, 1959). 12) *S. inframundus*, Hellyol Loch (Regan, 1909a). 13) *S. maxillaris*, Loch nr. Ben Hope (regan, 1909a). 14) *S. mallochi*, Loch Scourie (Regan, 1909a). 15) *S. alpinus*, Loch Eck (Friend, 1959). 16) *S. scharffi*, Ireland (Regan, 1908). 17) *S. trevelyani*, Ireland (Regan, 1908). 18) *S. colii*, Ireland (Regan, 1908). 19) *S. grayi*, Ireland (Regan, 1908), 20) *S. fimbriatus*, Ireland (Regan, 1908). 21) *S. obtusus*, Ireland (Regan, 1908).

Fig. 6.4 The range in the total number of gill rakers in arctic char from various populations.



1) Welsh lakes (present study). 2) Other British populations (Regan, 1908; 1909a). 3) *S. fimbriatus*, (Regan, 1908). 4) Tiefensaibling, Alpine lakes (Doerfel, 1974). 5) Normalsaibling, Alpine lakes (Doerfel, 1974). 6) Normal char, Sweden (Nilsson & Filippson, 1971). 7) Blattjen, Sweden (Nilsson & Filippson, 1971). 8) Eastern North America (Vladykov, 1954). 9) Western Arctic-Bering Sea (McPhail, 1961). 10) Eastern Arctic (McPhail, 1961). 11) Sagavanirktok River, Alaska (McCart & Craig, 1971). 12) Cache Creek, Alaska (McCart & Bain, 1974). 13) Canning River, Alaska (Craig, 1978). 14) Lake Nachikin, Kamchatka (Savvaitova, 1976a). 15) Kamchatka River benthophages (Savvaitova, 1973). 16) Kamchatka River predators (Savvaitova, 1973). 17) Stone char, Kamchatka (Savvaitova, 1973). 18) Brook char, Kamchatka (Savvaitova, 1973). 19) Okhota River, USSR (Savvaitova, 1976a). 20) Indigirka River, USSR (Savvaitova, 1976a). 21) Lake Frolikha, USSR (Savvaitova, 1976a). 22) Lake Taimyr, USSR (Savvaitova, 1976a). 23) Lake of Karelia, USSR (Savvaitova, 1976a).

'blattjen' char of Sweden; and also populations from North America and most riverine and lacustrine char of Kamchatka. The larger number of gillrakers found for S. fimbriatus are similar to the 'normalsaibling' of Alpine lakes, the stone char and brook char of Kamchatka, and those from the northern USSR (Okhota River, Lake Frolikh and Lake Taimyr).

The char populations of the British Isles have been isolated since the last Ice Age, about 8000 years ago. Whether they are relicts of anadromous populations which became landlocked due to the rise in the water temperature of the sea, or whether they were already non-migratory, perhaps living with anadromous populations as they still do in higher latitudes, is unknown. However, with the possible exception of S. fimbriatus, they all probably originated from a common ancestral population, which was possibly slightly divergent from the ancestors of the European mainland populations (Behnke, 1972).

As has been mentioned previously, the isolation of char populations and their ability to adapt to different environments has caused great plasticity in form which has resulted in their being given a large number of specific or subspecific names with little thought to their taxonomic position. Whether or not any populations are sufficiently divergent to warrant specific status is debatable. Even sympatric populations which are reproductively isolated and which may be morphologically different can interbreed readily under artificial conditions. The exact taxonomic position of British char populations is beyond the scope of this study, but the variation found within the British Isles is relatively small compared to the rest of the char's distribution. I would certainly agree with Friend (1959) that all the British arctic char are but a single species, Salvelinus alpinus, but I would also contend that the allocation of subspecific names is of little taxonomic value.

However, I agree with Behnke (1972) that attempts should be made to preserve genetic diversity within a species. The data presented in this study agree with the findings of Child (1977) that the Peris and Padarn char populations are genetically identical. Thus the loss of those from Llyn Peris alone would be of little consequence. These findings also support the contention that the two populations spawn in the same place and that there is no segregation between them. Therefore, unless the Llyn Padarn char change their habits, there is the probability that both populations would become extinct. The Llyn Cwellyn char are slightly divergent **from** the Llanberis ones, but havecertainly not diverged sufficiently to warrant subspecific classification.

CHAPTER 7 POSSIBLE EFFECTS OF THE PUMPED STORAGE SCHEME ON THE LLANBERIS CHAR

Behnke (1972) commented "postglacial salmonid communities are fragile and susceptible to destruction by man-induced changes .... Many distinct genotypes of trout, char and whitefish have been lost forever in the last 50 years. I strongly believe that every attempt should be made to preserve genetic diversity present within a species".

Arctic char as a species are probably not endangered in the British Isles, there being probably over 200 populations, but a number have become extinct in recent times (Maitland, 1979). Most char lakes are remote and suffer little from pollution or eutrophication, although Llyn Padarn and Lake Windermere (LeCren et al., 1972) may do so in the future, but many are being greatly modified by hydro-electric schemes, especially in Scotland (Friend, 1959). Examples of extinction include; Loch Leven, caused either through overfishing or the drop in water level (Regan, 1911); Heldale water, Orkney, probably due to the introduction of brown trout; Ullswater, through pollution by discharges from lead mines into their spawning streams (Frost, 1963); and Lough Neagh, possibly through overfishing. Friend (1959) reported that there were 12 lakes on record in Wales as holding char, but failed to name the source of information, but at the present time only four are definitely known to contain char; Llyn Peris, Llyn Padarn, Llyn Cwellyn and Llyn Bodlyn ; and all may soon suffer, directly or indirectly, by impoundment. Harvey (1975a) did not consider that the effects of a scheduled 2m fluctuation in water level would affect the Llyn Cwellyn population, although the char are thought to spawn in shallow water. He did concede that an entire year class could be destroyed in the event of a large drawdown immediately after spawning. However, apart from the spawning considerations, there is also that of food supply. Grimas (1961; 1965); Nilsson (1961); Hunt and Jones (1972), and others have shown that fluctuations in water level drastically reduce the littoral fauna. Although this would have little direct effect on the char, which are, in this country, planktivorous or benthophagic, it could cause the feeding habits of the more aggressive brown trout to alter into direct competition with char, especially if the food which the trout often revert to, terrestrial invertebrates, is scarce (Nilsson, 1960; 1961; 1963; 1964; 1965; Runnstrom, 1964; Lindstrom, 1965).

In 1776, Pennant, quoted by Gunther (1862), thought that all the Llanberis char had been destroyed by noxious water from coppermines. Certainly, prior to the Salmon Acts of 1873, they were in danger due to the practice of netting them off the spawning shallows every winter. However, there is now no doubt that the Llyn Peris char will not be able to survive after the completion of the scheme. Apart from considerations such as loss of food and spawning grounds, the water temperature during the winter would be above the lethal limit for char ova (Swift, 1965). The loss of the Peris char alone would probably be of little consequence; they are genetically identical to Llyn Padarn char and the latter grow larger and are a better sport fish. Unfortunately, evidence presented in this study indicates that the scheme may also affect the Padarn population, principally because access to their spawning grounds will be denied. The origin of their spawning behaviour is unknown, but is possibly innate and has remained since the lakes were separated. Vladykov (1943); Martin (1955b; 1960) and Frost (1963) have shown that species of <u>Salvelinus</u> home extremely well to their spawning grounds. Frost (1963; 1965) concluded that the meristic differences between autumn and spring spawning char in Lake Windermere were maintained by the infallibility of the homing. The exact mechanism by which homing is completed is unknown. Frost (1963) considered that it may be due to imprinting, that is that the newly hatched fry have their place of birth 'imprinted' on them and subsequently return to it to spawn. Doving et al. (1974) showed that fish odours, principally released from skin mucus, elicited responses from the olfactory bulb cells of char, different populations eliciting differential responses from the cells, and concluded that the odours could help guide homing. If the latter is true it does not explain, for instance, why char home to a pool on the River Brathay, flowing into Windermere, when there are no resident char in the stream (Frost, 1965). It could explain the initial migration from Llyn Padarn into Llyn Peris; the Padarn char responding to the odours of the resident char in Llyn Peris; but the homing onto the actual spawning beds is presumably imprinted. If odours are implicated in the migration of Padarn char, then the stimulus will be cut off after the completion of the scheme.

Little is known about the physical requirements of the spawning substrate for char, except that it is invariably stony and never composed predominantly of silt. Brown trout normally spawn on gravel, usually of a restricted size, and there is always a flow of water through the gravel to provide oxygenation (Frost and Brown, 1967). Such water flow through lake gravel is not possible except that due to wave action near the shore or by upwelling from springs. Because char eggs are rarely, if ever, deeply buried in the gravel, like those of trout, they possibly do not require a flow of water to ensure adequate oxygenation. There appears to be no reason why Llyn Padarn could not be used for spawning by char, there being large areas of apparently suitable substrate (Chapter 5). It could be that when access to Llyn Peris is denied and, if it is necessary, the odour stimulus from the Llyn Peris char is extinguished, then the Llyn Padarn char will spawn in Llyn Padarn itself. Fabricius (1950) reported that after the water level of Lake Storsjoute in Sweden was raised then, although some char spawned on the old grounds, others spawned nearer the new shoreline, on submerged streambeds and in tributaries, which was previously unrecorded. Martin (1955b; 1960) found similar evidence for lake trout (*Salvelinus namaycush*) in Ontario lakes, some even spawning on man-made artificial spawning beds after the lake level was lowered. It is apparent that char will alter their spawning habits after their original ones are denied to them or rendered unsuitable. It will therefore be necessary to observe the behaviour of the Padarn char to see if they also alter their habits. Frost (1963; 1965) provided some limited evidence that by planting eggs or alevins onto new sites then the resulting adults would return to those areas. It might be worthwhile to plant ova on suitable sites in Llyn Padarn in the hope that this behaviour will be apparent.

It has been suggested that attempts should be made to try and establish Llyn Peris char in other lakes. Apparently, earlier ettempts at this failed, although there are no details (Owen, 1809). Arctic char are apparently difficult to rear artificially, being particularly reluctant to take dry food. Preliminary attempts at rearing Llanberis char were unsuccessful (Harvey, 1975a), but Frost (1965) managed to hatch and grow on small numbers of Windermere char, feeding them on ground liver. Small scale laboratory experiments showed that young Llanberis char would also feed on ground liver as well as finely sieved *Daphnia*, *Cyclops*, and

Artemia, but all these methods would be too labour intensive to use on a larger scale.

A further problem is that of finding a suitable lake into which to stock char. Although char are occasionally found living sympatrically with brown trout in shallow waters in this country, they are normally found in deeper waters, mainly because of competition with the trout, as has been discussed. Most lakes in North Wales have large populations of brown trout, and a number of the larger, deeper lakes are impounded now or scheduled for it in the near future. Trout are highly regarded by anglers in the area, whereas char, because of their relatively small size and the specialised techniques required to catch them, are generally not, although they do have a novelty value with visitors to the area. Char have been shown to have a deleterious effect on the trout when introduced into new waters, especially where food supplies are limited (Somme, 1933; Schmidt-Nielsen, 1939; Grimas and Nilsson, 1962; Nilsson, 1963). This could cause hostility with anglers in whose lakes char might be stocked. A suitable lake for transplanting char should therefore be deep (large areas greater then 15m in depth); preferably have a small trout population; have stony or gravelly areas, probably in shallow water; and have an abundance of planktonic or benthic organisms. Shallow lakes could prove suitable if trout were removed or maintained at a low density. During the present study, several likely lakes were examined, but all proved deficient in one or more aspects. Harvey (1975b) investigated Llyn Bodgynydd and also found it unsuitable.

Thus it will be difficult to successfully maintain the Llyn Peris char in other lakes, and I would contend that efforts would be better directed to ensuring the survival of the Llyn Padarn char. Friend (1959) concluded

"How long the world's isolated colonies of freshwater charr (sic) are likely to persist cannot, of course, be guessed. As one of the many peripheral-glacial phenomema this fragmentation of Salvelinus alpinus in the freshwaters could be quite transient, for the small isolated populations that make it up are always liable both to local accidents and to the impact of more widespread changes such as climatic cycles. It is difficult to avoid the feeling that most subspecies of charr are, in all probability, heading for extinction ......". One can only hope that this does not apply to more than one Welsh population in the near future.

Acknowledgements.

I would like to thank my supervisor, Dr. J.W. Jones O.B.E., for his constant encouragement and advice; and the technicians of Liverpool University and the C.E.G.B., Dinorwic Power Station and the bailiffs of the Gwynedd River Division of the Welsh National Water Development Authority for their assistance in the field. I would also like to express my appreciation to Dr. J.W.Banks for his helpful criticism of the manuscript.

I would especially like to thank my wife, Margaret, and my daughters for their continued tolerance of my intolerances. The study was financed by a grant from the Central Electricity Generating Board.

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Fish. Mgmt (1976), 7, No. 3. Printed in Great Britain

The Use of Knotless Netting in Fisheries Research

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INTRODUCTION

In 1922 a knotless type of netting was invented by the Japanese Nippon Seimo Co. Ltd. With the advent of synthetic fibres, this type of netting has been used in many countries for the construction of various types of fishing gear, although it has not been used extensively for this purpose in Britain. In the past it has been difficult to obtain small mesh sizes in knotless netting, suitable for the construction of freshwater fishing gear. Recently, small-mesh knotless keepnets and landing nets have appeared on the market. Moore and O'Hara (1974) have demonstrated that these nets cause considerably less damage to fish than conventional knotted nets. If knotless netting, when used in fishing gear, caused less damage to the fish during capture, then nets of this material would be of considerable advantage for research purposes. Since small-meshed knotless netting was readily available, the Freshwater Fisheries Unit of Liverpool University decided to build various types of net with the material and assess its performance in the field.

CONSTRUCTION OF NETTING

Although there are many different kinds of knotless netting, "Micromesh"* with a mesh diameter of 3 mm and "Polynet"* with a mesh diameter of 6·5 mm were the only type used in the construction of our nets. The bars of the mesh are composed of five interlocking strands and the overall effect of this type of construction is to produce a hexagonal mesh. Each strand is made of 200 denier nylon. To prevent mesh slippage the material is heat set after it has been knitted.

Many advantages accrue from the use of nylon in net construction. As Lonsdale (1959) indicated, the ideal net fibre should be strong, when both wet and dry. He showed that when nylon twines were wetted they lost strength, but there was a corresponding increase in extensibility, which meant that the energy absorption actually increased when wet. Lonsdale suggested that the popularity of nylon for the construction of fishing gear was "largely due to its comparatively high energy absorption under dry, and even more so, wet conditions". Arzano (1959) has shown that the polyamide group of fibres, of which nylon is a member, have the highest resistance to abrasion in the whole field of textile fibres. The combination of a very low moisture absorption with a low specific gravity (1·14) means that the total weight of nylon nets, even when in use, is comparatively low. Arzano (1959) stated that nylon fibres are resistant to attack by fungi or bacteria and therefore do not rot. The only disadvantage with the use of nylon in the construction of fishing gear is that sunlight can cause loss of strength on prolonged exposure but this damage can be reduced by dying with a dark colour (Klust, 1959). All the knotless netting used in the construction of our nets had been dyed a dark green colour.

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* Available from C. J. Field (Polynet) Ltd., Union Road Estate, Macclesfield, England.

ADVANTAGES OF KNOTLESS NETTING

The cost of the "Micromesh" for a beach seine 120 feet long and 16 feet deep is £118 (February 1976) which is competitive with the price of knotted netting. Complicated nets are easy to make because sections can be sewn together mechanically, the resultant join being even stronger than the meshes. Additional strength can be provided by overlaying with a bias binding strip.

When synthetic fibres are knotted the loss in strength may be as much as 30–40 per cent (The Nippon Seimo Co. Ltd., 1959). Since the fibres are not sharply bent in knotless netting there is no reduction in strength, and for the same mass of netting per unit area, the mesh breaking load of knotless netting will be higher.

Knotted netting has the disadvantage that a large proportion of the yarn is used in making the knot. This proportion increases with decreasing mesh size, so that a knotted net with a small mesh, designed to capture fish larvae will be much heavier and bulkier than a similar sized knotless net. This reduction in both weight and bulk saves manpower, an important consideration for many research projects.

Moore and O'Hara (1974) showed that fish kept in conventional knotted keepnets suffered damage to their integument, because of the abrasive action of the protruding knots. With knotless keepnets such damage was reduced. Roberts (1975) has stated that physical damage makes fish more susceptible to fungal and bacterial infection and recommended the use of knotless keepnets. Damage to fish as a result of abrasion with the netting during capture is probably reduced when knotless fishing gear is used. This is an important consideration when fish are required alive and in good condition for restocking or as part of a mark-release-recapture experiment where the effect on the subsequent survival, by the method of capture, must be kept to a minimum.

Knotless netting is readily available in a mesh size as small as 3 mm, which makes it particularly suitable for investigations on fish larvae. Heron (1968) concludes that variations in mesh size were an important factor influencing samples. Klust (1973) has noted that knotless netting has a more constant and accurate mesh size than knotted netting, and therefore should be preferred for investigations involving fish larvae.

Any tears in nets can be easily repaired, either by sewing, or in the case of "Polynet" or "Micromesh", by glueing another piece over the hole with a suitable waterproof adhesive.

PRACTICAL APPLICATIONS

Nylon knotless netting has been used by members of the Freshwater Fisheries Unit of Liverpool University, over the last two years for the following purposes.

Beach seine

A net 36·5 m in length and 4·8 m in depth was constructed entirely of "Micromesh". The selvedge was formed by folding the bottom of the net upwards to produce a 5 cm turnover. A leaded line was threaded down this loop and stitched into position. Chain with 1·27 cm galvanized open links was then stitched below the selvedge. During a period of 10 months, 187 hauls were taken over a range of muddy and rocky substrates. For such a large net it proved surprisingly light and on many occasions only three people were used to take the hauls. The few tears which appeared in the main body of the net were quickly repaired by stitching. In places the selvedge had worn through completely, but this damage was also repaired by stitching. The fish caught by the net were in very good condition and even fragile perch larvae, *Perca fluviatilis* L., were still alive and undamaged after capture by this net.

Purse seine

A miniature purse seine was built entirely of "Micromesh" following a design by Hunter *et al.* (1966). The net was 36·5 m in length and 6·6 m deep, and was weighted with 22·7 kg of open link galvanized chain. Over a period of 6 months, 82 hauls were taken with this net. The weight of the net and corresponding ease of handling is indicated by the fact the it was operated by only two people. All the fish taken were taken in good condition and again the fragile perch larvae were undamaged.

Shimozaki (1959) pointed out that a high sinking velocity was important for the efficient operation of a purse seine. Although our net was constructed of nylon, which has a low specific gravity, the sinking velocity was sufficient to capture a large shoal of gwyniad, *Coregonus larvaretus* (L.), on two occasions and would therefore appear adequate.

Midwater trawl

A small otter trawl based on the design given by Rupp and de Roche (1960) has been constructed recently. Unlike all the other nets, the main body of the trawl was made from knotless polypropylene, with a different method of mesh formation than that used in "Polynet" and "Micromesh". The cod end was constructed of "Polynet". Very few trials have been performed with this net, so the effect of wear and tear cannot be assessed. It must be noted that on one occasion it was used as a bottom trawl in the River Dee, and no damage was sustained. All the fish caught in the net were apparently in excellent condition, with little loss of scales or fin damage.

Salmonid rearing cages

Pedley (pers. comm. 1975) has constructed cages made of "Polynet", used for the lake rearing of juvenile Salmonids. Nylon knotless netting was chosen for the construction material because of the high mesh strength and the lack of abrasive damage caused to the fish.

Other uses

"Polynet" has been used in the construction of fyke nets, once again because of its high mesh strength and the lack of damage caused to fish caught in the nets. Dip nets and keep boxes have also been constructed of "Micromesh" and found to be satisfactory.

DISCUSSION

Nylon knotless netting has obviously many uses in fisheries research. The only disadvantage is the lower resistance to abrasion than knotted netting. In knotted netting the knots are the points of strongest abrasion but Bobzin (1970) has shown from comparative tests with knotted and braided knotless netting in bottom trawls, that the degree of abrasion in knotless nets is not smaller, but extends over the whole surface of the netting. For this reason Klust (1973) suggests that knotless netting should not be used where it will be exposed to a great deal of abrasion, such as in a bottom trawl. The selvedge of the beach seine described in this paper was observed to have worn through in a few places. However it must be noted that a large number of hauls were performed before the effects of abrasion were noticeable. This disadvantage of knotless netting can be solved by overlaying points of strong abrasion such as the selvedge of a beach seine with nylon webbing.

The numerous advantages to be gained from the use of knotless netting in the construction of fishing gear, favour its use in net construction.

ACKNOWLEDGEMENTS

We would like to thank Dr J. W. Jones, OBE and Dr J. W. Banks, under whose supervision this work was carried out, and Mr K. O'Hara who criticized the manuscript. Thanks are also offered to Mr L. W. Balmer, Mr J. C. Gittins, Miss C. Dickson Barr and the many volunteers who helped in this field.

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Fish. Mgmt (1977), 8, No. 2. Printed in Great Britain

The Use of a Midwater Trawl to Sample Lacustrine Fish Populations

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I. INTRODUCTION

Sampling fish populations representatively from deep lakes often presents many problems. These were apparent in our efforts to capture immature gwyniad *Coregonus lavaretus* (L.) and coarse fish, especially perch *Perca fluviatilis* L. from Llyn Tegid, North Wales. Techniques were available for sampling the bottom, surface and shallow inshore areas, but the midwater region proved more difficult. However, echo-sounding revealed the presence of many fish in this area. It was therefore decided to attempt sampling with a midwater trawl.

Midwater trawls have undergone continual development over the past thirty years (Barraclough and Johnson, 1956, 1960; Parrish, 1959; Scharfe, 1964). Although the technique is commonly used in marine environments, it has been limited in freshwater to large lakes and rivers where boats of sufficient power were available (Netsch *et al.*, 1971; von Geldern jnr., 1972; Steinberg and Dahm, 1975; Ikusemiju, 1975).

This paper is an evaluation of the use of the midwater trawl in British waters for which, as far as the authors are aware, there are no published accounts.

II. MATERIALS AND METHODS

Net Design

The trawl was based on a design by Ruppe and de Roche (1960). This net was selected because it can be used from a boat with an engine smaller than 10 hp and may be retrieved by hand. Knotless netting was used in the construction of the net (Coles and Butterworth, 1971). The main body of the trawl was constructed from 32 mm mesh polypropylene and the cod-end from 6·5 mm mesh Polynet (C. J. Field (Polynet) Ltd., Macclesfield, England). The sweep lines were each continuous around the head and the foot of the trawl to evenly distribute the strain. The joins of the netting were reinforced with bias binding. A total of 10 kg of chain was attached to the foot rope and an extra float was fastened to the centre of the headline to keep the mouth open (Parrish, 1959). A funnel arrangement was incorporated into the mouth of the cod-end to aid retention of the catch.

Method of use

A 6·7 m clinker built boat powered by a 10 hp inboard engine was used for the experimental trawling. The method of setting differed from that described by Ruppe and de Roche (1960). With the boat travelling slowly forwards, the net was laid from a netting board, followed by the otterboards and side ropes. The gear was briefly held at this point to check that the net was fishing correctly. After the required length of towing warp had been paid

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out, it was secured to a bridle by a quick release knot. The bridle was fastened to either side of the transom of the boat, centralizing the pull whilst towing. The towing speed was set at 0·8 m sec^{-1}. The trawl was retrieved by hand while the boat slowly reversed. Since the net was stationary during hauling, the funnel arrangement was necessary to prevent the escape of fish. The depth of the trawl was computed from the length of the warp and its angle as measured by a clinometer. The accuracy of this estimate had been previously confirmed by echo-sounding over the net from a boat following the fishing vessel (Backus and Hersey, 1956; Wood and Parrish, 1950).

Sampling procedure

Samples were collected over 24 hour periods in March and April, 1976. On each occasion replicate 20 minute hauls were taken in random order at depths of 6 m, 12 m, 18 m, and 24 m in the main body of the lake. Ten minute hauls were also taken at 6 m and 12 m in Llanuwchlyn bay, a relatively shallow part of the lake with a maximum depth of 15 m. The fish caught were divided by species, enumerated and the fork length measured to the nearest mm.

To provide a comparison with the trawl catch data, bottom set gill-nets with mesh sizes 32 mm, 29 mm, 26 mm, and 19 mm were laid in similar locations to those trawled. These nets were manufactured from nylon monofilament which have proved efficient for capturing coregonids (McCombie and Fry, 1960).

III. RESULTS AND DISCUSSION

Length Frequencies

The gill-net mesh sizes chosen to provide a comparison with the trawl data were those that have been used previously to sample perch and gwyniad in Llyn Tegid (Haram, 1968; Ali, 1973). Because the mesh size of the smallest gill-net used was much larger than that of the cod-end of the trawl, direct comparisons of the length-frequencies of the catches is not possible. The purpose of such comparisons in this paper is merely to provide an evaluation of the two fishing methods. Heard (1962) has shown that small mesh gill-nets are highly selective and have very low catch efficiencies. Haram (1968), Ali (1973) and Andrews (pers. comm.) have used 91 mm gill-nets in Llyn Tegid, but found them inefficient for catching gwyniad and perch fry.

One of the main criteria for sampling fish populations adequately is to obtain a representative sample of fish from the entire length range of that population. Judged by this criterion, the trawl is a much better sampling device than the gill-nets (*Figs 1 and 2*).

No perch of the 1975 year class (age 0+) were captured in the gill-nets, whereas fish of this age group comprised 57 per cent of the total catch from the trawl (*Figs 1a and 1b*). The smallest perch of the 1974 year class (age 1+) were also not effectively sampled by the gill-nets. Therefore data obtained from gill-net catches alone would over estimate the mean length of two year old perch.

The range of lengths of gwyniad caught by the trawl was again much larger than those caught by gill-nets (*Figs 2a and 2b*). However, unlike the perch population, relatively few small fish were sampled. It is unlikely that this result is attributable to the loss of fish through the cod-end meshes, because large numbers of similar sized perch were retained. It is

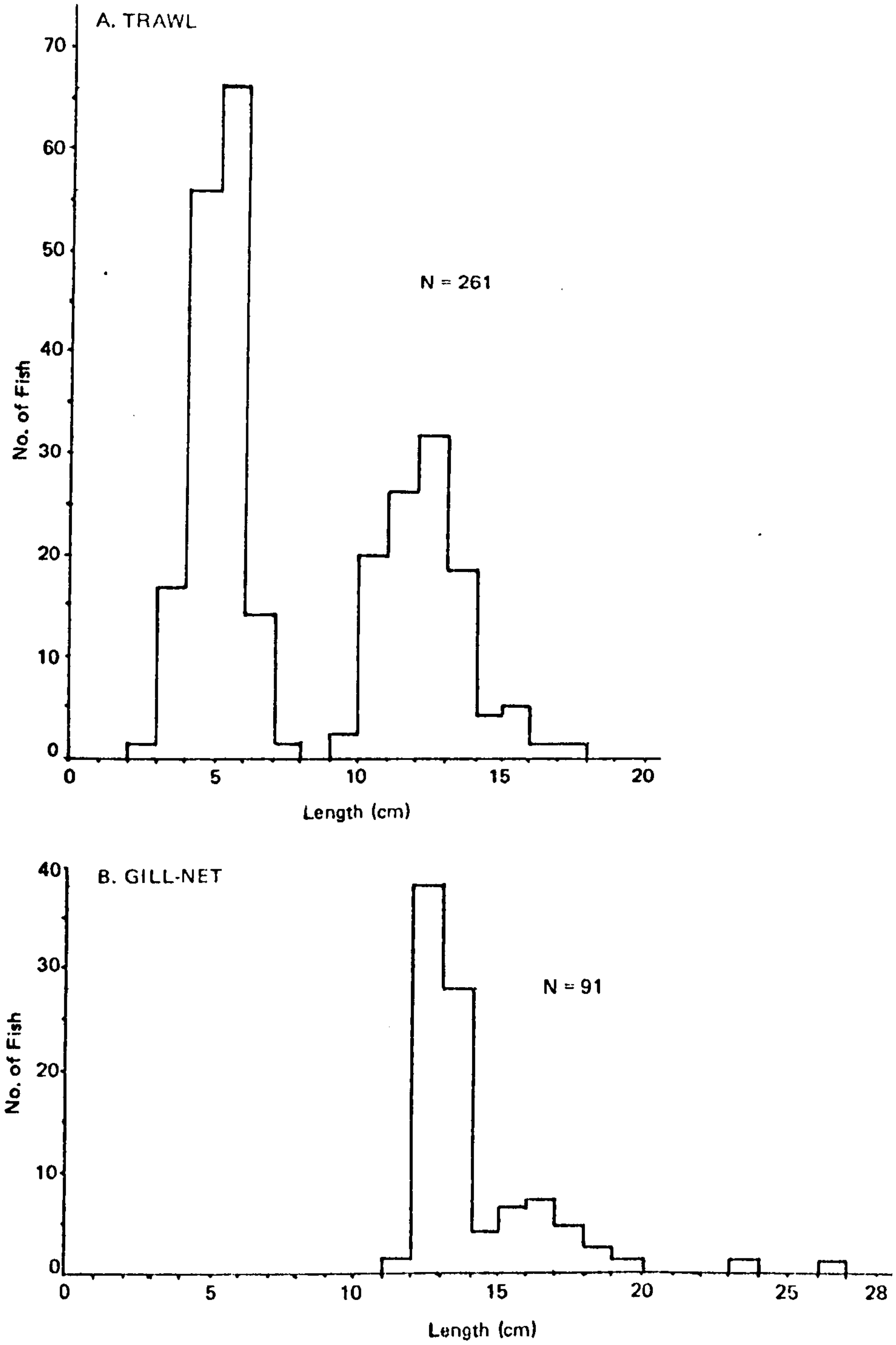

Fig. 1. Length Frequency distribution of perch catches.

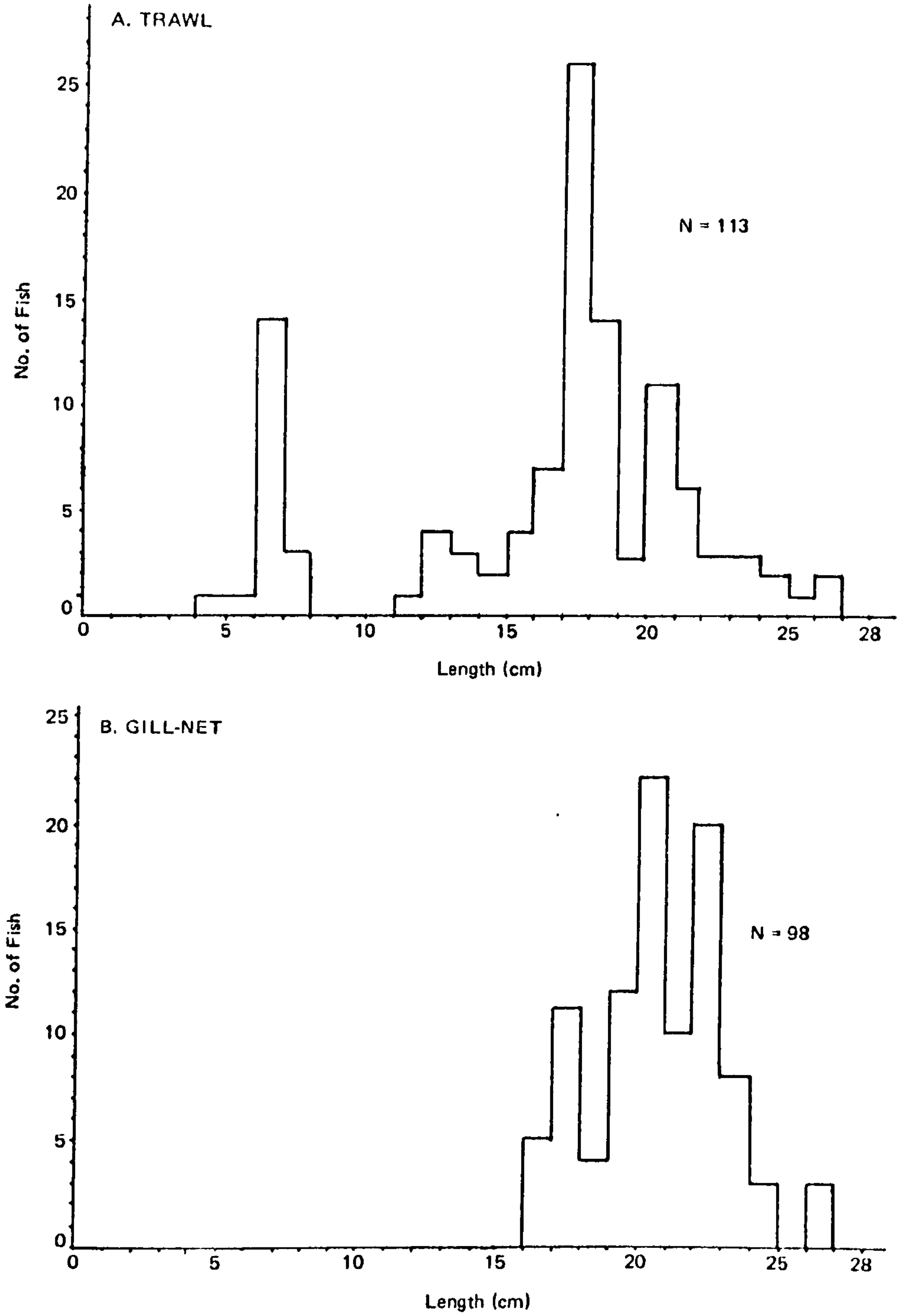

Fig. 2. Length frequency distribution of gwyniad catches.

possible that the depths and areas sampled were not commonly frequented by small gwyniad. Alternatively, the low numbers of small gwyniad could reflect a poor recruitment in recent years. If the latter explanation is correct, the reduction in numbers would not be apparent in gill-net catches until the fish have reached a length greater than 17 cm.

It is difficult to determine whether there was any avoidance of the trawl. Houser and Dunn (1967), in their production studies, assumed avoidance to be negligible, whereas Grubisic *et al.* (1974) estimated that 4/5 of the fish in the path of a pelagic trawl towed in shallow water were escaping. The largest gwyniad sampled by trawling fell within the same length group as the largest taken by gill-net. This does not indicate that there was no avoidance of thè net, but merely suggests that the whole length range of the population was sampled. Perch larger than those caught in the trawl were taken by gill-net, but the frequency of these captures was low.

Vertical Distribution

Many different techniques have been used to assess the vertical distribution of fish in large lakes including echo-sounding, vertical gill-nets and midwater trawls.

Echo-sounding has the advantage of allowing continual monitoring of fish populations over any time period, and has been used by many workers (Hergenrader and Hasler, 1966; Haram, 1968; Finnell and Reid, 1969; Dembinski, 1971). However, it is difficult to assess the size and abundance of fish present, making production studies impracticable. Species identification has also proved difficult. Dembinski (1971) equated echo-sounding traces with gill-net catches and concluded that different species caused different shaped marks on the traces. Other workers have used gill-nets (Haram, 1968; Finnell and Reid, 1969) and direct observation (Hergenrader and Hasler, 1966) for species identification. Television and film cameras have proved unsuccessful for this purpose (Chubb *et al.*, 1975).

Vertical gill-nets have been used for qualitative analysis of fish movement (Hartman, 1962; Horak and Tanner, 1964; Miller and Perrin, 1967; Lackey, 1968, 1970; Bartoo *et al.*, 1973). The entire water column can be sampled with these nets, but they may have very low catch efficiencies during the day (Finnell and Reid, 1969) and are highly selective. Difficulty may be encountered in setting and retrieving the nets during rough weather. Neutrally buoyant horizontal midwater gill-nets suffer from similar disadvantages (Hancock, pers comm.).

The assessment of the vertical distribution of fish by means of a midwater trawl has been determined previously as a preliminary to production studies (Houser and Bryant, 1967; Houser and Dunn, 1967; Houser and Netsch, 1971). In the present study only the vertical distribution has been considered. Data on the catch of the perch from Llanuwchllyn Bay and gwyniad from open water were analysed. Insufficient numbers of perch from open water and gwyniad from the bay were captured for analysis. A two-way model I analysis of variance (Zar, 1974) was used to examine the effect of depth and time of day on the catches. There is considerable evidence to show that the variance in the catch from trawls is related to the mean and therefore must be transformed before undergoing this type of analysis (Barnes and Bagenal, 1951; Taylor, 1953; Bagenal, 1958). Elliott (1971) gives the appropriate transformations where the distributions are unknown. The variance of the perch catch was considerably larger than the mean and therefore equation 1 was used to transform the data.

$$y = \log(x + 1) \qquad (1)$$

The variance of the gwyniad catches was not much larger than the mean and equation 2 (Bartlett, 1936) gave a more satisfactory transformation.

$$y = \sqrt{x + 0{\cdot}5} \qquad (2)$$

Tables I and II show the results of the analyses of variance. In both analyses, the within cells variation contributed a large amount to the total. The gwyniad showed a highly significant difference (0·001>p>0·0005) in catches between day and night. The hypothesis that these fish occurred in equal numbers at each depth is rejected (0·01>p>0·005). The amount of variability caused by changes in depth distribution with time contributed little to the total variation. These results could be explained by an increase in the efficiency of the trawl at night. Netsch *et al.* (1971) stated that night trawl catches were greater than by day, but that the relative distribution patterns were similar. An alternative explanation is that an upward movement of fish occurred from below the lower sampling zone at night, although the relative proportions of the population at each depth remained the same. Echo-sounding traces have shown such a movement of gwyniad towards the surface after dusk in Llyn Tegid (Haram, 1968). Similar observations were made by Dembinski (1971) for whitefish in Polish lakes and he discussed the abiotic and biotic factors that may be responsible.

Table I. Analysis of variance of trawl catch of gwyniad from open water

Source of variation	S.S.	d.f.	M.S.	F value
Total	28·07	31		
Cells	18·39	7		
Period	6·33	1	6·33	15·70*
Depth	11·12	3	3·37	9·19†
Period X depth	0·95	3	0·32	0·78
Residual	9·67	24	0·40	

* p = 0·001
† p = 0·01

Table II. Analysis of variance of trawl catch of perch from Llanuwchlyn bay

Source of variation	S.S.	d.f.	M.S.	F value
Total	5·23	11		
Cells	2·91	3		
Period	1·71	1	1·71	5·91‡
Depth	0·86	1	0·86	2·95
Period X depth	0·34	1	0·34	1·17
Residual	2·32	8	0·29	

‡ p = 0·05

The perch showed a significant difference (0·05>p>0·025) in catches between day and night. Although the hypothesis that equal numbers of perch occurred at each depth cannot be rejected, the F value is approaching significance (0·25>p>0·1). The data from the perch catches also indicate that the amount of variability caused by changes in depth distribution with time contributed little to the total variance. The explanations proposed to explain the distribution of gwyniad may also be true for the perch population.

IV. CONCLUSIONS

The results outlined in this paper indicate that a midwater trawl is a satisfactory device for sampling fish populations in large lakes. No attempt has been made to estimate production in this study, but other workers have shown that this is clearly feasible (Houser and Dunn, 1967; Houser and Netsch, 1971).

The most obvious disadvantage of this technique is that large fish may not be sampled representatively. It is therefore suggested that sampling programmes for lakes and reservoirs should include the use of a trawl in conjunction with large mesh gill-nets.

ACKNOWLEDGEMENTS

The authors would like to thank Dr J. C. Chubb and members of the Fisheries Unit of Liverpool University for their helpful criticism of the manuscript, and to Dr M. E. Begon for his help with the statistics. Our special thanks go to Mr J. C. Gittins and Mr L. Balmer for their assistance in the field. The work was carried out whilst the first author was in receipt of a research studentship from the Central Electricity Generating Board.

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