STUDIES ON SALMONID FISHES IN LLYN TEGID

AND THE WELSH DEE

Thesis submitted in accordance with the requirements

of the University of Liverpool for the degree of

Doctor in Philosophy

by

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Frontispiece

The River Dee at Llanderfel

CONTENTS

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CHAPTER I

NATURE AND PURPOSE OF THE RESEARCH

A. Introduction

The studies presented in this thesis were undertaken on a Water Resources Board grant, under the supervision of Dr. J.W. Jones, O.B.E., at the University of Liverpool. The work carried out formed part of a long term investigation into the effects of river regulation on aquatic organisms in the Welsh Dee and its tributaries. At the time of presentation of this thesis the Water Resources Board research programme is in its first stage, that is a detailed survey of the present biological, chemical and physical conditions prevailing in the River Dee. From an examination of these conditions predictions on the effects of further regulation may be possible, and data will be available for comparison with future research (stage 2 of the research programme) after the implementation of the proposed regulation schemes. Results obtained from the River Dee study will be used to derive general formulae applicable to any regulated river.

Regulation of the River Dee at present comprises two upland storage reservoirs which maintain a prescribed flow at a point approximately halfway along the river course. These reservoirs can be used for short-term flood detention capacity and one is also used for the generation of electricity. Further regulation of the River Dee is planned to include more storage reservoirs and an estuary barrage scheme.

My contribution to the research programme consists of studies on the ecology and population dynamics of grayling (*Thymallus thymallus* L.), trout (*Salmo trutta* L.) and juvenile salmon (*Salmo salar* L.) in the upper reaches of the River Dee, in Llyn Tegid (now a storage reservoir) and in the unregulated Llyn Tegid feeder streams. These studies were aimed at providing the Water Resources Board programme with information on the biology of indigenous fish species in the River Dee, especially of those species competitive with young salmon; on production of salmon in the area; and on factors affecting the distribution and migration of salmonid fishes. The work was carried out in close co-operation with the Dee and Clwyd River Authority, individual anglers, riparian owners and several angling societies.

B. Regulation of the River Dee

River regulation is here taken to mean "the storage in the headwater area of a river, and the controlled discharge of water from the storage into the river in such a way as to provide a desired flow, or sequence of flows, at some point or points in the river downstream" (Blezard *et al.*, 1970). The main purpose of this regulation is to support abstraction for public water supply at a point well down the river, by maintaining the flow there at a quantity sufficiently above the natural minimum to permit the abstraction without detriment to the river below this point. The system also provides for the detention of water in storage during wet weather to reduce the effects of flood water downstream. Releases of water from storage can be made in order to generate electricity, to improve water quality, and to provide conditions that will encourage the migration of salmon upstream. Detailed descriptions of the River Dee regulation schemes are given by Wright (1955), Boddington et al. (1962) and Blezard et al. (1970). The Bala regulation installations and river course alterations are shown in plate 1.

The first storage used to regulate the River Dee was Llyn Tegid. Regulation is by no means a recent phenomenon on the River Dee, sluices having been built at the Llyn Tegid outlet by Thomas Telford early in the 19th Century. These sluices impounded water in the lake to 0.75 metres above the normal level and supported abstractions from the River Dee to the Shropshire Union Canal at Llantysilio (Wright, 1955). The recent history of regulation commenced with the construction of the present Bala sluices (see plates 1 and 2) in 1953-56, which, by lowering the draw-off level, allow fluctuations of up to 4 metres in Llyn Tegid and provide about 4000 million gallons of storage. The water level of Llyn Tegid is controllable between the limits 159.5 metres A.O.D. and 163.5 metres A.O.D. The regulation of Llyn Tegid provides water for release to the river to maintain the flow at its principal gauging station at Erbistock at 55 million gallons per day (2.9 cumecs) during periods when it would naturally fall below this prescribed flow. This prescribed flow supports abstractions from the river of 38 m.g.d. (1.8 cumecs). In operation Llyn Tegid is kept as empty as possible during the winter, to provide flood detention capacity, and about one third full during the summer to provide augmentation storage during the potential drought period,

Plate 1

Aerial view of the Bala regulation scheme.

key:

A Llyn Tegid

B River Dee

C Afon Tryweryn main channel

D Afon Tryweryn flood relief channel

E Bala sluices

F Old course of Afon Tryweryn

G Old course of River Dee

H Bala gauging station

a Sampling site a, River Dee

b Sampling site b, River Dee

J Sampling site J, Llyn Tegid

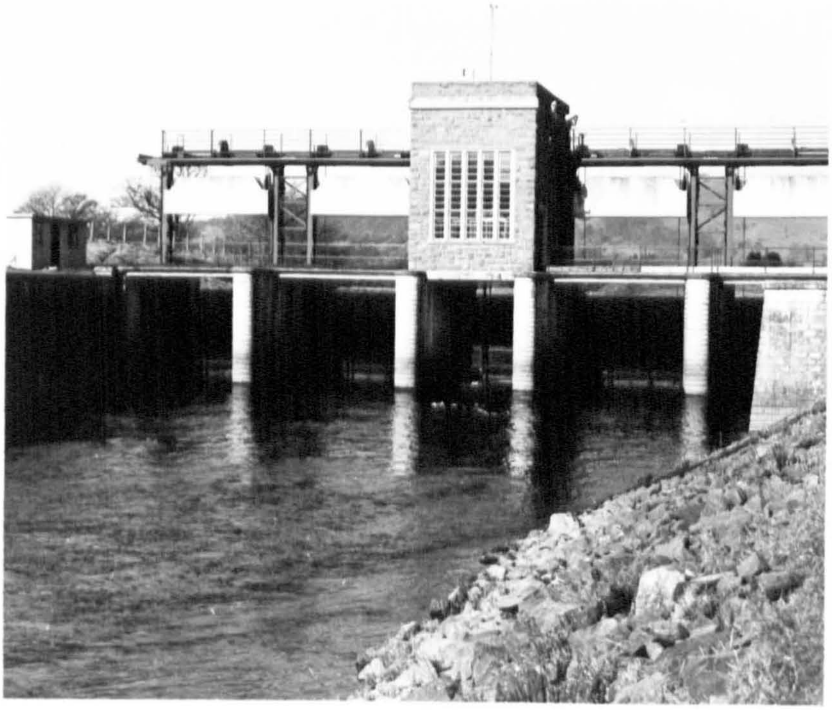

A
J
B
C
F
D
E
G
a
H
b

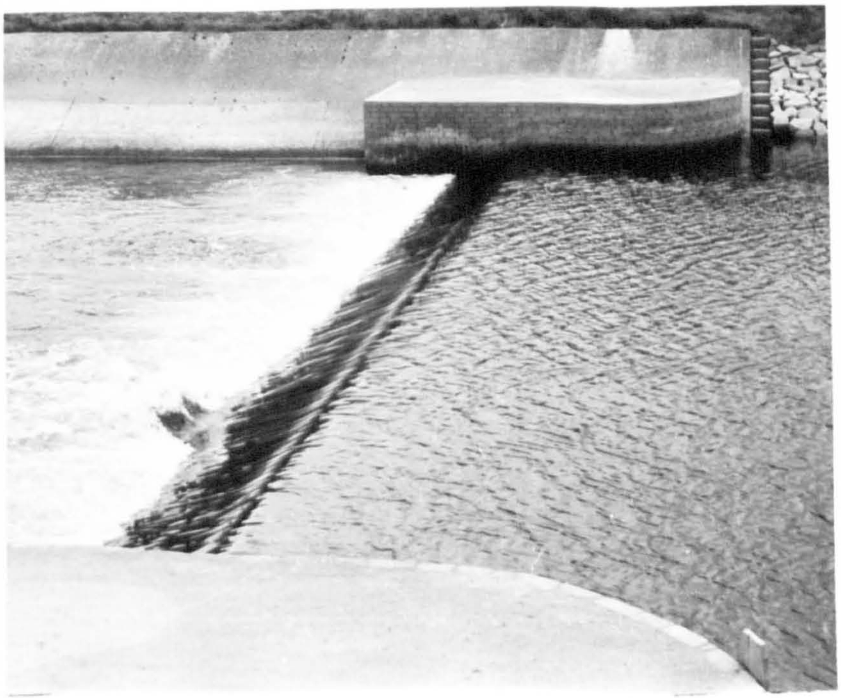
Plate 2

The Bala sluices

Plate 3

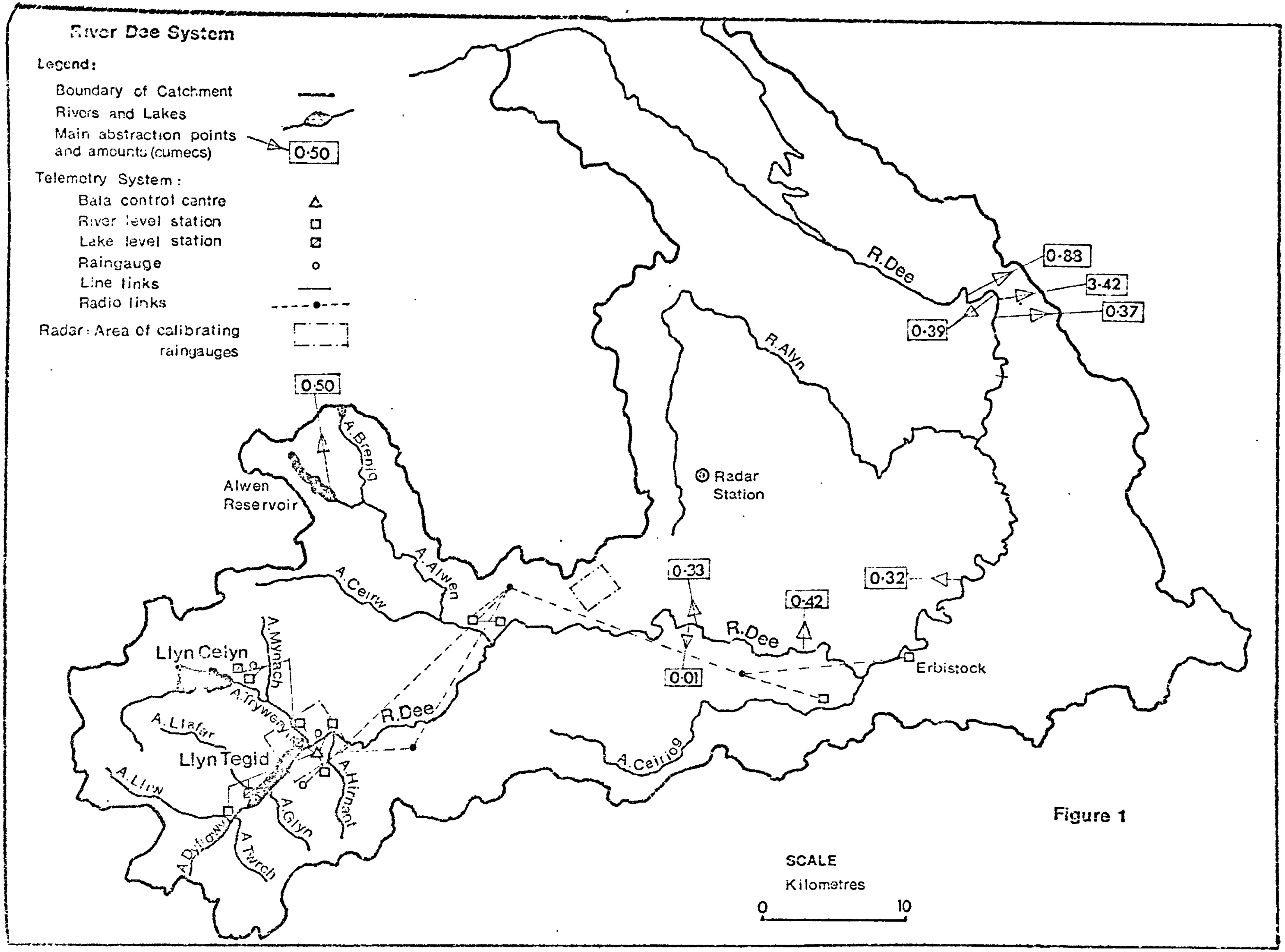
Bala gauging station weir





and some capacity for flood retention. This is the reverse of the pre-1955 situation when winter rains kept the lake level up.

The second storage, Llyn Celyn, was constructed by Liverpool Corporation and was brought into service in 1965, with the function of storing water necessary to maintain the flow at Erbistock of 150 m.g.d. (7.9 cumecs). The increase in the prescribed flow enabled a further 65 m.g.d. (3.4 cumecs) to be abstracted from the river by Liverpool Corporation. The minimum flow (compensation water) permitted from Llyn Celyn into the Afon Tryweryn is 7 m.g.d. from October to March and 14 m.g.d. from April to September. Llyn Celyn also provides flood detention capacity and is used to generate electricity. Water released from Llyn Celyn into the Afon Tryweryn in effect passes through Llyn Tegid, the Bala sluices controlling discharges from both lakes into the River Dee (see plate 1.). Water from Llyn Celyn can therefore be used to raise the level of Llyn Tegid if required. The operation of the regulation system is under the control of a centrally situated computer using information from rainguages, lake level and river level stations, relayed by a telemetry system. These features, together with the regulating reservoirs and principal abstractions, are shown in figure 1. It is hoped that the operational efficiency of the regulation schemes will be improved by the use of radar installations (also shown in figure 1) to measure the detailed distribution of rainfall in the catchment. Releases of water from Llyn Celyn and Llyn Tegid are under the day to day control of the Dee and Clwyd River Authority, acting in accordance with the general directions provided for in the Dee and Clwyd River


River Dee System
Legend:
Boundary of Catchment
Rivers and Lakes
Main abstraction points and amounts (cumecs)
0·50
Telemetry System:
Bala control centre
River level station
Lake level station
Raingauge
Line links
Radio links
Radar: Area of calibrating raingauges
0·50
A.Brenig
Alwen Reservoir
A.Alwen
A.Cerrw
A.Mynach
Llyn Celyn
A.Tryweryn
A.Llafar
Llyn Tegid
A.Lliw
A.Dyfrdwy
A.Twrch
A.Glyn
A.Hirnant
R.Dee
A.Ceiriog
Radar Station
R.Alyn
R.Dee
0·83
3·42
0·37
0·39
0·33
0·01
0·42
0·32
R.Dee
Erbistock
SCALE
Kilometres
0
10
Figure 1

Board Act 1951 and the Liverpool Corporation Act 1957. These general directions are outlined by Blezard et al. (1970).

The controlled releases of water used to regulate the River Dee are measured at a gauging station 300 metres downstream from the Bala sluices (see plates 1 and 3). The gauging station weir was originally constructed as a broad-crested weir, 20 metres wide, trisected by two flumes each 0.6 metres wide, for modular low flow measurement, and was modified in 1969 to a triangular crested weir of uniform level (1:1 upstream slope, 1:3.5 downstream slope) for modular low and medium range flow measurement.

The effects of regulation on the River Dee fisheries are discussed by Iremonger (1971) who lists the main factors involved as being loss of spawning ground, variations in flow, and obstructions to migration. The loss of spawning ground chiefly applies to the construction of Llyn Celyn and the subsequent loss of many miles of salmon spawning gravel in the Afon Tryweryn and its tributaries. The Dee and Clwyd River Authority have attempted to compensate for this loss by fairly extensive salmon rearing policies. Rapid decreases in river flows are considered by Iremonger (1971) to be more detrimental to fisheries than rapid increases in flow, and limits have been set for reductions in discharges, those from the Bala sluices being about 0.3 cumec/hour. Obstructions to the migration of salmon occur at the Bala sluices, the Afon Tryweryn mouth, and at Llyn Celyn dam. The Llyn Celyn dam does not incorporate provisions for the upstream passage of salmon, but the former two obstacles do have such provisions. Passage for salmon through the Bala sluices is provided by a fishlock, consisting of two gates in tandem. A closeable orifice in the upstream gate enables the lock to operate as a weir at low head differences; at larger head differences the downstream gate is opened and closed automatically on a regular cycle and permits fish alternately to swim into the lock from downstream and to swim out upstream. The main channel weir at the Afon Tryweryn mouth is provided with a conventional pool fishpass, and the flood channel incorporates diagonal baffles on a flat sloping weir. Iremonger (1971) states that the Bala lake scheme has had little effect on the natural migration of salmon into Llyn Tegid and its feeder streams, nor has it affected the eventual migration of salmon into the Afon Tryweryn. This would appear to be true since salmon were seen in Llyn Tegid during the spring of 1969 and 1970 only a few days after they were first reported ascending Chester weir. The Bala sluices do hold up runs of summer salmon for short periods under particularly wet weather conditions when high river flows prevail. In these circumstances most salmon do not use the fishlock but wait until the sluice gates are opened enough for their free passage into the Tryweryn and Llyn Tegid. The water quality aspects of river regulation and the development of future schemes are outlined by Blezard et al. (1970). The general effects of water storage on freshwater fisheries are discussed by Aass (1958), and the river flow conditions necessary for the preservation of migratory fish life are considered by Baxter (1961).

CHAPTER II

SPECIES OF FISH STUDIED

1. Grayling (*Thymallus thymallus* Linn.)

A. Previous Investigations

Few studies have been made of grayling in the British Isles. Some research has been carried out on age, growth and scales by Hutton (1923), Gerrish (1938,1939), Jones (1953a) and Hellawell (1969b); on food and feeding habits by Limbert (1939), Radforth (1940), Siddiqui (1969) and Hellawell (1971); on general biology by Hellawell (1969a); and on population structure by Mackay (1970). These studies are discussed in more detail in later chapters together with the greater amount of European literature on grayling. The present study was designed to investigate the biology of grayling in Llyn Tegid and the upper reaches of the River Dee, being the first study of grayling in the latter environment, and the first detailed study of Llyn Tegid grayling.

B. Classification

The classification of the European grayling according to Berg (1947) is as follows :

Phylum Vertebrata
  Subphylum Craniata
    Superclass Gnathostomata
      Series Pisces
        Class Teleostomi
          Sub Class Actinopterygii

Order Clupeiformes

Sub Order Salmonoidei

Family Thymallidae

Genus <u>Thymallus</u> Cuvier 1829

Species <u>Thymallus thymallus</u> (Linnaeus) 1758

C. <u>Origin of common and specific names</u>

The origin of the common name "Grayling" has been discussed by a number of authors (Yarell, 1836; Day, 1887; Pritt, 1888; Rolt, 1905; Platts, 1935, 1939; and Tutin, 1961) and is generally considered to be a corruption of "grey-lines", a reference to the characteristic markings on the sides of the fish produced by overlapping scales in serrated rows (Pritt, 1888). Tutin (1961) considers that the name comes from the German, Grau, or grey fish. The German name of the fish, Asche, refers to the ash-grey colour of the grayling.

No satisfactory etymological derivation for the grayling's alternative name, "Umber", has been found. Theories have been propounded that the fish takes this name from the Latin Umbra, a shadow; from "umber" a pigment; from Umbria, a district of ancient Italy; from "Umbro", an Italian river in which it abounded; and from "Humber", the Yorkshire river in whose tributaries it flourishes (Platts, 1935). Most authors favour the shadow theory, which refers to the grayling's habit of "fading from sight like a shadow upon being alarmed" (Platts, 1935). The French name, Ombre, also refers to the shadow-like appearance of the grayling. Tutin (1961) postulated that the River Humber was so-called because of the abundance of grayling ("umber") in it, rather than grayling being named after the river.

The scientific name, Thymallus, is supposed to refer to the resemblance of the odour of a freshly caught grayling to that of thyme. Pritt (1888) points out, however, that the plant originally referred to in this context, which is found in certain Italian rivers containing grayling (Italian name Temolo, a modern variation of the old Latin Thymallus) is the water-thyme, a plant having no scent. The freshly caught grayling does have a distinctive odour, and Rolt (1905) thought that the explanation of the name Thymallus was to be found in the adjective thymy, which can mean either "smelling of thyme", or more generally, just "fragrant".

D. Specific characters

The specific characters of grayling have been described by a number of writers and most recently by Jankovic (1964) in his general review of European grayling. During my study of grayling in the Welsh Dee a number of characters of 100 grayling were examined, and the results are shown in table 1. The comparative figures given by Jankovic (op.cit.) are shown in parenthesis.

Table 1. Specific characters of grayling from the Welsh Dee.

Number of scales along lateral line	77-90	(78-98)
Number of scales from dorsal fin to lateral line	7-9	(-)
Number of scales from ventral fin to lateral line	7-8	(-)
Number of rays in dorsal fin	18-21	(18-27)
Number of rays in anal fin	11-12	(8-16)
Number of gill rakers on first gill arch	20-26	(20-29)
Number of pyloric caeca	17-23	(12-37)

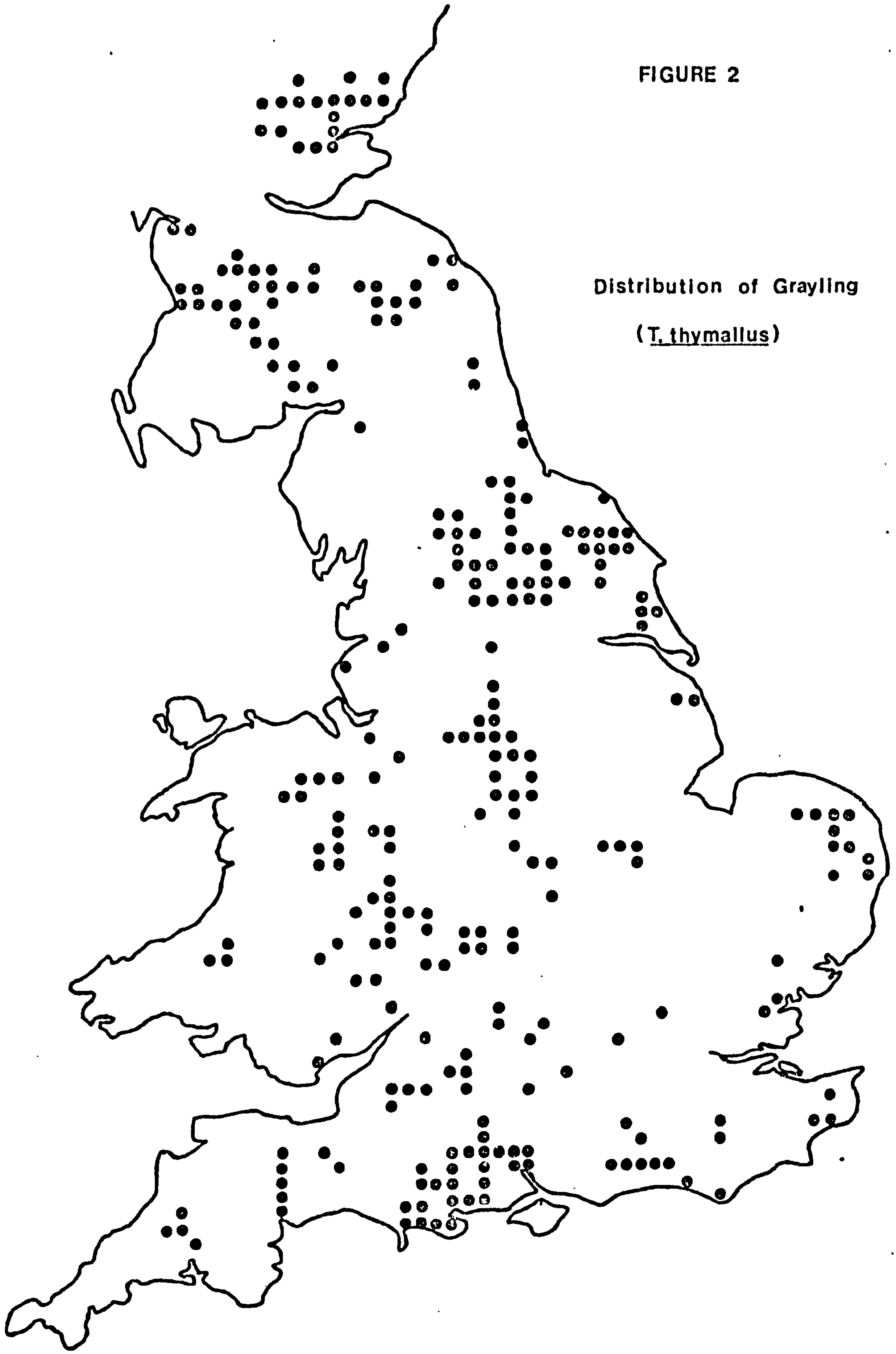
The large dorsal fin is a very distinctive characteristic of the grayling and instantly distinguishes it from other members of the Salmonoidei. At spawning time the posterior dorsal fin rays of male grayling became elongated, and the overall colour of the fish darkened.

E. Distribution

The present distribution of grayling in the British Isles is shown in figure 2 (by kind permission of Dr. P.S. Maitland). Pritt (1888) considered that grayling were originally introduced into Great Britain from the continent by monks, but subsequent authors (Rolt, 1905; Platts, 1939) pointed out that the grayling is a very difficult fish to handle and to transport, and that it was very unlikely that the monks had sufficient expertise or knowledge to successfully introduce these fish as Pritt suggested. These authors concluded that grayling were indigenous to British rivers.

P latts (1939) discussed the origins of grayling at some length and considered that grayling reached British rivers via the prehistoric North Sea River, of which our east coast rivers were tributaries. He thought that the Scottish rivers would have been too rapid for colonization by grayling, but that some of the English rivers, in particular the Humber, would have been ideally suited to the grayling's ecological requirements. In addition to the east coast rivers, grayling appear to have been indigenous to the Hampshire Avon, the Welsh Dee, the Ribble and the Severn/Wye system. Platts (op.cit.) considered that from their original distribution in the Humber and

FIGURE 2



Distribution of Grayling

(*T. thymallus*)

its tributaries, grayling found their way into the Severn and Ribble systems following geological upheavals resulting in the exchange of tributaries and/or connections between the headwaters of different river systems. In the same way he postulated that grayling reached the Hampshire Avon via the Severn and Thames tributaries. The headwaters of the Severn and Welsh Dee are in close proximity to one another and grayling may have been transplanted from the former to the latter. Lake (1900) considers the possibility that the upper reaches of the Afon Dyfrdwy (Dee) represent the original headwaters of the Afon Vyrnwy, and similarly that the Afon Lliw and Afon Llafar, and the Afon Tryweryn, represent the original headwaters of the Afon Banwy and Afon Tanat respectively. If this was so, then the presence of grayling in the Welsh Dee would be easily accounted for. Subsequent extension of the distribution in the British Isles has been brought about by the introduction of grayling by man into new environments. These introductions have been particularly successful in rivers such as the Exe (Devon), Test (Hampshire), Itchen (Hampshire), Eden (Cumberland), Clyde (Lanarkshire), Tweed and Border Esk.

The distribution of grayling in Europe is discussed by Berg (1962) and Jankovic (1964), the latter author also given an account of related species of the genus Thymallus in Asia and North America.

F. Sporting value

The regard in which grayling are held as a sporting fish varies considerably in different parts of the British Isles. In the south-country chalk streams they are largely regarded as vermin and detrimental to the well-being of the much preferred trout. These waters are in fact more suited to the grayling than to the trout (Brayshaw, 1971) and belong to the "grayling zone" of Huet's (1949) classification of western European streams. The trout are maintaining a precarious footing in this zone (Brayshaw, op.cit.) which can only continue if the stocks of grayling are regularly culled. Conversely, grayling are held in very high esteem in many Yorkshire and Derbyshire streams where they fulfil a popular demand for angling during the trout close season. The latter is also so in the Welsh Dee, the subject of this study, although many anglers consider that the increase in the grayling population, which has been apparent in recent years, is detrimental to trout fishing.

C. Grayling in the Welsh Dee

The River Dee from Glyndyfrdwy to Bala conforms closely to Huet's (1949) "grayling zone" and the dominance of grayling over trout is to be expected in this area, in the absence of management procedures. An inversion of the typical sequence of river zones occurs in the Dee with a "trout zone" occurring below the grayling zone in the stretch of river between Glyndyfrdwy and Erbistock weir (see Chapter 3, figure 3). Trout appear to dominate this stretch of river but evidence points to the continuing encroachment of grayling into this area (Dee and Clwyd River Authority reports).

Giraldus Cambrensis (in Itinerarium Kambriae, volume VI, p.33,1868) refers to the presence of grayling in the River Wye. The earliest reference found to grayling in the River Dee was Davy (1828) who observed that grayling were found "not near the Valle Crucis Abbey, but higher up between Corwen and Bala." King (1945), in the Annual Report of the River Dee Fishery Board, mentioned the abundance of grayling in the Dee between Corwen and Bala. He considered this stretch of river to be trout and salmon water, and grayling to be intruders which were more suited to the quieter reaches of the river below Erbistock weir. In fact the reverse is true, the upper reaches being ideally suited to the needs of the grayling. The 1952 Annual River Board report stated that grayling had shown a recent decline in numbers, being scarce at Corwen and not nearly so numerous in the Cynwyd-Llanderfel reaches as hitherto. Grayling appeared to remain scarce in the Dee until after the completion of theBala regulation works and from 1956 onwards increasing numbers of grayling were reported. The spreading of grayling downstream in the Dee and into tributaries such as the Tryweryn, Alwen and Ceiriog was also noted. In 1957 grayling were being caught above and below Llangollen weir; in 1960 below Newbridge; in 1963 around Bangor-on-Dee; and by 1964 a few fish were even being taken on the Groves at Chester. Reports from the Dee and Clwyd River Authority indicate that grayling are still on the increase in the River Dee, considerably outnumbering trout in the upper reaches, and are continuing to spread into the lower and middle reaches.

H. Grayling in Llyn Tegid

Llyn Tegid is the only natural lake in the British Isles in which grayling live, although grayling may be commonly found in

European lakes (Muller, 1961; Dahl, 1962; Jankovic, 1964). Grayling are also found in the British Isles in Gouthwaite Reservoir, Yorkshire. This reservoir was formed by the impoundment of the River Nidd, and grayling from this river continued to thrive in the new environment (Parry, pers.comm.).

The earliest River Board reference to grayling in Llyn Tegid was in the Annual Report for 1945 which mentioned the capture of several grayling in the lake and in the lower reaches of its feeder streams. The numbers of grayling caught in the lake appeared to increase each year from 1945 onwards, even at the time when these fish were reported to be scarce in the River Dee (Annual Report for 1952). A similar increase in netting captures was also recorded by research workers from the University of Liverpool, and some possible reasons for this increase were postulated by Siddiqui (1969). Further reference to these observations are made in later chapters.

2. Trout (*Salmo trutta* Linn.)

A. Previous investigations

A great deal of research has been carried out on brown trout, both in Great Britain and in other countries, and it is felt unnecessary to give a general account of this species here. No research has been carried out on trout in the River Dee but a considerable amount of work has been done on Llyn Tegid trout by Ball (1957, 1961), Ball and Jones (1960, 1962), Graham (1960), Graham and Jones (1962), and Siddiqui (1969). The work carried out by these authors was chiefly concerned with the age, growth, diet and movement of trout in Llyn Tegid, but included some investigations into the growth of trout in the Llyn Tegid feeder streams and the migration of trout from these streams into Llyn Tegid.

B. Present studies

In this study an attempt has been made to investigate the populations of trout in the Llyn Tegid feeder streams and in the upper reaches of the River Dee. This work was subsidiary to the main investigations on young salmon in the Llyn Tegid feeder streams, and grayling in the River Dee. Other studies are also being carried out on trout in small streams in the Dee and Clwyd catchment area by P.R. Lees, A. Cane and M.A. Rahim from the Department of Zoology, Liverpool University. This work is to be continued and further research on the lower and middle reaches of the River Dee is planned.

C. Management of trout fisheries

The Dee and Clwyd River Authority carry out limited stocking of brown trout using mostly 3-5" yearling fish from Chirk hatchery together with some wild trout transferred from the Afon Brenig salmon nursery stream. The numbers of trout stocked during recent years in the upper Dee area are shown in table 2.

Table 2. Numbers of Trout stocked in the upper Dee area by the Dee and Clwyd River Authority.

River	Site	No. in each year					
		1964	1965	1967	1968	1969	1970
A. Lliw	Llanuwchllyn	-	-	-	500	500	500
R. Dee	Bala	500	500	250	550	-	-
	Bodweni	-	-	-	-	500	500
	Llandrillo	300	-	500	-	-	-
	Cynwyd	-	450	-	-	-	-
	Corwen	800	500	500	500	250	250

D. Trout in the Welsh Dee

The apparent ousting of the trout population in the upper Dee by grayling (King, 1945) was mentioned in the previous section, but it seems likely that grayling have always dominated trout in this stretch of river, since conditions favour the grayling rather than trout. From an examination of River Authority records it does, however, appear that there has been a decline in the quality of trout fishing in the upper and middle Dee since the upsurge in the grayling population.

3. Juvenile Salmon (Salmo salar Linn.)

A. Previous investigations

A great deal of research has also been carried out on the Atlantic salmon, at all stages in its life history, and no attempt will be made here to review the vast volume of literature available. A recent bibliography of the Atlantic salmon was prepared by

Bergenon (1962), and a review of the literature was made by Pyefinch (1955). Jones (1959), in his book "The Salmon", gives a detailed account of the salmon's life history and biology, and Mills (1971) describes the ecology, conservation and management of salmon and trout in his recent book. Studies have been made on adult salmon in the Dee area by Jones (1939, 1950a, 1950b, 1951, 1953b) and Jones and King (1946, 1949, 1950a); and on juvenile salmon by Carpenter (1940), Jones (1940, 1947, 1949) and Jones and King (1939, 1950b, 1952). The studies made by Jones (op.cit.) and Jones and King (op.cit.) on juvenile salmon were concerned with the spawning of ripe male salmon parr, the passage of smolts into saltwater, and scale examinations in relation to growth, migration and spawning. Carpenter (op.cit.) studied the feeding of salmon parr in the River Dee.

B. Present studies

This study, together with the work being carried out on other streams by P.R. Lees and A. Cane, is the first detailed investigation of the populations of young salmon in the River Dee area. This work has involved the examination of the populations of salmon parr in the Llyn Tegid feeder streams; the migration of salmon smolts out of these streams into and through Llyn Tegid, together with the predation of pike (Esox lucius L.) on the smolts; and the examination of salmon parr caught from the River Dee whilst sampling for grayling. Other research workers from the University of Liverpool will be continuing studies on young salmon in the area, and will be extending the work to cover the middle reaches of the River Dee and further tributaries.

C. Management of the Dee salmon fisheries

The River Dee is a valuable salmon fishery and the preservation of this fishery is of prime importance to the Dee and Clwyd River Authority and to the Water Resources Board research programme outlined in Chapter 1.

Iremonger (1971) concludes that regulation has apparently had no deleterious effects on the salmon stocks in the River Dee and quotes salmon redd counts and catch records in support of his statements. The redd counts made by River Authority bailiffs in the Llyn Tegid feeder streams and the upper Dee during recent years are shown in table 3.

Table 3 Salmon redd counts in the upper Dee area.

(i) Llyn Tegid feeder streams

River	No. of redds counted each year				
	1964	1965	1968	1969	1970
A.Dyfrdwy	30	22	3	20	8
A.Glyn	24	-	1	7	5
A.Twrch	15	1	11	7	6
A.Llafar	20	15	6	17	8

(ii) River Dee (upper reaches)

Site	No. of redds counted each year	
	1961	1962
Bala/Llanderfel	537	452
Llanderfel/Cynwyd	605	685
Cynwyd/Corwen	304	243

As a result of the construction of Llyn Celyn (see chapter 1) and the subsequent loss by innundation of much of the salmon spawning grounds in the Afon Tryweryn, it was felt desirable for the Dee and Clwyd River Authority to augment the natural reproduction of salmon in the area by the artificial propagation of young salmon, in all stages of development, at least equal in number to those estimated to have been lost to the river system by the Llyn Celyn works. The River Authority use two methods to achieve this :-

(1) Rearing and distribution of hatchery bred fry, underyearling parr and pre-smolts.

(2) The utilization of specially selected streams, which are naturally inaccessible to salmon, as nursery streams, by stocking with salmon fry after the removal of predators and food competitors.

The supply of eggs reared in the hatchery are obtained from adult salmon caught in a fish trap below Llyn Celyn dam and in a weir fish trap at Pont Barcer.

The numbers of young salmon stocked in the Llyn Tegid feeder streams and the upper Dee during recent years are shown in table 4.

Table 4. Numbers of young salmon stocked by the Dee and Clwyd River Authoxity in the Llyn Tegid feeder streams and the upper Dee.

1964	Eyed ova	unfed fry	underyearling parr
A. Lliw	50,000	total 50,000	-
A. Twrch	50,000		-
A. Llafar	-		-

Table 4 cont.

1965	Eyed ova	unfed fry	underyearling par
A.Twrch	10,000	total 140,000 (A.Twrch, A.Lliw, A.Llafar)	-
A.Lliw	-		-
A.Llafar	-		-
R.Dee (Corwen)	-		15,000
1967			
A.Lliw	50,000	-	-
A.Llafar	50,000	-	-
A.Dyfrdwy	50,000	-	-

The planting out of eyed ova has been discontinued in the Dee area, but used to be carried out during January and February. Unfed fry are planted out during May, and underyearling parr in October and November. No stocking of the Llyn Tegid feeder streams or the River Dee has been carried out by the River Authority since 1967, most of the stocking efforts of the Authority now being directed towards the use of nursery streams. The eggs and fry planted in the Llyn Tegid feeder streams before 1967 were placed in the upper reaches of the streams and, where applicable, above impassable falls.

CHAPTER III

DESCRIPTIONS OF THE SAMPLING SITES

A. Introduction

Studies were made on the salmonid fishes in the following habitats :

1. Llyn Tegid feeder streams

    Afon Dyfrdwy

    Afon Lliw

    Afon Llafar

    Afon Twrch

    Afon Glyn

2. Llyn Tegid

3. River Dee

    Bala to Corwen (upper reaches), and several small tributary streams (Afon Hafhesp, Afon Meloch, Llanderfel brook, Afon Ceidiog, Afon Llynor, A. Cammddwr and Afon Morwynion).

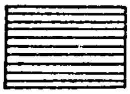
The location of these habitats can be seen in figure 1 (chapter 1) and detailed descriptions are given in the following pages.

B. Geology of the area

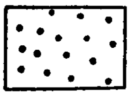
The geology of the upper Dee area is shown in figure 3. The Bala or Caradoc beds form the main feature of the area and consist of sandstones, slates and mudstones together with shales, flags, limestones and some interbedded volcanic rocks overlying the

Figure 3.

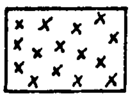
Legend:



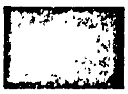
Llandovery-Tarannon beds (Valentian)
(Silurian)



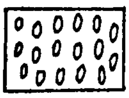
Wenlock limestone (Silurian)



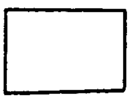
Felsite, Quartz-Porphyry, Lime,
Bostonite, Porphyrite and Andesite.



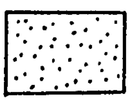
Basalt, Dolenite and Diabase.
(Igneous rocks)



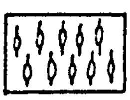
Horneblende and Glaucophane Schists.
(Pre-Cambrian)



Alluvium River Terraces and Peat.
(Recent)



Bala (Ashgill, Caradoc), Llandeilo and
Arenig Beds. (Ordovician)



Ludlow Beds. (Silurian)

The Geology of the upper Dee catchment area

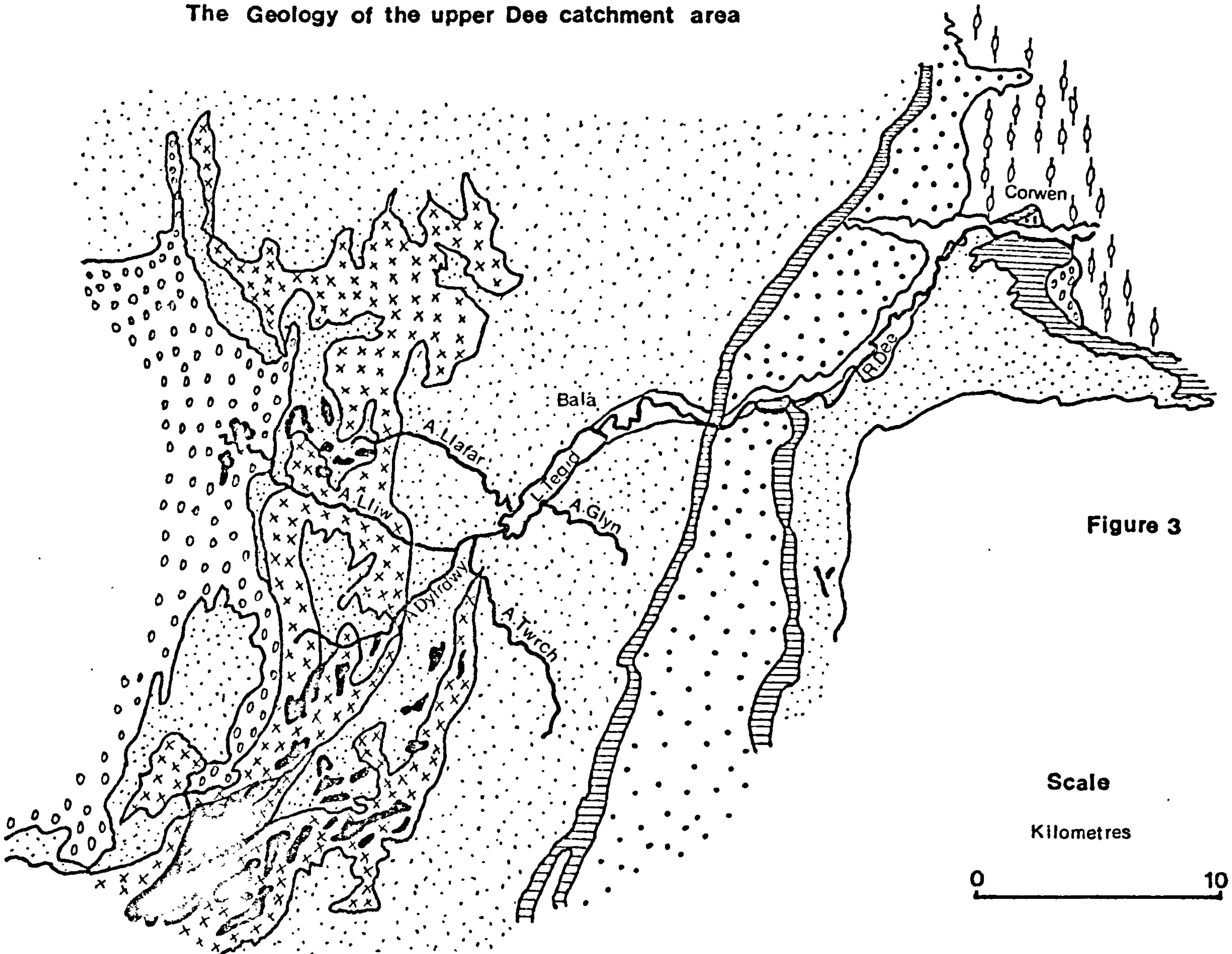


Figure 3

Llandeilo and Arenig beds. Bala limestone is generally very impure and rather localised. The Afon Glyn, in its upper reaches, flows through an accumulation of this limestone and consequently has a much higher calcium content than the other Llyn Tegid feeder streams (see Table 8). Intrusive and contemporaneous igneous rocks form much of the mountainous area to the west and southwest of Llyn Tegid.

The formation of Llyn Tegid and the development of its associated river systems were discussed by Lake (1900) who stated that Llyn Tegid lies in a trough between two faults, modified by other faults crossing the trough obliquely. The interrelationships of the Llyn Tegid feeder streams and tributaries of the River Severn considered by Lake (op.cit.) were referred to in chapter 2 (section 1E). Extensive areas of alluvial deposits occur at both the southwest and northeast ends of Llyn Tegid.

Below Llyn Tegid the River Dee flows for 5km. through an alluvial tract overyling the Bala beds. In the Llanderfel area the hills close in on the river for about 1½km. before the river again enters braod alluvial flats which then continue to Corwen. The Llanderfel hills consist largely of Llandovery and Wenlock grits, slates and limestones. The geological origins of the River Dee system were described by Ramsay (1876) and the drainage of the area by Brown (1960).

C. Characteristic features of the sampling sites

1. Llyn Tegid feeder streams

a. Location of sampling sites

The Llyn Tegid feeder streams were sampled principally for juvenile salmon (with the exception of the lower reaches of the Afon Dyfrdwy) and sampling sites were chosen accordingly. After preliminary surveys sites were chosen which were reasonably accessible, which contained large numbers of young salmon, and for which the necessary permission for sampling could be obtained. With the diversity of Welsh hill farms and language difficulties the latter factor was not always easily overcome! Sketch maps illustrating the position of the sites chosen are shown in figures 4 to 10.

b. Physical features

The physical features of the Llyn Tegid feeder stream sites are presented in table 5 using an adapted classification system based on that of Cuinat (1970).

Views of a number of the sites can be seen in plates 4 to 11. Note the extensive salmon spawning gravel in plate 6 (A.Lliw, site 2) and the gabion weirs in plates 9 and 10 (A.Glyn). These gabion weirs are used for the retention of gravel and limiting erosion, particularly in the lower reaches of the Afon Glyn and Afon Dyfrdwy following the lowering of the water level in Llyn Tegid. The series of weirs in the Afon Glyn conveniently divided the river up into a number of easily fishable sections. Sites 5 to 8 on the Afon Dyfrdwy can be seen in the aerial view of Llyn Tegid (plate 12), together with the Afon Glyn and Afon Llafar inlets. The Afon Glyn

Figures 4 to 10

Sketch maps to show the position of sampling sites on the Llyn Tegid feeder streams

SH903322	=	map reference - National Grid
p	=	pool
RB	=	Road Bridge
RyB	=	Railway Bridge
FB	=	Foot Bridge
	=	Gabion weir
g	=	Gabion groyne
.164	=	altitude (metres) above O.D.
1,2,3 etc.	=	sampling site numbers
	=	boundaries of sampling site.

(not to scale)

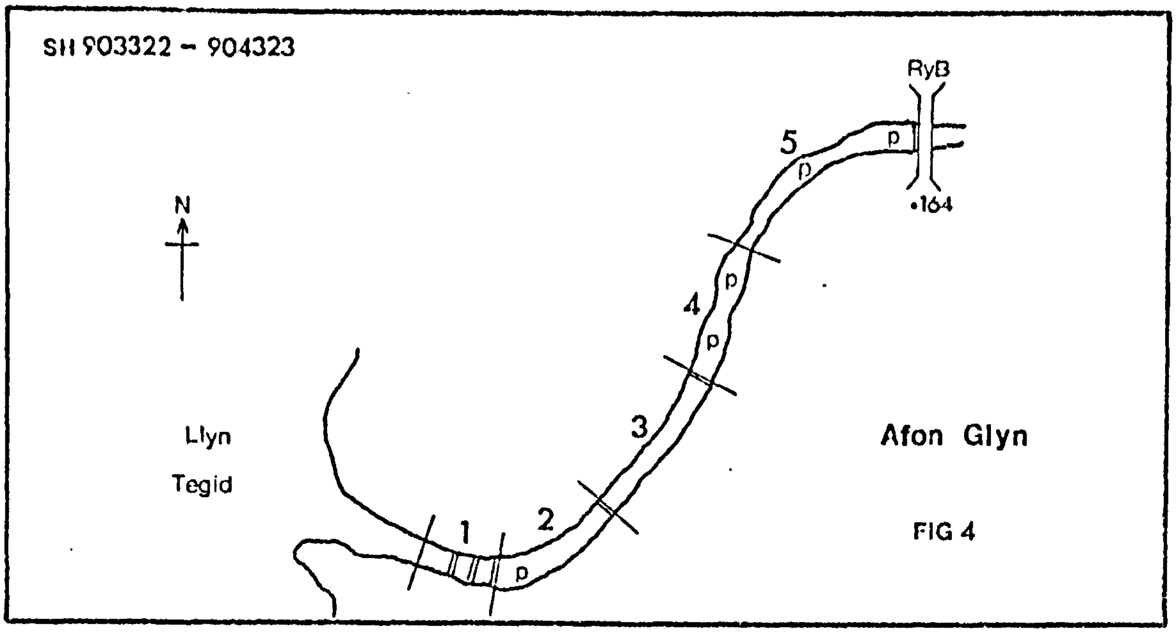


FIG 4

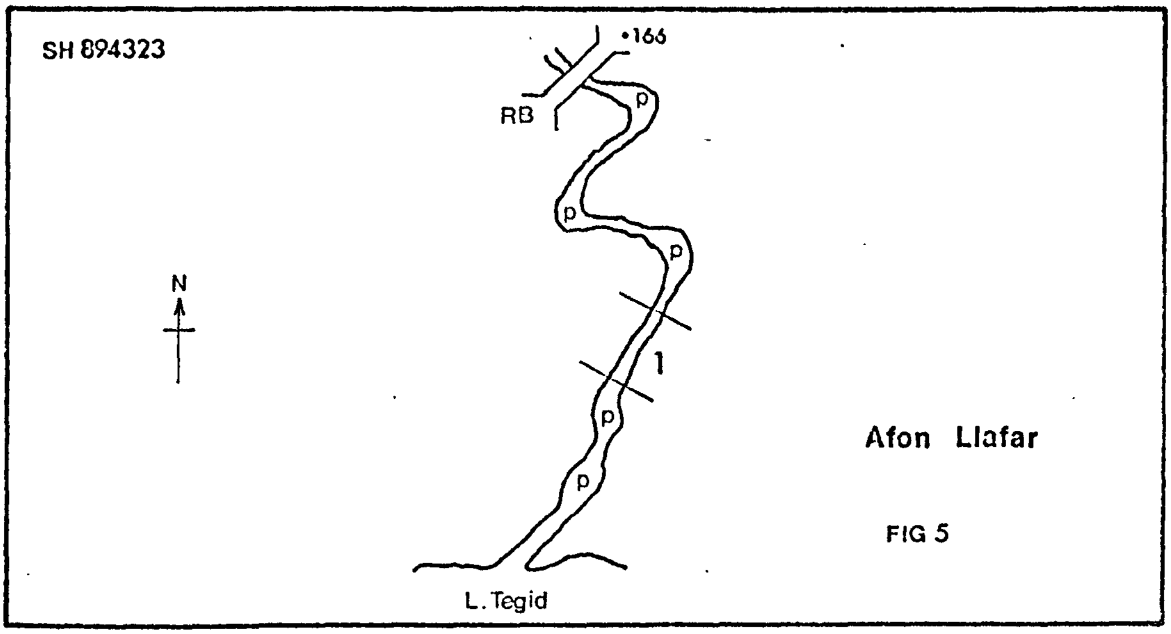


FIG 5

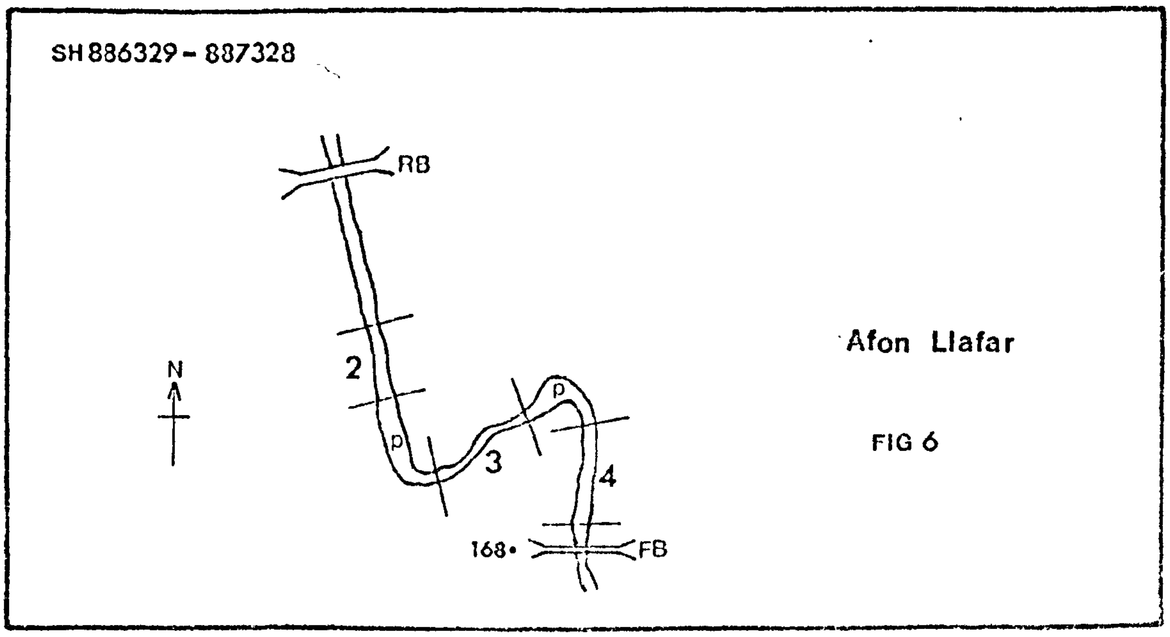


FIG 6

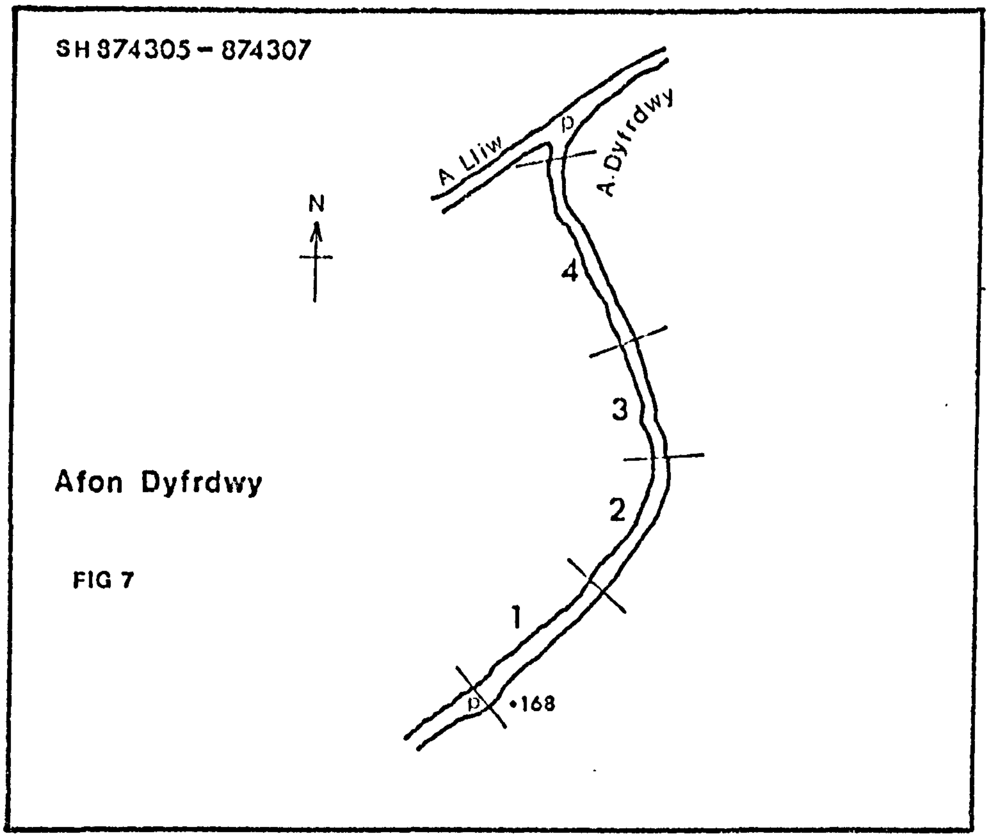


FIG 7

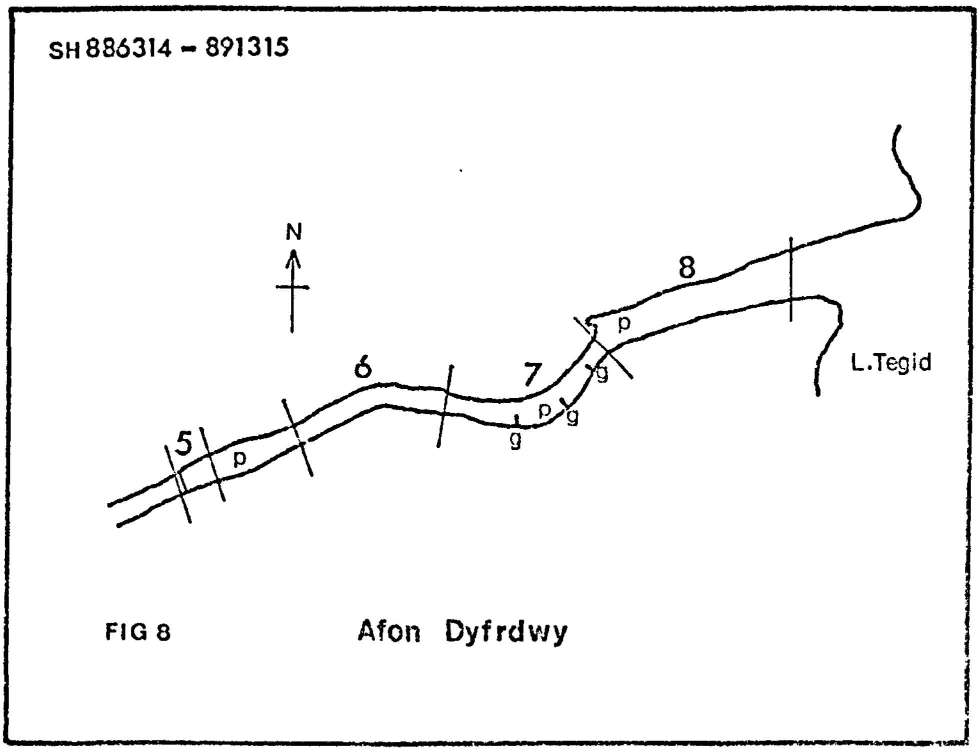


FIG 8 Afon Dyfrdwy

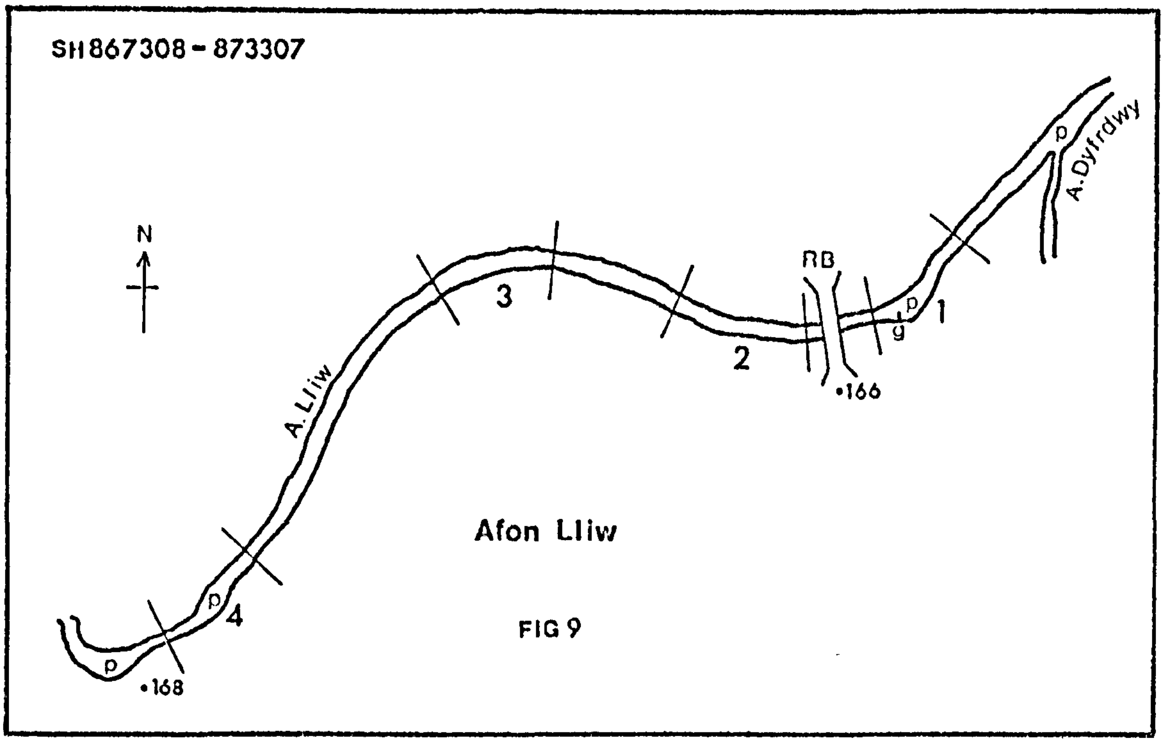

SH867308 – 873307
N
A.Lliw
A.Dyfrdwy
RB
•166
•168
p
g
1
2
3
4
Afon Lliw

FIG 9

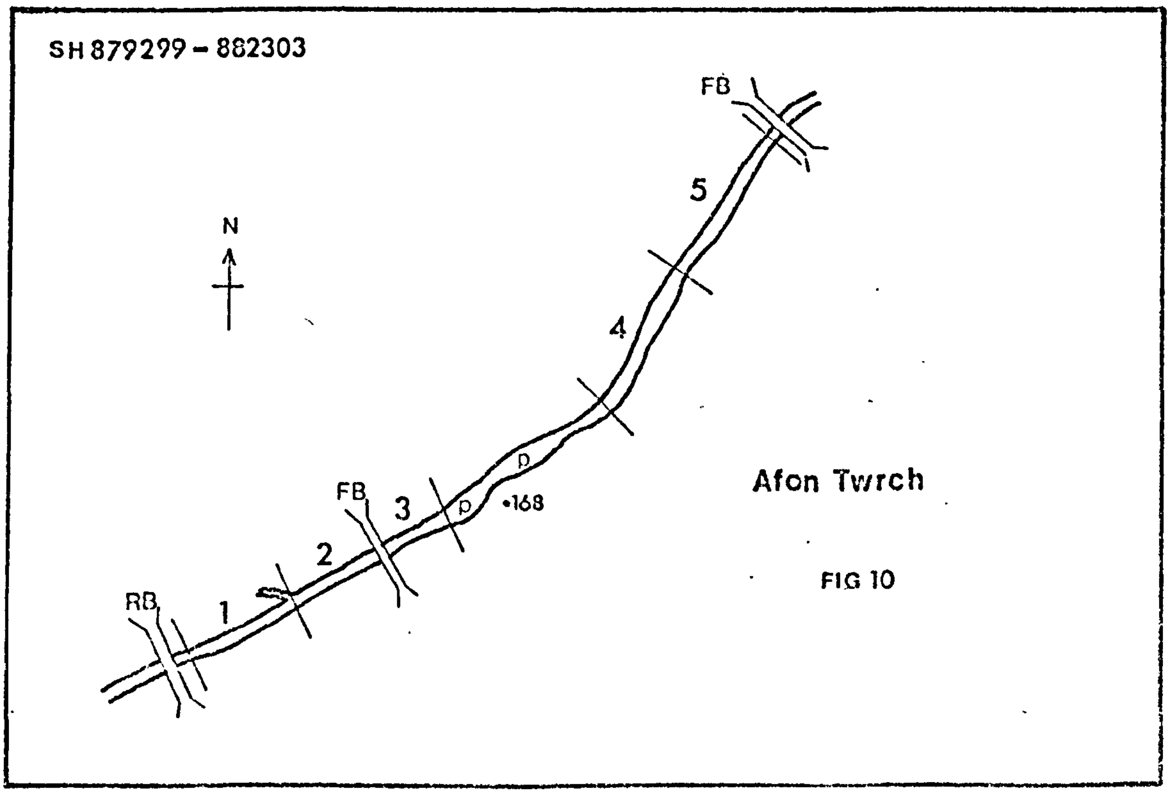

SH 879299 – 882303
N
FB
RB
p
•168
1
2
3
4
5
Afon Twrch

FIG 10

Table 5.

Key :

riffles	1	=	section of rapid water of moderate depth
flats			
Lbo		=	large boulders (diam. 500mm.)
Sbo		=	small boulders (diam. 200-500mm.)
Lpb		=	Large pebbles (diam. 50-200mm.)
Spb		=	Small pebbles (diam. 20-50mm.)
Lpb | Spb		=	Large and small pebbles present in equal quantities
-		=	none, absent
(+)		=	few, small quantity
+		=	moderate quantity
++		=	abundant, extensive

Table 5. Physical characteristics of sampling sites on the Llyn Tegid Feeder Streams.

	A. Llafar				A. Lliw				A. Dyfrdwy								A. Twrch					A. Glyn				
site number	1	2	3	4	1	2	3	4	1	2	3	4	5	6	7	8	1	2	3	4	5	1	2	3	4	5
Length (m)	41	41	46	46	114	46	64	82	64	50	41	58	25	85	105	130	41	38	38	59	64	27	27	37	45	73
Mean width (m)	6.1	7.6	4.0	6.4	7.3	7.6	7.0	8.2	5.8	5.5	4.3	5.2	12.3	14.2	16.0	18.1	6.1	6.1	7.6	7.9	8.5	7.3	6.1	6.3	4.6	4.6
Length x width (m^2)	250	312	184	294	832	350	448	672	371	275	176	302	307	1207	1680	2353	250	232	289	466	544	197	165	233	207	336
Mean slope (%)		0.5		0.7		0.4							0.4						1.1					0.9		
Mean depth in riffles (cm)	20	20	15	15	13	18	20	18	13	13	13	15	25	50	50	60	30	30	30	20	20	15	-	25	10	20
flats (cm)	60	-	60	56	-	-	40	-	30	30	-	25	|	|	|	|	|	|	76	|	|	|	46	|	46	38
pools (cm)	76	-	90	-	152	66	-	66	76	-	90	50	76	84	175	170	90	90	102	60	43	56	76	70	104	90
Number of riffles	2	1		1	2	1	1	2		1	2	2		-	-	-				1	2				1	2
			1						1				1				1	1	1			1	1	1		
flats	1	—		-	-	-	-	-		-	-	1		1	1	1				-	1				1	1
pools	-	-	-	-	1	1	-	1	1	-	2	1	-	-	1	1	-	-	1	1	-	-	1	-	2	2
Bottom Deposits dominant	Lpb	Lpb	Lbo	Lpb	Spb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lbo	Spb	Spb	Spb	Lbo	Lbo	Lbo	Lpb	Lpb	Lbo	Lbo	Lbo	Spb	Lpb
subdominant	Sbo	Spb	Sbo	Sbo	Lpb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Sbo	Lpb	Lpb	Lpb	Sbo	Sbo	Sbo	Spb	Spb	Lpb	Lpb	Lpb	Lpb	Spb
Fish shelter blocks & rocks	+	-	++	+	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	++	-	(+)	(+)	++	++	++	+	(+)	++	++	++	-	(+)
vegetation	-	-	-	-	+	-	-	-	-	-	-	-	-	+	(+)	-	-	-	-	-	-	-	-	-	-	-
roots and undermined banks	(+)	(+(	++	(+)	(+)	(+)	-	(+)	-	-	(+)	(+)	-	-	-	(+)	(+)	-	-	(+)	(+)	(+)	(+)	(+)	++	+
Spawning gravel (salmon)	+	+	(+)	(+)	++	++	++	++	++	++	++	++	-	+	(+)	-	-	-	-	+	+	-	(+)	(+)	(+)	+
Shade	-	-	++	+	-	-	-	(+)	-	-	-	-	-	-	-	-	+	+	+	-	-	(+)	(+)	(+)	++	++
Source of river	Arenig Fawr				Foel Boeth				Dduallt								Foel Rhudd					Foel y Geifr				
Map reference of source	SH 831365				SH 781349				SH 813270								SH 892237					SH 935300				
Altitude of source (m)	656				525				534								631					467				
Total Length of river (km) (excluding tributaries)	10.1				12.1				12.9								12.0					4.5				

Plate 4

Afon Llafar

Site 4

Plate 5

Afon Llafar

Site 2

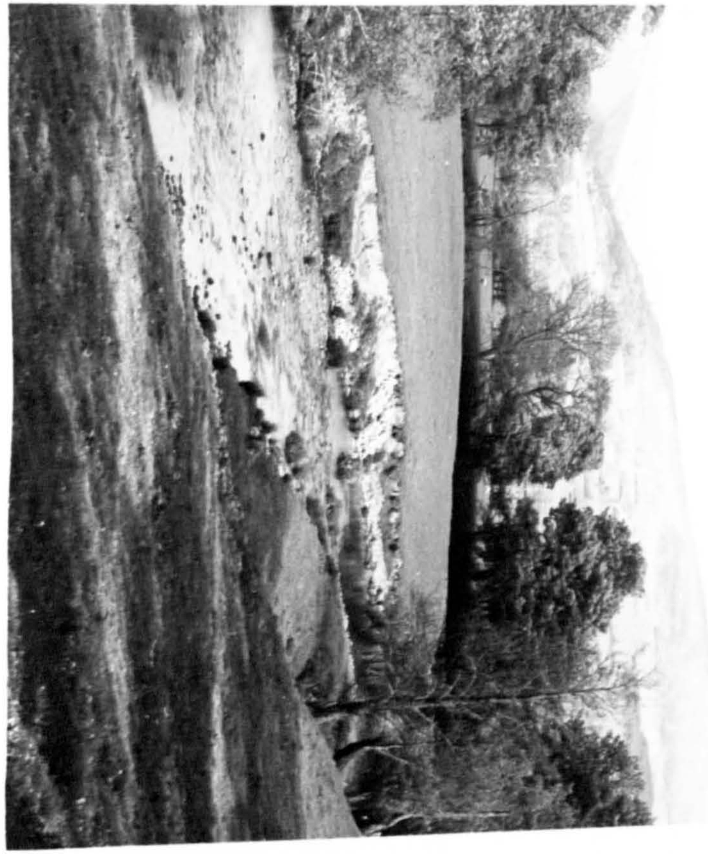


Plate 6

Afon Lliw

Site 2

Plate 7

Afon Dyfrdwy

Site 4 and Afon Lliw confluence

Plate 8

Afon Twrch

Site 1

Plate 9

Afon Glyn

Site 1

(Gabion weirs)

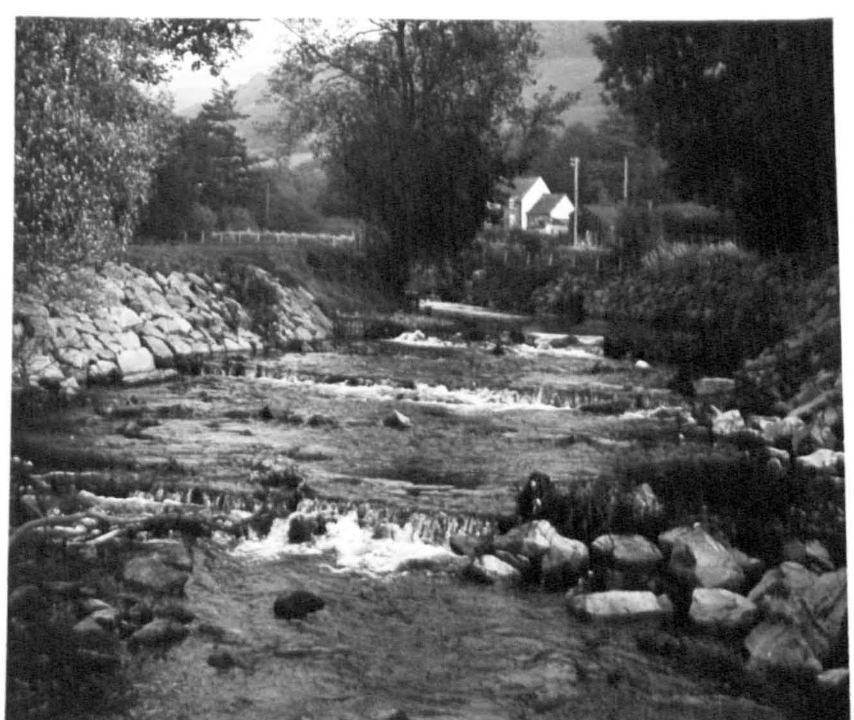


Plate 10

Afon Glyn

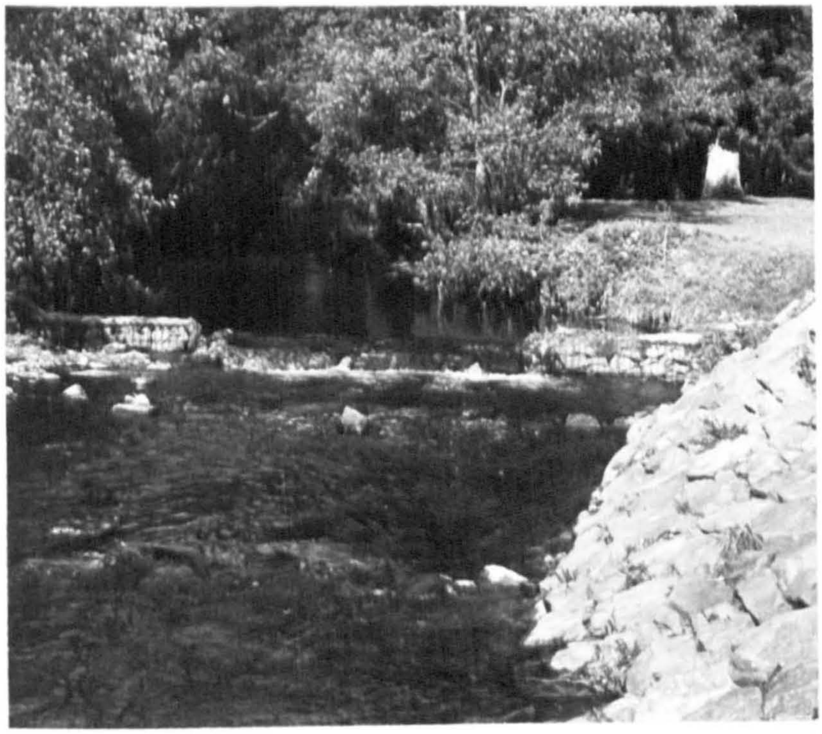
Site 3

(Gabion weir)

Plate 11

Afon Glyn

Site 5 (upper part)



and Afon Twrch both contain falls in the lower reaches which are impassable to salmon and my sampling sites were situated downstream of these falls. The slopes of the feeder streams in the sampling area fall into the lower trout and upper grayling zones of Huet (1949).

Water temperature s were taken on each sampling visit, around midday, by both M.A. Rahim (sampling invertebrates) and myself. The combined monthly results for all feeder streams are shown in Table 6.

Table 6. Monthly water temperatures in the Llyn Tegid feeder streams.

Month	Range of temperature °C	Mean temperature °C
Feb. 1969	1.5 - 3.0	2.1
Mar	3.0 - 4.5	3.5
Apr.	4.0 - 6.5	5.4
May	5.5 -13.5	9.6
Jun	10.4 -14.0	12.8
Jul	13.0 -20.0	14.5
Aug	13.5 -18.0	15.5
Sept	8.2- 14.0	12.0
Oct	8.5 -11.5	9.0
Nov	3.0 - 5.3	4.9
Dec	3.0 - 4.0	3.8
Jan 1970	2.8 - 5.0	4.0
Feb	2.3 - 5.0	4.1
Mar	2.0 - 5.5	4.7

Water flow measurements in the Afon Dyfrdwy at a gauging station just below the Afon Lliw confluence have been carried out since July 1969 by the Dee and Clwyd River Authority. The results of these measurements from July 1969 to June 1970 are given in Table 7.

Table 7. Monthly measured flow (cumecs) in the Afon Dyfrdwy.

Month	Total Monthly flow	Mean daily flow	Max. daily flow	Min. daily flow	Highest flow	Lowest flow
July 1969	8.938	0.288	0.963	0.154	2.01	0.15
Aug	25.286	0.816	2.178	0.183	8.01	0.18
Sept	21.743	0.725	3.459	0.244	5.85	0.24
Oct	41.856	1.350	6.670	0.537	12.78	0.51
Nov	164.215	5.297	24.733	0.726	41.02	0.64
Dec	129.700	4.184	21.104	0.740	40.10	-
Jan 1970	96.719	3.120	11.973	0.598	31.19	0.36
Feb	175.180	6.256	25.793	0.984	52.60	0.79
Mar	96.011	3.097	13.558	1.083	34.16	0.98
Apr	169.149	5.638	27.285	0.728	44.30	0.70
May	17.887	0.557	1.437	0.240	1.56	0.21
Jun	13.363	0.445	2.812	0.140	6.72	0.13

The cathcment area of the Afon Dyfrdwy (Little Dee) is given by the Dee and Clwyd River Authority at 53.9 sq.km. and an estimate for the total inflow into Llyn Tegid (excluding that from the Afon Tryweryn) can be obtained by multiplying the A. Dyfrdwy flow figures by a factor of 3.1.

c. Chemical characteristics

Chemical analyses of the Llyn Tegid feeder streams carried out by Dr. Abdullah of the Oceanography Department, University of Liverpool, and M.A. Rahim (pH and oxygen concentrations) are shown in Table 8.

d. Biological characteristics

The vegetation of the Llyn Tegid feeder streams is shown in

Table 8. Water Chemistry of the Llyn Tegid Feeder Streams.

	A.Glyn		A.Twrch		A.Dyfrdwy		A.Lliw		A.LLafar	
	meq/l.	ppm	meq/l.	ppm	meq/l.	ppm	meq/l.	ppm	meq/l.	ppm
Cations										
Calcium	0.751	-	0.510	-	0.300	-	0.186	3.96	0.195	3.80
Magnesium	-	-	0.15	-	0.066	-	0.045	0.61	0.046	0.56
Sodium	-	-	-	-	-	-	0.193	4.44	0.195	4.53
Potassium	-	-	-	-	-	-	0.112	0.56	0.103	0.56
Carbon	-	1.85	-	1.86	-	1.567	-	1.52	-	1.52
Iron	-	0.14	-	-	-	0.13	-	0.13	-	0.14
Anions										
Alkalinity(HCO_3)	0.402	-	0.201	-	0.146	-	0.113	-	0.112	-
Calcium carbonate	-	-	-	-	-	-	-	5.7	-	5.6
Chloride	0.157	-	0.152	-	0.148	-	0.184	6.87	0.195	6.98
Sulphate	0.161	-	0.146	-	0.158	-	0.145	7.00	0.147	7.01
Nitrate	-	-	-	-	-	-	0.030	0.272	0.021	0.291
pH range	6.4 - 8.2		6.4 - 8.2		6.4 - 8.4		6.4 - 8.2		6.0 - 8.5	
pH mean	7.1		6.9		7.0		7.0		6.8	
Oxygen concentration (% saturation)	65 - 125		71 - 110		63 - 116		63 - 118		65 - 115	
Copper	-		none		none		-		-	
Manganese	-		none		none		-		-	

table 9. The most abundant moss present in the streams is *Fontinalis antipyretica*. Trees commonly occurring on the bank-sides are alder (*Alnus glutinosa*), sycamore (*Acer pseudoplanatus*) hawthorn (*Crataegus monogyna*), mountain ash (*Sorbus aucuparia*), beech (*Fagus sylvatica*) and birch (*Betula pendula*).

The invertebrate fauna of the Llyn Tegid feeder streams is the subject of a study at present being carried out by M.A. Rahim.

The fish species present in the Llyn Tegid feeder streams are salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.), eels (*Anguilla anguila* L.), stoneloach (*Nemacheilus barbatula* L.), bullheads (*Cottus gobio* L.) and minnows (*Phoxinus phoxinus* L.). In the lower reaches of the rivers, pike (*Esox lucius* L.) and gudgeon (*Gobio gobio* L.) occur. Perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.) enter the lower reaches from Llyn Tegid during the summer, and grayling (*Thymallus thymallus* L.) migrate from Llyn Tegid into the feeder streams to spawn in April and May. Some grayling also enter the Afon Dyfrdwy and Afon Llafar during the summer and migrate up as far as the lower reaches of the Afon Twrch and Afon L_1iw. These grayling drop out of the feeder streams into Llyn Tegid during the autumn. The riffle and rapid areas of the streams support a mixed population of young salmon and trout, with salmon predominating. Young salmon are particularly numerous around the blocks and rocks used in the construction of gabion weirs. Trout are more numerous than salmon in pools under overhanging banks and near tree roots. Adult salmon do not enter the feeder streams until shortly before spawning time, in November and December. Salmon smolts descend from

Table 9

Key :

submerged macrophytes	A	*Myriophyllum spicatum*
	B	*Callitriche aquatica*
	C	*Ranunculus aquatilis*
emergent macrophytes	D	*Juncus* sp.
	E	*Phalaris arundinacea*

Table 9. Vegetation of the Llyn Tegid feeder streams.

	A. Llafar				A. Lliw				A.Dyfrdwy								A.Twrch					A. Glyn				
Site number	1	2	3	4	1	2	3	4	1	2	3	4	5	6	7	8	1	2	3	4	5	1	2	3	4	5
Aquatic Vegetation																										
mosses	+	+	+	+	+	+	+	+	+	+	+	+	+	(+)	(+)	(+)	++	++	++	+	+	(+)	(+)	(+)	(+)	(+)
submerged macrophytes	A (+) B (+)	B (+) C (+)	–	B (+) C (+)	B (+) C (+)	A (+) B (+)	–	–	A (+)	–	–	A (+) B (+)	–	A + B +	A (+) B (+)	–	–	–	–	–	–	–	–	–	–	–
emergent macrophytes	D (+)	D (+) E (+)	–	D (+) E (+)		D(+)	E(+)				D (+)		E(+)				D(+)		E(+)			D(+)		E(+)		
Bankside Vegetation																										
trees	(+)	(+)	++	+	(+)	(+)	1	(+)	–	–	–	–	(+)	–	–	–	+	+	+	(+)	–	(+)	(+)	(+)	++	++
bushes & shrubs	(+)	(+)	–	–	(+)	(+)	(+)	(+)	–	–	–	–	(+)	–	–	–	(+)	–	(+)	(+)	(+)	–	–	(+)	(+)	–
(1 or 2 banks) meadows	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	2	2	2	1

the streams to Llyn Tegid in late April and early May, and at the same time large numbers of young trout (2 to 4 years old) migrate into the lake.

e. Previous research

Morris (1967) compared the biology of minnows, stoneloach and bullheads in the Afon Llafar, a soft-water stream, with the biology of these species in Willow brook, a hard-water stream in southern England. Ball and Jones (1960, 1962) in their studies on the brown trout of Llyn Tegid included some observations on the growth rates of trout in the Afon Lliw and Afon Glyn and on the movement of trout out of the Llyn Tegid feeder streams into Llyn Tegid.

2. Llyn Tegid

a. Location of sampling sites

The location of the Llyn Tegid sampling sites (A to J) are shown in the aerial view of Llyn Tegid (plate 12). These sites were chosen according to their suitability for shore seine-netting operations. The ideal sites were those with a gently sloping gravel bottom and an absence of snags such as large boulders. Prevailing southwest winds render northeast facing shores more suitable for netting and in strong southwesterlies station J could not be sampled.

b. Physical features

Llyn Tegid, the largest natural Welsh lake, is 6km. long, 0.9km. wide and has an area of approximately 4.5 sq.km. The lake

Plate 12

Aerial view of Llyn Tegid from the southwest end of the lake.

A to J	:	sampling stations
5 to 8	:	Afon Dyfrdwy sampling sites nos. 5 to 8
Tw	:	Afon Twrch
La	:	Afon Llafar
Gl	:	Afon Glyn
RD	:	River Dee outlet


J
G
H
I
A
B
C
Tw

lies in a southwest/northeast direction at an altitude of 161m. above O.D. and is roughly rectangular in shape with steep sides and more gradually sloping ends falling to a flat bottom at approximately 35 metres. The maximum depth of the lake is about 47m.

Llyn Tegid is fed by five main streams (Afon Dyfrdwy, Afon Lliw, Afon Twrch, Afon Llafar and Afon Glyn), four of which can be seen in plate 12, and several smaller streams. The lake is drained at the northeast end by the River Dee (Plate 1, chapter 1, and plate 12). The surrounding land is agriculturally poor, largely consisting of hill and moorland, and is mainly used for sheep grazing. Mountains surrounding the southwest end of the lake rise to 884m. above O.D. (Aran Benllyn).

A bathymetric survey of Llyn Tegid was carried out by Jones (1951) and the resulting contour map is shown in figure 11. The areas of the lake floor within each contour are shown in table 10. These figures are representative of pre-Bala scheme measurements since which time there has been a reduction in the area of the 0-3 metre zone.

Dunn (1952) divided the lake floor into three zones according to the composition of the benthic fauna and the extent of rooted vegetation. These zones were : littoral, approximately 0-3 metres; sublittoral, approximately 3-15 metres; and profundal, below 15 metres. From the figures in table 10 it can be seen that about 60% of the lake floor lies in the profundal zone. The lake temperature was taken on each sampling visit (usually weekly) at a depth of 1 metre in mid-lake.

Figure 11

Contours of Llyn Tegid

surveyed October 1951 by the Department of Zoology, University of Liverpool. Depths in feet. Surface of water 530 ft. above mean level of sea at Liverpool. Dotted lines represent coast lines in 1960. Present coast lines from aerial photographic (AM.1948).

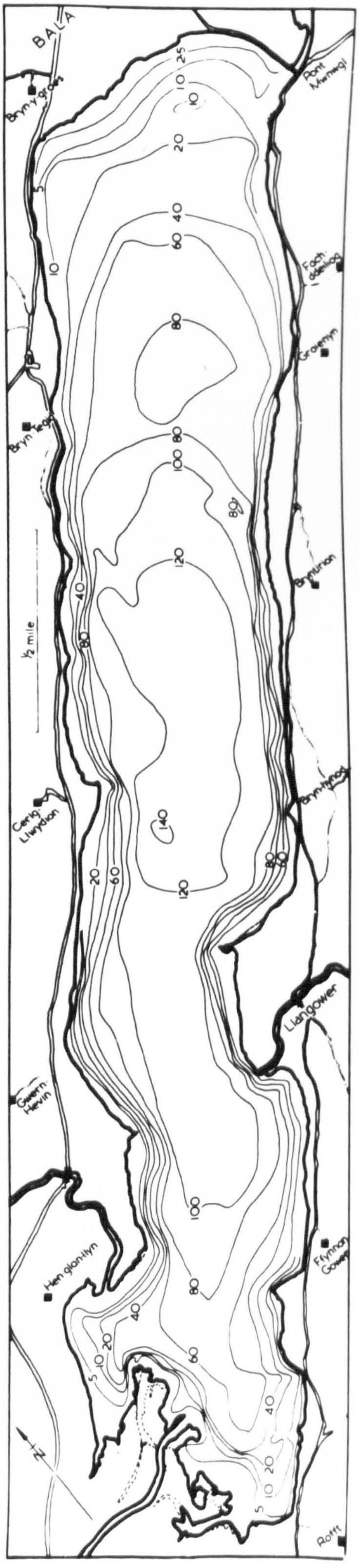

BALA
Bryn-y-groes
Pont Mwnwgl
Fach-ddeiliog
Bryn-Tegid
½ mile
Cerig-Llwydion
Llangower
Gwern-Hefin
Hen-glan-llyn
N
Rofft

Table 10. Approximate areas of lake floor within each contour.

Depth in metres	(in feet)	Area sq.km.	% of total area
0-3	(0 - 10)	0.649	14.47
3-6	(10 - 20)	0.395	8.80
6-13	(20 - 40)	0.482	10.74
13-18	(40 - 60)	0.438	9.77
18-26	(60 - 80)	0.676	15.07
26-32	(80 - 100)	0.533	11.90
32-38	(100 - 120)	0.781	17.41
38-44	(120-140)	0.526	11.71
44	(140)	0.006	0.13

total area 4.486

Table 11. Monthly water temperatures at a depth of 1 metre in Llyn Tegid.

Month	Range of Temperature °C	Mean temperature °C
Oct 1968	10.5 - 13.0	12.5
Nov	8.0 - 11.0	9.3
Dec	6.0 - 7.0	6.7
Jan 1969	4.5 - 6.5	5.8
Feb	3.0 - 5.0	4.1
Mar	1.0 - 5.0	1.50
Apr	5.0 - 8.0	9.5
May	9.0 - 11.5	10.7
Jun	12.5 - 17.5	14.5
Jul	15.0 - 21.0	17.5
Aug	16.5 - 18.5	17.5
Sep	13.8 - 16.0	15.7
Oct	12.0 - 14.0	13.0

The monthly temperatures recorded are shown in table 11.

Hunt (1970) found that a thermocline formed in the lake during late summer, the depth of which fell as the summer progressed. In September 1968 the thermocline was located at a depth of 11-15 metres, and by 2nd November 1968 the water temperature was uniform from the surface to the lake floor. Approximate depth/temperature recordings were made in mid-July 1969. At depths above 6 metres the temperature was 16-17°C, between 6 metres and 10 metres the temperature fell from 15°C to 10°C, and below 10 metres the temperature was a uniform 9°C to the lake floor.

Fluctuations of up to 4 metres (from 159.5 to 163.5 metres A.O.D.) are possible in Llyn Tegid but in practice are generally much less. In the early days of regulation large erratic level fluctuations were common (Hynes, 1961a), but since the completion of Llyn Celyn the level fluctuations have been considerably reduced (Hunt, 1970). Hunt (1970) found level fluctuations in 1967 to 1969 similar to those in the pre 1955 period but with a mean water level 2 metres lower. The actual 3 day mean lake level fluctuations (Dee and Clwyd River Authority) from October 1968 to September 1970 are shown in figure 12. The mean winter level during this period was lower than the mean summer level (approximately 160 metres and 160.7 metres respectively). Fluctuations were greater in the winter than in the summer because of heavy winter rains and the retention of flood water. Mean winter fluctuations were about 0.7 metres and mean summer fluctuations about 0.35 metres.

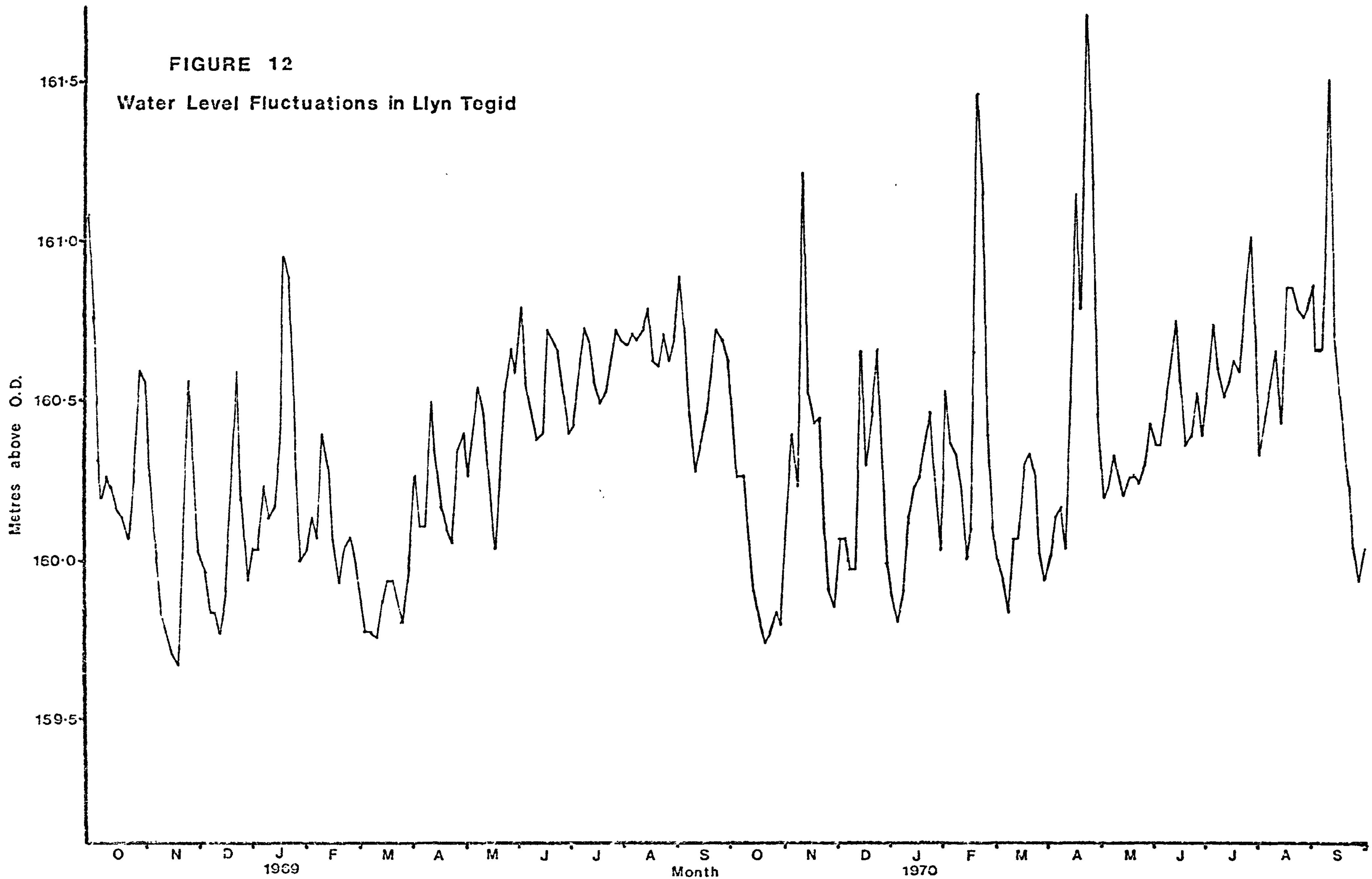


FIGURE 12
Water Level Fluctuations in Llyn Tegid
161·5
161·0
160·5
160·0
159·5
Metres above O.D.
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
1969
Month
1970

Maximum fluctuations recorded during the sampling period (October 1968 to October 1970) were 2.1 metres in the winter and 0.9 metres in the summer.

Figures for the monthly rainfall at the meteorological office, Bala, from October 1968 to October 1970 are shown in table 12.

Table 12. Monthly rainfall at Bala

Month	Total rainfall (mm)	Days with > 0.2mm	Days with > 1.0mm
Oct 1968	154.6	20	16
Nov	79.6	15	13
Dec	103.3	18	13
Jan 1969	119.5	22	20
Feb	124.1	21	19
Mar	63.7	14	9
Apr	79.2	14	11
May	150.3	24	21
Jun	81.7	13	10
July	41.4	8	6
Aug	84.1	17	12
Sep	42.7	9	7
Oct	54.5	14	6
Nov	205.8	25	21
Dec	117.9	21	13
Jan 1970	133.1	27	25
Feb	169.6	21	20
Mar	107.6	27	23
Apr	187.0	28	24
May	35.6	11	9
Jun	72.6	16	13
Jul	77.7	22	14
Aug	103.7	14	13
Sep	113.4	16	11
Oct	167.4	23	19

c. Chemical characteristics

Ball and Jones (1960) described the lake water as soft, slightly acid or neutral, and poor in electrolytes. Water chemical analyses were carried out by Dr. Abdullah monthly from July 1968 to April 1969. His results, together with additional information from the Dee and Clwyd River Authority and the electrical conductivity figures from Hunt (1970), are shown in table 13. A small amount of sewage enters the lake from the town of Bala and from Glanllyn hostel (Welsh League of Youth). When thermal stratification occurs the hypolimnion is large in comparison with the total volume of the lake, and there is little dimunition in oxygen content in deeper waters at this time (Dunn, 1952; Hynes, 1961a; Hunt, 1970).

d. Biological characteristics

Rooted vegetation in Llyn Tegid occurs to a depth of 3 metres and is composed of Isoetes lacustris, Littorella uniflora, Callitriche sp. some Elodea canadensis and Potamogeton sp. The moss Fontinalis antipyretica forms extensive beds attached to stones on rocky shores. Emergent vegetation is sparse and consists mosly of Juncus sp. and Sparganium simplex.

The invertebrate benthic fauna of Llyn Tegid has been the subject of a number of studies (Dunn, 1952; Hynes, 1961; Hunt, 1970). The most recent work (Hunt, 1970) indicates that the commonest littoral organisms are oligochaetes, ephemeropteran nymphs (particularly Ephemera danica and Leptophlebia marginata) and chironomid larvae.

Table 13. The Chemistry of the water of Llyn Tegid.

Nitrate	75-347 u gm/l
Silicate	0.25 - 1.01 ppm
Sulphate	10 ppm
Chloride	8 ppm
Potassium	0.43 - 0.9 ppm
Sodium	3.24 - 5.45 ppm
Magnesium	0.78 - 0.99 ppm
Calcium	1.91 - 2.36 ppm
Manganese	2.1 - 55.0 u gm/l
Copper	1.6 - 11.6 u gm/l
Zinc	16.3 - 67.2 u gm/l
Lead	2.4 - 4.3 u gm/l
Nickel	0.83 - 1.88 u gm/l
Cadmium	0.27 - 1.15 u gm/l
Iron	2.98 - 70.0 u gm/l
Conductivity	39 - 47 u mhos
pH	6.1 - 7.7 (mean 6.7)
Calcium Hardness	4 - 13 mg/l
Magnesium Hardness	0 - 21 mg/l
Total Hardness	7 - 27 mg/l
B.O.D. (5 days at 20°C)	0.2 - 6.3 mg/l
Permanganate value (4hrs at 27°C)	1.7 - 8.3 mg/l
Dissolved oxygen, % saturation	83 - 121

A large increase in the numbers of oligochaetes in the littoral zone followed the lowering of the lake level for regulation purposes. The muddly lub-littoral zone then became the littoral zone with the consequent influx of oligochaetes. It is expected that these worms will mostly disappear as the mud is washed away by wave action (Hunt, 1970). Further details of the relative numbers of littoral benthic organisms is given in chapter 7 in connection with the feeding habits of grayling. The profundal and sub-littoral fauna is largely composed of oligochaetes and chironomid larvae (Hunt, 1970). Pugh-Thomas (1959) made a study of the zooplankton of Llyn Tegid.

The fish species present in the lake are brown trout (Salmo trutta L.), perch (Perca fluviatilis L.), roach (Rutilus rutilus L.), eels (Anguilla anguilla L.), grayling (Thymallus thymallus L.), gudgeon (Gobio gobio L.), minnows (Phoxinus phoxinus L.), pike (Esox lucius L.) and gwyniad (Coregonus clupeoides pennatii Cuvier & Valenciennes). Adult salmon (salmo salar L.) enter the lake from the River Dee during the spring and summer, and remain in the lake until autumn when they migrate into the feeder streams to spawn. Small numbers of sea trout (Salmo trutta L.) have also been recorded in Llyn Tegid. Salmon fry and parr are rarely found in the lake, but salmon smolts migrate through the lake in shallow water during late April and May. Trout and grayling are the most common species present in the shore zone from autumn to spring. In early summer large numbers of perch and roach enter the shallows and the trout and grayling mostly disappear. Gudgeon are also found in the shallows during the summer, particularly around the Afon Dyfrdwy inlet. Gwyniad remain in deep water except at spawning time (Haram, 1968).

Dunn (1952) on the basis of electical conductivity (38-45 u mhos) and the number of benthic organisms per m^2 (Thienemann, 1925) classified Llyn Tegid as being in the late oligotrophic condition. On the basis of rooted vegetation the lake may be regarded as being in the late mesotrophic state (Pearsall, 1921), and the mixed salmonid and coarse fish populations support the view that Llyn Tegid is in an intermediate phase.

e. Research on Llyn Tegid

Llyn Tegid has been subject to a considerable amount of research and a list of publications from this research is given below.

Ball, J.N. (1957)	The biology of the brown trout of Llyn Tegid. Ph.D. Thesis, University of Liverpool
Ball, J.N. (1961)	On the food of the brown trout of Llyn Tegid. Proc.Zool.Soc.Lond. 137 (4), 599-622.
Ball, J.N. & Jones, J.W. (1960)	On the growth of the brown trout of Llyn Tegid. Proc.Zool.Soc.Lond. 134 (1), 1-41.
Ball, J.N. & Jones, J.W. (1962)	On the movements of the brown troutof Llyn Tegid. Proc.Zool.Soc.Lond. 138 (2), 205-224.
Chubb, J.C. (1961)	A preliminary investigation of the parasite fauna of the fish of Llyn Tegid, Merionethshire. Ph.D. Thesis, University of Liverpool.
Chubb, J.C. (1962)	The parasite fauna of the fishes of Llyn Tegid, an oligotrophic lake. Parasitology (1962) 52.
Chubb, J.C. (1963)	On the characterization of the parasite fauna of the fish of Llyn Tegid. Proc.Zool.Soc. Lond. 141 (3), 609-621

Dunn, D.R. (1952) An investigation of the bottom fauna of Lake Bala, Merionethshire. Ph.D. Thesis, University of Liverpool.

Dunn, D.R. (1954) The feeding habits of some of the fishes and some members of the bottom fauna of Llyn Tegid (Lake Bala), Merionethshire. J.Anim.Ecol. 23, 224-233.

Dunn, D.R. (1961) The bottom fauna of Llyn Tegid (Lake Bala) Merionethshire. J.Anim.Ecol. 30, 267-281.

Graham, T.R. (1960) The biology of Llyn Tegid trout. M.Sc. Thesis, University of Liverpool.

Graham, T.R. & Jones, J.W. (1962) The biology of Llyn Tegid trout 1960. Proc.Zool. Soc.Lond. 139 (4), 657-683.

Haram, O.J. (1968) A preliminary investigation of the biology of the Gwyniad (*Coregonus clupeoides pennantii* Cuv.et Val.) of Llyn Tegid. Ph.D. Thesis, University of Liverpool.

Haram, O.J. & Jones, J.W. (1965) The gwyniad - an "ice age" fish. Animals 7, 298-301.

Hunt, P.C. (1970) Biological investigations in regulated reservoirs. Ph.D. Thesis, University of Liverpool.

Hynes, H.B.N. (1961) The effect of water level fluctuations on littoral fauna. Verh.int.Ver.Limnol 4, 652-656.

Jones, J.W. (1951) A bathymetric survey of Llyn Tegid.

Jones, J.W. (1953) Part I. The scales of roach. Part II. Age and growth of trout, grayling, perch and roach of Llyn Tegid (Bala) and roach of the river Birket. Fish.Invest.Lond. (I) 5 (7).

Jones, J.W. (1956) The biology of brown trout. 3. Rate of growth. Trout Salm.Mag 2 (19), 12-13.

Pugh-Thomas, M. (1959) A study of the freshwater zooplankton of Llyn Tegid. Ph.D. Thesis. University of Liverpool

Siddiqui, M.S. (1967) Perch, rudd and grayling in trout waters. Proc.3rd Brit.Coarse Fish Conf., University of Liverpool.

Siddiqui, M.S. (1969) Studies on the brown trout (Salmo trutta L.), the grayling (Thymallus thymallus L.) and the rudd (Scardinius erythrophthalmus L.) of the natural regulated waters and regulated reservoirs in North Wales. Ph.D. Thesis, University of Liverpool.

Williams, E.G. (1939) Micro-organisms of Bala Lake, Merionethshire. North Western Naturalist.

Research is at present being carried out on the roach and perch populations in the lake, and on aspects of the biology of the eels. A further one year study of trout and grayling has been started and work on underwater photography techniques is in progress.

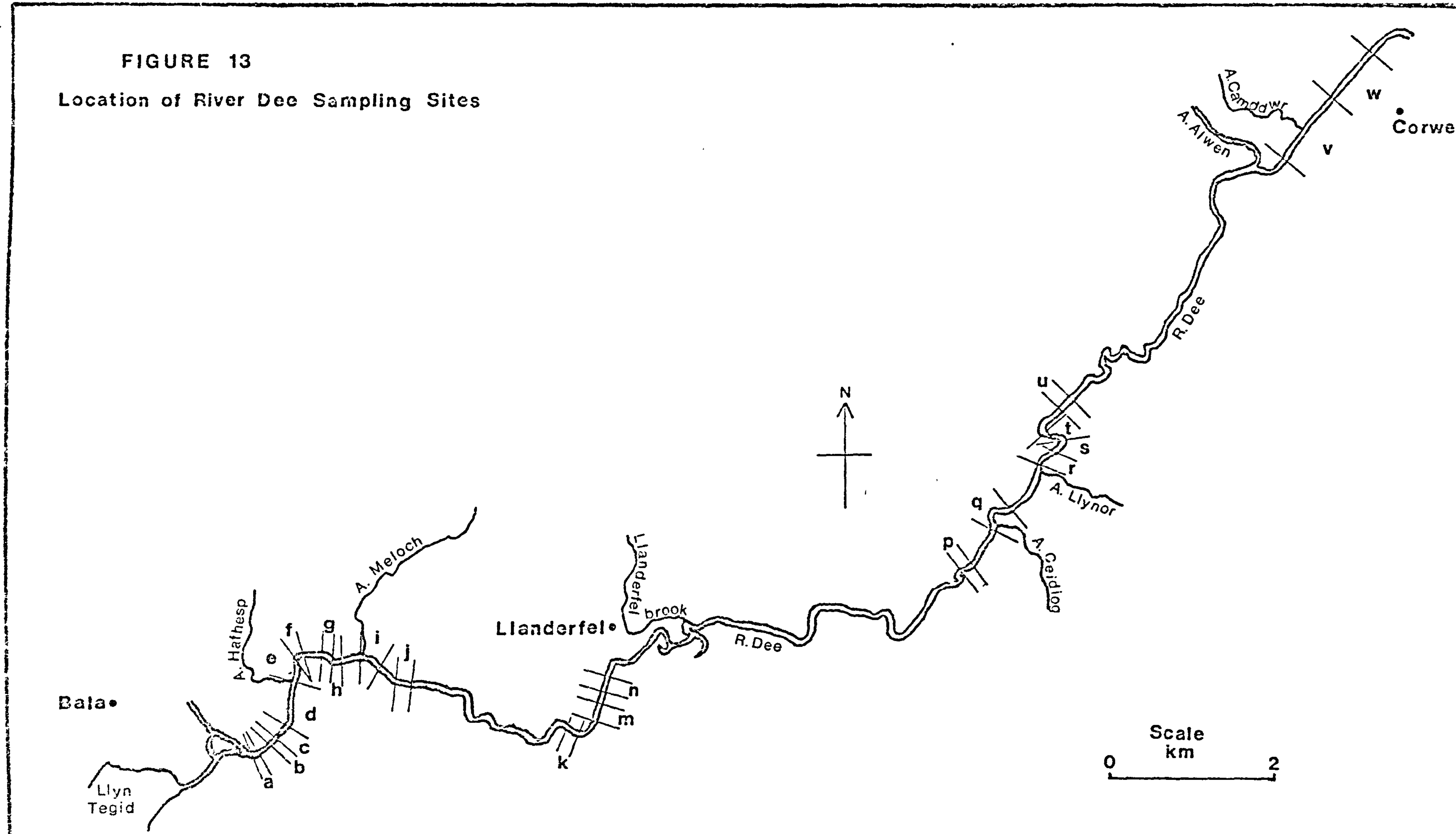
3. River Dee

a. Location of sampling sites

Sampling of the River Dee was chiefly carried out for grayling and sites were chosen where the most grayling could be caught. Attempts were made to include as wide a range of habitats as possible, particularly in the first 3 km. below Llyn Tegid. Twenty one main sampling stations were chosen along the river between the Bala sluices and Corwen. The location of these sites (a to w) is shown in figure 13. Sites a and b can also be seen in plate 1 (chapter 1), and the frontispiece shows the River Dee at Llanderfel (site m). A number of small tributary streams were occasionally sampled and these are labelled in figure 13.

FIGURE 13

Location of River Dee Sampling Sites



b. Physical features

The physical features of the River Dee sampling sites are shown in table 14 (after Cuinat, 1970). The slope of 0.12% falls into the lower part of Huet's (1949) grayling zone. The profile of the River Dee is shown in figure 14. The source of the River Dee was considered by Ramsay (1876) to be Llyn Tegid. To avoid confusion the river below Llyn Tegid will be referred to as the River Dee, and above Llyn Tegid, the so-called Little Dee, will be referred to as the Afon Dyfrdwy.

Water temperatures were taken on each visit to the sampling sites (about twice weekly), and monthly by M.A. Rahim and the Dee and Clwyd River Authority. The combined results of these recordings are given in Table 15.

Table 15. Monthly temperature of the River Dee.

Month	Range of temperature °C	Mean temperature °C
Oct. 1969	9.1 - 14.0	13.0
Nov	4.8 - 10.0	8.0
Dec	3.0 - 7.0	6.1
Jan 1970	2.0 - 7.0	4.5
Feb	3.0 - 5.0	3.6
Mar	1.7 - 5.0	4.4
Apr	4.0 - 8.0	6.0
May	5.8 - 14.5	12.4
Jun	13.0 - 18.0	14.5
Jul	11.7 - 20.0	15.5
Aug	14.5 - 19.1	16.6
Sep	12.8 - 16.9	14.5
Oct	8.8 - 13.0	11.5

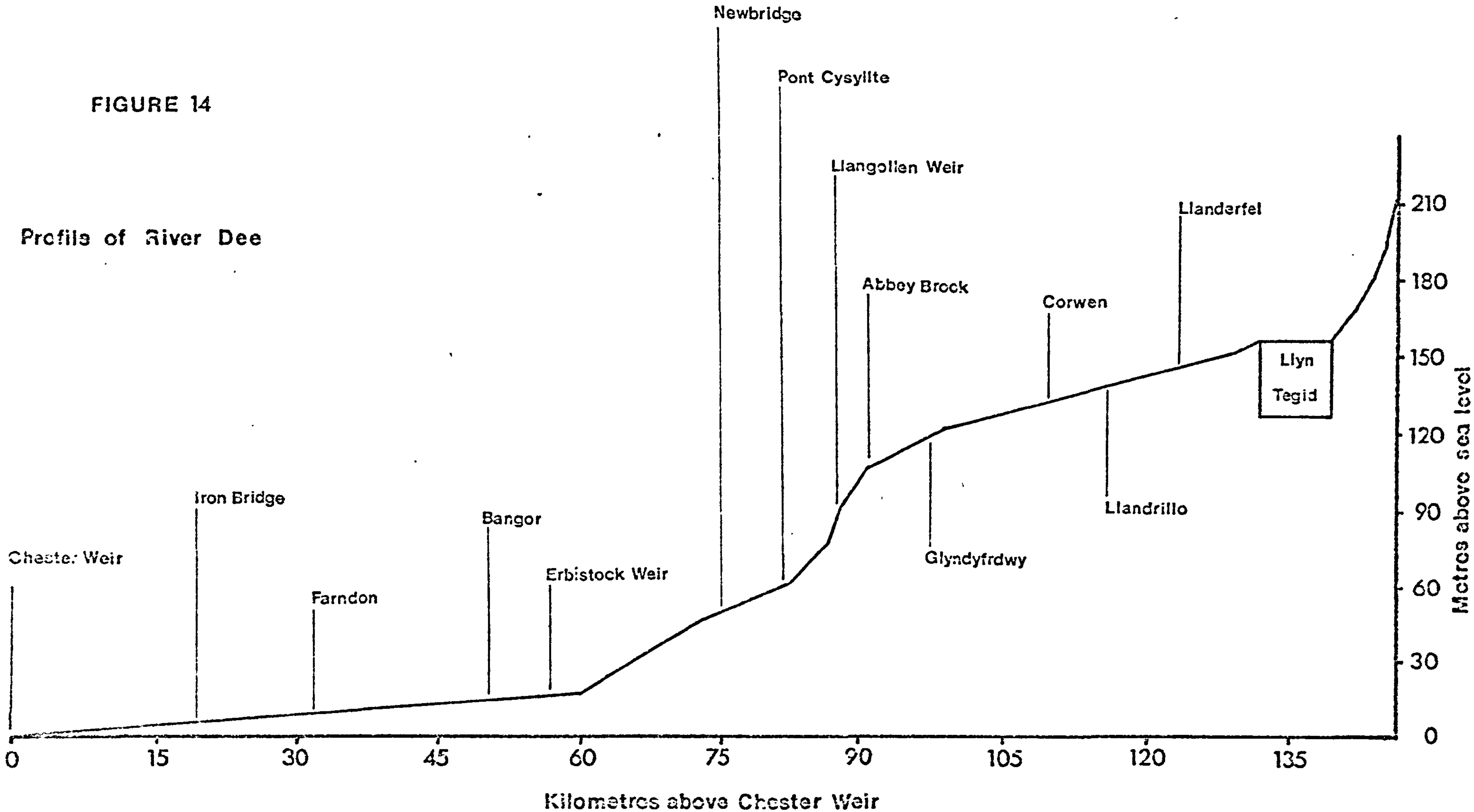
Table 14. Physical characteristics of sampling sites on the River Dee.

	River Dee																				
site number	a	b	c	d	e	f	g	h	i	j	k	m	n	p	q	r	s	t	u	v	w
Length (m)	80	80	129	402	181	80	101	201	266	201	121	161	120	101	101	160	110	120	120	885	482
Mean width (m)	36.6	29.3	29.3	32.0	35.1	35.1	29.3	33.5	33.5	29.0	30.5	41.2	35.1	32.0	36.6	24.4	24.4	45.8	42.7	41.2	42.7
Length x width (m^2)	2928	2344	3780	12845	6353	2808	2959	6734	8911	5829	3691	6633	4212	3232	3697	3904	2684	5496	5124	36462	20581
Slope (%)										0.12											
Mean depth (cm) in																					
riffles	30	25	–	30	33	38	–	46	27	30	38	30	30	51	38	43	38	41	51	51	51
flats	81	76	76	76	76	81	71	91	85	64	90	71	90	71	64	66	74	70	90	97	97
pools	114	102	–	114	102	122	110	118	120	–	137	140	122	180	132	136	127	175	150	165	183
Number of riffles	1	1	–	2	1	1	–	1	3	2	2	1	1	1	2	2	2	1	1	2	1
flats	2	1	1	3	1	1	1	2	3	1	2	1	1	1	1	2	2	1	1	1	1
pools	1	1	–	1	1	1	1	1	3	–	2	1	1	1	1	2	2	1	1	1	1
Bottom deposits																					
dominant	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Spb	Lpb	Lpb
subdominant	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Lpb	Spb	Spb
Fish shelter																					
blocks and rocks	(+)	(+)	(+)	(+)	(+)	–	(+)	(+)	(+)	(+)	(+)	(+)	–	–	(+)	(+)	–	–	(+)	–	–
vegetation	+	+	(+)	+	(+)	(+)	+	(+)	(+)	(+)	–	+	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)	(+)
roots & undermined banks	(+)	(+)	–	(+)	–	(+)	–	–	(+)	(+)	(+)	–	(+)	(+)	–	(+)	(+)	(+)	(+)	(+)	(+)
Spawning gravel	(+)	++	+	+	++	(+)	(+)	(+)	+	++	+	++	+	+	++	+	+	++	(+)	++	++
Shade	(+)	–	–	–	–	(+)	(+)	–	(+)	–	+	+	(+)	(+)	–	(+)	(+)	–	(+)	(+)	(+)

(key as for table 5).

FIGURE 14

Profile of River Dee



Water flow measurements for the River Dee, taken by the Dee and Clwyd River Authority at the gauging station below the Bala sluices (see plates 1 and 3, chapter 1), are given in table 16.

Table 16. Monthly measured flow (cumecs) in the River Dee at Bala.

Month	Total monthly flow	Mean daily flow	Max. daily flow	Min. daily flow	Highest flow	Lowest flow
Oct 1969	185.79	5.99	9.10	4.25	9.26	4.03
Nov	561.09	18.70	45.32	5.00	46.00	4.90
Dec	506.57	16.34	39.70	7.03	41.50	5.90
Jan 1970	425.44	13.72	28.10	6.05	29.60	5.56
Feb	653.57	23.34	62.36	8.29	65.52	7.70
Mar	379.48	12.34	20.43	6.30	24.04	5.98
Apr	787.59	26.26	62.83	8.30	67.42	8.10
May	141.58	4.57	18.91	2.54	20.33	2.48
Jun	171.50	5.73	14.88	3.89	18.14	1.84
Jul	234.89	7.58	23.54	4.74	25.65	4.60
Aug	213.10	6.87	24.61	2.26	30.20	0.54
Sep	355.07	11.84	54.25	4.51	55.37	4.52
Oct	397.05	12.81	48.11	5.02	51.06	4.94

Note the high winter flows (November to April) which led to sampling difficulties (chapter 4, section A1c). The drainage area of the River Dee above the gauging station is given by the Dee and Clwyd River Authority as 262 sq.km. and the altitude at the gauging station weir crest is 159.194 metres above O.D.

c. Chemical characteristics

The results of chemical analyses carried out by the Dee and Clwyd River Authority at the Bala sluices, Llanderfel and Corwen, between October 1969 and October 1970 are given in Table 17. A fuller

Table 17. Water Chemistry of the River Dee

	Bala sluices	Llanderfel	Corwen	Glyndrfrdwy
Colour, hazen units	15-30			10-18
Turbidity (as Fuller's Earth)	2.5-11.7			4.5-39.0
pH range (mean)	6.4(7.0)8.2	6.4(6.9)7.7	6.4(6.9)7.7	6.5(6.9)7.5
Dissolved oxygen (%saturation)	94-110	90-120	92-120	93-118
B.O.D. (five days at 20°C)	0.1-1.7	0.4-2.0	0.3-2.1	0.3-1.7
Permanganate value (4 hrs at 27°C)	2.3-9.7	2.2-8.2	2.1-9.5	2.2-9.8
C.O.D. (Dichromate value)				6.2-11.6
Nitrogen, as N, ammoniacal	0.01-0.15			0.011-0.34
Nitrogen, as nitrite	0.001-0.019			0.001-0.010
Nitrogen, as total oxidised				0.18-1.40
Chlorides, as Cl	8	8	8	9-17
Solids, dissolved				32-76
suspended				1-44
Hardness, total as $CaCO_3$	25			15-35
Hardness, calcium, as $CaCO_3$	10			10-20
Hardness, Magnesium, as $CaCO_3$	15			5-20
Alkalinity, as $CaCO_3$				4.8-14.0
Sulphates, as SO_4				1.2-21.0
Phenols, as C_6H_5OH				<0.002-0.003
Detergents, Anionic, As Manaxol O.T.				<0.05-0.07
Silicates, reactive, as SiO_2				1.0-3.5
Phosphates, total, as PO_4				0.04-0.66
Phosphates, Ortho, as PO_4				Nil-0.14
Iron, total, as Fe				0.15-2.30
Iron, soluble, as Fe				0.08-0.42
Manganese, total, as Mn				Nil - 0.25
Manganese, soluble, as Mn				Nil - 0.05

(Results, except where otherwise stated, in Mg/l).

analysis carried out at Glyndyfrdwy (9km. below Corwen) is also included in this table.

d. Biological characteristics

The abundance of vegetation at the River Dee sampling sites is given in table 18. The most common mosses are Fontinalis antipyretica and Eurhynchium riparoides. The most abundant submerged macrophytes are Ceratophyllum demersum and Callitriche aquatica. Ranunculus aquatilis is locally common and Myriophyllum spicatum occurs occasionally. Submerged macrophytes are most abundant in shallow and riffle areas of the river as opposed to flats and pools. The opposite is the case in the small Llyn Tegid feeder streams where shallow areas are composed of unstable gravel which plants are unable to colonise. Emergent macrophytes are generally sparse and mostly comprise Juncus sp. and Phalaris arundinacea. Beds of Sparganium ramosum occur at site v and beds of Phragmites communis at site h. Trees along the banksides are much the same as those at the Llyn Tegid feeder stream sites (section C.3c) with the addition of numerous oaks (Quercus sp.) at sites k,m and n. Alders (Alnus glutinosa) are particularly abundant at Corwen.

The invertebrate fauna of the upper reaches of the River Dee is being studied by M.A. Rahim.

The most abundant fish species present in the upper Dee are salmon (Salmo salar L.), grayling (Thymallus thymallus), brown trout (Salmo trutta L.), eels (Anguilla anguilla L.), minnows (Phoxinus phoxinus L.) and bullheads (Cottus gobio L.). Pike (Esox lucius L.) occur in

Table 18. Abundance of vegetation at the River Dee sampling sites.

	River Dee																				
site number	a	b	c	d	e	f	g	h	i	j	k	m	n	p	q	r	s	t	u	v	w
Aquatic vegetation																					
mosses	+	+	(+)	+	+	(+)	+	(+)	+	+	(+)	+	(+)	+	(+)	(+)	+	(+)	(+)	(+)	(+)
submerged macrophytes	+	+	(+)	+	+	(+)	+	(+)	(+)	(+)	(+)	+	(+)	+	(+)	+	+	(+)	(+)	(+)	(+)
emergent macrophytes	(+)	(+)	(+)	(+)	(+)	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
Bankside vegetation																					
trees	(+)	-	-	-	-	+	(+)	-	+	(+)	++	++	+	(+)	(+)	(+)	+	-	+	+	+
bushes and shrubs	(+)	-	-	-	-	(+)	(+)	-	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)
(1 or 2 banks) meadows	1	2	2	2	2	1	2	2	1	2	1	1	1	2	2	2	1	2	1	1	1

(key as for table 9)

considerable numbers and stone loach (Nemacheilus barbulata L.) are present. Some perch (perca fluviatilis L.), roach (Rutilus rutilus L.) and gudgeon (Gobio gobio L.) are found in the river, particularly in the area just below the Bala sluices. Young salmon are most common in rapid riffle areas, grayling in midstream at the tail end of pools where the water shallows and in flats less than 90 cm. deep, and trout in turbulent water around rocks, in pools, and in the vicinity of overhanging banks and tree roots.

e. Research on the River Dee

No previous research has been carried out on the River Dee above Corwen. Carpenter (1940) investigated the feeding habits of salmon parr in the Dee at Corwen and Newbridge, and in several tributary streams (A. Hirnant, A. Ceidiog, A. Alwen, A. Ceiriog). She included some benthic fauna surveys in her studies. Jones (1939, 1949, 1950a, 1950b, 1951, 1953) and Jones & King (1946, 1949, 1950a, 1950b, 1952) investigated the runs of adult salmon in the Dee, the spawning behaviour of salmon in a tributary of the Dee (A. Alwen), and the scale structure of juvenile salmon from the Dee area. Further studies on the Dee salmon runs are being made by P.R. Lees. Badcock (1949) investigated the benthic fauna of the Ceirw and Merddwr, tributaries of the Afon Alwen, and Hynes (1961b) studied the invertebrate fauna of the Afon Hirnant. Edmonds (1939) made a study of the plankton of the River Dee together with observations on the benthos in polluted stretches of the middle Dee. Barnabus (1971) investigated the feeding habits of coarse fish in the lower Dee.

Research at present in progress on the Dee includes work on the invertebrate fauna of the upper reaches, and studies on the dace (Leuciscus leuciscus L.) and other coarse fish in the middle reaches of the river. The work on dace is to be extended and investigations are planned to study the salmonid populations and invertebrate fauna of the middle Dee.

CHAPTER IV.

METHODS AND TERMINOLOGY

A. Field Studies

1. Sampling methods.

a. Llyn Tegid feeder streams

The Llyn Tegid feeder stream sites described in chapter 3, with the exception of the Afon Dyfrdwy stations 6,7 and 8, were all sampled for trout and juvenile salmon, by means of a Honda A.C/D.C. generator (model E300, A.C. output 240 volts, 1.5 amps.) using partially rectified alternating current. This partially rectified current produced galvanotaxis in fish in the same way as a full direct current, and was found suitable for nearly all of the conditions encountered on the relatively small feeder streams. Two electrodes were used, a stationary negative earth plate, and a moveable positive plate mounted on a pole, supplied with 100 metres of electric cable. Fish within a 1-2 metre range of the positive electrode swam towards the electrode and were scooped out of the water by means of hand nets. The fish were then transferred to large plastic bins containing water in which they quickly recovered from the effects of the electric current.

Sites on the Afon Glyn were sampled monthly from January 1969 to March 1970, the lower part of the Afon Llafar (site 1) bimonthly from February 1969 to February 1970 and the upper part (sites 2-4) bimonthly from March 1969 to March 1970. The Afon Lliw was sampled in November and December 1968 then bimonthly from January 1969 to

March 1970, and the upper Afon Dyfrdwy (sites 1-4) also bimonthly from November 1968 to March 1970. Samples were taken from Afon Dyfrdwy site 5 in February, May, July and September 1969, and from sites 6, 7 and 8 in July, September and October 1969. Sampling of the Afon Dyfrdwy sites 6, 7 and 8 was carried out principally for grayling, using the small seine net described in the following section on Llyn Tegid. Samples were obtained from the Afon Twrch in February 1969, then bi-monthly from March 1969 to March 1970 with the addition of a sample taken in August 1969. The main sampling period was considered to be March 1969 to March 1970, during which time all of the above rivers were sampled.

Each section of river (described in chapter 3) was sampled as an individual unit and fish from one section were dealt with separately from those caught in other sections. On a number of occasions successive sampling runs were carried out in the same river section, for use in population estimates, and fish caught during each run were kept in separate containers. Efforts were made to prevent the movement of fish between different sites during sampling. Gabion weirs in a number of the Afon Clyn sections provided suitable barriers to such movement, but in the absence of such obstacles stop nets (mesh size 10 mm.) were erected at the site boundaries. Sampling was carried out by starting at the downstream end of the lowest river section and working upstream, so that the fish caught would not have eaten organisms disturbed from the river bed by the sampling team. This procedure also helped to prevent the escape of fish which swam downstream over gabion weirs in the Afon Olyn sites, but not upstream over such obstacles.

Few difficulties were encountered in the sampling of the Llyn Tegid feeder streams except during flood and high water conditions. Water levels in these streams quickly fell after floods, however, and samples were obtainable at some time during every month of the sampling period. Under conditions of very low water the Afon Glyn section 1 was unfishable, the stream at this point being reduced to subsurface trickles between the rocks and blocks of the gabion weirs. All sampling sites were within short walking distances of roads, and in dry weather some sites could be approached by motor vehicle across the surrounding meadows. Sampling was usually carried out singly or with the help of one other person.

b. Llyn Tegid

Sampling for grayling was carried out in Llyn Tegid by means of shore seine-netting. The method of netting used on Llyn Tegid has been developed over the years by University of Liverpool workers. One end of the seine net was held by a team of men on the shore, and the other end was towed round in a large semi-circle by an engine powered boat. The net was also towed for some distance parallel to the shoreline before the offshore end was finally brought into the shore. This procedure considerably speeded up netting operations and permitted a greater area of lake to be sampled in a given period of time. Two sizes of seine net were used according to the pulling capacity of the towing boat. The larger net used was 55 metres long, 3.7 metres deep, with a mesh of 37mm. in the arms and 10mm. at the bag. The smaller net was 46 metres long, 2.8 metres deep, with a mesh of 25mm. in the arms and 13 mm. at the bag. Netting operations could be carried out in all conditions except during periods of strong onshore winds or when an ice covering was present. The latter condition occurred only twice during the sampling period.

Seine netting was carried out on Llyn Tegid, at the sites listed in chapter 3, weekly or twice weekly from October 1968 to October 1969, and monthly from November 1969 to October 1970. Fish caught at different times during any particular month were considered together as a monthly sample. The number of seine net hauls and the number of grayling caught per haul were recorded, together with prevailing weather conditions, lake levels and lake temperatures. A regular team of workers was available for assistance with the netting operations on one day per week, and additional work was carried out using a small team of one to three people.

Sampling for salmon smolts descending through Llyn Tegid was carried out by shore seine netting (as described above) during April and May of 1969 and 1970. At the time of the main smolt runs (late April and early May) samples were taken daily, and factors which may have affected the size of the runs (e.g. rainfall, water temperature, river flows) were recorded. At this time a seine net was also left overnight around the mouth of the Afon Glyn to determine the numbers of smolts descending from the river during each night. Smolts were sometimes caught in large numbers and handling mortalities were initially high. This problem was largely overcome by retaining the smolts in large perforated plastic ("Netlon") keeps, placed in the lake, until the samples could be processed. Pike caught whilst fishing for smolts were retained for stomach analysis.

Extensive gill netting was carried out from July to September during 1969 and 1970, in an effort to trace the summer disappearance of grayling from the Llyn Tegid shore zone. Bottom set nylon twine gill nets, each 27 metres long and 1.9 metres deep, of mesh sizes 19.5mm., 26mm. and 32 mm. were used for a total of 1554 net hours at depths ranging from 1 - 30 metres. Only two grayling were captured by this method, one at a depth of 1 metre near the Afon Glyn inlet, and one at a depth of 7 metres at site B. Seine netting of the Afon Dyfrdwy sites 6, 7 and 8 was also carried out in connection with the summer disappearance of grayling, and efforts were made to trace the spawning migrations of Llyn Tegid grayling by careful observation in the feeder streams.

c. <u>River Dee</u>

The River Dee is a relatively large river (see frontispiece) with a high mean winter flow (table 16, chapter 3), presenting considerable sampling difficulties. Few bridges are present in the upper reaches and access to suitable sampling sites is limited, often involving a trek of up to ½ mile across meadows which become waterlogged for much of the winter. Sampling was carried out principally for grayling and several methods were tried before any success was achieved. Electrofishing with the equipment used in the Llyn Tegid feeder streams were found to be unsuitable for sampling the River Dee. A few salmon parr, trout, pike and eels were caught by this method in shallow regions near the river banks, but no grayling were ever stunned and indeed none were ever seen! Juvenile salmon and trout tend to seek refuge under stones, in weed beds and amongst tree roots when disturbed rendering them susceptible to capture by electrofishing. Grayling, however, remain in midstream and dart off when disturbed, always keeping out of range of the electrical field. The development of electrofishing machines for use in large rivers is in its very early stages at the University of Liverpool, and moreover requires accessibility to the river and a large team of workers. Such a team, which could turn out regularly on the many dates that were required for adequate sampling of the Dee, was not available.

Attempts were made to seine net the river, but accessible sites were generally unsuitable and in the absence of an adequate labour force, further efforts in this direction were postponed. It was somewhat in desperation that I decided to try angling for grayling; this proved extremely successful. All parts of the river could be sampled and the necessary equipment for sampling and for the subsequent processing of samples, could easily be carried by one person. After a short time catches of 50 grayling per day became fairly commonplace, and a great deal of information on the habits of these fish was obtained from the close observation that is so integral a part of angling. The angling methods used for the capture of grayling were wet and dry fly fishing from April to November, and longtrotting with worms and maggots from December to March. A considerable number of trout and juvenile salmon were also caught by these methods. Fish caught by angling were generally kept for a short time in keep nets placed in the river until a small number had accumulated which were then processed accordingly. The selectivity of angling in this study is discussed in later chapters on growth rates and feeding habits.

The River Dee was sampled, from October 1969 to October 1970, on up to 3 days per week, and all sites (a-w) were sampled in any one month. All data for a particular month were combined. In addition, a number of local anglers were kind enough to assist in my research programme by sending relevant details of their catches to me. During the summer of 1970 it was possible to drive a motor vehicle across the previously water logged meadows to the river bank, thus enabling heavy equipment to be taken to sites which were formerly inaccessible. Renewed attempts at seine netting were therefore made, and two suitable sites (a and c) in the stretch of river downstream from the Bala sluices were found. Seine net hauls, using the small net described in section A1(b), were made at these sites in June, July, August and September 1970. A boat was not required for this work as the river was wadeable in chest waders at the selected sites. One end of the net was hauled quickly across the river and then downstream and back across the river to a place where the net could be conveniently drawn in (preferably a gentle sloping gravel bank in slack water). This method was most successful in conditions of low water and low river flows.

Investigations into pike predation on salmonids in the River

Dee were undertaken and samples of pike were caught by gill netting (mesh size 90mm.) and electrofishing in, and around the mouth of, the Afon Tryweryn flood relief channel (see plate 1) during the spring of 1969 and 1970. Electrofishing was carried out using the equipment described in section Al(a) mounted in a small boat. A few pike were caught in other parts of the upper Dee using this equipment from the bankside. Some pike were also provided by the Dee and Clwyd River Authority from their annual gill netting operations carried out in the proximity of pike spawning grounds in the upper and middle Dee during early spring.

Some electrofishing, using the equipment described in section Al(a) was carried out in the small tributary streams listed in chapter 3, section a, following the discovery of numbers of mostly small grayling in some of these streams by other workers from the University of Liverpool. This work was carried out in March 1969 and from February 1970 to April 1970. After early April grayling disappeared from the streams and electrofishing was discontinued.

2. Treatment of samples

a. General procedure

Captured fish were transferred, in small batches, from the large bins or keeps to small buckets containing a 1:20,000 solution of tricaine methanesulphonate (MS222), in which they became anaesthetized. The length of the fish to the nearest 1mm below was then measured, using a standard ½ metre measuring board, from the tip of the snout to the fork of the tail (fork length). In the early stages of field work measurements of fish braght back to the laboratory were made after freezing, but freezing was found to cause a decrease in length and all subsequent measurements were made in standard conditions after anaesthetising in MS222. Corrections were applied to the early post-freezing measurements.

Fish to be taken back to the laboratory for post-mortem examinations were at this stage placed in suitably labelled polythene bags. On arrival at the laboratory these bags were placed in a deep freeze (-20°C) until such time as they could be dealt with. Fish which were to be returned alive to the river or lake were next weighed on a Salter balance to the nearest gram. It was found to be impractical to weigh small fish in the field because of the large errors which occurred, and consequently only fish of fork length greater than 15cm. were weighed. No significant difference ($p > 0.10$) was found between fresh and frozen fish weights, so fish taken back to the laboratory were weighed after freezing.

The data on length and weight were recorded on small envelopes (one per fish), together with details of sampling station, date and any other relevant information (e.g. tag number, recapture details). Samples of scales from each fish were then placed in the envelopes. Replacement scales occur frequently in trout (Tesch, 1956; Ball & Jones, 1960) and at least 20 scales were therefore taken from each fish. Replacement scales were found less frequently in juvenile salmon and grayling, and samples of 10 and 5 scales respectively, from each fish, were found to be adequate. Scales were removed, by scraping with a scalpel blade, from a position approximately halfway between the posterior base of the dorsal fin and the lateral line, always on the left hand side of the fish in the case of grayling, but also on the right hand side in the case of recaptured trout and juvenile salmon.

b. Marking and tagging methods

Fish which were returned alive to the river or lake were marked or tagged in one or more of the following ways :

(i) Fin clipping.

Total removal of the adipose fin and partial removals of pectoral and pelvic fins were carried out. Little or no regeneration of the adipose fin occurred (Mills, 1971), and regeneration of the clipped paired fins was deformed in such a way as to be easily recognisable (Stuart, 1958).

(ii) Dye inoculation.

Indian ink was injected subdermally by means of a panjet inoculator (Hart & Pitcher, 1969). Marks were made in various positions on the fish according to sampling site, date and recaptures.

(iii) Individual tagging.

Individual tagging was carried out using 5mm. square, numbered ivorine discs mounted on stainless steel (diameter 0.3mm.) or silver wire (diameter 0.5mm.), to Ministry of Agriculture, Fisheries and Food specifications (Rounsefell & Everhart, 1953). Tags were attached with the aid of a hypodermic needle in the musculature immediately anterior to the dorsal fin. Wounds caused by tagging were slight in the case of trout and juvenile salmon, and quickly healed. Some grayling, however, showed more permanent damage with wounds increasing in size and becoming infected with fungus. Such cases occurred more frequently in Llyn Tegid than in the River Dee and when found, were treated with a 1% solution of mercurochrome. Better results were achieved with the use of silver wire which, being thicker, showed less tendency to cut through the flesh. Floy tags mounted on polythene thread might have given even better results, but unfortunately these tags were not available until the end of the experimental period.

The tagging programmes carried out in the upper Dee area were publicized in the angling press and letters were written to local angling clubs and to individual anglers offering a reward of 25p for the return of the tags from recaptured fish, together with details of the capture. This procedure met with considerable success but reports of anglers throwing back tagged fish were all too common and undoubtedly more publicity should have been given to the programme.

Ideally marking and tagging methods should make a fish permanently and unmistakably recognisable, preferably individually, to anyone examining it, and should have no effect on growth, mortality or liability to capture by predator or by fishing gear (Stott, 1968). No such ideal methods exist and the effects of my tagging methods on growth, mortality and capture, together with the frequency of tag losses, is discussed in later chapters. Various colours of ministry tags were used, light coloured tags were easier to read on recapture but possibly attracted the undue attention of predators such as pike

(Carlin, 1955), and dark tags (brown) were very difficult to read on recapture. The use of brown tags was discontinued after initial trials. Individual ministry tags were only used on trout and salmon parr over 9cm. fork length and on grayling over 15cm. fork length. Smaller fish were marked by fin clipping or dye inoculation. Where fish were not individually marked then schemes of different batch marks for different sampling sections were developed so that movements could be followed. Some tagged fish were also marked by fin clipping or dye inoculation in order to facilitate the assessment of tag losses, and batch marked fish were given an additional mark when captured away from their "home" section. Salmon smolts captured in Llyn Tegid proved to be very delicate to handle and were only marked by dye inoculation. Recaptures of smolts in Llyn Tegid, originally tagged in the feeder streams, were recorded.

After marking or tagging, fish were placed in containers of fresh water until they had recovered from the effects of the anaesthetic. The fish were then placed back into the centre of the section from which they were caught and details of subsequent recaptures were recorded. Several experiments were also carried out in which tagged fish were transferred to other sampling sections to investigate the possible occurrence of "homing" migrations.

B. Laboratory procedures

1. General treatment of fish samples

The fork lengths of fish broght back from the field were measured to the nearest 1mm. below after thawing, and a table of corrections for converting frozen lengths to fresh lengths was compiled. These corrections are shown in table 19.

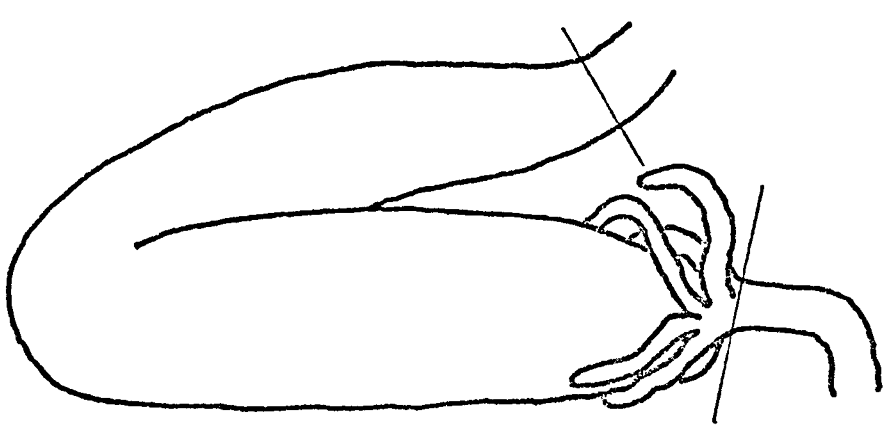
Table 19. Length corrections for frozen fish.

Frozen length (cm)	Added length correction (cm)
3-5	0.20
5-7	0.25
7-9	0.30
9-11	0.35
11-13	0.40
13-15	0.45
15-17	0.50
17-19	0.55
19-21	0.60
21-23	0.65
23-25	0.70
25-27	0.75
27-29	0.80
29-31	0.85
31-33	0.90

Fish weights were measured on an "Avery" balance to the nearest 0.1gm. below. Scale samples were taken in the manner described in section A2(a). The body cavity was opened by a longitudinal ventral slit from the anal opening to the pectoral girdle. The standard 'U'-shaped stomach region (Ball, 1961) shown in figure 15 was removed and stored in 10% formalin. The stage of development of the gonads (section B4) was recorded and the ovaries of mature grayling were removed and stored in modified Gilson's fluid (Simpson, 1951). Any

FIGURE 15

The alimentary tract of a salmonid fish showing the region removed for a stomach analysis.



obvious parasites were recorded.

2. Treatment of scales for age and growth studies

All age determinations were made from scales mounted on glass slides in euparal and examined under a binocular microscope at magnifications of x43 and x72. The validity of the age determination methods used, and the reviews of the relevant literature, are given for grayling and for trout and juvenile salmon in chapters 5 and 6 respectively.

Measurement of trout and salmon scales for the back calculation of length was carried out using the microscope described above, fitted with a graduated eyepiece micrometer. Measurements of grayling scales were obtained from an enlarged horizontal image formed by means of an "Enbeeco" portable microprojector. Scales were measured from the scale nucleus to the anterior edge along the antero-posterior axis in trout and salmon, and from the scale nucleus to the anterior ventral corner along a diagonal anterior axis (see plate 13, chapter 5) in grayling. The scale axis used in grayling was determined after a series of trials, and scales from only the left side of the fish were examined in order to ensure consistent use of the chosen axis. The antero-posterior axis is not suitable for measurement in grayling because of the lobed anterior scale border. Fork length/scale length relationships for trout, grayling and juvenile salmon were constructed from the scale measurements. Measurements were also made from the scale nucleus to the end of each "winter band" of rings (annual check) and the mean scale lengths of each year class at the end of each year of life were calculated. The corresponding mean fish lengths were determined from the fish length/scale length relationships.

The occurrence of false checks (summer checks) was recorded and any scale erosion, particularly in connection with spawning activities, was noted. Ring counts were made on all scales to determine the seasonal formation of scale growth rings. Scales used for photographic purposes (chapter 5) were cleaned in a saturated solution of trypsin.

3. Treatment of stomachs for diet analyses

The stomach contents were examined by :

(i) the number method, whereby the number of individuals in each food category were counted.

(ii) the volume method, whereby the total volume of each food category was measured.

(iii) the occurrence method, whereby the number of occurrences of each food category in all of the stomachs examined was assessed.

The degree of fullness of the stomachs and the mean volume of food per stomach each month provided ways of following seasonal changes in the amount of food eaten.

Feeding intensity was based on a series of categories of stomach fullness, ranging between an empty stomach and a distended stomach, given below.

0	empty	no food in stomach
1	¼full	pronounced ridges on the inside of the stomach wall. Food filling lumen without appreciable increase in stomach size above that of a similar empty stomach, or with only regional distortion of the stomach

		wall by the contained food, this distortion not occupying more than one quarter of the total length of the stomach.
2	½ full	ridges on the inside of the stomach wall less well defined but still obvious. Food in the lumen of the stomach distending the stomach appreciably as when compared with a similar empty stomach. If the food has a regional distribution in the stomach lumen the ridges in the stomach wall may have disappeared in that region of the stomach but then be very pronounced in the remainder of the stomach.
3	¾ full	ridges on the inside of the stomach wall more or less absent or only present in limited areas. Stomach wall appearing thick and relatively opaque. Food filling much of the stomach lumen but there may be regions of limited size containing little or no food.
4	full	No ridges on the inside of the stomach wall. Wall of the stomach thin and more or less translucent with food filling the lumen of the stomach, but without obvious distension of the stomach wall.
5	distended	No ridges on the inside of the stomach wall. Stomach wall taking the shape of the food contained in the stomach lumen.

In addition to the categories outlined above intermediate conditions were frequently found. These were described by selecting the nearest category and adding a plus or minus sign after the category number, depending on whether or not the intermediate condition was above or below the category.

As the stomach lumen fills with food the stomach wall expands to accommodate more food within the stomach lumen. This expansion is made possible by the muscle layers within the stomach wall which in the empty contracted stomach produce the ridged appearance of the inside of the stomach wall. As the lumen fills with food and the muscles expand, the ridges become less pronounced and finally disappear. Preserved stomachs maintain their appearance at the death of the fish.

Following the estimation of feeding intensity, the stomach contents were emptied into a petri-dish and the food animals were sorted, identified and counted. When large numbers of small animals (e.g. Chironomid larvae) were present in a stomach an estimate of the total number was made by extrapolating counts in sub-samples of smaller volume as described by Siddiqui (1969). The volume of individual food categories in each stomach was measured using the method described by Chubb (1961). The occurrence of food items was determined by the number of stomachs in which a particular food item occurred expressed as a percentage of the total number of stomachs examined (Hynes, 1950). The results of number, occurrence and volume analyses were expressed as percentages and considered in terms of annual and seasonal diet, variation in diet with age and the relationship between the food eaten and the invertebrate fauna present in the environment.

The relative merits of the various methods of analysing the food of fishes have been discussed by many authors, notably Hynes (1950), Occurrence methods tend to overestimate the importance of small organisms or those occurring in low numbers (Hynes, 1950). The number method takes no account of the size of organisms and therefore overestimates the importance of small organisms which may occur in large numbers (Hynes, 1950; Graham, 1960). The number method may, however, give a good indication of the amount of effort expended in selecting and capturing food organisms (Ball, 1943). The volume method is considered by a number of authors to show most accurately the importance of the various food items as far as the nutritive values are concerned (Ball, 1961; Graham & Jones, 1962; Hunt, 1970), but it does not allow for differential rates of digestion (Hess and Rainwater, 1939), and the volume of food found will depend on the stage of feeding at which the fish was caught (Jones, 1959). It is generally agreed that most methods of analysing the food of fishes have their advantages and their drawbacks, and that a combination of methods will probably give a better picture of the importance of different food organisms than any single method (Windell, 1968).

The identification of food organisms was taken to various taxonomic levels. Most of the food items were identified to species or genus, some to family (e.g. Ceratopogonidae) and a few only to order (e.g. Coleoptera). Chironomid larvae in the stomachs of fish from the River Dee were not identified further, but those in stomachs of fish from Llyn Tegid were identified to genera in order to determine the lake zone from which they were eaten. Terrestrial insects were sometimes identified to genus (e.g. <u>Bibio</u>, <u>Hilara</u>) or family (e.g. Aphidae), and others were classified as terrestrial Diptera, Hymenoptera or Hemiptera

Identification of food organisms was greatly aided by information on the invertebrate faunae of the River Dee and Llyn Tegid supplied by M. A. Rahim and Dr. P.C. Hunt, respectively.

4. Treatment of gonads

a. Sexual maturity

The stage of development of the gonads was determined in male salmon parr using the classification of Orton & Jones (1933), and in trout using the system described by Frost and Brown (1967). The stages of sexual maturity in grayling are shown in table 20 (after Jankovic, 1964).

b. Fecundity

Egg counts were made on the grayling ovaries (stages IV and V, table 20) which had been preserved in modified Gilson's fluid (section B1). Gilson's fluid hardens eggs and breaks down ovarian tissue (Simpson, 1951). Ovaries were left in the fluid for up to 6 months and were shaken vigorously to help liberate the eggs from ovarian tissue, which were then stored in 10% formalin.

Counting of eggs was carried out by means of the weight and volume subsampling methods of McGregor (1922) and Kandler & Pirwitz (1957), described by Bagenal & Braum (1968). Fecundity was considered in terms of the number of eggs/weight of fish relationship and the number of eggs/ length of fish relationship. The weights of ovaries from grayling caught throughout the year were also recorded.

Table 20. Sexual maturity stages of grayling.

Sexual maturity stage	Appearance of testes	Appearance of ovaries
I	Very narrow, ribbon like white testes; milky-white colouration on antero-dorsal margin.	Ovary thread like or narrow, lobate, pale yellow.
II	Testes still white and ribbon like; milky-white edge to the testes.	Ovary in strip, lobate, yellow, somewhat larger than stage I. Eggs minute, hardly visible to the naked eye.
III	Testes rapidly increasing in weight and occupying a considerable part of the unoccupied body cavity. A large part of the testes milky-white.	Ovary lobate with a yellow colouration. Small eggs clearly visible.
IV	Testes completely milky-white. The milt, in the form of dense drops, appears under pressure. The testes not yet fully developed.	Ovary fills large proportion of unoccupied body cavity. Eggs large, pigmented. Minute, barely visible white roe occur between large grains.
V	Testes fully developed, milky-white with a pink appearance becuase of increased hyperaemia. Milt, in the form of dense drops, is extruded under the slightest pressure.	Running ripe. Eggs flow on slight pressure.

Table 20 continued.

Sexual maturity stage	Appearance of testes.	Appearance of ovaries.
VI	Spawning; dimension of testes decreasing; weight reducing.	Spent, ovary gray, flaccid, with some unspawned eggs.
VII	Spent; testes of minimum dimensions and weight; gray and flaccid.	Regenerating; ovary gray, flaccid. New smal[l] white roe visible.
VIII	Regenerating	-

C. Terminology

The meaning of the following terms used in this thesis is the same as that given by Ball & Jones (1960) and Hellawell (1969).

Year of life.
Year class.
Age group.
Rings and ring counts (winter, wide summer and narrow summer rings)
Scale checks (annual, and false or summer checks).
Erosion (spawning marks).
Redd.

The hatching time for salmon and trout was taken as March 1st (Ball & Jones, (1960), and as June 1st for grayling (see chapter 9). The 1969 year class of grayling was thus composed of all fish which hatched at the end of May 1969 from eggs laid at the beginning of May 1969. A 3+ fish had completed three years and was in its fourth year of life. Ring counts were only carried out at the margin of the scale, beyond the last annual check.

CHAPTER V

THE AGE AND GROWTH OF GRAYLING IN LLYN TEGID AND THE RIVER DEE.

1. Introduction

Very little research has been carried out on grayling in the Welsh Dee area. Jones (1953) examined the scales of 93 grayling from Llyn Tegid and described the seasonal scale growth ring cycle. The scales examined by Jones (op.cit.) together with 478 sets he collected in subsequent years, were re-examined in my study. Siddiqui (1969) investigated the feeding habits of 486 grayling from Llyn Tegid and gave the sets of scales from these fish to me. In addition to this material I examined a total of 1014 grayling scale sets from Llyn Tegid and 1935 sets from the River Dee collected from October 1968 to October 1970.

Other studies on the age and growth of British grayling have been made by Hutton (1923), Gerrish (1933, 1939), Hellawell (1969a, 1969b), Mackay (1970) and Mills (1970). European work on this topic was carried out by Gustafson (1949), Muller (1961), Balon (1962), Solewski (1963), Jankovic (1964), Peterson (1968) and Micha (1971). Studies have been made on the age and growth of Arctic grayling (Thymallus arcticus Pallas) by Brown (1943), Miller (1946) and Kruse (1959).

2. Age determination

a. Description of the scales

A detailed description of the scales of grayling was given by

Plate 13

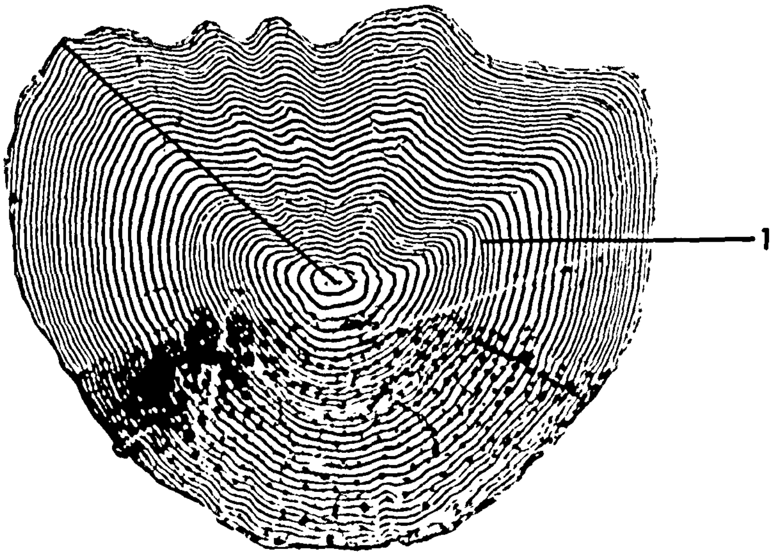
Scale from a grayling aged 1+ years, showing two winter bands of rings, caught on 28th January 1969 in Llyn Tegid. The axis used for back calculation measurements is shown.

Plate 14

Scale from the same grayling as above recaptured on 13th May 1969. Two annual checks can be seen, together with 2 wide summer rings at the scale margin.

Plate 15

Scale from a grayling aged 1+ years, showing two winter bands of rings, caught on 13th April 1970 in the River Dee at Llandrillo.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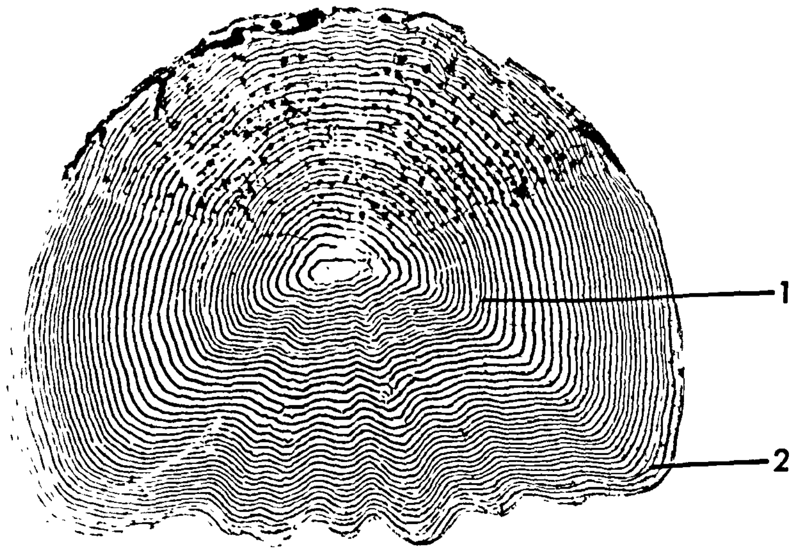
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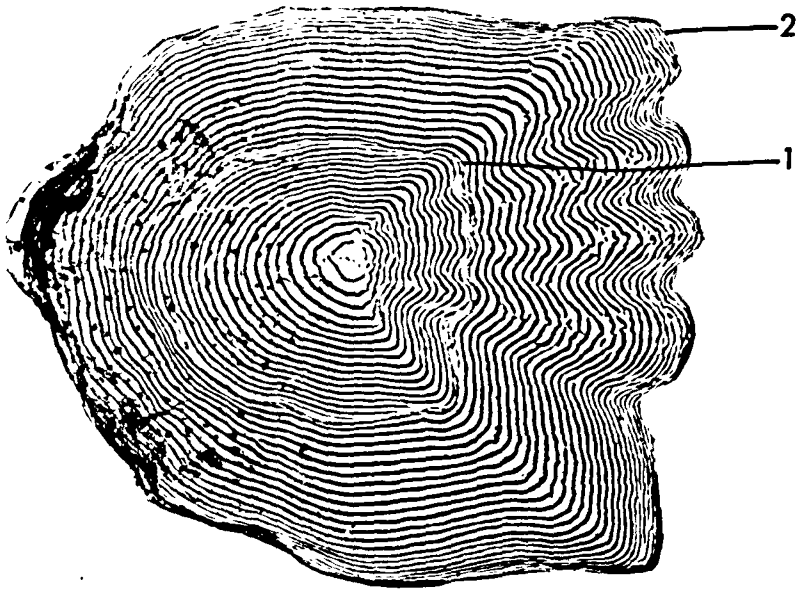
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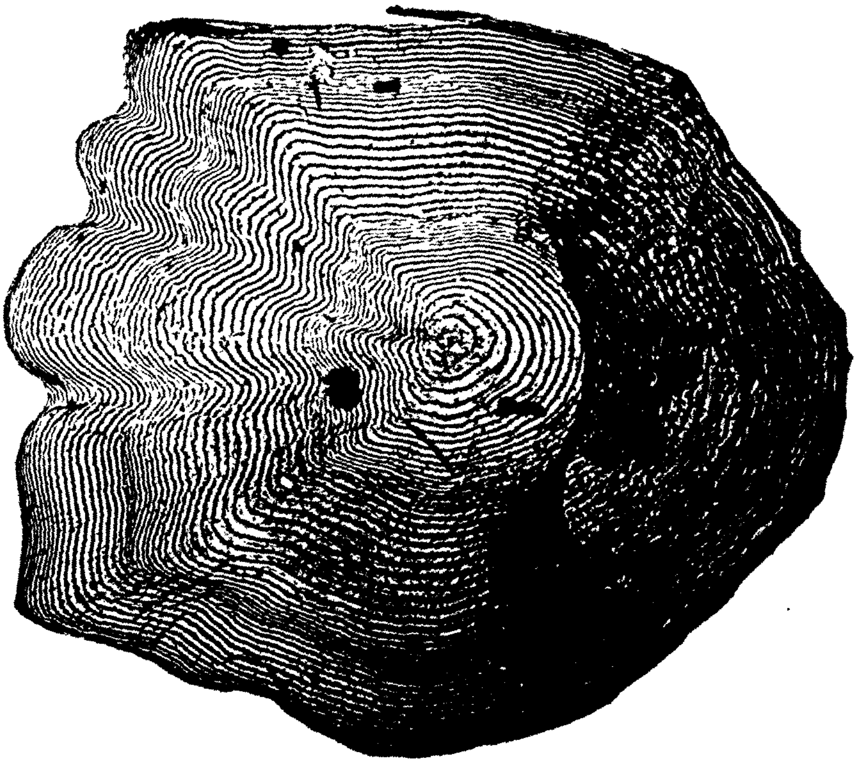
Plate 16

Scale from a grayling aged 2+ years, showing three winter bands of rings, caught on 26th, February 1970 in the River Dee at Llanderfel.

Plate 17

Scale from the same grayling as above, aged 3+, with four winter bands of rings, recaptured on 6th April, 1971.



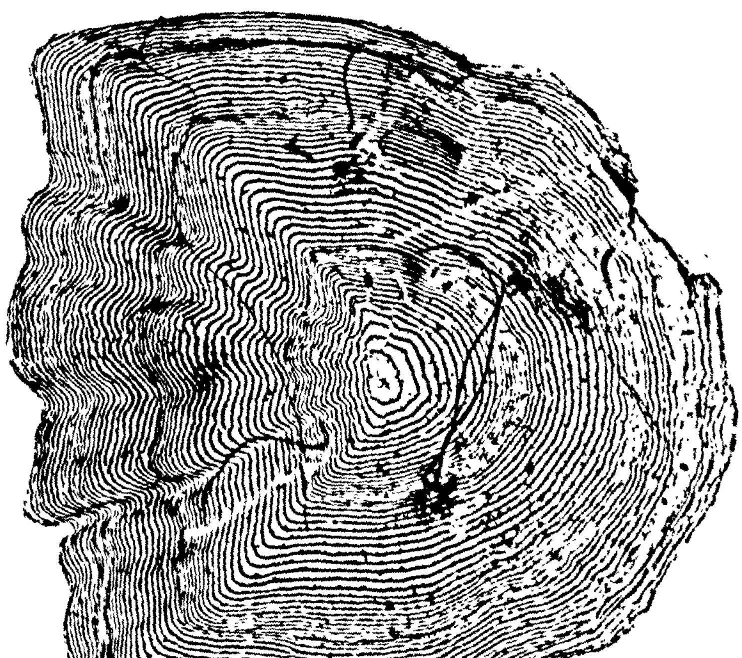
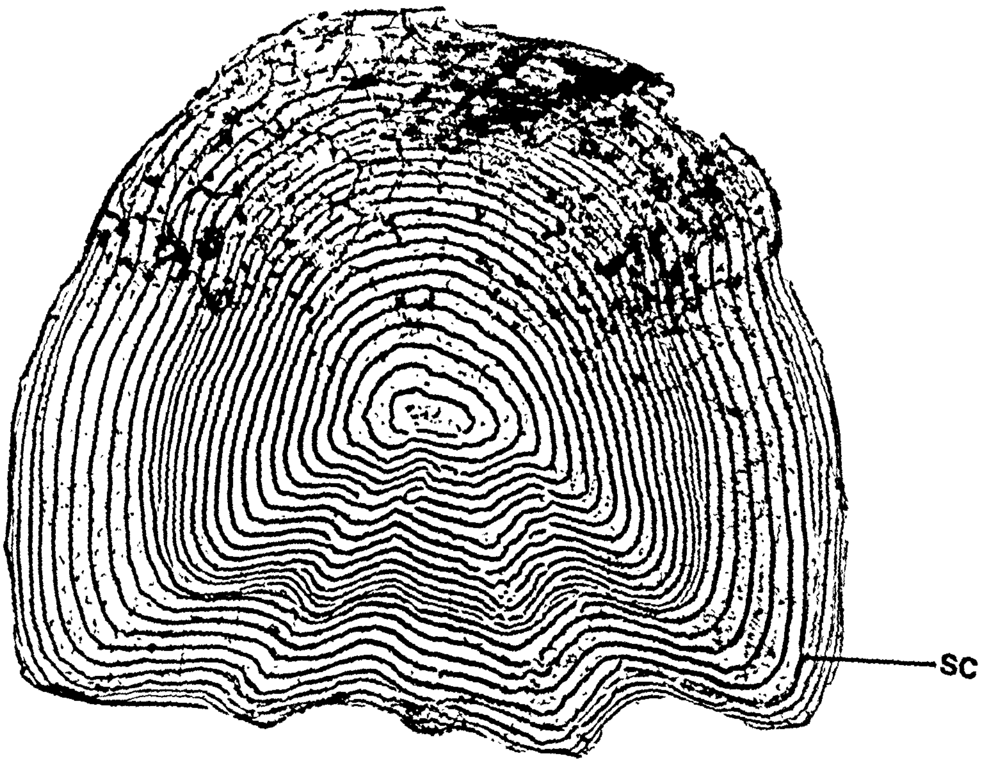


Plate 18

Scale from a grayling aged 1+ years, caught in Llyn Tegid on 22nd July 1969, showing a "summer check".

Plate 19

Scale from a grayling aged 1+ years, caught in the River Dee, (site h) on 8th July 1970, showing a "summer check".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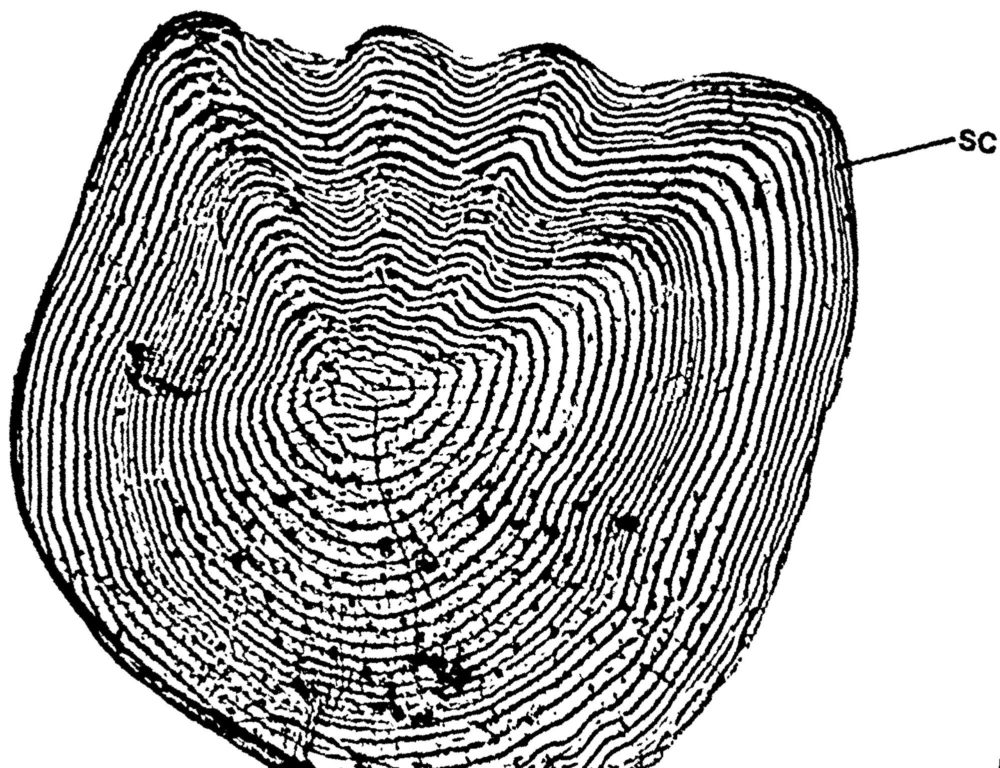
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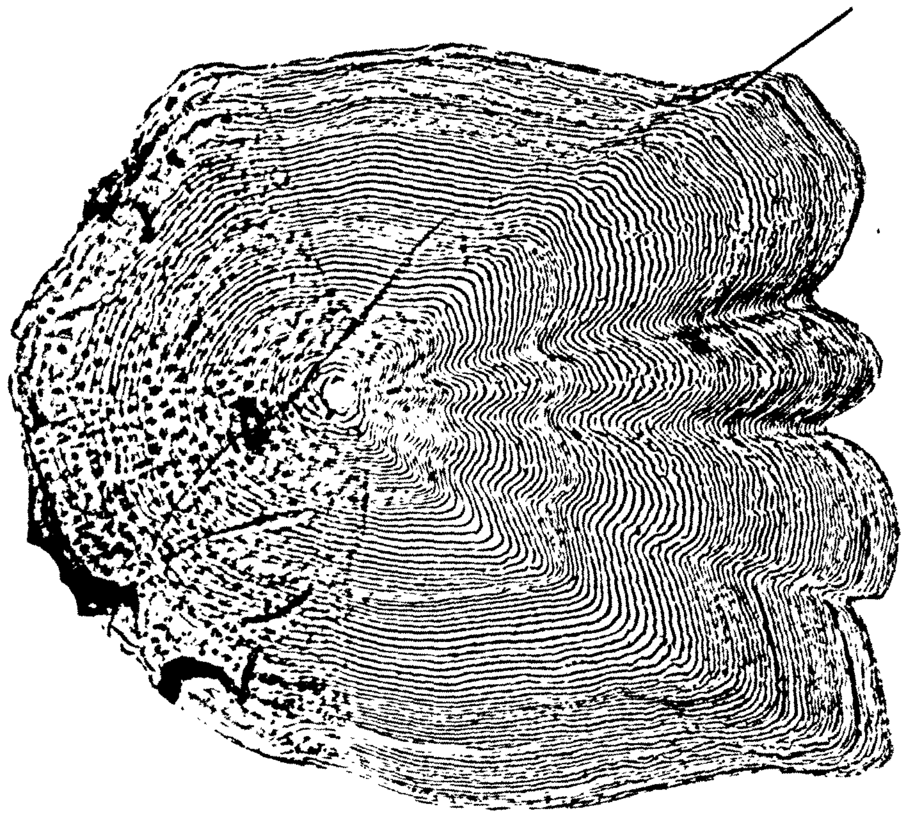
Plate 20

Scale of 5+ year old grayling caught in Llyn Tegid on 15th October 1970, showing a possible "spawning mark" at the fifth annulus.

Plate 21

Scale of 5+ year old grayling caught in the River Dee at Llandrillo on 24th September, 1970, showing possible "spawning marks" at the fourth and fifth annulus.



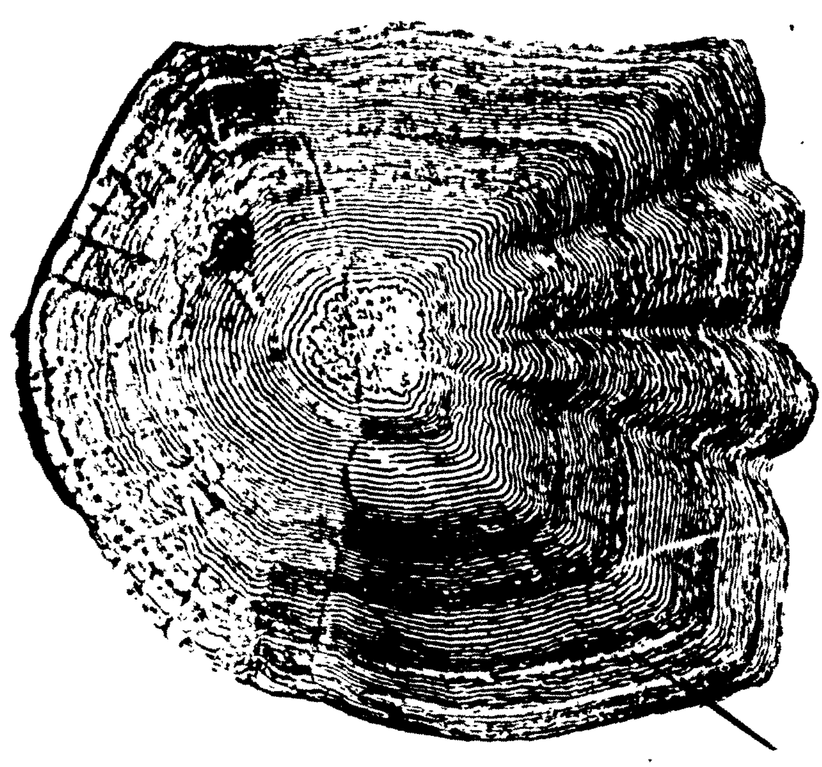


Plate 22

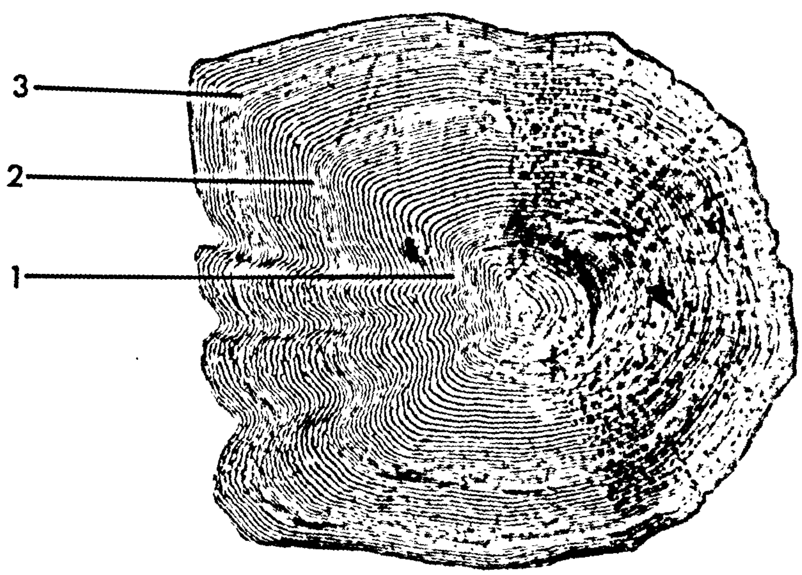
Scale of 0+ year old grayling (length 40mm) caught in Llyn Tegid on 15th July 1969, showing four growth rings.

Plate 23

Scale of 3+ year old grayling (length 300mm) caught in the River Dee at Llandrillo on 15th July 1970.

Plate 24

Scale of 4+ year old grayling (length 345mm) caught in the River Dee at Llandrillo on 19th August 1970.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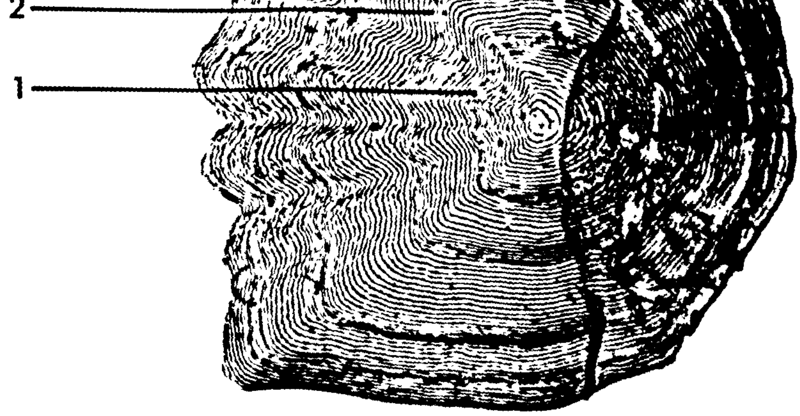
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Plate 25

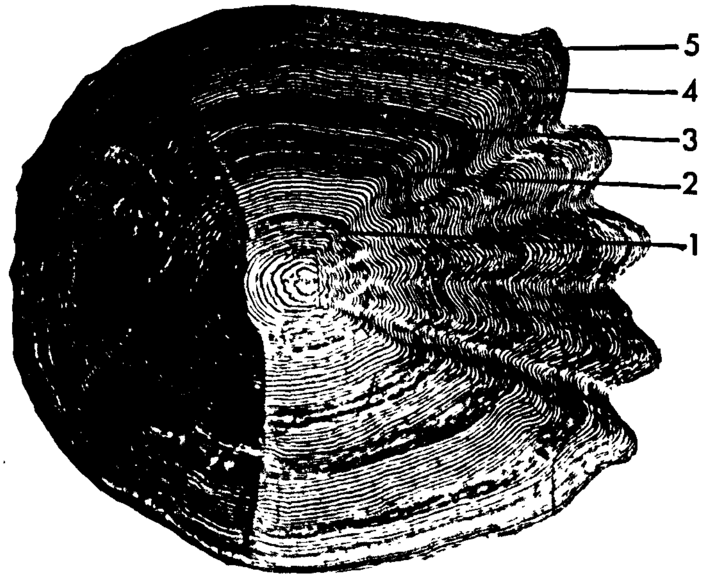
Scale from 5+ year old grayling (length 373mm) caught in the River Dee at Llandrillo on 19th August, 1970.

Plate 26

Scale from 6+ year old grayling (length 435 mm) caught in Llyn Tegid on 3rd June 1966.

Plate 27

Scale from 7+ year old grayling (length 373mm) caught in the River Dee at Llandrillo on 22nd October, 1970.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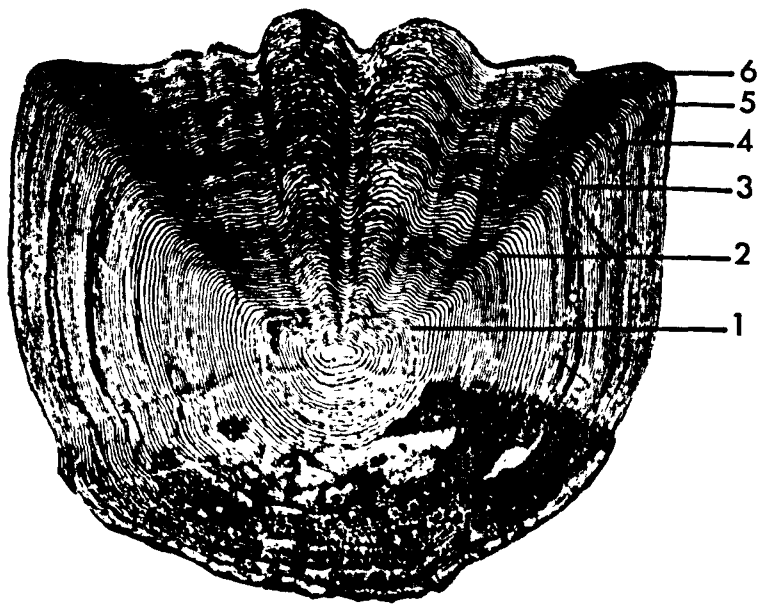
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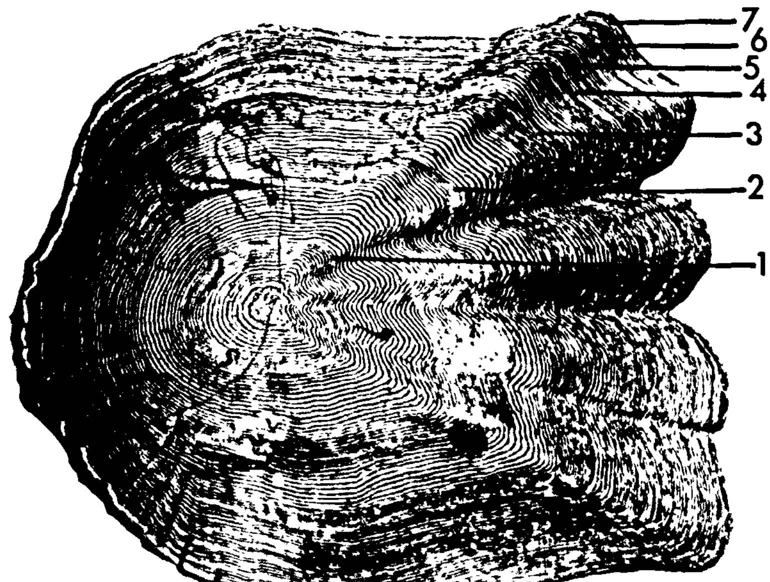
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that grayling first spawned at that time. Gerrish (1938, 1939) indicated the first occurrence of spawning marks at the end of the 2nd–4th years of life in his data tables, but gave no account of these marks in the text of his papers. Jones (1953) found no evidence of scale erosion associated with spawning activities in Llyn Tegid grayling, and considered that this was because grayling were actively feeding and growing rapidly during the spawning period. Peterson (1968) also found no noteworthy scale erosion, but Balon (1962) found distinct "spawning annuli" which he described in some detail. Grayling from Llyn Tegid and the River Dee have, in recent years, laid down their annual scale check during the spring (see section 2(b)) at approximately the same time as when they spawned, and some evidence was found of spawning marks being formed at this time. Such marks are shown in plates 20 and 21, and first occurred at the end of the third or fourth year of life, corresponding with the first time of spawning (see chapter 9). The slight erosion that can be seen at the anterior corners of the annuli, together with the frequently interrupted rings and large light interspaces in the lateral region, closely fits the description given by Balon (1962) and resembles the spawning marks shown by Hutton (1923, figures vi and vii). "Spawning marks" were relatively common, but were not present on the scales of all mature grayling, even of those which had recently spawned.

b. <u>The use of scales in age determination</u>

Hutton (1923) assumed that grayling scales were suitable for age determination merely because of the clarity of their markings. Jones

(1953) followed the seasonal cycle of growth ring formation in Llyn Tegid grayling and found that the annual check was laid down during early autumn (September) in contrast to the spring check formation in Scandinavian grayling (Muller, 1961; Peterson, 1968) and in North American species (Brown, 1943; Kruse, 1959). Gerrish (1939) found that the "winter" band of rings started to appear on the scales of grayling from the Hampshire Avon in early July. Hellawell (1969a) sought to confirm the apparent difference between British grayling and those in Scandinavia and North America, by a study of River Lugg grayling over a period of twelve consecutive months. He found that the check was laid down in November/December, somewhat later than in Llyn Tegid grayling (Jones, op.cit). Brown (1943) stated that different check times of Montana grayling in various waters probably resulted from temperature differences. The variation of the check time observed in European grayling within the British Isles, and between the British Isles and Scandinavia, may also be caused by this factor.

The results of my studies on grayling in the Welsh Dee area vary strikingly from those of previous British workers, but more closely resemble those of Scandinavian authors. The seasonal occurrence of scale growth rings in River Dee grayling from September 1969 to October 1970 is shown in table 21. Observations made on small samples of scales in March, April andDecember 1971 are also included.

The check was laid down during early May in 1969/70 and during early April in 1970/71, the onset of wide ring formation coinciding with the time of increased growth rates (section 2a,ii), increased food consumption (chapter 7, section 3,i) and rising water temperatures. The scales of two fish from a sample of ten examined in December 1971 had one wide summer ring at the margin, suggesting that the 1971/72 check would be laid down earlier than in the previous two years. A scale from a 1+ grayling (showing two winter bands) caught during April 1970 in the River Dee at Llandrillo is shown in plate 15.

Table 21. Seasonal cycle of scale growth rings in River Dee grayling.

Year	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec
1969	-	-	-	-	-	-	-	-	NS	NS	W	W
1970	W	W	W	W	S 1-5	S 1-10	S 4-13	NS 5-19	NS 11-19	W	-	-
1971	-	-	W	W/s 1-2	-	-	-	-	-	-	-	W

where : S = wide "summer" rings
NS = narrow "summer" rings
W = "winter" rings
1-5 = number of rings beyond last annulus
red line = time of check formation

The seasonal occurrence of scale growth rings in Llyn Tegid since 1950 is shown in table 22.

During my sampling period the scale check in Llyn Tegid grayling was laid down, like in River Dee grayling, during the spring (early May 1968/69; early April 1969/70). Plates 13 and 14 show scales from a fish caught in late January 1969 (winter rings at margin) and recaptured in mid-May 1969 (2 wide rings at margin). The time

Table 22. Seasonal cycle of scale growth rings in Llyn Tegid grayling.

Year	Jan	Feb	Mar	Apr	May	Jun	July	Aug	Sept	Oct	Nov	Dec
1950	-	-	-	-	S 3	S +	-	NS	W	S 1-3	-	-
1951	-	S 4-11	-	S 2-14	S +	S +	S +	NS	W	-	-	-
1952	-	-	S 2-13	S 2-14	S +	S +	-	-	-	-	S 1-8	S 2-6
1953	S 2-7	S 4-11	S 2-13	S 2-14	S +	S +	-	-	W	S 1-6	S 2	S 1-11
1955	S 1-8	S 4-6	-	S 2-10	-	-	-	-	-	-	-	-
1957	-	S 2-7	-	-	-	-	-	-	W	W	S 1-8	-
1958	W	-	S 1-5	S 5	-	S 4-12	-	NS	-	-	-	-
1959	-	-	-	-	-	S 5-10	-	NS	W	W	W	S 2-7
1960	S 2-4	-	-	-	-	-	-	-	-	-	-	-
1966	W	W	W/S 2-5	S 1-9	S 1-8	S 2-8	S 8-16	NS	NS	W	W	W
1967	W	-	-	S 4-11	S +	-	-	-	-	-	-	-
1968	-	-	-	-	-	-	-	-	-	NS	W	W
1969	W	W	W	W	S 1-8	S 2-9	S 6-12	S 7-14	NS	NS	W	W
1970	W	W	-	S 1-5	-	-	-	-	-	S 1-5	-	-
1971	-	-	-	S 1-10	-	-	-	-	-	-	-	-
1972	S 3-5											

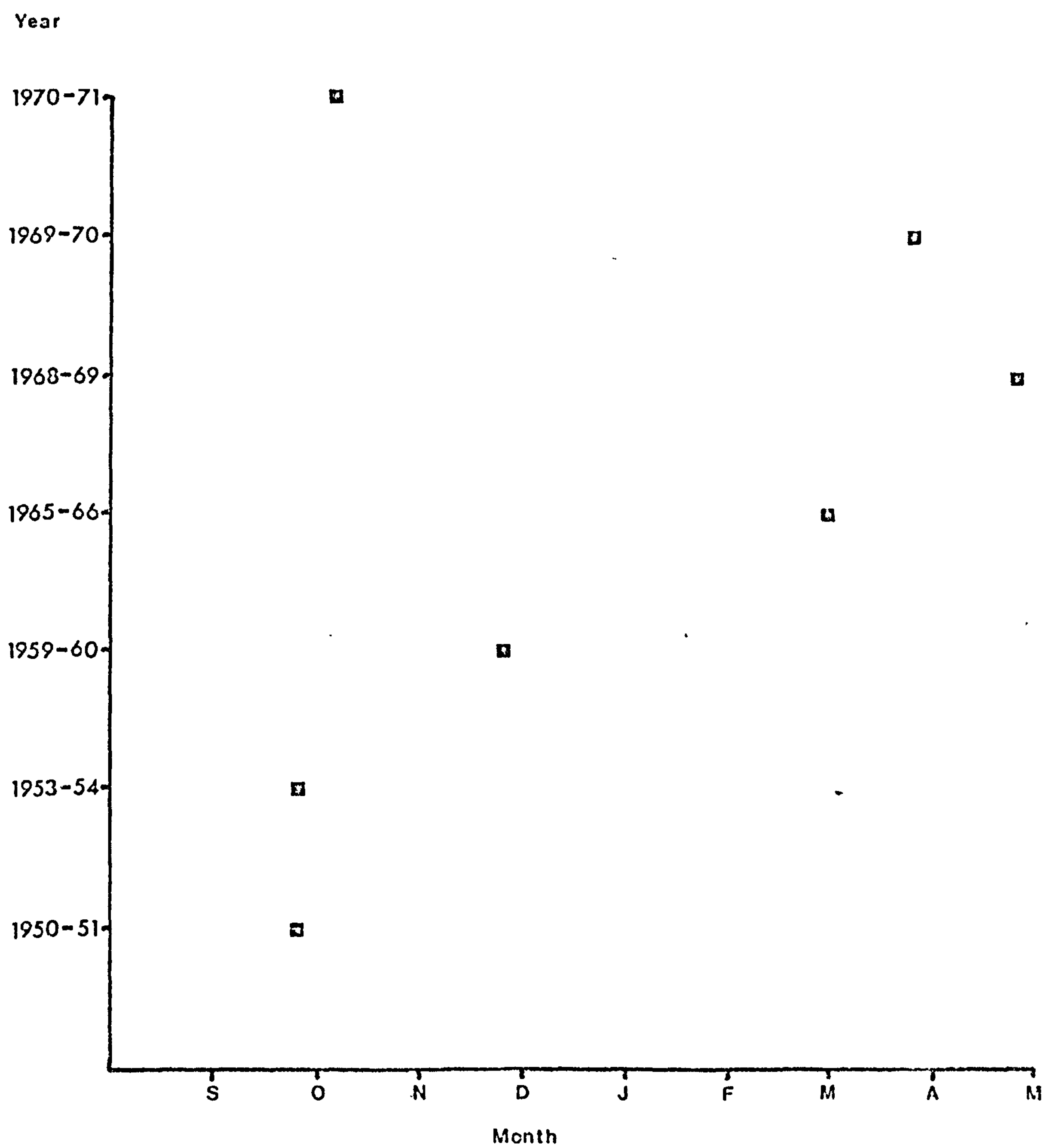
key as for table 21.

+ = many "summer" rings beyond last annulus of check formation in other years varied considerably, as shown in figure 16. In October 1970 Llyn Tegid grayling had 1-5 wide rings at the margin, resembling those examined by Jones (1953), and in January 1972 an average of 4 wide rings were present at the scale margin, indicating an autumn or early winter check time. It is suggested that temperature may have been an important contributory factor to the observed variation of check time in different years. The winters of 1968/69 and 1969/70 were severe and prolonged, with snow present on the mountains surrounding Llyn Tegid almost continuously from November to mid or late April. The following winter was much less severe, and the autumns of 1970 and 1971 were particularly mild.

Grayling often feed actively throughout the winter, except during severe weather (chapter 7), and Llyn Tegid fish which check in the autumn grow rapidly at this time (section 3a). During very cold weather feeding activity is low and little winter growth occurs as found in the years 1968-70. The growth of Llyn Tegid grayling scales during the winter of 1969/70 (table 22) contrasts with the lack of scale growth in the River Dee (table 21), and may result from richer feeding conditions in the lake. The winter food of grayling in Llyn Tegid consists principally of <u>Ephemera danica</u> nymphs, Crustacea and gwyniad eggs, which are more nutritious than the Trichoptera larvae that form the main winter food of River Dee fish (see chapter 7). Grayling leave Llyn Tegid in the summer and return to the lake from the River Dee and the Llyn Tegid feeder streams during the autumn (chapter 10). The rich feeding conditions found on

FIGURE 16

Time of Scale Annulus Formation in Llyn Tegid Grayling



the return to Llyn Tegid may give rise to an upsurge in feeding activity and growth which can continue throughout the winter. It is interesting to note that underyearling grayling, which check later than older fish (also recorded by Hellawell, 1969b), eat little of the nutritious food listed above (see chapter 7). In conclusion, it appears that both winter temperatures and the quantity and quality of the available food supply are important factors in determining the time of scale check formation in grayling.

The formation of the scale check in the spring, during the breeding season, facilitated age determination of grayling. The allocation of year classes was not related to the number of winter bands of rings in grayling which checked at other times, since a fish caught during the winter might have two checks but would only be 1+ years old (Hellawell,1969a, 1969b). The designation of year class was therefore generally given with reference to the hatching time (taken as 1st June). The validity of the scale method for ageing grayling was demonstrated by the seasonal sequence of scale growth rings shown in tables 21 and 22, together with the examination of scales from fish recaptured over a one year period. Scales from a grayling caught at Llanderfel in February 1970, and recaptured at the same place in April 1971, are shown in plates 16 and 17. Two other such fish, recaptured over a one year period, had one scale check in March 1969 and two scale checks in March 1970. False scale checks were found in a number of the grayling examined. These checks, termed "summer checks", were formed during periods of high water temperature which occurred in mid-July 1969, when the surface temperature of Llyn Tegid reached 22°C, and in the first week of July 1970, when the River Dee temperature rose to 20°C. Scales with such checks are shown in plates 18 and 19. Brown (1943) also recorded summer checks in Montana grayling, formed during hot weather.

The time of scale formation was unknown, but a fish of 40mm., captured in Llyn Tegid on 15th July 1969, had scales with only one wide growth ring. Plate 22 shows a scale, with four wide growth rings, from a grayling of 48mm. also captured in Llyn Tegid on 15th July 1969. Gustafson (1949) stated that scale formation took place at a length of 33.5mm., and Peterson (1968) first found scales, along the lateral line, in grayling of 37mm. Fish of 40mm. examined by Peterson (op.cit.) had about two scale growth rings.

The oldest fish found in Llyn Tegid and the River Dee were 6+ and 7+ respectively, the scales of which can be seen in plates 26 and 27. Scales from fish of 3+, 4+ and 5+ are shown in plates 23 to 25. The oldest recorded British grayling seems to be one of nearly 8 years (Hutton, 1923), and Gerrish (1938, 1939) found grayling of 7+ in the Hampshire Avon. In Scandinavia, Peterson (1968) examined grayling of 8+ and Müller (1961) found one of 10 years. The longest lived European grayling appear to be those in Yugoslavian rivers which may live to an age of 13 years (Svetovidov, 1936). Arctic grayling of 11 years have been recorded (Miller, 1946). Most authors agree that grayling have a relatively short life span (Jankovic,1964), and the scarcity of fish older than 4+ or 5+ in most of the data presented is very noticeable. The relative numbers of grayling of different ages in Llyn Tegid and the River Dee can be seen in the seasonal length frequency distributions given in figures 17 and 18. The dominance of the 0+, 1+ and 2+ age groups seen in these figures, was also recorded by Peterson (1968) and Hellawell (1969b).

3. Growth

a. Seasonal growth

(i) Material

The numbers of Llyn Tegid grayling and River Dee grayling examined each month are shown in tables 23 and 24.

Data from River Dee grayling were treated in two groups;

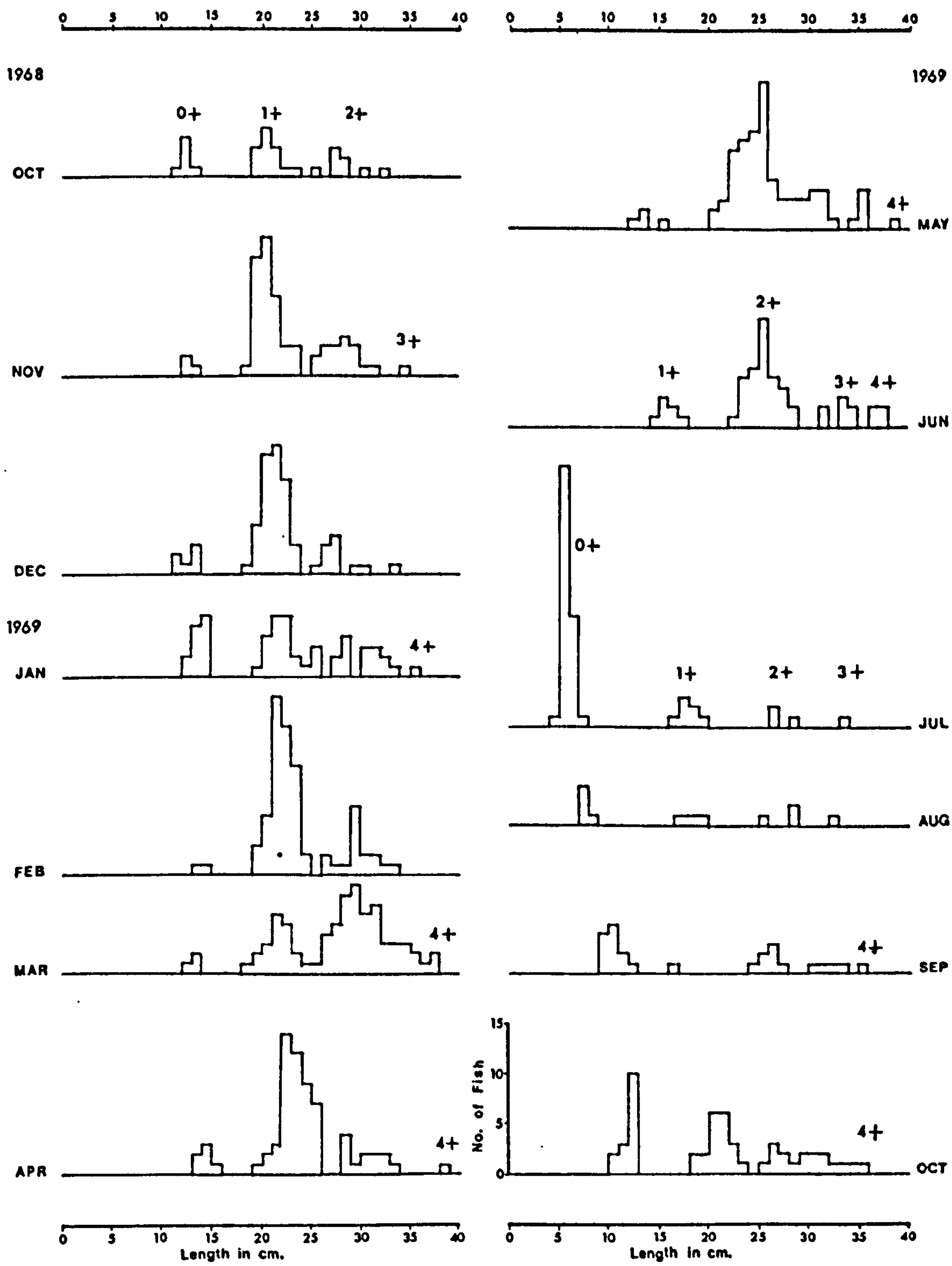
(1) Above Corwen (sites a to u),

(2) Corwen (sites v and w).

No significant difference ($p > 0.10$) was found between the growth rates of grayling in any of the sites a to u, but the difference between the growth rates in sites a to u (upper Dee) and v to w (Corwen) was very significant ($p < 0.001$ in most age groups, see section b,iii). Sites a to u are hereafter referred to as the "upper Dee", and sites v and w as "Corwen".

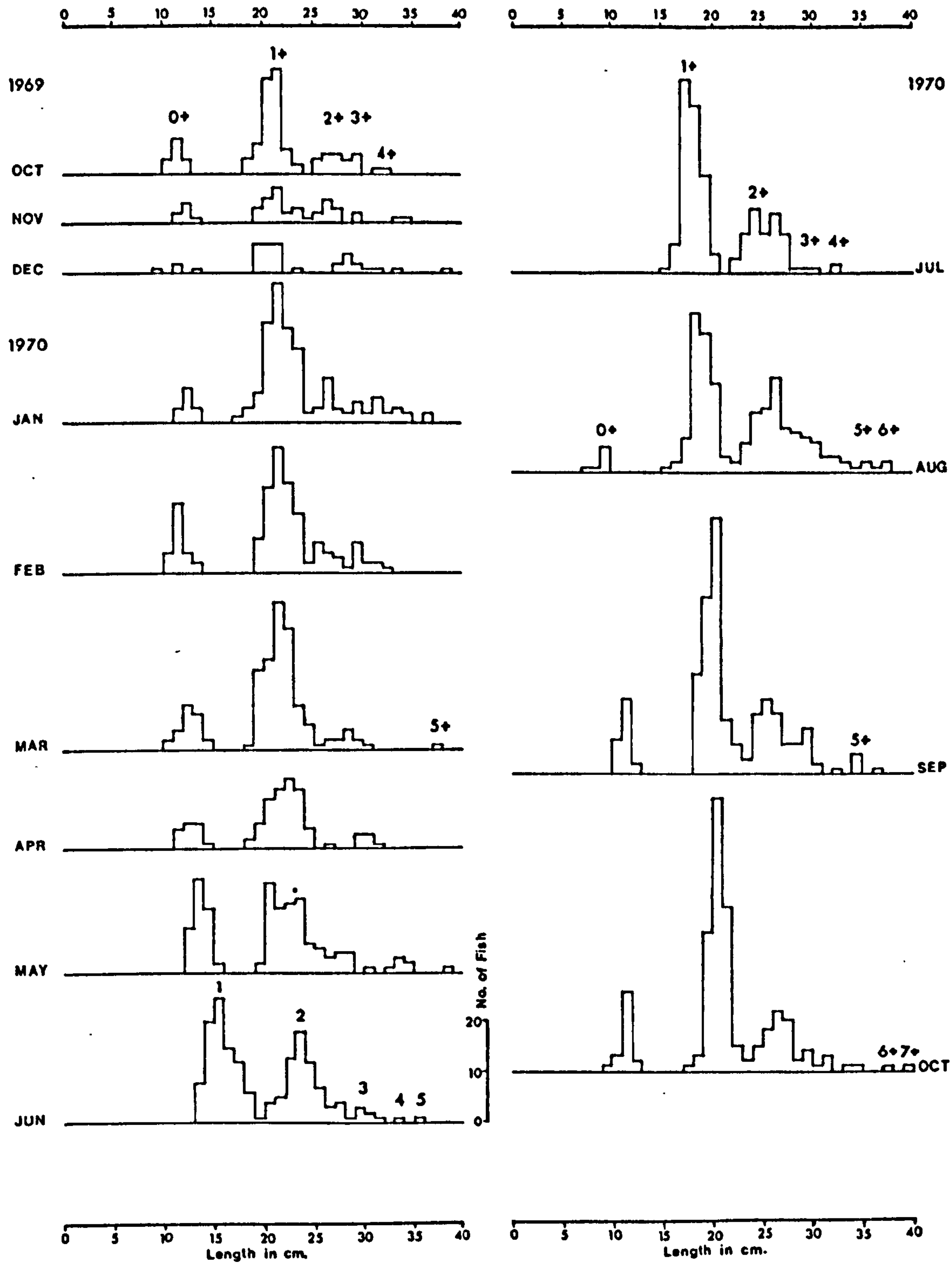
(ii) Growth in length

The seasonal growth in length of grayling in Llyn Tegid and the upper Dee is shown in figures 19 and 20. A comparison of the seasonal growth of grayling in Llyn Tegid, the upper Dee and the Dee at Corwen, is given in figure 21. The seasonal increase in length can also be followed from the length frequency histograms shown in figures 17 and 18. The results from the 1966/67 samples donated by M.S. Siddiqui were not significantly different ($p > 0.10$)



Seasonal Length/Frequency Distribution of Llyn Tegid Grayling (0+ to 4+ age groups)

FIGURE 17



Seasonal Length/Frequency Distribution of River Dee Grayling (0+ to 7+ age groups)

FIGURE 18

Table 23. Numbers of Llyn Tegid grayling examined each month.

Month	Total	Numbers in each year class						
		1964	1965	1966	1967	1968	1969	1970
October 1968	26	-	-	8	12	6	-	-
November	64	-	2	16	43	3	-	-
December	59	-	-	11	42	6	-	-
January 1969	51	1	5	14	18	13	-	-
February	77	-	3	16	56	2	-	-
March	77	1	9	43	21	3	-	-
April	67	1	-	12	48	6	-	-
May	82	2	4	16	56	4	-	-
June	51	-	3	7	33	8	-	-
July	63	-	-	1	3	7	52	-
August	14	-	-	1	5	3	5	-
September	26	-	1	5	7	1	12	-
October	53	-	1	10	8	19	15	-
November	15	-	-	-	1	12	2	-
December	54	-	1	2	7	42	2	-
January 1970	40	1	0	1	1	33	4	-
February	3	-	-	-	-	3	-	-
March	2	-	-	1	-	1	-	-
April	48	-	-	-	4	39	5	-
May	99	-	2	2	8	76	11	-
June	1	-	-	-	-	1	-	-
July	2	-	-	-	-	1	1	-
August	0	-	-	-	-	-	-	-
September	0	-	-	-	-	-	-	-
October	40	-	1	2	6	28	1	2
Total nos. of fish	1014	6	32	168	379	317	110	2

Table 24 Numbers of River Dee grayling examined each month

a. Above Corwen

Month	Total	numbers in each year class							
		1963	1964	1965	1966	1967	1968	1969	1970
October 1969	89	-	-	1	4	15	56	13	-
November	42	-	-	2	1	11	21	7	-
December	36	-	-	2	5	5	20	4	-
January 1970	143	-	-	6	9	23	92	13	-
February	130	-	-	1	6	18	81	24	-
April	80	-	-	-	3	5	57	15	-
May	133	-	-	1	7	15	67	43	-
June	164	-	-	2	4	6	67	85	-
July	176	-	-	-	3	6	60	107	-
August	188	-	1	3	7	11	66	93	7
September	213	-	-	4	3	4	55	123	24
October	199	1	-	-	2	4	41	129	22
Total nos. of fish	1733	1	2	22	55	134	785	681	53

b. At Corwen

	Total	1963	1964	1965	1966	1967	1968	1969	1970
May 1970	8	-	-	-	-	1	3	4	-
June	0	-	-	-	-	-	-	-	-
July	8	-	-	-	1	-	5	2	-
August	21	-	1	-	1	2	4	12	1
September	27	-	-	-	4	6	8	8	1
October	6	-	-	-	-	-	2	3	1
Total nos. of fish	70	0	1	0	6	9	22	29	3

FIGURE 19

Seasonal Growth of Llyn Tegid Grayling

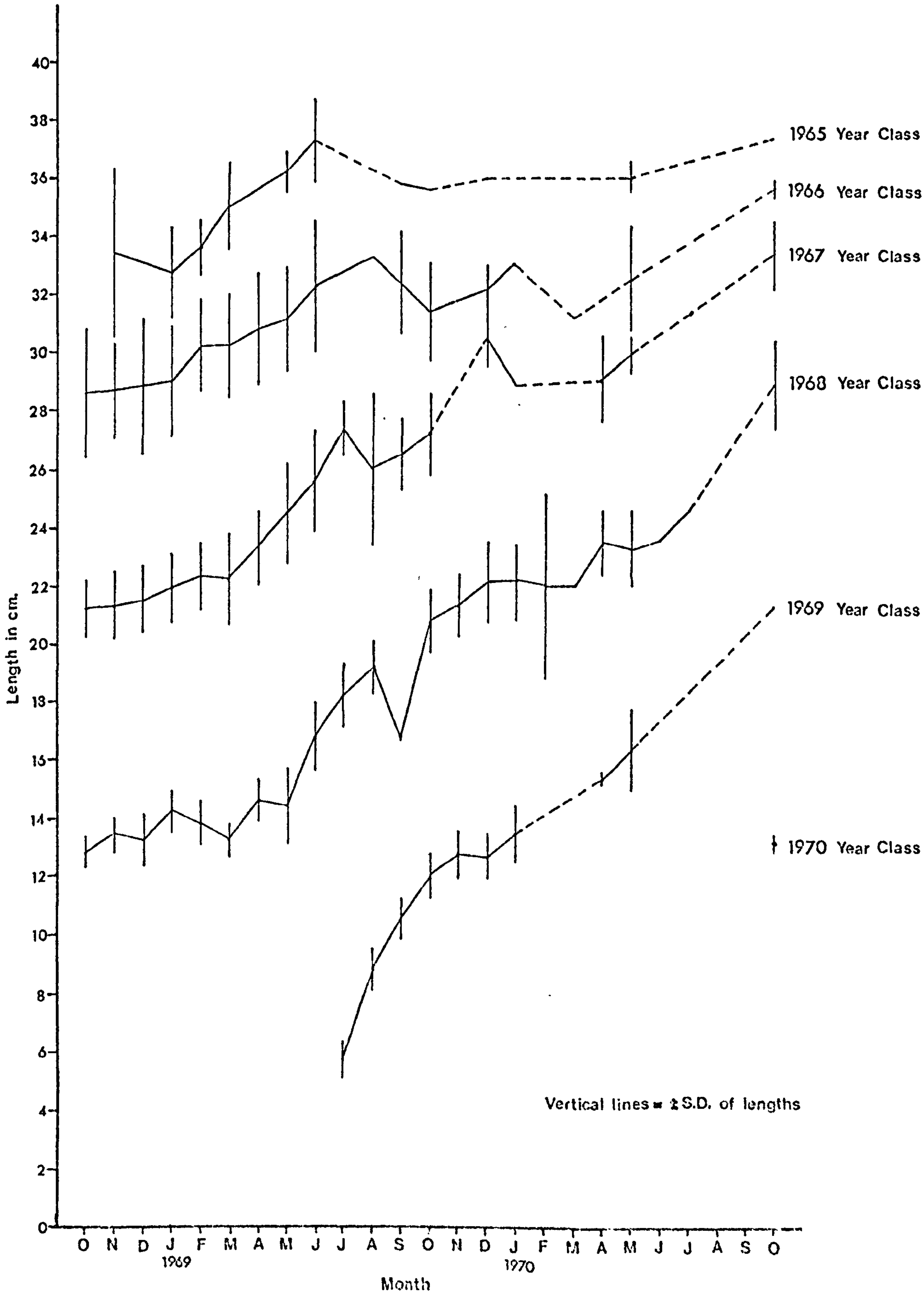


FIGURE 20

Seasonal Growth of Upper Dee Grayling

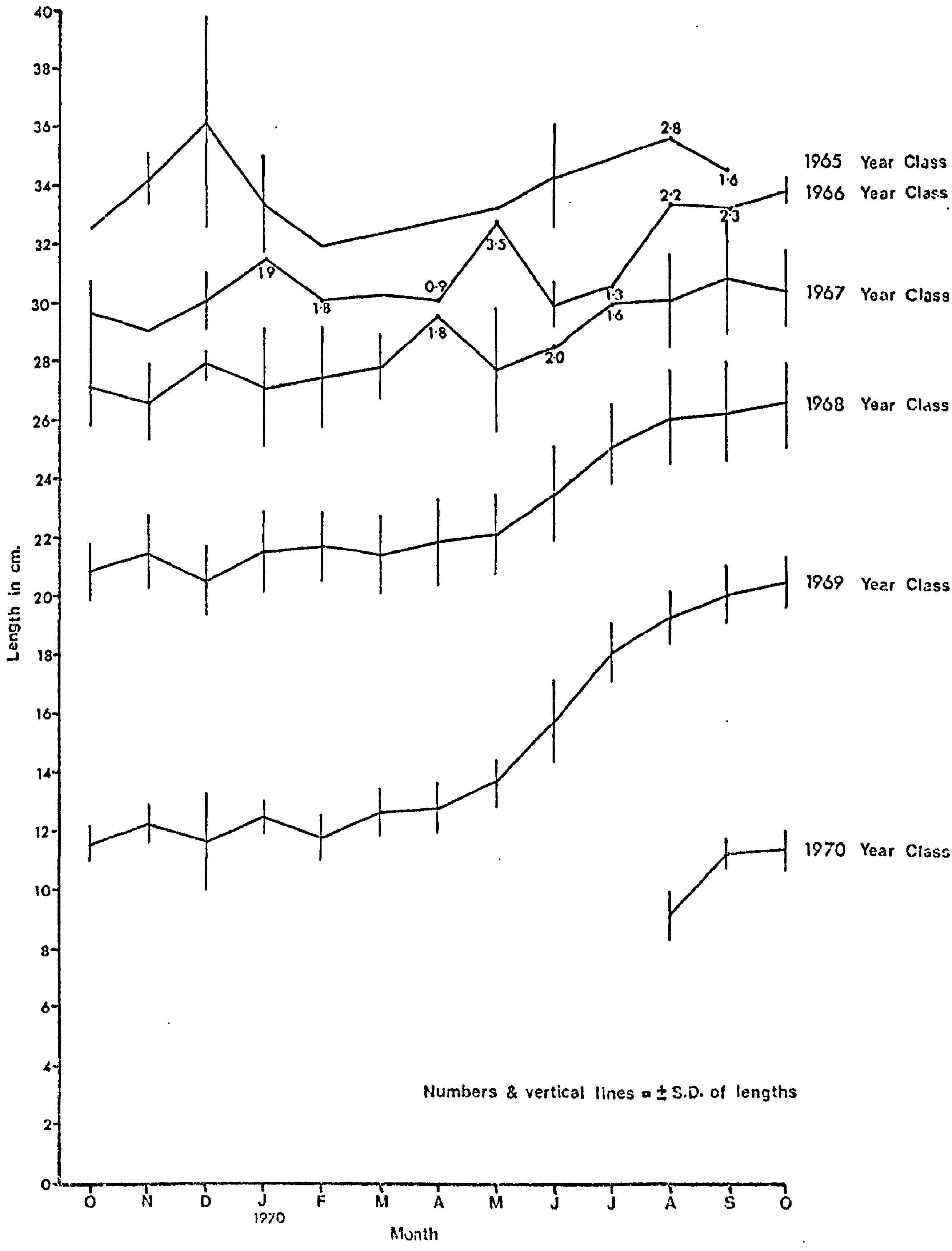
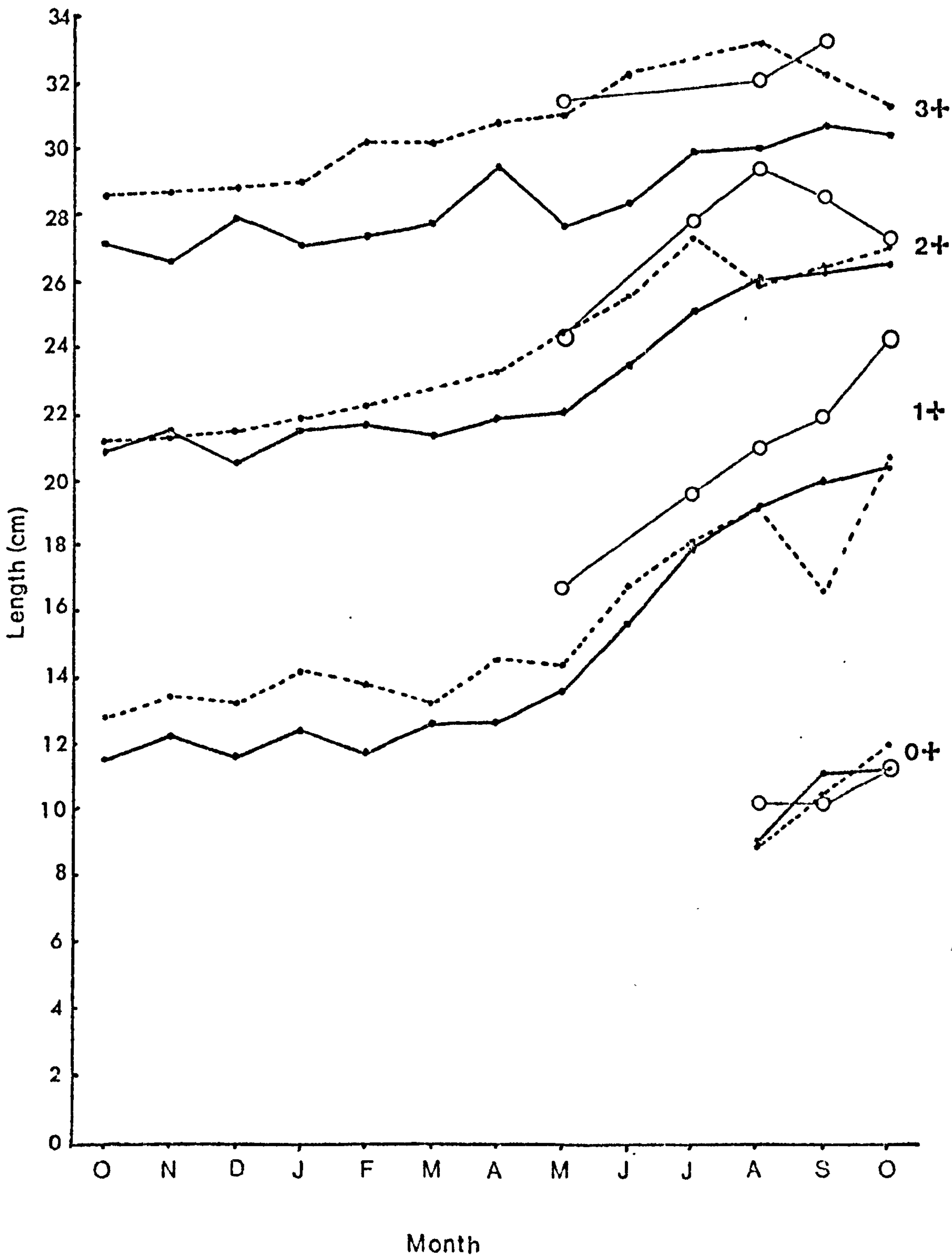


FIGURE 21

Seasonal growth of grayling from the upper Dee (•——•), Llyn Tegid (•- - - -•) and the Dee at Corwen (O—O).



from those shown in figure 19 and have, therefore, been excluded from this section. The grayling collected by Dr. J.W. Jones from Llyn Tegid were generally too few in number and too unevenly distributed during the year for determination of monthly growth cycles but the results for 1+ year old grayling from December 1953 to June 1954 are shown in figure 22.

Figures 17-21 indicate that the main growth period of Llyn Tegid and River Dee grayling was from April/May to October/November. Growth during the winter was very slow, River Dee 0+ grayling, for instance only grew about 5mm. between November 1969 and April 1970. Figure 22 shows, however, that fish which checked in the autumn (see table 22 and figure 16) grew much more rapidly during the winter than those which checked in the spring. Grayling of the 1+ age group grew 28mm. in length from December 1953 to April 1954. Hellawell (1969a) stated that the period of accelerated growth in River Lugg grayling occurred from May to August.

The seasonal growth cycles of grayling in Llyn Tegid and the River Dee were very similar (Figure 21). The differences in growth rates of grayling from Llyn Tegid, the upper Dee and Corwen which are evident in figure 21, are discussed in section 3bv.

The seasonal length/frequency distributions of rod-caught and net-caught grayling in the River Dee are shown in figure 23. No significant difference ($p > 0.10$) was found between the growth rates of the two groups of fish and, although the age structure of the samples varied considerably in different months, the total numbers of each year class captured from June to September 1970 were very

FIGURE 22

Growth of 1+ Grayling in Llyn Tegid during Winter and Spring 1953-54

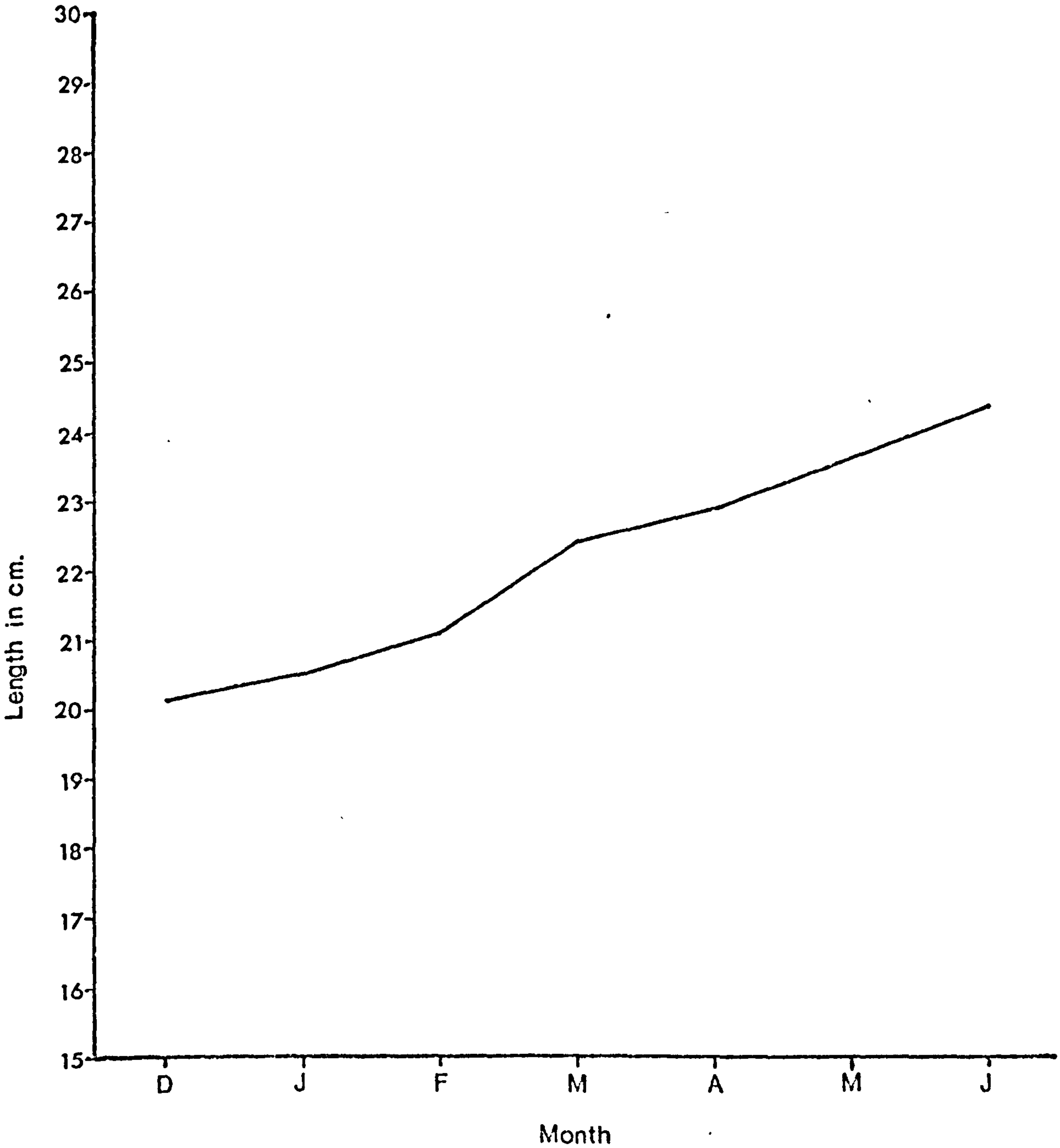
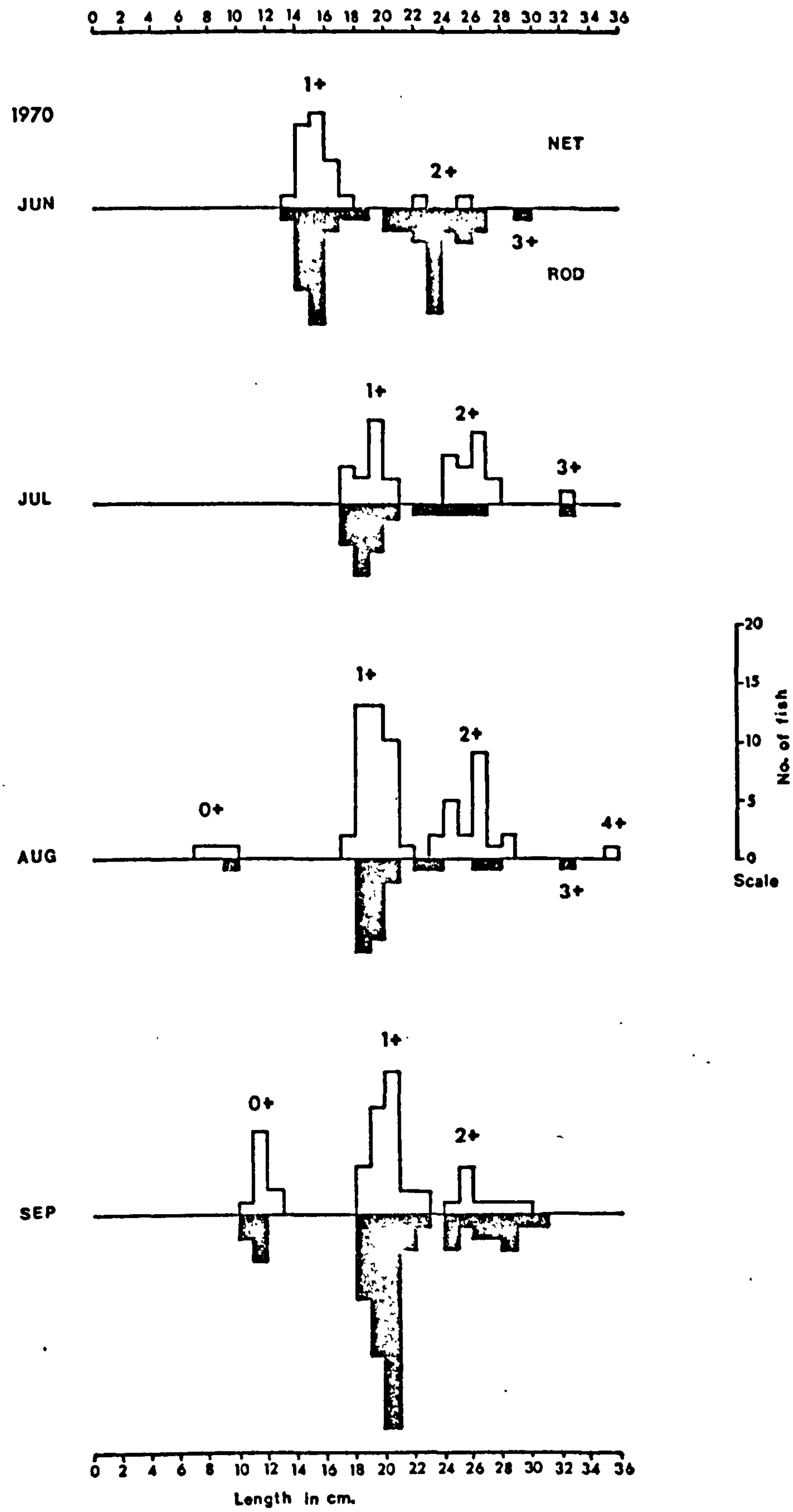


FIGURE 23

Length/Frequencies of Seine Net and Rod Caught Grayling in the River Dee (sites a and c)



similar. The numbers of fish captured during this period are shown in table 25.

Table 25. The numbers of grayling caught by angling and by seine-net in the River Dee (sites a and c) between June and September 1970.

Year class	No. of rod-caught grayling.	No. of net-caught grayling.
1966	0	1
1967	3	1
1968	45	47
1969	95	103
1970	7	13

A χ^2 test showed that these figures were not significantly different ($p > 0.10$).

The seasonal growth in length of tagged fish is shown for Llyn Tegid in figure 24, and for the River Dee in figure 25. 51.9% of recaptured Llyn Tegid grayling were shorter than the mean untagged fish length, 21.5% were the same length, and 26.6% grew faster than the mean. Recaptured fish were on average only 0.12cm. shorter than untagged fish (not significant, $p > 0.10$). The comparative figures for the River Dee grayling were 57.8%, 12.8%, 29.4% and 0.25cm ($p > 0.10$). The tagging methods used in this study, therefore, had a small but non-significant effect on the growth in length of grayling. Gustafson (1949) using individual tags similar to those described in chapter 4, section 2(b), together with pelvic fin clips, found little or no difference between the growth of tagged and untagged grayling.

FIGURE 24

The Effect of Tagging on the Growth of Llyn Tegid Grayling

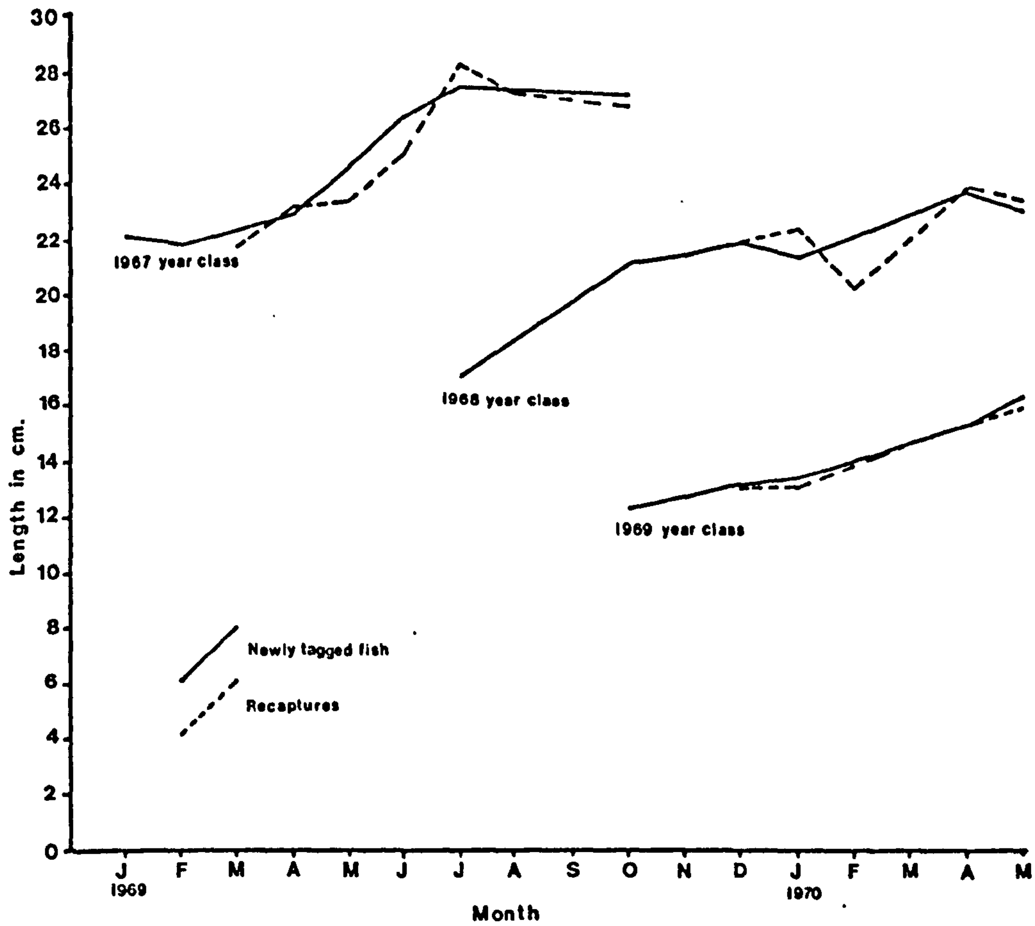
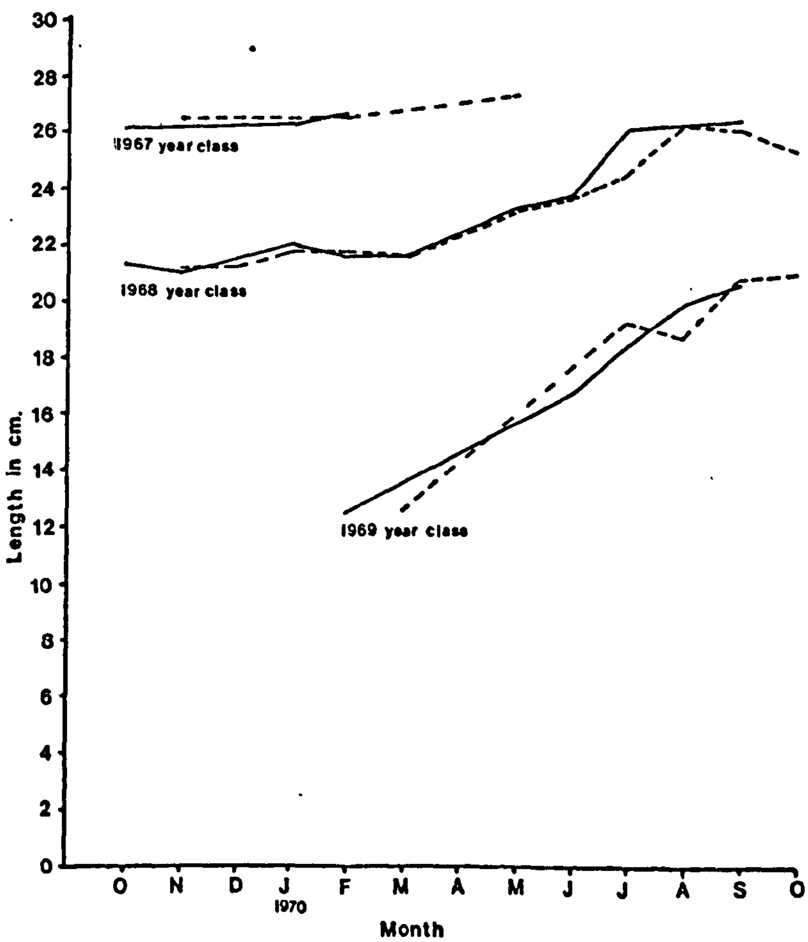


FIGURE 25

The Effect of Tagging on the Growth of River Dee Grayling



(iii) Growth in weight

The seasonal growth in weight of grayling in Llyn Tegid and the upper Dee is shown in figures 26 and 27. The seasonal weight of Corwen grayling is given in table 26.

Table 26. Seasonal growth in weight of Corwen grayling.

Month	No. in sample	Mean weight (gm) of each year class: 1964	1965	1966	1967	1968	1969	1970
May 1970	8	-	-	-	370.0	160.0	43.6	-
June	0	-	-	-	-	-	-	-
July	8	-	-	700.0	-	257.0	90.5	-
August	21	845.0	-	623.0	403.0	302.0	103.5	8.0
September	27	-	-	470.0	415.0	267.0	116.4	9.0
October	6	-	-	-	-	211.0	143.0	14.0

The seasonal growth weight of grayling was found to closely follow the seasonal cycle of growth in length.

(iv) Condition

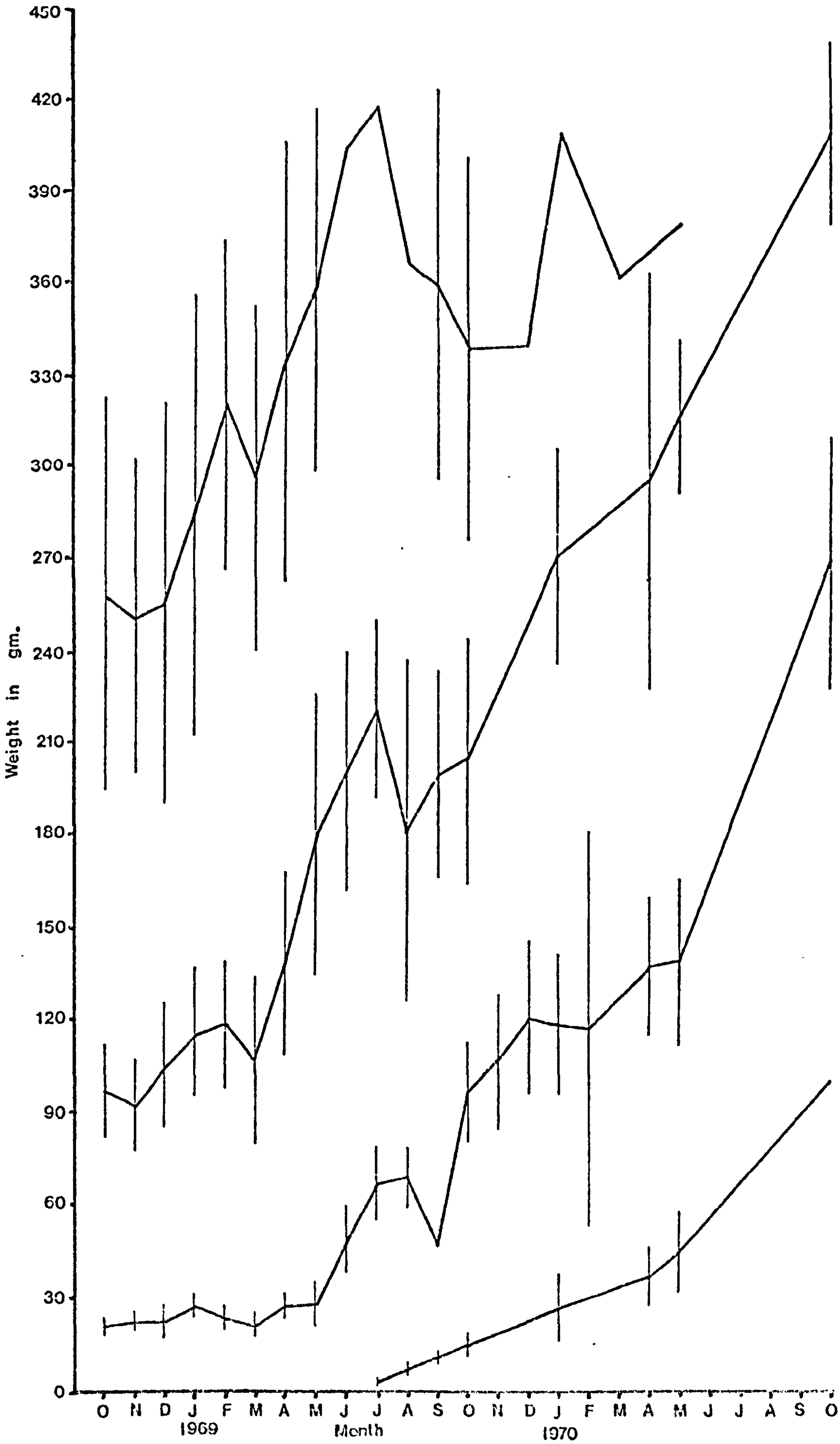
The condition factor (k) of grayling was calculated as follows :

$$k = \frac{\text{Weight (in grammes)}}{\text{Length (in centimetres)}^3} \times 10^4$$

The seasonal change of k for Llyn Tegid and River Dee grayling of different ages is shown in figures 28 and 29. The seasonal k cycles shown in these figures were found to be superimposed on a general upward trend in k with increasing length and age of the fish. This upward trend reflects changes in the length-weight relationship which occur during the life of the fish (see section 3b,vi). The data

FIGURE 26

Seasonal Growth in Weight of Llyn Tegid Grayling



Vertical lines = ± S.D. of weights

FIGURE 27

Seasonal Growth in Weight of Upper Dee Grayling

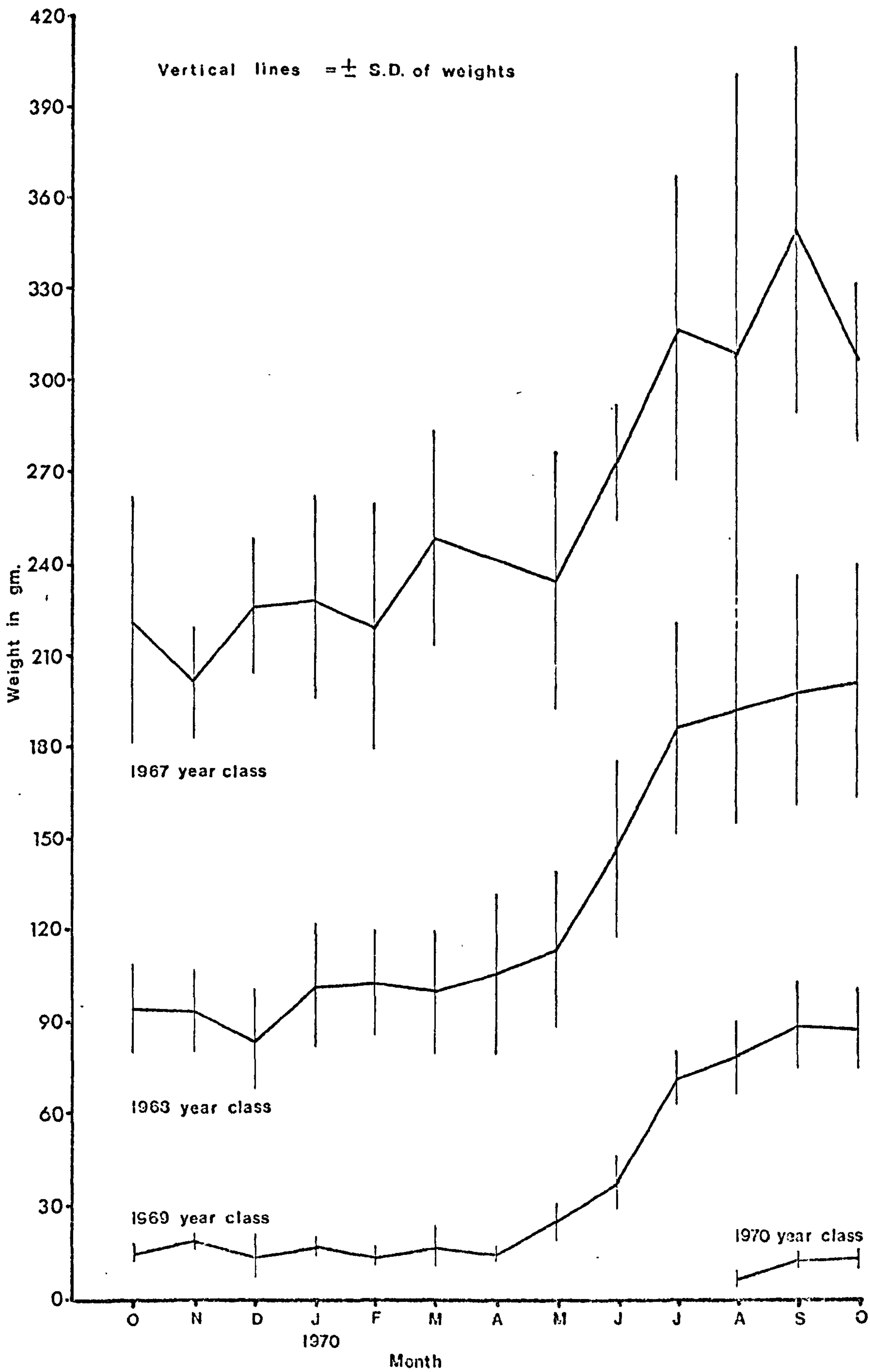


FIGURE 28

Seasonal Condition of Llyn Tegid Grayling

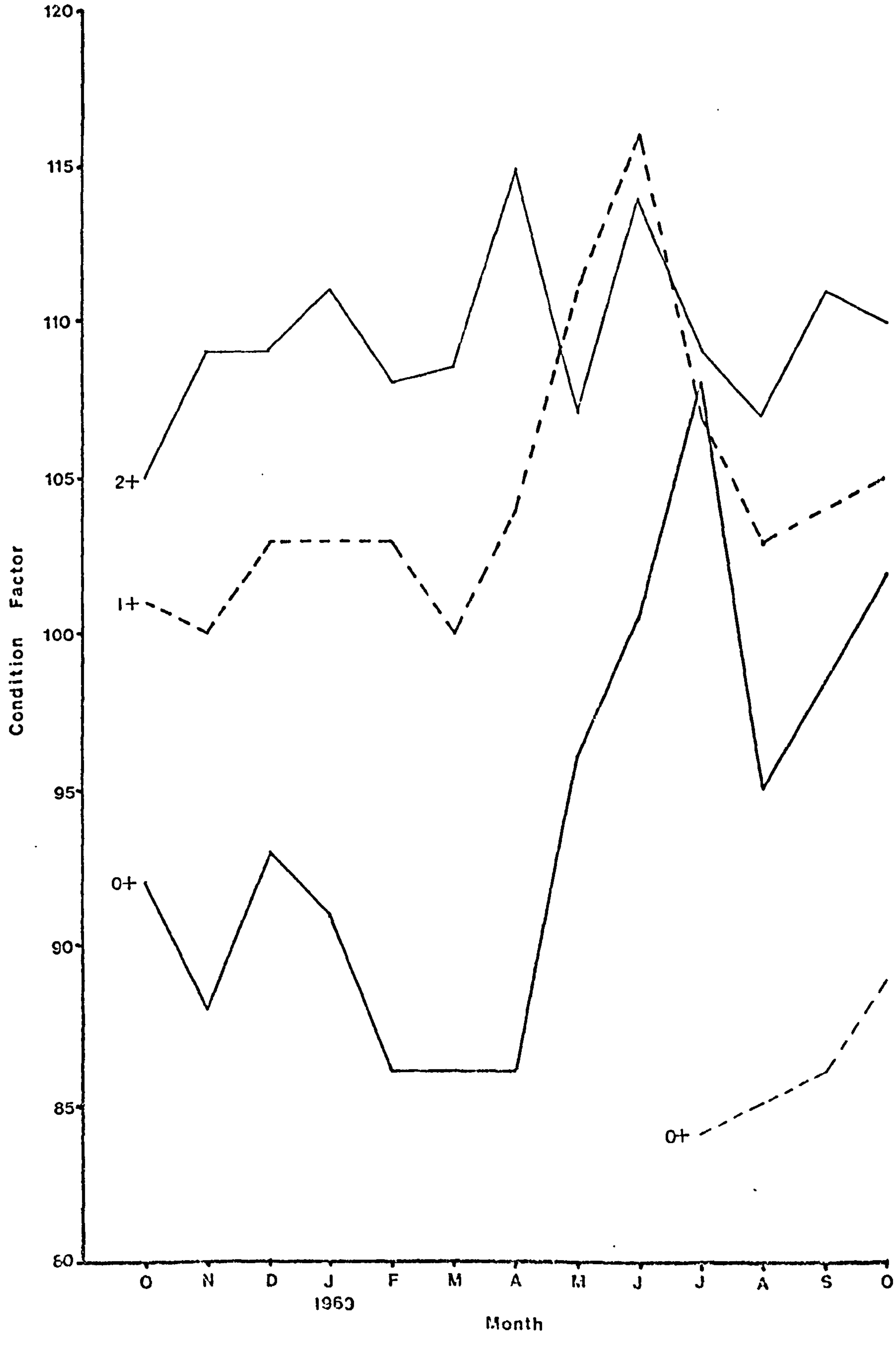
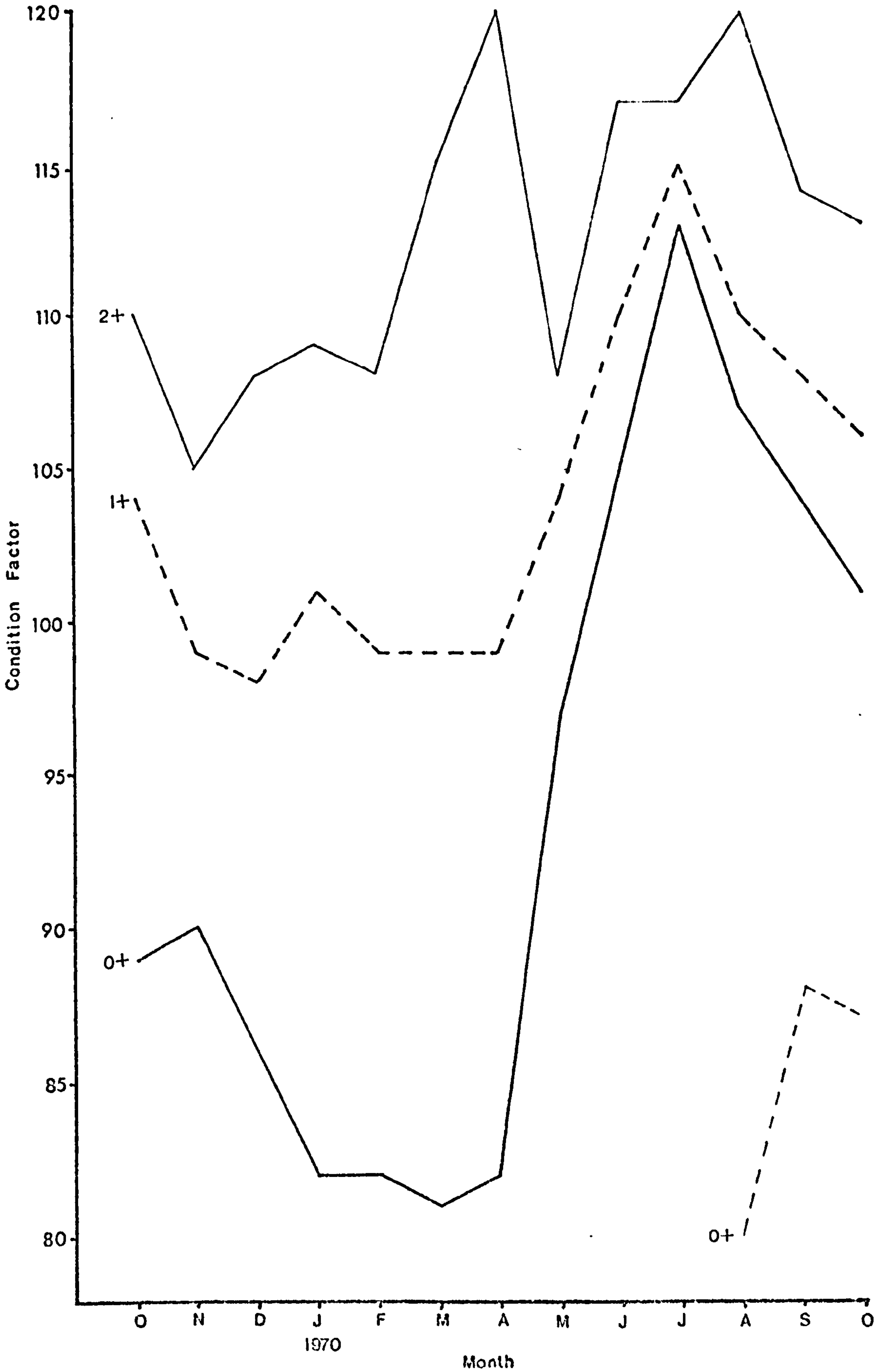


FIGURE 29

Seasonal Condition of River Dee Grayling



from figures 28 and 29 were combined to give theoretical condition factor curves for the first 3+ years of life as shown in figures 30 and 31. The general trend which emerged showed high summer condition and low winter condition. The highest K occurred in 1+ and 2+ fish during June and July, but 0+ grayling continued to increase in condition until November or December. A sharp fall in K occurred in Llyn Tegid grayling during August, followed by a rise to a higher autumn level. Unsuitable living conditions in Llyn Tegid probably accounted for the summer disappearance of grayling from the lake (chapter 10) and also for the poor condition of the few fish which remained. Grayling first matured at the end of the third year of life (chapter 9) and the condition of maturing fish increased through the winter to a maximum just before spawning. Condition fell sharply with spawning, but quickly rose again in the early summer.

The growth in length of grayling was unaffected by tagging (section ii) but the mean condition of tagged fish was significantly lower ($p < 0.05$) than that of untagged fish. The condition of recaptured and newly tagged grayling in Llyn Tegid and the River Dee is shown in figures 32 and 33. Figure 33 shows the effects of tagging on two year classes in which recaptures were well represented. Only one age group (1+) from Llyn Tegid contained large numbers of recaptures, and data from 1+ grayling in successive years were combined to some extent in figure 32. The loss of condition following tagging was greater in Llyn Tegid grayling than in River Dee grayling, and this was reflected in the poor appearance and large tag wounds

FIGURE 30

Change in Condition of Llyn Tegid Grayling with Age

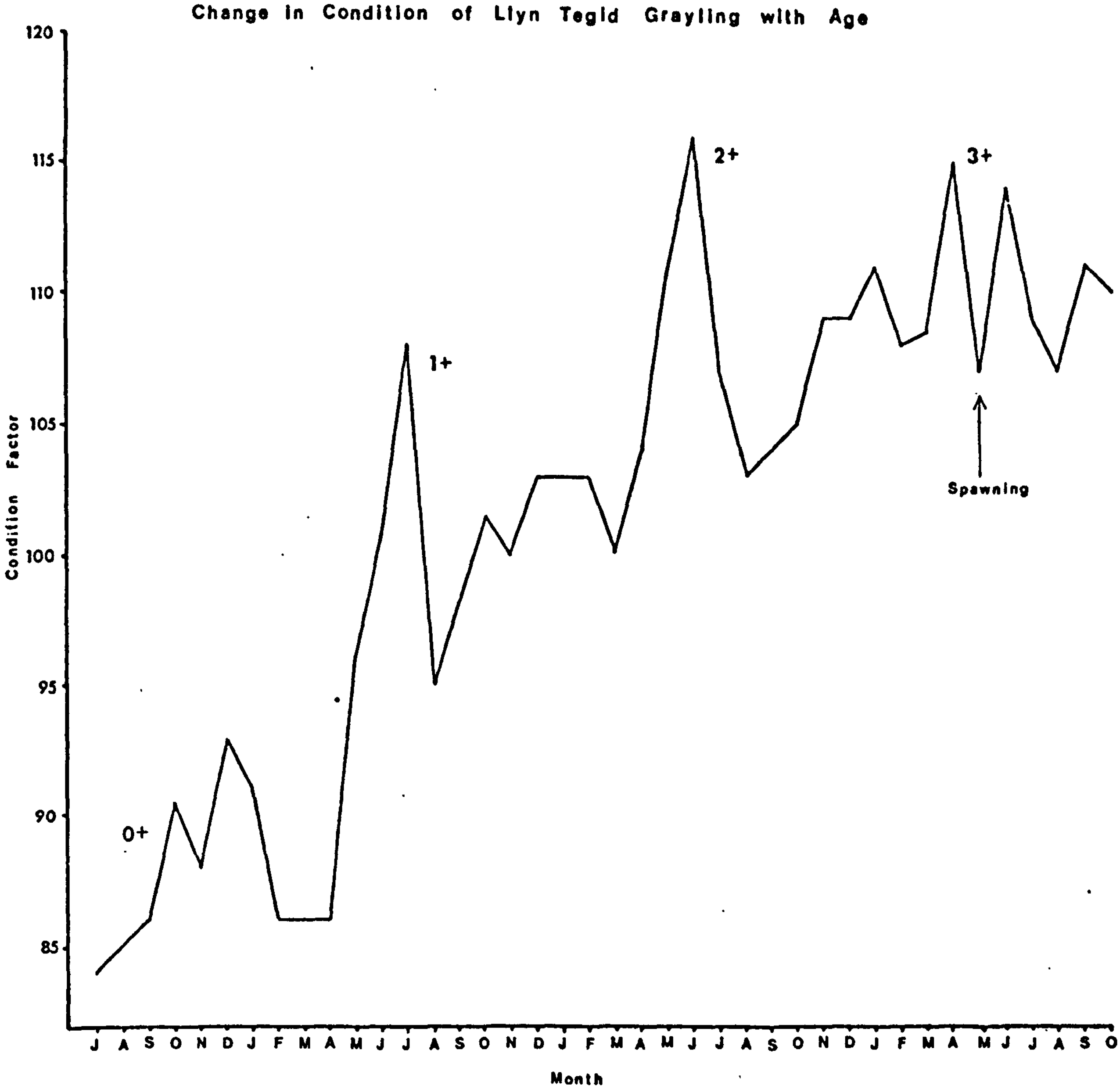


FIGURE 31

Change in Condition of River Dee Grayling with Age

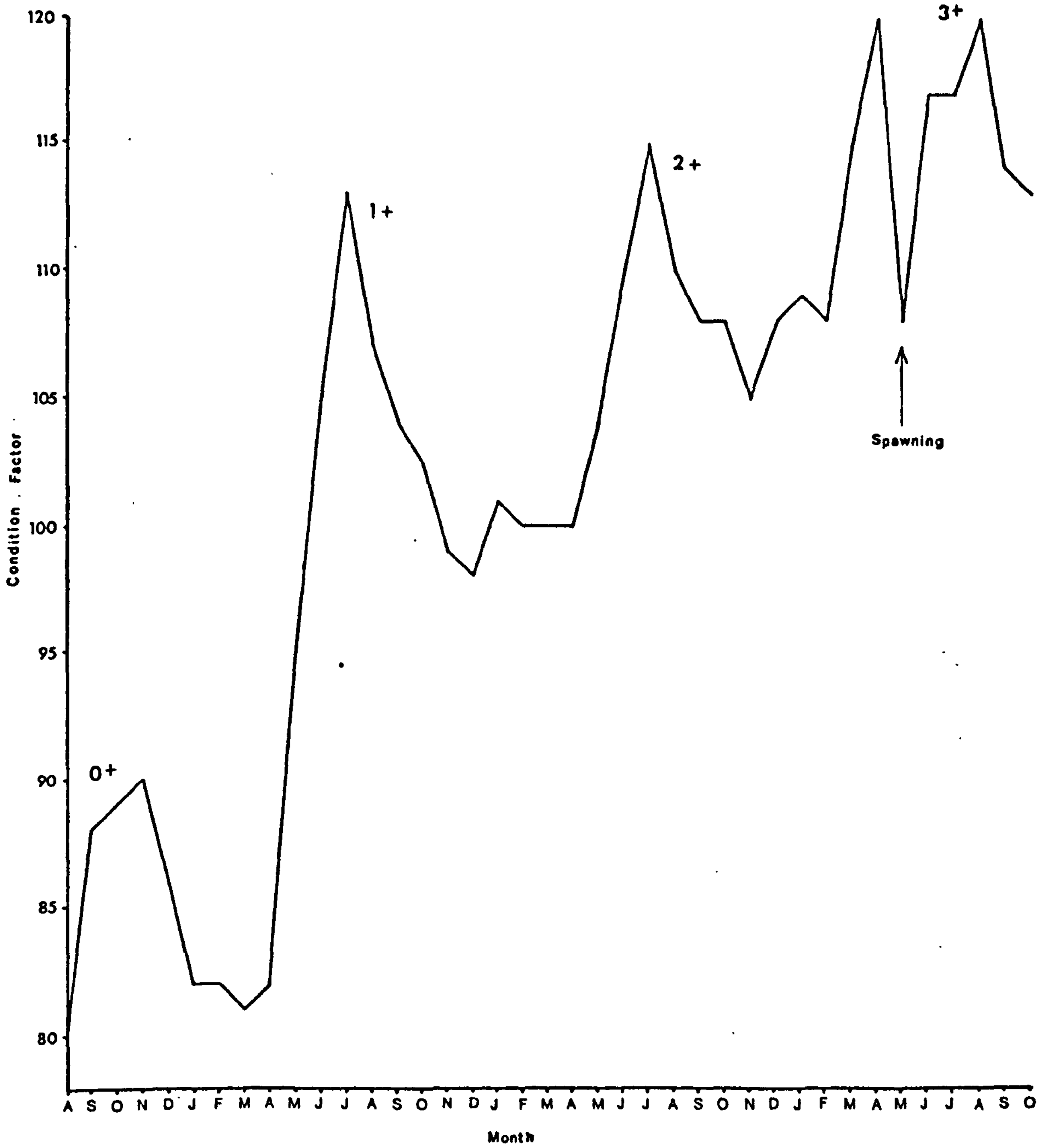
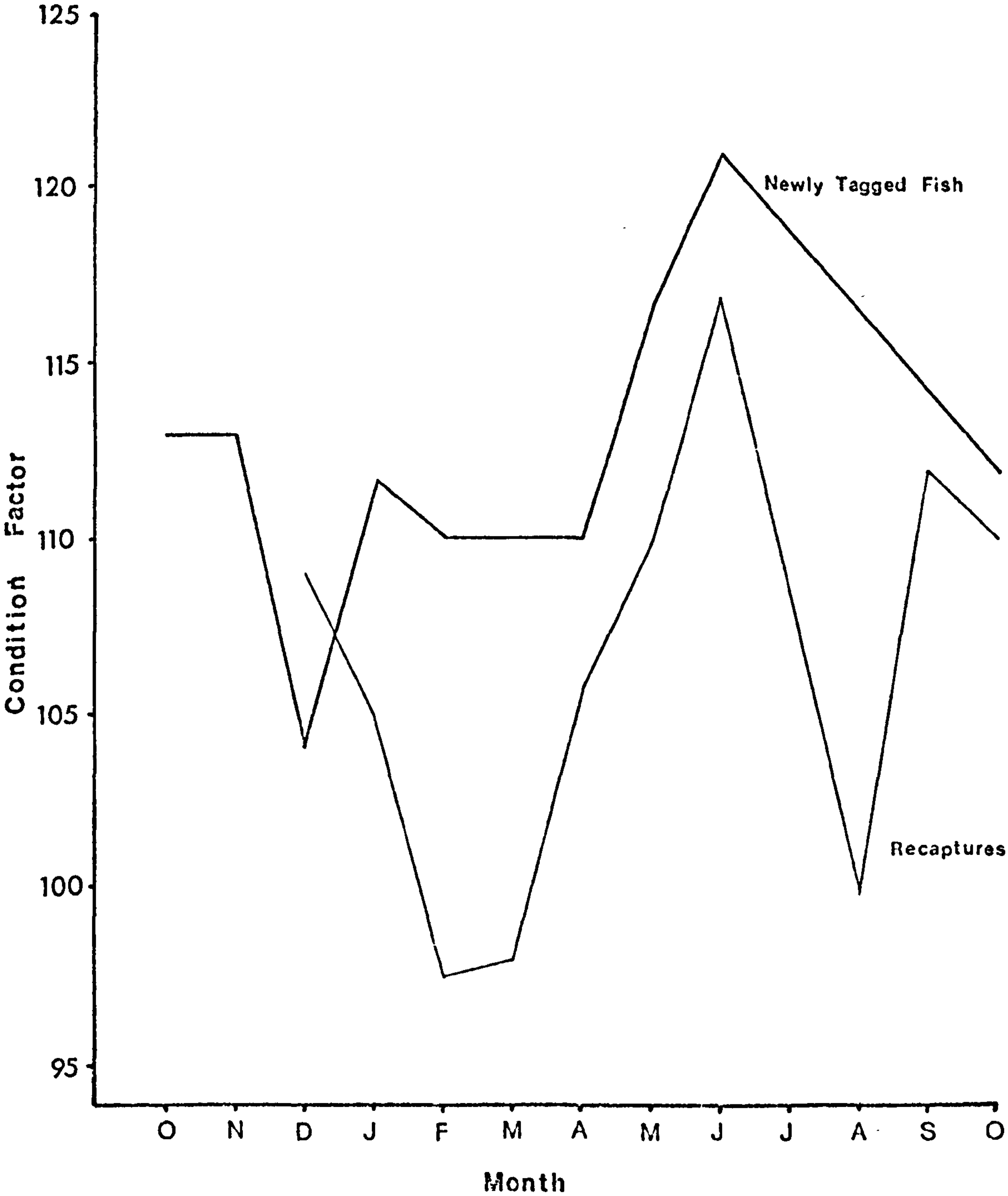


FIGURE 32

Effect of Tagging on the Condition of Llyn Tegid Grayling



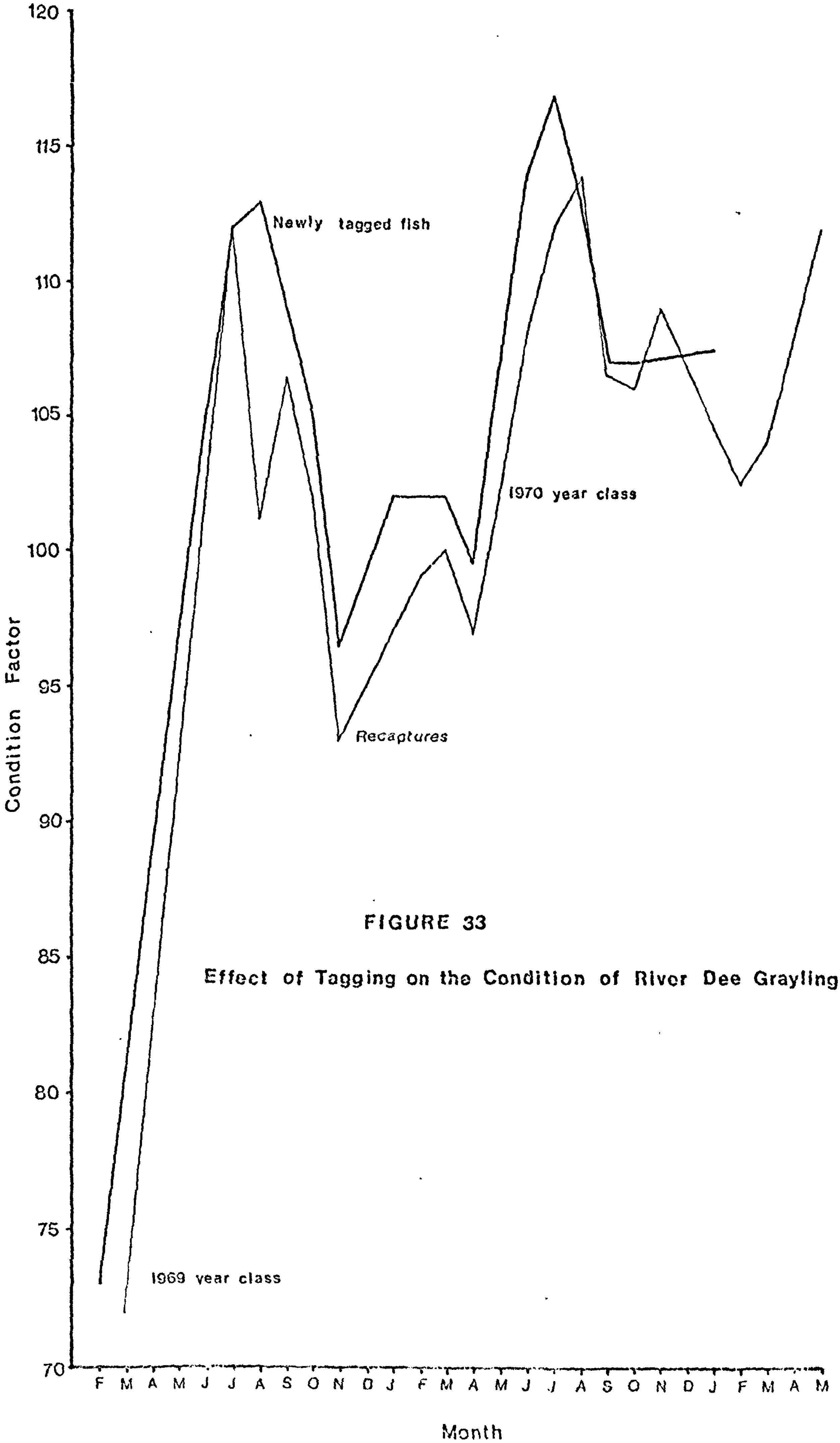


FIGURE 33

Effect of Tagging on the Condition of River Dee Grayling

of a number of the recaptured fish.

b. Annual growth

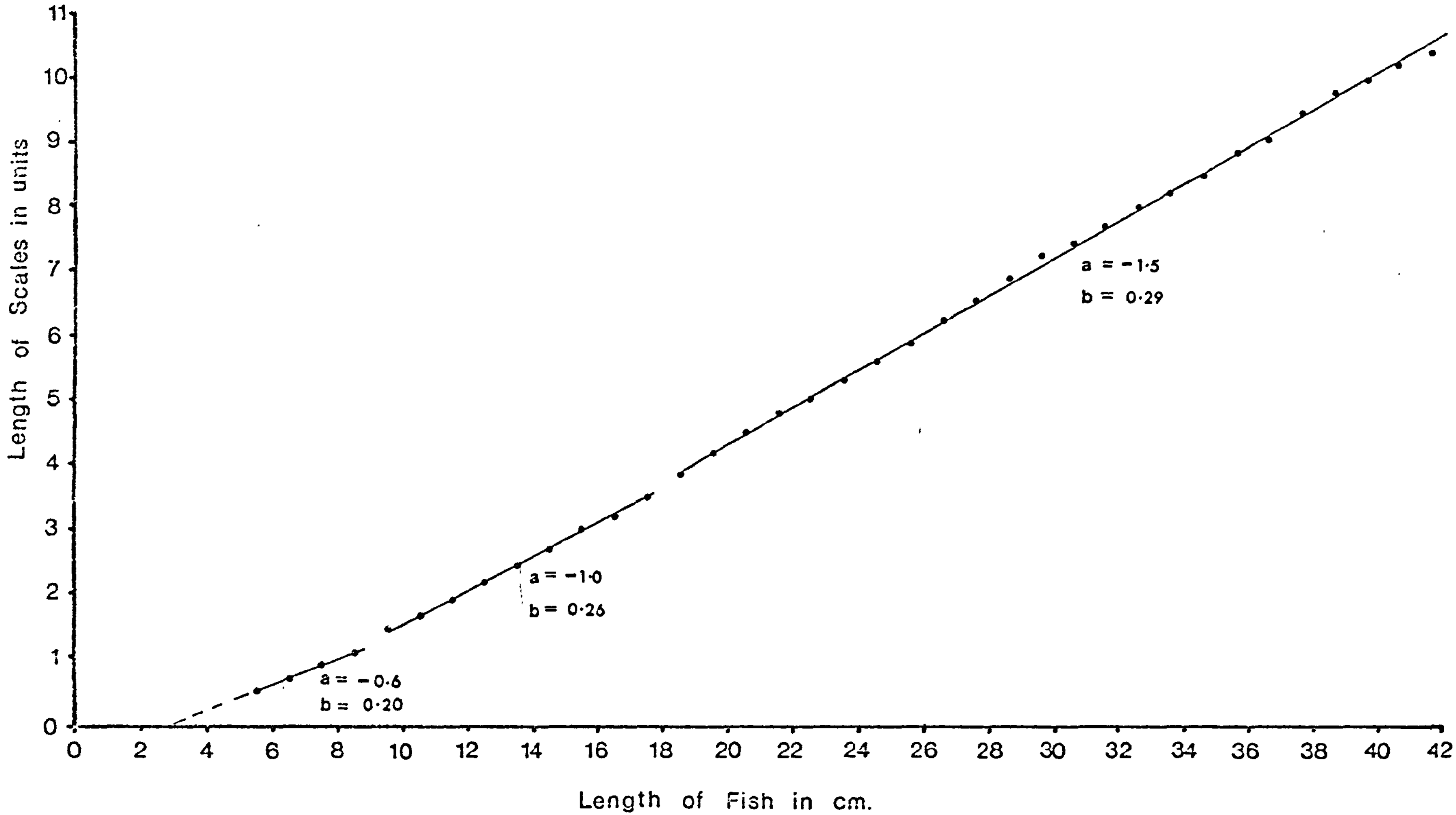
(i) The scale length/fish length relationship

The relationship between the grayling's body length and scale measurements has been investigated by a number of authors. Balon (1962) considered that his data, from measurements of the ventral diagonal scale radius, closely fitted a straight-line relationship, as did Brown (1943) in his work on Montana grayling. Svetovidov (1936) and Gustafson (1949), using an anterior scale radius and total fish length, found that the scale length/fish length relationship took the form of a parabolic curve, and Micha's (1971) data fitted a logarithmic curve.

The scale length/fish length relationship for Llyn Tegid and River Dee grayling is shown in figure 34. The data used to construct figure 34 were treated in three groups, and the parameters a and b for the equation $y = a + bx$ (where y = scale length in units, and x = fish fork length in centimetres) are included, for each group, in the figure. The regression lines were calculated from all of the accumulated data, but only the mean scale lengths for each 10mm. fish length group have been given in figure 34. The variation about the regression line was small with the standard deviation of the scale measurements varying from $\pm$ 0.2 units at 10cm fork length, to $\pm$ 0.7 units at 40 cm fork length. The results shown in figure 34 are intermediate between the straight line relationship found by Brown (1943) and Balon (1962), and the parabolic curve described by Svetovidov (1936) and Gustafson (1949).

FIGURE 34

Fish Length/ Scale Length Relationship of Grayling



(ii) Calculated lengths of Llyn Tegid grayling

The lengths of Llyn Tegid grayling at the end of each year of life were calculated by the method described in chapter 4, section B2, and are shown in figure 35. The data given in this figure were compiled from scale examinations of grayling caught between May 1950 and December 1953, January 1966 and January 1967, and October 1968 and October 1970. The results obtained were roughly divisible into two groups, the 1946 to 1952 year classes, and the 1962 to 1968 year classes. Growth rates within these two groups were very similar, but there appeared to be a large difference between the two groups, with the more recent group growing considerably faster than the early group.

Back calculated lengths showed little or no evidence of Lee's phenomenon (Lee, 1920), so data for successive years was combined to give mean lengths at the end of each year of life for the 1950-53, 1966-67 and 1968-70 grayling. The "end of each year of life", in terms of scale check time, occurred at very different times of the year in 1950-53 grayling and 1966-70 grayling (autumn and spring, respectively, see section 2b), and a correction for this factor was considered necessary. Calculated lengths were therefore plotted, with allowance made for the scale check time, as shown in figure 36. This graph showed very little difference between the growth rates of any of the Llyn Tegid grayling examined. Further comparisons between the different groups of Llyn Tegid fish were made in terms of specific growth rates (section (v)).

FIGURE 35

Calculated Lengths of Llyn Tegid Grayling

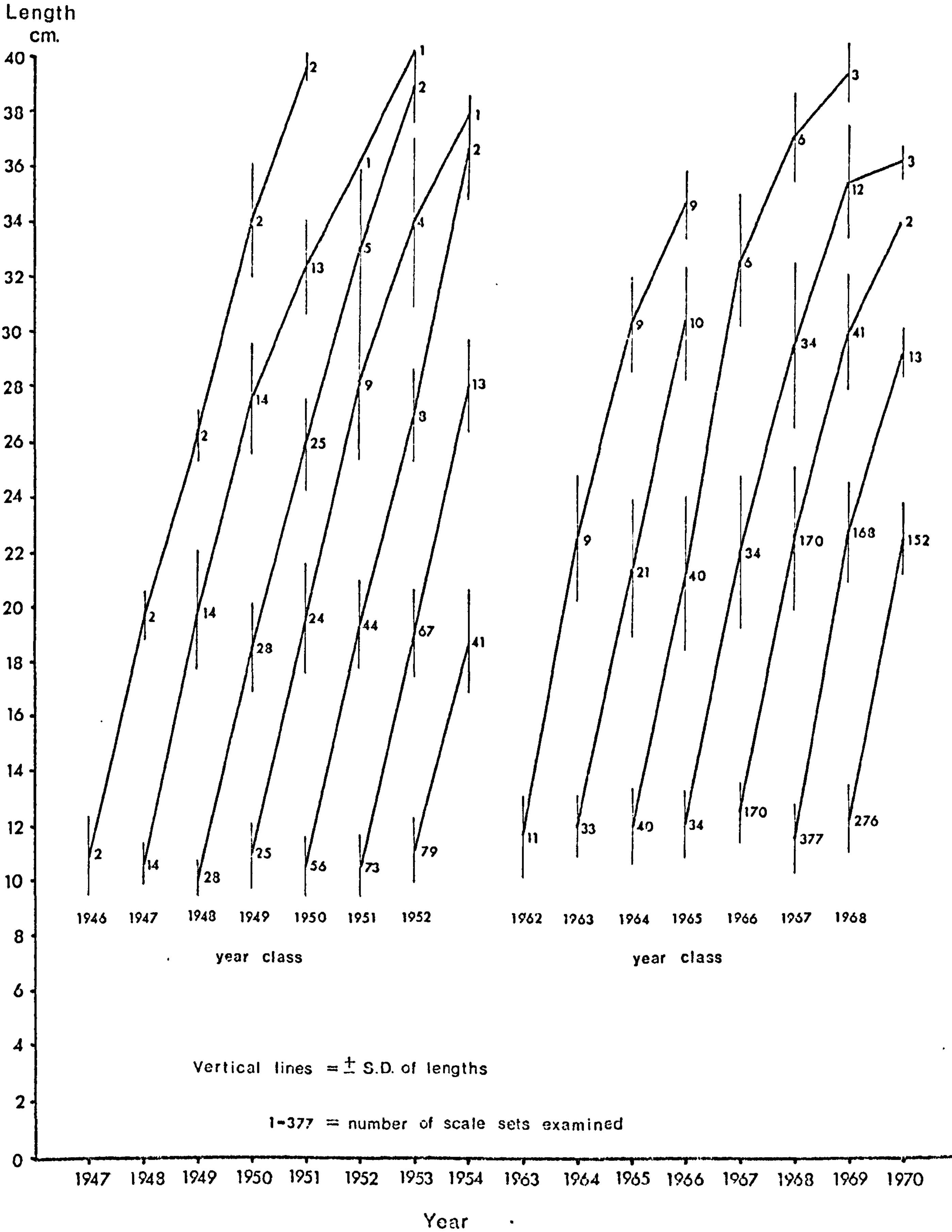
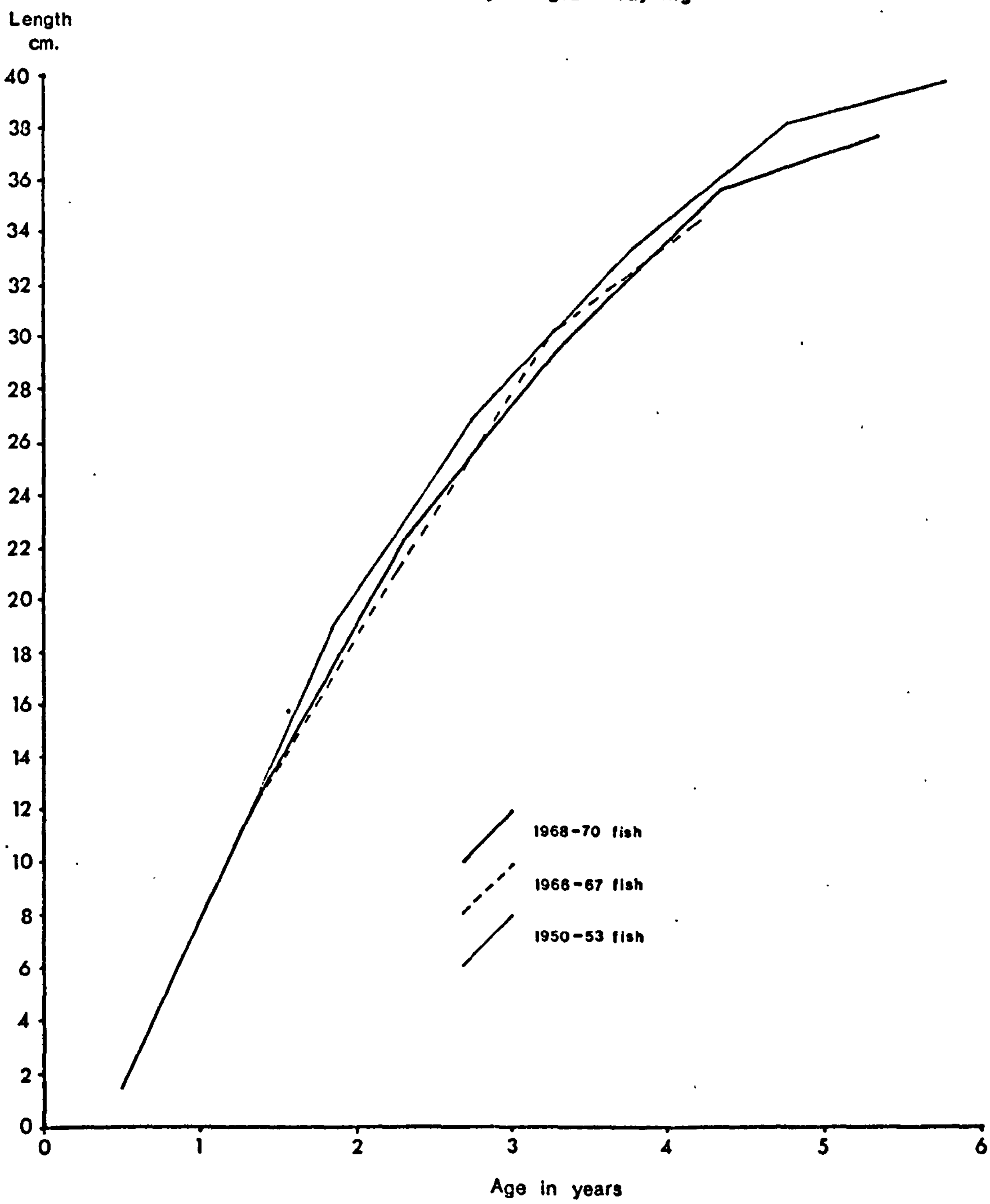


FIGURE 36

Calculated Growth of Llyn Tegid Grayling



(iii) Calculated lengths of River Dee grayling

The calculated lengths of upper Dee grayling are shown in figure 37. No evidence was found of Lee's phenomenon so data for successive year classes of upper Dee and Corwen grayling were combined and the results, together with those from Llyn Tegid grayling (1968–70), are given in figure 38.

Corwen grayling grew faster than upper Dee grayling at all ages ($p < 0.001$ to < 0.05), and faster than Llyn Tegid grayling for the first two years of life ($p < 0.002$ and < 0.001). The growth of Llyn Tegid and Corwen grayling was the same ($p > 0.1$) from the age of 3 years onwards, and Llyn Tegid grayling grew faster than upper Dee grayling ($p < 0.001$ to < 0.01) except during the first year of life.

(iv) Growth of male and female grayling

The calculated lengths of male and female grayling in Llyn Tegid and the upper Dee are shown in figure 39. The growth of male and female grayling was identical ($p > 0.10$) for the first two years of life in both Llyn Tegid and the River Dee, but from the age of 3 years onwards the males grew faster ($p < 0.001$) than the females. The observed differences in growth rate were correlated with the onset of sexual maturity, and similar findings have been recorded by Gustafson (1949), Solewski (1963), Jankovic (1964) and Peterson (1968). The relationship between maturity, size and age in fishes (including data on grayling) was discussed in detail by Alm (1959).

FIGURE 37

Calculated Growth of Upper Doe Grayling

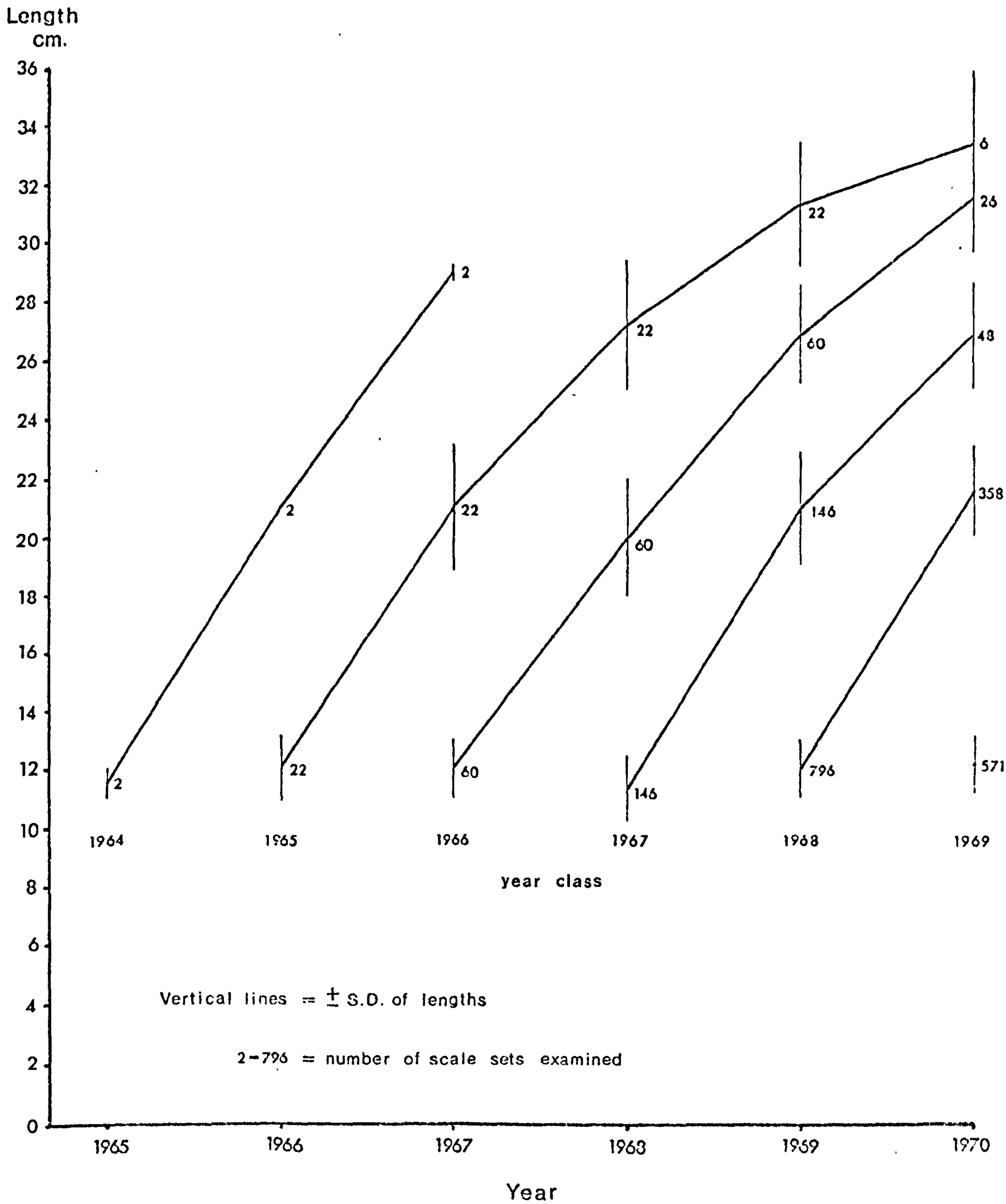


FIGURE 38

Calculated Growth of Grayling in Llyn Tegid and the River Dee

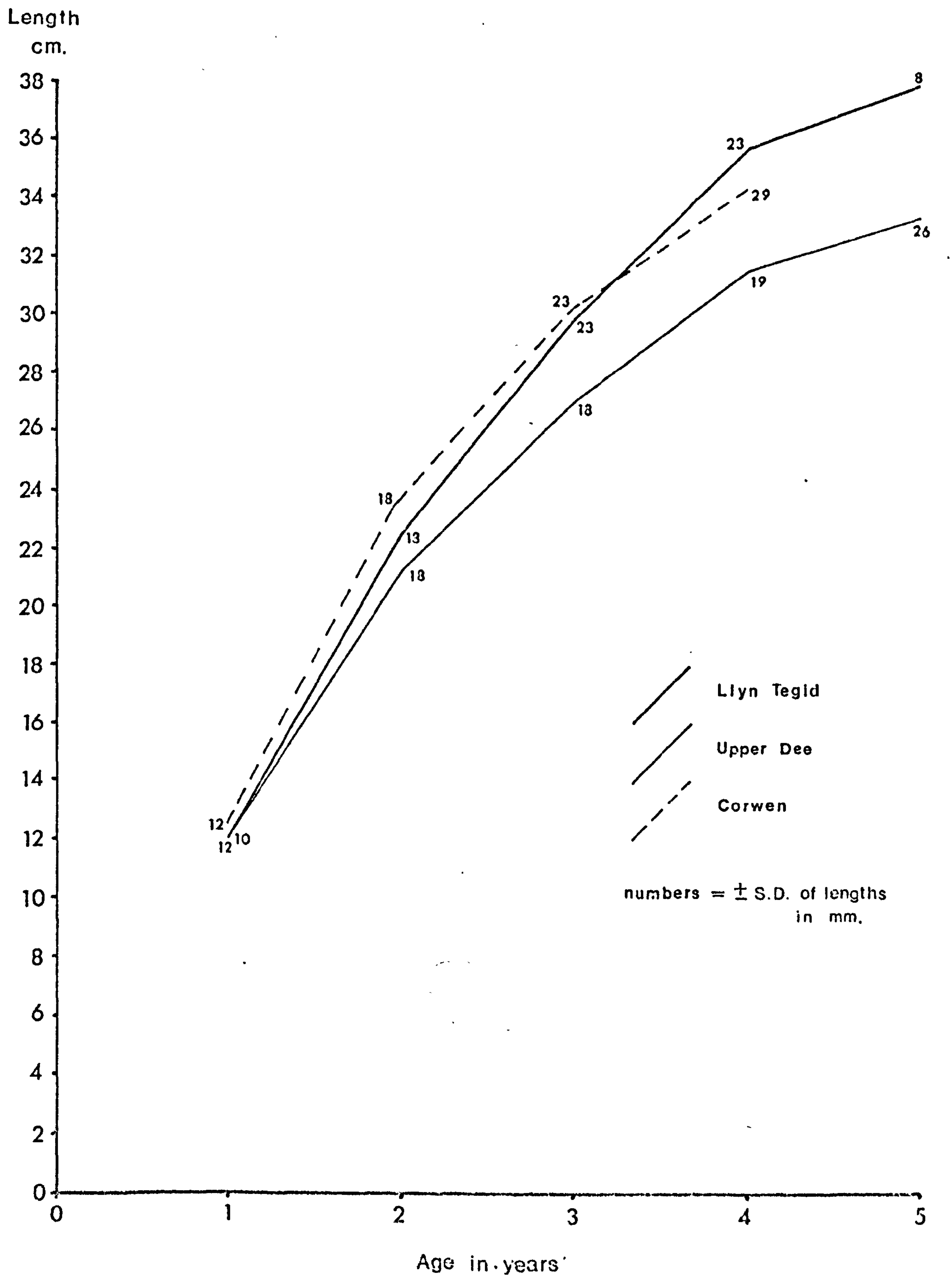
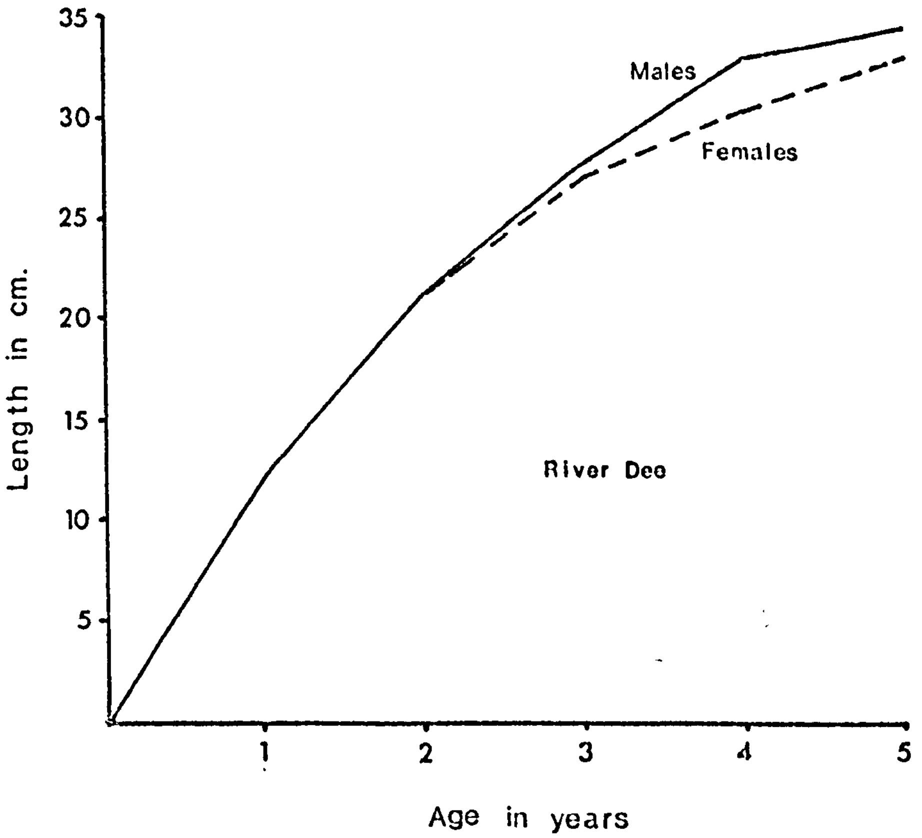
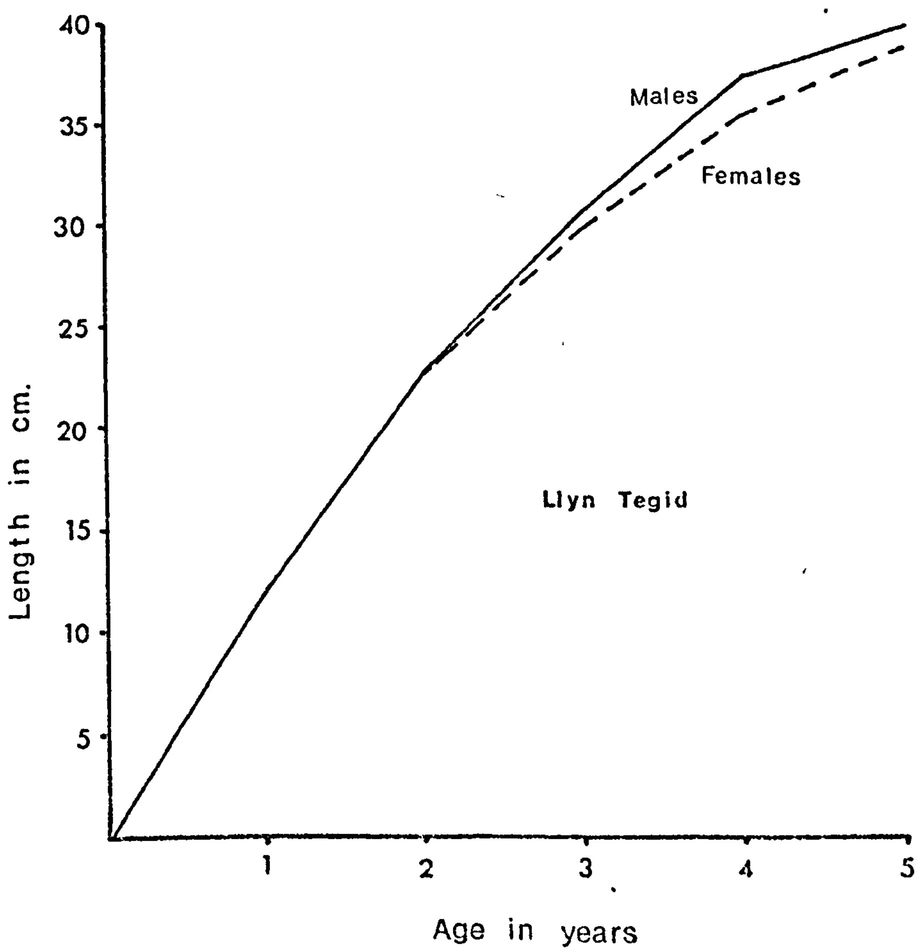


FIGURE 39

Calculated Growth of Male and Female Grayling





(v) Specific growth rates

Specific growth rates of grayling were calculated from the formula :

$$G = \frac{\log_e YT - \log_e Yt}{T - t} \times 100$$

where G = specific growth rate
YT = length at time T
Yt = length at time t
and T - t = one year

The specific growth rates of Llyn Tegid and River Dee grayling are shown in tables 27 and 28 respectively. The mean figures shown at the bottom of the table were calculated from mean lengths and not from mean specific growth rates. The specific growth rate in the first year of life was calculated after assigning an arbitrary initial length of 1.5 cm. This was considered to be the approximate length of grayling fry when they first began to feed.

Because of the differences in scale check times of Llyn Tegid grayling, the mean 0 — 1 year specific growth figures given in table 27, for the 1950-53 fish (1946-52 year classes) and for the 1966-70 fish (1962-68 year classes), are not comparable. The figures given for subsequent years, however, each represent a complete year's growth.

Specific growth rates were found to be high in the first year of life and to decline in later years with a decreasing negative

Table 27. Specific growth rates of Llyn Tegid grayling.

Year Class	Percentage increase in length per annum					
	0-1 year	1-2 years	2-3 years	3-4 years	4-5 years	5-6 years
1946	197.4	59.6	28.7	26.4	15.2	-
1947	193.6	63.4	33.9	16.4	10.8	10.8
1948	188.7	62.0	34.2	24.2	16.5	-
1949	197.4	59.1	36.5	19.1	10.9	-
1950	193.6	61.8	33.2	32.2	-	-
1951	193.6	60.3	38.8	-	-	-
1952	199.2	53.7	-	-	-	-
1962	203.7	67.1	29.8	13.6	-	-
1963	207.1	58.7	34.8	-	-	-
1964	207.1	58.3	34.5	12.9	6.3	-
1965	207.9	60.6	29.3	18.5	2.0	-
1966	211.2	59.6	28.4	12.9	-	-
1967	203.7	68.0	24.5	-	-	-
1968	209.6	61.2	-	-	-	-
Mean for 1946-52	194.7	59.3	34.8	21.7	13.7	4.1
Mean for 1962-68	207.9	60.3	31.5	16.3	7.0	-

Table 28. Specific growth rates of River Dee grayling.

	Year Class	Percentage increase in length per annum				
		0-1 year	1-2 years	2-3 years	3-4 years	4-5 years
Upper Dee	1964	203.5	60.3	32.3	-	-
	1965	207.9	56.0	25.9	14.4	6.2
	1966	207.9	51.1	29.6	16.1	-
	1967	201.9	62.0	24.8	-	-
	1968	207.9	58.8	-	-	-
	1969	209.6	-	-	-	-
Corwen	1964	207.9	66.8	31.3	-	-
	1966	212.0	61.4	27.1	12.7	-
	1967	207.9	66.8	25.8	-	-
	1968	209.6	66.4	-	-	-
	1969	214.4	-	-	-	-
	Mean for Upper Dee	207.9	57.4	23.7	15.7	5.5
	Mean for Corwen	212.0	64.4	24.2	12.7	-

acceleration. The highest rates were found in Corwen grayling during the early years of life, but Llyn Tegid grayling maintained a higher rate in later years. Llyn Tegid grayling had a higher specific growth rate than upper Dee grayling in all years except the first, and upper Dee grayling had a higher rate than Corwen grayling in later life.

A number of workers (Frost, 1945; Ball & Jones, 1960; Thomas, 1964) found that the overall growth pattern of trout was greatly influenced by the specific growth rate during the first year, and Thomas (op.cit.) found that trout with the highest specific growth in the first year always attained greater lengths at the end of each subsequent year. These observations were found to be only partially true for grayling. Corwen grayling showed a high specific growth rate in early years and maintained higher lengths than upper Dee grayling at all ages, but Llyn Tegid grayling reached the same length as Corwen grayling by the fourth year of life and from then on grew as fast as Corwen fish, or slightly faster. Grayling growth patterns were therefore affected not only by the specific growth in the first year of life, but also by the rate of decline of specific growth in subsequent years. Thus the relatively high specific growth rates maintained throughout life by Llyn Tegid grayling enabled these fish to achieve greater lengths than Corwen grayling which had higher rates of specific growth during the first two years of life, but more rapidly decreasing rates in later years.

The slower growth rates of upper Dee grayling in comparison with Corwen grayling probably resulted from the higher population density of grayling in the upper reach (chapter 10), and differences in population densities, together with the quantity and quality of the available food supply (chapter 7), may have accounted for the slower growth of upper Dee grayling in comparison with Llyn Tegid fish. The specific growth rates of the 1950-53 and 1966-70 groups of Llyn Tegid grayling were similar during the second year of life but from then on the 1950-53 group grew quicker. These differences may have resulted from an increased population of grayling in the lake (chapter 10), changes in the invertebrate fauna since regulation (Hynes, 1961a; Hunt, 1970), or differences in the seasonal growth cycle. The first and last of these factors probably had the greatest effect on growth rates, as most invertebrate animals have become re-established in the lake since regulation, and some have even increased in number (Hunt, 1970). One of the major changes which occurred in the seasonal growth cycle from the 1950-53 group of grayling to the 1966-70 group was the shortening of the "summer" growth phase (section 2a). The higher specific growth rate of the former fish was therefore spread over a longer growing period, and may not have been higher at any one instant during the accelerated growth phase than that of the latter group. Nevertheless, the 1950-53 fish had a higher annual specific growth rate than the 1966-70 group and consequently achieved a greater overall size.

(vi) Length/weight relationships

The length /weight relationship of most fish can be adequately represented by

$$W = a L^{b} \qquad (1)$$

where a is a constant, and b is an exponent with a value nearly always between 2 and 4, often close to 3 (Tesch, 1968).

Expression (1) can be transformed to :

$$\log w = \log a + b \log L \qquad (2)$$

A plot of weight against length on double logarithmic graph paper should therefore approximate to a straight line.

The logarithmic regressions of weight on length for Llyn Tegid grayling and River Dee grayling are shown in figures 40 and 41, together with the mean weights for each 10mm length group, the regression coefficients b, and the y-axis intercepts a.

Micha (1971) found that the length/weight relationship of grayling comprised two parts, one for fish above 19cm. and one for fish below 19cm., each with different regression coefficients and y-axis intercepts. He considered that the single straight line logarithmic relationship shown by Hellawell (1969b) resulted from the inadequacy of the data on fish below 15cm. The general upward trend of K with increasing length found in my study (section 3a,iv, figures 30 and 31), suggests that changes in the length/weight relationship occur throughout the life of the fish. Regression coefficients and y-axis intercepts were calculated for each age group of grayling from Llyn Tegid and the River Dee, and are given

FIGURE 40

Length/Weight Relationship of Llyn Tegid Grayling

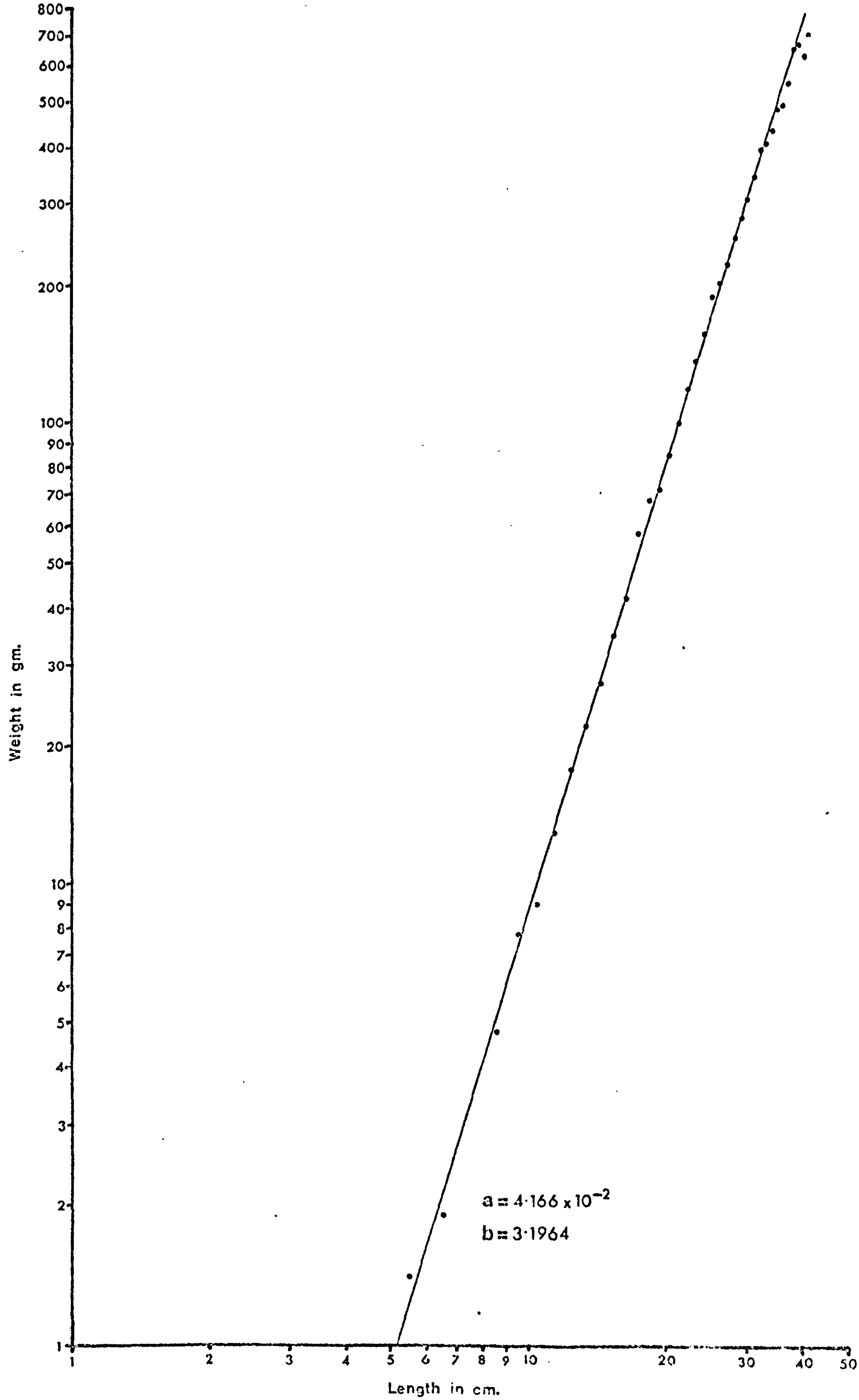
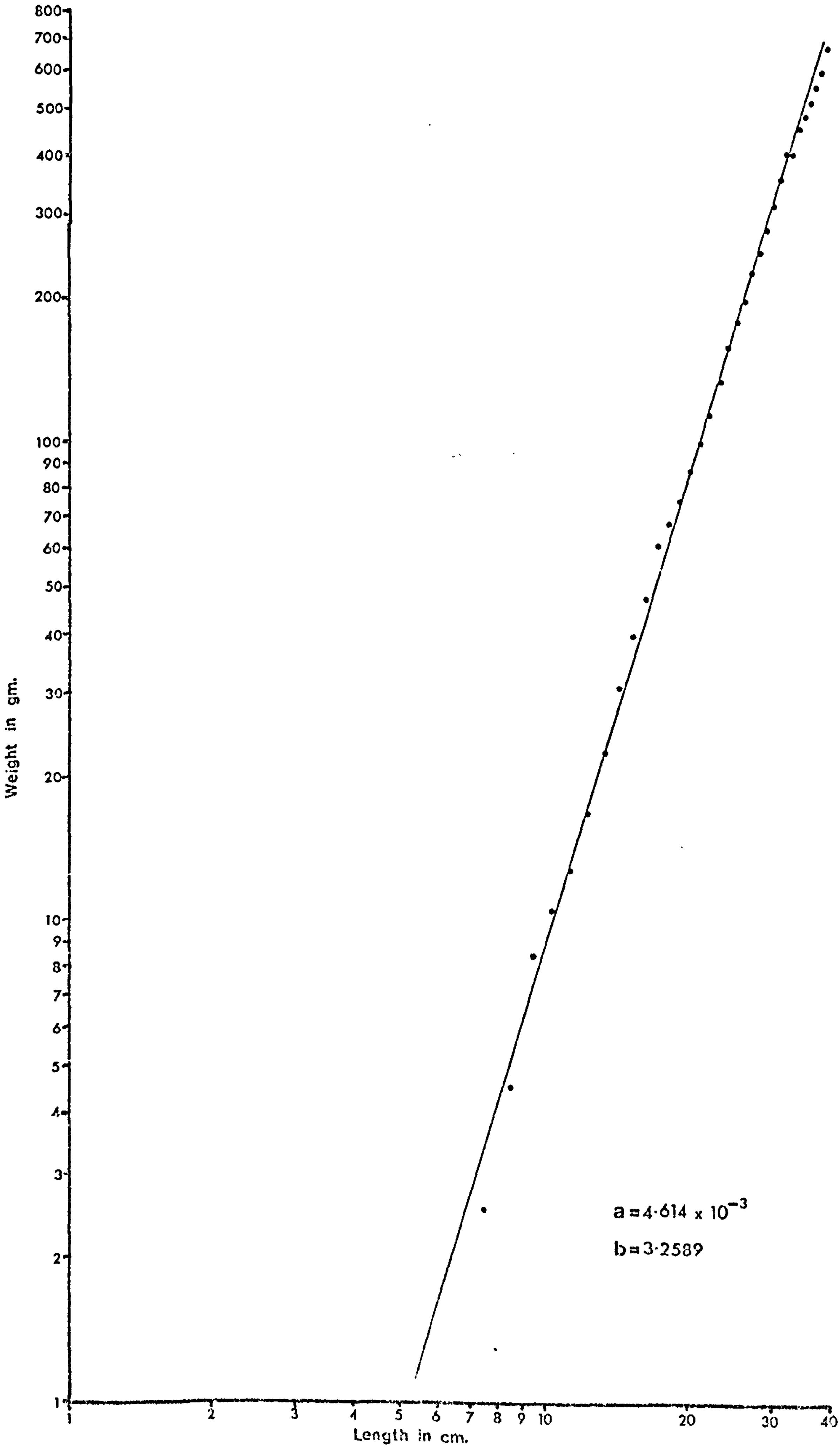


FIGURE 41

Length/Weight Relationship of River Dee Grayling



in tables 29 and 30.

Table 29. Variation of the logarithmic length/weight relationship with age in Llyn Tegid grayling.

Age in (years)	length group (cm)	y-axis intercept a	regression coefficient b
1	11-13.5	1.074×10^{-2}	2.9227
2	20-24	2.424×10^{-3}	3.4694
3	27-32	8.039×10^{-3}	3.0909
4	33-38	3.518×10^{-2}	2.6667

Table 30. Variation of the logarithmic length/weight relationsip with age in River Dee grayling.

Age in years	length group (cm)	y-axis intercept a	regression coefficient b
1	10-13	1.605×10^{-2}	2.7569
2	19-22	1.701×10^{-2}	2.8300
3	25-28	7.389×10^{-3}	3.1041
4	29-33	5.214×10^{-3}	3.8776
5	31-36	6.397×10^{-2}	2.5060

These tables indicate that changes do occur in the length/weight relationship throughout the life of grayling. Hunt (1970) found that the parameters a and b changed seasonally in trout, and this could also be expected to occur in grayling. The overall logarithmic lenght/weight relationship of grayling showed an increasing weight per unit length up to 3 or 4 years of age, follwed by a decrease in subsequent years.

The annual growth in weight of Llyn Tegid and River Dee grayling was calculated from the length/weight relationships described above, and is shown in figure 42.

(vii) Maximum size of grayling in Llyn Tegid and the River Dee.

The Walford plots shown in figure 43 indicate that $L\infty$ for grayling is 37.6 cm. in the upper Dee, 40.8 cm. at Corwen, and 45.0 cm. in Llyn Tegid. Grayling were captured at Corwen and in the upper Dee which exceeded these asymptotic lengths. The largest grayling caught during my study were 43.5 cm. (910gms) in Llyn Tegid (scale shown in plate 26), 42.2 cm. (845 gms) at Corwen, and 39.2 cm. (680 gms) in the upper Dee. Grayling of about 900-1000 gm. have been reported by anglers fishing in the River Dee at Corwen, but the alleged capture of a fish of 2000 gm. (4½lbs) at Bodweni seems highly improbable, the only British rivers producing grayling of this size are the very productive south-country chalk streams and possibly a few Scottish rivers such as the Tweed and the Ida (Perthshire).

In Yugoslavian rivers Jankovic (1964) found grayling of 42.0 cm (800-1000gm.), and Muller (1961) caught one of 52.0 cm. (ten years old) in the Lule Alv. Hutton (1923) examined scales of a grayling 43.2 cm. in length from the Hampshire Avon. Table 31 shows the growth rates of grayling in a number of British and European waters.

4. Summary

(1) The age and growth of grayling was assessed from the measurements and scale examinations of 1585 Llyn Tegid grayling caught between 1950-1970, and 1935 River Dee grayling caught between

FIGURE 43

Walford Plots for Grayling in Llyn Tegid and the River Dee

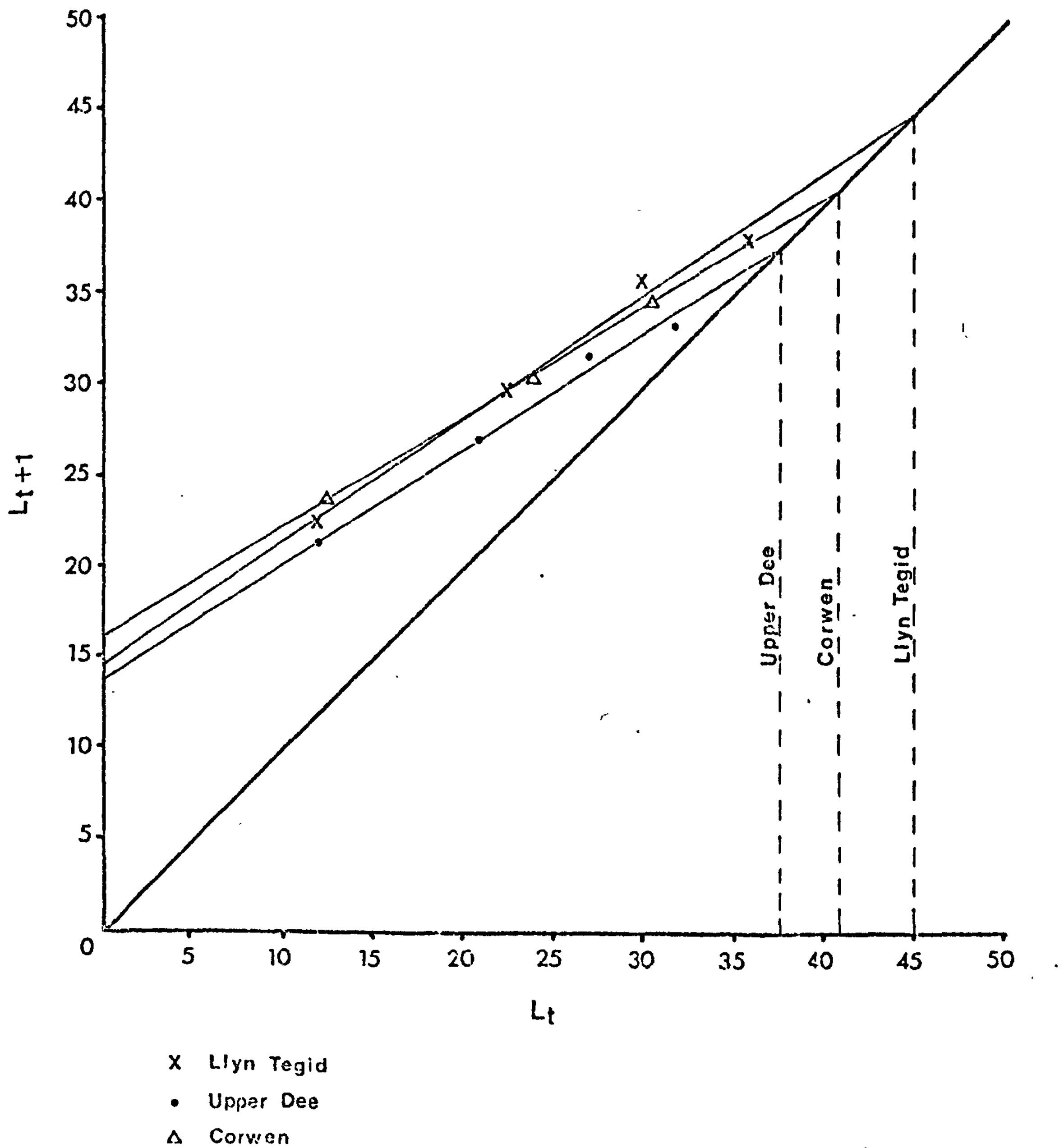


FIGURE 42

Annual Growth in Weight of Llyn Tegid and River Dee Grayling

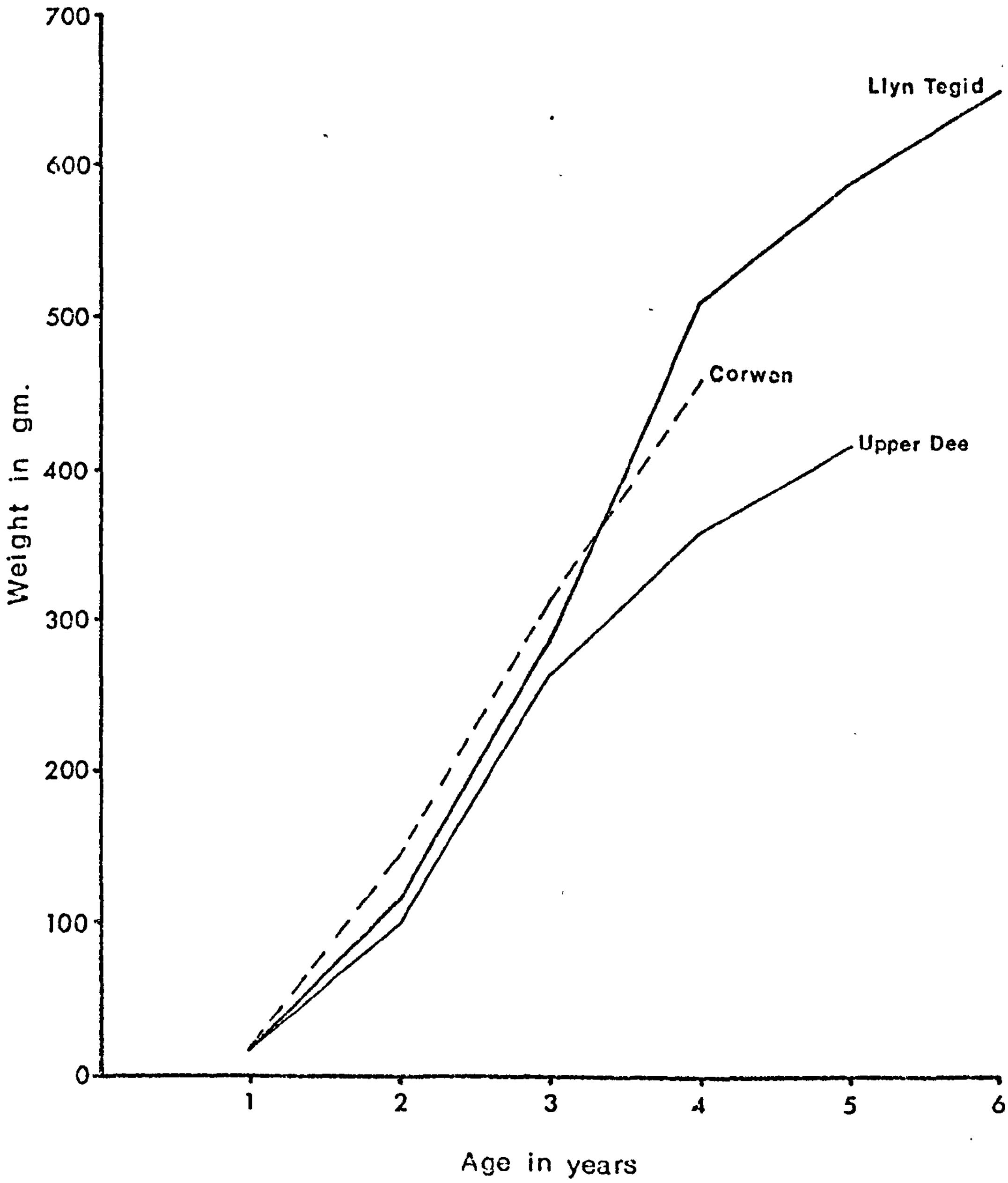


Table 31. Comparative growth rates of grayling in various waters.

Location	Length (cm.) at the end of each year of life 1	2	3	4	5	6	7	8
Upper Dee	12.0	21.3	27.0	31.6	33.4	-	-	-
River Dee at Corwen	12.5	23.8	30.3	34.4	-	-	-	-
Llyn Tegid	12.0	22.5	29.8	35.8	37.9	39.9	-	-
River Gryfe (Mackay, 1970)	12.0	20.0	25.0	30.0	-	-	-	-
Douglas Water (Mackay, 1970)	7.6	16.8	22.7	25.3	29.0	-	-	-
River Lugg (Hellawell, 1969a)	11.0	16.7	26.0	30.3	-	-	-	-
River Test (Hutton, 1923)	15.9	28.6	33.5	38.7	41.3	43.2	-	-
Lake Storsjo (Gustafson, 1949)	8.4	15.9	23.2	28.5	31.7	33.7	37.8	-
Drobsinska riverine lake (Balon, 1962)	14.7	22.4	26.9	29.4	31.1	-	-	-
River Indalsalven (Peterson, 1968)	9.4	17.2	23.9	29.6	34.9	38.6	40.8	41.3
Yugoslavian rivers (Jankovic, 1964)	15.6	24.1	30.6	35.1	39.0	41.2	42.0	-
Ourthe River (Micha, 1971)	14.5	23.5	29.5	-	-	-	-	-

October 1969 and October 1970.

(2) The scales of grayling were described and the occurrence of "spawning marks" was discussed.

(3) A study of the seasonal scale growth ring cycle showed that the annual check of Llyn Tegid and River Dee grayling during the 1966-70 period was laid down in the spring. The annual check of Llyn Tegid grayling in the 1950-53 period, and again in the 1970-72 period, was formed during the autumn.

(4) Age determination from grayling scales, the occurrence of summer checks, and the time of scale formation were discussed.

(5) The main period of accelerated growth in length and weight was found to be April/May to October/November. Grayling with autumn scale checks grew throughout the winter. No significant difference was found between the growth rates of net and rod caught fish, or between the growth rates of tagged and untagged fish.

(6) The condition (K) of grayling showed marked seasonal fluctuations in addition to a general increase with age. Condition rose quickly in the early summer and declined during the autumn and winter. Llyn Tegid grayling showed a sharp fall in condition during August. The condition of mature fish was highest just before spawning and lowest immediately after spawning. The condition of grayling was found to be adversely affected by tagging.

(7) The calculated lengths of upper Dee grayling were lower than those of Corwen and Llyn Tegid grayling. Corwen grayling grew

faster than Llyn Tegid grayling during early life, but slower in later years. Llyn Tegid grayling caught in the 1950-53 period grew slightly faster than those caught in the 1966-70 period.

(8) Mature male grayling grew faster than mature females.

(9) The length attained by grayling at the end of each year of life was found to depend not only on the specific growth rate (G) in the first year, but also on the rate of decline of G in subsequent years.

(10) The logarithmic length/weight relationship of grayling was found to approximate to a straight line, but changes occurred in the regression coefficient b and the y-axis intercept a throughout life. The annual growth in weight of Llyn Tegid and River Dee grayling was calculated from the length/weight relationships.

(11) The maximum size of grayling in Llyn Tegid and the River Dee was discussed, and the growth rates of grayling in various waters were compared.

CHAPTER VI

THE AGE AND GROWTH OF TROUT AND YOUNG SALMON

1. Introduction

Some previous research has been carried out in the Welsh Dee area on the age and growth of both trout and young salmon. Jones (1949) studied the scales of 1500 young salmon from the River Dee and paid particular attention to the seasonal growth ring cycle, the effects of spawning on scales, the growth of young salmon, and the age at smolt migration. Ball & Jones (1960, 1962) in their studies on Llyn Tegid trout included observations on the growth of trout in the Afon Lliw and Afon Glyn. These authors also investigated the age at which trout migrated from the feeder streams into Llyn Tegid, and the effects of migration on the length/frequency distributions of trout which remained in the streams. Jones (1950a, 1950b, 1951, 1953) made studies on adult Dee salmon and determined the duration of river life in the juvenile stages, and the relative proportions of the different smolt age groups. In my study I have examined the scales and measurements of 1830 salmon parr and 1306 trout from the Llyn Tegid feeder streams, together with 316 salmon parr and 148 trout from the River Dee between Corwen and Bala. The Llyn Tegid feeder stream material was collected from November 1968 to March 1970, and the River Dee material was captured whilst fishing for grayling between October 1969 and October 1970.

Many studies have been made on the age and growth of trout and young salmon in other British waters. Studies made in British rivers on young salmon include those of Carr (1913), Allen (1940, 1941b), Frost & Went (1940) and Mills (1964); on trout, Southern (1935), Gerrish (1938, 1939), Went & Frost (1942), Frost (1945), Horton (1961), Thomas (1962, 1964) and Kennedy & Fitzmaurice (1971); and on both species, Frost (1950), Spence & West (1964), Egglishaw (1967), Robins (1967) and Vickers (1969). Pyefinch (1955) reviewed the literature on atlantic salmon, and recent books which give details of age and growth studies are those of Jones (1959) on salmon, Frost & Brown (1967) on trout, and Mills (1971) on salmon and trout. Went (1964) reviewed the investigations that had been carried out on Irish salmon up to 1963.

2. Age determination

The use of scales for ageing salmon and trout is a well established procedure and has been described in detail for salmon by Jones (1959), and for trout by Frost & Brown (1967). The scales of young salmon and trout in the Welsh Dee area, and the validity of their use for age determination were described by Jones (1949) and Ball & Jones (1960). The terminology used by these authors has been adopted in my study. The "birthday" of both salmon and trout was considered to be March 1st (Ball & Jones, op.cit.) and the length at commencement of feeding as 2.4 cm (Frost & Brown, op.cit.).

"Cutting over" of incomplete winter rings by the first summer ring (Frost & Went, 1940; Ball & Jones, 1960) was found on the scales of both salmon and trout, and allowed the quick and certain identification of completed winter bands. Ball & Jones (op.cit.) were unable to identify spawning marks on the scales of Llyn Tegid trout and non were found in my study, either in River Dee trout or in Llyn Tegid feeder stream trout. Summer checks were recorded on a small number of trout and salmon scales and appeared to have been laid down during July or August. These checks are related to above optimum temperatures acting either through the respiratory system (Fry, 1957; Swift, 1961) or the digestive system (Pentelow, 1939).

The seasonal scale growth ring cycles of the 1968 year classes of trout and young salmon in the Llyn Tegid feeder streams and the River Dee are shown in figure 44. This figure clearly shows that the annual scale check was formed in early April by both species in both habitats. This time closely corresponds with that found by Jones (1949) and Ball & Jones (1960). Since the scale check time almost coincided with the allotted "birthday" the age classes could be allotted according to the number of completed winter bands. Fish were considered to be at the end of year year of life in March, and to be in the next year of life in April when "summer" growth rings first appeared on the scales.

The age structure of the samples of salmon and trout can be seen in tables 32 and 33, and in the length/frequency distributions shown in figures 45 and 46. Most salmon smolted at 2 years of age (see chapter 12) and few fish over that age were captured after May. Many 2-4 year old trout migrated during the spring from the

FIGURE 44

Seasonal Scale Growth of Salmon Parr and Trout

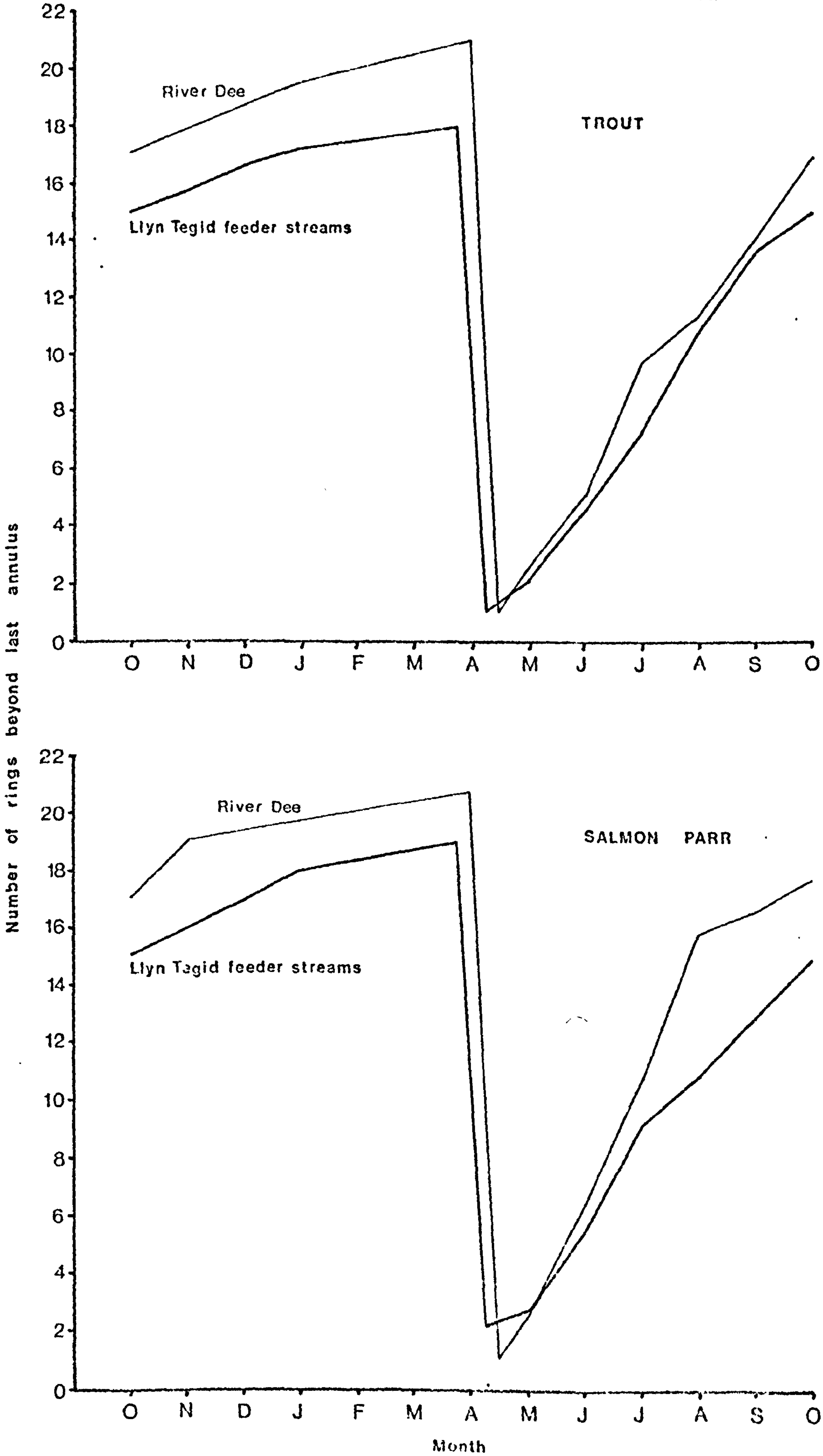


Table 32. Numbers of young salmon examined each month

(a) Llyn Tegid feeder streams.

Month	Total number	Numbers in each year class 1966	1967	1968	1969
November	17	2	9	6	-
December	30	-	18	12	-
January 1969	45	-	24	21	-
February	37	3	27	7	-
March	178	4	114	60	-
April	79	4	55	20	-
May	87	1	21	65	-
June	42	-	1	41	-
July	179	-	28	125	26
August	119	-	13	105	1
September	197	-	14	154	29
October	71	-	5	56	10
November	156	2	22	101	31
December	127	1	5	103	18
January 1970	202	-	12	143	47
February	36	-	1	28	7
March	228	1	18	174	35
Total nos. of fish	1830	18	387	1221	204

Table 32. cont. Numbers of young salmon examined each month.

(b) River Dee

Month	Total no. Upper Dee (Corwen)	Numbers in each year class: 1967	1968	1969	1970
October	31	2	24	5	-
November	28	-	14	14	-
December	1	-	-	1	-
January 1970	13	1	7	5	-
February	-	-	-	-	-
March	3	-	3	-	-
April	14	-	12	2	-
May	22(3)	3	15 (3)	4	-
June	33(7)	1	10	22 (7)	-
July	41(6)	1	3	37 (6)	-
August	27(6)	-	-	27 (6)	-
September	36(4)	1	6 (2)	27 (2)	2
October	34(7)	-	-	32 (6)	2 (1)
Total nos. of fish	283 (33)	9	94 (5)	176 (27)	4 (1)

Table 33. Numbers of trout examined each month.

(a) Llyn Tegid feeder streams.

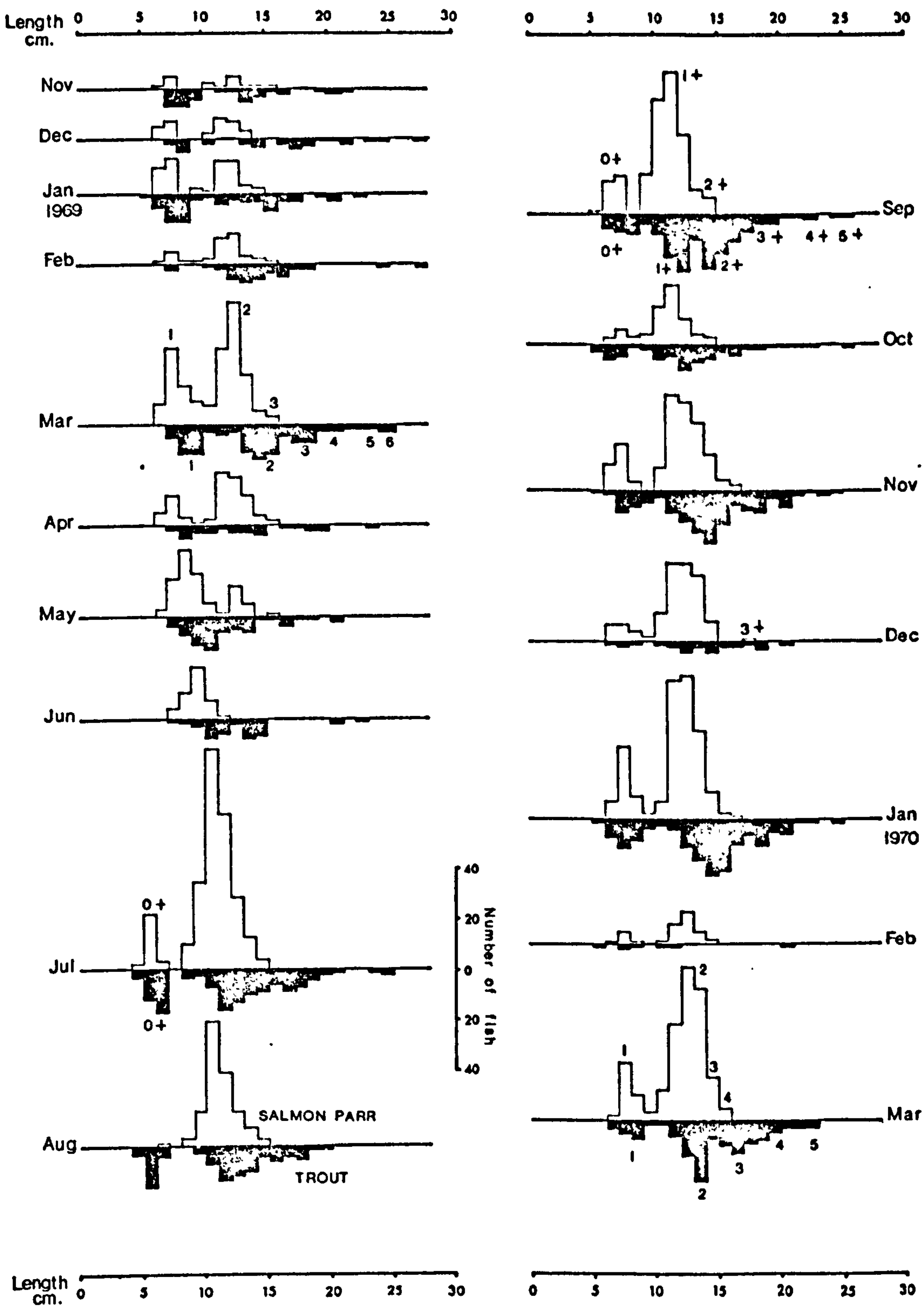
		Numbers in each year class						
Month	Total	1963	1964	1965	1966	1967	1968	1969
November	35	-	-	2	3	12	18	-
December	27	-	-	2	10	6	9	-
Jan 1969	63	-	-	2	12	17	32	-
February	37	1	-	1	7	26	2	-
March	106	1	1	9	25	39	31	-
April	30	-	-	-	7	10	13	-
May	61	-	-	-	3	18	40	-
June	45	-	-	1	2	14	28	-
July	126	-	-	4	8	33	49	32
August	87	-	-	-	4	18	42	23
September	158	-	1	1	14	49	72	21
October	76	-	-	3	3	13	38	19
November	141	-	-	3	9	36	71	22
December	24	-	-	-	-	5	15	4
Jan 1970	150	-	-	1	6	39	72	32
February	7	-	-	-	1	-	2	4
March	133	-	3	8	8	34	63	17
Total nos of fish	1036	2	5	37	122	369	597	174

Table 33. contd. Numbers of trout examined each month.

(b) River Dee

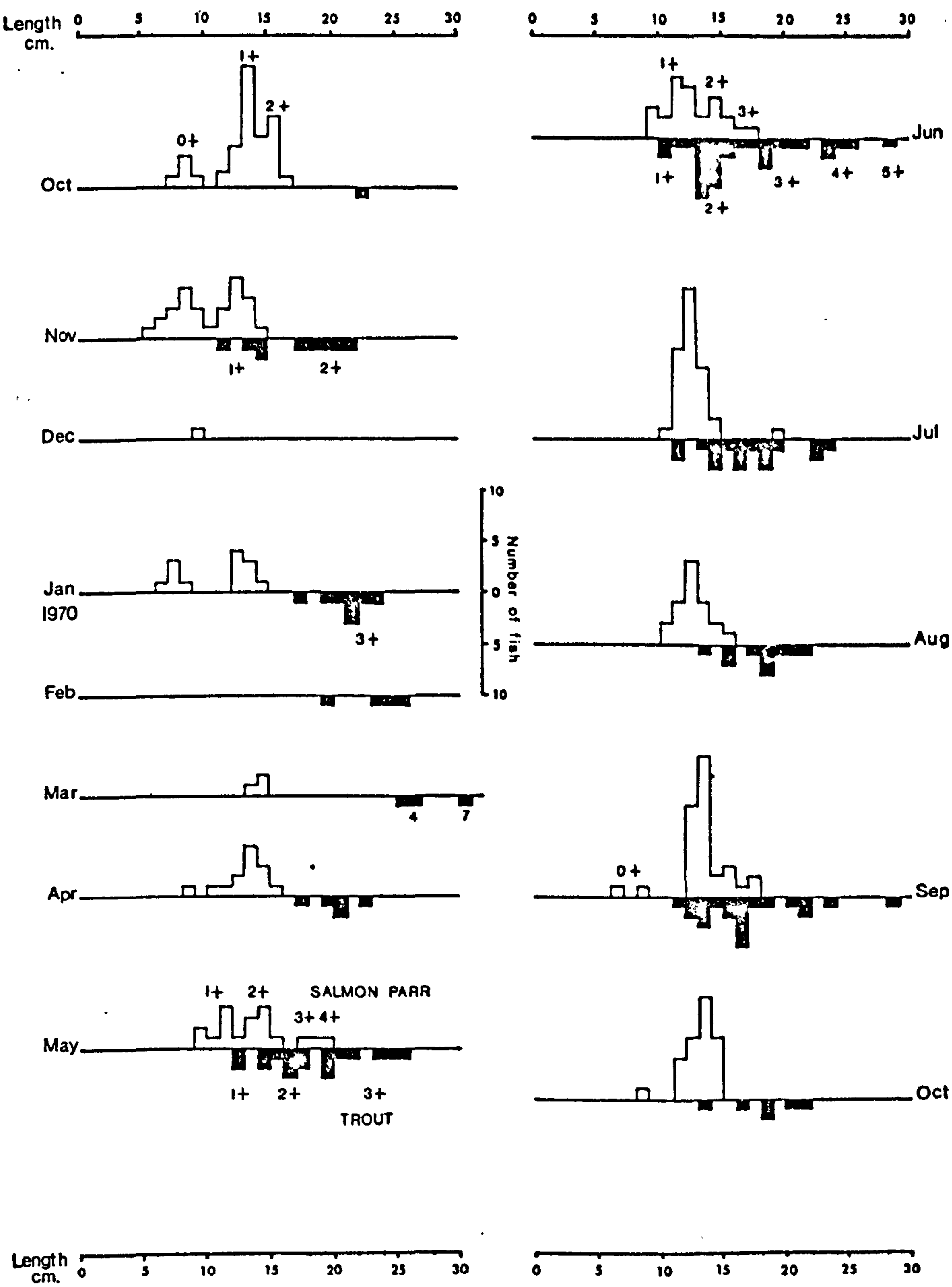
Month	Total Upper Dee (Corwen)	1963	1964	1965	1966	1967	1968	1969
October	1	-	-	-	-	1	-	-
November	9	-	-	-	-	4	5	-
December	8	-	-	-	2	5	1	-
Jan 1970	5	-	-	1	-	4	-	-
February	4	-	-	-	1	3	-	-
March	3	1	-	-	1	1	-	-
April	7	-	-	1	-	4	2	-
May	16(7)	-	-	-	- (4)	6 (1)	10 (2)	-
June	26(3)	-	-	-	2	2	11 (3)	11
July	19	-	-	-	1	2	11	5
August	10	-	-	-	-	-	9	1
September	21 (2)	-	-	1	-	3	8	9 (2)
October	6	-	-	-	- (1)	-	5	1
Total nos of fish	135(13)	1	0	3	7 (5)	35 (1)	62 (5)	27 (2)

FIGURE 45



Seasonal Length/Frequency Distribution of Salmon Parr and Trout in the Llyn Tegid Feeder Streams

FIGURE 46



Seasonal Length/Frequency Distribution of Salmon Parr and Trout in the River Dee feeder streams into Llyn Tegid (Ball & Jones, 1962) and trout of 4+ years and older comprised only 2.1% of the total sample number from the feeder streams. In the River Dee, trout over 4 years of age comprised 8.1% of the total sample number.

3. Growth

(a) Seasonal growth

(i) Material

The numbers of salmon and trout examined each month from the Llyn Tegid feeder streams and the River Dee are shown in tables 32 and 33. The Corwen samples were considered separately from the Upper Dee samples in the same way as for grayling (chapter 5, section 3a).

(ii) Growth in length

The seasonal growth in length of trout and juvenile salmon in the Llyn Tegid feeder streams and the Upper Dee is shown in figures 47-50. Data on salmon parr and trout older than 3 years have not been included in these figures because of the small number of old fish captured. The seasonal growth of Corwen fish is excluded for the same reason. The data from the Llyn Tegid feeder streams have been combined since no significant difference ($p > 0.10$) was found between the lengths of salmon parr from the different streams, and the length differences of trout were only significant ($p = 0.05$) from the fourth year of life onwards (see section 3B).

The accelerated growth period of salmon parr and trout started during April and coincided with the first appearance of wide summer

FIGURE 47

Seasonal Growth in Length of Young Salmon in the Llyn Tegid Feeder Streams

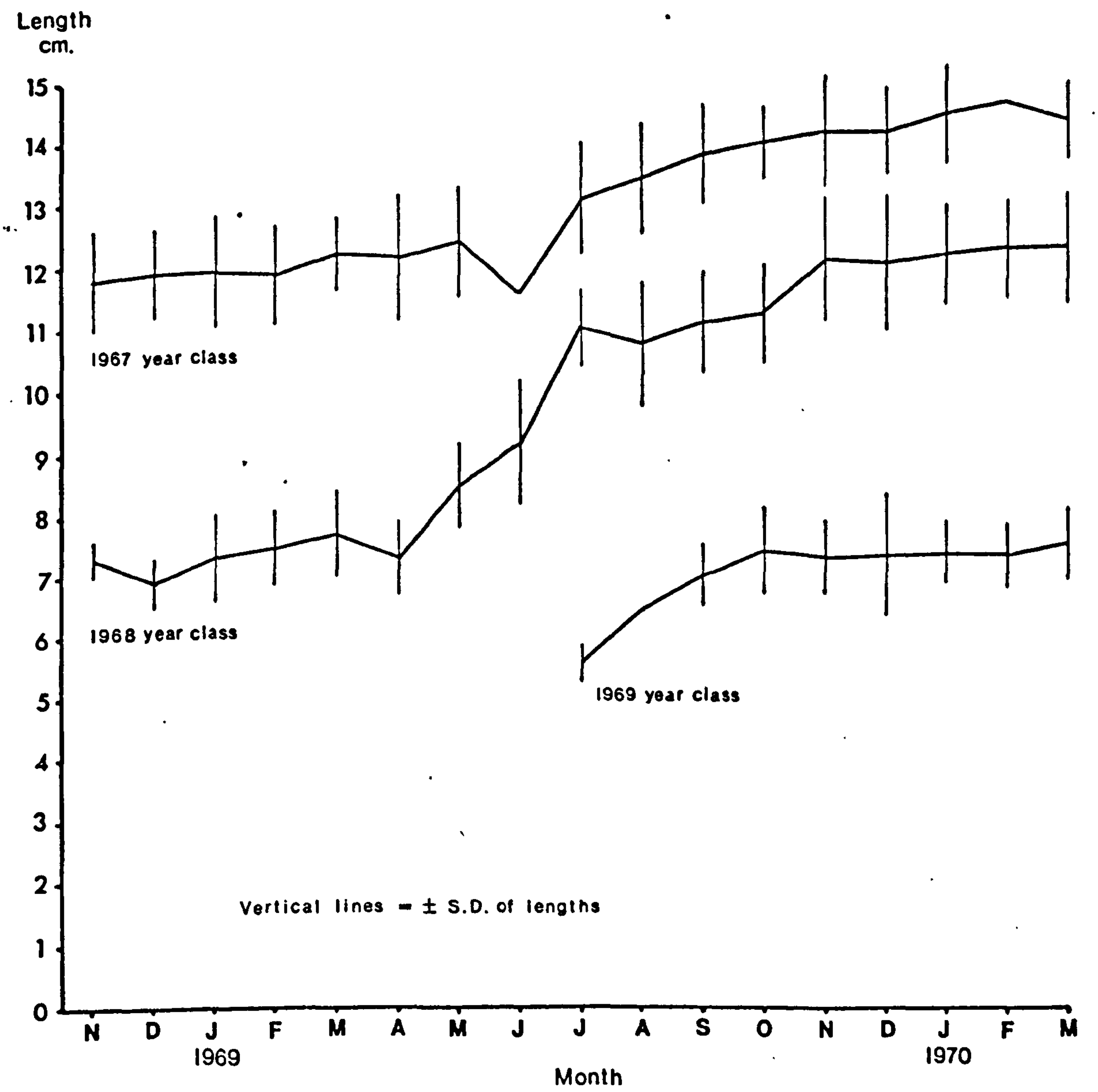


FIGURE 48

Seasonal Growth in Length of Young Salmon in the Upper Dee

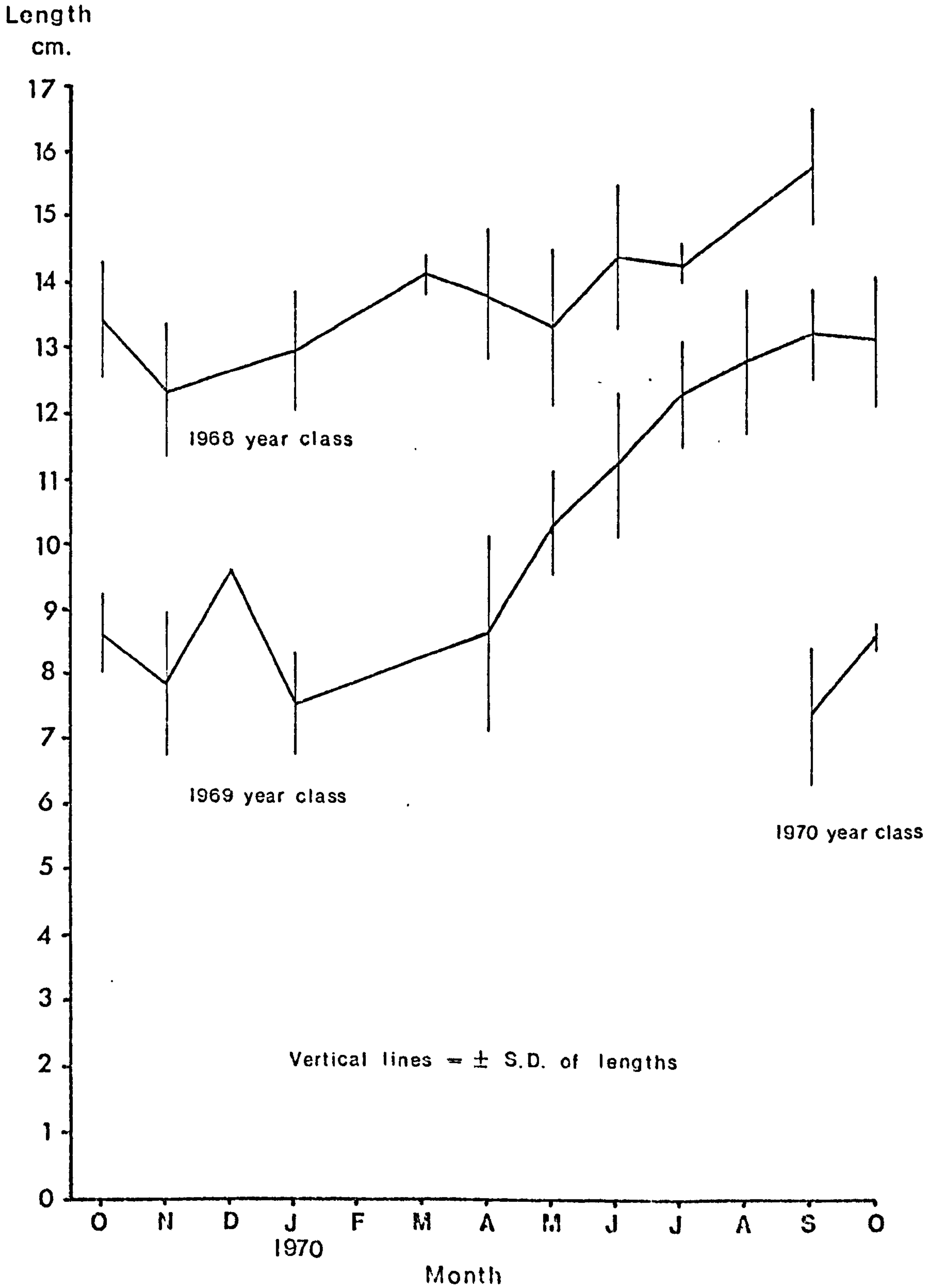


FIGURE 49

Seasonal Growth in Length of Trout in the Llyn Tegid Feeder Streams

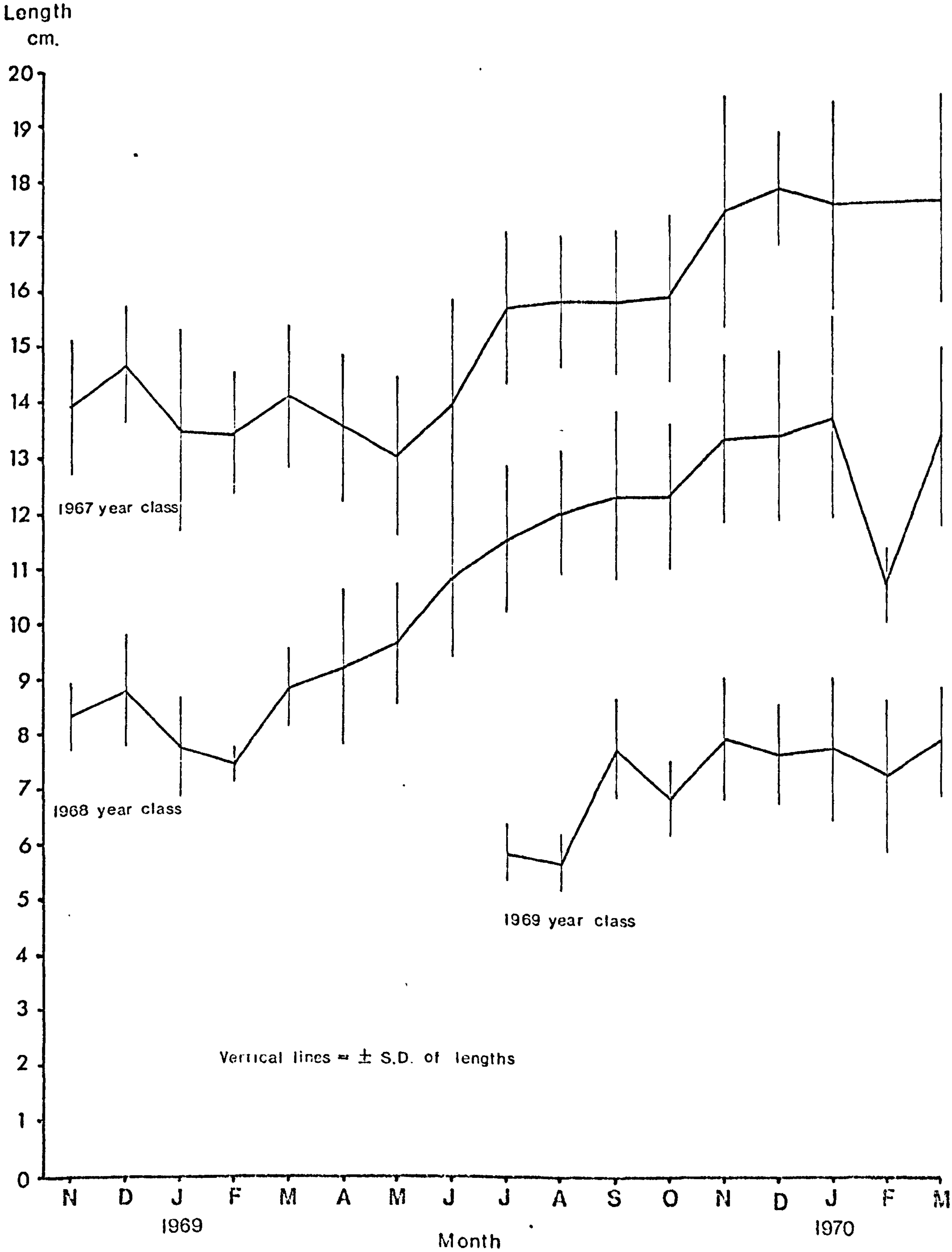
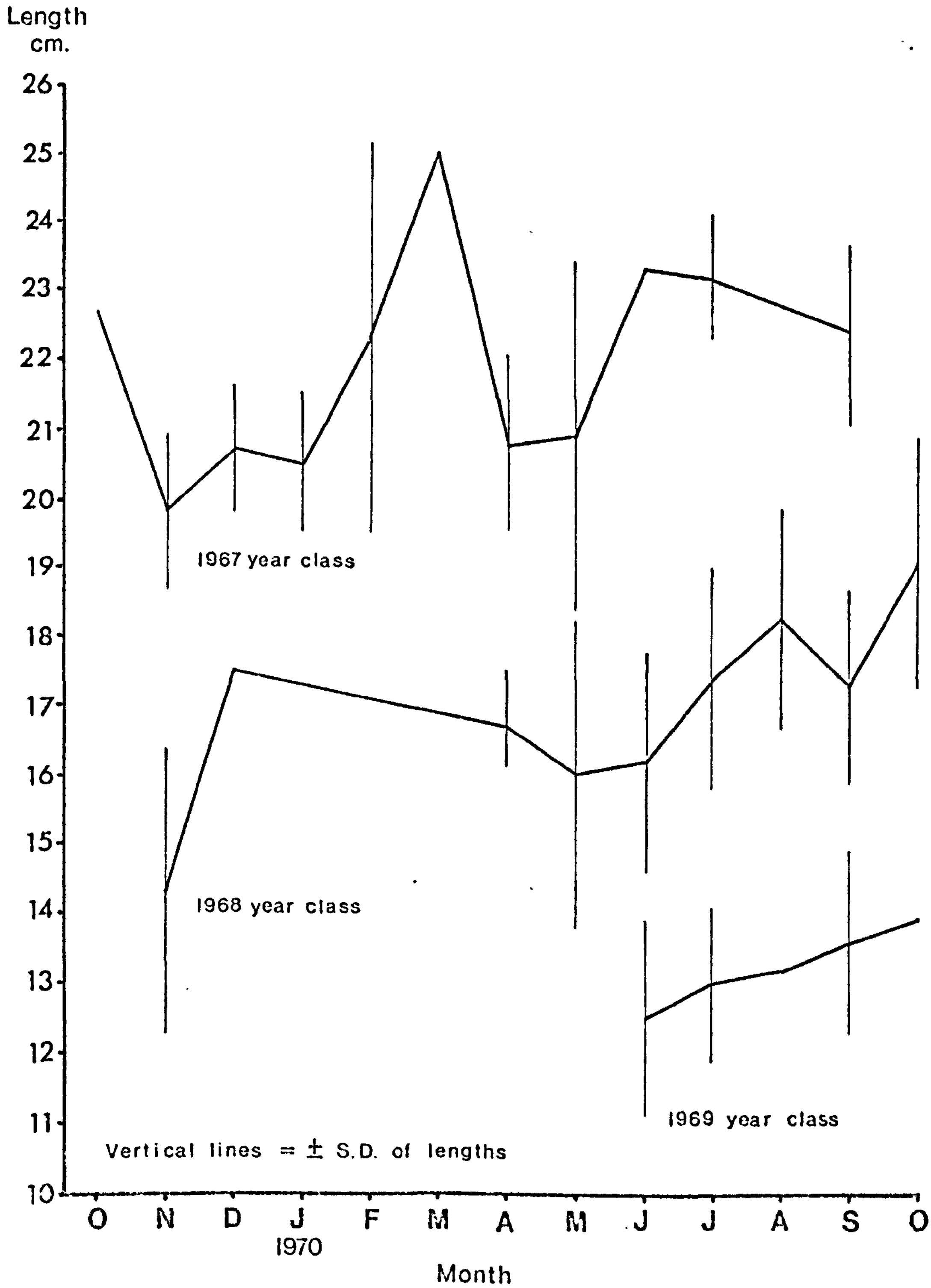


FIGURE 50

Seasonal Growth in Length of Trout in the Upper Dee



scale rings (section i) and the increase in feeding intensity (chapter 8). These findings closely agreed with those of Jones (1949) and Ball & Jones (1960), and with those of other workers in different waters (Frost & Went, 1940; Thomas, 1964; Egglishaw, 1967). The early growth of 0+ fry could not be determined since fry were not captured in the feeder streams until July, and in the River Dee until September. Ball & Jones (1962) first observed trout fry in the feeder streams during May, but were unable to catch any until August. No trout under the age of 1+ were caught from the River Dee, and this reflects the selectivity of the sampling method (rod). The accelerated growth period of salmon and trout started approximately one month earlier than in grayling. Gerrish (1938) found the reverse to be true in the Hampshire Avon.

A number of authors have discussed the effects of water temperature on the growth and general activity of salmonids. Jones (1959) found that salmon parr fed at water temperatures as low as 2°C and Allen (1940, 1941b) considered that the critical temperature for commencement of active feeding and growth in salmon parr was 7°C. Brown (1946b) found two optimum temperature ranges for the growth of trout, 7-9°C and 16-19°C, but Swift (1961) criticised these results on the grounds of inadequate data and concluded that the optimum temperature for the growth of brown trout was about 12°C. In my study the growth rate started to accelerate rapidly during April when the water temperature ranged from 4-8°C (chapter 3) and fell sharply when the water temperature rose above about 17°C

(July/August). Thomas (1964) recorded a similar decrease in the growth rate of a number of trout that he examined. A small increase in growth rate occurred in the Llyn Tegid feeder stream fish during the autumn at water temperatures of 8-14°C. Little or no growth occurred during the winter.

Ball & Jones (1962) referred to the significant decrease which occurred in the mean lengths of feeder stream trout following the spring migration of the larger trout of each age group from the streams into Llyn Tegid. A similar decrease was found in the mean length of the 1967 year class during April and May 1969, and can be clearly seen in figure 49. A decrease was not apparent in other year classes at that time because two year old trout alone comprised the vast majority of the migrant fish (Ball & Jones, op.cit.). A corresponding decrease in the mean length of salmon parr remaining after smolt migration may also be expected to occur (Allen, 1940), and such a decrease can be seen in figures 47 and 48 for 2 year old fish from both the River Dee and the Llyn Tegid feeder streams during May and June. The two year old fish again comprised the bulk of the migrants.

The growth of rod caught and net caught fish in the River Dee was not significantly different ($p>0.10$). The effects of tagging on the growth rate of trout and salmon depended on the tagging method used. Fin clips and dye innoculation had no significant effect ($p>0.10$) on the growth rate of trout or salmon, but the individual ministry tags described in chapter 4 (section A 2b) caused a significant decrease ($p<0.001$) in the growth rates of salmon parr.

The effects of tagging on the growth of salmon parr are shown in figure 51. The change from little or no effect in salmon below 10.5cms. to the marked effect in fish above that length, closely corresponds to the change from fin clipping and dye innoculation to individual tagging. Figure 51 thus shows the effects of both types of marking or tagging on the growth of young salmon. Ministry tags were not used in trout, but similar tags used by Fagerstrom et al. (1969) were found to retard the growth of trout.

(iii) Growth in weight

The seasonal growth in weight of trout and juvenile salmon in the Llyn Tegid feeder streams and the upper Dee is shown in figures 52-55. Fish older than 3 years, and all Corwen fish, have been excluded from these figures for the reasons given in the previous section.

The seasonal growth in weight of trout and juvenile salmon was found to closely follow the seasonal cycles of growth in length.

(iv) Condition

The seasonal condition factor (K), calculated as described in chapter 5 (section 3a,iv), of salmon parr and trout is shown in figures 56-59. Figure 56 shows that the condition of salmon parr rises rapidly from April to July, decreases in August, rises again in the autumn and falls sharply after November. A general upward trend of K with increasing age is also apparent. Hoar (1939) found that the condition of salmon parr increased with length up to the

FIGURE 51

Effect of Tagging on the Growth of Salmon Parr in the Llyn Tegid Feeder Streams

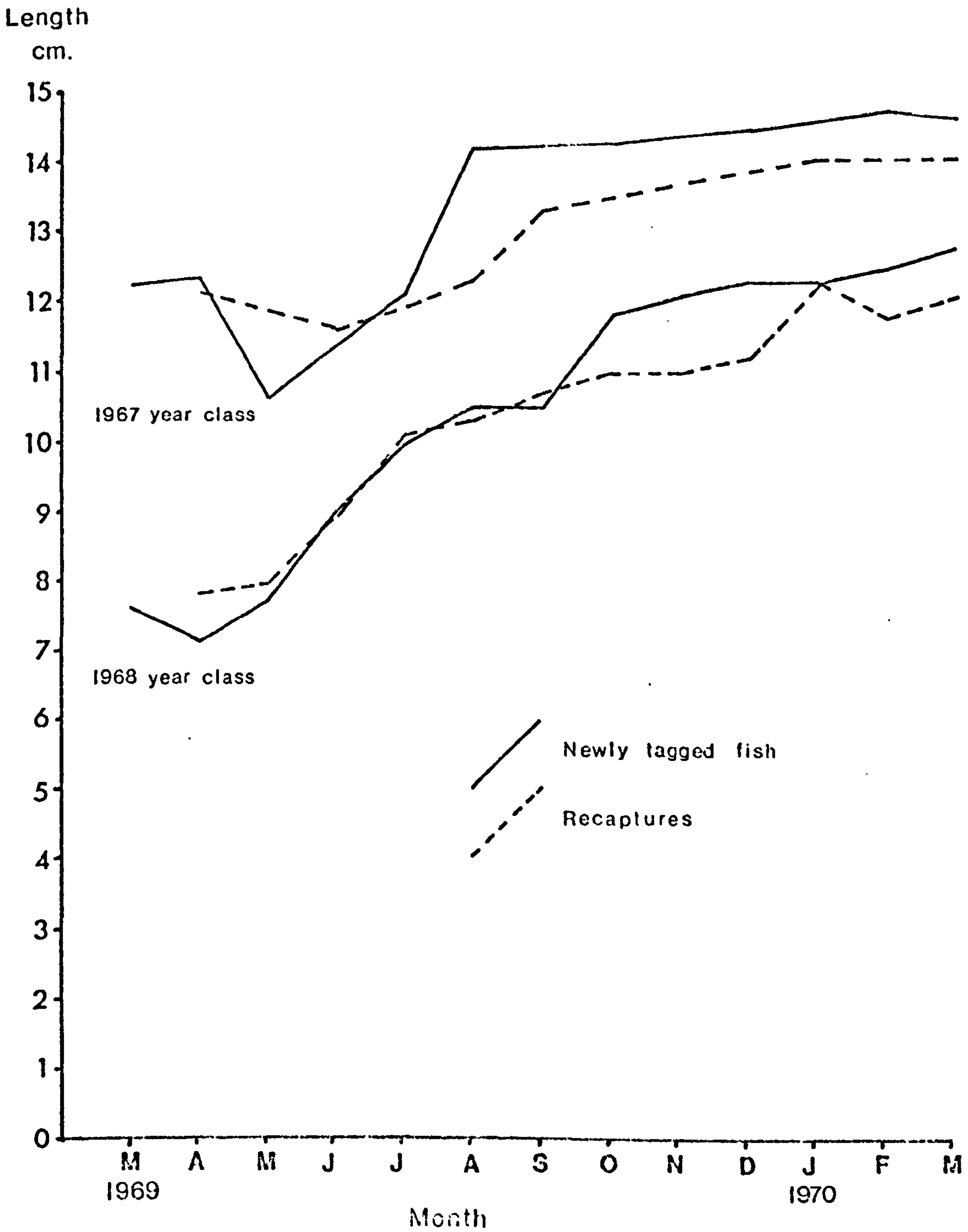


FIGURE 52

Seasonal Growth in Weight of Salmon Parr in the Llyn Tegid Feeder Streams

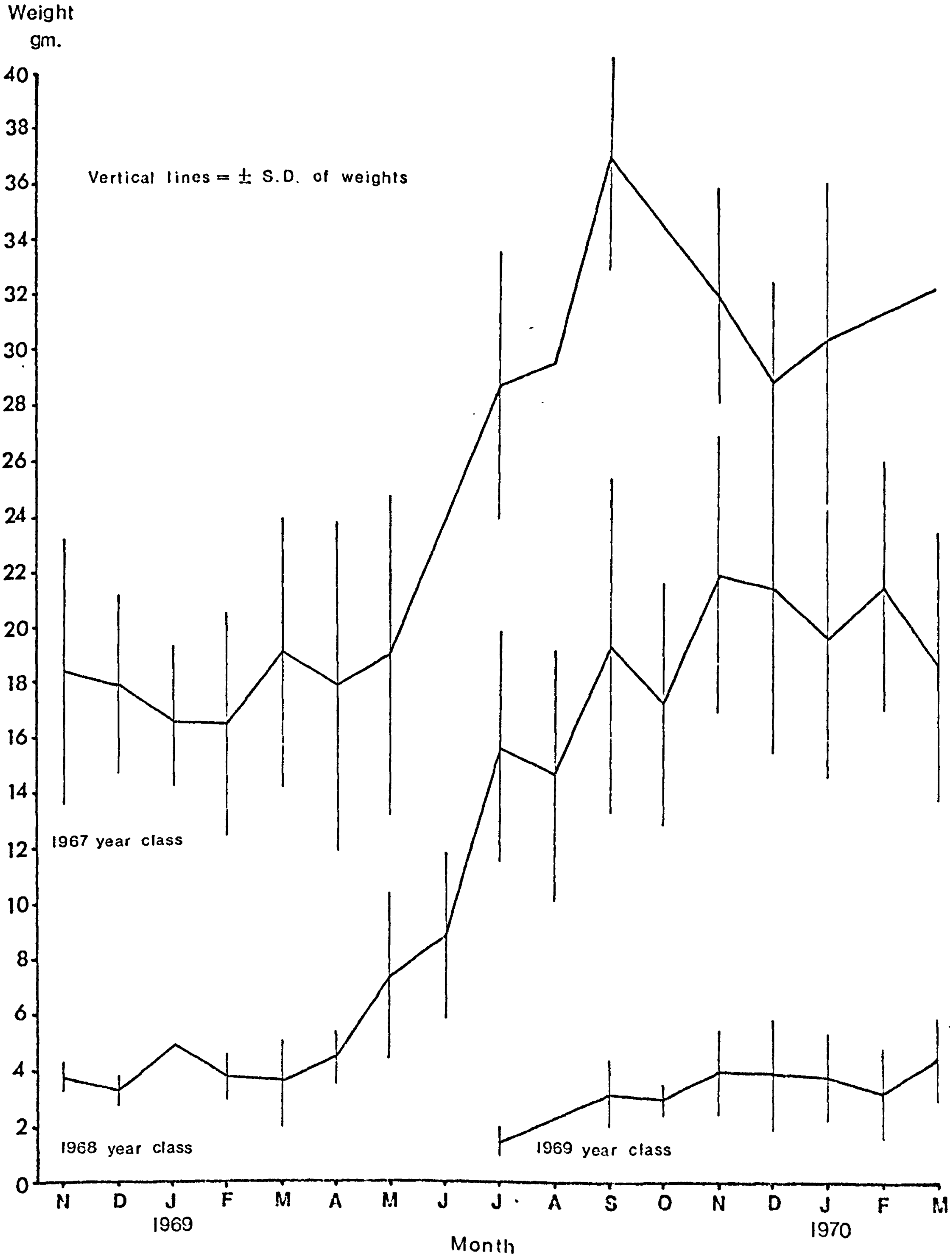


FIGURE 53

Seasonal Growth in Weight of Trout in the River Dee

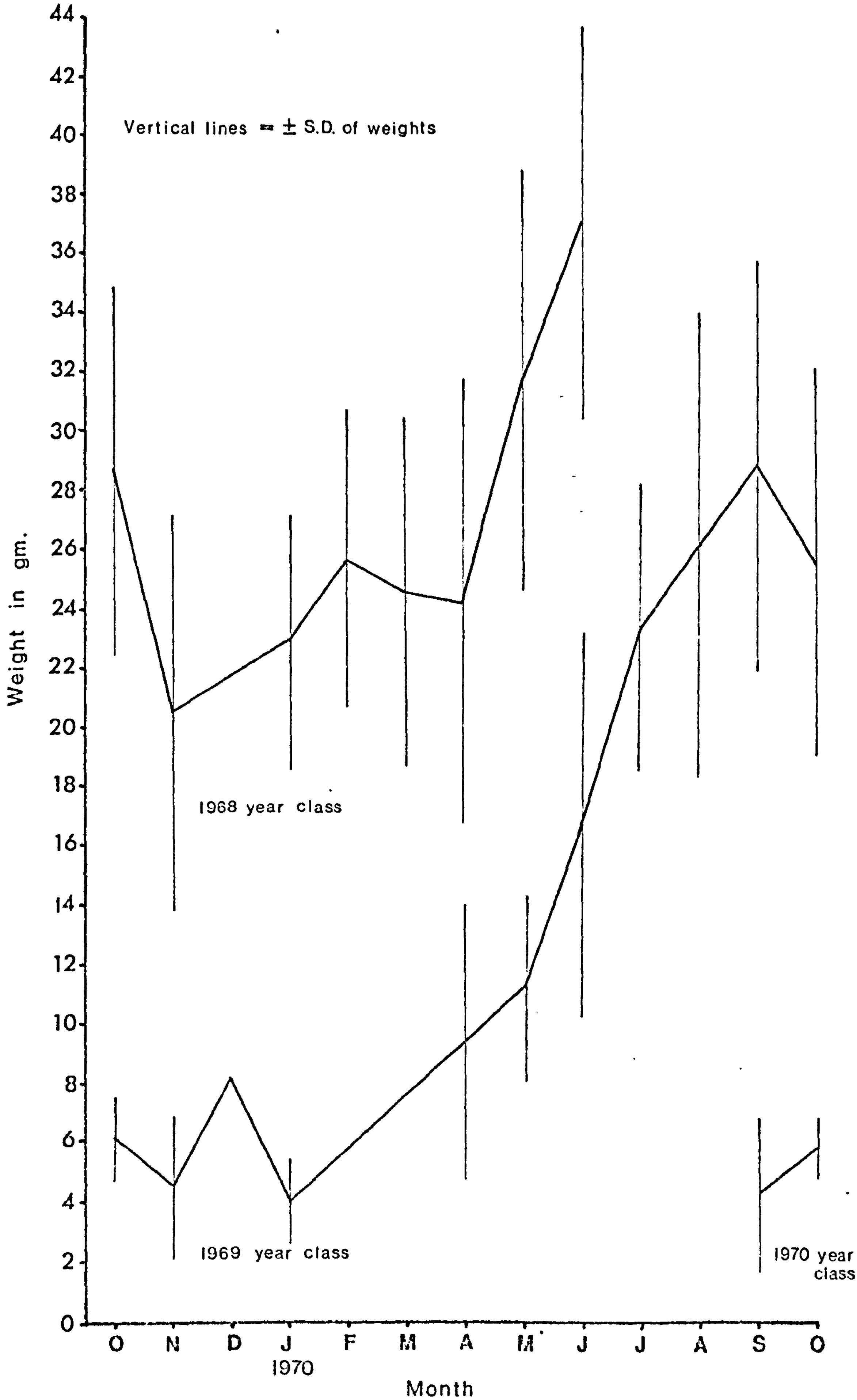


FIGURE 54

Seasonal Growth in Weight of Trout in the Llyn Tegid Feeder Streams

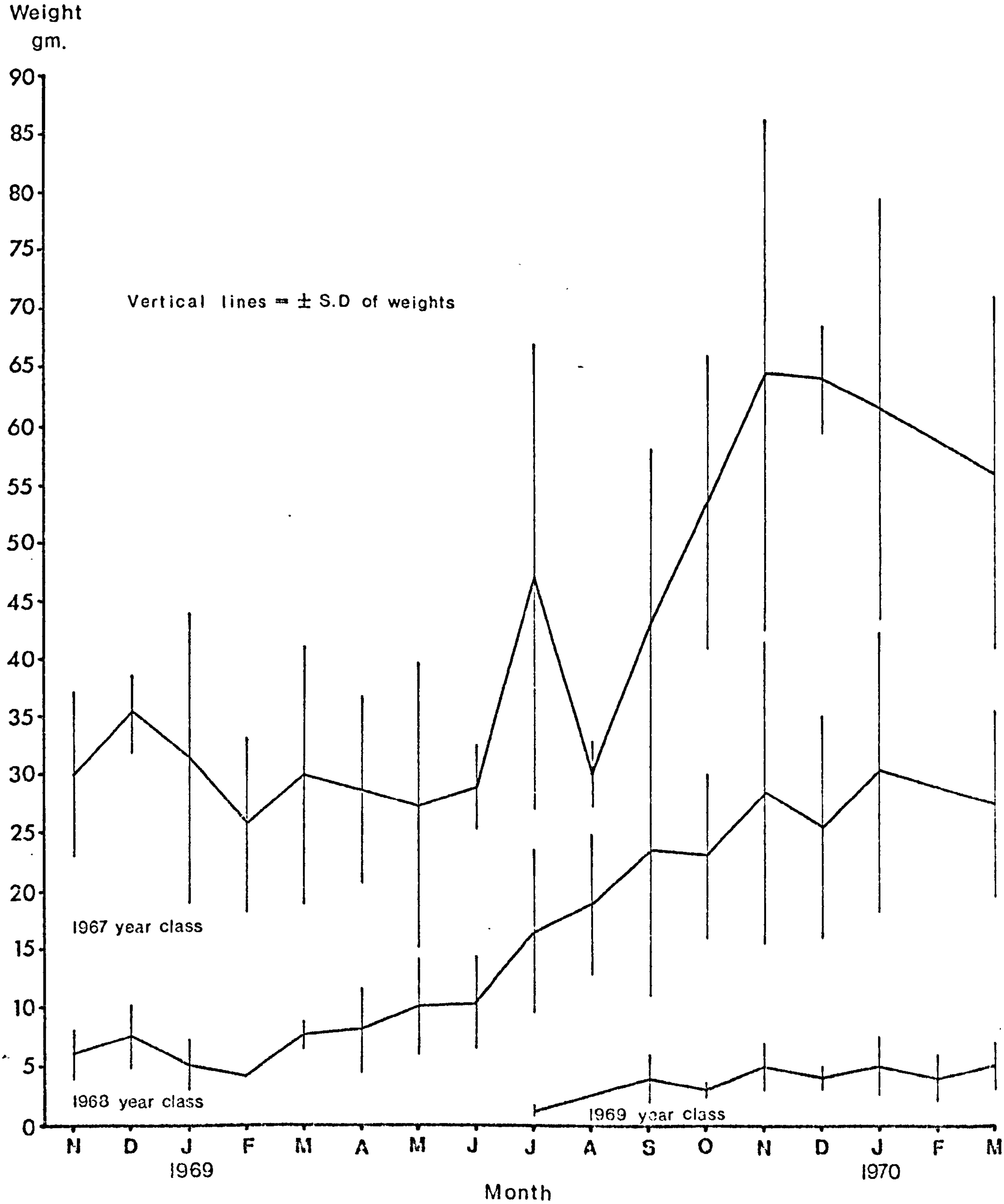


FIGURE 55

Seasonal Growth in Weight of Trout in the River Dee

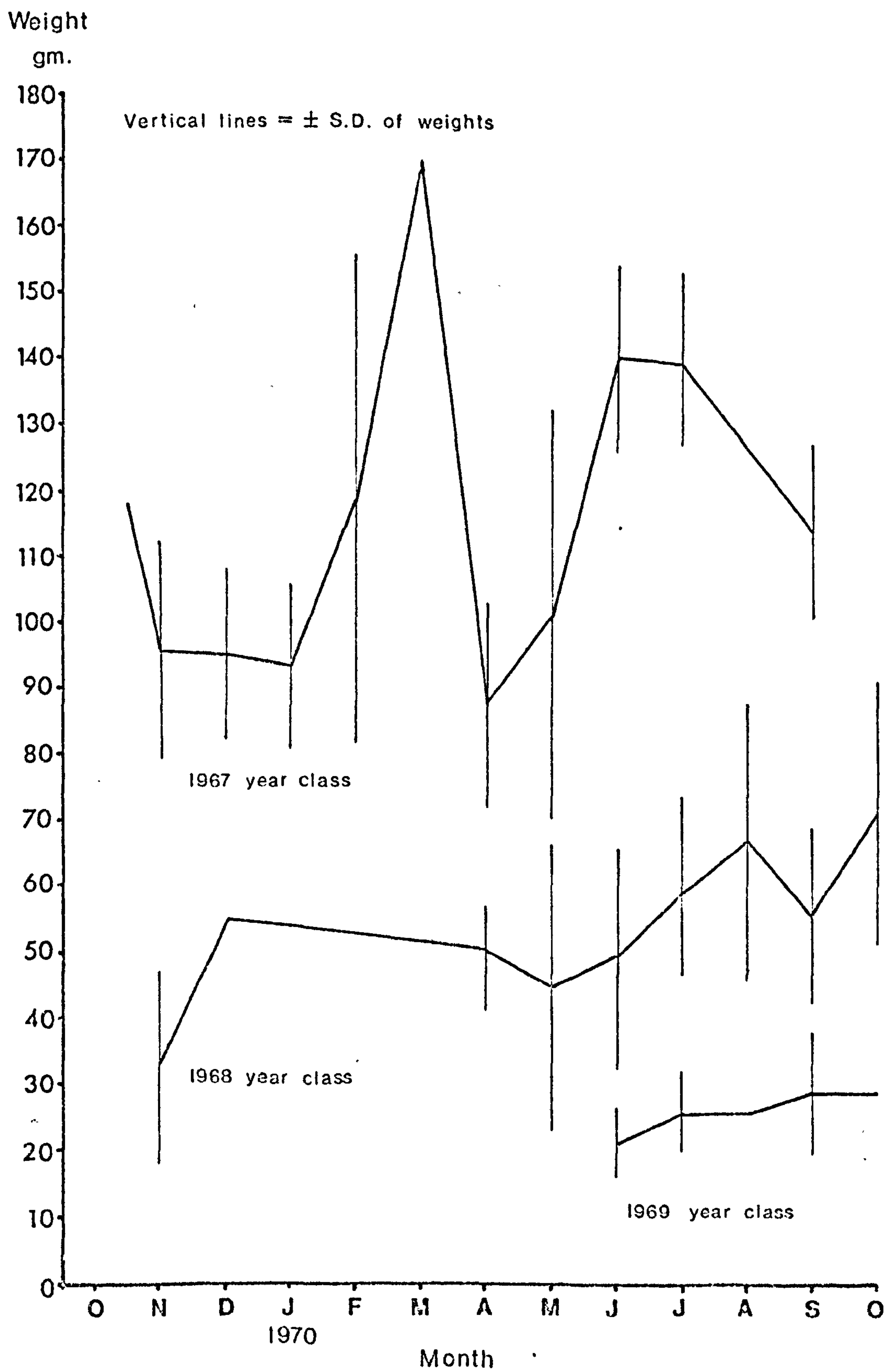


FIGURE 56

Seasonal Condition of Salmon Parr

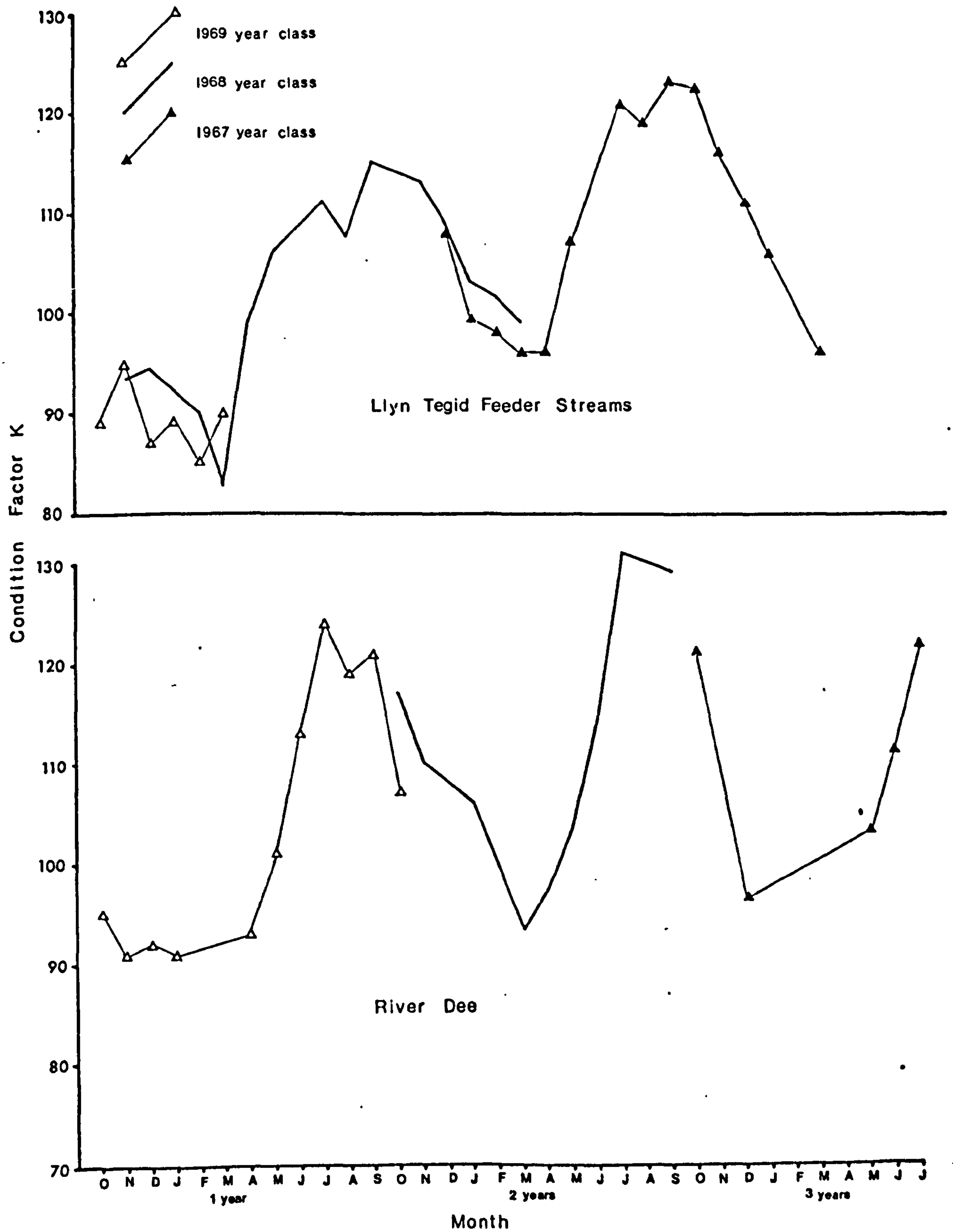
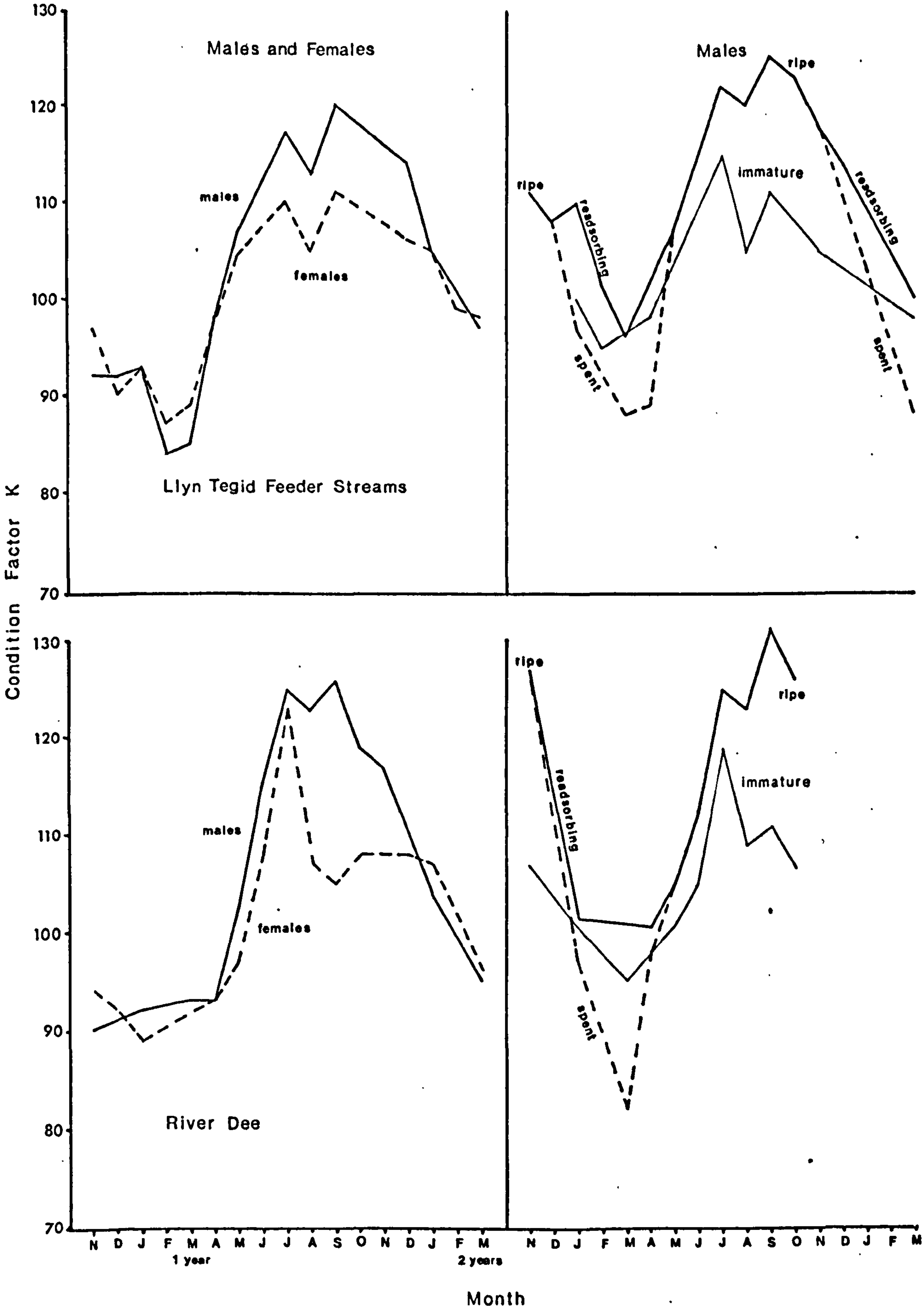


FIGURE 57



Effect of Sex and Maturity on the Condition of Salmon Parr

FIGURE 58

Seasonal Condition of Trout in the Llyn Tegid Feeder Streams

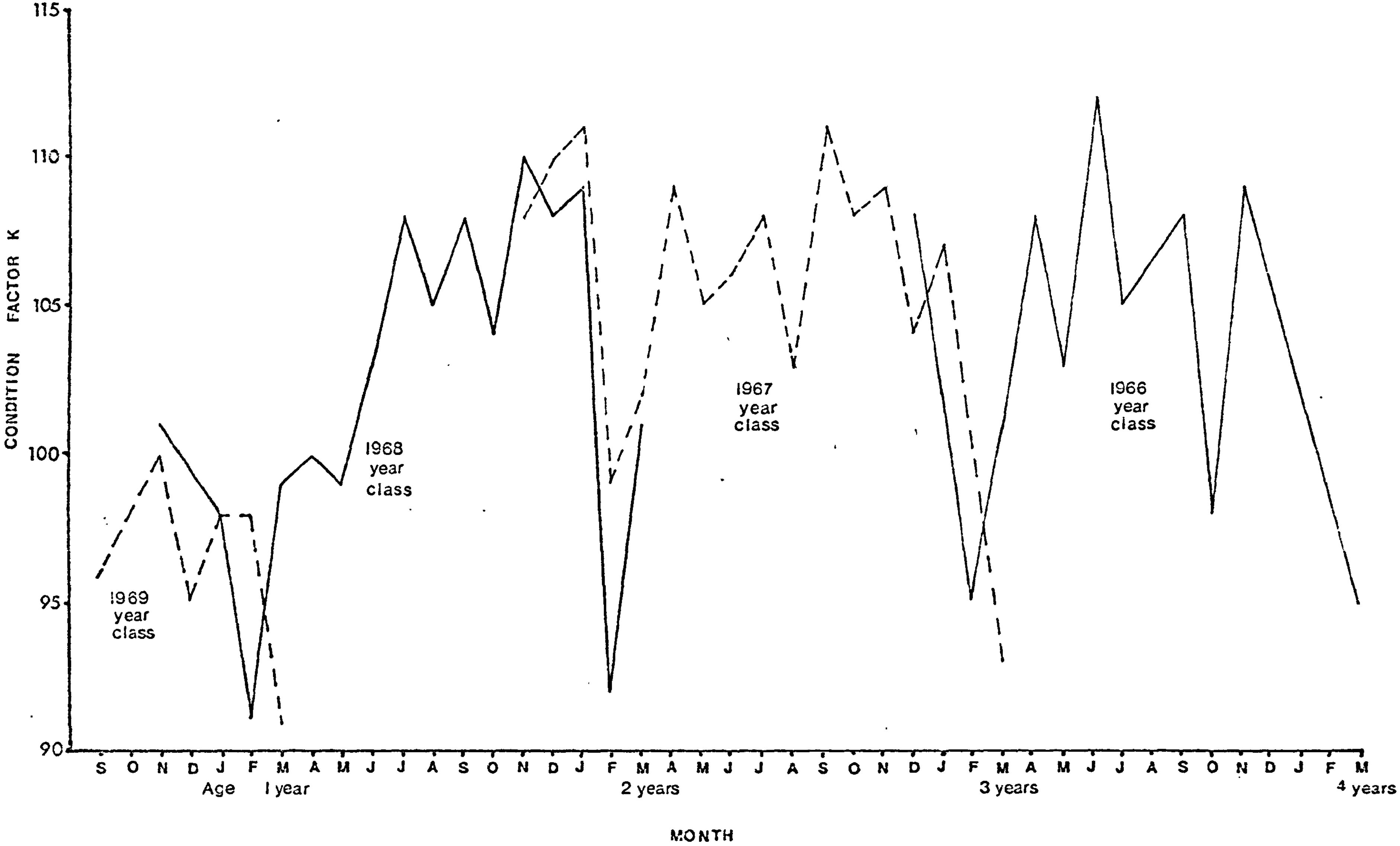
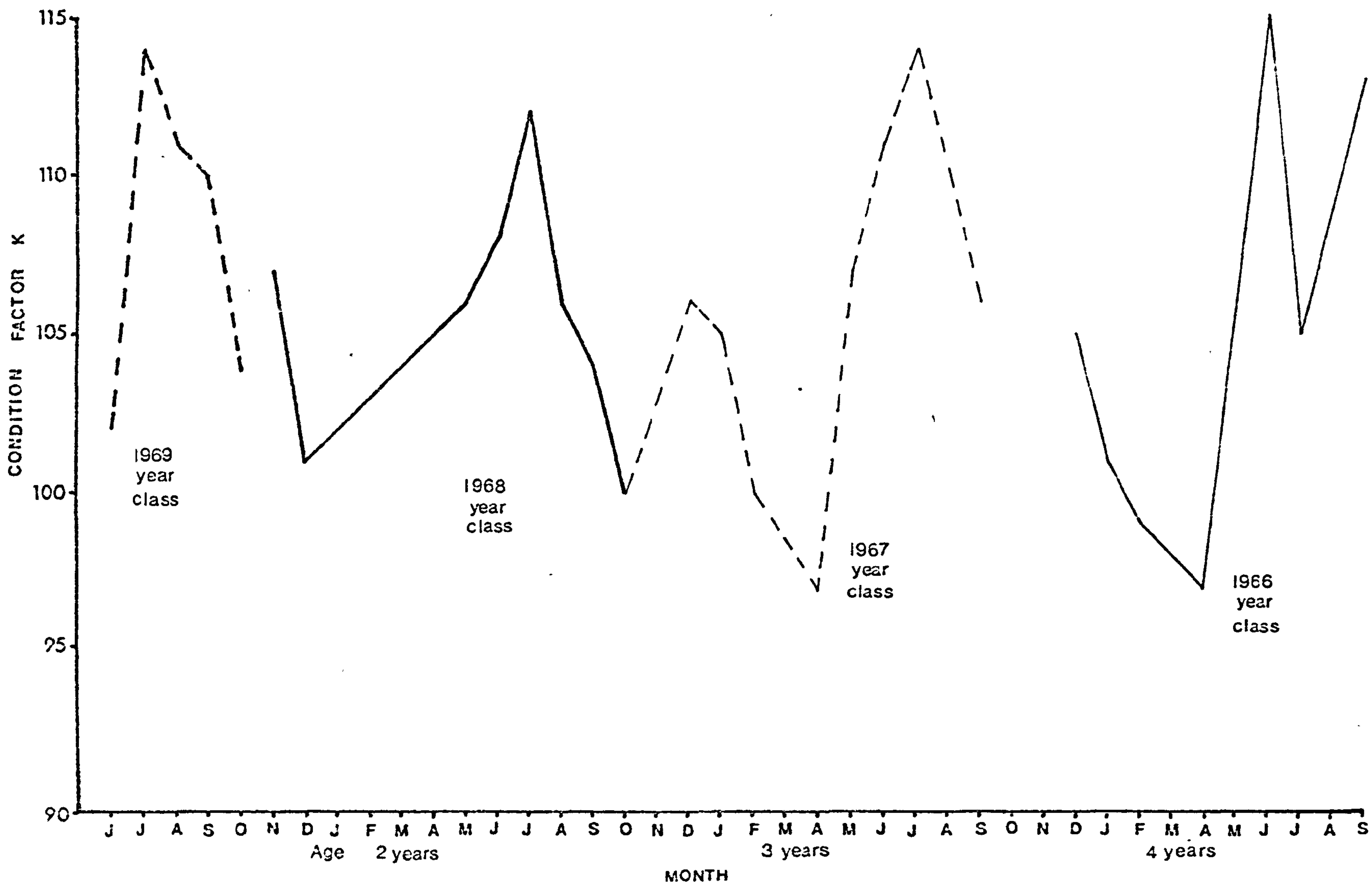


FIGURE 59

Seasonal Condition of Trout in the River Dee



time of smolt transformation. Hoar (op.cit), Allen (1940) and Frost & Went (1940) all found that the condition of salmon parr reached a maximum in July and declined thereafter. In my study the time of highest condition was dependent on sex and maturity, as shown in figure 57. Male salmon parr first reached maturity during the second year of life in the Llyn Tegid feeder streams and the River Dee, and samples of fish of this age and older contained mature males, immature males and immature females. The condition of immature males was always less than that of ripening or readsorbing (unspent) males, but greater than that of spent males during the winter. The condition of immature males and females was very similar and followed the same seasonal pattern, with a maximum in July and a decrease thereafter. Maturing male salmon parr, however, reached their maximum condition in September and October, just before the spawning season! The August decrease in condition probably resulted from above optimum water temperatures.

The seasonal condition cycles of trout in my study (figures 58 and 59) were very similar to those found by Ball & Jones (1960), with a spring increase to a maximum in July, followed by a decline thereafter. Secondary condition maxima were sometimes found in the November-January period. Ball & Jones (op.cit.) related such peaks to the large early winter fat reserves, and considered that the rapid rise in condition between May and July might have resulted from faster growth in weight than in length at that time. A rise in mean condition occurred in the trout of the Llyn Tegid feeder streams up to the age of 1+ years followed, in contrast to salmon parr, by a slow decline in subsequent years. This decline was also found in River Dee trout (figure 59) and was recorded previously by Allen (1951), Ball & Jones (1960) and Thomas (1964). Thomas (op.cit.) related the declining condition of trout to decreasing specific growth rates. The effect of maturity on the condition of trout was not assessed in my study because of the very small number of mature fish examined. Very few salmon parr or trout were weighed in the field (chapter 4, section A2b), so the effects of tagging on K could not be determined.

b. <u>Annual growth</u>

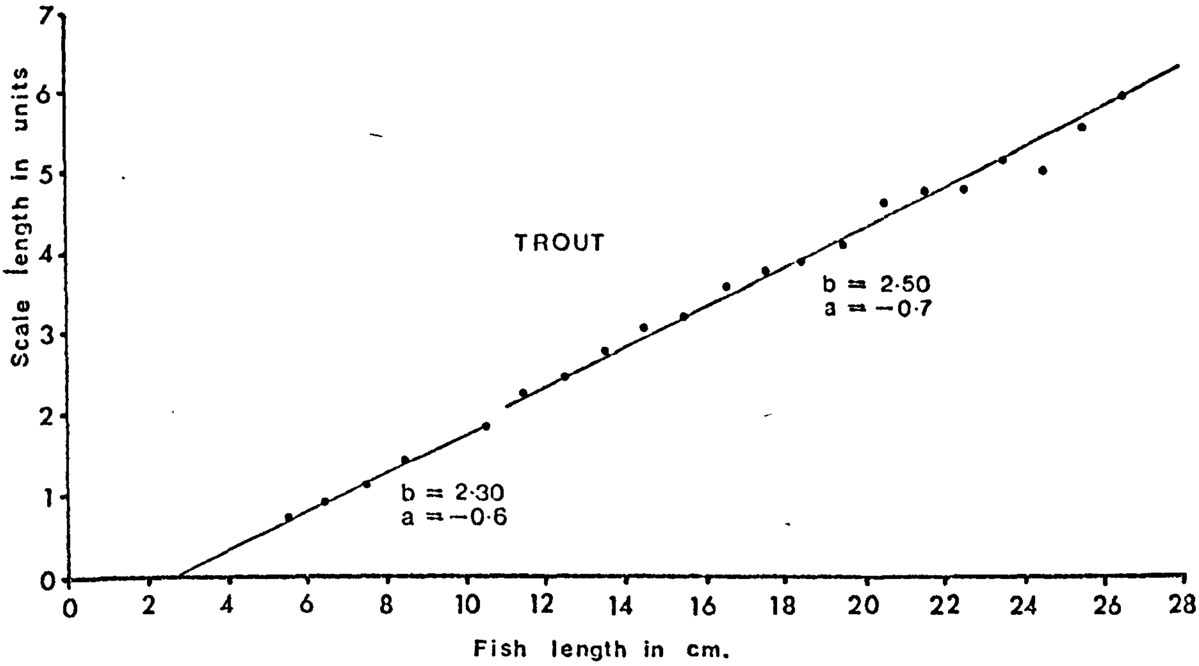
(i) <u>Scale length/fish length relationships</u>

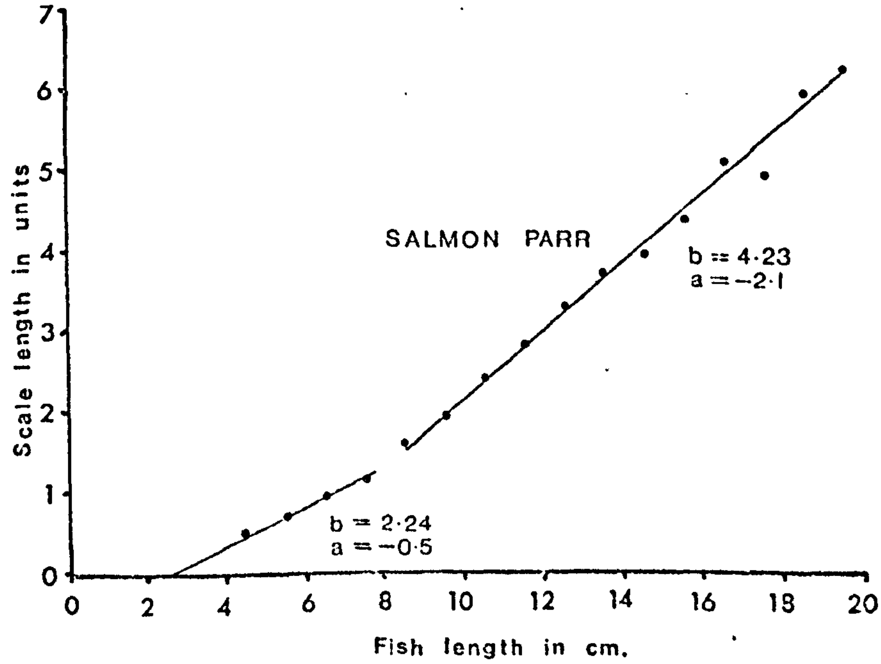
Wide use has been made in the past of the back calculation of lengths for age of salmonid fishes, with the general assumption that the scales and body grew in direct proportion and that the ratio of scale length to fish length remained constant whatever the length of the fish. This assumption may not always be justified and corrections must often be applied to compensate for allometric growth (Kipling, 1962).

The fish length/scale length relationships of trout and salmon parr in my study are shown in figure 60, together with the regression slopes (b) and the y-axis intercepts (a). It can be seen that allometry of scale growth did occur in both trout and salmon. Trout below about 10cm. showed a different body-scale relationship to those above 10cm. as did the trout examined by Kipling (~~1962~~ loc. cit.). Allometry in the scale growth of salmon parr occurred below 8cm. These results indicate that corrections for allometry should be applied to back

FIGURE 60

Body/Scale Relationships of Salmon Parr and Trout





calculations by direct proportion (Dahl-Lea equation) for all fish under these lengths (i.e. most fish at age 1). In my study, however, only the mean lengths of fish at the end of each year were considered, enabling mean lengths of the scales to be related directly to mean lengths of fish using the body-scale relationships shown in figure 60. Some small errors (<0.5cm) can arise in the interpretation of the scale lengths of trout and salmon around 10cm. and 8cm. respectively, and variations in scale measurements make length estimates from small samples unreliable.

(ii) Calculated lengths of trout and salmon parr

The calculated lengths of trout and salmon parr are shown in tables 34 and 35. The actual lengths at the end of each year, where known, have also been included in these tables. No significant difference ($p > 0.10$) was found between the lengths of salmon parr from the upper Dee and Corwen, so data from all River Dee salmon were combined. Strong evidence of "Lee's phenomenon" (Lee, 1920) can be seen in the data presented in tables 34 and 35, with each successively older age group giving smaller values of back calculated lengths for corresponding years of life. To minimise the effects of Lee's phenomenon the calculated lengths of trout at the last scale annulus only were plotted against age as shown in figure 61. This method should give the best estimate of the actual size of surviving fish at successive ages. Considerable discrepancies exist between the calculated lengths and true lengths of the feeder stream trout, the former generally being less than the latter. This may partly be accounted for by the migration of the largest fish of each age

Table 34 Calculated growth in length of trout

(a) Upper Dee.

Year class	Length in cm(±s.d) at the end of each year of life. 1	2	3	4	5
1965	7.4(±0.4)	14.0(±1.2)	19.9(±2.3)	23.4(±2.4)	25.8(±2.0)
1966	7.8(±1.6)	13.6(±2.4)	19.5(±2.7)	24.0(±2.4)	-
1967	9.0(±1.6)	16.0(±2.4)	20.7(±3.5)	-	-
1968	9.2(±1.6)	16.0(±2.9)	-	-	-
1969	9.9(±1.9)	-	-	-	-
Actual lengths	-	16.0(±2.2)	20.8(±1.3)	-	-

(b) Corwen.

Year class	Length at end of year 1	2	3	4
1966	9.5(±2.4)	16.4(±5.4)	20.7(±4.0)	24.3(±3.5)
1967	9.3	17.8	22.1	-
1968	9.6(±1.9)	18.6(±3.1)	-	-
1969	10.1(±1.0)	-	-	-

(c) Llyn Tegid feeder streams

Year class	Length at end of year 1	2	3	4	5
1964	6.5	12.4	15.6	18.7	20.7
1965	7.0(±0.8)	11.6(±1.0)	15.4(±2.2)	18.8(±1.8)	-
1966	7.4(±1.2)	12.8(±2.0)	16.8(±2.4)	-	-
1967	7.8(±1.2)	13.0(±2.0)	-	-	-
1968	8.4(±1.6)	-	-	-	-
Actual lengths	7.8(±1.0)	13.4(±1.6)	17.7(±1.9)	20.3(±1.3)	23.4(±0.6)

Table 35. Calculated growth in length of salmon parr.

(a) River Dee

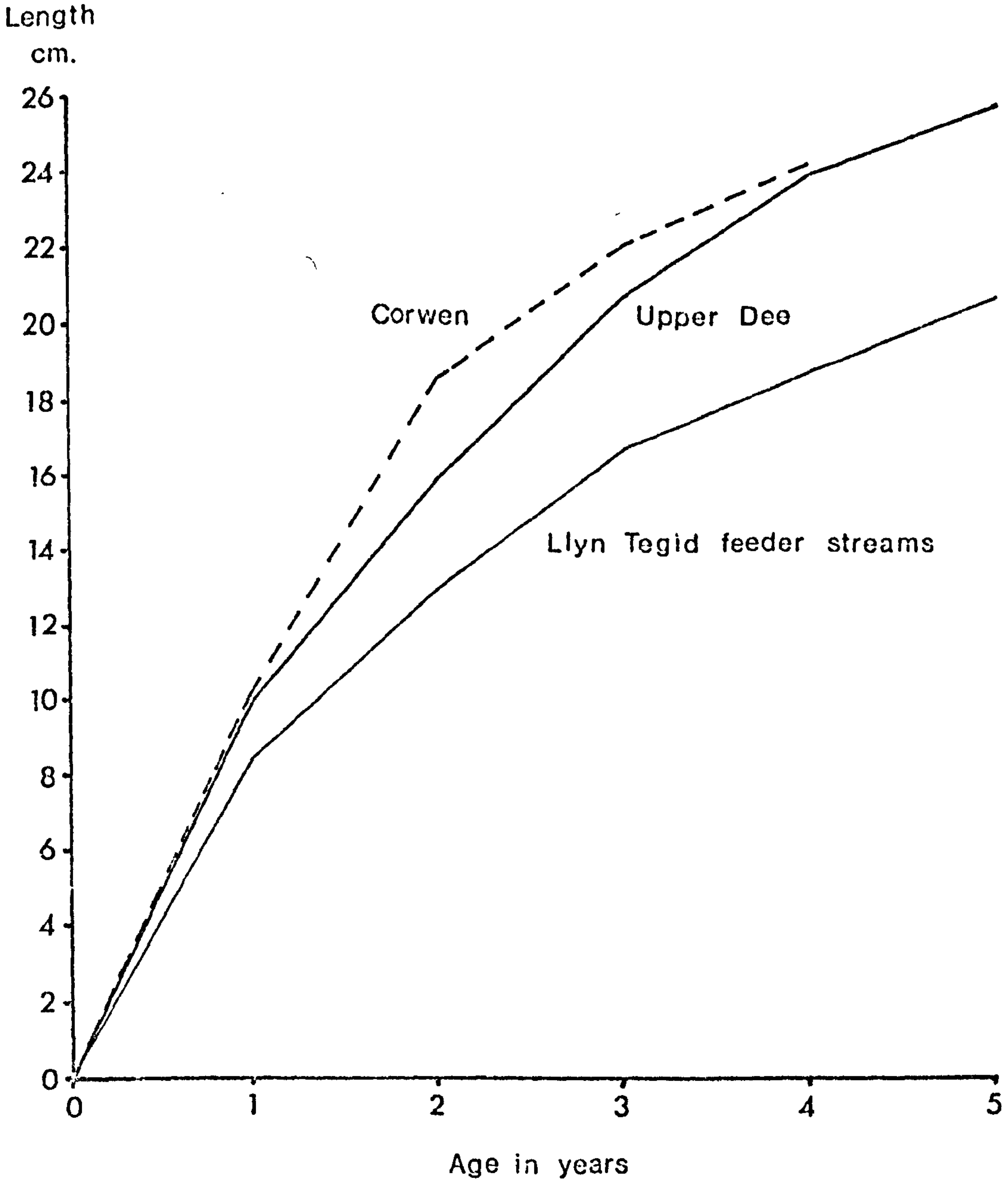
Year Class	Length in cm (±s.d) at the end of each year of life 1	2	3
1967	8.1(±0.6)	12.5(±2.1)	16.1(±2.7)
1968	8.5(±1.0)	13.0(±1.7)	-
1969	8.7(±1.1)	-	-
Actual lengths	8.6(±0.6)	13.5(±1.3)	-

(b) Llyn Tegid feeder streams

Year Class	Length in cm (±s.d) at the end of each year of life. 1	2	3
1966	7.1(±1.6)	10.9(±1.6)	12.9(±1.8)
1967	7.4(±1.3)	11.2(±1.5)	-
1968	8.0(±1.0)	-	-
Actual lengths	7.4(±0.6)	12.4(±0.9)	14.5(±0.8)

FIGURE 61

Calculated Growth of Trout



group from the streams into Llyn Tegid (Ball & Jones, 1962, and section 3a,ii), and is most marked after the second year. Figure 61 does, however, show that upper Dee trout grew quicker than Llyn Tegid feeder stream trout ($p < 0.001$), and Corwen trout grew faster than upper Dee trout ($p < 0.05$). No significant difference ($p > 0.10$) was found between the calculated lengths of trout from the Afon Lliw, Afon Dyfrdwy and Afon Llafar, but trout from the Afon Glyn and Afon Twrch grew significantly slower ($p = 0.05$) than in the other streams during the fourth year of life. The mean lengths of Glyn and Twrch trout were 16.4 cm. and 17.9 cm. at age 3 and 4, as compared with 17.3cm. and 19.4cm. in the other feeder streams. These variations were probably the result of population size differences (see chapter 11). The actual lengths of Afon Lliw trout given by Ball & Jones (1960) did not differ significantly from those found in the Lliw during my study. These authors recorded a slower growth rate in Glyn trout as compared with Lliw trout, but considered that this might have resulted from the Glyn samples being taken after the spring migration to the lake, and the Lliw samples being taken before the migration. They also found that trout grew much slower in the upper reaches of the Lliw, where the river took on the character of a moorland stream, than in the lower reaches.

The calculated lengths of salmon parr also show strong evidence of "Lee's phenomenon" (table 35), and this may largely be a result of smolt migration which annually removes the largest fish of each age group. Annual growth figures based on back calculations from scales are therefore of little use, but may give some indication of the growth rates of the different migrant groups. Calculated lengths were found to be much lower than actual lengths, and the annual growth was therefore assessed in terms of the latter, as shown in figure 62. River Dee salmon parr were found to grow significantly faster ($p<0.001$) than Llyn Tegid feeder stream salmon parr, but no differences in growth rates were found within the feeder streams. The actual lengths of the smolt migrant groups and the back calculation of their growth in earlier years is considered in chapter 12. The lengths of 2 year old salmon parr given by Jones (1949) agree substantially with those found in the River Dee during my study. A comparison of figures 61 and 62 shows that trout grew faster than salmon parr in all habitats.

(iii) Specific growth rates

Specific growth rates (G) were determined, using the formula given in chapter 5 (section 3bv), from the calculated lengths of trout shown in figure 61, and from the actual lengths of salmon parr shown in figure 62. The initial length at age 0+ was taken as 2.4cm. (Frost & Brown, 1967). The annual specific growth rates of trout and salmon parr are given in tables 36 and 37.

The specific growth was found to be high in the first year of life and to decline in subsequent years with a decreasing negative acceleration. A strong correlation was found between specific growth rates in the first year and the overall growth patterns of fish throughout life. Ball & Jones (1960) considered that differences in growth rates in the first year were very important

FIGURE 62

Annual Growth of Salmon Parr

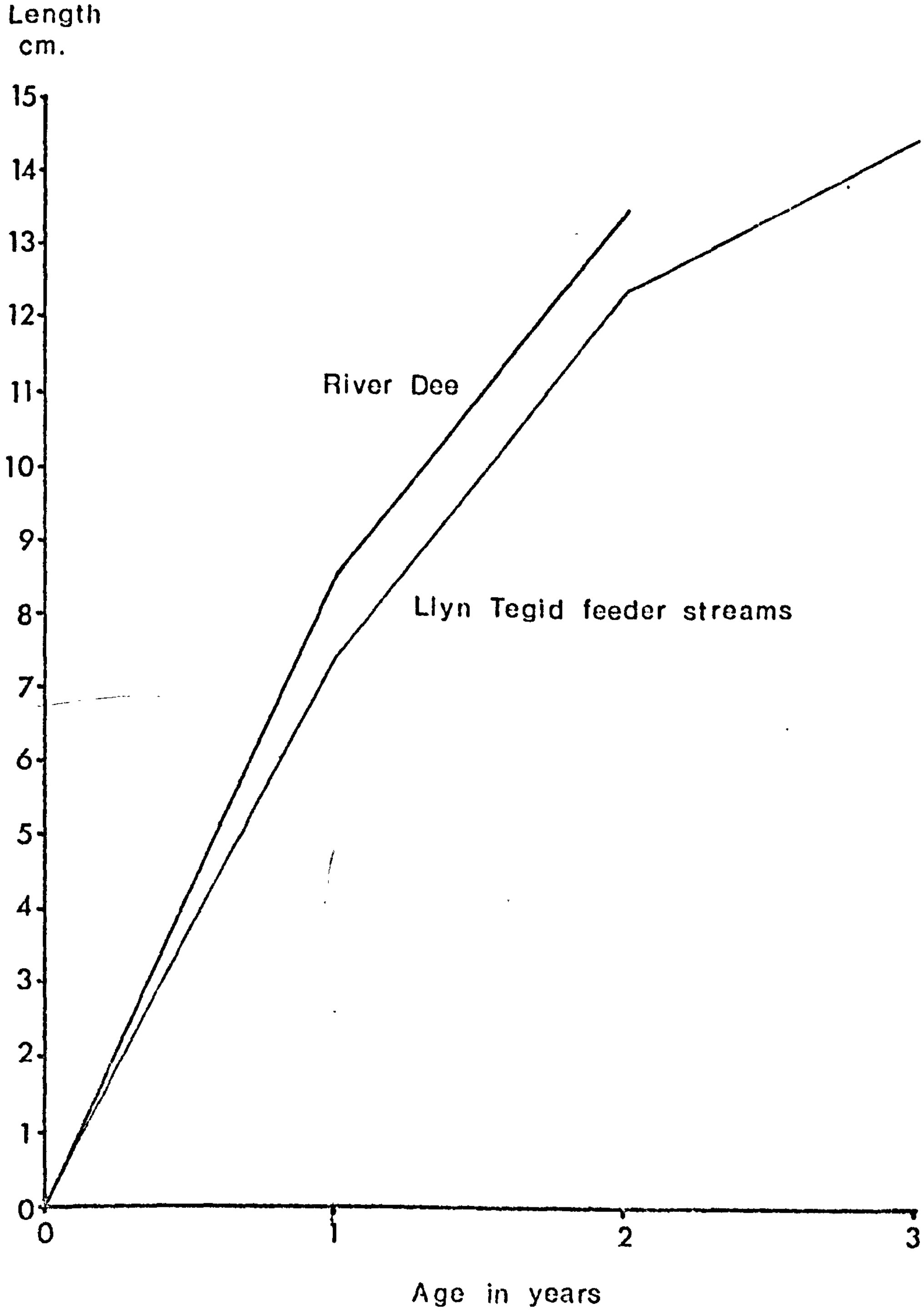


Table 36. Specific growth rates of trout.

Locality	Percentage increase in length per annum. 0-1 year	1-2 year	2-3 years	3-4 years	4-5 years
Corwen	153.7	30.8	17.2	9.5	-
Upper Dee	141.7	48.0	25.8	14.8	7.2
Llyn Tegid feeder streams	125.3	43.6	25.6	11.3	9.6

Table 37. Specific growth rates of salmon parr.

Locality	Percentage increase in length per annum. 0-1 year	1-2 year	2-3 year
River Dee	127.6	45.1	-
Llyn Tegid feeder streams	112.6	51.6	15.7

in producing subsequent size differences of trout, and my findings agree substantially with these authors' and with those of Frost (1945) and Thomas (1964). Trout and salmon parr which showed the highest specific growth rate in the first year of life always attained greater lengths at the end of each subsequent year. Thus Corwen trout, which had a higher value for G in the first year than upper Dee trout grew faster throughout life despite the fact that G was higher in the upper Dee trout from the second year of life onwards. The same observations can be applied to the differences in growth rates between River Dee and feeder stream salmon parr, and to some extent between upper Dee and feeder stream trout. The specific growth rate of feeder stream trout remained lower than that of upper Dee trout throughout most of life, but it should be remembered that the calculated lengths of feeder stream trout were much lower than their actual lengths (for reasons discussed in section 3b,ii), and the values of G from the second year onwards should be higher than indicated.

(iv) Length/weight relationships

The rise in the condition factor of salmon parr with increasing age found in this study, and also by Hoar (1939), suggests that the length/weight relationship changes with size. Figure 63 shows that this relationship does change as the length increases. Figure 63 was constructed in the same way as for grayling (chapter 5, section 3b,vi), and shows the mean weights for each 10mm. length group. The regression lines have not been drawn, but the regression coefficients (b) and y-axis intercepts (a) have been included for three groups of data from each habitat. These three groups of data ($<$ 9.5cm., 10.5-12.5cm., 13.5-15.5cm.) roughly correspond to the 0-1, 1-2 and 2-3 age classes. The length/weight relationships of River Dee and Llyn Tegid feeder stream salmon parr were found to be very similar.

A marked change in the condition of trout occurred after the first year of life (section 3a,iv) and this was reflected in a corresponding change in the length/weight relationship at a length of approximately 12cm., as shown in figure 64. As with salmon parr,

FIGURE 63

Length/Weight Relationship of Salmon Parr in the River Dee (Δ) and the Llyn Tegid Feeder Streams (•)

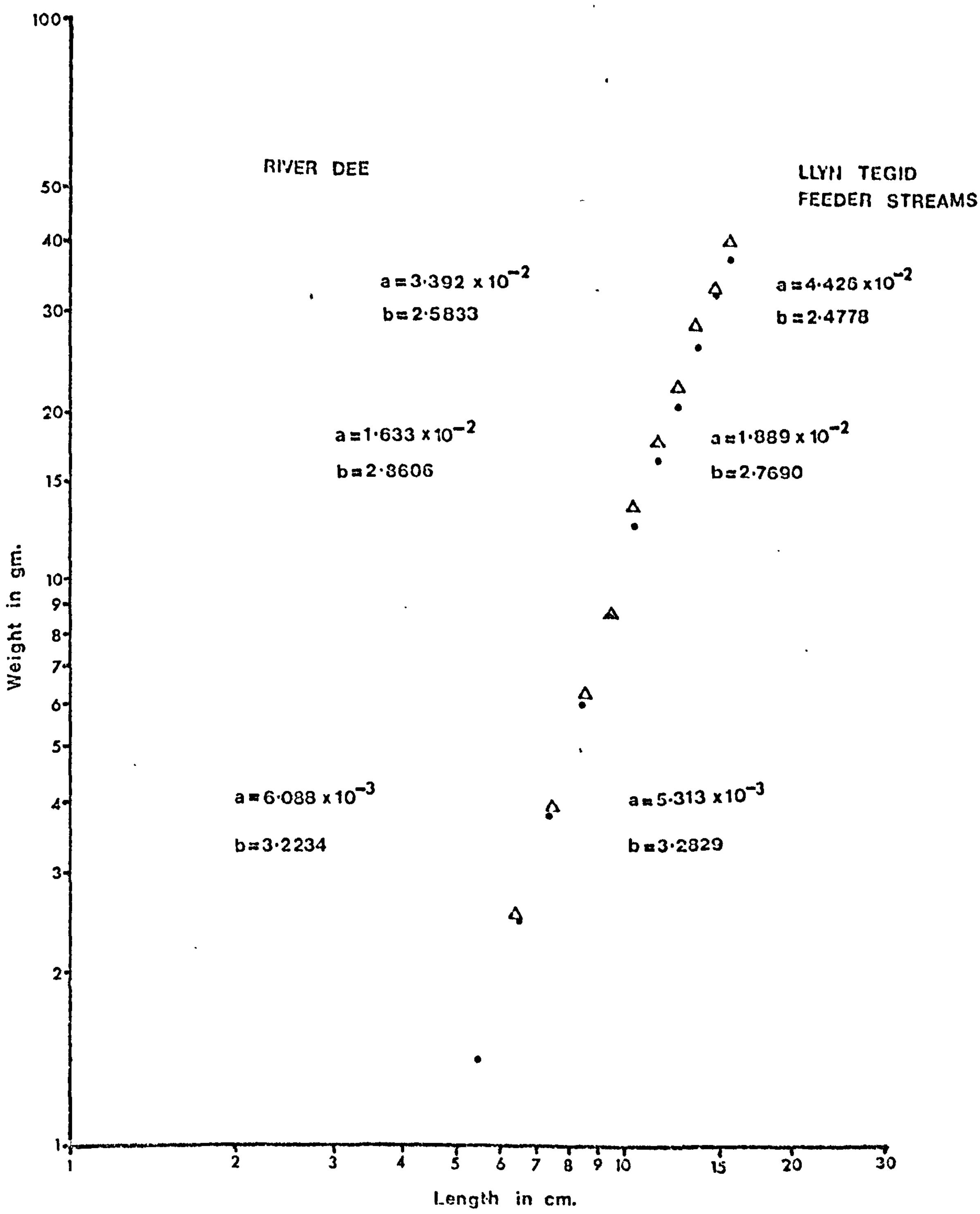
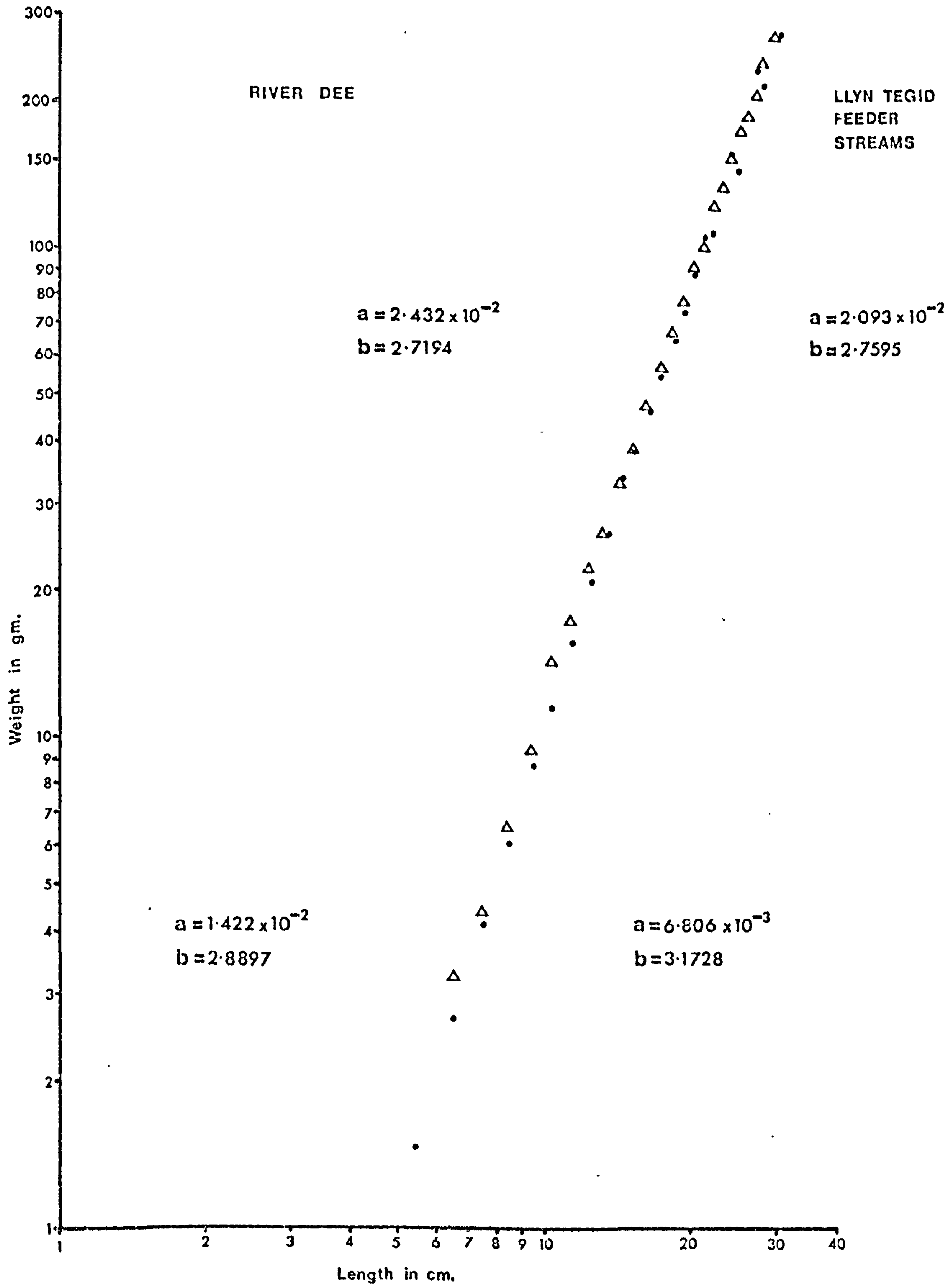


FIGURE 64

Length/Weight Relationships of Trout in the River Dee (Δ) and the Llyn Tegid Feeder Streams (•)



the regression lines have not been drawn but the values of b and a are shown. The length/weight relationships of River Dee and Llyn Tegid feeder stream trout were almost identical above 12cm. but smaller fish were slightly heavier in the River Dee at any given length. Ball & Jones (1960) found that the length/weight relationships of the trout they examined were identical in all habitats, and that the slope of the logarithmic relationship was 2.92. Graham & Jones (1962) found a slope of 2.86 for Llyn Tegid trout, and considered that the difference between their findings and those of Ball & Jones (op.cit.) may have resulted from the detrimental effects of regulation on the food supply. The slope of 2.76 found in the feeder stream trout in my study is rather less than that found by Ball & Jones (op.cit.) and Graham & Jones (op.cit.), and may reflect the betar feeding conditions of lake trout as compared with the river trout.

The annual growth in weight of salmon parr and trout, calculated from the length data shown in figures 61 and 62, and from the length/weight relationships shown in figures 63 and 64, is shown in figure 65.

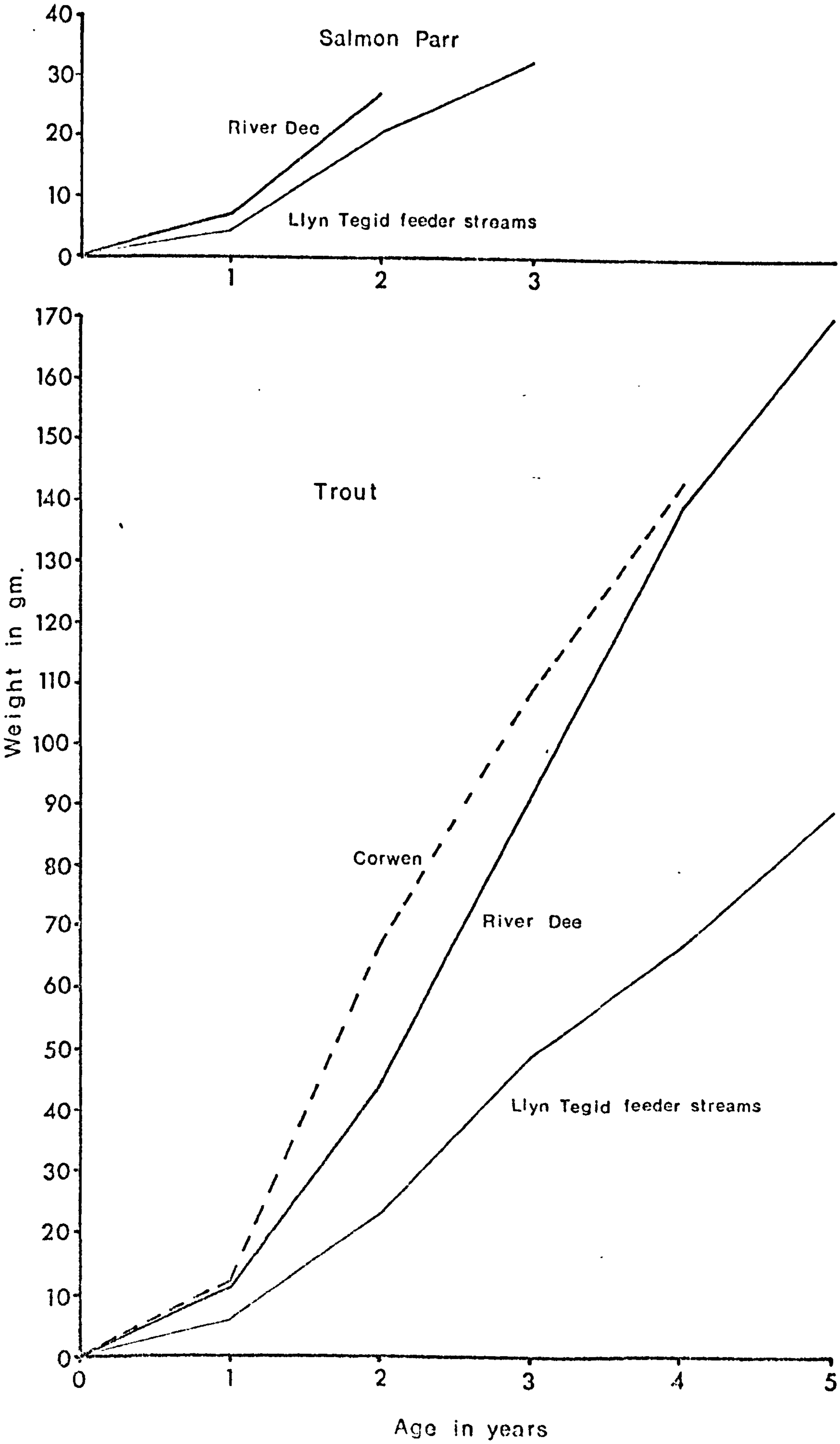
4. Summary

(1) The annual scale check was laid down in salmon parr and trout during early April.

(2) Few salmon parr over 2 years of age and few trout over 4 years of age were caught in the Llyn Tegid feeder streams because of smolt migration and migration to Llyn Tegid respectively.

FIGURE 65

Annual Growth in Weight of Salmon Parr and Trout



(3) Growth in length and weight increased rapidly from April to July, slowed down in late summer and autumn, and almost ceased during the winter. Growth of some fish stopped in August as a result of above optimum water temperatures.

(4) An apparent decrease in size occurred in two year old salmon parr and in Llyn Tegid feeder stream trout during the spring. This resulted from the removal of the largest fish of each age group from the population by the smolt migration and the migration to Llyn Tegid of salmon and trout respectively.

(5) Individual "ministry" tags significantly reduced the growth rate of salmon parr, but other tagging methods had no effect on the growth of either salmon parr or trout.

(6) The condition (K) of salmon parr showed a similar seasonal cycle to that of growth in length and weight. The K of immature male and female salmon parr reached a maximum in July and declined thereafter. Maturing male salmon parr, after an August decrease, showed maximum k values in the autumn, just before the spawning period. The condition of all salmon parr showed a general upward trend with increasing age.

(7) The condition of trout rose sharply in April, reaching a maximum in July and declining thereafter. A secondary rise in K from November to January may have been related to early winter fat reserves. After the age of 1+ the condition of trout gradually declined.

(8) Allometry was found in the growth of scales of trout below

10cm., and of salmon parr below 8cm.

(9) "Lee's phenomenon" was apparent in the calculated lengths of trout and salmon parr, and was most marked in salmon parr and Llyn Tegid feeder stream trout because of the migrations mentioned above. Annual growth of trout was determined from the calculated lengths at the last scale annulus only, and the annual growth of salmon parr was determined from the actual lengths of fish at the end of each year of life.

(10) Trout grew faster than salmon parr in all habitats. Trout and salmon parr grew faster in the River Dee than in the Llyn Tegid feeder streams, and Corwen trout grew faster than upper Dee trout. No significant difference was found between the growth rates of salmon parr within the feeder streams, but Glyn and Lliw trout grew slower after the third year of life than in the other streams.

(11) The specific growth rates in the first year of life was found to be an important factor in determining the size of trout and salmon parr in later years. Fish with the highest first year specific growth rates attained greater lengths at the end of each subsequent year of life.

(12) The length/weight relationship of salmon parr was found to change with age, and different relationships were found for trout above and below 12cm. These differences were related to the upward trend in condition of salmon parr with increasing size, and the change in condition of trout after the first year of life. The logarithmic regression slope for the length/weight data of trout was found to be lower than that found for Llyn Tegid trout by Ball & Jones (1960) and Graham & Jones (1962).

CHAPTER VII

THE FOOD AND FEEDING HABITS OF GRAYLING

1. Introduction

Few studies have been made of the diet of grayling and those that have mainly consider the grayling in terms of competition with other salmonids. In the British Isles, investigations have been carried out by Gerrish (1938, 1939), Radforth (1940), Dunn (1954), Siddiqui (1967, 1969) and Hellawell (1969a, 1971). The diet of grayling in Europe has been studied by many authors and Dahl (1962) gives a comprehensive review of the literature on European grayling and related species in Asia and North America, together with a detailed account of the diet of grayling in Danish streams. Other recent continental work includes that of Muller (1961), Jankovic (1964) and Peterson (1968).

In this study the food and feeding habits of grayling in the River Dee and Llyn Tegid have been assessed by the examination of 411 and 242 stomachs respectively, taken over thirteen month periods. The diet of Llyn Tegid grayling is of particular interest since Llyn Tegid is the only natural lake in the British Isles containing grayling. The competition for food between grayling and other salmonids in the River Dee is discussed in chapter 8, and the competition for food between brown trout and grayling in Llyn Tegid has been previously discussed by Ball (1961) and Siddiqui (1969).

2. Materials

The stomachs of 242 grayling caught between October 1968 and October 1969 from the Llyn Tegid netting stations shown in plate 12 (chapter 3), and the stomachs of 411 grayling caught during October 1969 to October 1970 from the River Dee sampling sites between Bala and Corwen (chapter 3, section C3a), were examined in order to determine the food and feeding habits of grayling in these differing environments. Table 36 shows the number of stomachs examined each month.

Table 36. The number of grayling stomachs examined each month.

Month:	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct.
Llyn Tegid	20	20	20	20	20	20	20	20	18	13	13	20	19
River Dee	30	11	25	40	26	30	16	39	35	40	39	40	40

The numbers of grayling stomachs examined from each main sampling area of the River Dee are given in table 37. Fewer stomachs were examined from Corwen than from the other sampling areas because this area was only fished between May and October 1970.

Table 37 The monthly distribution of grayling stomachs examined from the River Dee

Site :	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Total
Bala sluices	10	3	1	10	-	10	-	2	10	10	14	11	9	90
Bodwen	8	3	9	10	20	19	1	10	5	4	-	8	8	105
Llanderfel	12	5	-	10	-	-	8	10	10	9	10	8	9	91
Llandrillo	-	-	15	10	6	1	7	9	10	9	3	5	8	83
Corwen	-	-	-	-	-	-	-	8	-	8	12	8	6	42

3. Results of food analyses

(i) Seasonal variation in feeding intensity

Previous workers have generally found that the feeding intensity of grayling is high and that grayling with empty stomachs are rare (Dahl, 1962). The seasonal feeding intensity of grayling in the River Dee and Llyn Tegid is shown in figures 66 and 67. The mean monthly stomach fullness never fell below one third full and was rarely less than half full. No empty stomachs were found in the River Dee grayling and only two empty stomachs were found in Llyn Tegid grayling, one in August and one in September, at the time when the water temperature was at its highest. Siddiqui (1969) recorded no empty stomachs in the 104 Llyn Tegid grayling which he examined.

The number and volume representations of the feeding activity showed a similar basic pattern to the fullness variation, with the exception of the January and August peaks in the River Dee samples, and the large number of organisms in the autumn 1968 Llyn Tegid samples. The January peak of volume and number of organisms in stomachs from the River Dee resulted from an above average number of large fish in that month's sample. Large numbers of small terrestrial Diptera accounted for the August and July peaks in the River Dee and Llyn Tegid, and the autumn peak in Llyn Tegid was related to the consumption of large numbers of chironomid larvae. These observations indicate that the fullness index method shows most clearly the pattern of feeding activity, since this method was unaffected by the size of the fish or by the presence of large numbers

Figure 66

Seasonal Variation in the Fullness Index of Grayling Stomachs in the River Dee and Llyn Tegid.

———	=	mean fullness index
- - - - - -	=	mean water temperature
Vertical lines	=	± S.D. of fullness indices

FIGURE 66

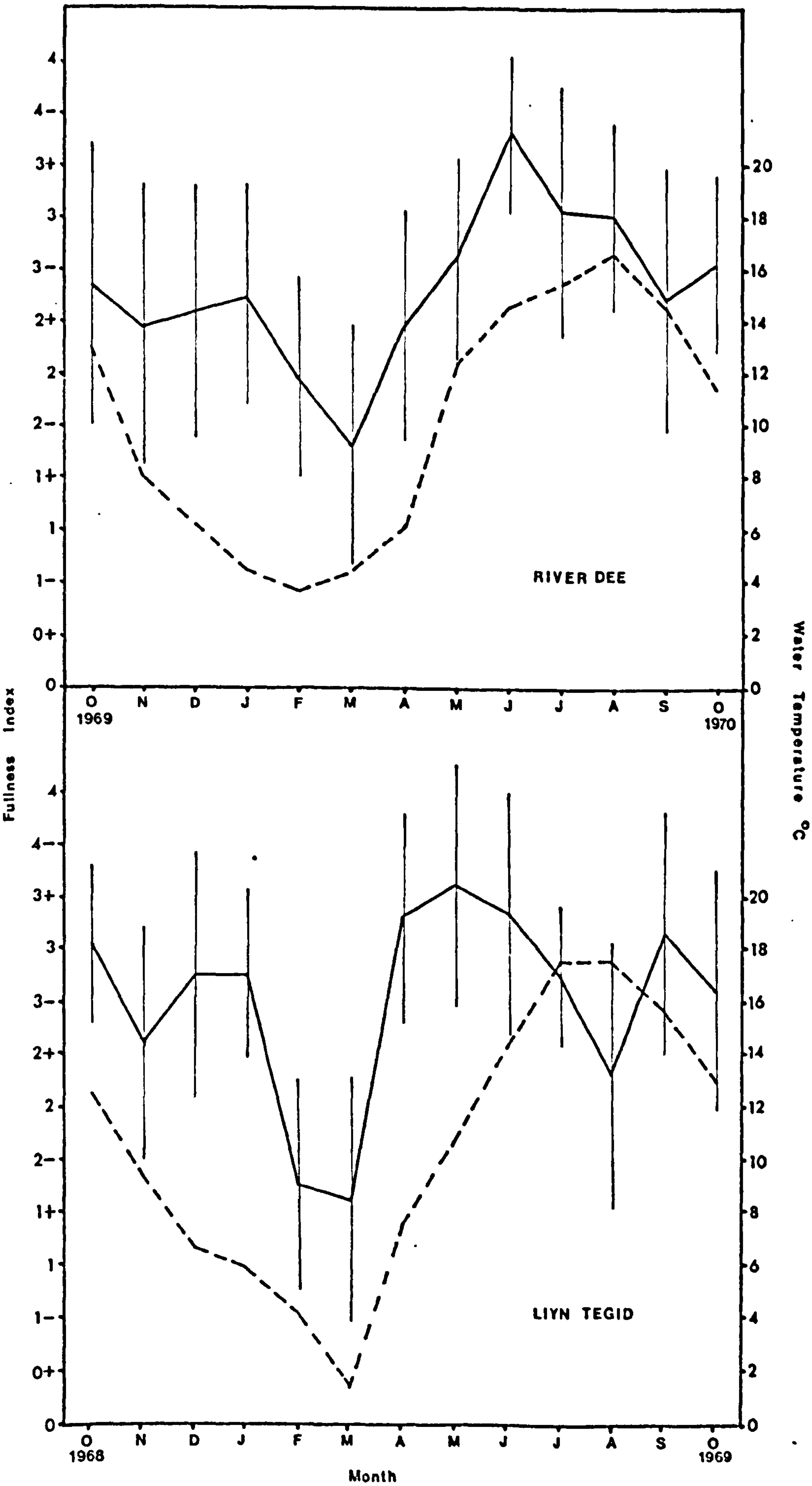
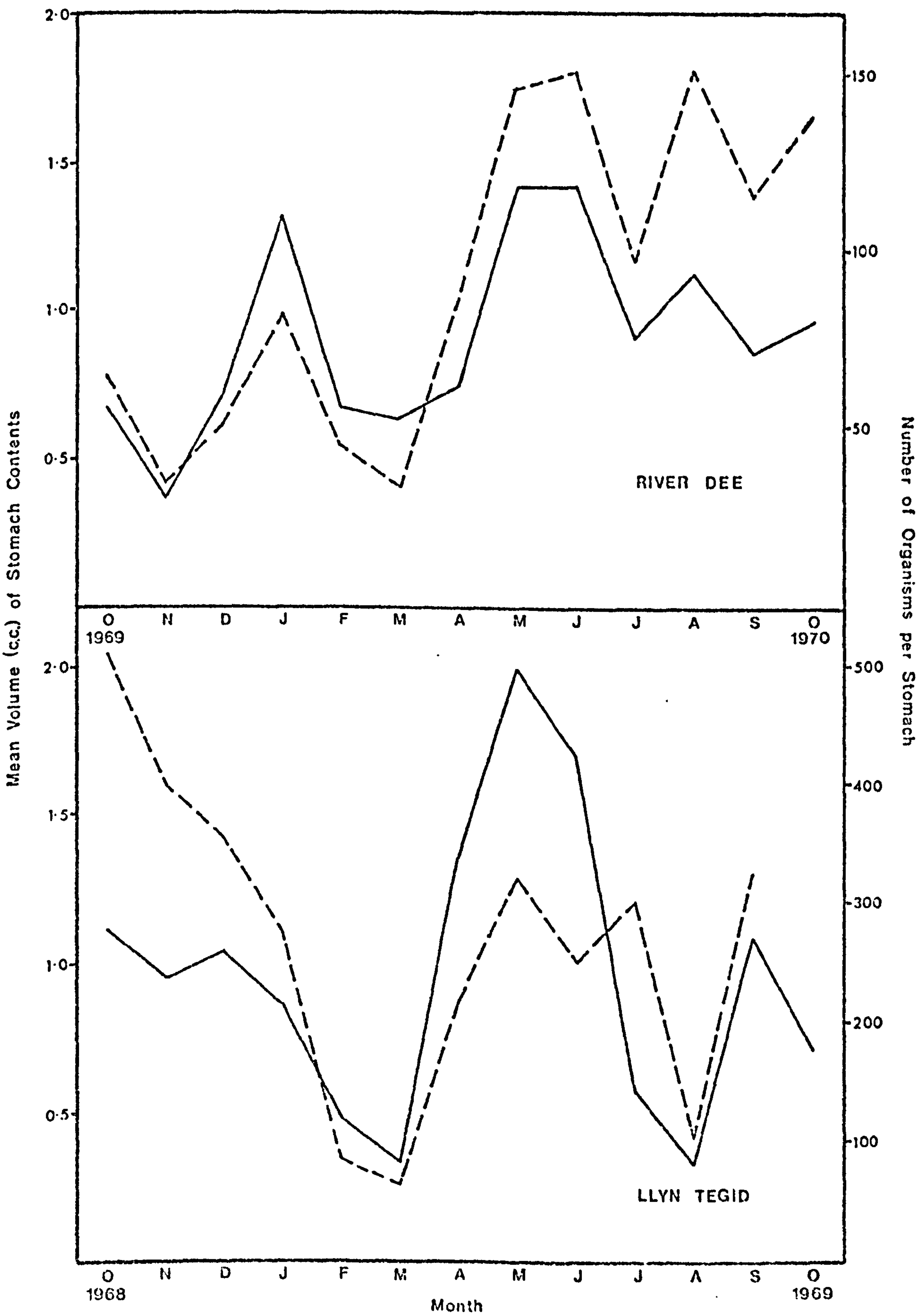

RIVER DEE
LIYN TEGID
Fullness Index
Water Temperature °C
Month
O N D J F M A M J J A S O
1969
1970
1968
1969
0
0+
1−
1
1+
2−
2
2+
3−
3
3+
4−
4
0
2
4
6
8
10
12
14
16
18
20

Figure 67

Seasonal Variation in the Volume of Stomach Contents and Number of Organisms eaten by Grayling in the River Dee and Llyn Tegid.

———	=	mean volume of stomach contents
– – – – –	=	mean number of organisms per stomach

FIGURE 67


Mean Volume (c.c.) of Stomach Contents
Number of Organisms per Stomach
2·0
1·5
1·0
0·5
150
100
50
RIVER DEE
O N D J F M A M J J A S O
1969
1970
2·0
1·5
1·0
0·5
500
400
300
200
100
LLYN TEGID
O N D J F M A M J J A S O
1968
1969
Month

of small organisms.

Feeding intensity was closely related to water temperature. Periods of low feeding activity coincided with minimum and maximum temperatures, and periods of high feeding activity coincided with intermediate temperatures. A summer depression of feeding activity was evident and was most marked in Llyn Tegid during August, a factor which may have contributed to the summer migration of grayling out of the lake (chapter 10). Ball (1961) pointed out that a summer depression of feeding intensity may be an artefact partly accounted for by increased digestive rates at high summer temperatures. The Llyn Tegid mean water temperature, however, was identical in July and August but the feeding intensity was considerably lower in August. Siddiqui (1969) and Hellawell (1971) both found that feeding activity was greatest in the winter and least during the summer and autumn. Nikolskii (1963) stated that Arctic fishes, such as the genus _Thymallus_, usually feed all the year round and may even increase their activity during the winter. The findings of Siddiqui (1969) and Hellawell (1971) support this statement, and Hellawell (op.cit.) adds that since _Thymallus_ is essentially an Arctic or cold-water genus, a depression of feeding activity at high summer temperatures would not seem unreasonable. Although a summer depression of feeding activity was found in both Llyn Tegid and the River Dee, the lowest feeding activity in these habitats occurred during February and March when the water temperature was at its lowest. The winters of 1968/69 and 1969/70 were severe and may account for this, as well as for the spring scale check formation discussed in chapter 5 (section 2b).

The peak of feeding activity was found to be in late spring and early summer with feeding activity high throughout the year, except during February and March when the water temperature was at its lowest, and July and August when the water temperature was at its highest. Seasonal changes in stomach fullness (figures 66 and 67) were closely correlated with seasonal changes in condition factor (figures 28 - 31, chapter 5).

(ii) The composition of the diet

a) River Dee. The composition of the diet of River Dee grayling by percentage number, volume and occurrence is shown in table 38. Detritus was excluded from the calculations of percentage volume and number since it was considered to be of no nutritious value. The percentage contribution of detritus by volume and occurrence to the total stomach contents is, however, included in table 38. The wide variety of dietary organisms was very obvious and the catholic feeding habits of grayling have been noted by most previous workers (Radforth, 1940; Dahl, 1962; Hellawell, 1971). The voracity of the grayling's feeding habits was reflected in the large number of individual food items consumed with a mean figure of 101 food items per stomach. Radforth (1940) recorded an average of 318 food items per stomach.

Trichopteran larvae (particularly Potamophylax latipennis, Glossoma conformis, Goera pilosa, Hydropsyche instabilis and Agapetus fuscipes) were found to be the most important food by volume (49.7%) and occurrence (92.5%). A number of previous

Table 38. - The composition of the diet of River Dee grayling by percentage number, volume and occurrence.

(+ = less than 0.1%)

	% Number	% Volume	% Occurrence
Ephemeropteran nymphs	8.5	5.9	48.8
Baetis spp.	2.0	1.0	46.0
Ecdyonurus venosus	0.4	0.3	9.7
Ephemerella ignita	5.0	3.8	26.0
Heptagenia sulphurea	1.0	0.8	8.3
Leptophlebia vespertina	+	+	4.4
Centroptilum luteoleum	+	+	2.2
Caenis moesta	+	+	0.5
Ephemera danica	+	+	0.2
Plecopteran nymphs	8.6	4.2	51.1
Chloroperla torrentium	4.6	1.6	34.1
Isoperla grammatica	1.8	1.3	23.6
Brachyptera risi	0.1	0.1	1.5
Perlodes microcephala	+	0.2	2.7
Leuctra fusca	1.0	0.4	2.9
Leuctra hippopus	+	+	1.0
Leuctra inermis	0.8	0.4	6.1
Nemoura erratica	+	+	0.2
Taeniopteryx nebulosus	+	0.1	2.4
Amphinemura sulcicollis	0.2	+	7.8
Trichopteran larvae	20.0	49.7	92.5
Goera pilosa	0.6	4.9	10.9
Potamophylax latipennis	1.2	15.8	21.7
Sericostoma personatum	0.2	1.3	7.5
Athripsodes bilineatus	2.3	1.4	33.6
Agapetus fuscipes	3.8	2.8	25.3
Stenophylax sp.	0.3	1.6	14.4
Anabolia nervosa	+	0.2	1.7
Halesus digitatus	1.9	3.0	19.0
Glossoma conformis	1.8	8.4	14.4
Tinodes waeneri	+	+	0.2

Table 33 continued :

	% Number	% Volume	% Occurrence
Glyphotaelius pellucidus	+	0.1	1.7
Mystacides nigra	+	0.1	3.2
Lepidostoma hirtum	1.8	3.1	6.3
Triaenodes bicolor	0.4	0.5	1.9
Hydroptilidae	+	+	2.7
Unidentified cases	0.6	1.1	15.1
Total cased larvae	15.1	44.4	78.8
Hydropsyche instabilis	4.3	4.5	51.6
Rhyacophila dorsalis	0.3	0.6	12.9
Polycentropus flavomaculatus	0.2	0.2	6.6
Plectronemia conspersa	+	+	2.4
Total uncased larvae	4.9	5.3	57.4
Dipteran larvae	14.4	4.5	80.3
Chironomidae	13.1	2.8	65.2
Simulium spp.	0.2	+	7.5
Tipula spp.	0.3	1.4	15.6
Ceratopogonidae	0.4	+	17.0
Other larvae	0.3	0.2	10.2
Mollusca	2.4	2.2	26.9
Limnaea pereger	+	0.3	4.4
Ancylastrum fluviatile	2.2	1.8	20.2
Pisidium spp.	0.1	+	3.9
Planorbis complanatus	+	+	0.2
Hydrobia jenkinsi	+	+	0.2
Crustacea	5.9	5.4	34.6
Gammarus pulex	1.3	2.4	16.1
Asellus meridianus	4.4	3.0	29.0
Planktonic Crustacea	0.2	+	0.5
Hirudinea			
Erpobdella octoculata	0.1	0.2	5.4
Megaloptera			
Sialis fuliginosa	0.1	0.3	6.3

Table 38 continued:

	% Number	% Volume	% Occurrence
Dipteran pupae	2.1	0.5	17.0
Chironomidae	2.1	0.5	16.3
Other pupae	+	+	1.0
Arachnida	1.1	0.1	20.2
Hydracarina	1.0	0.1	18.8
Aquatic & terrestrial spiders	0.1	+	6.8
Coleoptera	2.8	2.2	47.4
Larvae	1.0	0.5	28.0
Adults (aquatic & terrestrial)	1.8	1.7	35.7
Corixidae	0.1	0.2	10.0
Fish	+	0.3	1.0
Fish eggs	+	+	0.7
Aquatic aerial insects	8.5	7.6	47.4
Ephemeroptera :	4.5	3.7	29.5
Baetis spp.	1.7	1.4	17.3
Ephemerella ignita	2.7	2.2	15.8
Heptagenia sulphurea	+	0.1	0.7
Caenis moesta	+	+	1.5
Plecoptera :	1.7	2.5	17.1
Chloroperla torrentium	+	+	1.7
Isoperla grammatica	0.1	0.2	1.2
Perlodes microcephala	+	0.1	0.5
Leuctra fusca	1.0	1.6	7.5
Leuctra geniculata	0.2	0.3	12.2
Leuctra hippopus	0.2	0.3	4.1
Leuctra inermis	+	+	1.7
Nemoura cinerea	+	+	1.2
Taeniopteryx nebulosus	+	+	0.2
Amphinemura sulcicollis	+	+	0.5
Nemurella picteti	+	+	0.2
Protonemura meyeri	+	+	1.7
Trichoptera	0.3	0.8	12.2

Table 38 continued :

	% Number	% Volume	% Occurrence
Diptera: Chironomidae	2.0	0.5	19.7
Simuliidae	+	+	0.5
Terrestrial aerial insects	25.1	14.4	46.9
Diptera	9.5	8.0	41.8
Hymenoptera	0.6	1.0	20.0
Hemiptera	15.0	5.4	34.1
Miscellaneous			
Lepidopteran larvae	+	+	0.5
Millipedes	+	+	0.7
Centipedes	+	+	0.2
Forficula	+	+	0.2
Orthoptera	+	+	0.2
Earthworms	+	0.4	0.7
Unidentified fragments	-	1.7	23.4
Detritus	-	10.1	64.9
Pebbles, sand etc.	-	7.9	54.5
Vegetable matter	-	2.2	31.4
Total: Ephemeroptera	13.0	9.6	63.0
Plecoptera	10.3	6.7	62.2
Trichoptera	20.3	50.5	93.1
Aquatic Diptera	18.5	5.5	86.6
Aerial insects	33.6	22.0	61.8
Mean no. organisms/stomach	101		
Mean volume/organism (mm^3)		8.6	

workers also recorded trichopteran larvae as a major food of grayling (Dahl, 1962; Peterson, 1963; Hellawell, 1971). Aerial insects (aquatic and terrestrial) were the second main food category by volume (22%) and the dominant food by number (33.6%). Terrestrial insects were more important than aquatic aerial insects by number and volume, although of similar importance by occurrence. The most commonly eaten aquatic aerial insects were Ephemerella ignita, Baetis rhodani and Leuctra fusca. The terrestrial insects consumed were from the orders Diptera (mostly Empididae and Bibionidae, with some Calliphora and Muscidae), Hymenoptera (Ichneumonidae, Apidae, Formica and Vespa) and Hemiptera (mostly Aphidae). Peterson (1968) found aerial insects to be the dominant food of young grayling and a common food of older grayling. Hellawell (1969a) found fewer aerial insects in River Lugg grayling and considered that Peterson's (op.cit.) findings might have resulted from selective sampling by angling. A comparison of the stomachs of grayling caught from the River Dee during August and September revealed that in fact grayling caught by netting contained slightly more aerial insects than those caught by angling. No definite conclusions can be drawn from these observations, however, since net and rod samples were not taken at the same time and the consumption of aerial insects was partly dependent on climatic conditions. No evidence was found of regurgitation of food by rod-caught grayling as found in trout by Phillips (1929). Scheuring, (1936) (quoted in Dahl, 1962), found a high consumption of surface food, mainly of terrestrial origin, in fish from rivers [illegible], [illegible] but in [illegible] which flowed through forrested areas. Grayling from Llanderfel (River Dee, sites k and m) ate the most terrestrial food, and this was the most heavily wooded river section sampled (see table 14, chapter 3). Dahl (1962) considered that aerial insects (particularly those of terrestrial origin) were an emergency food necessary in rivers where aquatic food was insufficient in either quantity or quality.

Ephemeropteran nymphs (chiefly Ephemerella ignita, Baetis rhodani and Heptagenia sulphurea), plecopteran nymphs (mainly Isoperla grammatica, Chloroperla torrentium and Leuctra spp.) and dipteran larvae (mainly Chironomidae) were next in dietary importance to trichopteran larvae and aerial insects. The numbers, volume and occurrence of plecopteran and ephemeropteran nymphs were very similar to each other and peaks of consumption occurred just before and during their respective emergence periods. The volume of dipteran larvae eaten (4.5%) was similar to that of plecopteran and ephemeropteran nymphs, but the number (14.4%) and occurrence (80.3%) were much greater. Occurrence and number analyses thus exaggerate the dietary contribution of dipteran larvae (and aerial insects), particularly in comparison with trichopteran larvae which contribute a large percentage volume. Much of the volume of trichopteran larvae, however, consists of indigestible case material, and the nutritional value of these organisms is overestimated by the volume method. A number of previous workers recorded Simulium as the main dipteran larva eaten by grayling (Radforth, 1940; Dahl, 1962; Hellawell, 1971), but in my study far more chironomid larvae were eaten than Simulium larvae, as was found by Peterson (1968). Crustaceans (Gammarus pulex and Asellus meridianus) were of similar dietary importance to ephemeropteran nymphs by volume (5.4%) but occurred less frequently and in smaller numbers. The incidence of Gammarus in stomachs was found to be higher in the lower River Dee sampling sites than in the upstream sections, and a similar distribution of this organism was found in the benthic fauna by M.A. Rahim (pers.comm.). Planktonic Crustacea (Bythotrephes) were found in the stomachs of two fish caught immediately below the outfall of the River Dee from Llyn Tegid. The only mollusc commonly found in the diet was Ancylastrum fluviatile. Coleoptera (larvae and adults) were consumed in similar quantities to molluscs, but occurred in more stomachs. Dipteran pupae, Megaloptera (Sialis fuliginosa), Hirudinea (Erpobdella octoculata), Arachnida and Corixidae were of only minor importance to the diet, as were the miscellaneous food items recorded (Myriapoda, Lepidoptera, Forficula, Orthoptera and earthworms).

Four grayling of age groups 2+ to 4+ had one fish in their stomachs, these were two bullheads (Cottus gobio), a stickleback (Gasterosteus aculeatus) and a minnow (Phoxinus phoxinus). Most previous workers have recorded few fish (Radforth, 1940; Dahl, 1962; Peterson, 1968) or no fish (Hellawell, 1971) in grayling stomachs. Peterson (op.cit.) found larger numbers of fish in grayling from Sundsvall Bay than from the River Indalsalven, and Muller (1961) considered that grayling older than age group 6 tended to change to a fish diet, particularly in lakes and pond-like regions of streams. Only nine fish eggs (grayling) were found in the stomachs examined.

No salmon or trout eggs were found but anglers reported finding small numbers of these eggs in grayling they had examined. Fish eggs, including those of trout, salmon, grayling, coregonids and coarse fish, have been recorded in grayling stomachs by a number of workers (Dahl, 1962; Peterson, 1968; Hellawell, 1971) and it is generally considered that the salmon and trout eggs which are eaten are those that have been washed out of the redds and which would not have survived.

Detritus in the form of pebbles, sand, other substrate material and vegetable matter (mostly twigs), was present in many stomachs and has been recorded, often in considerable quantities, by previous workers (Radforth, 1940; Dahl, 1962; Hellawell, 1971). Margreiter, 1938 (quoted in Dahl, 1962), considered that the vegetable matter he often found in grayling stomachs had some definite nutritive value to the fish, but most workers consider material to have little or no nutritive value to grayling. Hellawell (op.cit.) thought that pebbles might be eaten accidentally or perhaps deliberately to help in the mastication of food. Detritus in River Dee grayling was considered to have been accidentally ingested since it was most common in stomachs containing a lot of bottom organisms, particularly trichopteran larvae, and least common when aerial insects were the dominant food. Pebbles were particularly numerous in the stomachs of grayling feeding on Glossosomatidae. These trichopteran larvae may be difficult to detach from stones, and thus smaller stones and pebbles with larvae attached may be ingested together. Some of the twigs found in stomachs may have been mistaken for trichopteran larvae (Hellawell, 1971).

b) Llyn Tegid. The composition of the diet of Llyn Tegid grayling by percentage number, volume and occurrence is shown in table 39. The wide variety of food organisms was again evident and the mean number of food items per stomach (270) was even higher than that for River Dee grayling. The overall mean volume of the stomach contents of Llyn Tegid fish was 0.99cc. compared with that of 0.96cc. in the River Dee fish. Individual age groups of grayling ate a larger volume of food in Llyn Tegid than in the River Dee. The mean volume of stomach contents was 0.74cc. in Llyn Tegid and 0.65cc. in the River Dee for the 1+ age group, and 1.50cc. and 1.34cc. respectively, for the 2+ age group.

Previous investigations into the diet of Llyn Tegid grayling have been carried out by Dunn (1954), Jones (unpublished, 1957) and Siddiqui (1969). Dunn (1954) examined only 4 grayling caught during March 1952 and found the dominant foods to be Limnaea, Gammarus and Asellus. Jones (1957) examined 16 grayling caught in October and November 1957 and found that the main foods were Asellus, Gammarus, Diptera and planktonic Crustacea. Siddiqui (1969) found that the main food items of 104 grayling caught during 1966 were planktonic Crustacea, dipteran larvae and pupae, Asellus and to a lesser extent, aerial insects, ephemeropteran nymphs, trichopteran larvae and gwyniad eggs. Kruse (1959) found that the main food of Arctic grayling in Grebe lake was ephemeropteran nymphs, chironimid larvae and pupae, and Gammarus together with some planktonic Crustacea, trichopteran larvae and aerial insects.

Table 39. The percentage composition by number, volume and occurrence of the diet of Llyn Tegid grayling.

(+ = less than 0.1%)

	% Number	% Volume	% Occurrence
Ephemeropteran nymphs	8.0	25.5	59.1
Ephemera danica	2.5	13.8	39.3
Leptophlebia marginata	5.5	11.7	34.7
Caenis moesta	+	+	5.0
Ectyonurus venosus	+	+	0.4
Plecopteran nymphs	+	0.1	7.9
Leuctra hippopus	+	0.1	7.0
Nemoura sp.	+	+	0.8
Chloroperla torrentium	+	+	0.4
Trichopteran larvae	2.3	5.1	55.0
Atripsodes aterrimus	1.2	1.5	31.2
Glyphotaelius pellucidus	+	+	0.8
Goera pilosa	+	+	0.4
Hydroptilidae	+	+	0.4
Lepidostoma hirtum	0.5	2.0	9.1
Limnephilus spp.	0.2	0.7	18.3
Mystacides azurea	+	+	0.4
Sericostoma personatum	+	0.3	4.5
Tinodes waeneri	+	+	2.5
Polycentropus flavomaculatus	0.1	0.2	14.2
Cyrnus trimaculatus	0.1	0.2	14.1
Total cased larvae	2.1	4.7	43.9
Total uncased larvae	0.2	0.4	22.5
Dipteran larvae	39.1	18.5	71.9
Chironomidae	39.0	18.1	71.9
Tipulidae	+	0.4	5.8
Ceratopogonidae	0.1	+	16.5
Amphipoda			
Gammarus pulex	1.4	5.1	19.4
Isopoda			
Asellus meridianus	19.6	21.3	65.3

Table 39 continued

	% Number	% Volume	% Occurrence
Planktonic Crustacea	11.3	3.9	22.7
Mollusca	0.5	1.8	24.4
Limnea pereger	0.4	1.6	18.6
Ancylastrum fluviatile	+	0.1	3.3
Valvata sp.	+	+	1.7
Pisidium sp.	+	+	1.2
Physa sp.	+	+	1.2
Hirudinea	0.3	0.5	18.2
Helobdella stagnalis	0.3	0.5	16.1
Erpobdella octoculata	+	+	2.5
Megaloptera			
Sialis lutaria	0.2	1.6	17.4
Dipteran pupae: Chironomidae	4.7	2.5	35.1
Arachnida	0.1	+	7.0
Hydracarina	+	+	4.5
Aquatic & terrestrial spiders	0.1	+	6.2
Corixidae	0.3	0.3	20.2
Coleoptera	0.5	1.1	30.9
Larvae	+	+	3.3
Aquatic and terrestrial adults	0.5	1.1	28.9
Fish eggs	1.8	2.8	16.9
Aquatic aerial insects	1.5	1.8	26.0
Chironomidae	1.1	0.7	23.6
Plecoptera : Leuctra hippopus	+	+	0.8
Ephemeroptera :			
Leptophlebia marginata	0.3	0.7	2.9
Caenis moesta	+	+	1.7
Baetis sp.	+	0.1	1.7
Trichoptera	+	0.2	2.5

Table 39 continued

		% Number	% Volume	% Occurrence
Terrestrial aerial insects		8.0	7.9	36.8
Diptera		3.9	4.9	31.0
Hymenoptera		0.4	0.6	14.5
Hemiptera		3.7	2.4	14.9
Miscellaneous				
Oligochaetes		-	+	0.4
Ostracods		+	+	1.7
Algae		-	+	6.6
Unidentified fragments		-	0.4	5.0
Detritus		-	13.1	70.7
Pebbles, sand etc.		-	11.8	65.3
Vegetable matter		-	1.3	7.9
Total	Ephemeroptera	2.8	26.3	61.2
	Plecoptera	+	0.2	8.7
	Trichoptera	2.3	5.3	57.5
	Crustacea	32.3	29.3	74.4
	Aquatic diptera	44.9	21.7	88.5
	Aerial insects	9.6	9.7	43.4
Mean organisms/stomach		270	985	
Mean volume (mm^3)/organism			3.2	

My study of the food and feeding habits of Llyn Tegid grayling agrees substantially with the findings of Dunn (1954), Jones (1957) and Siddiqui (1969), except for ephemeropteran nymphs which formed 25.5% of the total volume of food eaten by my fish, compared with the 8.0% recorded by Siddiqui (op.cit.) and the single occurrence of an unidentified nymph found by Jones (op.cit.). The increasing numbers of ephemeroptera nymphs in the diet is a reflection of the gradual re-establishment of these organisms, together with many others, in the littoral zone of Llyn Tegid since regulation. Mud and silt have also increased in the littoral zone as a result of the lowering of the lake level, and this has resulted in increased numbers of Ephemera danica in this zone (Hunt, 1970). Chironomid larvae were by far the most common food by number and occurrence, and the enormous increase in the numbers of these organisms was another of the effects of regulation recorded by Hunt (op.cit.).

Ephemeropteran nymphs (mostly Ephemera danica and Leptophlebia marginata) were the most common food by volume, followed by Asellus (21.3%), dipteran larvae (18.5%) and aerial insects (9.7%). Of lesser dietary importance by volume were trichopteran larvae (5.1%), Gammarus (4.1%), planktonic Crustacea (3.9%), gwyniad eggs (2.8%), dipteran pupae (2.5%), molluscs (1.8%), Megaloptera (1.6%) and Coleoptera (1.1%). The most common food items by number were dipteran larvae, Asellus, planktonic Crustacea and aerial insects, and by occurrence dipteran larvae, ephemeropteran nymphs, trichopteran larvae and aerial insects. The number method overestimates the value of dipteran larvae and planktonic Crustacea and underestimates the value of ephemeropteran nymphs. The occurrence method overestimates the contribution of dipteran larvae and trichopteran larvae to the diet, together with that of some of the minor food items such as Coleoptera and molluscs.

Ball (1961) examined a number of grayling stomachs for comparison with those of Llyn Tegid trout, and found that the main trichopteran larvae eaten were Polycentropus flavomaculatus together with Agraylea multipunctata, Tinodes waeneri, Lepidostoma hirtum and Limnephilus lunatus. Of these only Lepidostoma was commonly found in my study, the main trichopteran larvae eaten by grayling being Athripsodes aterrimus. Jones (1957) noted that more Gammarus pulex were found in stomachs of grayling caught at the north-east end of Llyn Tegid than in those from the south-west end. Similar trends were recorded in my study and result from the enrichment of the lake at the north-east end by the Bala sewage outfall. The littoral fauna at the south-west end of Llyn Tegid is more restricted than at the north-east end, and this is reflected by differences in the diet of grayling from opposite ends of the lake. No fish were found in any of the stomachs examined, and none were found by Siddiqui (1969).

Detritus was found in many stomachs and formed 13% of the total stomach contents. The frequent occurrence of large amounts of grit and other substrate material was also recorded by Dunn (1954) and Siddiqui (1969). In my study, this material was most commonly present in the stomachs of grayling which had been eating the burrowing nymphs of *Ephemera danica*. It was therefore concluded that substrate material was accidentally ingested. One stomach contained a number of plant shoots which appeared to have been eaten deliberately, and in May and June a number of stomachs contained algae (small clumps of *Nostoc* sp.) which also appeared to have been eaten deliberately, but which were considered by Eaton (1971, pers. comm.) to be of little or no nutritional value to the fish.

The diet of the grayling in Llyn Tegid and those of the River Dee was, as might have been expected, substantially different. The main differences were the greater consumption of ephemeropteran nymphs, Crustacean and dipteran larvae in Llyn Tegid, together with a smaller consumption of trichopteran larvae and aerial insects. The mean volume of organisms eaten was considerably less in Llyn Tegid ($3.2mm^3$) than in the River Dee ($8.6mm^3$), mainly because of the large number of small chironomid larvae in the diet of Llyn Tegid grayling, and the large trichopteran larvae in the diet of River Dee grayling. It is of interest to note that Dahl (1962) found a faster growth rate in grayling which ate *Gammarus*, Chironomidae and ephemeropteran nymphs, than in grayling which ate trichopteran larvae and aerial insects. He considered that trichopteran larvae were nutritionally of less value than the other foods, and that where fish had to resort to aerial food, because aquatic food was scarce, the growth rate was poor. These observations agree closely with the results of my study. Growth was slower in River Dee grayling, where the main foods eaten were trichopteran larvae and aerial insects, than in Llyn Tegid grayling which ate mostly ephemeropteran nymphs, dipteran larvae and Crustacea. A comparison of the relative calorific values of the two diets (using data from Geng, 1925, quoted in Stube, 1958) showed relative values of 447 x 10^3 and 413 x 10^3 by percentage volume in Llyn Tegid and River Dee grayling respectively. The relative calorific value of the diet of River Dee grayling was thus approximately 8% less than that of Llyn Tegid grayling and the smaller volume of food eaten by River Dee grayling was noted earlier.

(iii) Seasonal variation in the composition of the diet

a) River Dee. The seasonal variation in the composition of the diet of River Dee grayling by volume, number and occurrence is shown in figures 68 to 70. Muller (1961) and Dahl (1962) were able to show some seasonal trends in food consumption although their samples, unlike those of Hellawell (1971), were not taken over a period of consecutive months. In my study grayling were examined in approximately equal numbers for each of 13 consecutive months (table 36) from October 1969 to October 1970. The most common winter foods were found to be trichopteran larvae, Crustacea, dipteran larvae and plecopteran nymphs, whilst during the summer trichopteran larvae, aerial insects and ephemeropteran nymphs formed the bulk of the food eaten.

Trichopteran larvae were the main food of River Dee grayling throughout the year, particularly during the winter. Muller (1961) also recorded more trichopteran larvae in the winter, but Hellawell (1969) found them most commonly in spring, early summer and autumn. The greatest numbers of trichopteran larvae were found in River Dee

FIGURE 68

Seasonal Variation in the Diet of River Dee Grayling by Volume

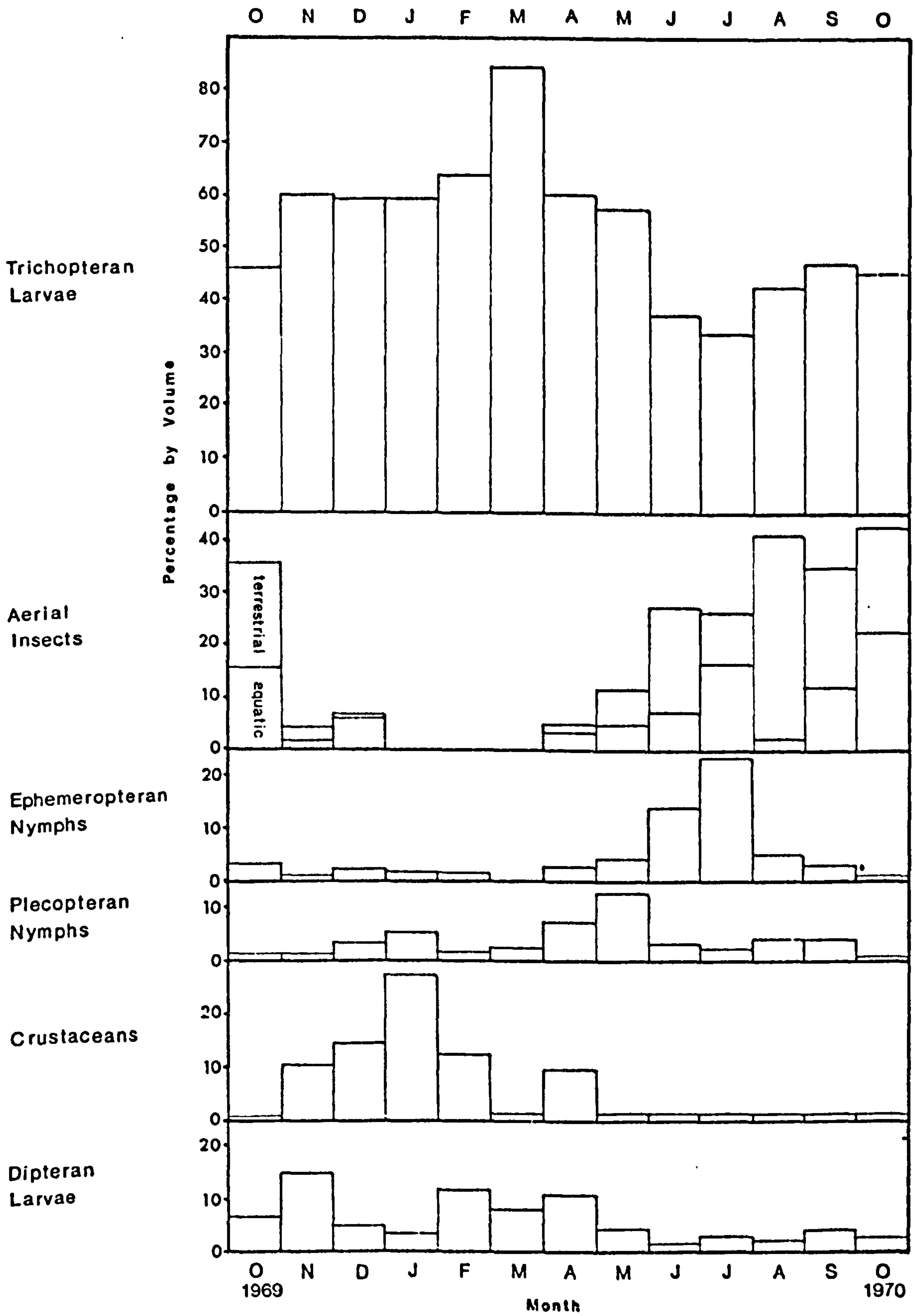


FIGURE 69

Seasonal Variation in the Diet of River Dee Grayling by Number

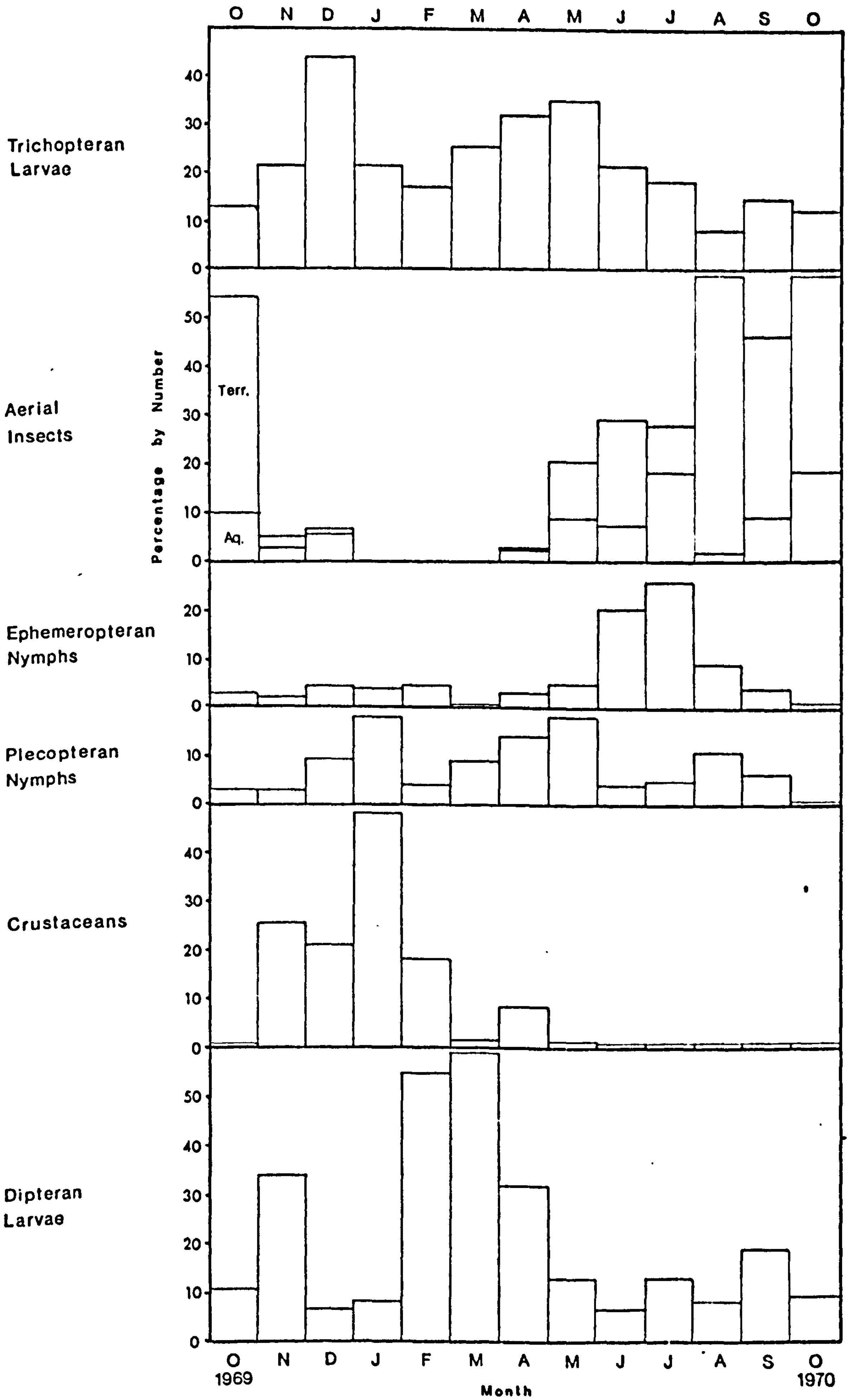
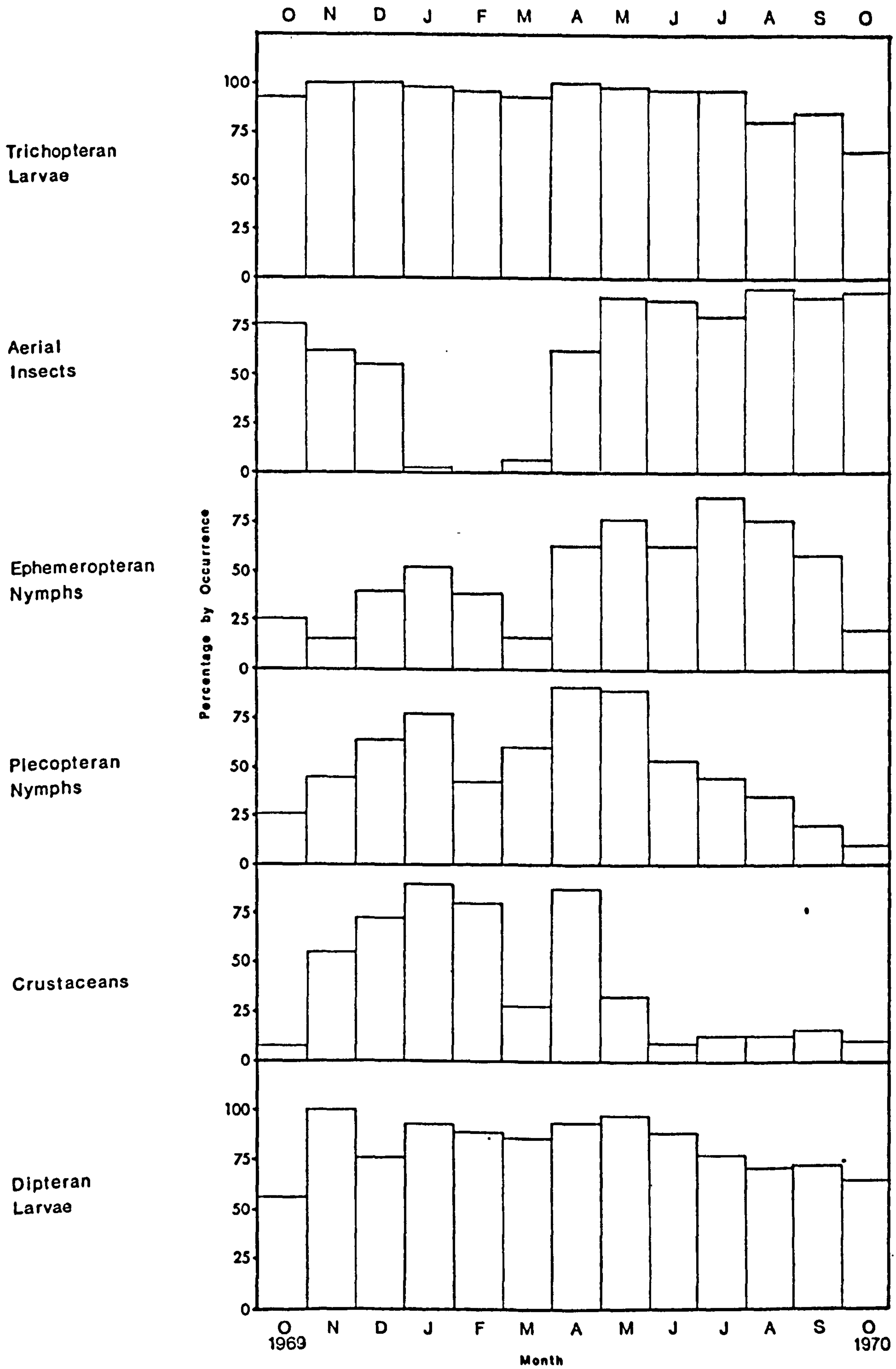


FIGURE 70

Seasonal Variation in the Diet of River Dee Grayling by Occurrence



grayling stomachs during December, when small *Agapetus fuscipes* were the dominant larvae. The greatest volume, however, occurred in March when large *Potamophylax latipennis* larvae were the main food eaten. *Agapetus fuscipes* and *Hydropsyche instabilis* were present in stomachs throughout the year, *Agapetus* being most common in autumn, early winter and spring, and *Hydropsyche* during April and May. *Potamophylax latipennis* and *Halesus digitatus* occurred chiefly in the winter and were almost absent from stomachs during the summer. Lepidostoma hirtum, a predominantly still-water species, was only found in stomachs during the summer, and *Glossoma conformis* was eaten mostly in the summer and autumn.

Aerial insects formed a major part of the diet from May to October and were consumed in smaller quantities in November, December and April. Ephemeroptera and Plecoptera adults were eaten during the spring, summer and autumn according to their respective emergence periods. *Baetis rhodani* sub-imagines and adults of the genus *Leuctra* were eaten in the spring and autumn whilst other *Baetis* spp., *Chloroperla torrentium* and *Isoperla grammatica* were eaten during the summer. *Ephemerella ignita* sub-imagines were consumed mainly in June and July, and in July formed 15% by number and 14% by volume of the total food intake. Trichoptera adults were eaten in small numbers throughout the summer. Except for *Baetis rhodani* in October, December and April, and *Ephemerella ignita* in July, aquatic aerial insects were of secondary importance to terrestrial insects in the diet throughout the period when surface feeding occurred. The most common terrestrial Diptera were Empididae and Bibionidae which were found in very large numbers in grayling stomachs during August and June respectively, and in smaller numbers in July and September. Ichneumon flies and bees (Apidae) occurred chiefly in early summer, whilst unwinged ants (Formicidae) were common in stomachs from August to October. The main Hemiptera found in grayling stomachs were small Aphidae which occurred in very large numbers in late summer and autumn.

Ephemeropteran nymphs were eaten in the greatest quantities during June and July, just before and during the emergence period of Ephemerella ignita. Ephemerella nymphs formed up to 23% by volume of the total food intake at this time. The only other Ephemeropteran nymphs found frequently in grayling stomachs were Baetis rhodani and Heptagenia sulphurea which were most common in April, May and early June. Baetis rhodani nymphs were also consumed, but to a lesser extent, in the autumn and small numbers of other Baetis spp. were found in stomachs during the summer. The importance of ephemeropteran nymphs in the diet declined rapidly after July and very few were eaten during the winter. Hellawell (1969) also found ephemeropteran nymphs most frequently in the summer, and Dahl (1962) found the peak of consumption during September in streams where Baetidae were the main Ephemeroptera present. Other organisms eaten mainly during the summer were molluscs and Coleoptera. Molluscs (mostly Ancylastrum fluviatile) were most common in the diet during June and July when they formed 9% and 5% respectively of the total volume of the stomach contents. Coleoptera formed a maximum of 4% of the diet by volume in May and were more common in the summer, when terrestrial species were also eaten, than in the winter. The main aquatic Coleoptera found in grayling stomachs were *Hydraena*, with smaller numbers of *Latelmis*, *Deronectes*, *Hydroporus*, *Haliplus* and *Laccobius*. Grayling eggs were the only fish eggs found in the stomachs examined and were found in grayling caught on 12th May 1970.

Plecopteran nymphs, Crustacean and dipteran larvae were consumed to a greater extent in the winter and spring than during the summer. Consumption of plecopteran nymphs was highest in April and May prior to the emergence period of *Chloroperla torrentium* and *Isoperla grammatica*, and together these two organisms formed 11% of the diet by volume during May. Plecopteran nymphs formed a significant part of the diet throughout the winter but few were found in stomachs during the summer. Dahl (1962) also found the greatest consumption of plecopteran nymphs during the winter and the least in May and July when consumption of adult Plecoptera was at its highest. Crustaceans (*Gammarus pulex* and *Asellus meridianus*) formed a maximum of 27% of the diet by volume in January and very few were eaten by grayling in the summer. Hellawell (1969) found that the greatest consumption of *Gammarus* by River Lugg grayling occurred during the winter, and Dahl (1962) considered that Crustacea were less important to the diet in the summer because of the high availability of other organisms at that time. Dipteran larvae (mostly Chironomidae) formed the main winter food by number but few were eaten during the summer. Chironomid larvae were also found to a considerable extent in November. Dipteran pupae and adults were most common in May, June and October, at times when the consumption of dipteran larvae was at its minimum.

Hellawell (1969) found an increased consumption of detritus and debris during the summer months and thought that this material might be eaten for an associated fauna. In this study, detritus was ingested to a slightly greater extent in the winter, with a maximum of 21% by volume in December, and appeared to have been eaten accidentally whilst feeding on benthic organisms.

b) Llyn Tegid. The seasonal variation, by volume, number and occurrence, of the main food items in the diet of Llyn Tegid grayling from October 1968 to October 1969 is shown in figures 71 to 73. Dipteran larvae, Crustacea, *Ephemera danica* nymphs and gwyniad eggs form the main winter food, whereas aerial insects, *Leptophlebia marginata* nymphs and dipteran pupae form the bulk of the summer food. Siddiqui (1969) found that Chironomidae, *Asellus* and Gastropods were eaten all the year round, ephemeropteran nymphs mostly in the winter and spring, planktonic Crustacea in the autumn and winter, aerial insects from June onwards and gwyniad eggs during the appropriate season.

Dipteran larvae (mostly Chironomidae) were the main food by volume and number throughout most of the autumn and winter, but few were eaten during the summer. Dipteran pupae and adults (mostly Chironomidae) were most common in July and August respectively, the latter also being eaten to some extent in June, September and October. Crustacea were most common in the diet during the autumn, winter and spring and were totally absent in July and August. Most

FIGURE 71

Seasonal Variation in the Diet of Llyn Tegid Grayling by Volume

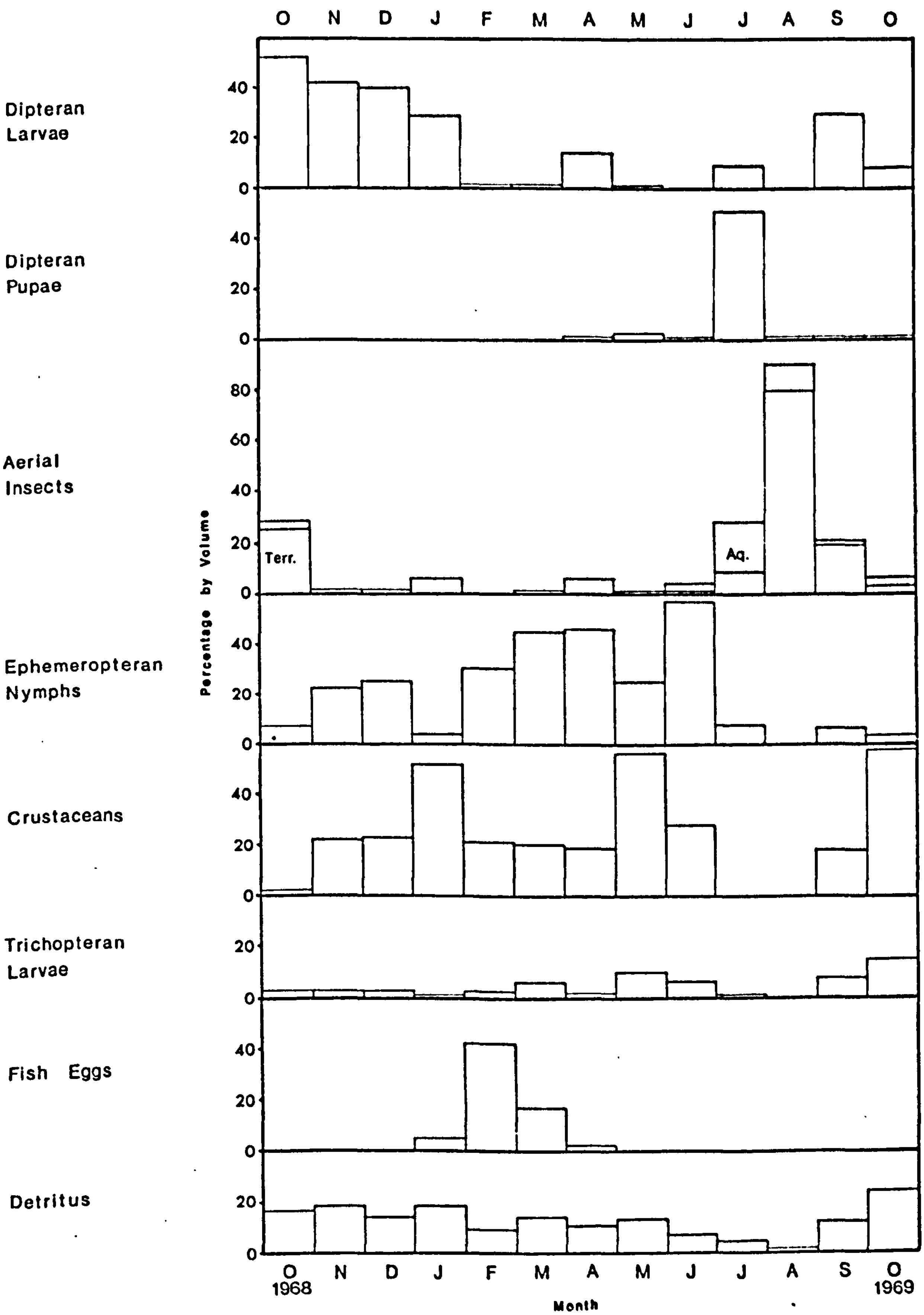


FIGURE 72

Seasonal Variation in the Diet of Llyn Tegid Grayling by Number

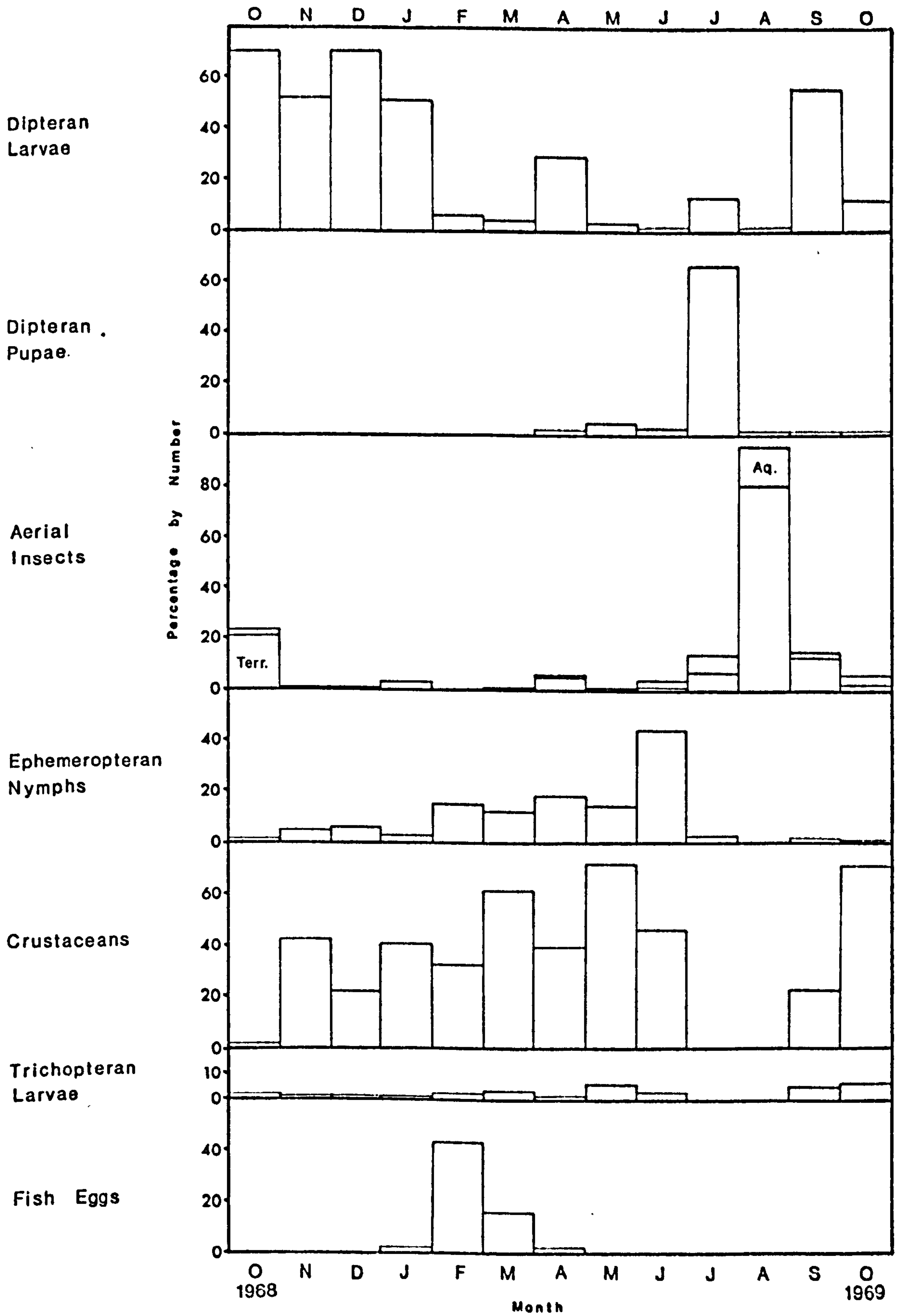
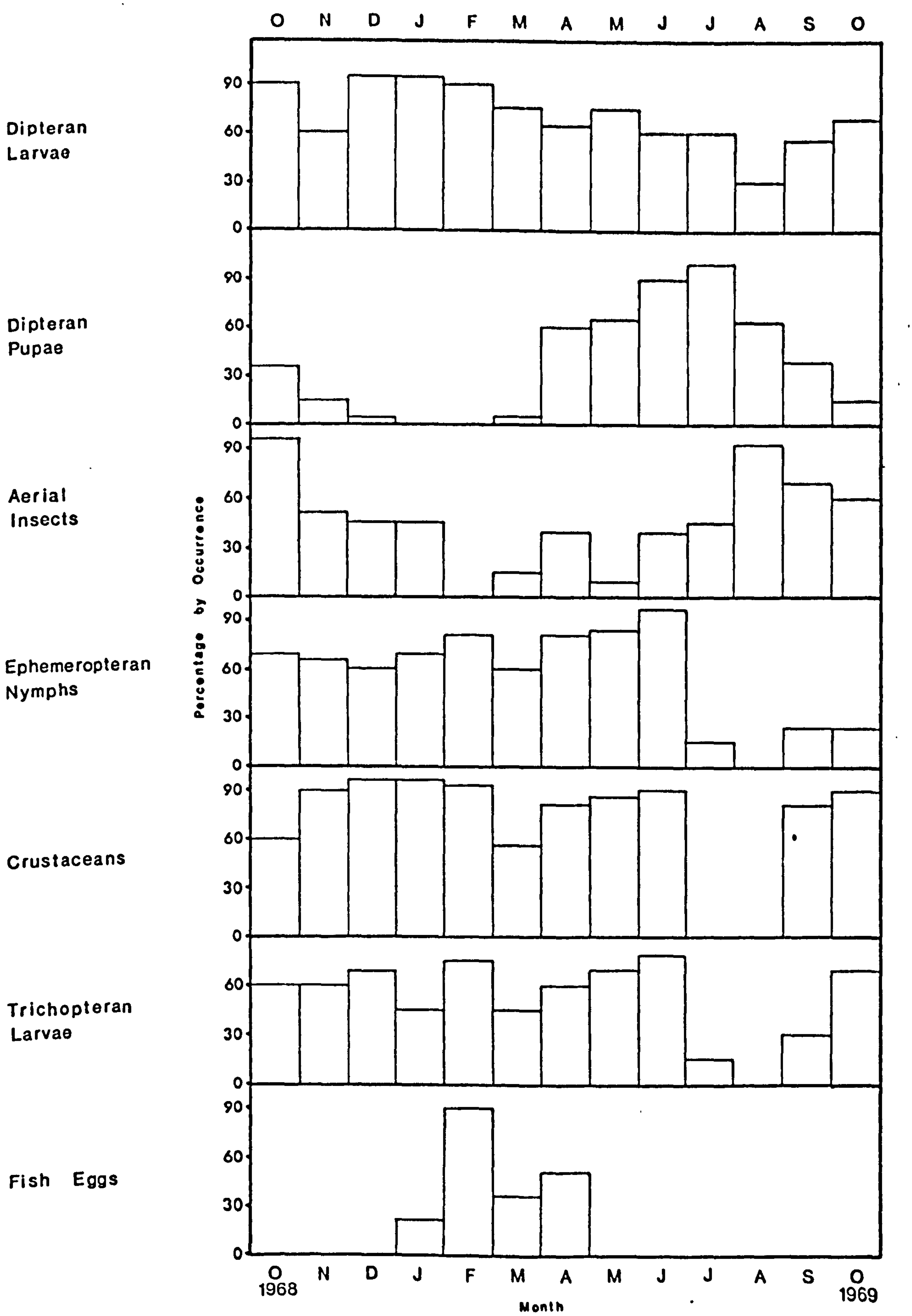


FIGURE 73

Seasonal Variation in the Diet of Llyn Tegid Grayling by Occurrence



of the fish examined in May and October 1969 were caught at the north-east end of the lake where Asellus and Gammarus are particularly abundant. This resulted in the high consumption of Crustaceans observed during these months. The large volume of Crustacea (mostly Asellus) found in January were eaten during a spell of mild weather. Large numbers of planktonic Crustacea (Bythotrephes) were consumed in November and March, and these organisms were also eaten during September, October, December and April. Gwyniad eggs were found in the diet from January to April, and in February they were the main food eaten. Mollusca (Limnaea pereger) were most commonly found in stomachs during September, when they formed 11% of the diet by volume. They occurred in small numbers at other times of year but were generally more abundant in the autumn and winter, and were completely absent from the diet during July and August. Megaloptera (Sialis lutaria) were found throughout the winter and spring forming 8% by volume of the total food intake in March and April. Hirudinea (mostly Helobdella stagnalis) were most common in the diet during the winter and formed 2.7% by volume of the food eaten in December. Detritus and debris was found in stomachs throughout the year, but was least abundant in the summer when aerial insects were the dominant food.

The consumption of ephemeropteran nymphs by Llyn Tegid grayling showed a different seasonal pattern than in the River Dee. Large Ephemera danica nymphs were a major food by volume throughout the winter, and disappeared from the diet after the emergence period in late May. Ephemeropteran nymphs were never of significance in the diet of River Dee grayling during the winter. *Leptophlebia marginata* nymphs were seldom found in the stomachs of Llyn Tegid grayling during the winter, but they became increasingly common in the spring and formed a maximum of 59.5% of the total volume of food eaten in June. These nymphs disappeared from the diet after the emergence period in June and July. Plecopteran nymphs occurred in small numbers, mostly during the spring and early summer, and were only found in fish caught in the vicinity of inflowing feeder streams. Trichopteran larvae were eaten during the spring, early summer and early autumn, and were absent from the diet in August. *Athripsodes aterrimus* was most common in the autumn and *Lepidostoma hirtum* was only of dietary importance in May and June. *Limnephilus* spp. occurred throughout the autumn, winter and spring, but were absent from the diet in July and August. Coleoptera (aquatic and terrestrial adults) were only common in the diet during August (7% by volume) and Corixidae (mostly *Micronecta poweri*) formed a maximum of 1% by volume in July.

Aerial insects became numerous in the diet after June and formed 95% by number and 90% by volume of the diet in August. In July aquatic aerial insects (*Leptophlebia marginata*, *Baetis* spp. *Caenis moesta*, Chironomidae and Trichoptera) were of greater dietary importance than terrestrial insects, but in August the latter formed 80% of the diet by number and volume. The great reduction in feeding intensity of Llyn Tegid grayling during the summer has already been mentioned and the utilization of aerial organisms, particularly of terrestrial origin, as an emergency food (Dahl, 1962) has been discussed. Few grayling remained in Llyn Tegid during July and August (chapter 10) and those that did were found to be in very poor condition as a result of the inferior feeding conditions which occurred at that time. The terrestrial insects eaten in Llyn Tegid were similar to those eaten by River Dee grayling, with Aphidae predominating in the early autumn and Empididae, Bibionidae and Formicidae during the summer. Aerial insects were generally less numerous in the diet of Llyn Tegid grayling than in River Dee grayling except during August when the only other food items eaten were Coleoptera (many of terrestrial origin) and a small number of Diptera larvae and pupae. Siddiqui (1969) also found aerial insects to be the dominant food of Llyn Tegid grayling during August.

(iv) Variation in the diet with age

(a) River Dee. The variation in the diet with age, by volume and number, is shown for River Dee grayling in tables 40 and 41, together with the mean volume of stomach contents and food items, and the mean number of food items per stomach. The 5+ and 6+ age groups are represented by only two and one individuals respectively, caught during the summer.

Previous workers generally agree that the bottom feeding habits of grayling become more pronounced with increasing age, and the contribution of aerial food to the diet correspondingly decreases. (Dahl, 1962; Jankovic, 1964; Peterson, 1968). Young grayling (0+ to 2+ age groups) in the River Dee, unlike the older fish, ate large quantities of aerial insects. Small Chironomidae, Ephemeroptera and Aphidae comprised the main surface food of young

Table 40 Variation in the diet by percentage volume of River Dee grayling with age.

(+ = less than 0.1%)

	Age groups						
	0+	1+	2+	3+	4+	5+	6+
No. of stomachs examined	78	173	102	32	23	2	1
Ephemeropteran nymphs	4.5	6.0	6.4	4.9	5.1	30.7	-
Baetis	2.5	1.3	0.6	0.7	1.4	-	-
Ephemerella	1.0	3.6	5.3	2.5	1.2	27.4	-
Heptagenia	0.6	0.8	0.3	0.8	1.9	3.3	-
Other nymphs	0.4	0.3	0.2	0.9	0.6	-	-
Plecopteran nymphs	3.0	5.0	3.3	4.7	4.6	4.4	-
Chloroperla	1.2	2.2	1.2	1.7	1.0	4.4	-
Isoperla	1.2	1.4	0.7	2.4	1.7	-	-
Leuctra	0.1	0.5	1.2	0.2	1.1	-	-
Other nymphs	0.5	0.9	0.2	0.4	0.8	-	-
Trichopteran larvae	23.5	38.1	53.9	53.9	63.6	35.2	95.7
Goera	0.4	2.7	8.6	4.7	1.8	13.7	-
Potamophylax	0.8	9.5	17.2	24.9	22.2	5.5	-
Athripsodes	1.5	1.3	1.7	0.7	2.0	0.2	-
Agapetus	7.6	4.7	2.6	1.4	+	-	-
Halesus	0.2	4.7	1.1	1.2	7.8	-	-
Glossoma	1.0	4.4	8.5	10.1	8.2	0.7	93.4
Lepidostoma	0.2	0.1	3.3	1.2	12.0	0.4	-
Other cased larvae	1.2	4.0	5.3	7.2	5.8	11.2	2.3
Uncased larvae	10.6	6.7	5.6	2.5	3.8	3.5	-
Diptera : Larvae	19.9	6.4	3.1	2.7	1.8	1.1	-
Pupae	1.4	1.0	0.3	+	-		-
Crustacea	2.4	4.8	2.5	8.5	11.5	-	-
Gammarus	0.1	1.2	1.2	4.1	6.8	-	-
Asellus	2.3	3.6	1.3	4.4	4.7	-	-
Hirudinea	0.3	0.5	+	+	+	-	-
Megaloptera	-	0.4	0.1	0.5	0.4	-	-

Table 40 continued

	Age groups						
	0+	1+	2+	3+	4+	5+	6+
Arachnida	1.1	0.1	+	+	-	-	-
Coroxidae	0.5	0.4	0.3	+	+	-	-
Coleoptera	2.6	3.6	2.1	1.5	0.7	3.7	0.2
Mollusca	2.5	1.2	1.8	6.3	0.7	7.1	-
Fish	-	-	0.2	0.7	0.7	-	-
Aerial insects	34.9	29.6	24.3	12.9	9.6	13.4	4.0
Aquatic:	20.2	9.1	7.0	5.5	5.3	12.3	0.5
Ephemeroptera	9.6	5.1	4.2	1.8	1.0	-	0.1
Plecoptera	3.2	2.5	1.7	2.8	3.6	12.3	0.2
Trichoptera	0.9	0.9	0.8	0.8	0.7	-	0.2
Diptera	6.5	0.6	0.3	0.1	+	-	-
Terrestrial :	14.7	20.5	17.3	7.4	4.3	1.1	3.5
Diptera	4.0	10.8	9.8	4.7	4.2	0.3	2.4
Hymenoptera	0.2	0.7	1.7	0.7	+	-	0.9
Hemiptera	10.5	9.0	5.8	2.0	+	0.8	0.2
Other organisms	1.4	1.2	+	0.2	0.2	1.6	-
Unidentified fragments	2.0	1.7	1.7	2.2	1.1	2.6	-
Detritus	1.9	8.6	10.2	13.8	10.6	11.0	8.7
Mean volume/stomach (cc)	0.19	0.65	1.34	2.00	2.45	1.83	5.23
Mean volume/organism (mm^3)	3.0	6.0	10.9	12.6	16.6	7.6	44.7

Table 41. Variation in the diet by percentage number of River Dee grayling with age.

(+ = less than 0.1%)

	Age groups						
	0+	1+	2+	3+	4+	5+	6+
Ephemeropteran nymphs	3.8	6.6	9.9	9.9	12.1	62.5	-
Baetis	2.5	2.0	1.1	2.2	4.2	-	-
Ephemerella	0.9	3.6	3.2	4.2	3.3	41.7	-
Heptagenia	0.1	0.6	0.4	1.3	3.4	20.8	-
Other nymphs	0.3	0.4	0.2	0.2	1.2	-	-
Plecopteran nymphs	2.2	8.2	10.1	11.4	12.3	8.3	-
Chloroperla	1.3	5.1	4.5	5.9	4.4	8.3	-
Isoperla	0.5	1.8	1.3	4.4	3.0	-	-
Leuctra	+	0.7	4.1	0.8	4.5	-	-
Other nymphs	0.4	0.6	0.2	0.3	0.4	-	-
Trichopteran larvae	12.2	17.0	23.6	19.5	37.2	5.4	85.4
Goera	+	0.3	1.4	0.9	0.5	1.3	-
Potamophylax	+	0.6	1.8	2.7	2.8	0.2	-
Athripsodes	1.5	1.8	3.0	1.6	5.2	0.4	-
Agapetus	4.3	5.0	3.5	2.5	0.2	-	-
Halesus	+	2.4	0.9	1.5	6.9	-	-
Glossoma	0.1	0.9	2.4	3.2	3.0	0.2	84.0
Lepidostoma	0.1	+	2.3	1.3	12.9	0.6	-
Other cased larvae	0.7	1.2	2.3	3.0	2.0	1.0	1.4
Uncased larvae	5.5	4.8	6.0	2.8	3.7	1.7	-
Diptera: Larvae	38.0	14.1	9.6	10.9	2.3	4.2	-
Pupae	2.7	3.2	1.6	0.3	-	0.2	-
Crustacea	1.6	4.8	3.7	12.6	16.9	-	-
Gammarus	+	0.5	0.9	3.2	7.1	-	-
Asellus	1.6	4.3	2.8	9.4	9.8	-	-
Hirudinea	0.1	0.3	+	+	+	-	-
Megaloptera	-	+	+	0.4	0.3	-	-
Arachnida	3.6	1.2	0.4	0.5	-	-	-
Corixidae	0.1	0.1	0.2	+	+	-	-

Table 41 continued

	Age groups						
	0+	1+	2+	3+	4+	5+	6+
Coleoptera	1.6	3.1	3.1	2.8	1.8	3.1	0.9
Molluscs	2.3	0.9	2.2	8.8	1.7	8.3	-
Fish	+	-	+	+	+	-	-
Aerial insects	30.1	40.5	35.3	22.4	15.3	7.5	13.7
Aquatic:	14.2	7.5	9.3	6.0	6.6	6.3	3.4
Ephemeroptera	4.1	4.6	6.1	2.6	2.3	-	0.9
Plecoptera	1.1	1.2	1.5	2.5	4.0	6.3	0.9
Trichoptera	0.1	0.4	0.5	0.4	0.2	-	1.7
Diptera	8.9	1.3	1.2	0.5	+	-	-
Terrestrial :	15.9	33.0	26.0	16.4	8.7	1.2	10.3
Diptera	2.0	12.3	10.1	7.1	8.6	0.4	2.6
Hymenoptera	0.3	0.7	0.7	0.9	+	-	6.8
Hemiptera	13.6	20.0	15.2	8.4	+	0.8	0.9
Other organisms	1.7	+	+	0.1	0.1	0.2	-
Mean number of organisms /stomach	62.5	100	111	137	132	240	117
No. of stomachs examined	78	173	102	32	23	2	1

grayling, whereas older grayling ate larger Diptera and Plecoptera. Bottom foods, particularly trichopteran larvae and Crustacea, became more common in the diet of grayling as they grew older. Dahl (1962) and Hellawell (1971) also recorded more Crustacea in older grayling than in young grayling. The main species of trichopteran larvae eaten varied between the different age groups, young fish ate small larvae such as *Agapetus fuscipes*, and older grayling ate larger larvae, in particular *Potamophylax latipennis*. Hellawell (1971) found that young grayling in the River Lugg ate most dipteran larvae and plecopteran nymphs than older grayling. The consumption of dipteran larvae and pupae decreased in River Dee grayling with increasing age, but plecopteran nymphs were eaten in similar quantities by all age groups of fish. Fish were only found in the stomachs of older grayling and were absent from the 0+ and 1+ age groups. Muller (1961) found fish in the stomachs of grayling older than 6 years.

The size (mean volume) of food organisms shown in table 40 clearly indicates that older grayling ate larger food organisms. Young grayling ate mostly small trichopteran larvae, dipteran larvae and aerial insects, whilst older fish ate large trichopteran larvae and Crustacea. The mean volume of stomach contents also increased with age as did the number of organisms eaten. Dahl (1962) used the length of food organisms to determine differences in food size, but errors arose in the use of this method as a result of the presence of very long ptychopterid larvae in a number of young grayling. Hellawell (1971), using volume measurements, was able to show a correlation between increasing amounts of large food items and increasing age.

Dahl (1962) drew attention to the fact that grayling of a similar size tend to shoal together and feed in different parts of the river according to their size. Small grayling tend to congregate in the fast shallows, whereas large grayling often inhabit the pools and deeper slow flowing river sections. Dahl (op.cit.) considered that differences in diet were thus largely related to differences in habitats. A similar distribution of size groups was found to some extent in the River Dee and variations in the feeding habits of the groups may have been partially a result of differential distribution of food organisms. Thus the consumption of _Agapetus_ which occurred mainly in riffle areas, by small grayling, and the consumption of _Potamophylax_, which occurred mostly in deeper and slower water, by large grayling, was related to the distribution as well as to the size of the organism. Large grayling were caught in fast shallow water during the spring, whilst these areas were chiefly populated by small grayling in the summer. During the winter the size groups were more mixed and large and small grayling were often caught in close proximity to each other, mostly in water of moderate depth (1 - 2 metres).

(b) _Llyn Tegid_. The variation in diet with age, by volume and number, is shown for Llyn Tegid grayling in tables 42 and 43. Only 7 fish of the 4+ age group were examined (caught in the period May to October)

Table 42 Variation in the diet by percentage volume of Llyn Tegid grayling with age.

(+ = less than 0.1%)

	Age groups				
	0+	1+	2+	3+	4+
Ephemeropteran nymphs	2.6	15.9	35.0	25.6	18.3
Ephemera danica	1.8	10.3	19.0	15.0	0.3
Leptophlebia	0.2	5.6	16.0	10.6	18.0
Other nymphs	0.6	+	-	+	-
Plecopteran nymphs	+	0.1	0.1	+	-
Trichopteran larvae	2.3	3.3	4.1	6.1	17.0
Athripsodes	1.4	2.1	1.7	0.3	1.4
Lepidostoma	-	+	0.9	3.8	12.7
Limnephilus	-	0.3	0.7	0.8	2.7
Tinodes	0.4	+	+	-	-
Other cased larvae	+	0.3	0.6	0.6	-
Uncased larvae	0.5	0.6	0.2	0.6	0.2
Diptera: Larvae	3.2	28.6	18.1	15.0	2.4
Pupae	10.4	2.5	1.7	3.6	+
Crustacea	22.4	22.8	28.0	32.6	56.9
Gammarus	-	0.8	3.7	5.3	17.7
Asellus	7.4	13.8	22.0	27.3	39.2
Planktonic Crustacea	15.0	8.2	2.3	+	-
Molluscs	0.2	1.2	1.9	3.3	1.2
Hirudinea	+	0.7	0.3	0.9	0.1
Megaloptera	1.1	1.6	1.7	1.9	+
Arachnida	0.3	0.1	+	+	-
Corixidae	0.2	0.5	0.2	0.2	+
Coleoptera	0.9	1.8	0.9	1.2	0.3
Fish eggs	0.1	2.7	2.5	5.4	-
Aerial Insects	55.5	16.9	4.6	3.8	-
Aquatic:	5.9	5.0	0.1	0.4	-
Ephemeroptera	-	3.0	+	+	-

Table 42 continued

	Age groups				
	0+	1+	2+	3+	4+
Plecoptera	-	+	+	-	-
Chironomidae	5.9	1.4	+	0.4	-
Trichoptera	-	0.6	+	-	-
Terrestrial:	49.6	11.9	4.5	3.3	-
Diptera	34.4	5.3	3.7	2.3	-
Hymenoptera	2.0	0.3	0.5	0.9	-
Hemiptera	13.2	6.3	0.3	0.1	-
Unidentified fragments	0.5	0.9	0.1	0.1	0.2
Detritus	1.0	13.5	11.8	17.9	13.2
Other organisms	+	+	0.4	0.4	3.4
Mean vol./organism (mm^3)	2.4	2.2	3.8	3.8	5.4
Mean vol./stomach (cc)	0.18	0.74	1.47	1.79	2.50
No. of stomachs examined	52	89	69	25	7

Table 43 Variation in the diet by percentage number of Llyn Tegid grayling with age.

(+ = less than 0.1%)

	Age groups				
	0+	1+	2+	3+	4+
Ephemeropteran nymphs	0.5	4.3	12.1	9.2	13.0
Ephemera danica	0.2	1.7	3.7	3.4	-
Leptophlebia	0.2	2.6	8.4	5.8	13.0
Other nymphs	+	+	-	+	-
Plecopteran nymphs	+	+	0.1	+	-
Trichopteran larvae	1.2	1.8	2.5	2.2	7.8
Athripsodes	0.5	1.4	1.6	0.2	1.1
Lepidostoma	-	+	0.3	1.4	4.9
Limnephilus	-	+	0.2	0.2	1.6
Tinodes	0.5	+	+	-	-
Other cased larvae	+	0.1	0.2	0.1	-
Uncased larvae	0.2	0.3	0.2	0.3	0.2
Diptera : Larvae	5.2	43.9	44.2	36.5	8.6
Pupae	8.9	3.6	3.9	8.7	0.1
Crustacea	41.5	29.7	28.7	32.8	69.3
Gammarus	-	0.3	1.4	2.4	9.0
Asellus	6.9	9.1	23.5	30.4	60.3
Planktonic Crustacea	34.6	20.3	3.8	+	-
Molluscs	+	0.3	0.6	0.8	0.6
Hirudinea	+	0.3	0.2	0.4	0.1
Megaloptera	0.1	0.1	0.2	0.3	+
Arachnida	0.4	0.2	+	+	-
Corixidae	0.5	0.5	0.2	+	+
Coleoptera	0.2	0.7	0.4	0.5	0.1
Fish Eggs	+	1.2	1.9	4.1	-
Aerial Insects:	41.0	13.0	4.4	4.0	-
Aquatic :	7.2	2.5	0.1	0.6	-
Ephemeroptera	-	1.0	+	+	-

Table 43 continued

	Age groups				
	0+	1+	2+	3+	4+
Plecoptera	-	+	+	-	-
Chironomidae	7.9	1.4	0.1	0.6	-
Trichoptera	-	+	+	-	-
Terrestrial:	33.1	10.5	4.3	3.4	-
Diptera	14.9	3.8	3.4	2.5	-
Hymenoptera	0.9	0.1	0.4	0.7	-
Hemiptera	17.3	6.6	0.5	0.2	-
Other organisms	-	+	+	-	-
Mean no. organisms/ stomach	72.1	285.0	343.7	336.2	402.4
No. of stomachs examined	52	89	69	25	7

and the diet of this group was, therefore, poorly represented by the results shown. Siddiqui (1969) did not show variations in the diet with age in his study of Llyn Tegid grayling. Kruse (1959) found that Arctic grayling of the O+ age group started feeding in Grebe lake on planktonic Crustacea (mostly Daphnia) and later ephemeropteran nymphs, dipteran larvae and pupae, aerial insects and some amphipods were added to the diet. Older fish ate dipteran larvae and pupae, more Gammarus and some trichopteran larvae, and Kruse (1959) was able to show an increase in food size with age.

In Llyn Tegid O+ grayling were first found feeding in July principally on chironomid pupae, and in August on aerial insects. Later planktonic Crustacea (Bythotrephes) became the main food and ephemeropteran nymphs, Asellus and trichopteran larvae were added to the diet. Muller (1961) found planktonic Crustacea to be the dominant food of O+ grayling in slow, lake-like regions of the Lule Alv. The 1+ age group in Llyn Tegid ate fewer aerial insects, planktonic Crustacea and dipteran pupae than O+ grayling but ate more dipteran larvae, Asellus, ephemeropteran nymphs, gwyniad eggs and Trichoptera. This change to bottom feeding continued as the grayling got older, with increasing consumption of ephemeropteran nymphs (Ephemera danica and Leptophlebia marginata), Crustacea (Gammarus and Asellus), trichopteran larvae, gwyniad eggs and molluscs, and decreasing consumption of aerial insects, dipteran pupae and planktonic Crustacea. Dipteran larvae decreased in dietary importance after the 1+ age group, probably because of their small size, but continued to be a major component of the diet in older fish. Some variation in the species of trichopteran larvae consumed in the different age groups was observed, young grayling eating small larvae such as *Athripsodes aterrimus*, *Tinodes waeneri* and Polycentropidae, and older fish eating larger larvae, in particular *Limnephilus spp.* and *Lepidostoma hirtum*.

The mean size (volume) of food organism increased with age (see table 42) but less so than in River Dee grayling. The increase in food size was mainly attributable to the increased consumption of ephemeropteran nymphs, *Gammarus* and *Asellus*. The greater increase in food size with age in River Dee grayling was due to the greater consumption of trichopteran larvae in that environment. There appeared to be no segregation of size groups in Llyn Tegid, both large and small grayling being caught in the same netting operation. Grayling fry, however, were found to be in separate shoals in very shallow water when they first appeared in the lake.

(v) Utilization of the fauna

The use of forage ratios, availability factors and selection factors to show the relationship between available food supply and dietary composition has been discussed by many previous workers (Neill, 1938; Allen, 1941; Hynes, 1950; Jones, 1952; Maitland, 1965; Elliot, 1967; Hunt, 1970) and involves the comparison of the percentage representation of an animal in the food with its percentage representation in the fauna. Neill (1938), Allen (1941), Jones (1952) and Hunt (1970) compared percentage numbers of organisms in the food and fauna, while Hynes (1950) concluded that percentage bulk should be used to determine availability factors, this method being adopted by Maitland (1965) and Elliot (1967). Results obtained from the use of such availability factors have been further considered by Neill (1938), Allen (1941), Thomas (1964) and Hunt (1970) in terms of accessibility, with classifications of food categories ranging from highly accessible organisms, such as Asellus and ephemeropteran nymphs, which are both mobile and exposed, to organisms which may never be accessible, such as burrowing oligochaetes and Pisidium.

In the present study the ratio, percentage by number of the animal in the food : percentage by number of the animal in the fauna, has been used to determine availability factors since numbers of organisms were the only comparable data available. Data on the invertebrate fauna of the River Dee between Llyn Tegid and Corwen from March 1969 to April 1970 was provided by M.A. Rahim, and data on the littoral fauna of Llyn Tegid from March 1968 to March 1969 by P.C. Hunt. The availability factors of the various food items are shown for River Dee grayling in table 44, and for Llyn Tegid grayling in table 45. The percentage representation of an animal in the food was determined as its proportion of the benthic fauna eaten, other food items such as aerial insects and planktonic Crustacea being excluded from such calculations. An availability factor of 1 indicates that a food item is eaten strictly in accordance with its occurrence in the benthos. No previous references to the availability factors of grayling food

Table 44 The availability factors of the benthic fauna in the diet of River Dee grayling.

Organism	% by no. in fauna A	% by no. in diet B	Availability Factor B/A
	(+ = less than 0.1%)		((+) = less than 0.01)
Oligochaetes	15.2	-	-
Corixidae	6.2	0.2	0.03
Asellus	5.6	6.8	1.21
Dipteran pupae	0.9	3.2	3.56
Coleoptera	3.7	3.1	0.84
Gammarus	0.6	2.0	3.33
Megaloptera	0.5	0.2	0.40
Turbellaria	0.4	-	-
Hydracarina	0.2	1.5	7.50
Dipteran larvae	24.9	22.2	0.89
Chironomidae	23.5	20.2	0.86
Simulium	0.2	0.3	1.50
Tipula	0.2	0.5	2.50
Ceratopogonids	0.5	0.6	1.20
Other larvae	0.5	0.5	1.00
Trichoptera	17.5	30.8	1.76
Hydropsyche	2.6	6.6	2.54
Agapetus	2.9	5.8	2.00
Plectronemia	0.3	+	0.15
Stenophylax	0.2	0.5	2.50
Potamophylax	1.0	1.8	1.80
Rhyacophila	+	0.4	4.67
Sericostoma	0.2	0.3	1.50
Anabolia	4.2	+	(+)
Mystacides	0.4	+	0.15
Glyphotaelius	5.5	+	(+)
Halesus	0.2	2.9	14.50
Silo	+	-	-
Diplectrona	+	-	-

Table 44 continued

	% by no. in fauna	% by no. in diet	Availability Factor
Limnephilus	+	-	-
Goera	-	0.9	-
Atrhipsodes	-	3.5	-
Glossoma	-	2.8	-
Tinodes	-	+	-
Lepidostoma	-	2.8	-
Triaenodes	-	0.6	-
Hydroptilidae	-	0.1	-
Polycentropus	-	0.3	-
Ephemeroptera	13.5	13.1	0.97
Ecdyonurus	0.2	0.6	3.00
Baetis	3.8	3.1	0.81
Procloeon	+	-	-
Ephemerella	5.3	7.7	1.45
Cloeon	+	-	-
Centroptilum	2.6	+	0.02
Leptophlebia	0.5	+	0.25
Caenis	0.5	+	0.02
Rhithrogena	+	-	-
Heptagenia	0.3	1.5	5.00
Paraleptophlebia	0.1	-	-
Siphlonurus	+	-	-
Ephemera	+	+	0.37
Plecoptera	7.1	13.2	1.86
Isoperla	0.9	2.8	3.11
Protonemura	0.2	-	-
Amphinemura	3.3	0.3	0.09
Leuctra	0.9	2.8	3.11
Nemoura	+	+	0.17
Chloroperla	1.7	7.1	4.17
Perlodes	+	+	3.03
Brachyptera	+	0.1	9.86
Nemurella	+	-	-

Table 44 continued

	% by no. in fauna	% by no. in diet	Availability Factor
Mollusca	2.9	3.6	1.24
Limnaea	0.2	0.1	0.50
Ancylastrum	+	3.4	13.79
Hydrobia	+	+	0.37
Pisidium	2.7	+	(+)
Planorbis	-	+	-
Hirudinea	0.7	0.2	0.29
Glossiphonia	+	-	-
Erpobdella	0.4	0.2	0.50
Helobdella	0.2	-	-
Piscicola	+	-	-

Table 45 The availability factors of the littoral fauna in the diet of Llyn Tegid grayling.

Organism	% by no. in fauna A	% by no. in diet B	Availability Factor B/A
	(+ = less than 0.1%)		((+) = less than 0.01)
Oligochaetes	34.9	+	(+)
Hydracarina	4.9	+	0.01
Gammarus	2.3	1.9	0.83
Asellus	2.3	27.0	11.74
Megaloptera	1.7	0.3	0.18
Plecoptera	1.1	0.1	0.09
Coleoptera	0.4	0.4	1.00
Turbellaria	0.3	-	-
Ephemeroptera	19.4	11.0	0.57
Leptophlebia	1.5	7.6	5.07
Caenis	8.8	+	(+)
Ephemera	8.9	3.4	0.38
Baetis	0.2	-	-
Diptera	17.5	53.9	3.08
Ceratopogonidae	4.0	0.1	0.03
Tipuliidae	0.5	+	0.01
Chironomidae	12.6	53.8	4.27
Other Diptera	0.4	-	-
Molluscs	5.2	0.7	0.14
Limnaea	2.5	0.6	0.24
Ancylastrum	0.2	+	0.02
Pisidium	2.5	+	0.01
Corixidae	5.1	0.4	0.08
Sigara	1.0	+	(+)
Micronecta	4.1	0.4	0.10
Trichoptera	2.6	3.2	1.23
Athripsodes	0.3	1.7	5.67
Potamophylax	0.2	-	-

Table 45 continued

	% by no. in fauna	% by no. in diet	Availability Factor
Limnephilus	0.2	0.3	1.50
Mystacides	0.2	+	(+)
Tinodes	1.3	+	0.03
Lepidostoma	+	0.7	7.00
Cyrnus	0.4	0.1	0.25
Hirudinea	2.3	0.4	0.17
Erpobdella	1.7	+	(+)
Helobdella	0.5	0.4	0.80
Glossiphonia	0.1	-	-

organisms have been found in the literature.

(a) River Dee. Oligochaetes, Turbellaria, some leeches and trichopteran larvae and a number of ephemeropteran and plecopteran nymphs were present in the fauna but absent from the diet. Oligochaetes were abundant in the fauna but high power observation for chaetae (Kennedy, 1969) failed to reveal the presence of remains of these worms in any of the stomachs examined. Oligochaetes were considered generally inaccessible to grayling because of their burrowing habit. Turbellaria, if eaten by grayling, would probably be quickly digested to an unrecognisable form (Hunt, 1970). Helobdella stagnalis and Glossiphonia complanatus are species of leeches which occur under stones in relatively small numbers and which are therefore not readily accessible, whilst Piscicola geometrica is a fish parasite. The absence from the diet of a number of trichopteran larvae, ephemeropteran nymphs and plecopteran nymphs was because of the scarcity of these organisms in the fauna.

A second group of organisms showed a considerably higher percentage representation in the fauna than in the food. This group included Corixids, Megaloptera and Erpodella octoculata, together with a number of trichopteran larvae, ephemeropteran nymphs, plecopteran nymphs and molluscs. Corixids were considered by Frost & Macan (1948) to be generally unacceptable to fish because they secrete substances distasteful to fish. Hunt (1970), however, found corixids to be a common food of Llyn Alaw trout. Most of the corixids recorded by M.A. Rahim in the

River Dee were from a sampling site at the mouth of a backwater contining large amounts of macrovegetation and silt, and generally with no water flow. (A. Tryweryn flood relief channel, plate 1). Megaloptera (Sialis fuliginosa) are burrowing organisms which are not very numerous in the fauna and which are not readily accessible to grayling. Erpobdella was the only leech eaten by River Dee grayling but was unimportant in the diet and relatively infrequent in the fauna. Trichopteran larvae with low availability factors included Anabolia nervosa, a large organism incorporating long twigs in its case, and Glyphotaelius pellucidus, a species occurring in still or slow flowing parts of the river which grayling do not generally frequent. The low availability factors of Plectrocnemia and Mystacides may be because of their relative scarcity in the fauna since other larvae of similar size and habits were eaten by grayling to a considerable extent. The small nymphs of Centroptilum luteolum, Leptophlebia vespertina and Baetis spp. showed low availability factors, as did the small, silt dwelling nymphs of Caenis moesta which occur in still or slow flowing water. Only one Ephemera danica nymph was found in both the fauna and the stomachs examined. Plecopteran nymphs showing low availability factors were Amphinemura sulcicollis which were small, and Nemoura erratica, which were scarce in the fauna. The most common mollusc in the fauna was Pisidium, but this organism was rare in the stomachs because of its burrowing habits. Hydrobia was rare in the fauna and Limnaea was only abundant in the Afon Tryweryn flood relief channel sampling site described above.

Asellus, Coleoptera and most dipteran larvae were eaten approximately in accordance with their occurrence in the benthos. Chironomid larvae were abundant in both the fauna and the food and were more available to young grayling than to old grayling because of their small size. Asellus, on the other hand, was more available to older fish, and was not eaten during the summer despite its presence in the benthos.

Organisms showing a high availability factor were generally mobile, of large size, and occurred in exposed situations. Some, however, occupied concealed habitats (e.g. Hydropsyche instabilis and Tipula larvae) and their availability to grayling reflects the ability of these fish to "root out" food items from among stones and bottom deposits. Organisms which are firmly attached to stones and which are relatively immobile (e.g. Agapetus fuscipes and Ancylastrum fluviatile) may also be eaten to a considerable extent by grayling. Trichopteran larvae such as Potamophylax, Sterophylax, Lepidostoma, Sericostoma and Halesus are relatively large animals easily accessible on the river bottom, and their increased availability to older grayling shows the ability of larger fish to consume larger organisms, and to deal with hard cases. Dipteran pupae and Hydracarina show a high availability to young grayling because of their exposure and mobility, but are eaten much less by older grayling because of their small size. Gammarus is readily available to grayling because of its size and mobility. Most ephemeropteran nymphs only become readily accessible just before and during their emergence period (e.g. Ephemerella, Heptagenia and Baetis), at a time when they are most numerous, of maximum size and mobility, and are most exposed. Ecdyonurus, however, was only common in the diet during the winter, possibly because of the similarity of its habits with those of lithophilic plecopteran nymphs. The availability of plecopteran nymphs also increased just before the emergence periods (Chloroperla, Isoperla, Leuctra and Amphinemura) but these organisms continued to be accessible to grayling throughout the autumn, winter and spring. The misleadingly high availability factors of Perlodes and Brachyptera resulted from the very small numbers of these nymphs in both the stomachs and the fauna. It should also be noted that organisms with high availability factors are not necessarily important in the diet (e.g. Hydracarina) whereas organisms with low availability factors may be of considerable dietary value (e.g. chironomid larvae).

A number of organisms (mostly trichopteran larvae) were found in fish stomachs but not in the fauna. Planorbis, Tinodes, Hydroptilidae and Polycentropus were relatively scarce in the diet and may have been easily missed in faunal examinations. Athripsodes, Glossoma, Lepidostoma and to a lesser extent Goera and Triaenodes were common in the diet and their apparent absence from the benthos can only be due to incomplete sampling of the whole fluviatile environment. This factor may also account for the very high availabilities of Halesus and Ancylastrum. The patchy distribution of Simulium larvae was noted by Egglishaw (1967) and it seems likely that their numerical representation in the River Dee fauna should be higher than that shown.

Excluded from the above discussion are emerging aquatic insects and terrestrial organisms. Both of these food categories form a major part of the diet during the appropriate seasons. At such times these food items are very accessible to grayling and are often available in large numbers.

River Dee grayling were found to be primarily bottom feeders eating considerable quantities of surface food when this was available. Grayling were mostly found feeding in mid-stream over a gravel bottom, rather than amongst weed beds or at the river edges. Food organisms were taken from exposed positions on the river bed, and from among stones and bottom deposits. Large bottom dwelling animals became increasingly important in the diet of older grayling, and full advantage was taken of the high seasonal accessibility of aquatic insects just before their emergence periods. Organisms which were most numerous in the diet were generally those which were most numerous in the fauna, except when such organisms were, for one reason or another, inaccessible to grayling (e.g. oligochaetes).

(b) Llyn Tegid. Turbellaria, Baetis, Potamophylax, Glossiphonia and some dipteran larvae were present in the fauna but absent from the diet. The relative scarcity of these organisms, digestion of Turbellaria to an unrecognisable form, and the inaccessibility of Glossiphonia (under stones) and burrowing dipteran larvae, account for this absence.

Organisms showing low availability factors (<1) were oligochaetes, Hydracarina, Megaloptera, Plecoptera, Corixids, Erpobdella, molluscs and certain ephemeropteran nymphs and trichopteran larvae. Some of these organisms, notably oligochaetes, Caenis, Ephemera, Micronecta, Hydracarina and ceratopogonids, were numerous in the littoral fauna. Oligochaetes and Pisidium were generally inaccessible because of their burrowing habits, and were probably ingested accidentally whilst grayling were feeding on other bottom organisms. Some burrowing organisms, in particular Ephemera danica and to a lesser extent Sialis lutaria, were eaten by grayling, however, the former nymph being of great dietary importance by volume despite its low numerical availability factor. Caenis moesta nymphs are small, dull coloured and slow moving (Ball, 1961), and carry mud and epiphytes on their backs which may camouflage them and protect them from predation (Frost, 1939). Micronecta, Hydracarina and Ceratopogonids, despite their mobility and exposure, are probably too small to be of interest to grayling. Most of the plecopteran nymphs recorded by Hunt (1970) were found in the vicinity of the Afon Glyn inflow, an area from which few grayling were examined. Limnaea peregar, a large and relatively mobile organism, was the mollusc most commonly eaten by Llyn Tegid grayling, whilst Ancylastrum fluviatile was scarce in both the diet and the fauna. Trichopteran larvae showing low availability factors were Mystacides azurea, which were relatively scarce in the fauna, Cyrnus trimaculatus, which is small and occurs under stones, and Tinodes waeneri, the most common trichopteran in Llyn Tegid. Tinodes occurs in tunnels on or under stones (Hunt, 1970), and may be inconspicuous to grayling or difficult to detach.

Gammarus, Coleoptera and Helobdella stagnalis were eaten in approximate accordance with their occurrence in the fauna. *Gammarus* is not very numerous in the littoral fauna of Llyn Tegid except at the north-east end of the lake where increased numbers in the fauna are parallelled by increased numbers in the diet. Adult Coleoptera are readily accessible to grayling but many of the larvae are buried in bottom deposits or occur beneath stones. The consumption of *Helobdella* by Llyn Tegid grayling rather than *Erpobdella* is opposite to the situation found in the River Dee. *Helobdella* is a leech occurring under stones, whereas *Erpobdella* is a relatively mobile species found on the upper surface of stones and bottom deposits.

A final group of animals showed availability factors considerably in excess of 1. These were *Asellus*, *Leptophlebia marginata* nymphs, chironomid larvae and certain trichopteran larvae. The high consumption of chironomid larvae is a reflection both of the abundance of these organisms in the littoral fauna, and of the grayling's ability to "root out" food items from bottom deposits. The consumption of *Ephemera* nymphs and *Helobdella* is also accounted for by this characteristic. Chironomid larvae continue to be of considerable food value to older grayling, but there is evidence of a decrease in consumption with increasing age, probably because of the small size of these larvae. *Stictochironomus* was by far the most numerous chironomid larva in both the littoral fauna and the diet. Other chironomids found in grayling stomachs were *Dicrotendipes* and *Cryptochironomus*, together with very small numbers of *Orthocladiinae* and *Procladius*. *Stictochironomus*, *Dicrotendipes* and *Cryptochironomus* occur almost exclusively in the littoral zone of the lake, and *Orthocladiinae* and *Procladius* occur in both the littoral zone and the profundal zone. None of the strictly profundal larvae (*Chironomus* and *Sergentia*) were found in grayling stomachs. *Asellus meridianus* showed the highest avilability factor of any of the organisms eaten by Llyn Tegid grayling. This organism is both mobile and exposed, and is of sufficient size to form a major part of the diet of all age groups of grayling. As in the case of *Gammarus*, an increase in the numbers, both in the fauna and the diet, occurred at the north-east end of the lake. *Leptophlebia nymphs* showed a very high availability factor just before and during the emergence period, when they were most abundant in the littoral zone and when they were largest and most active. Trichopteran larvae showing high availability factors were *Athripsodes*, *Lepidostoma* and *Limnephilus*, all of which were of moderate size and easily accessible on the lake bottom. *Athripsodes* and *Lepidostoma* were particularly abundant in the stomachs of grayling from the north-east end of the lake.

Food items not included in the above discussion were aerial insects, planktonic Crustacea, gwyniad eggs and dipteran pupae. All of these organisms were eaten to a considerable extent at those times of year when they were available in large numbers and were readily accessible.

In my study, Llyn Tegid grayling have been found to be predominantly bottom feeders of the shallow littoral zone, supplementing their diet with surface food, mid-water food and coregonid eggs at times of the year when these items became abundant and accessible. Whilst some of the benthic food eaten was mobile and exposed (e.g. *Asellus*), other items were buried or partially buried (e.g. *Ephemera danica* nymphs and chironomid larvae) and could only be obtained by grubbing about in bottom deposits. The latter method of feeding was more pronounced in Llyn Tegid grayling than in River Dee grayling, probably because of differences in the faunal compositions.

4. Summary

(1) The food and feeding habits of grayling were assessed by the examination of 411 and 242 stomachs from the River Dee and Llyn Tegid respectively. The value of the various food items in the diet was estimated in terms of percentage number, volume and occurrence.

(2) Feeding activity was found to be greatest in the late spring and early summer with a high rate of feeding throughout the year except during February and March, when the water was coldest, and July and August, when the water temperature was at its highest.

(3) The main food items of River Dee grayling were trichopteran larvae and aerial insects, together with smaller quantities of ephemeropteran nymphs, plecopteran nymphs, dipteran larvae and Crustacea.

(4) In Llyn Tegid the main food items of grayling were Crustacea, ephemeropteran nymphs and dipteran larvae. Fewer aerial insects and

trichopteran larvae were eaten than in the River Dee.

(5) Plecopteran nymphs, dipteran larvae and Crustacea were mostly eaten in the winter and spring, whilst aerial insects and ephemeropteran nymphs (except *Ephemera danica*) were eaten during the summer and early autumn. Trichopteran larvae were found in stomachs throughout the year, but were generally more common in the winter. Gwyniad eggs were also consumed by Llyn Tegid grayling during the winter, and dipteran pupae in the summer.

(6) As grayling get older more large bottom foods (e.g. *Potamophylax latipennis* and *Ephemera danica*) and fewer aerial insects and small aquatic organisms (e.g. chironomid larvae) were eaten. Large and small grayling were, to some extent, found in different habitats in the River Dee.

(7) Grayling in the River Dee and Llyn Tegid were found to be predominantly bottom feeders, with considerable quantities of mid-water and surface food being added to the diet when this was available. Food organisms were taken from exposed positions on the river or lake bed, and were also rooted out from among stones and bottom deposits. Grayling generally fed on organisms which were most numerous or most accessible.

CHAPTER VIII

THE FOOD OF SALMON PARR AND TROUT IN THE RIVER DEE.

1. Introduction

Investigations before 1948 into the feeding relationships between different species of fishes in the same community have been reviewed by Hartley (1948). The feeding relationships between salmonids have been studied recently by Thomas (1962), Maitland (1965), Egglishaw (1967) and Mann & Orr (1969). Maitland (1969) emphasises the importance of examining fish caught close together both in time and space when attempting to assess the competition for food between two or more species, and he considers the comparisons of the food of different species of fish given by Hartley (1948) and Thomas (1962) to be unjustifiable on this account.

In my study the stomachs of 161 salmon parr and 105 brown trout, caught whilst fishing for grayling, were examined in order to compare the diets of these fish with each other and with grayling. The competition for food between salmon parr, trout and grayling was assessed. The diet of salmon parr in the Cheshire Dee has been studied previously by Carpenter (1940).

2. Materials

The stomachs of 161 salmon parr and 105 brown trout caught between October 1969 and October 1970 were examined to determine the food and feeding habits of these fishes in the River Dee. All fish were caught by angling and Table 46 shows the number of stomachs examined each month.

Table 46. The numbers of salmon parr and brown trout stomachs examined each month.

	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
salmon parr	15	15	1	15	0	10	15	15	15	15	15	15	15
brown trout	1	6	8	9	4	10	10	10	10	10	10	10	10

The numbers of fish examined from each main sampling area are shown in table 47.

Table 47. The numbers of salmon parr and trout examined from different reaches of the River Dee.

Site	Salmon parr	Brown trout
Bala sluices	42	42
Bodweri	25	21
Llanderfel	54	32
Llandrillo	14	3
Corwen	26	7

The use of angling methods for the capture of samples has been criticised on the grounds that this method might be selective (Pentelow, 1932) and that captured fish might regurgitate their food (Phillips, 1929), but Thomas (1962) states that these criticisms were discounted by Dimick & Mote (1934), Neill (1938) and Frost (1939). More recently Macan et al. (1969) showed that trout caught by angling and by netting could be treated together for dietary analyses. No evidence of regurgitation of food by rod-caught salmon parr and trout was observed in the River Dee, and comparisons of rod and net caught grayling were discussed in the previous chapter.

3. Results of food analyses

(i) Seasonal variation in feeding activity

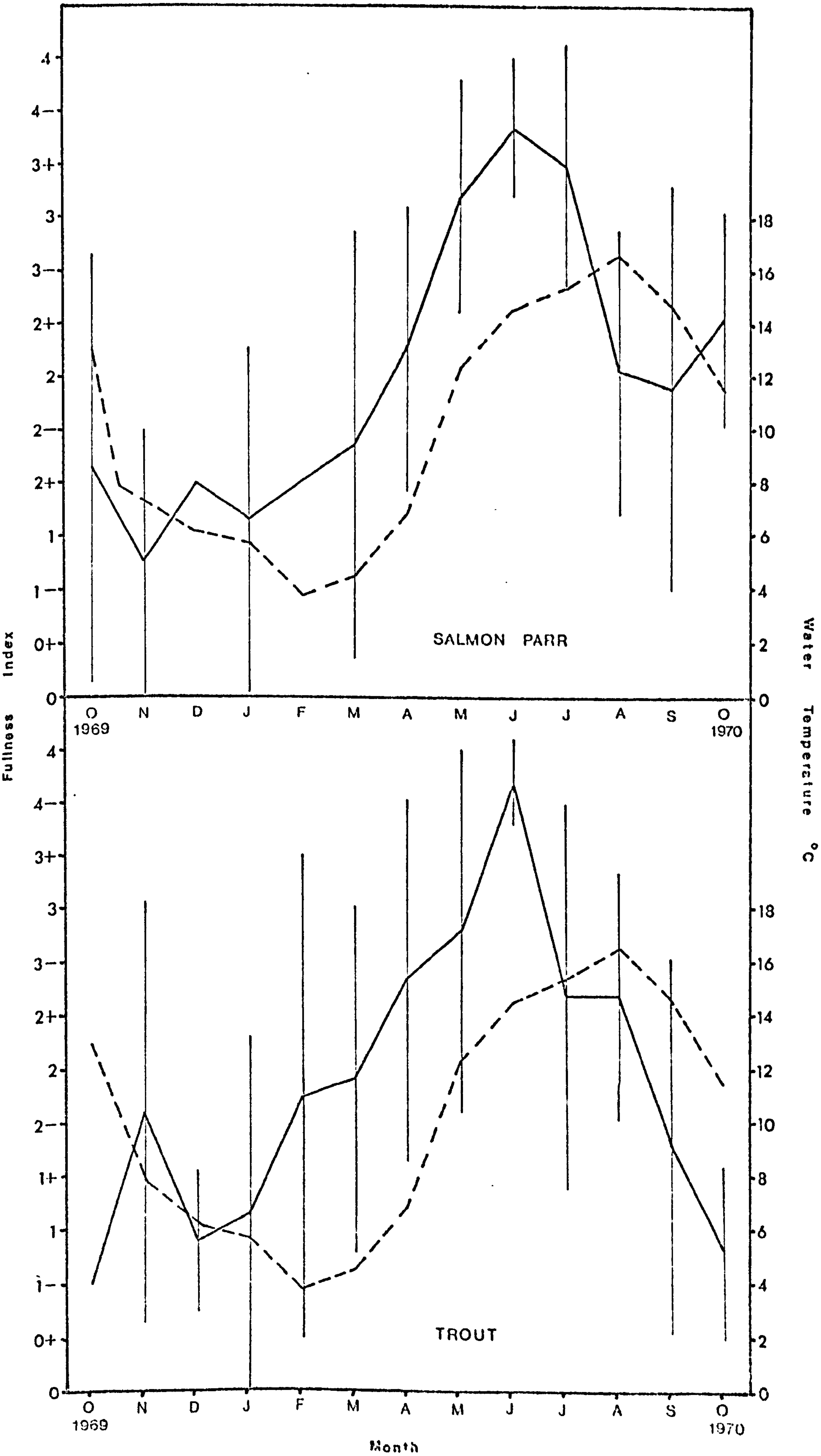
The seasonal variation in the feeding activity of salmon parr and trout is shown in figure 74 in terms of fullness index, and in figure 75 in terms of volume of stomach contents and number of organisms eaten. These figures show that feeding activity is at a minimum during the winter and increases during the spring, rising to a maximum in June. Feeding intensity drops rapidly after July and remains low throughout late summer and autumn. The period of maximum food intake coincides with the period of maximum growth and the increased spring rate of feeding commences earlier than in grayling, at a time when water temperatures are at their lowest. 6.2% of salmon parr stomachs were found to be completely empty and 5.6% contained only a trace of food. 3.8% of trout stomachs were empty and the same proportion contained only a trace of food. All empty stomachs were found in the period October to March, as were most of the stomachs containing only a trace of food. Some stomachs in the latter category were also found in August and September when water temperatures were at their highest.

McCormack (1962) found extensive feeding in trout even at very low water temperatures and Elliot (1967) found no correlation between water temperature and the amount of food in trout stomachs. Thomas (1962) found that salmon parr and trout fed actively at all seasons regardless of temperature but that more food was found in the

Figure 74

Seasonal Variation in the Fullness Index of Salmon Parr and Trout Stomachs in the River Dee

———	=	mean fullness index
-----	=	mean water temperature
Vertical lines	=	± S.D. of fullness indices



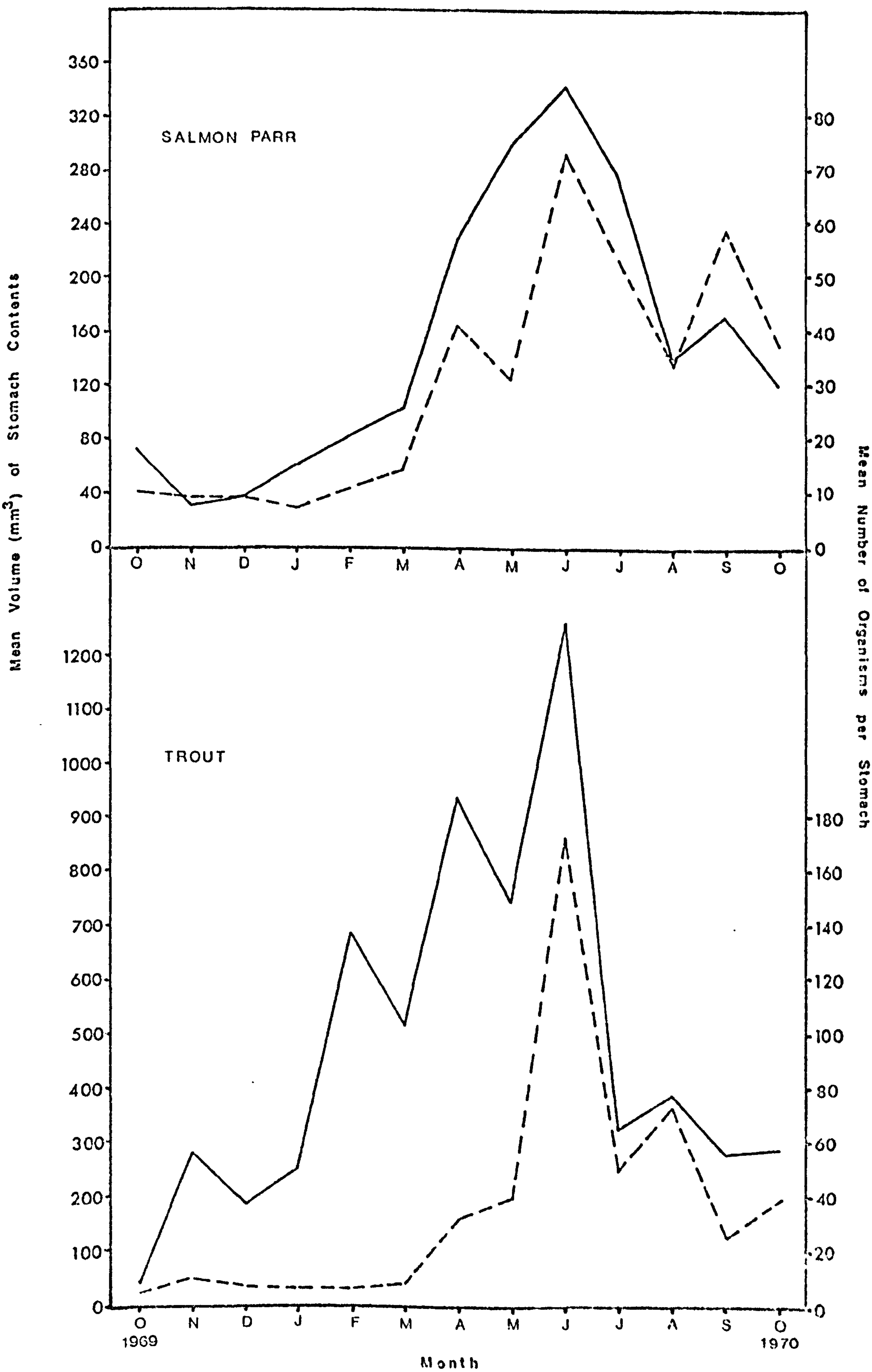
SALMON PARR
TROUT
Fullness Index
Water Temperature °C
O 1969
N
D
J
F
M
A
M
J
J
A
S
O 1970
Month

Figure 75

Seasonal Variation in the Volume of Stomach Contents and Number of Organisms Eaten by Salmon Parr and Trout in the River Dee.

———	=	mean volume of stomach contents
------	=	mean number of organisms per stomach.

FIGURE 75



SALMON PARR
TROUT
Mean Volume (mm³) of Stomach Contents
Mean Number of Organisms per Stomach
0
40
80
120
160
200
240
280
320
360
10
20
30
40
50
60
70
80
100
200
300
400
500
600
700
800
900
1000
1100
1200
140
160
180
O
N
D
J
F
M
A
M
J
J
A
S
O
1969
1970
Month

stomachs during the summer than in the winter. Summer food consumption is probably even higher than stomach analyses indicate because of increased rates of digestion at high temperatures. Carpenter (1940) and Thomas (1962) found an August decrease in food consumption and the former author related this decrease to the low availability of food organisms at this time. Ball (1961) considered that the main factors concerned in the spring rise in food intake of Llyn Tegid trout were increasing day length, temperature, appetite and availability of the food supply. Brown (1946b) showed that much less food was eaten by trout in excess of the maintenance requirements at 5°C and 20°C than at intermediate temperatures, and Egglishaw (1967) considered that low winter feeding activity was due to a physiological loss in capacity of the alimentary system of salmonids to digest food at low winter temperatures, and not to a decrease in the numbers of food organisms.

In this study there appears to be a definite correlation between feeding activity and water temperature. Salmon parr and trout fed throughout the year but less intensively at times of low and high water temperatures. The period of maximum feeding coincided with the time of maximum availability of aquatic insects, and in late summer when many of these organisms were inaccessible, the feeding intensity decreased despite the abundance and high availability of terrestrial food. The depression of feeding intensity in August was more marked in salmon parr than in trout and may be correlated with the trout's greater tendency to feed on surface organisms.

(ii) <u>The composition of the diet.</u>

The composition of the diet of River Dee salmon parr and trout by percentage number, volume and occurrence is shown in tables 48 and 49. These tables also indicate that the mean number and volume of stomach contents, and the mean volume of food items consumed, is greater in trout than in salmon parr. The main food items of salmon parr, by all methods of diet analysis, were trichopteran larvae, ephemeropteran nymphs, dipteran larvae and aerial insects. Carpenter (1940) found the same main food items in the River Dee salmon parr she examined but recorded a greater number of dipteran larvae (71%) and fewer ephemeropteran nymphs (11%), trichopteran larvae (6%) and aerial insects (7%). Other workers have also found the most common foods of salmon parr to be ephemeropteran nymphs, trichopteran larvae and dipteran larvae (Frost & Went, 1940; Allen, 1941a), together in some cases with plecopteran nymphs (Maitland, 1965; Egglishaw, 1967) and molluscs (Thomas, 1962). In the case of River Dee trout the dominant food items were trichopteran larvae, aerial insects, fish (by volume) and to a lesser extent, ephemeropteran nymphs and dipteran larvae. The major foods of river trout have been recorded by previous workers as being trichopteran larvae, aerial insects and ephemeroptera nymphs (Frost, 1939; Thomas, 1962; Maitland, 1965; Egglishaw, 1967; Elliot, 1967; Mann & Orr, 1969) together, in some cases, with plecopteran nymphs (Frost, 1939; Thomas, 1962; Elliot, 1967), molluscs (Mann & Orr, 1969), dipteran larvae (Frost, 1939; Maitland, 1965; Mann & Orr,

Table 48 The percentage composition of the diet of River Dee salmon parr by number, volume and occurrence.

(+ = less than 0.1%)

	% Number	% Volume	% Occurrence
Ephemeropteran nymphs	21.9	27.9	57.9
Baetis spp.	9.5	9.4	39.1
Ecdyonurus venosus	0.1	0.2	2.5
Ephemerella ignita	10.7	14.1	29.2
Heptagenia sulphurea	1.5	4.1	13.0
Ephemera danica	+	0.2	1.2
Plecopteran nymphs	2.1	4.5	31.2
Chloroperla torrentium	0.4	0.3	9.3
Isoperla grammatica	0.9	1.5	13.7
Brachyptera risi	0.1	0.1	2.5
Leuctra fusca	+	+	0.6
Leuctra inermis	0.3	0.2	5.6
Amphinemura sulcicollis	0.3	0.2	4.3
Perlodes microcephala	+	0.4	1.2
Protonemura meyeri	+	0.2	1.9
Perla bipunctata	+	1.5	1.2
Trichopteran larvae	16.8	30.7	73.3
Athripsodes bilineatus	3.7	3.4	28.6
Agapetus fuscipes	6.4	7.1	20.5
Stenophylax sp.	0.2	2.5	6.8
Anabolia nervosa	+	0.6	1.9
Halesus digitatus	0.2	0.5	6.2
Glossoma conformis	0.3	1.5	6.2
Mystacides nigra	+	0.1	1.2
Lepidostoma hirtum	0.3	1.2	8.1
Triaenodes bicolor	+	+	0.6
Hydroptilidae	0.1	0.1	2.5
Unidentified cases	0.2	0.6	4.3
Hydropsyche instabilis	5.0	12.0	36.0

Table 48 continued

	% Number	% Volume	% Occurrence
Rhyacophila dorsalis	0.2	0.[illegible]	5.6
Polycentropus flavomaculatus	0.1	0.2	2.5
Cyrnus trimaculatus	+	+	0.6
Total cased larvae	11.5	17.6	57.0
Total uncased larvae	5.3	13.1	43.9
Dipteran larvae	29.6	10.9	51.8
Chironomidae	23.3	7.3	49.1
Simulium spp.	6.1	3.1	8.1
Tipula spp.	+	0.4	1.2
Other Diptera larvae	0.2	+	4.3
Crustacea	0.7	1.0	11.8
Gammarus pulex	0.1	0.4	2.5
Asellus meridianus	0.6	0.6	9.3
Mollusca			
Ancylastrum fluviatile	1.3	1.3	9.9
Hirudinea			
Erpobdella octoculata	+	0.2	1.9
Megaloptera			
Sialis fuliginosa	+	0.1	0.6
Dipteran pupae	5.5	1.9	21.2
Chironomidae	5.4	1.8	19.9
Simuliidae	0.1	0.1	1.9
Arachnida	0.2	+	3.1
Hydracarina	0.2	+	2.5
Aquatic & Terrestrial spiders	+	+	0.6
Corixidae	+	+	0.6
Coleoptera	0.2	0.5	6.2
Larvae	0.1	0.4	3.1
Aquatic & Terrestrial adults	0.1	0.1	3.1

Table 48 continued

	% Number	% Volume	% Occurrence
Aerial insects	21.4	20.3	44.9
Aquatic :	7.3	10.5	34.6
Ephemeroptera:	2.0	3.4	15.1
Baetis spp.	0.9	1.3	10.6
Ephemerella ignata	0.6	0.9	3.1
Heptagenia sulphurea	0.5	1.2	2.5
Plecoptera:	1.3	2.3	10.9
Chloroperla torrentium	0.2	0.3	3.1
Isoperla grammatica	+	0.2	1.9
Leuctra fusca	0.8	1.3	5.6
Leuctra geniculata	+	0.2	1.2
Leuctra hippopus	+	0.2	1.9
Amphinemura sulcicollis	+	0.1	1.2
Trichoptera:	0.9	3.5	11.2
Diptera: Chironomidae	2.9	1.2	14.3
Simuliidae	0.2	0.1	3.7
Terrestrial:	14.1	9.8	28.5
Diptera	4.0	4.3	20.5
Hymenoptera	0.1	0.1	2.5
Hemiptera	10.0	5.4	14.9
Miscellaneous			
Lepidopteran larvae	+	0.1	1.9
Millipede	+	+	0.6
Earthworms	+	0.5	0.6
Pebbles	-	0.2	1.9
Mean organisms/stomach number and volume (cc)	33.8	0.17	
Mean volume (mm^3)/organism		4.9	

Table 49 The percentage composition of the diet of River Dee trout by number, volume and occurrence.

(+ = less than 0.1%)

	% Number	% Volume	% Occurrence
Ephemeropteran nymphs	6.8	3.5	32.4
Baetis spp.	1.8	0.7	7.6
Ecdyonurus venosus	0.2	0.2	5.7
Ephemerella ignita	4.7	2.5	21.0
Heptagenia sulphurea	+	+	2.9
Plecopteran nymphs	1.1	0.5	11.4
Chloroperla torrentium	0.2	+	4.8
Isoperla grammatica	0.5	0.3	6.7
Brachyptera risi	+	+	1.0
Leuctra hippopus	+	+	1.0
Leuctra inermis	0.1	+	2.9
Amphinemura sulcicollis	0.3	0.1	4.8
Trichopteran larvae	18.5	41.7	75.2
Goera pilosa	0.2	0.6	2.9
Potamophylax latipennis	1.8	14.1	20.0
Sericostoma personatum	0.3	0.7	3.8
Athripsodes bilineatus	3.9	1.7	26.7
Agapetus fuscipes	1.4	0.6	10.5
Glossoma conformis	0.1	0.4	1.9
Stenophylax sp.	2.3	6.9	21.0
Anabolia nervosa	1.4	6.8	7.6
Halesus digitatus	0.9	1.3	10.5
Glyphotaelius pellucidus	+	0.1	1.9
Lepidostoma hirtum	1.3	1.3	13.3
Mystacides nigra	0.2	0.5	1.9
Hydroptilidae	+	+	1.0
Unidentified cases	0.2	0.3	5.7
Hydropsyche instabilis	4.3	6.1	20.0
Rhyacophila dorsalis	+	0.2	2.9
Polycentropus flavomaculatus	+	+	1.9
Total cased larvae	14.1	35.4	67.6

Table 49 continued

	% Number	% Volume	% Occurrence
Total uncased larvae	4.4	6.3	22.9
Dipteran larvae	1.3	2.9	17.1
Chironomidae	0.9	0.1	5.7
Simulium spp.	0.1	+	2.9
Tipula spp.	0.3	2.8	7.6
Crustacea	1.2	0.8	12.0
Gammarus pulex	0.1	0.2	2.9
Asellus meridianus	1.1	0.6	11.4
Mollusca			
Ancylastrum fluviatile	0.5	0.4	5.7
Hirudinea			
Erpobdella octoculata	+	+	1.0
Megaloptera			
Sialis fuliginosa	+	0.1	1.9
Dipteran pupae			
Chironomidae	0.8	0.2	6.7
Arachnida			
Aquatic & Terrestrial spiders	0.1	+	3.8
Corixidae	+	0.1	2.9
Coleoptera	1.5	1.2	19.1
Larvae	+	+	2.9
Aquatic & Terrestrial adults	1.5	1.2	16.2
Aerial insects	67.1	34.2	55.2
Aquatic:	13.1	11.0	41.0
Ephemeroptera:	6.6	3.9	21.9
Baetis spp.	3.6	2.0	13.3
Ephemerella ignita	3.0	1.9	13.3
Plecoptera:	3.1	2.5	15.2
Chloroperla torrentium	1.8	1.0	6.7

Table 49 continued

	% Number	% Volume	% Occurrence
Isoperla grammatica	0.6	0.7	3.8
Leuctra geniculata	0.3	0.3	1.0
Leuctra hippopus	0.3	0.3	4.8
Leuctra inermis	0.1	+	1.9
Amphinemura sulcicollis	+	+	1.9
Protonemura meyeri	+	+	1.0
Taeniopteryx nebulosus	+	+	1.0
Trichoptera	1.8	4.2	23.8
Diptera	1.6	0.4	6.7
Terrestrial:	54.0	23.2	43.8
Diptera	36.8	17.0	38.1
Hymenoptera	0.5	0.5	9.5
Hemiptera	16.7	5.7	21.9
Miscellaneous			
Fish	0.6	12.2	20.0
Lepidopteran larvae	0.1	0.4	2.9
Millipedes	0.1	0.2	1.0
Earthworms	0.1	1.3	1.9
Unidentified fragments	-	0.1	1.0
Detritus	-	0.2	4.8
Pebbles	-	0.1	1.9
Vegetable matter	-	0.1	2.9
Mean volume/organism (mm^3)		12.2	
Mean organisms/stomach number and volume (cc)	42.7	0.52	

1969), Crustacea (Soong, 1939; Maitland, 1965; Mann & Orr, 1969) and oligochaetes (Elliot, 1967).

Ephemeropteran nymphs comprise one of the two major food items of River Dee salmon parr, the commonest nymphs found in stomachs being Ephemerella ignita and Baetis rhodani. Ephemeropteran nymphs were eaten much less by trout. These nymphs were most accessible to trout and salmon just before and during their emergence periods and at this time trout were feeding predominantly on surface food, both of aquatic and terrestrial origin. Maitland (1965) found that ephemeropteran nymphs comprised approximately 46% of the diet of salmon parr but only 14% of the diet of trout in the River Endrick.

Plecopteran nymphs were of minor dietary importance to both trout and salmon parr but were of greater importance to salmon parr. Salmon parr were found to have consumed a greater variety of plecopteran nymphs than trout but the dominant species were the same in both fish, the most common being Isoperla grammatica.

Trichopteran larvae were the dominant food by volume and occurrence in both trout and salmon parr, and were more commonly eaten by trout than by salmon parr. Salmon parr ate more of the small larvae such as Athripsodes bilineatus and Agapetus fuscipes, together with uncased larvae (mostly Hydropsyche instabilis), whereas trout ate larger larvae, in particular Potamophylax latipennis, Stenophylax sp. and Anabolia nervosa. Thomas (1962) found similar differences in the consumption of Trichopteran larvae by salmon parr and trout, but found few caseless larvae, such as Hydropsyche, which he considered were not easily accessible. Frost (1939) and Frost & Went (1940) found Hydropsyche to be the most common trichopteran eaten by River Liffey salmon parr and trout.

Dipteran larvae were of much greater dietary importance to salmon parr than to trout. Chironomid larvae, and to a lesser extent Simulium larvae, were the dominant Diptera found in salmon parr stomachs, whereas Tipula was the most common in trout. The same differences in the consumption of dipteran larvae by salmon parr and trout were recorded in the River Teify by Thomas (1962). Other workers have emphasised the importance of Simulium larvae in the diet of salmon parr and trout (Frost, 1939; Frost & Went, 1940; Allen, 1941a; Egglishaw, 1967) but Simulium larvae were found to be less common in the diet than chironomid larvae in my study, a situation also found by Carpenter (1940), and by Maitland (1965) in the River Endrick. Dipteran pupae were more common in salmon parr than in trout.

Aerial insects were a major food of both salmon parr and trout, but especially of the latter. Trout ate slightly more adult Ephemeroptera, Plecoptera and Trichoptera, and slightly fewer adult aquatic Diptera than salmon parr, but ate a great deal more terrestrial food, particularly Diptera (mostly Bibionidae and Empididae). Other workers have generally recorded more aerial food in trout than in salmon parr, particularly of terrestrial origin (Frost, 1939; Frost & Went, 1940; Thomas, 1962; Maitland, 1965; Mann & Orr, 1969), but Frost (1950) found similar quantities of aerial insects in salmon parr and trout from the River Forss, Caithness.

Molluscs, Crustacea, Coleoptera and earthworms were of minor dietary importance to both salmon parr and trout. Molluscs and Crustacea were more common in salmon parr, whereas Coleoptera (particularly of terrestrial origin) and earthworms were more common in trout. Earthworms were most commonly found in stomachs after periods of high water and floods. Hirudinea, Megaloptera, Arachnida, Corixids and miscellaneous foods (Lepidoptera and Myriapoda) were found to be of very little dietary importance to either trout or salmon parr.

A number of previous workers have recorded the presence of fish in trout stomachs (Thomas, 1962; Mann & Orr, 1969) and Frost & Went (1940) found a minnow in the stomach of a large salmon parr. No fish were found in any of the River Dee salmon parr examined but fish were important by volume (12%) in the diet of trout. Bullheads (Cottus gobbio), minnows (Phoxinus phoxinus) and occasionally young salmon (Salmo salar) and trout (Salmo trutta), were found in small numbers in 20% of the trout examined. Fish eggs were not found in any of the salmon parr or trout examined. Egglishaw (1967) found that young salmon and trout fed on eggs released by adult salmon and on those disturbed from the redds during the spawning season.

(iii) Seasonal variation in the composition of the diet.

The seasonal variation of the diet by volume, number and occurrence is shown for salmon parr in figures 76 to 78, and for trout in figures 79 to 81. The main winter foods of salmon parr were trichopteran larvae, plecopteran nymphs and dipteran larvae,

FIGURE 76

Seasonal Variation in the Diet of River Dee Salmon Parr by Volume

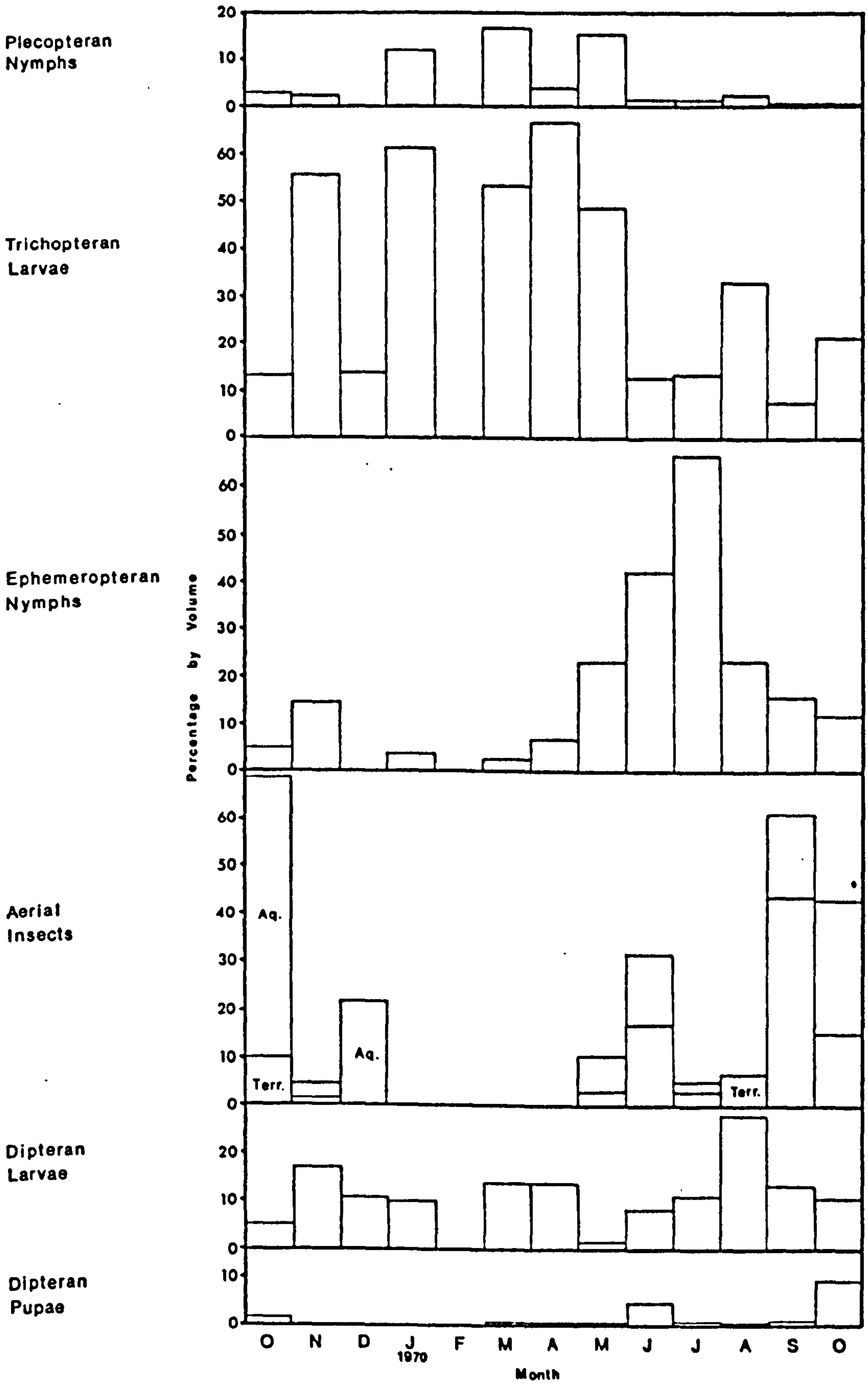


FIGURE 77

Seasonal Variation in the Diet of River Dee Salmon Parr by Number

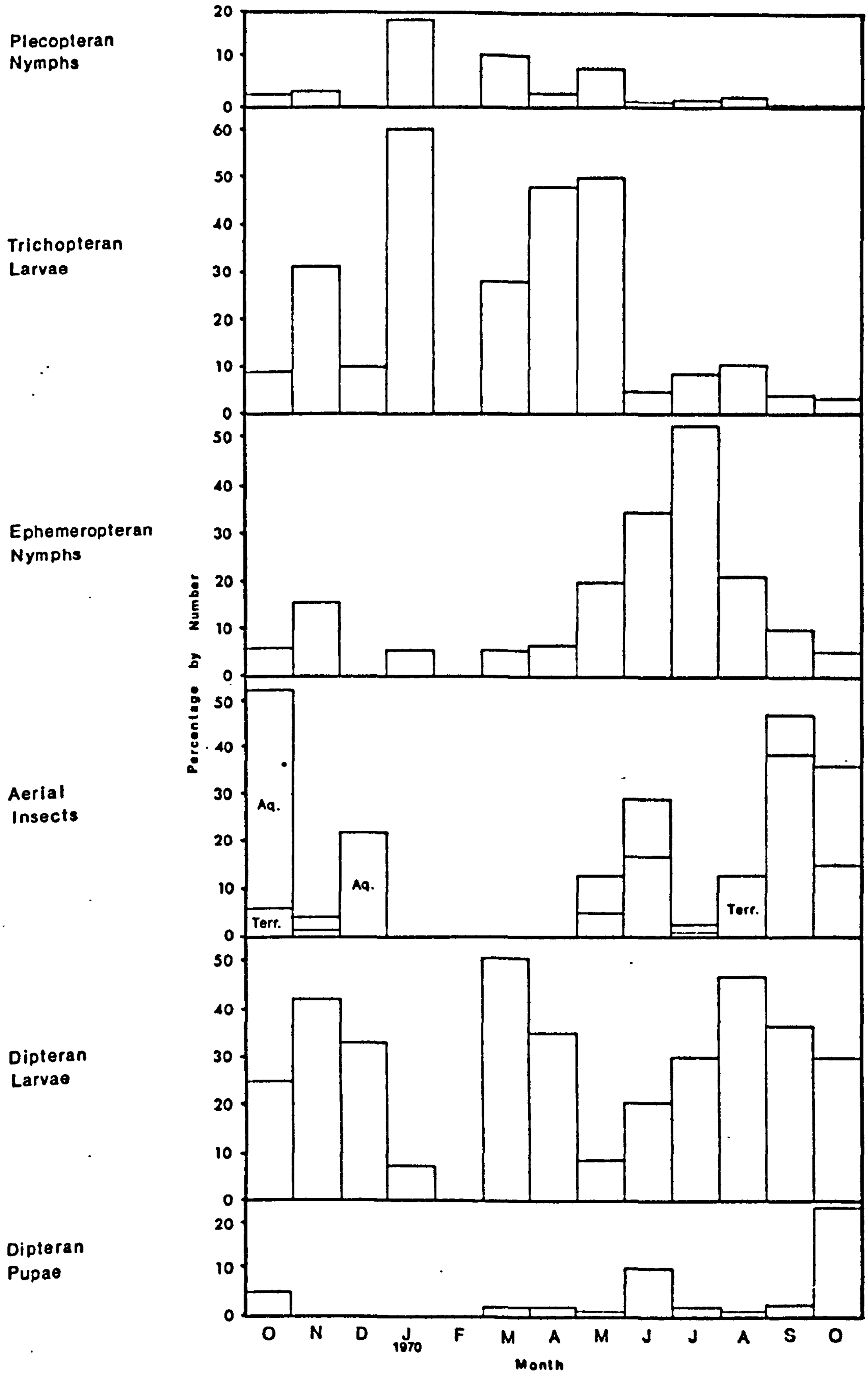


FIGURE 78

Seasonal Variation in the Diet of River Dee Salmon Parr by Occurrence

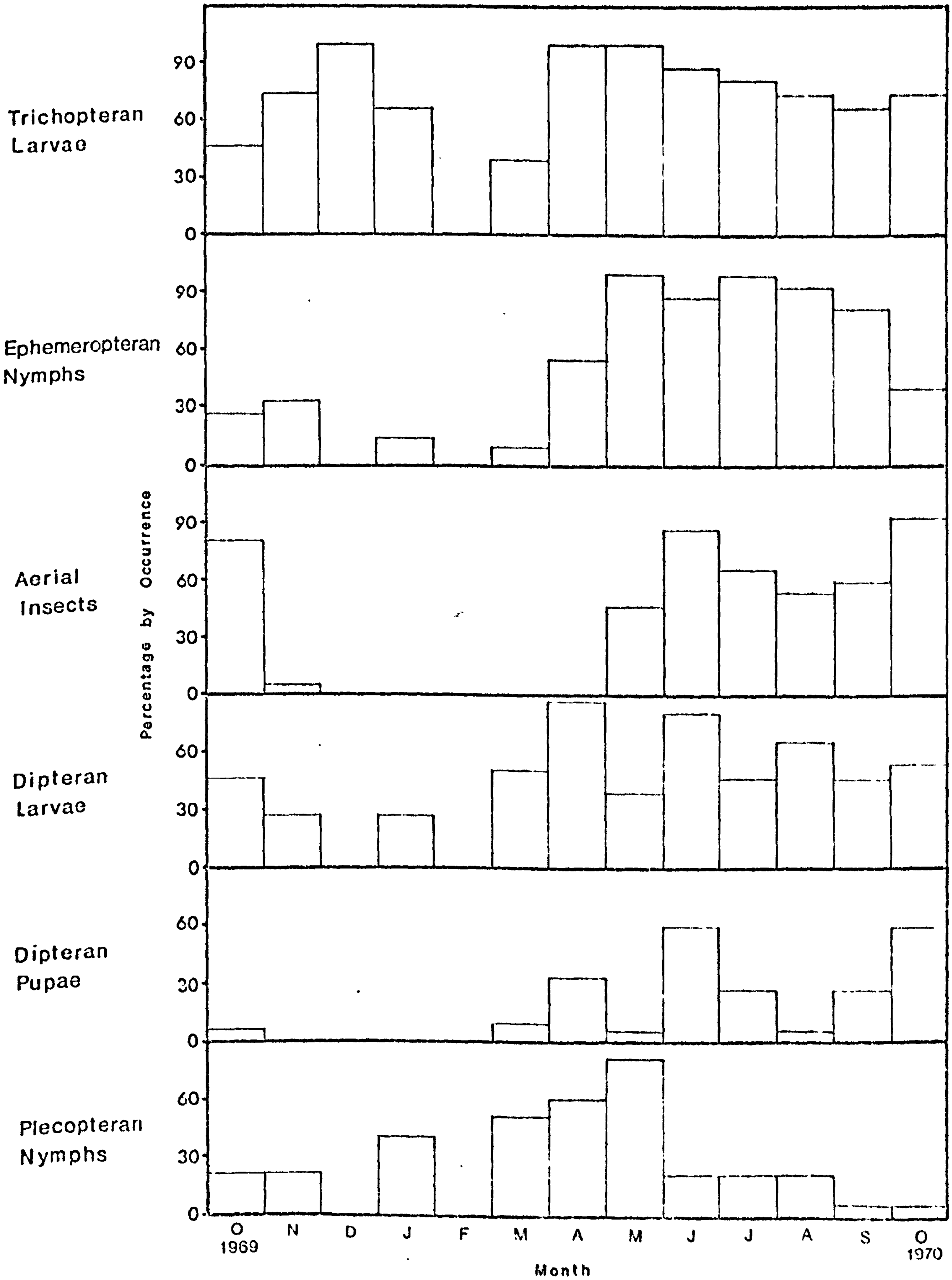


FIGURE 79

Seasonal Variation in the Diet of River Dee Trout by Volume

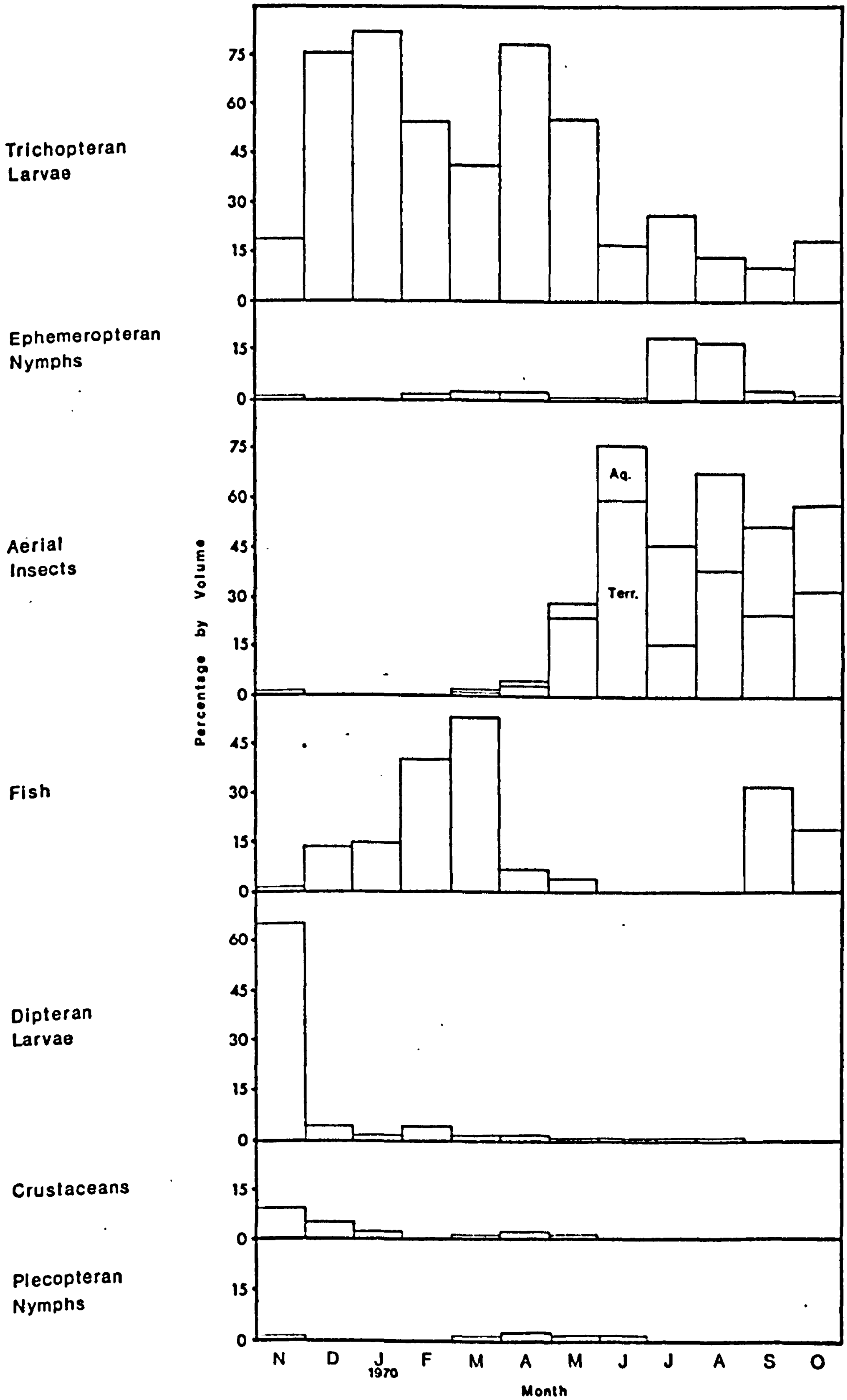


FIGURE 80

Seasonal Variation in the Diet of River Dee Trout by Number

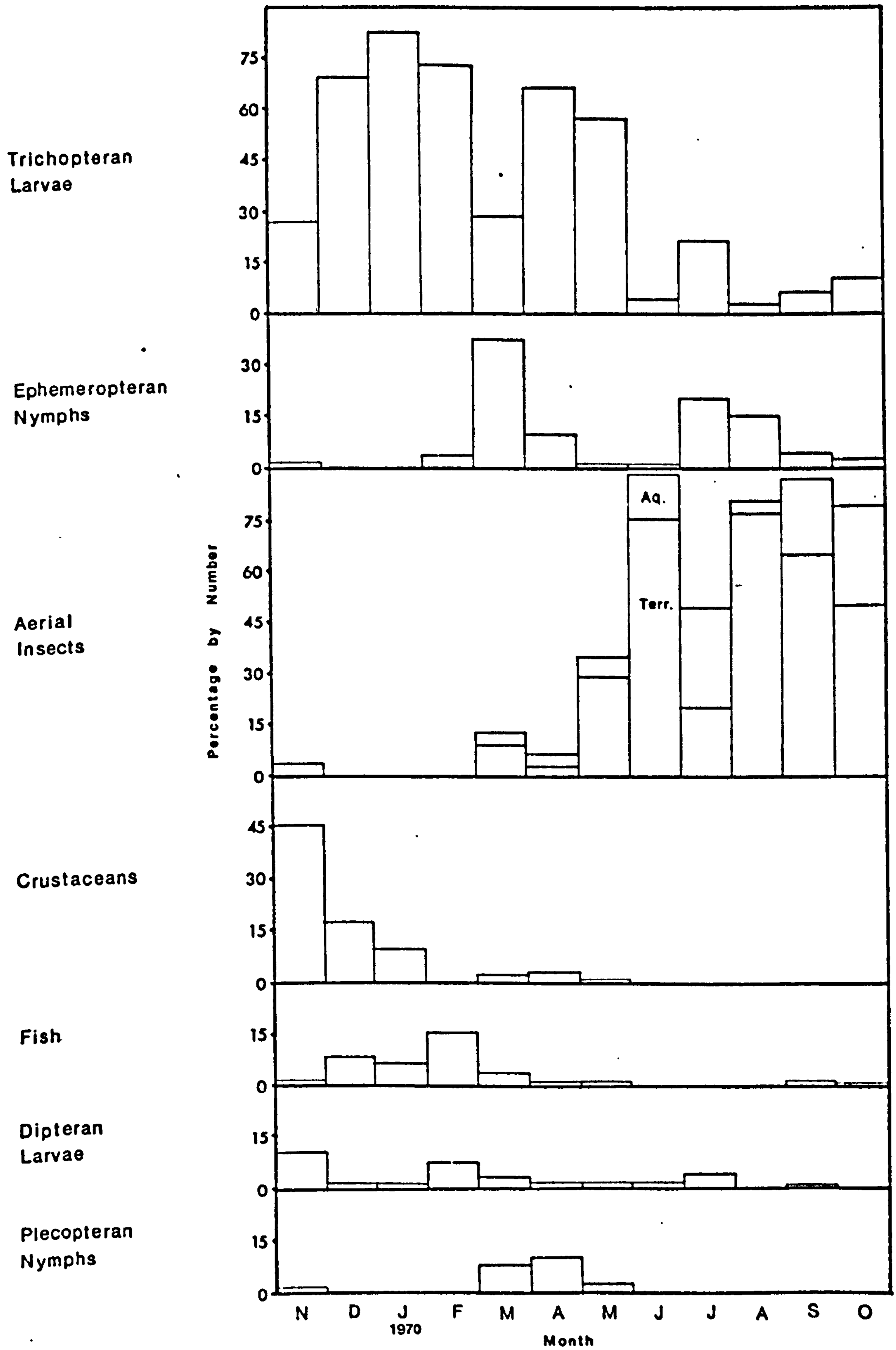
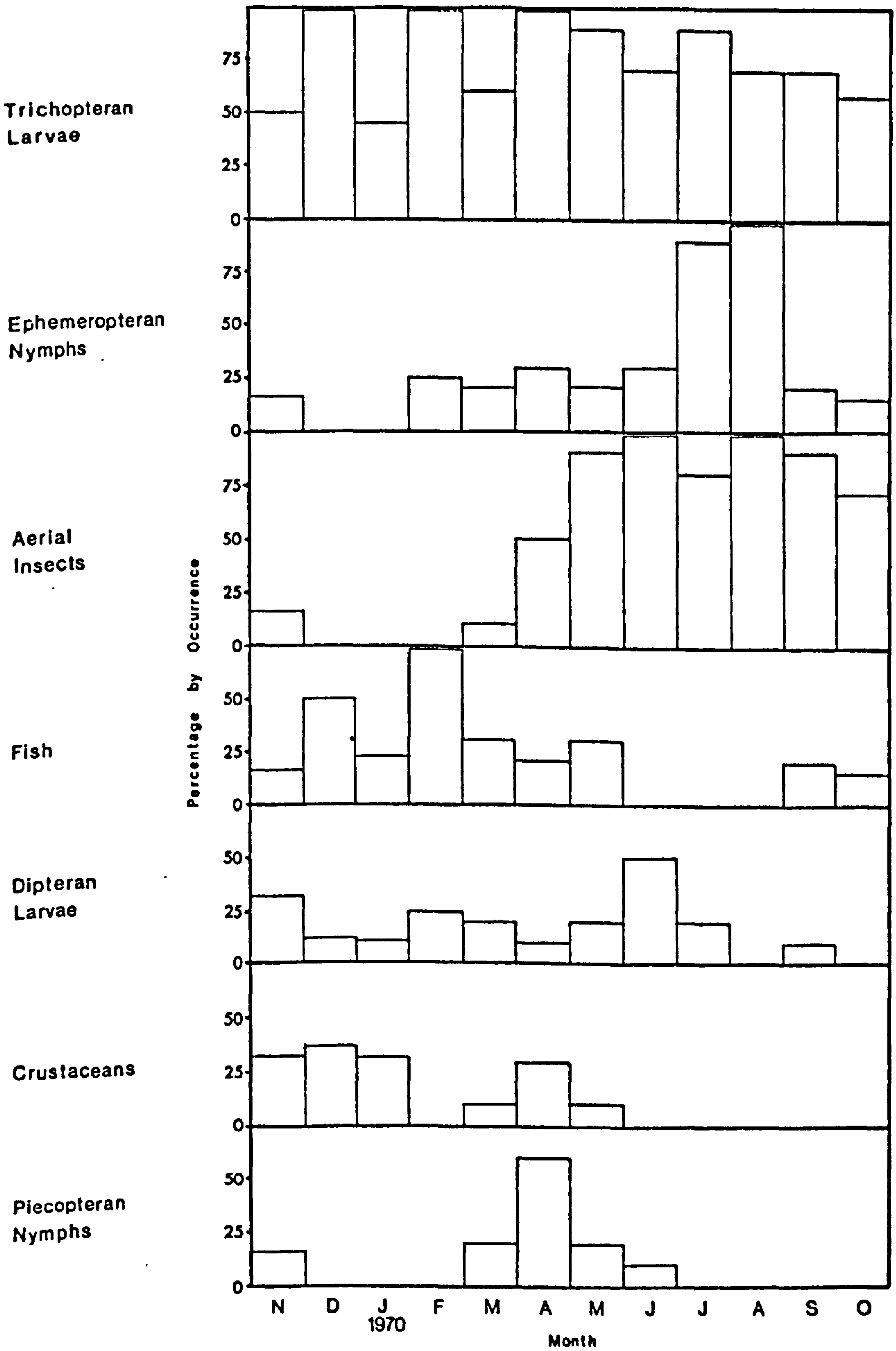


FIGURE 81

Seasonal Variation in the Diet of River Dee Trout by Occurrence



and those of trout were trichopteran larvae, fish, dipteran larvae and Crustacea. Dipteran larvae continued to be eaten by salmon parr during the summer, but trichopteran larvae and plecopteran nymphs were replaced in the diet by ephemeropteran nymphs and aerial insects. The greatest consumption of dipteran pupae occurred in June and October. Aerial insects became the dominant food of trout during the summer, together with smaller quantities of trichopteran larvae and ephemeropteran nymphs.

Trichopteran larvae were eaten throughout the year, but were of greatest dietary importance to both salmon parr and trout during the winter. In the winter trout ate mostly Potamophylax latipennis and Stenophylax sp. whereas salmon parr ate Agapetus fuscipes. Hydropsyche instabilis was found in stomachs throughout the autumn, winter and spring but was most common in April and May, forming 30% by volume of the diet of both trout and salmon parr at that time. Lepidostoma hirtum was only consumed during the summer and formed 10% by volume of the diet of trout in July. Frost (1939), Frost & Went (1940) and Thomas (1962) also recorded trichopteran larvae as major food of salmon parr and trout throughout the year, but more so during the winter than the summer. Crustacea (Asellus meridianus and Gammarus pulex) were found in stomachs from November to May. Asellus was particularly abundant in the stomachs of trout in November. These trout were caught in a slow flowing section of the river at Llanderfel, where the bottom was littered with plant debris. Plecopteran nymphs were of greatest dietary importance during the winter and spring, particularly to salmon parr, a situation also recorded by Frost (1939), Maitland (1965), Egglishaw (1967) and Elliot (1967). A number of *Chloroperla torrentium* nymphs and *Isoperla grammatica* nymphs were eaten by salmon parr in May, just before their emergence period, and *Leuctra* nymphs were consumed in the autumn. Chironomid larvae were of greatest dietary importance to salmon parr during the spring and autumn, and *Simulium* larvae in July and August. Carpenter (1940) found *Simulium* larvae most commonly in July, and chironomid larvae during the spring. Chironomid larvae and *Simulium* larvae were not common in the diet of trout, but were eaten most frequently in June and March respectively. Of greater dietary importance to trout were *Tipula* larvae which formed 70% by volume of the diet in November. Fish were found in trout stomachs mostly during the autumn and winter and were the dominant food in March.

Ephemeropteran nymphs were eaten to the greatest extent by salmon parr and trout during the summer, particularly in July. Different species were eaten at different times of the year according to their emergence periods. Thus *Baetis rhodani* was found in stomachs during the spring and autumn, other *Baetis* spp. during the summer (particularly August), *Ephemerella ignita* in June and July and *Heptagenia sulphurea* in May. Aerial insects were eaten during the spring, summer and autumn, with a summer decrease in consumption of these organisms by salmon parr at the time when the consumption of ephemeropteran nymphs (*Ephemerella ignita*) was at a maximum. This decrease was also recorded in salmon parr by Carpenter (1940) and Thomas (1962), but trout showed only a slight decrease in consumption of aerial insects during July and ate more Ephemerella sub-imagines than nymphs. Carpenter (1940) found that aquatic Diptera formed the main aerial food of salmon parr in the spring and terrestrial organisms (especially Hemiptera) in the autumn. Thomas (1962) and Egglishaw (1967) also recorded large amounts of terrestrial food during the autumn and considered the possibility of much of this food being introduced to the river via the leaf fall. Terrestrial food in River Dee salmon parr was most common in September (mostly Aphidae) and of much greater dietary importance to trout particularly during August (Diptera), September and October (Hemiptera). Aquatic aerial insects eaten by salmon parr consisted mainly of Heptagenia sulphurea in May, Ephemerella ignita, Chloroperla torrentium and Isoperla grammatica in June and Trichoptera, Leuctra spp., Baetis rhodani and Chironomidae in September and October. Aquatic aerial food was eaten by trout from June to October. In addition to the organisms eaten by salmon parr, trout ate Ephemerella ignita sub-imagines in July and Trichoptera in August, together with greater numbers of Ephemeroptera than salmon parr and fewer Plecoptera in September and October. Molluscs (Ancylastrum fluviatile) were only common in trout during July (6% by volume) and in salmon parr during August (6% by volume). Coleoptera larvae were chiefly consumed from September to April, and the adults from June to October. The latter category included many terrestrial species taken, along with other surface food, particularly in June.

(iv) Variation in the diet with age

The variation in the diet with age by percentage volume and number is shown for salmon parr in tables 50 and 51, and for trout in tables 52 and 53. The numbers of 3+ salmon parr and 4+, 5+ and 7+ trout examined were too small to be representative of these age groups as a whole. The mean volume of stomach contents and the mean number of food items per stomach increased with age, as did the mean size (volume) of organisms eaten. Corresponding age groups of salmon parr and trout ate similar numbers of food organisms but trout stomachs contained a greater volume of food and the mean size of the food items was larger.

Trichopteran larvae and aerial insects increased in dietary importance with age in both salmon parr and trout, whereas *Simulium* larvae and chironomid larvae became less common with increasing age. In addition, older trout ate more fish and *Tipula* larvae than young trout. A number of previous workers record the decreasing consumption of dipteran larvae by salmon parr and trout with increasing age, and the greater consumption of trichopteran larvae and aerial insects by older fish (Alln, 1941a; Maitland, 1965). Young trout and salmon parr in the River Dee ate mostly small trichopteran larvae such as *Athripsodes bilineatus*, whilst older salmon parr ate mostly *Hydropsyche instabilis* and *Agapetus fuscipes*, and older trout ate larger larvae, in particular *Potamophylax latipennis*, *Stenophylax* sp. and *Anabolia nervosa*. More terrestrial insects and adult Trichoptera were eaten by older

Table 50 Variation in the diet by volume % of River Dee salmon parr with age.

(+ = less than 0.1%)

	Age Group			
	0+	1+	2+	3+
Ephemeropteran nymphs	9.6	36.8	18.7	31.8
Baetis	8.8	11.7	6.1	12.9
Ephemerella	0.8	22.3	7.4	7.9
Heptagenia	-	2.4	4.9	10.4
Other nymphs	-	0.4	0.3	0.6
Plecopteran nymphs	3.2	1.6	6.3	10.1
Chloroperla	0.7	0.1	0.4	0.3
Isoperla	1.5	0.5	2.3	2.5
Leuctra spp.	0.3	0.4	+	-
Perla	-	-	2.3	6.1
Amphinemura	-	-	0.2	1.2
Other nymphs	0.7	0.6	1.1	-
Trichopteran larvae	24.9	22.2	41.6	25.7
Athripsodes	5.6	3.6	3.5	1.1
Agapetus	2.8	3.0	12.8	3.5
Stenophylax	-	2.8	2.3	2.4
Glossoma	-	1.2	2.2	-
Lepidostoma	-	1.0	1.6	0.6
Other cased larvae	8.4	0.8	3.2	-
Uncased larvae	8.1	9.8	16.0	18.1
Dipteran larvae	31.5	14.5	7.6	-
Chironomidae	25.9	8.0	6.8	-
Simuliidae	-	6.5	0.2	-
Other larvae	5.6	-	0.6	-
Dipteran pupae	2.2	3.0	1.1	-
Crustacea	4.7	0.8	1.1	0.7
Mollusca	2.9	2.3	0.3	-
Coleoptera	1.7	0.3	0.6	0.2

Table 50 continued

	Age Group			
	0+	1+	2+	3+
Aerial insects	19.1	17.9	20.7	31.0
Aquatic:	13.9	11.8	7.0	18.6
Ephemeroptera	4.8	2.7	2.5	9.6
Plecoptera	6.5	3.4	0.7	2.7
Diptera	2.6	1.3	0.7	3.2
Trichoptera	-	4.3	3.1	3.1
Terrestrial:	5.2	6.1	13.7	12.4
Diptera	2.2	3.8	4.5	7.3
Hymenoptera	1.0	+	-	0.3
Hemiptera	2.0	2.2	9.2	4.8
Other organisms	-	0.5	1.6	-
Pebbles	0.6	+	0.4	-
Mean volume/stomach (cc)	0.04	0.14	0.25	0.41
Mean volume/organism (mm^3)	2.6	0.14	0.25	0.41
Number of stomachs examined	22	88	45	6

Table 51 Variation in the diet by % number of River Dee Salmon parr with age.

(+ = less than 0.1%)

	Age Group			
	0+	1+	2+	3+
Ephemeropteran nymphs	7.2	27.3	15.3	28.8
Baetis	6.6	11.7	6.1	13.1
Ephemerella	0.6	14.6	6.9	9.5
Heptagenia	-	0.8	2.3	5.9
Other nymphs	-	0.2	+	0.3
Plecopteran nymphs	2.1	1.2	3.1	4.9
Chloroperla	0.6	0.1	0.7	0.7
Isoperla	0.9	0.5	1.5	1.6
Leuctra	0.3	0.4	0.1	-
Perla	-	-	+	0.3
Amphinemura	-	-	0.4	2.3
Other nymphs	0.3	0.2	0.4	-
Trichopteran larvae	14.1	10.6	26.7	18.6
Athripsodes	6.1	3.5	3.7	2.0
Agapetus	1.4	2.4	13.5	5.2
Stenophylax	-	0.2	0.3	0.3
Glossoma	-	0.2	0.5	-
Lepidostoma	-	0.3	0.5	0.3
Other cased larvae	2.8	0.3	1.0	-
Uncased larvae	3.7	3.7	7.2	10.8
Dipteran larvae	57.9	35.6	20.2	-
Chironomidae	57.6	24.3	19.2	-
Simuliidae	-	11.3	0.3	-
Other larvae	0.3	-	0.6	-
Dipteran pupae	4.9	7.6	3.2	-
Crustacea	0.9	0.4	0.8	1.0
Molluscs	1.4	2.0	0.2	-
Coleoptera	0.6	0.1	0.4	0.3

Table 51 continued

	Age groups			
	0+	1+	2+	3+
Aerial insects	11.0	14.9	29.4	46.1
Aquatic:	7.8	7.6	4.3	22.9
Ephemeroptera	2.3	1.5	1.7	7.8
Plecoptera	1.4	1.7	0.4	2.9
Diptera	4.0	3.5	1.5	8.5
Trichoptera	-	0.9	0.7	3.6
Terrestrial:	3.2	7.3	25.1	23.2
Diptera	0.3	3.6	4.0	11.8
Hymenoptera	0.9	0.1	-	0.3
Hemiptera	2.0	3.6	21.1	11.1
Other organisms	-	0.2	0.6	-
Mean number of organisms / stomach	15.8	33.0	42.1	51.0
Number of stomachs examined	22	83	45	6

Table 52 Variation in the diet by %volume of River Dee trout with age.

(+ = less than 0.1%)

	Age Groups					
	1+	2+	3+	4+	5+	7+
Ephemeropteran nymphs	14.9	3.9	3.7	1.7	-	-
Baetis	0.8	0.4	2.2	-	-	-
Ephemerella	12.4	3.2	1.1	1.7	-	-
Heptagenia	1.1	+	-	-	-	-
Ecdyonurus	0.6	0.3	0.4	-	-	-
Plecopteran nymphs	0.7	0.3	1.2	0.2	0.5	-
Chloroperla	0.4	+	+	0.1	-	-
Isoperla	-	0.2	0.7	-	0.5	-
Leuctra	-	+	0.1	-	-	-
Amphinemura	0.3	+	0.2	0.1	-	-
Brachyptera	-	-	0.1	-	-	-
Trichopteran larvae	16.8	40.0	26.8	30.8	88.5	78.3
Potamophylax	-	8.3	11.6	3.1	37.1	78.3
Athripsodes	10.2	2.4	0.3	0.5	-	-
Agapetus	0.5	1.5	0.1	-	-	-
Stenophylax	-	8.9	4.6	-	19.7	-
Anabolia	-	1.6	1.0	25.3	15.1	-
Lepidostoma	2.7	1.2	1.2	1.8	0.5	-
Other cased larvae	0.4	4.6	7.8	-	3.3	-
Uncased larvae	2.9	11.5	0.2	0.1	12.8	-
Dipteran larvae	2.3	5.9	2.0	0.1	-	-
Chironomidae	2.0	+	-	0.1	-	-
Simuliidae	0.3	-	+	-	-	-
Tipulidae	-	5.9	2.0	-	-	-
Dipteran pupae	0.8	0.2	+	+	-	-
Crustacea	4.6	0.5	1.7	-	-	-
Mollusca	2.6	0.6	-	-	-	-
Coleoptera	3.2	0.8	1.8	1.3	0.9	-
Fish	-	10.9	22.2	12.2	-	21.7

Table 52 continued

	Age groups					
	1+	2+	3+	4+	5+	7+
Aerial insects	51.9	36.7	35.7	47.1	9.9	-
Aquatic:	19.8	10.9	9.8	19.7	1.5	-
Ephemeroptera	10.4	3.0	5.0	5.8	-	-
Plecoptera	0.7	0.4	1.9	10.3	1.5	-
Diptera	4.1	0.1	-	1.1	-	-
Trichoptera	4.6	7.3	2.9	2.5	-	-
Terrestrial:	32.1	25.8	25.9	27.4	8.4	-
Diptera	20.3	21.8	17.0	17.9	4.6	-
Hymenoptera	+	0.9	0.5	-	0.5	-
Hemiptera	11.8	3.1	8.4	9.5	3.3	-
Other organisms	1.5	0.3	4.7	5.6	0.2	-
Unidentified fragments	-	-	-	0.9	-	-
Detritus	-	0.2	0.3	0.6	-	-
Mean volume/stomach (cc)	0.17	0.41	0.57	1.12	1.65	2.30
Mean volume/organism (mm^3)	5.1	10.5	14.2	12.3	29.1	143.8
No. of stomachs examined	18	52	22	8	4	1

Table 53 Variation in the diet by number% of River Dee trout with age.

(+ = less than 0.1%)

	Age groups					
	1+	2+	3+	4+	5+	7+
Ephemeropteran nymphs	12.6	6.3	9.1	2.9	-	-
Baetis	1.7	1.0	5.7	-	-	-
Ephemerella	10.3	5.2	2.8	2.[illegible]	-	-
Heptagenia	0.3	+	-	-	-	-
Ecdyonurus	0.3	0.1	0.6	-	-	-
Plecopteran nymphs	1.0	0.5	2.8	0.7	1.8	-
Chloroperla	0.5	+	0.3	0.3	-	-
Isoperla	-	0.3	1.1	-	1.8	-
Leuctra	-	+	0.6	-	-	-
Amphinemura	0.5	0.1	0.7	0.4	-	-
Brachyptera	-	-	0.1	-	-	-
Trichopteran larvae	11.3	24.2	10.4	7.6	46.2	93.7
Potamophylax	-	1.3	1.6	0.4	10.1	93.7
Athripsodes	8.4	5.4	0.7	1.4	-	-
Agapetus	0.5	2.9	0.2	-	-	-
Stenophylax	-	2.9	2.2	-	11.0	-
Anabolia	-	0.8	0.2	5.2	7.0	-
Lepidostoma	1.0	1.3	1.2	1.5	0.9	-
Other cased larvae	0.2	1.9	4.2	-	4.0	-
Uncased larvae	1.2	7.7	0.1	0.1	13.2	-
Dipteran larvae	6.0	0.5	0.7	0.8	-	-
Chironomidae	5.5	+	-	0.8	-	-
Simuliidae	0.5	-	0.1	-	-	-
Tipulidae	-	0.4	0.6	-	-	-
Dipteran pupae	1.7	0.9	0.2	0.6	-	-
Crustacea	3.9	0.6	1.8	-	-	-
Mollusca	1.8	0.6	-	-	-	-
Coleoptera	0.8	1.1	2.3	1.7	3.5	-
Fish	-	0.8	0.6	0.6	-	6.3

Table 53 continued

	Age groups					
	1+	2+	3+	4+	5+	7+
Aerial insects	60.2	64.2	70.0	85.0	47.6	-
Aquatic:	19.0	7.8	14.2	25.2	3.5	-
Ephemeroptera	9.1	4.9	9.2	8.2	-	-
Plecoptera	0.5	0.5	3.3	12.2	3.5	-
Diptera	6.7	0.3	-	3.4	-	-
Trichoptera	2.7	2.1	1.7	1.4	-	-
Terrestrial:	41.2	56.4	55.8	59.8	44.1	-
Diptera	18.2	47.7	34.2	31.5	18.1	-
Hymenoptera	0.2	0.4	1.1	-	1.8	-
Hemiptera	22.8	8.3	20.5	28.3	24.2	-
Other organisms	0.6	+	1.5	0.3	0.9	-
Mean No. organisms/ stomach	33.1	39.1	40.0	91.4	56.8	16.0
No. of stomachs examined	18	52	22	8	4	1

salmon parr than by young salmon parr but the consumption of most aquatic aerial insects decreased with increasing age. The number of aerial insects found in trout stomachs was generally greater in older fish, the large quantities present in 1+ fish being attributable to the fact that most of the 1+ trout examined were caught during the summer. Thomas (1962), McCormack (1962) and Maitland (1965) all recorded an increased consumption of terrestrial food in older trout. Ephemeropteran nymphs were consumed to a greater extent by older salmon parr than by young salmon parr, but these organisms declined in dietary importance with increasing age in trout. Older salmon parr ate more plecopteran nymphs than young fish, Perla bipunctata being absent from the diet of the 0+ and 1+ age groups, presumably because of its large size. Amphinemura sulcicollis, a small plecopteran nymph, was also absent from the stomachs of younger fish. The importance of molluscs and Crustacea showed an apparently reverse trend to that found by other workers (Allen, 1941a; Thomas, 1962; Mann & Orr, 1969). These observations, however, resulted from small numbers of relatively large organisms occurring in a very few stomachs, and such discrepancies would probably be eliminated by the examination of larger samples.

(v) Utilization of the fauna

The availability factors of benthic organisms in the diet of salmon parr and trout in the River Dee were calculated in the same way as for grayling (chapter 7), and are shown in tables 54 and 55.

Table 54 The availability factors of the benthic fauna in the diet of River Dee salmon parr.

	% by no. in fauna A	% by no. in diet B	Availability factor B/A
	(+ =	0.1%)	((+)= 0.01)
Oligochaetes	15.2	-	-
Corixidae	6.2	+	(+)
Asellus	5.6	0.8	0.14
Dipteran pupae	0.9	7.0	7.78
Coleoptera	3.7	0.2	0.05
Gammarus	0.6	0.1	0.17
Megaloptera	0.5	+	0.04
Turbellaria	0.4	-	-
Hydracarina	0.2	0.3	1.50
Dipteran larvae	24.9	37.8	1.52
Chironomidae	23.5	29.8	1.27
Simulium	0.2	7.8	39.00
Tipula	0.2	+	0.20
Other larvae	1.0	0.3	0.30
Trichoptera	17.5	21.5	1.23
Hydropsyche	2.6	6.4	2.46
Agapetus	2.9	8.2	2.83
Plectrocnemia	0.3	-	-
Stenophylax	0.2	0.2	1.00
Potamophylax	1.0	-	-
Rhyacophila	+	0.3	5.00
Sericostoma	0.2	-	-
Anabolia	4.2	+	0.02
Mystacides	0.4	+	0.10
Glyphotaelius	5.5	-	-
Halesus	0.2	0.3	1.50
Silo	+	-	-
Diplectrona	+	-	-
Limnephilus	+	-	-

Table 54 continued

	% by no. in fauna A	% by no. in diet B	Availability factor B/A
Athripsodes	–	4.7	–
Glossoma	–	0.4	–
Lepidostoma	–	0.4	–
Triaenodes	–	+	–
Hydroptilidae	–	0.1	–
Polycentropus	–	0.1	–
Cyrnus	–	+	–
<u>Ephemeroptera</u>	<u>13.5</u>	<u>28.0</u>	<u>2.07</u>
Ecdyonurus	0.2	0.1	0.50
Baetis	3.8	12.1	3.18
Procloeon	+	–	–
Ephemerella	5.3	13.7	2.58
Cloeon	+	–	–
Centroptilum	2.6	–	–
Leptophlebia	0.5	–	–
Caenis	0.5	–	–
Rhithrogena	+	–	–
Heptagenia	0.3	1.9	6.33
Paraleptophlebia	0.1	–	–
Siphlonurus	+	–	–
Ephemera	+	+	4.00
<u>Plecoptera</u>	<u>7.1</u>	<u>2.7</u>	<u>0.38</u>
Isoperla	0.9	1.1	1.22
Protonemura	0.2	+	0.30
Amphinemura	3.3	0.4	0.12
Leuctra	0.9	0.4	0.44
Nemoura	+	–	–
Chloroperla	1.7	0.5	0.29
Perlodes	+	+	2.00
Brachyptera	+	0.1	10.00
Nemurella	+	–	–
Perla	–	+	–

Table 54 continued

	% by no. in fauna	% by no in diet	Availability factor
	A	B	B/A
Mollusca	2.9	1.7	0.59
Limnaea	0.2	-	-
Ancylastrum	+	1.7	42.50
Hydrobia	+	-	-
Pisidium	2.7	-	-
Hirudinea	0.7	+	0.13
Glossiphonia	+	-	-
Erpobdella	0.4	+	0.23
Helobdella	0.2	-	-
Piscicola	+	-	-

Table 55 The availability factors of the benthic fauna in the diet of River Dee trout.

Organism	% by no. in fauna A	% by no. in diet. B	Availability factor B/A
	(+ = 0.1%)		((+) = 0.01)
Oligochaetes	15.2	-	-
Corixidae	6.2	0.2	0.03
Asellus	5.6	3.5	0.63
Dipteran pupae	0.9	2.6	2.89
Coleoptera	3.7	2.6	0.70
Gammarus	0.6	0.3	0.50
Megaloptera	0.5	0.1	0.20
Turbellaria	0.4	-	-
Hydracarina	0.2	-	-
<u>Dipteran larvae</u>	<u>24.9</u>	<u>4.2</u>	<u>0.17</u>
Chironomidae	23.5	2.9	0.12
Simulium	0.2	0.3	1.50
Tipula	0.2	1.0	5.00
Other larvae	1.0	-	-
<u>Trichoptera</u>	<u>17.5</u>	<u>59.7</u>	<u>3.41</u>
Hydropsyche	2.6	13.9	5.35
Agapetus	2.9	4.5	1.55
Plectrocnemia	0.3	-	-
Stenophylax	0.2	7.4	37.00
Potamophylax	1.0	45.5	45.50
Rhyacophila	+	0.2	3.33
Sericostoma	0.2	1.0	5.00
Anabolia	4.2	4.5	1.07
Mystacides	0.4	0.6	1.50
Glyphotaelius	5.5	0.1	0.02
Halesus	0.2	2.9	14.50
Silo	+	-	-
Diplectrona	+	-	-
Limnephilus	+	-	-
Athripsodes	+	-	-

Table 55 continued

	% by no. in fauna A	% by no in diet B	Availability Factor B/A
Glossoma	-	0.3	-
Lepidostoma	-	4.2	-
Hydroptilidae	-	+	-
Polycentropus	-	+	-
Goera	-	0.6	-
Ephemeroptera	**13.5**	**21.9**	**1.62**
Ecdyonurus	0.2	0.6	3.00
Baetis	3.8	5.8	1.53
Procloeon	+	-	-
Ephemerella	5.3	15.2	2.87
Cloeon	+	-	-
Centroptilum	2.6	-	-
Leptophlebia	0.5	-	-
Caenis	0.5	-	-
Rhithrogena	+	-	-
Heptagenia	0.3	0.2	0.67
Paraleptophlebia	0.1	-	-
Siphlonurus	+	-	-
Ephemera	+	-	-
Plecoptera	**7.1**	**3.5**	**0.49**
Isoperla	0.9	1.6	1.78
Protonemura	0.2	-	-
Amphinemura	3.3	1.0	0.30
Leuctra	0.9	0.3	0.33
Nemoura	+	-	-
Chloroperla	1.7	0.6	0.35
Perlodes	+	-	-
Brachyptera	+	+	6.00
Nemurella	+	-	-
Mollusca	2.9	1.6	0.55
Limnaea	0.2	+	-

Table 55 continued

	% by no in fauna A	% by no. in diet B	Availability factor B/A
Ancylastrum	+	1.6	40.00
Hydrobia	+	-	-
Pisidium	2.7	-	-
Hirudinea	0.7	0.1	0.14
Glossiphonia	+	-	-
Erpobdella	0.4	0.1	0.25
Helobdella	0.2	-	-
Piscicola	+	-	-

Oligochaetes, despite their abundance in the fauna, were not found in any of the stomachs examined. High power observation failed to reveal any chaetae remains (Kennedy, 1969). The absence of oligochaetes from the diet was undoubtedly a result of their burrowing habits, although Elliot (1967) found a considerable quantity of these worms in trout stomachs from Dartmoor. Corixids were rejected by both salmon parr and trout, possibly because of the secretion of substances distasteful to fish (Frost & Macan, 1948). The high proportion of corixids in the fauna is largely accounted for by the high numbers of these organisms at the backwater sampling site described in the previous chapter. Salmon parr and trout seldom frequent this type of habitat. Asellus and Gammarus were more available to trout than to salmon parr, but in both cases these Crustacea were eaten to a lesser extent than their occurrence in the fauna. If the backwater sampling site fauna is excluded from the overall River Dee invertebrate fauna then the availability factor of Asellus in the diet of trout becomes approximately 1. Maitland (1965) also found Crustacea to be more available to trout than to salmon parr, whereas Frost & Went (1940) found very few Crustacea in River Liffey salmon parr and trout, despite the abundance of these organisms in the fauna. Coleopteran larvae were not easily accessible to trout or salmon parr, since many of these larvae are buried in bottom deposits or occur beneath stones. Adult Coleoptera, particularly of terrestrial origin, are more available to trout than salmon parr and the consumption of terrestrial species reflects the greater utilisation of surface food by trout.

Sialis fuliginosa, a burrowing organism, showed a low availability to trout and salmon parr, and Turbellaria were not found in any of the stomachs examined. Hydrocarina were eaten occasionally by salmon parr, but were probably too small to be of interest to trout.

Marked differences in the consumption of dipteran larvae were observed between salmon parr and trout. Chironomid larvae and *Simulium* larvae were much more available to salmon parr, whereas *Tipula* larvae were more available to trout. Chironomid larvae and *Simulium* larvae were eaten more by small trout than by large trout and their high availability to salmon parr is a reflection of the greater degree of bottom feeding by salmon parr, particularly in fast riffles where *Simulium* larvae are often present in dense aggregations (Egglishaw, 1967), and occur in exposed positions. *Tipula* larvae are burrowing organisms and most of those found in trout stomachs were too large to have been eaten by salmon parr. Dipteran pupae were of high availability to both salmon parr and trout, but less so to the latter, and to larger fish, because of the size factor. These organisms were probably eaten as they ascended to the water surface, at a time when their mobility would attract the attention of the fish.

Most trichopteran larvae showed a high availability to trout, especially to the older age groups, and the smaller species were eaten to a considerable extent by salmon parr. *Hydropsyche* larvae showed a high availability to both trout and salmon parr, despite their concealed habitat. Allen (1941a) and Thomas (1962) considered

Hydropsyche to be relatively inaccessible because of its habitat, but a number of workers have recorded this organism in salmonid stomachs, and Frost & Went (1940) found it to be the most common trichopteran eaten by salmon parr in the River Liffey. Differences in the availability of *Potamophylax*, *Anabolia*, *Stenophylax* and *Sericostoma* to salmon parr and trout are mainly attributable to the ability of larger fish to consume larger organisms and to deal with organisms in hard cases (Allen, 1941a). Large trout are the only salmonids in the River Dee capable of consuming *Anabolia* to any extent. The large gape of the trout enables it to ingest the very large cases of these larvae, whereas the mouth of the salmon parr, and even of large grayling, is too small to deal with them. *Glyphotaelius* is common in still or slow flowing reaches of the river, but these areas are not often frequented by salmon parr and trout and this larva is therefore rarely found in the stomachs. A number of trichopteran larvae were recorded in stomachs but not in the fauna. Some of these larvae were found in considerable quantities in the stomachs (e.g. *Athripsodes* and *Lepidostoma*) and their apparent absence from the fauna has been discussed in the previous chapter.

Baetis rhodani and *Ephemerella ignita* nymphs showed high availability factors for both salmon parr and trout just before and during their emergence periods, when they were largest, most active and most exposed. A number of previous workers have emphasised that the transition from aquatic to aerial life in Ephemeroptera is the time of maximum availability (Carpenter, 1940;

Frost & Went, 1940; Ball, 1961; Thomas, 1964). Heptagenia sulphurea nymphs were particularly available to salmon parr during May, but were eaten to a lesser extent by trout. Species of the genus Baetis, other than Baetis rhodani, were eaten to some extent during the summer by salmon parr, but much less so by trout which were feeding predominantly on surface food at that time. Egglishaw (1967) found Baetis to be a major component of the drift fauna, and thus of high accessibility. Small size and retiring habits give rise to low availability of an organism (Carpenter, 1940) and this may explain the absence of Centroptilum from the diet, and the scarcity of ephemeropteran nymphs in stomachs during the winter. Badcock (1949) stated that Ephemerella ignita have a long incubation period, and that from November to May the populations consist chiefly of small nymphs. Other ephemeropteran nymphs which were absent from the diet were generally scarce in the fauna or only occurred in situations where they were generally unavailable to salmonids (e.g. Caenis).

Small numbers of a particular organism in the fauna and the food may give rise to misleading availability factors; such is the case with Ephemera danica in salmon parr, and with several of the plecopteran nymphs (Perlodes and Brachyptera). Isoperla grammatica was the only plecopteran nymph which actually showed a high availability factor to salmon parr and trout. This organism was consumed to the greatest extent during April and May, just before its emergence period. Other plecopteran nymphs also showed maximum availability before their emergence periods, the small size and retiring habits of most of these nymphs accounting for their low availability at other times. *Ancylastrum fluviatile* was the only mollusc eaten by salmon parr and trout, and it was consumed to a far greater extent than its occurrence in the fauna. This organism occurrs predominantly on stones and pebbles in riffles and moderately fast flowing water (Thomas, 1962), areas which were frequented by salmon parr and young trout, but not by older trout which rarely ate this mollusc. *Limnaea* and *Hydrobia* are mostly found on vegetation in slow flowing water, and *Pisidium* is a burrowing organism which is inaccessible to salmon parr and trout. *Erpobdella* was eaten to a small extent by salmon parr and trout. The other leeches present in the fauna occur under stones (*Helbodella* and *Glossiphonia*) or are parasitic (*Piscicola*).

Excluded from the above discussion are emerging aquatic insects, terrestrial organisms and, in the case of trout, fish. All of these organisms are of considerable importance in the diets, particularly aerial insects which form up to 47% and 90% by number of the summer diet of salmon parr and trout respecively. At appropriate times these organisms are present in large numbers and are very accessible to salmonids, in particular to trout. Kalleberg (1958), in his stream tank experiments, found that salmon parr laid in close contact with the river bottom, whereas trout took up station in mid-water from where they were more easily able to obtain surface food. He also found that trout feeding intensively on aerial insects sometimes left their stations and roamed about just below the surface. This phenomenon was occasionally observed in the River Dee. Ball (1961) considered that trout preferred surface food to bottom food when both were available. This may also be true in the River Dee since during June salmon parr fed extensively on Ephemeropteran nymphs which were very abundant and accessible at that time, whereas trout ate relatively few nymphs and fed predominantly on the sub-imagines and other surface food.

The important factors governing the type and amount of food eaten by salmon parr and trout in the River Dee are the numerical representation of organisms in the fauna, together with their accessibility in terms of size, mobility and habits. The type of habitat in which the fish are feeding and the different distributions of benthic organisms (Egglishaw, 1967) also appear to be of importance. The degree to which surface food is utilized may be influenced by the vertical position normally taken up by the fish in the water.

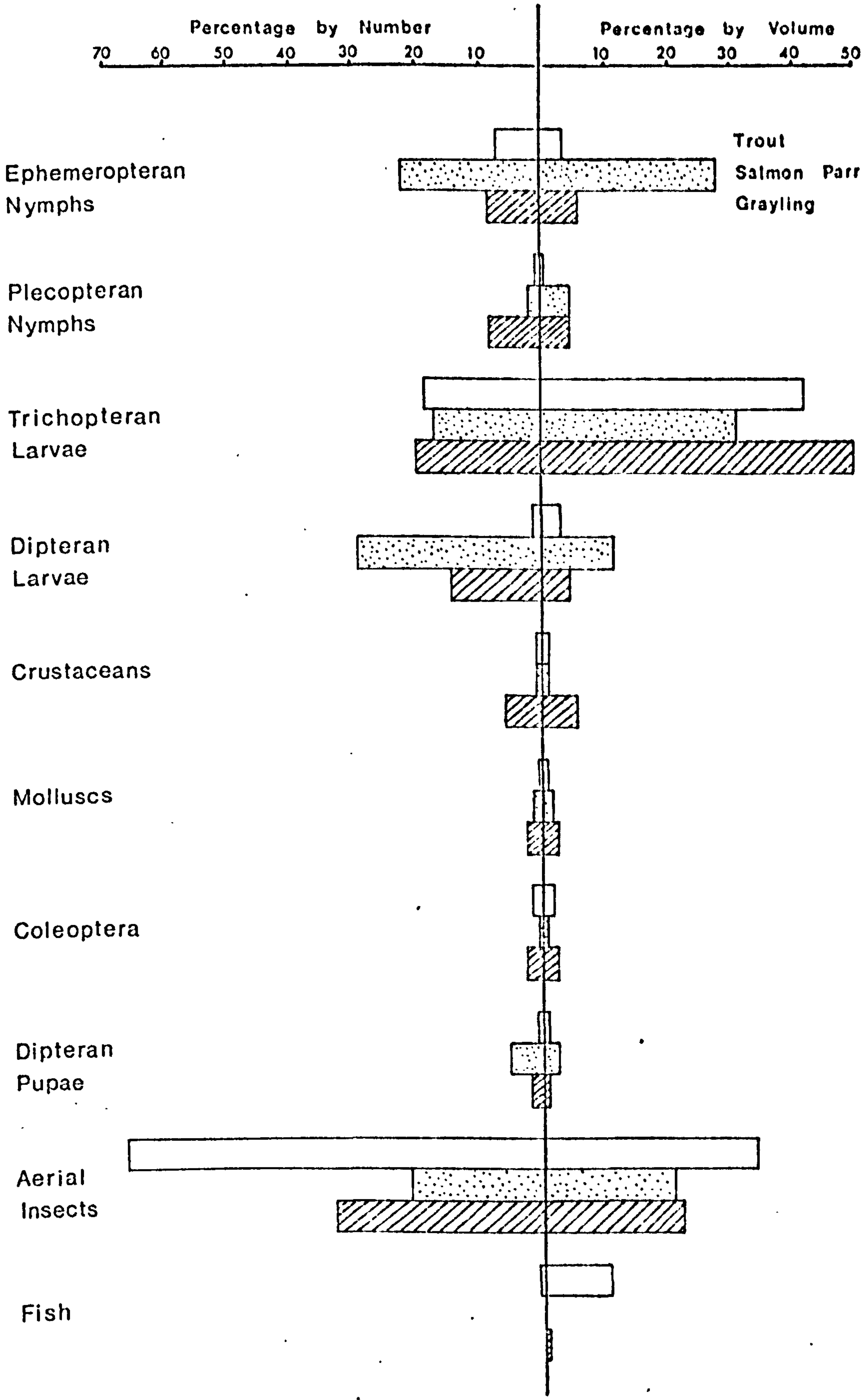
(vi) The feeding relationships of trout, salmon parr and grayling in the River Dee.

Ball (1961) found that Llyn Tegid grayling fed principally by rooting about amongst bottom deposits, whereas trout were superficial feeders eating the more obvious and readily accessible organisms. He considered that these feeding differences virtually eliminated competition for food between Llyn Tegid trout and grayling, and he suggested that the same would probably be true in a riverine habitat. Siddiqui (1967, 1969), however, found considerable overlapping between the diets of trout and grayling in Llyn Tegid and thought that some competition did occur between the two species. Many European authors have regarded the feeding of grayling and trout as being distinctly similar (Jankovic, 1964), but Muller (1954, quoted in Jankovic, 1964) found that trout and grayling occupied different niches in north Swedish rivers, and that there was no similarity between them regarding the selection of bottom fauna as food. Hartley (1948) found that there was no complete identity of feeding habit between any two species of fish in a mixed community, and much general competition occurred between the fish for certain staple foods. Many subsequent authors have recorded similar observations in mixed communities of fishes (Thomas, 1962; Cragg-Hine, 1964; Mills, 1964; Maitland, 1965; Sinha & Jones, 1967; Mann & Orr, 1969) and this feeding pattern was found in salmonid fishes during my study.

The diets of grayling, trout and salmon parr in the River Dee overlapped not only in the general types of food eaten, but also in the actual species consumed. Figure 82 shows the variation of the main food categories in the diets of the three species. Differences occurred in the proportions of these categories, thus salmon parr ate more ephemeropteran nymphs and aquatic Diptera, trout ate more aerial insects (particularly of terrestrial origin), and trout and grayling ate more trichopteran larvae. Grayling ate more Crustacea and plecopteran nymphs than trout or salmon parr, and fish were only of importance to the diet of trout. Differences in the diets also varied with age, thus young grayling ate similar quantities of dipteran larvae to salmon parr, and young trout ate similar quantities

FIGURE 82

Comparative Diets of Salmonid Fishes in the River Dee



of ephemeropteran nymphs to salmon parr. Young grayling and trout ate the same species of trichopteran larvae as salmon parr, but older trout and grayling ate much larger larvae, in particular Potamophylax latipennis. This resulted from the increase of gape size in older fish, and the larger gape of trout as compared with that of grayling (Jankovic, 1964) enabled trout to consume the very large larvae of Anabolia nervosa. The consumption of surface food increased with age in trout and salmon parr, but decreased with age in grayling.

Egglishaw (1967) emphasised the importance of the feeding locality in determining the diet, and thought that many of the differences between salmon parr and trout were a result of this factor. The habitats occupied by trout, salmon parr and grayling were to some extent different in the River Dee (chapter 4, section A1c) and these differences obviously gave rise to variations in the diets. Thus the large trichopteran larvae eaten by trout (e.g. Potamophylax) were those which inhabited the slower reaches of the river, whereas the small larvae eaten by salmon parr (e.g. Agapetus) were those which inhabited riffle areas. The consumption of Glossoma by older grayling in riffle areas, rather than Agapetus, was a function of the size of the food organism as well as its distribution.

A number of authors have recorded the occurrence of vertical stratification between salmon parr and trout (Stuart, 1953; Kalleberg, 1958; Maitland, 1965; Mann & Orr, 1969), and have related this to differences in the utilization of surface food. Salmon parr, and also grayling, lie close to the river bed and eat fewer aerial insects than trout which feed from a mid-water position.

It is somewhat surprising in this context that grayling often rise to surface food from depths of up to 2 metres, and that aerial food (particularly of terrestrial origin) is more important to the diet of grayling than to salmon parr.

The occurrence of interspecific competition, as defined by Andrewartha & Birch (1954) and Larkin (1956), is difficult to demonstrate adequately under natural conditions because of the complexity of most ecosystems. One of the criteria of competition is that food must be in short supply, but this is very difficult to assess and Maitland (1965) assumed that when two species ate the same food then that consumed by one species could be used to advantage by the other. Nilsson's (1967) concept of "interactive segregation" infers that food differences between sympatric species become more prounounced when food resources are limited. The close similarities in the diets of salmonid fishes in the River Dee suggests therefore that food may not in itself be a limiting factor in this instance.

If interspecific competition does occur then it should be reflected in the growth rates of the respective competitiors at different population densities. Data on the population sizes of salmonids in the Dee at Corwen are scanty but density indices, based on the number of fish per 100 seine net hauls, indicate that in comparision with the upper Dee, more salmon parr, considerably fewer grayling, and about the same number of trout are present (see chapter 10). Grayling are by far the most numerous fish in the upper Dee, and salmon parr are the most abundant fish at Corwen. These variations in population density are reflected in the growth rates of the three species in the two habitats (see chapters 5 and 6). Grayling, and to a lesser extent trout, grow faster at Corwen than in the upper Dee, but salmon parr grow at the same rate in both reaches. It would appear from these findings that competition does occur between these species, and that this competition operates in favour of the grayling. It would also appear that strong intraspecific competition occurs within the grayling population since these fish grow very much faster at Corwen than in the upper Dee. Competition between grayling and salmon parr probably occurs in the upper Dee, but intraspecific competition would seem to be the main factor limiting the growth of salmon parr at Corwen. It is difficult to know whether or not the increased population of salmon parr adversely affects the growth of trout, but Frost (1950) thought that inter-specific competition was unlikely to be the primary cause of poor growth of brown trout in base deficient waters, and suggested that the growth of trout would not improve if salmon were eliminated. This suggestion seems rather improbable because of the very similar diets of the two species in the River Dee, particularly during the early stages. Kalleberg (1958) found that trout were more aggressive than juvenile salmon and that trout consequently occupied the best feeding stations. As a result of this trout attained a size advantage and therefore and increased dominance over salmon parr, and this was reflected in the faster growth of trout throughout freshwater life. Aggressive territorial behaviour of grayling (Fabricius & Gustafson, 1955) similarly results in the dominance of grayling over trout in the "grayling zone" of the upper Dee (chapters 2 and 4).

4. Summary

(1) The food and feeding habits of salmon parr and trout in the River Dee were assessed by an examination of 161 and 105 stomachs respectively, between October 1969 and October 1970. The value of the various food items to the diet was estimated in terms of percentage number, volume and occurrence.

(2) Feeding intensity of salmon parr and trout was at a minimum during the winter, increased during the early spring, rising to a maximum in June, and decreased markedly after July remaining low throughout late summer and autumn. The spring increase in feeding started in February /March, about one month earlier than in grayling.

(3) The main food items of salmon parr were trichopteran larvae, ephemeropteran nymphs, dipteran larvae and aerial insects. Trout ate more aerial insects and trichopteran larvae than salmon parr, but ate fewer ephemeropteran nymphs and dipteran larvae. Fish formed an important part of the diet of trout by volume, but were not eaten by salmon parr.

(4) The main winter foods of salmon parr were trichopteran larvae, plecopteran nymphs and dipteran larvae, and those of trout were trichopteran larvae, fish, dipteran larvae and Crustacea.

Trichopteran larvae and plecopteran nymphs were replaced in the diet of salmon parr during the summer by ephemeropteran nymphs and aerial insects. Aerial insects (particularly of terrestrial origin) formed the major part of the summer food intake of trout. The consumption of the nymphs of Plectopera and Ephemeroptera was greatest just before their emergence periods.

(5) Trichopteran larvae and aerial insects became more common in the diet of salmon parr and trout with increasing age. The species of Trichoptera eaten also changed from small larvae such as Athripsodes bilineatus in the diet of young fish, to larger larvae such as Hydropsyche instabilis and Potamophylax latipennis in the diets of the older salmon parr and trout respectively. Dipteran larvae decreased in dietary importance with age, and older trout ate more fish. Ephemeropteran nymphs were less common in the diet of older trout, but more common in older salmon parr.

(6) The main factors governing the type and amount of food eaten by salmon parr and trout in the River Dee were the numerical representation of organisms in the fauna, together with their accessibility in terms of size, mobility and habits.

(7) The diets of salmon parr, trout and grayling in the River Dee were found to show considerable overlapping, suggesting inter-specific competition for food. This suggestion was further enhanced by the observed effects of high population densities of grayling on the growth rates of the other two species. Intraspecific competition for food also occurred and was most marked in the grayling population of the upper Dee, and probably also in the salmon parr population at Corwen.

CHAPTER IX

REPRODUCTIVE BIOLOGY OF SALMONID FISHES

A. Grayling

1. Introduction

Few investigations have been carried out on the reproductive biology of grayling. Some studies have been made on spawning migrations (Gustafson, 1949; Balon, 1962), spawning behaviour (Fabricius & Gustafson, 1955), fecundity and seasonal gonad development (Jankovic, 1960, quoted in Jankovic, 1964), and a number of authors have recorded sex ratios and the age at maturity (Gustafson, 1949; Balon, 1962; Jankovic, 1964; Peterson, 1968; Hellawell, 1969a; Micha, 1971). The reproductive biology of North American grayling was studied by Brown (1938), Kruse (1959) and Bishop (1971).

2. Sex ratios

The sex ratio of grayling has usually been recorded as being close to 1:1 (Gustafson, 1949; Peterson, 1968; Hellawell, 1969a), but the spawning shoal of grayling studied by Balon (1962) comprised approximately 7 females to 1 male, and Stepanek (1960, quoted in Jankovic, 1964) found males predominating over females by from 2:1 to 6:1.

In my study the ratios of males to females were 1.05:1 in the River Dee and 1:1.13 in Llyn Tegid. Neither these values, nor those for males and females in any of the age groups studied, differed significantly from a 1:1 ration (χ^2 test, $p > 0.05$).

3. Age at maturity

Jankovic (1964) stated that sexual differentiation of grayling began in the first year of life, and in my study the sexes could be distinguished by eye at the end of the first summer. Yugoslavian grayling mostly matured at 3 years of age, but a few males matured at 2 years (Jankovic, op.cit.). Sexual maturity was also reached by males in 2 years and by females in 3 years in the fish studied by Gustafson (1949), and Balon (1962) recorded that male grayling spawned one year earlier than female grayling. Sømme (1936, quoted in Peterson, 1968) found that grayling in northern Norway did not reach sexual maturity until 5 or 6 years of age, and thereafter spawned every year. The youngest spawning fish found by Peterson (op.cit.) were 5 years of age. Hellawell (1969a) and Micha (1971) both recorded that grayling reached maturity towards the end of the third year of life. The age at which River Dee and Llyn Tegid grayling reached maturity is shown in table 56.

Table 56 Percentage of grayling which mature at the end of each year of life.

Age	Males	Females
1	0	0
2	0	0
3	64.5	73.9
4 & older	100.0	100.0

This table indicates that most grayling matured at the end of the third year of life, and that all grayling were mature by the end of the fourth year. Since no non-spawning fish were recorded after the age of 4 it was concluded that grayling spawn every year after sexual maturity is attained. Slightly more females were mature at age 3 than males, but this difference was not significant (χ^2 test, $p > 0.05$).

4. Sexual cycle

The seasonal development of the gonads of male and female grayling is shown in figure 83. The gonad stages shown refer to those given for female grayling in chapter 4 (section B4a), and for males the x-axis should read one stage higher.

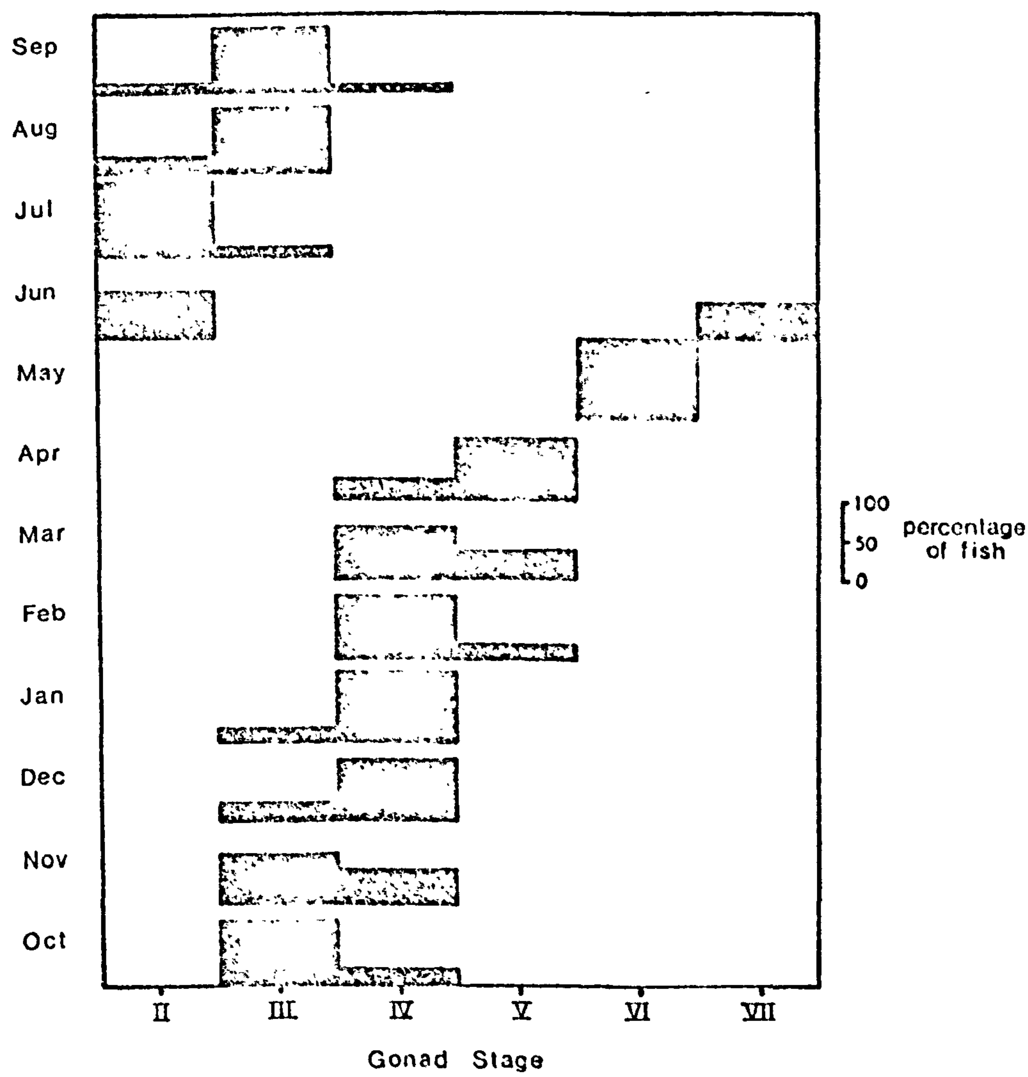
Jankovic (1964) considered that the sexual cycle of grayling had four stages which he gave as :

(1) Spawning period of males and females - 4 to 6 weeks.
(2) Regeneration period of males and females - 4 to 6 weeks.
(3) Period of active spermatogenesis and ovogenesis - up to 5 months.
(4) Period of final spermatogenesis and ovogenesis - up to 4 months.

These features can be seen fairly clearly in figure 83, with rapid development of the gonads to stage III-IV between July and December, a relatively stationary phase throughout the winter at gonad stage IV, a final ripening phase in the spring, spawning in May, and regenerating and redeveloping in June. Seasonal data on the contribution of ovary weight to total body weight were incomplete and only the relative weights of mature ovaries were considered to be of importance in this study. During March and April ovaries which had been preserved in Gilson's fluid formed 9.9% of the total body weight (S.D. ± 1.3%).

FIGURE 83

Seasonal Gonad Development in Grayling



5. Fecundity

The fecundity of grayling was estimated from counts of the eggs in 35 stage IV-V ovaries (see chapter 4, section B4b). Reference to section 4 of the present chapter shows that ovaries at this stage of maturity occurred during the winter months when body growth was at a minimum. If eggs are collected from fish during a period of active somatic growth then fecundity in relation to length will appear to decrease (Bagenal, 1967). This factor should be taken into account in grayling fecundity studies if growth occurs during the winter period, (see chapter 5, section 3a,ii).

Fecundity of fish can be related to a number of parameters, the most commonly used being fish length and weight. Typical results of a fecundity investigation show that fecundity is approximately proportional to the cube of the length, or linearly proportional to the weight (Bagenal & Braum, 1968). Bagenal (op.cit.) consideres that fecundity should preferably be related to length rather than to weight. If fecundity is related to total weight this can lead to a spurious correlation (Bagenal, 1967, p67), while if gonad weight is not included, difficulties may arise if there are marked seasonal changes in condition. In my study, the fecundity of grayling was related to length and total weight after logarithmic transformations had been carried out. These transformations enabled a straight line regression to be fitted to the length data, and also removed the dependance of the standard deviation on the mean (Pope et al., 1961). The equations for the regression lines were :

$$\log F = \log a + b \log L$$

and

$$\log F = \log a + b \log W$$

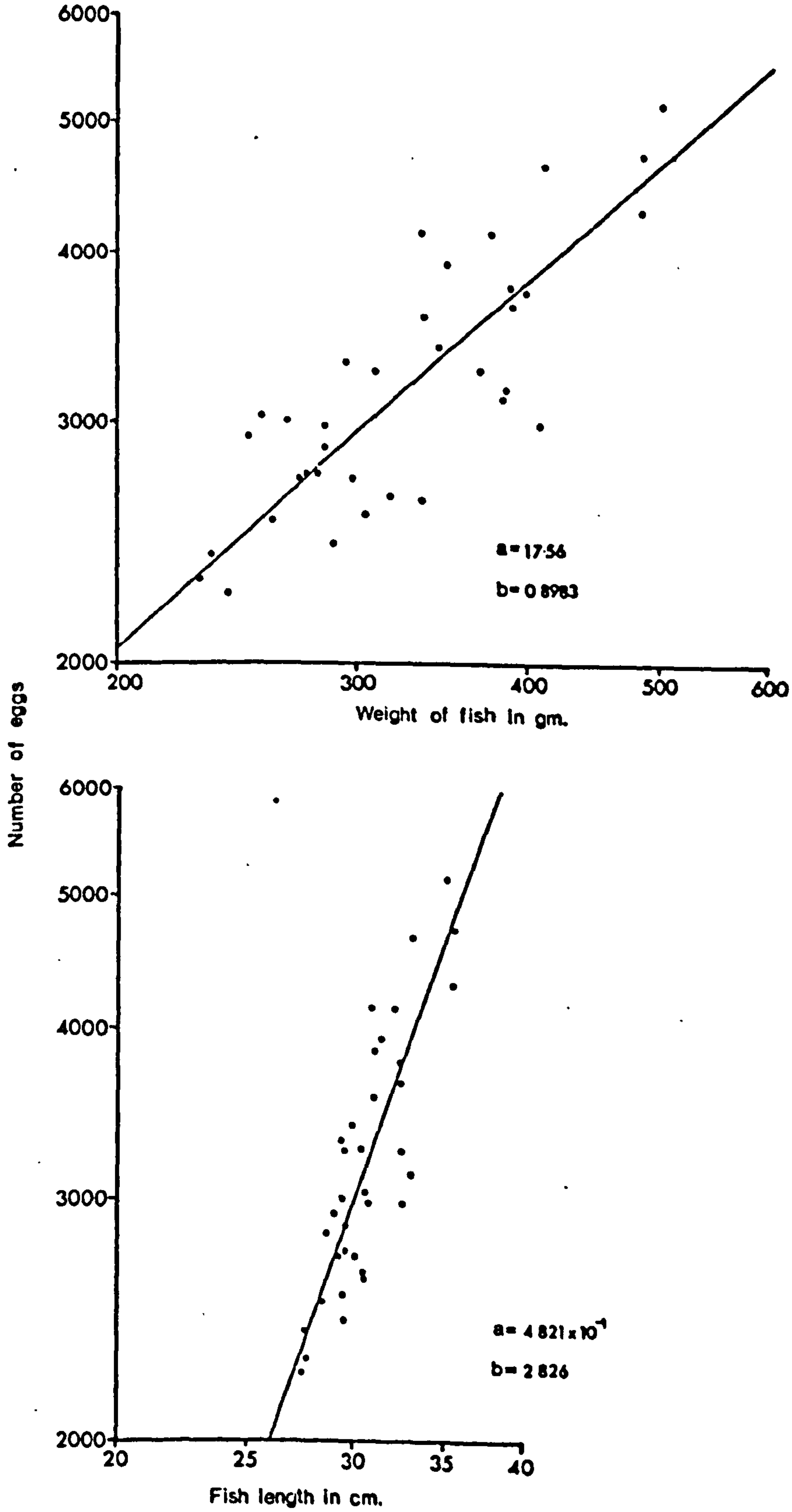
where F = fecundity, L = fish length, and W = fish weight.

The logarithmic transformations of fecundity in relation to length and weight are shown in figure 84, together with the regression slopes (b) and the y-axis intercepts (a). The logarithmic values for the standard deviation of the regression lines were 0.056 and 0.055 for the length and weight relationships respectively. The scatter of points about the regression line was greater in the weight relationship than in the length relationship and reflected individual variations in condition (K) which constitute one of the main objections to the use of weight measurements in fecundity studies.

Bagenal (1967) gave a range for the value of b in the fecundity/length relationship of 2.34 to 5.28, with the most usual values being a little above 3. The value of b obtained for grayling in my study was 2.83 and no comparable values for grayling from other workers have been found in the literature. Grayling fecundity has been recorded by other workers simply as the range in the number of eggs, or more occasionally, as the number of eggs per unit of body weight. A table of such recordings given by Jankovic (1964) shows that the number of eggs per fish ranged from 1000 to 36,240, and that one investigator found 6000 to 10,000 eggs per Kgm. body weight. In River Dee and Llyn Tegid grayling egg counts of from 2200 to 5200 were recorded, and

FIGURE 84

Fecundity of Grayling



extrapolation of the weight regression line in figure 84 gave an estimate of 8700 eggs per Kgm. body weight.

6. Spawning localities

Fabricius & Gustafson (1955) made a comprehensive study of the spawning behaviour of grayling and concluded, from observations under natural conditions and in a stream tank, that spawning grayling preferred shallow places where there was a swift current of water over the top of a bank of fine gravel. Spawning took place in water 5-25 cm. deep, flowing at approximately 0.75 metres per second, over a substrate comprising pebbles 1-3 cm. in diameter which was usually located, in contrast to the spawning gravels of salmon and trout, at the upstream end of pools. Grayling from lakes have been observed to migrate into feeder streams to spawn (Gustafson, 1949; Balon, 1962) and those studied by Gustafson (op.cit.) spawned at a distance of 3 km. from Lake Storsjo after ascending a height of 38 metres. Similar migrations of lake dwelling North American grayling were recorded by Brown (1938), Kruse (1959) and Bishop (1971), and the spawning gravels used by these fish were very similar to those described for European grayling by Fabricius & Gustafson (op.cit.). Peterson (1968) recorded spawning migrations of grayling from Sundsvall Bay (Baltic Sea) into the River Indalsalven.

From the above observations it appeared likely that Llyn Tegid grayling also migrated into feeder streams to spawn, and the 1952 Dee and Clwyd River Board Report stated that numerous grayling had been seen apparently spawning in the lower reaches of the Afon Llafar and Afon Lliw. An angler also reported the presence of numbers of grayling in the Afon Glyn during the second week of May, 1969. Grayling are not generally present in the feeder streams at this time of year (chapter 10) and the fish observed were probably grayling which had entered the Glyn from Llyn Tegid for spawning purposes. Despite daily observations in the feeder streams throughout the probable spawning season in 1969 and 1970 no spawning was seen. A number of large grayling were, however, seen cruising in the shallows of the Afon Dyfrdwy above the weir at site 5 (see chapter 3, section C1a) during the second week of May 1969, and one of these fish had been tagged in Llyn Tegid. Mature grayling were caught in Llyn Tegid around the feeder stream inlets during April, and fry were first observed in these areas in early July (see section 8). Morris (1967) recorded the presence of grayling fry in the lower reaches of the Afon Llafar in June 1962. Spent fish were caught in the lake during May around the feeder stream inlets and also near the River Dee outlet. These observations clearly indicate that grayling do leave Llyn Tegid to spawn in the feeder streams and probably also in the River Dee, and moreover that grayling may ascend small weirs to do so.

Grayling in the River Dee were thought to spawn in the main river since no mature grayling were ever caught or seen in any of the small tributaries. Grayling have been reported spawning in the Afon Alwen below Rhug bridge (J.W.Jones, pers.comm.) but these fish are resident in the lower reaches of the river throughout the year. No spawning was observed in the River Dee but some evidence was accumulated concerning the likely whereabouts of a number of spawning sites. On 11th and 12th May 1970 a number of large grayling were seen actively cruising about in very shallow water at site t (chapter 3, section C3a), causing a considerable disturbance in the water. The area occupied by these fish could not be reached without the aid of a boat, but a number of the grayling were captured by fly fishing and were found to have newly spent gonads. The fish had been feeding intensively and the stomachs contained a number of grayling eggs (see chapter 7). It seems likely that these fish had only recently spawned, particularly since one fish had only partly spent ovaries, and the area in which they were located closely fitted the description of spawning sites given by Fabricius & Gustafson (1955). The site consisted of a bank of fine gravel about 3 square metres in area, at the side of a pool in fast flowing water less than 10cm. deep. Accumulations of mature grayling were found during late April and early May in a number of very similar situations at sites c,k and h, the fish being caught on the upstream side of the gravel banks as well as on the downstream side. Extensive digging in a number of likely areas failed to reveal the presence of eggs, and whether or not these gravel banks were actually used for spawning remains uncertain. From this discussion, it is clear that more studies need to be carried out in order to ascertain the exact spawning areas and spawning requirements of both River Dee and Llyn Tegid grayling.

7. Spawning time and conditions

Grayling have generally been found to spawn during the spring, and in many parts of Scandinavia spawning activity commences with the spring ice-thaw (Gustafson, 1949; Fabricius & Gustafson, 1955; Muller, 1961; Peterson, 1968). Fabricius & Gustafson (op.cit.) found that grayling spawned in late May and early June, and that nearly all of the observed spawning acts took place at water temperatures between 9.1 and 11.6°C. Muller (1961) recorded the water temperature at 10.5°C during spawning, but Peterson (1968) found the largest number of grayling spawning during mid-May at a temperature of 5°C. Dyk (1959, quoted in Jankovic, 1964) said that grayling in mountain areas spawn at 7°C, whilst in lower hilly regions spawning begins only at 10°C. Jankovic (1964) stated that the spawning period lasted from four to six weeks.

The exact time of spawning of River Dee and Llyn Tegid grayling was uncertain since no spawning was observed. The occurrence of ripe and spent fish, however, enabled the time to be fairly accurately estimated. During 1969 mature fish (almost ripe) were last caught in Llyn Tegid on 29th April at the Afon Dyfrdwy and Afon Llafar inlets, when the lake temperature was 7.5°C. Spent fish were first caught in the lake on 13th May 1969, when the lake temperature was 10.5°C. It was therefore concluded that spawning took place in the feeder streams at some time between 29th April and 13th May. It is suggested that grayling in fact spawned only a few days before the 13th May, since heavy rains caused some flooding during the first week of

May making conditions unsuitable for spawning at that time. In 1970 the last occasion on which mature fish were caught in Llyn Tegid was on 20th April and the first spent fish were caught on 12th May. Daily sampling for salmon smolts was being carried out in the lake at this time and the first recording of spent grayling was probably fairly accurate. The environmental conditions during late April and early May 1970 were water temperature 9-11°C, rainfall very low, river flows low and water clear.

In the River Dee during 1970 relatively large numbers of mature grayling were caught at site k on 30th April at and site h on 1st May, and spent fish were caught at the same sites on the 5th and 4th of May respectively. The water temperature at this time was 8.0-12.5°C, and at the end of April the river level was falling after a small flood and the water was coloured. The water flows in cumecs from 30th April to 5th May were 21.5, 18.9, 15.5, 8.8, 51 and 3.4. On the 3rd, 4th and 5th May the water was low and clear and spawning probably took place in a concentrated period at this time. Fabricius & Gustafson (1955) found that most grayling completed their spawning in from ½ to 4 days, with a few fish continuing for up to a week. Grayling at sites q and t were thought to spawn slightly later than those in sites k and h, since the evidence suggested that the fish caught there on 11th and 12th May had just spawned (see section 6). At this time the river flow was between 8 and 9 cumecs, and the water temperature was 11-12.5°C. Thus it appears that although spawning in a particular locality may take place in a short period of time, spawning activities throughout the upper Dee may continue for about two weeks. No evidence of any spawning after 12th May was recorded.

A small number of observations were also made in the River Dee in 1971. Four running ripe fish were caught at site n on the 21st April and spent fish were caught at this site, and also at site t, on the 29th April. The water temperature at this time was 8.5–11.0°C.

8. Hatching and early stages

The incubation period for grayling eggs was quoted by Muller (1961) as being from 20–25 days and a period of about three weeks was given for North American grayling by Kruse (1959) and Bishop (1971). Assuming an incubation period of three weeks the eggs of River Dee and Llyn Tegid grayling would have hatched in late May or early June.

Kruse (1959) found that the fry of Arctic grayling drifted down into Grebe lake from the feeder streams within a ten day period from hatching. The first fry were seen in Llyn Tegid on 8th July 1969 approximately one month after hatching, and were first caught on 11th July when they measured from 4.1 to 5.7 cm. in length. The fry were caught at the main feeder stream inlets and also at the inlet of a small unnamed brook situated between sites b and c (see plate 12). In the spring of 1970, three pairs of ripe grayling were introduced into a fenced off section of this brook in which it was hoped they would spawn. I intended to observe the spawning activity of these fish, and by collection of the resulting fry in a downstream trap, to assess mortality between the egg and fry stages. Unfortunately, a very large flood occurred in the last week of April and the experiment was washed out. A similar experiment in the Afon Alwen stream tank (Jones & King, 1950a) failed when the fish contracted a fungal disease and died. Kruse (1959) gave a figure of 2.5% survival from egg to fry for Grebe lake grayling.

The first grayling fry were seen in the River Dee on 8th June 1970. One of these fish, which measured about 2cm. in length, was captured by hand in very shallow water close to the bankside, but managed to escape before accurate measurements could be made. Young grayling were first caught by angling and by netting during August when they were about 7cm. in length.

Very little information is available in the literature on the embryonic and juvenile stages of grayling (Jankovic, 1964), and it is suggested that some work should be carried out in this field on River Dee grayling, possibly along the lines of the trial experiments described above.

9. <u>The effects of river regulation on grayling spawning</u>

Assuming that River Dee grayling do spawn in similar places to those described by Fabricius & Gustafson (1955), then it is possible that river regulation has had some effect on the breeding success of grayling. The eggs of grayling are deposited under 4cm. or less of fine gravel, whilst those of trout are laid at twice this depth (Jones & Ball, 1954) and those of salmon at depths of up to 30cm. (Jones, 1959). The eggs of salmon and trout are laid in much coarser gravel than those of grayling, and trout often spawn in small tributary streams rather than in the main river.

It follows from this that the eggs of grayling in the River Dee are more susceptible to the effects of floods and droughts than are those of salmon and trout. The fine gravel in which the eggs are laid is easily washed out by floods, and since it is situated in shallow water it is quickly exposed and dessicated during periods of drought.

The occurrence of even a moderately severe flood during the incubation period could lead to large scale destruction of eggs and subsequently a weak or missing year class. The hatching time of grayling eggs, however is very much shorter than that of salmon and trout, and this probably offsets the apparently disadvantageous susceptibility to environmental conditions. Nevertheless, any reduction in the frequency of adverse conditions, as may be brought about by regulation, must lead to substantially lower mortality rates in the redd. Kruse (1959) found that the greatest part of the mortality in the early stages of Grebe lake grayling was attributable to dislodgement of the eggs during the incubation period either by subsequent spawners or by changes in water level and current velocity.

It is arguable whether or not lower mortality rates in the redd and the resulting increased numbers of hatching fish (recruits) gives rise to any overall increase in the population. Many fishery scientists believe that the number of eggs laid by a fish has little bearing on the number of adults that result (Le Cren, 1965; Beverton, 1962), since population regulating mechanisms act mainly during the first few weeks of life and are mostly density dependent (McFadden, 1969; Mills, 1969).

Increased numbers of recruits may result in a lower percentage survival, but the actual numbers surviving may increase, particularly when environmental conditions become favourable. Two of the main factors which constitute such favourable conditions are increased food supplies and increased living space. Both of these factors can arise from river regulation.

Invertebrate animals will survive better in the more stable conditions which exist in a regulated river system, particularly as a result of the reduction in the harmful scouring effects of floods, and territories for fish will generally increase because of the higher mean and minimum river flows discussed in chapter 1.

Regulation may also effect the breeding success of Llyn Tegid grayling, in both the adult and fry stages. Considerable erosion occurred at the feeder stream inlets following the general lowering of the lake level, and gabion weirs were constructed to limit this erosion (see chapter 3). It is possible that these weirs may impede the upstream migration of lake grayling to suitable spawning sites, but evidence from tagging experiments (chapter 10) suggests that grayling readily surmount such small obstacles.

The lake level is raised during the summer (chapter 1) and the time of this operation roughly coincides with the time of fry descent into the lake. Grayling fry spend their early life in shallow water (Muller, 1961) and the summer raising of the lake level greatly increases the area of shallow water available to the fry, as well as providing an increased food supply in the form of terrestrial organisms.

It seems likely from this discussion that the Bala regulation scheme has been beneficial to the breeding success of River Dee and Llyn Tegid grayling, and that this in turn has contributed to the increasing stocks which have been observed since regulation.

B. Salmon and Trout

1. Introduction

Many studies have been made on the reproductive biology of salmon and trout (e.g. Jones, 1940; White, 1942; Jones & King, 1949, 1950a, 1950b, 1952; Allen, 1951; Stuart, 1953; Jones & Ball, 1954; Pope et al., 1961; Robins, 1967) and further studies are being conducted in the Welsh Dee area as part of the Water Resources Board programme (see chapter 1). In this investigation observations were only made on sex ratios, ages at maturity, seasonal gonad development and salmon redd counts (chapter 2, section 3c).

2. Sex ratios

The sex ratios of salmon parr and trout in the Llyn Tegid feeder streams and in the River Dee are shown in tables 57 and 58.

Table 57. Sex ratios of salmon parr

Year Class	Ratio of males to females: Llyn Tegid Feeder streams	P	River Dee	P
1966	2.33 : 1	< 0.05	-	
1967	2.30 : 1	< 0.001	9.00 : 0	< 0.01
1968	0.87 : 1	> 0.05	1.71 : 1	< 0.05
1969	0.82 : 1	> 0.05	1.23 : 0	> 0.05
1970	-	-	0 : 2.00	> 0.05
Total	1.05 : 1	> 0.05	1.43 : 1	< 0.05

(P = probability of observed results conforming to a 1:1 ratio, χ^2 test)

Table 58. Sex ratios of trout.

Year Class	Llyn Tegid Feeder streams	P	River Dee	P
1965	0.73 : 1	> 0.05	0.33 : 1	> 0.05
1966	0.63 : 1	< 0.05	0.56 : 1	> 0.05
1967	0.79 : 1	> 0.05	0.45 : 1	< 0.05
1968	1.17 : 1	> 0.05	1.03 : 1	> 0.05
1969	1.65 : 1	< 0.05	1.40 : 1	> 0.05
Total	0.98 : 1	> 0.05	0.72 : 1	< 0.05

(p = probability of observed results conforming to a 1:1 ratio, χ^2 test)

Male salmon parr outnumbered female salmon parr in the older age groups, but not in the young age groups. The overall ratio of males to females in the Llyn Tegid feeder streams did not differ significantly from 1:1, but males outnumbered females in the River Dee.

The results obtained in this study were substantially the same as those found by Jones (1949). In his study, the numbers of male and female salmon parr were not significantly different in the 1+ - 2 year age group, but males greatly outnumbered females (2.77:1) in the 2+ - 3 year age group. He considered that the increasing dominance of males over females in older age groups was a reflection of the attainment of sexual maturity by male fish in their second year of life. He thought that the high proportion of 3 year old male fish reflected and probably accounted for the high proportion of females amongst 2 year old smolts. This predominance of females amongst 2 year old smolts was also found in my study (see chapter 12). Jones (op.cit.) suggested that 3 year old males may spawn more than once in the river before migrating seawards.

The sex ratios of trout followed almost reverse trends to those of salmon parr, females outnumbering males in older age groups, and males outnumbering females amongst the younger fish. The overall ratio of male trout to female trout in the Llyn Tegid feeder streams did not differ significantly from 1:1, but females outnumbered males in the River Dee.

Variations were found in the sex ratios of salmon parr in the different Llyn Tegid feeder streams, and also in different parts of these streams. Table 59 shows the sex ratios of salmon parr in the Llyn Tegid feeder streams.

Table 59 Sex ratios of salmon parr in the Llyn Tegid feeder streams.

River Site	Observed ratio of males to females	Probability of results conforming to 1:1 ratio	Abundance of spawning gravel
A. Lliw	2.80 : 1	< 0.01	++
A. Dyfrdwy (upper)	1.75 : 1	< 0.05	++
A. Dyfrdwy (lower)	0.32 : 1	< 0.001	(+)
A. Glyn	0.79 : 1	> 0.05	+
A. Twrch	2.64 : 1	< 0.001	+
A. Llafar (upper)	0.57 : 1	< 0.05	(+)
A. Llafar (lower)	0.66 : 1	< 0.005	(+)

(Abundance of spawning gravel from table 5, chapter 3)

There appeared to be a correlation between the proportions of the sexes and the abundance of spawning gravel. Males greatly outnumbered females in areas where spawning gravel was abundant, and the reverse was true where spawning gravel was scarce. This differential distribution may be related to the participation of male salmon parr in the spawning activities of the adult fish (Jones & King, 1952).

Male salmon parr outnumbered female salmon parr at all sites in the River Dee. The numbers of male and female trout did not differ significantly in any of the Llyn Tegid feeder stream sites, except in the Afon Lliw where males outnumbered females by 1.86 : 1 ($p<0.001$), and in the Afon Glyn where females outnumbered males by 1.54 : 1 ($p<0.05$).

3. Age at maturity

The age at which maturity was reached by trout and male salmon parr in the Llyn Tegid feeder streams and the River Dee is shown in table 60.

Table 60. Attainment of sexual maturity by trout and male salmon parr.

a) Trout

Age	Percentage of mature fish at the end of each year of life	
	males	females
1	0	0
2	0.03	0
3	22.40	12.40
4	76.50	50.00
5	96.80	83.30
6 & older	100.00	100.00

b) Male salmon parr

Age	Percentage of mature fish at the end of each year of life
1	0.2
2	86.8
3 & older	100.0

Male trout were found to mature at a younger age than female trout, most male fish maturing during the fourth year of life, and females maturing during the fifth year.

Sexual maturity was first reached by the majority of male salmon parr at the end of the second year of life. The 1+ to 2 year age group of salmon parr comprised 6.2% immature males, 40.2% mature males and 53.1% females. Jones (1949) found a larger proportion of immature males in this age group and recorded the proportions of the three categories as 21.9%, 24.5% and 53.6% respectively. Following the first attainment of sexual maturity both trout and male salmon parr were found to spawn (or ripen) annually.

4. Sexual cycles

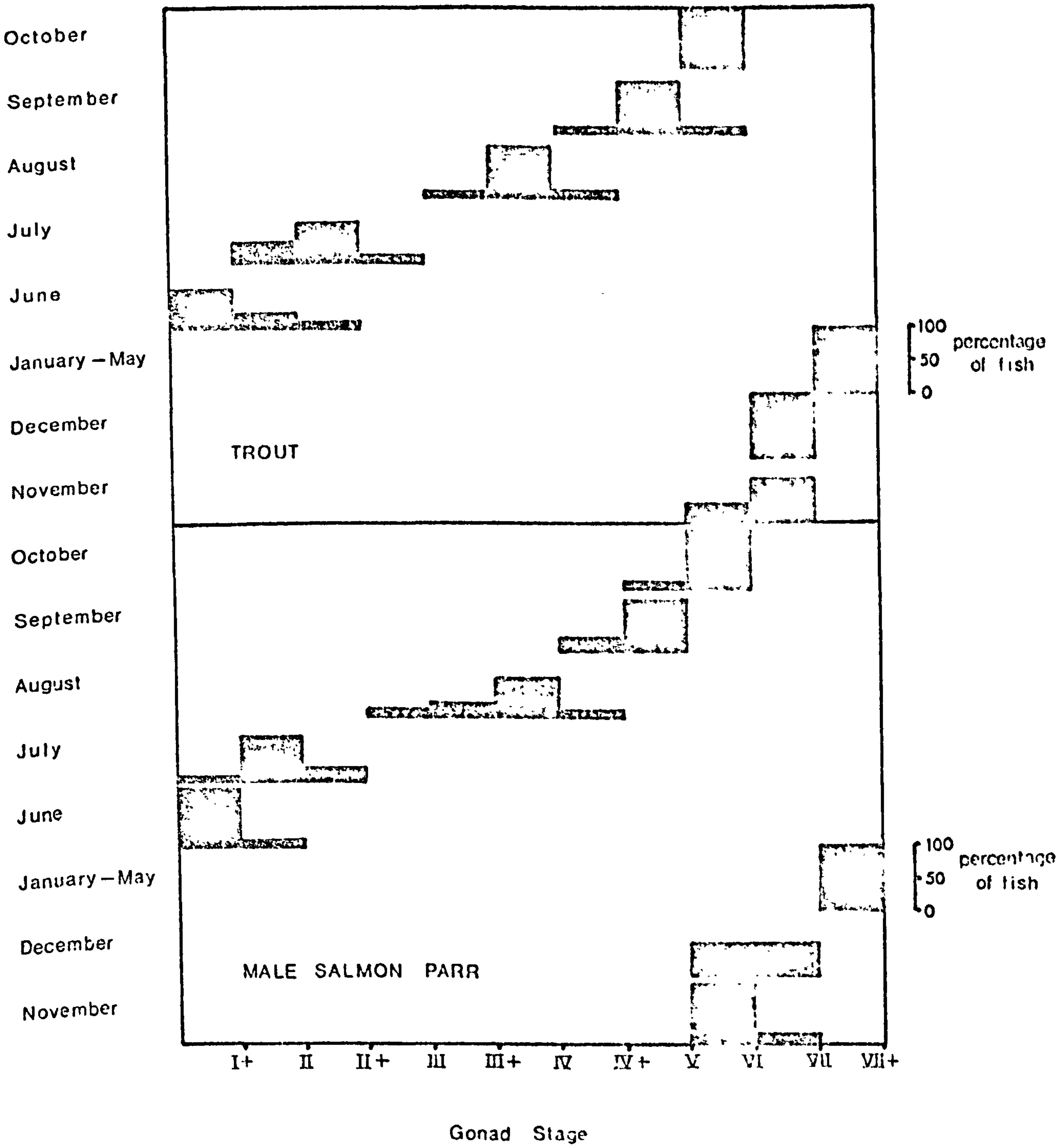
The seasonal development of the gonads of trout and male salmon parr are shown in figure 85. The gonad stages given in this figure ar those referred to in chapter 4 (section B4a). Gonad development started in June; by October most trout were ripe and by November most male salmon parr were ripe. Trout spawned in the latter half of November, and salmon spawned in early December. The gonad devlopment and spawning of trout thus took place slightly earlier in the year than in salmon parr. Reabsorption and regeneration of gonads took place in both trout and salmon parr from January to May.

C. Summary

1. The sex ratio of grayling in both Llyn Tegid and the River Dee did not differ significantly from 1:1. The sex ratios of salmon parr and trout varied according to age and differed in different habitats. Male salmon parr predominated over female salmon parr in older age classes and in areas containing abundant spawning gravel, but the numbers of males and females were similar in younger age groups. Female trout outnumbered males in the older age groups and the reverse was true amongst younger fish.

FIGURE 85

Seasonal Gonad Development of Trout and Salmon Parr



2. Most grayling matured at 3 years of age, and all were mature at 4. Most male salmon parr (86.8%) attained sexual maturity during the second year of life. Male trout matured earlier in life than female trout, most males maturing during the fourth year of life and females in the fifth.

3. The gonads of grayling developed rapidly from July to December, remained at stage IV (V in males) throughout the winter and ripened in the spring. Spawning took place in May, and readsorption and regeneration in June.

4. Salmon parr gonads developed more slowly than those of trout, trout ripening in October and spawning in November, salmon parr ripening in November and spawning in early December. Readsorption and regeneration took place from January to May in both species, and redevelopment commenced in June.

5. The fecundity of grayling was expressed in relation to fish length and weight in terms of the following equations :

$$\log \text{Fecundity} = \log 17.56 + 2.826 \log \text{length}$$

and

$$\log \text{Fecundity} = \log 0.4821 + 0.8933 \log \text{weight}$$

Extrapolation of the fecundity on weight regression gave an estimate of 8700 eggs per Kgm. body weight.

6. Grayling were found to leave Llyn Tegid to spawn at unknown localities in the Llyn Tegid feeder streams and in the River Dee. The location of some possible spawning sites of River Dee grayling, which corresponded closely with those described by Fabricius & Gustafson (1955), were considered.

7. Grayling in 1969 and 1970 were found to spawn during early May at water temperatures between 8.0 and 12.5°C, when river flows were low and when the river water was clear. In 1971 spawning apparently took place in late April at water temperatures of 8.5 to 11.0°C.

8. Grayling eggs were considered to hatch in late May or early June. The first fry were caught in Llyn Tegid on 11th July 1969, and in the River Dee on 8th June 1970.

9. River regulation was thought to have had a beneficial effect on the breeding success of River Dee grayling, and also on the survival of fry in both the River Dee and Llyn Tegid.

CHAPTER X

STUDIES ON THE POPULATIONS OF GRAYLING IN THE RIVER DEE AND LLYN TEGID

1. Movements of grayling

A. Introduction

The few studies that have been carried out on the movements of grayling populations have mostly been concerned with spawning migrations from lakes (Gustafson, 1949; Kruse, 1959; Balon, 1962) but in addition Peterson (1968) made some observations on non-spawning movements. He found two genetically identical sub-populations in the River Indalsalven, one which originated from Sundsvall Bay, and the other a "pure" river population. The Sundsvall Bay grayling entered the River Indalsalven to spawn and stayed in the river for varying periods of up to one year. This group of fish moved extensively within the river, but the "pure" river population moved very little, all recaptures of such fish being made very close to the places where they were released. Peterson (op.cit.) also found that very little movement occurred of grayling in Sundsvall Bay outside of the spawning period.

The populations of grayling in Llyn Tegid and the River Dee showed some similarities to the two groups of fish described by Peterson (1968), as well as some interesting differences. Spawning migrations were dealt with in the previous chapter and the present chapter deals principally with non-spawning movements. The numbers of grayling tagged at each sampling site in Llyn Tegid and the

River Dee, and the location of subsequent recaptures can be seen in figure 86. The methods of tagging were discussed in chapter 4. For the purposes of this study it has been assumed that marked fish behaved in the same way as unmarked fish.

B. Movements of grayling in the River Dee

(i) General movements

The movements of tagged grayling can be seen in figure 86. This figure includes the movements of fish used in transfer experiments (sites a–c, see section 1B,ii) and such movements have not been included in the assessment of general movements. Excluding the results attributable to the transfer experiments, a total of 117 (84.8%) grayling were recaptured in their site of origin, and 21 (15.2%) were recaptured elsewhere. These results indicate that the distribution of grayling in the River Dee was not random (χ^2 test, $p < 0.001$) and that movement was restricted.

This type of restricted movement has been recorded for many stream fishes (Gerking, 1953, 1959) and indicates that such fish occupy a "home range". Hayne (1949) defined home range as "the area over which an animal normally travels", and this definition has been adopted here.

The demonstration of home range does not necessarily mean that territoriality is involved but it does indicate the possibility of this phenomenon (Gerking, 1953). Evidence for the occurrence of territoriality in the River Dee grayling population is presented in the following section in connection with transfer experiments.

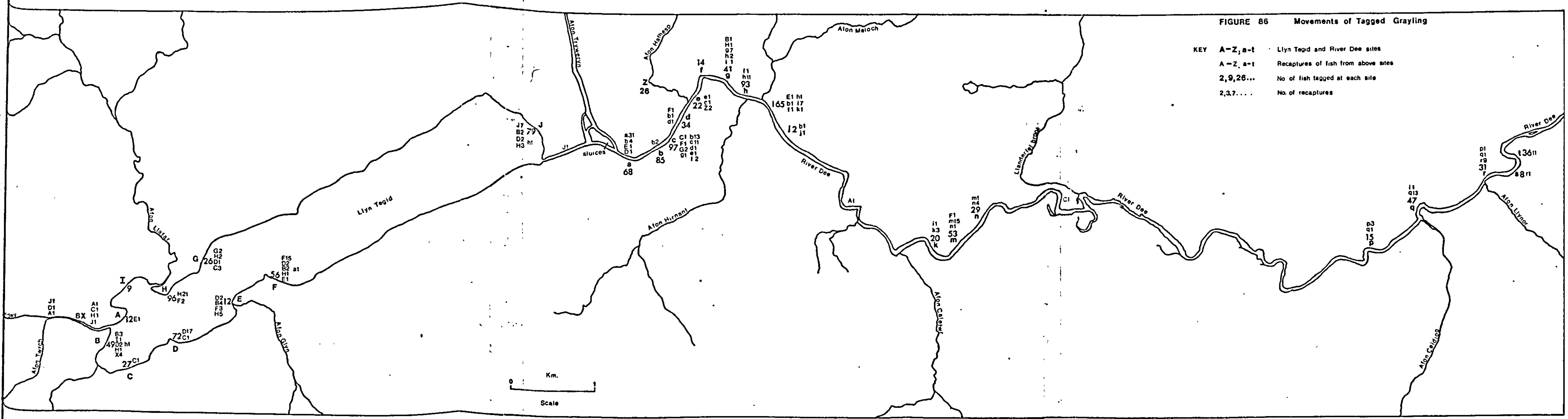


FIGURE 86 Movements of Tagged Grayling
KEY
A–Z; a–t Llyn Tegid and River Dee sites
A–Z, a–t Recaptures of fish from above sites
2,9,26... No of fish tagged at each site
2,3,7.... No. of recaptures
Afon Tryweryn
Afon Hatheso
Afon Meloch
Llyn Tegid
sluices
River Dee
Afon Hirnant
Afon Llafar
Afon Glyn
Afon Twrch
Afon Celyn
Afon Ceidiog
Afon Llynor
Km.
Scale

PULLOUT

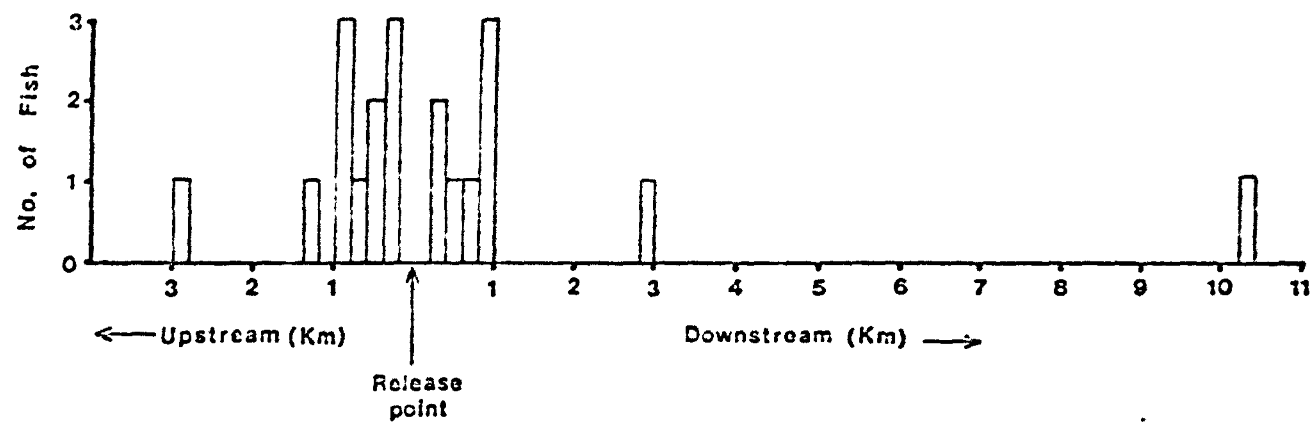
The distances moved by those grayling which did leave the home area are shown in figure 87 for each 200 metre interval. Eleven of the recorded movements occurred in an upstream direction, and 10 were downstream of their site of origin. It was found that 76% of the recorded movements were within 1 Km. of the "home area".

Some bias towards negative movement will have been introduced as a result of the absence of samples from stretches of the river between certain of the sampling sections (see figure 13, chapter 3), but this error is likely to be small since any large scale movement into such areas would undoubtedly have shown up in angler's catches. Some error may also result from the arbitrary allocation of site boundaries which may not coincide with home ranges. The longest recorded movement was of a grayling tagged at site i in February 1970 and recaptured at site q, about 10 Km. downstream, in July 1970.

Stott (1967) described the populations of coarse fish in the River Mole, Surrey, as comprising two components, a static group normally distributed with a narrow dispersion, and a smaller mobile group which wandered more widely. Some evidence of this phenomenon was found in the River Dee grayling populations. Thus a grayling originally tagged at site k on October 29th, 1969, was recpatured for the first time at site i, 2900 metres upstream, on 1st June 1970, and for the second time on 9th July 1970 back at site k. In addition, a fish tagged at site m in January 1970 was recaught in March of the same year at site n, and subsequently returned to

FIGURE 87

Movement of Grayling in the River Dee



site m where it was caught in May. The fact that both of these grayling returned to their sites of origin after moving away suggests the possibility that some grayling may alternate between two home areas. This, however, was considered to be an unlikely explanation for the first example given, because of the long distances travelled.

The occurrence of a mobile portion of the population may result from the inability of such fish to accept a home range, or to maintain territories in competition with other fish, the less aggressive fish being forced to move from one temporary position to another temporary position (Kalleberg, 1958). Evidence of the inability of "foreign" grayling to obtain territories in competition with permanent residents was found during transfer expreiments (section 1 B,ii).

Since the degree of aggressive behaviour, and thus of territoriality, is often a function of size (Kalleberg, 1958) it would seem reasonable to expect non-sedentary grayling to be smaller than sedentary fish. This was not found to be true of those grayling which moved in the River Dee. The numbers of movements recorded were very small, however, and no conclusions can be reached on the possible benefits, or otherwise, of territoriality to growth and feeding. Gerking (1953, 1959) emphasised the importance of stray fish in providing a reserve supply available for occupying vacant territories, repopulating decimated areas, and distributing the species over its geographical limits of tolerance.

(ii) Transfer experiments

The occurrence of territoriality, where territory is defined as any defended area (Noble, 1939), is difficult to observe in a large river such as the Dee. Experiments were therefore conducted along the lines suggested by Gerking (1953) who considered that territoriality could be demonstrated if:

(1) fish move rapidly into an underpopulated area;

(2) a "foreign" population, on suddenly entering a well-established population, competes with the others, but the residents have some advantage in the competition. As a result "foreign" fish move to a greater extent than the others;

(3) the well-established individuals move more than they usually do as a result of the competition.

The experiments were carried out in sites a, b and c, and grayling caught at one site were tagged and released at another site. The effects of such transfers were assessed from subsequent recaptures. Grayling were only caught in large numbers from site c during the experimental period (January 1970–April 1970), and most of the transfers were made from that site. Table 61 shows the relevent details of the transfer experiments, together with the distances between the centres of each site. It should also be noted that the Bala gauging station weir (plate 3, chapter 1) forms the upstream boundary of site b.

Table 61. Results of transfer experiments with River Dee grayling.

site of origin	site to which trans-ferred	Dist-ance between sites (metres)	No. of fish moved	Recaptured in sites: a	b	c	d	elsewhere
a	b	250	4	1	0	0	0	0
b	a	250	7	1	2	0	0	0
c	b	160	80	3	0	13	1	site i – site j –

If no competition for territories occurred between resident and introduced fish, then the subsequent distribution of recaptures following the transfers should have been random. Table 61 clearly shows that this was not so (χ^2 test, $p<0.001$) as only one fish was captured in the site to which it was transferred, compared with 22 recaptured elsewhere.

The results also show a distinct tendency towards the "homing" of displaced fish, where "homing" refers to the choice a fish makes between returning to a place formerly occupied instead of going to equally probable places (Gerking, 1959). If movements were only attributable to the repopulation of an artificially under populated area then some fish from sites a and c should have been found in site c, and the proportion of fish returning to c would hot have been so high.

Taking the transfer of site c fish as being most representative then 63.4% of the recaptures of fish released in site b were recorded suggesting that "homing" fish had reoccupied their former territories.

back in the "home" section c, 15.8% went upstream from b to a, and 15.8% went downstream below site c. Some bias towards "homing" may occur with site c fish because of the relatively short distance from b to c and because of the necessity of ascending the gauging station weir when leaving site b in an upstream direction.

"Homing" of site a grayling after transference to site b, and the movement of some of the site c grayling into site a, suggests that the gauging station weir does not seriously impede the movements of grayling. This finding is of particular interest since grayling, unlike salmon and trout, are not generally noted for their ability to ascend obstacles such as weirs and falls.

Not shown by table 61 are 3 grayling which, after returnig to site c from site b, were released again in site b. Of these fish, 2 returned for the second time to site c, and one was recaught in site j. In addition the site c fish recpatured in site d (see table 61) was the same fish as the one recaptured at a later date in site i. These findings provided further evidence of territoriality, and indicated that "foreign" fish introduced into site b were unable to obtain territories in competition with resident fish. Fish which did not "home" successfully were at a similar disadvantage, and showed a continuing tendency to move.

Of the grayling which returned to c from b and which were not transferred back to b, 3 were recaptured for a second time. All of these second recaptures were recorded in the home section (c), suggesting that "homing" fish had re-occupied their former territories.

The experiments did not reveal increased movement amongst resident fish following the introduction of foreign fish. This was because of the complete absence of home tagged site b fish, and the small number of fish transferred from b to a. Some evidence of the increased movements of resident fish was obtained, however, in connection with the summer immigration of grayling from Llyn Tegid (1B,iii).

(iii) Seasonal movements

(a) Movements of grayling between Llyn Tegid and the River Dee.

Fourteen recaptures of Llyn Tegid grayling were recorded in the River Dee, and three recaptures of River Dee grayling were recorded in Llyn Tegid (see figure 86). All of the recaptures of Llyn Tegid fish in the River Dee were made between July and early October, and of River Dee fish in Llyn Tegid between late October and early May. These movements were associated with the observed summer disappearance of grayling from Llyn Tegid, and the autumn return to the lake (see section 1C,iii).

Recaptures of Llyn Tegid grayling were made throughout the upper 7 Km. of the River Dee, but 71% of the recaptures were made in the upper 2Km. suggesting that most of the grayling which enter the River Dee from Llyn Tegid during the summer occupy this part of the river.

It is apparent from the observations on movements between Llyn Tegid and the River Dee, that the Bala sluices do not constitute a serious obstacle to the migrations of grayling. Sidliqui (1969) suggested that the increasing numbers of grayling in Llyn Tegid may have arisen from the difficulty of downstream movement through the sluices, resulting in fish being "trapped" in the lake. The tagging experiments I have carried out, however, suggest that movement through the sluices may be easier in the downstream direction than in the upstream direction.

(b) Seasonal movements within the River Dee.

Recaptures of tagged grayling which had moved from their sites of origin showed no obvious seasonal trends except for an increase in June and July when 7 of the 21 movements were recorded. These movements may have arisen as a result of the general increase in activity associated with rising water temperatures, but may also have been brought about by the influx of grayling from Llyn Tegid. The latter suggestion conforms to Gerking's (1953) hypothesis, that the introduction of "foreign" fish into a well-established population will not only give rise to movements of the "foreign" fish, but will also result in increased movements of the well-established individuals.

Movements of grayling within sections showed some seasonal trends from deep to shallow water and vice versa. During the winter most grayling were located in water of moderate depth (1-2 metres), large fish moved into the shallows during the spring, and in the summer the shallow regions of the river were principally occupied by small grayling.

Fish tended to congregate during the winter in places which gave them some shelter from the current, such as a depression in the river bed. In the summer the grayling became more scattered as was apparent from "rise" patterns and rod catches, and fish occupied all areas of the river, especially the mid-stream positions.

Many angling writers have regarded the grayling as a shoaling fish but this type of behaviour was not generally recorded in River Dee grayling, except possibly during the winter when fish tended to congregate in certain places, but not necessarily to shoal. The occurrence of territoriality, demonstrated in my study, and the aggressive behaviour of this species recorded by Fabricius & Gustafson (1955), suggests that riverine grayling do not normally form shoals. Observations on the distribution of grayling "rising" to take surface food indicated that individual fish were well separated, at least during the summer months.

The spring movement of large grayling into the shallows was associated with spawning activities. No migration of mature fish out of ho areas was recorded, the available information suggesting that fish moved only to nearby shallows to spawn. Few mature grayling were tagged, however, and emigration to suitable spawning areas may occur from places where spawning gravel is limited.

In addition to the above movements, some migration of grayling into a number of small tributary streams was recorded during the winter months. The first indications of such movements occurred during routine sampling of the Afon Hafhesp by P.R. Lees on 4th March 1969. Twenty four 0+ grayling were caught on this occasion, and a further 21 0+ fish were caught and tagged on 12th March. None of these fish were recaptured in the Afon Hafhesp and subsequent visits on 17th April and 22nd May produced catches of 3 and 2 0+ grayling respectively. It appeared that the grayling had moved out of the stream, but direct evidence of this was not obtained until the following year when two of the grayling tagged in the Afon Hafhesp were recaptured in the River Dee close to the stream inlet (see figure 86).

Small catches of grayling were also made during the early months of 1969 by Lees in the lower reaches of the Afon Morwynion, Llanderfel brook and Druid brook (a small tributary of the Afon Alwen). The catch of grayling from the Afon Morwynion comprised 3 0+ fish and 3 1+ fish, and one 0+ fish was caught in each of the other two streams.

Grayling were caught in the Afon Camddwr during the winter of 1969/70 by R.S. Pritchett whilst sampling for eels. These grayling were first recorded on 25th February and further catches were made in April. No grayling were caught in the stream after 19th April. The total catch of grayling from the Afon Camddwr comprised 17 0+, 5 1+, one 2+ and one 3+ fish. One 1+ grayling was recorded in the Emral Brook (a tributary of the middle Dee) by D.R. Wilkinson in January 1970, and I caught 2 0+ grayling in the Afon Llynor, and one 0+ grayling in the Afon Ceidiog, by electrofishing during February 1970.

The reasons for the migration of grayling into small tributary streams during the winter months, and the spring movement of fish back to the main river, are not known. Since no spawning fish were ever seen in the tributaries and no fry were caught there, it was concluded that these were not nursery streams. I think that grayling enter these streams to avoid strong winter flows in the main river, and that such movements are most marked in young fish.

C. Movements of grayling in Llyn Tegid

(i) Location of fish

Grayling in Llyn Tegid were principally found in the littoral zone (0-3 m.) and small numbers of fish were sometimes caught in the sublittoral region (3-15m.). During my study only one grayling was caught in the latter region, at a depth of 7 metres, but other workers have recorded a few grayling in gill nets at depths of about 10 metres. Grayling therefore occupy less than 30% of the total lake area (see chapter 3), and most fish are concentrated in about 15% of the lake area (littoral zone).

The sites at which grayling were most commonly found were those which had a gently sloping bottom of fine gravel or silt. They were most commonly caught in sheltered positions such as sites D and F, but this may have been because of difficulties in sampling windward shores (see chapter 4), and fish were often caught on exposed shores, such as site J, under suitable conditions.

Some exploratory netting was carried out in the shore zone of the central part of the lake, but very few grayling were caught there. The bathymetric survey of Llyn Tegid (Jones, 1951) showed that the lake bottom fell steeply from the shore in the central region, and this area was considered generally unsuitable as a habitat for grayling. The main areas containing suitable grayling habitats occurred at each end of the lake.

Because of its nearness to the laboratory, the southwest end of the lake was netted most frequently, but site J (at the northeast end) was sampled in most months from May 1969 onwards. From the large catches of grayling obtained at this site it is evident that future studies would be well directed towards more thorough sampling at the northeast end of the lake. Such sampling would also give more detailed information of movements of grayling between Llyn Tegid and the River Dee.

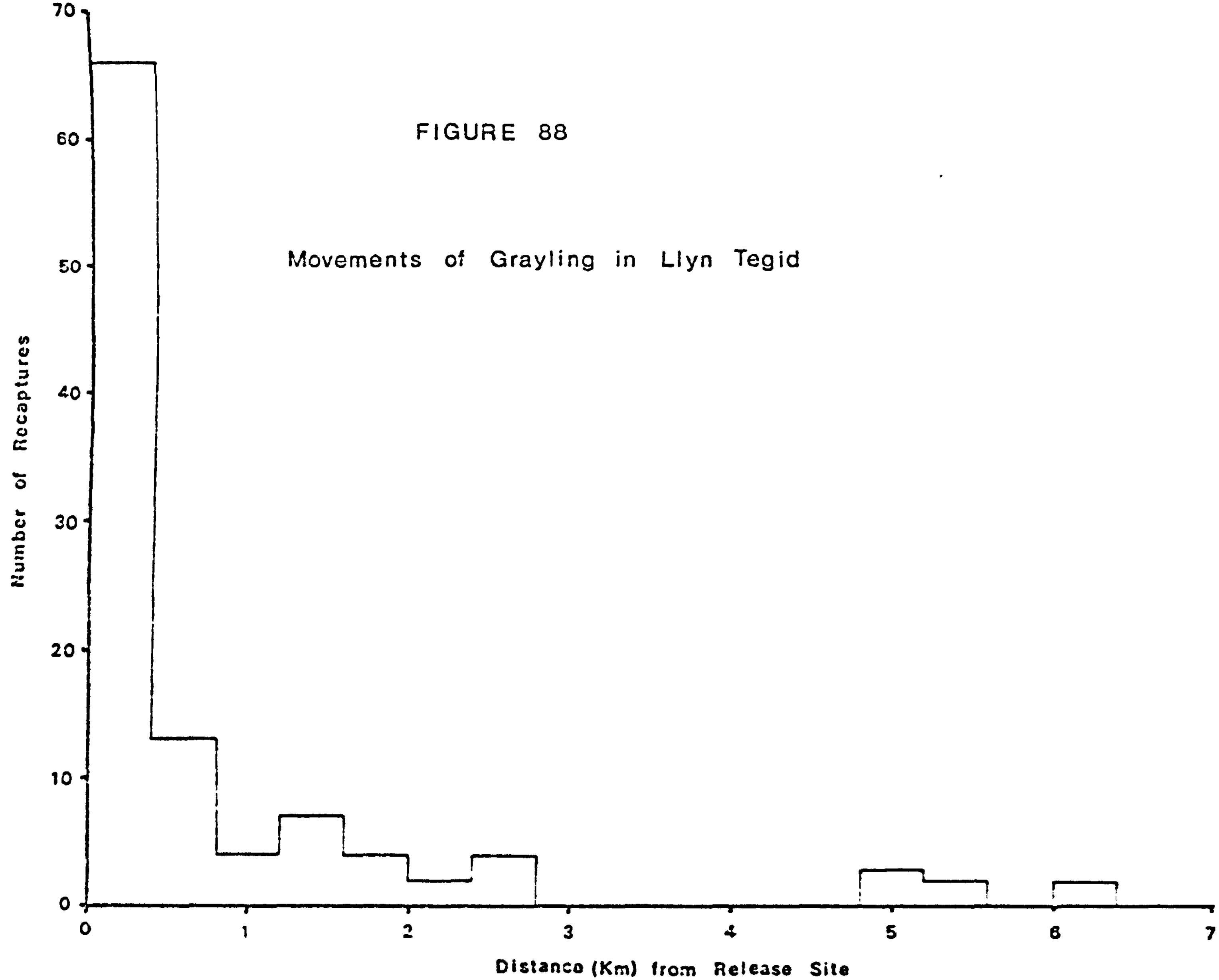
(ii) General movements

Movements of grayling were found to occur more frequently in Llyn Tegid than in the River Dee. Sixty six (61.7%) of the recaptures were at or near the point of release, and 41 (38.7%) were recorded elsewhere. This distribution of recaptures was significantly different from random at the 1% probability level (χ^2 = 7.958 with 1 d.f.).

Although most grayling tended to remain within the "home" area many fish moved away, the distances moved are shown in figure 88. These distances were compiled from measured shore distances between the various sites, but from the distribution

FIGURE 88

Movements of Grayling in Llyn Tegid



of recaptures between site H on one side of the lake, and sites E and F on the other (see figure 86), it seemed possible that fish may have moved directly across the lake, not around the shore line. The distance moved by fish recaptured on the opposite side of the lake to that at which they were released was therefore taken as the shortest distance between release and recapture points. The distances shown in figure 88 are therefore arbitrary, and it was concluded that grayling move randomly from one position to any other suitable area. Recaptures of grayling within the "home-area" are also included in figure 88.

(iii) Seasonal movements

(a) Movements within Llyn Tegid.

The distribution of "home" (61.7%) and "away" (38.7%) recaptures given in the preceding section reflected the mean occurrence of movements during the year. The frequency of movements changed extensively, however, at different times of year. During the winter virtually all recaptures were made within the home area. From January to April 1969 all recaptures were made at the points of release, and from December 1969 to late April 1970 only one recapture was recorded elsewhere.

During late spring, early summer and autumn, however, large scale movements occurred within the lake and at these times "away" recaptures often exceeded "home" recaptures. In June 1969, for example, 4 "home" recaptures and 8 "away" recaptures were recorded. Nearly all of the movements of Llyn Tegid grayling shown in figures

86 and 88 thus occurred between May and October, and at such times the distribution of grayling was clearly random.

The above results indicate that grayling in Llyn Tegid, unlike those in the River Dee, have no definite home area. The lack of movement during the winter is probably a result of the low level of activity at that time, which is assochted with low winter water temperatures. It was apparent that as the water temperature rose in the spring and early summer, the grayling began to move extensively.

A number of transfer experiments were carried out with grayling in Llyn Tegid, in the same way as with River Dee grayling in an attempt to assess the occurrence, or lack of territoriality and home range. The results of such transfers are shown in table 62.

Table 62. Results of transfer experiments with Llyn Tegid grayling.

Site of origin	Site to which transferred	Number of fish moved	(Number) of recaptures and site of recapture
B	H	18	(2) H
E	H	5	(2) River Dee
E	I	1	(1) B
F	D	9	(1) A, (1) B
H	I	8	-
J	G	2	(1) G

Excluding those fish which left the lake it can be seen that 3 fish were recaptured at the site to which they were transferred, and 3 were recaptured elsewhere. No evidence of "homing" was found and it was concluded that displaced grayling distributed themselves randomly after release.

These results suggest that grayling in Llyn Tegid do not occupy a restricted home range and that no apparent territoriality occurs within the population. It seems probable that grayling show a decrease or loss of aggressive territorial behaviour in lakes, in the same way as did the juvenile salmon and trout studied by Kalleberg (1958) when water flows ceased. Grayling in lakes may therefore adopt a shoal-like behaviour pattern, and may subsequently roam around in search of food. Ball & Jones (1962) found that trout in Llyn Tegid moved freely about the lake and did not form home areas for periods longer than one week, although trout in streams were considered to occupy definite home areas (Allen, 1951).

A good example of a grayling which moved extensively, and in an apparently random fashion, was provided by a grayling which was captured on five occasions. This fish was originally caught at site H on 22nd April and was subsequently caught at site H on 3rd June, at site J on 10th June, at site E on 12th August, and in the Afon Dyfrdwy (site 6) on 25th August.

Little movement of grayling occurred during mid-summer in the lake, the few fish that were caught being located at or near river inlets. The summer distribution was related to the general disappearance of grayling from the Llyn Tegid shore zone at that time (section Ciii,b).

Some of the early summer movements of grayling may have been correlated with the search for an outlet from Llyn Tegid, but the distribution of recaptures of Llyn Tegid grayling outside of the lake suggested that this was not the case. Thus, some fish tagged at the northeast end of the lake (site J) were recaptured above the lake in the Afon Dyfrdwy, and some fish tagged at the southwest end of the lake were recaptured below the lake in the River Dee (see figure 86). Most of the movements recorded during the autumn occurred at a time when grayling were returning to the Llyn Tegid shore zone (see section Ciii,c).

(b) The summer disappearance of grayling from the Llyn Tegid shore zone.

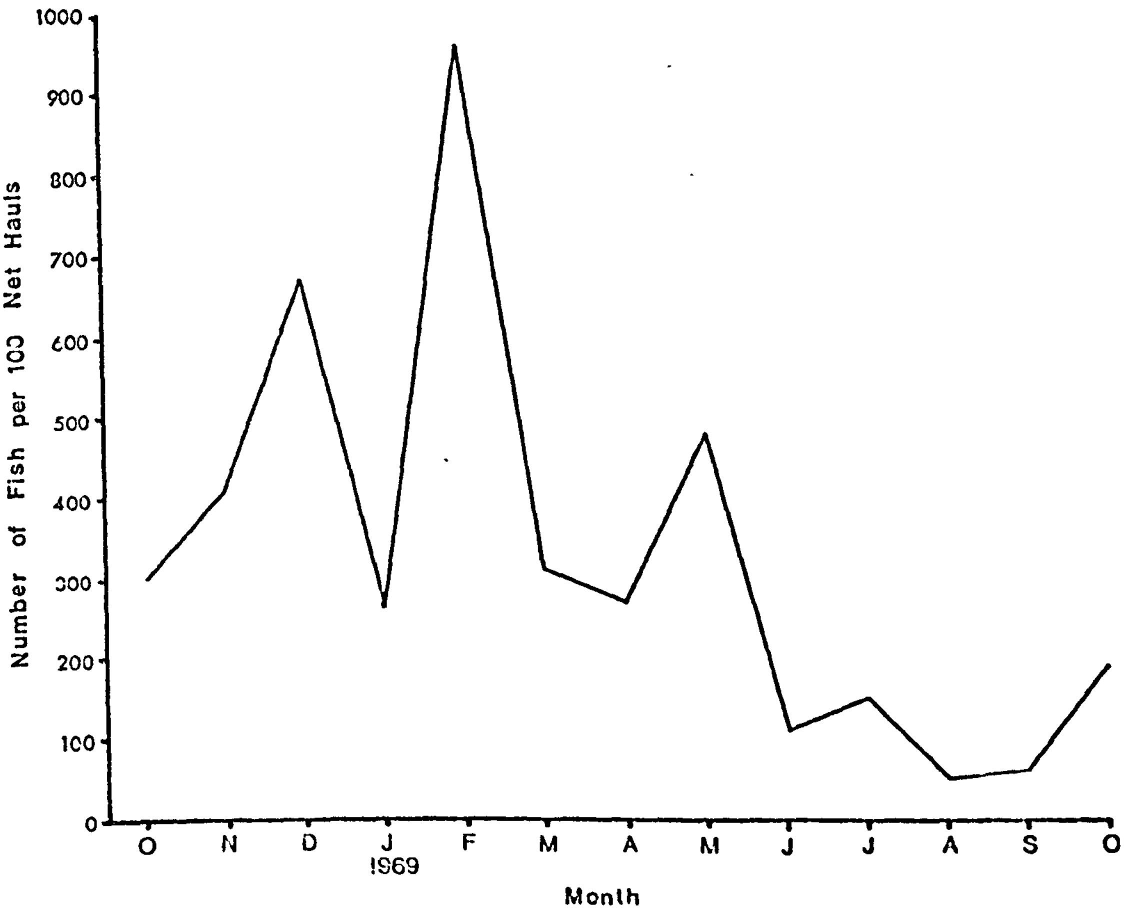
Ball & Jones (1962) found that the catches of trout in the littoral zone of Llyn Tegid decreased markedly during the summer (July-September). From gill net catches in deep water and observations in the feeder streams, they concluded that most trout left the shore zone and went into deeper water, but that a few left the lake and went into the feeder streams.

During my study it was found that the catches of grayling also fell sharply during the summer, and similar findings were reported by Siddiqui (1969). The seasonal density index of grayling in the Llyn Tegid shore zone is shown in figure 89. The density index refers to the catch per 100 net hauls (Gulland, 1955).

Figure 89 shows that catches of grayling were greatest in the

FIGURE 89

Seasonal Density Index of Grayling in the Llyn Tegid Shore Zone



shore zone during the winter months and fell to a minimum from June to September. In fact the large decrease in June occurred during the second half of the month, relatively large numbers of grayling being caught in the first half of the month, particularly at site J. The small rise in catches during July resulted from the influx of fry from nursery streams.

Extensive gill netting was carried out throughout the summer of 1969 (see chapter 4) in an attempt to discover whether or not grayling went into deep water. These netting operations produced only one grayling at a depth of 7 metres at site B, and one grayling at a depth of 1 metre at the Afon Glyn inlet. The grayling caught at site B was captured on 11th July and may have been on the point of leaving the lake via the Afon Dyfrdwy. Grayling were not recorded in deeper water during the summer, nor at any other time of the year, and it was concluded that the summer disappearance of grayling from the shore zone could not be attributed to a migration to deeper offshore water.

Nearly all of the grayling caught in Llyn Tegid during the summer were caught at or near the feeder stream inlets in very shallow water. This suggested that some grayling may have left the lake and gone into the rivers. Evidence for such an emigration was obtained by the capture of 14 tagged lake grayling in the River Dee, 4 tagged fish in the Afon Dyfrdwy site X, and 3 tagged fish by anglers at the Afon Dyfrdwy-Afon Twrch junction. These captures, which were all recorded between July and early October, can be seen in figure 86. In addition, seine netting operations in the Afon Dyfrdwy site X (sites 6-8, figure 8) only caught grayling during July, August and September, and although relatively few fish were caught (2) at this time, it was apparent that many more were present, both below and above the weir at site 5 (figure 8).

Grayling were also observed, but not captured, in the pools in the lower reaches of the Afon Llafar (see chapter 5) during the summer. No grayling were ever seen or captured in the Afon Glyn during the summer except in the area below site 1 (figure 4) at the outlet to Llyn Tegid. No grayling were caught or seen in any of the feeder streams during the winter.

It was concluded from these results that most grayling left Llyn Tegid during the summer, migrating out of the lake into the feeder streams and also into the River Dee. Population estimates of graling in the River Dee were not generally reliable (see section Bii) but some indication was found of increasing numbers of fish during the summer which could possibly be attributed to the influx of Llyn Tegid grayling.

The reasons for the summer migration of grayling from Llyn Tegid are not certain. Ball & Jones (1962) postulated that the summer departure of trout from the shore zone may have resulted from the increased activity of trout associated with rising temperatures, and the effects of competition with spring migrants from the feeder streams. This may have led to a general extension of the distribution of trout away from the shore zone with fish congregating, and becoming "trapped", in the optimum temperature gradient of the thermocline region.

Since the grayling is essentially an Arctic, cold-water species (Hellawell, 1969a), the effects of above optimum temperatures on the behaviour are likely to be most marked. Although water temperatures, as recorded in chapter 3, were not very different in the lake and the surrounding rivers, the temperature in the shallow littoral zone was often considerably higher than that shown in table 11 (chapter 3), and this may have been an important contributory factor to emigration from the lake.

The migration out of the lake may also have been correlated with the lower summer oxygen concentration of the relatively static lake water in comparison with the turbulent rivers, and the extreme susceptibility of grayling to low oxygen concentrations was noted by Brayshaw (1971). The summer location of grayling in Llyn Tegid, in close proximity to relatively cool, well oxygenated inflows, provided further evidence in support of these theories. It is also possible that the large influx of perch and roach into the shore zone during the summer may have had some effect on the behaviour of grayling, and the extent of competition between these three species is as yet unknown. Grayling which did remain in the lake during the summer became heavily infested with lice (Argulus sp.), but this parasite was very much less common on river fish.

(c) The autumn return of grayling to the Llyn Tegid shore zone.

Grayling catches in the Llyn Tegid shore zone rose sharply from early October onwards (figure 89), fish first being captured near river inlets (sites B,H and J) and then quickly spreading throughout the lake. The initial capture of fish near river inlets suggested a return of grayling from the rivers to the lake, and further evidence of this was obtained from the recapture in the lake of fish tagged in the rivers. Thus, of 8 grayling tagged in the Afon Dyfrdwy in September 1969, 4 were subsequently recaptured in Llyn Tegid at site B during October 1969 (see figure 86). In addition, 3 fish tagged in the River Dee in the autumn of 1969 were recaptured in Llyn Tegid during the winter and early spring of 1970.

Captures were also made during October 1969 of 2 grayling at the River Dee outlet, 2 grayling at the Afon Llafar inlet and 4 grayling at the Afon Dyfrdwy inlet, all of which had been tagged at other sites during the previous winter. It seems likely that these fish had spent the summer in the respective rivers, and were captured as they were returning to the lake.

It is more difficult to account for the return of grayling to Llyn Tegid during the autumn than their summer departure, particularly for fish which undergo the comparatively arduous return from the River Dee over the gauging station weir and through the Bala sluices. The motivating force which initiates the return is not known, no large increase in river flows occurred at this time and temperatures (see chapter 3) were very similar in both the lake and the rivers. The water temperatures at the time of the return to the lake (12-14°C) were very similar to those at the time of departure (13-15°C).

It seems possible that Llyn Tegid grayling have become adapted to a lacustrine existence, and only leave the lake when conditions become unsuitable, for one reason or another, and for spawning purposes. The intestinal tracts of nearly all Llyn Tegid grayling were infested during the winter months with the encysted plerocercoid larvae of Diphyllobothrium ditremum, or Diphyllobothrium dendriticum, but neither of these parasites was ever recorded in River Dee grayling. It seems likely, therefore, that undetected movements of grayling from Llyn Tegid to the River Dee did not occur during the winter, and that grayling only left the lake in the summer.

2. Population structures and densities

A. Introduction

The tagging experiments carried out to assess the movements of grayling in Llyn Tegid and the River Dee also enabled some estimates of population size to be made. Because of the large area covered in the surveys, and the preliminary nature of the studies, the information available for such estimates was necessarily limited. The numbers of fish caught and tagged at any one site on any single occasion were small, and the resulting population estimates were not considered very reliable. Fish were being continuously removed from the populations during the sampling period for dietary analyses, thus reducing the number of fish available for tagging, and of those tagged 134 were used in transfer experiments. In addition the tagging experiments were carried out over long periods of time, a procedure which introduces numerous complications into the estimates (see section 2B,ii).

Despite the many drawbacks it was decided to attempt a number of population density estimates since, as pointed out by Le Cren (1969), approximate data are distinctly better than no data at all, and it is only by making such estimates that one can see where the major inaccuracies lie and then take steps to eliminate them.

Estimates were made using the methods of Schnabel (1938), as modified by Chapman (1952), and Schumacher & Eschmeyer (1943). These methods and their application have been adequately described by Ricker (1958) and recent reviews on the methods of estimating population sizes have been made by Jones (1964), Reiger & Robson (1967), and Robson & Reiger (1968). The material available was not suitable for use with the more sophisticated estimate methods such as that of Jolly (1965). In addition to the density estimates details of the population structures were recorded, and attempts were made to assess the relative proportions of grayling, trout and juvenile salmon in different parts of the River Dee.

No estimates of population densities of European grayling from mark recapture experiments have been found in the literature, but Solewski (1963) gave an approximate density of 0.041 grayling per square metre in the Rogoznik stream. Mackay (1970) gave the density of grayling in the Douglas Water and the River Gryfe, Scotland, as 125 per Km. and 23 per Km. respectively. He did not indicate the width of these rivers but judging from the mean flows given in his paper, these streams were nearer in size to the Llyn Tegid feeder streams than to the River Dee. Assuming a very approximate width of 10 metres, then the density of grayling in the two rivers would be 0.0125/metre^2 and 0.0023/metre^2. These relatively low densities may have occurred because grayling are not indigenous to these rivers. The River Gryfe population had also been subjected to frequent pollutions, and the density estimates were both made following pollutions in which Mackay (1970) assumed that all fish had been killed. Kruse (1959) used Schnabel estimates to assess the population density of *Thymallus arcticus* in Grebe lake from mark-recapture experiments. He gave the density of grayling in the lake as approximately 4500 per hectare.

B. The grayling population of the River Dee

(i) Population structure

The catches of grayling made at each site in the River Dee are shown in table 63. The results obtained show that the 0+ age group was not caught efficiently by the methods used, and that the catches of these fish were not representative of their proportion

Table 63. Catch statistics for River Dee grayling (excluding anglers' catches).

Site		Total Catch	0+	No. in each age group 1+	2+	3+	4+	5+	6+	7+	No. of samples
Bala	a	122									15
	b	47									7
	c	339									21
	d	64									4
	e	45									5
	f	25	126	710	203	17	2	1	0	0	4
	g	62		(76.1)	(21.8)	(1.8)	(0.2)	(0.1)	0	0	3
	h	184									16
	i	159									20
	j	12									2
Llanderfel	k	77									4
	m	160	22	139	81	18	9	3	0	0	12
	n	35		(55.6)	(32.4)	(7.2)	(3.6)	(1.2)			5
Llandrillo	p	37									5
	q	77									7
	r	93	22	206	73	22	8	4	1	1	10
	s	15		(65.4)	(23.2)	(7.0)	(2.5)	(1.3)	(0.3)	(0.3)	4
	t	98									9
	u	17									2
Total for upper Dee		1668	170	1055	357	57	19	8	1	1	154
				(70.4)	(23.8)	(3.8)	(1.3)	(0.5)	(0.1)	(0.1)	
Corwen (v+w)		70	7	28	20	8	6	0	1	0	13
				(44.5)	(31.7)	(12.7)	(9.5)		(1.6)		

(Percentage numbers of fish in each age group, excluding the 0+ age group, are shown in parenthesis).

in the population. The percentage representation of each age group shown in table 63 was therefore calculated with the 0+ group omitted. If these figures are taken as being representative of the survival rates of each successively older age group (Ricker, 1958), then it can be seen that survival rates are lowest at Bala and generally increase downstream, reaching a maximum at Corwen.

It is considered that the differences in survival rates may have resulted from differences in population densities (section 2B, ii and iii). It should be noted that survival was lowest in the Bala area where the largest numbers of grayling occurred, and where the effects of present regulation are likely to be most marked. The high proportion of young fish in the upper reaches is indicative of overcrowding. Table 63 also suggests that the greatest period of mortaility after the age of 1 year occurred between 2+ and 3+ years, coinciding with the onset of maturity.

The age and length composition of the River Dee grayling stocks can also be seen in figure 18 (chapter 5), and the sex ratios were given in chapter 9.

(ii) <u>Population densities</u>

(a) Methods.

Population estimates were made using the multiple census methods of Schnabel (1938, as modified by Chapman, 1952) and Schumacher & Eschmeyer (1943).

The Chapman modification of the Schnabel estimate is given by the equation :

$$\hat{N} = \frac{\Sigma(Ct\ Mt)}{(\Sigma Rt) + 1} \qquad (1)$$

where $\hat{N}$ = estimated population size
Ct = catch at time t
Mt = number of marked fish at large at time t
Rt = Recaptures of marked fish at time t.

Schumacher & Eschmeyer's formula for estimating population size is :

$$\frac{1}{\hat{N}} = \frac{\Sigma(Mt\ Rt)}{\Sigma(Ct Mt^2)} \qquad (2)$$

where $\hat{N}$, Mt, Ct and Rt are the same as in formula (1).

The formulae for estimating the variance of the Schnabel method are more appropriate to large samples and have not been calculated. The variance of the Schumacher estimate is given by the equation :

$$s^2 = \frac{\Sigma(Rt^2/\ ct) - (\Sigma RtMt^2)\ /\ \Sigma Ct\ Mt^2}{m - 1} \qquad (3)$$

where m is the number of samples included in the summations. Confidence limits are best computed for $^1/\hat{N}$ (Ricker, 1958). The standard error for $^1/\hat{N}$ is :

$$\frac{s}{\sqrt{Ct\ Mt^2}}$$

Confidence limits of 95% are obtained by multiplying by a t value for m-1 degrees of freedom. The limits of confidence for $\hat{N}$ are found by inverting those found for $^1/\hat{N}$.

The use of these and other methods has been well discussed by Ricker (1958), but some of the drawbacks of the methods relevant to this study should be mentioned. The methods of estimating population size used here require :

(1) that marked fish suffer the same natural mortality as unmarked fish;

(2) that marked and unmarked fish are equally as vulnerable to the sampling method being used;

(3) that the marked fish do not lose their mark;

(4) that marked fish become randomly mixed with unmarked fish;

(5) that all marks are recognised and reported on recovery;

(6) that there is only a negligible amount of recruitment to the catchable population during the period in which recoveries are being made.

It was shown in chapter 5 that tagging caused a significant decrease in the condition (K) of grayling, and it is possible that tagged fish may have suffered a higher mortality than unmarked ones, although no direct evidence of this was found. Higher mortality of tagged fish will produce overestimates.

Since most of the mark-recapture programmes included fish caught by angling, it is likely that the availability of tagged fish for recapture decreased as a result of the grayling becoming less catchable. Beukema (1970a, 1970b) demonstrated the ability of pike (Esox lucius L.) and carp (Cyprinus carpio L.) to learn to avoid baits on hooks, and this phenomenon may also occur amongst grayling.

Reference to the methods by which multiple recaptures were made suggested that this assumption was correct. Thus only one fish was recaptured more than once on maggots, 11 fish were recaptured once on maggots and subsequently by fly fishing, and 6 multiple recaptures occurred on fly alone.

Maggots are not a normal food of grayling in this part of the river and the greatest decrease in catchability would be expected with this bait. Flies (surface food), however, form a major part of the diet of grayling (chapter 7) and more multiple recaptures would be expected on artificial flies than on maggots. One particular grayling was caught on two successive days in the same pool on the same fly! The much higher proportion of multiple recaptures of grayling on two different types of bait suggests that some avoidance of artificial flies occurred as well as that of maggots. Beukema (1970a) found that pike learnt to avoid artificial spinning lures, but not live fish baits. Decreases in catchability reduce the number of marked fish available for recaptrue and, like mortality, result in population estimates that are too high.

In addition to the recaptures shown in figure 86, a total of 13 fish were caught which bore tag wound scars. It was therefore assumed that about 8.0% of tagged fish lost their tags. The highest rate of tag loss occurred in sites a and c and was associated with the seine netting operations which were carried out in those sites. Grayling caught by this method were sometimes found to have become entangled in the net meshes by the tags, and tags were ripped out of the fish as they struggled to free themselves. Nine of the recorded tag losses occurred in the above sites after the onset of netting procedures. Tag losses were even higher in Llyn Tegid (11%, see section 2C,ii) where all fish were caught by seine netting. Tag losses again result in overestimates of population size, as does the failure of anglers to report the removal of tagged fish (chapter 4).

No evidence was found to suggest that tagged fish did not become randomly mixed with untagged fish, or that they behaved differently to other fish apart from showing a decreasing catchability, as mentioned above.

Large scale recruitment of fish into the catchable population did occur during the study period, in the form of the 1969 year class and the increasing catchability of 1968 0+ grayling. It was decided to eliminate this source of error by excluding all such fish from the estimate computations. The estimates of population sizes given later thus refer only to fish older than 1 year of age.

Schnabel & Schumacher estimates also assume that no mortality or emigration occurs during the study period. These conditions were not satisfied in my tagging experiments which extended over long periods of time. The effect of mortality equally affecting marked and unmarked fish during the experimental period results in Schnabel type estimates being initially too low and finally too large (Ricker, 1958). This trend can be seen in a number of the estimates given in the following pages.

It was considered that, in the absence of some correction, the sources of error discussed above would result in population estimates that were too high, and probably meaningless. The main inaccuracy which occurred was in the overestimation of the number of marked fish at large (M) which were available for recapture. Stott (1967) reduced the value of M in his population estimates according to the observed extent of emigration. The emigration of tagged fish was only one of many factors which reduced the true value of M in my study, and it was decided that a more comprehensive correction was required.

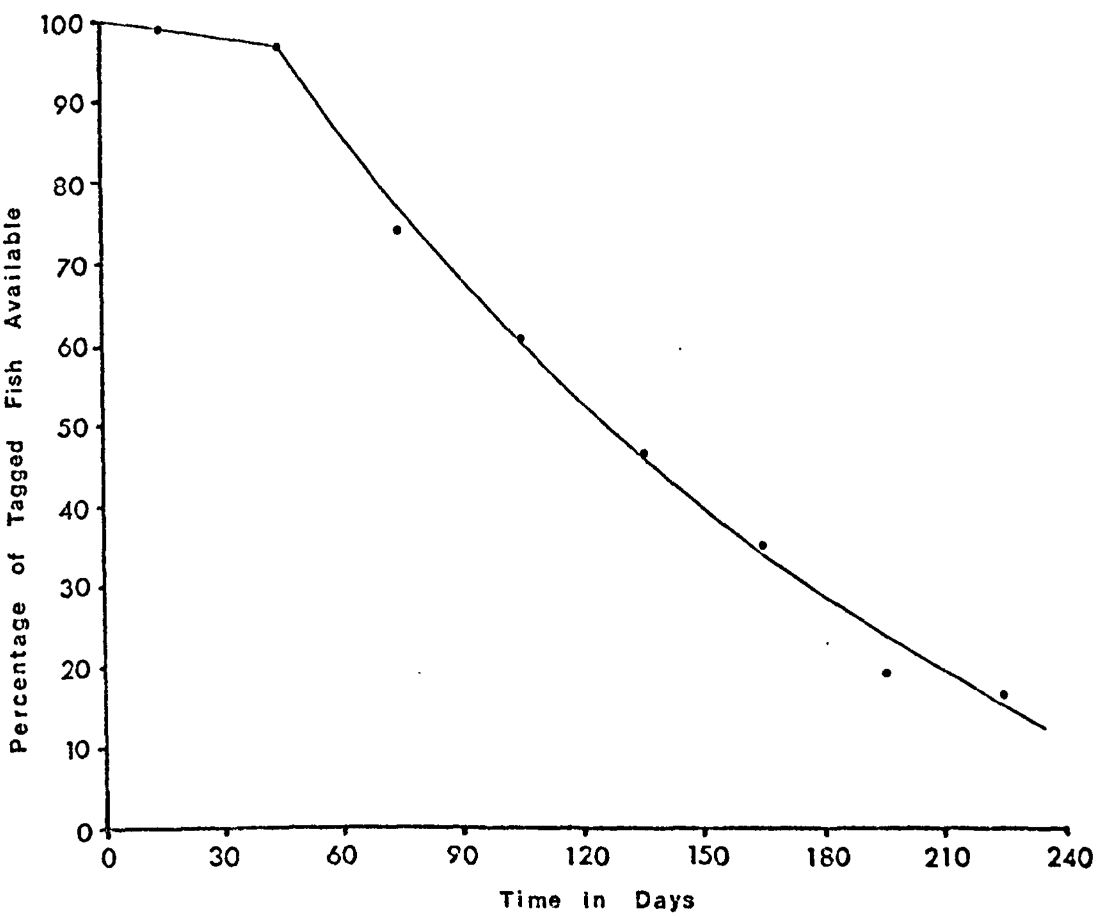
Theoretically the decreasing availability of tagged fish for recapture, from whatever cause, should be reflected in the decreasing proportion of such fish in successive catches. This assumption was tested by assessing the extent to which the proportion of recaptures (R) to catch (C) changed between 30 day intervals. Only "home" recaptures were used whilst assessing R/C, and data from all sites were combined by considering each release date as day 0. Since the numerical value of R/C depends on the number of marked fish at large (M) it was necessary to weight each proportion by a factor of $^1/_M$. This procedure may negatively bias the R/C value, because emigration reduced the value of M.

The mean values obtained for R/C decreased only slightly between the first and second 30 day periods, but fell sharply thereafter. The rate at which R/C declined during the first two periods was assumed to be constant and this rate extrapolated to day 0 gave a hypothetical value for R/C at day 0. This value was taken to represent a 100% availability of tagged fish for recapture on day 0, and the mean R/C values for each of the following 30 day periods were expressed as percentages with reference to this. The resulting "availability" curve is shown in figure 90. The results obtained indicate, for example, that less than 30% of the tagged fish released on day 0 were still available for recapture after 180 days.

The value of Mt in the Schnabel & Schumacher estimates was reduced with time (figure 90). Theoretically this correction should allow for differential mortality of tagged and untagged fish, decreases in catchability of tagged fish, tag losses, and, since only "home" recaptures were used in the calculations, the emigration of tagged fish. The correction is probably an over-simplification and the assumption of a small and constant rate of decline in R/C during the first two 30 day periods may be incorrect. Observations did indicate that the recapture rate remained high during this period and the error from this source was therefore unlikely to have been very great. Although the correction was based on a relatively small amount of data it was considered to show at least the general trend. The necessity for the correction, however, demonstrates the general unsuitability of such data for population estimates.

FIGURE 90

Changes in the Availability of Tagged Grayling in the River Dee



It is apparent from the above discussion that many of the problems encountered in the estimation of population sizes could be overcome if such estimates were made in a short period of not more than a few weeks.

(b) Results.

Most of the data available from tagging experiments were unsuitable for use in population estimates and attempts at such estimates were only made on data from sites a,c,h and m. Only "home" recaptures were used in the estimates.

Site a provided the best data for such estimates and the results obtained are shown in table 64. Schnabel & Schumacher estimates were both very similar, the latter being slightly larger. Confidence limits were initially high, but decreased with successive estimates. The best single estimate was considered to be that from the 13th August sample, for two mean reasons. Firstly, the sample was taken less than one month after the largest release of tagged fish in section a (on 20th July) and recaptures in the sample were high. Secondly the product CtMt was greater than 4N and the negative bias on the estimate was therefore less than 2% (Reiger & Robson, 1967). The value of CtMt also exceeded 4N on 20th July but confidence limits for this estimate were much wider than for the August 13th estimate.

Using the August 13th Schumacher estimate and referring to the area of site a given in table 14 (chapter 3), a density of 0.024 grayling/m^2 (95% confidence limits 0.021-0.028/m^2) was obtained. Using the proportions of age groups shown in table 63,

Table 64. Population estimates of grayling in the River Dee site a.

$\hat{N}_1$ = Schnabel (Chapman modification) estimate. $\hat{N}_2$ = Schumacher & Eschmeyer estimate.

Sampling date	Mt	Ct	Σ(CtMt)	(ΣRt)+1	$\hat{N}_1$	Σ(Mt Rt)	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% confidence limits	No. of fish removed
15 Oct.'69	0	7	0	0	-	0	0	-	-	0
27 Jan.'70	4.3	5	21.5	0	-	0	92.5	-	-	5
19 Mar.	2.8	4	32.7	0	-	0	123.7	-	-	0
2 Apr.	3.4	4	46.3	0	-	0	170.1	-	-	0
18 May	5.8	3	63.7	0	-	0	270.9	-	-	0
2 Jun.	7.7	4	94.5	2	47	7.7	508.1	66	32 - ∞	2
11 Jun.	7.1	5	130.0	5	26	29.0	760.1	26	14 - 303	0
8 Jul.	7.9	3	153.7	5	31	29.0	947.3	33	16 - ∞	1
13 Jul.	7.6	4	184.1	6	31	36.6	1178.3	32	18 - 175	0
20 Jul.	10.3	30	493.1	9	55	67.5	4361.5	65	51 - 833	0
13 Aug.	34.5	29	1493.6	23	65	550.5	38880.2	71	63 - 81	5
14 Sep.	36.1	6	1710.2	24	71	586.6	46699.4	80	61 - 115	4
16 Sep.	35.6	6	1923.8	25	77	622.2	54303.8	87	63 - 141	0
23 Sep.	34.1	6	2128.4	26	82	656.3	61280.6	93	63 - 180	0
7 Oct.	35.5	4	2270.4	26	87	691.8	66321.8	96	68 - 161	3

and the mean weights of these fish during August (figure 27, chapter 5), the estimated biomass of grayling older than 1 year of age in site a at this time was 2.586 g/m^2 (95% confidence limits 2.263 - 3.017 g/m^2).

The estimated density of grayling in site a, was less than that found by Solewski (1963) in the Rogoznik stream, and more than that found by MacKay (1970) in Scottish rivers. Approximately one third of the area of site a was very shallow, relatively static water on a bend of the river. Grayling did not generally occupy this region, but were concentrated in the remaining area of site a.

The results of both types of estimates show a general upward trend in successive samples. This may have resulted from the effects of mortality on such estimates (section 2B,iia), or from inaccurate assessment of the reducing availability of tagged fish (figure 90). It would be tempting to attribute the sudden increase in population size between early and late July to the influx of grayling from Llyn Tegid (section 1B,iii) but the accuracy of the results does not justify such a conclusion. Evidence from site h estimates, which were carried out before this time, and which showed no general upward trend, suggested, however, that this may have been the cause.

It was apparent from rod-catches that densities of grayling were often much higher at other sites than at site a. Grayling appeared to be particularly numerous at site c but the data from this site were unfortunately complicated as a result of the transfer experiments described earlier (section 1B,ii). "Home" recaptures were in themselves too limited for use with the estimate methods, but it was evident that much more data would be available if recaptures of fish "homing" from site b to site c could be included. From the results of the transfer experiments it was estimated that 68.4% of the displaced fish "homed" in this manner. It was therefore assumed that this proportion of displaced tagged fish was available for recapture at site c at any one time, subject to the same general decrease in availability as other fish (figure 90). It is thought that this figure was probably an overestimate, since some bias towards the capture of "homing" fish occurred as a result of intensive sampling in site c, and the population estimates for section c given in table 65 may be too high.

The confidence limits for site c estimates were much wider than for site a estimates, but the results do indicate that grayling were much more numerous at site c. Using the 13th August estimate to obtain a direct comparison with the site a results, shows that the density of grayling at site c was $0.143/m^2$ (95% confidence limits $0.087-0.499/m^2$), which was equivalent to a biomass of 15.421 g/m^2 (95% confidence limits 9.382-53.811 g/m^2). This estimate is probably too high, as a result of the overestimation of "homing" fish, but angling and netting catches did suggest that there were more grayling at site c than at site a.

Site c estimates also showed an increasing size in successive

Table 65. Population estimate of grayling in the River Dee site c.

Sampling date	Mt	Ct	Σ(CtMt)	(ΣRt) + 1	$\hat{N}_1$	Σ(MtRt)	$\Sigma(Ct\ Mt^2)$	$\hat{N}_2$	95% confidence limits	No. of fish removed
29 Aug.1969	0	-	0	0	-	0	0	-	-	0
11 Sep.	2.0	8	16.0	0	-	0	32.0	-	-	0
10 Nov.	8.3	2	32.6	0	-	0	169.8	-	-	2
27 Jan.1970	4.6	33	184.4	0	-	0	869.4	-	-	3
3 Mar.	23.2	37	1042.8	2	521	23.2	2078.3	90	-	11
19 Mar.	37.4	9	1379.4	4	345	98.0	33372.0	34.1	154 - ∞	0
2 Apr.	37.7	20	2133.4	5	427	135.7	61798.0	455	216 - ∞	0
7 Apr.	48.8	5	2377.4	7	340	233.3	73705.0	316	148 - ∞	0
5 May	45.7	3	2514.5	8	314	279.0	79970.5	287	144 - ∞	2
18 May	41.8	8	2843.9	9	317	320.8	93948.1	293	159 - ∞	4
2 Jun.	40.3	3	2969.8	9	330	320.8	98820.4	308	164 - 2500	3
8 Jun.	38.9	24	3903.4	11	355	398.6	135137.2	339	229 - 1833	0
23 Jun.	56.7	13	4640.5	12	387	455.3	176930.9	389	219 - 1754	1
7 Jul.	53.1	5	4906.0	12	409	455.3	191028.9	419	225 - 1563	0
13 Jul.	51.7	17	5784.9	12	482	455.3	236468.2	519	305 - 1724	14
13 Aug.	41.6	32	7116.1	14	508	538.5	291847.4	542	327 - 1563	1
14 Sep.	57.7	9	7635.4	14	545	538.5	321811.1	598	267 - 1695	9
16 Sep.	57.2	24	9003.2	15	600	595.7	400334.3	672	415 - 1754	1
23 Sep.	53.9	32	10733.0	17	631	703.5	493300.7	701	438 - 1736	0
7 Oct.	74.9	15	11856.5	19	624	853.3	577450.7	677	429 - 1639	5
5 Feb.1971	23.4	20	12324.5	21	587	900.1	588402.7	654	417 - 1515	0

samples, the largest increase again occurring during July. The last two estimates showed evidence of decreasing size in spite of the general upward trend, but whether this decrease represented a real decrease in the population, as a result, for instance, of grayling returning to Llyn Tegid, was unknown.

Data available for population estimates from sites h and m were even more limited, and only the final two estimates for each site are shown in Table 66. The confidence limits for both sets of estimates were wide, and the difference between Schnabel and Schumacher estimates for site m suggested that the figures were not very reliable. The density estimates at each site were, however, remarkably similar, and this was generally borne out by angling catches.

The estimated densities, using the final Schumacher estimates, were 0.057 grayling/m^2 at site h (95% limits 0.032-0.252/m^2) and 0.050 grayling/m^2 at site m (95% confidence limits 0.030 - 0.079/m^2). These densities represneted biomasses of 5.760 g/m^2 (95% confidence limits 3.233 - 25.467 g/m^2) at site h, and 7.764 g/m^2 (95% confidence limits 4.658 - 12.267 g/m^2) at site m. The higher biomass at site m resulted from the larger proportion of older fish at that site (see table 63). From observations made whilst sampling, it appeared that the densities of grayling at sites h and m were more typical of the upper Dee as a whole than were those of either site a or site c.

It is interesting to note that despite the very wide confidence

Table 66. Population estimates of grayling in the River Dee sites h and m.

Site	h		m	
Sample number	12	13	10	11
Date	1.6.70	9.7.70	21.9.70	14.10.70
Mt	35.4	31.4	33.9	35.2
Ct	11	5	39	10
Σ (CtMt)	3946.2	4103.2	2473.2	2825.2
$(\Sigma Rt) + 1$	10	11	9	11
$\hat{N}_1$	395	373	275	257
Σ(MtRt)	370.9	402.3	177.1	243.1
$\Sigma(CtMt^2)$	148914.2	153844.2	69996.3	80886.3
$\hat{N}_2$	401	382	395	333
95% C.L.	219-2381	213-1695	212-2860	197-521
No. of fish removed	2	1	28	10

$\hat{N}_1$ - Schnabel (Chapman modification) estimate

$\hat{N}_2$ - Schumacher & Eschmeyer estimate limits, the estimates of population size made at site h on previous occasions were all similar to those shown in table 66. Schumacher estimates for site h grayling were 432 (February 12th), 280 (March 2nd), 304 (March 3rd), 439 (March 16th), 374 (March 23rd), 363 (April 9th) and 403 (May 5th). These estimates showed no general upward trend and since they were made before the main influx of Llyn Tegid grayling, the summer rise in estimates for sites a and c may have represented actual increases in the population, in terms of Llyn Tegid immigrants, rather than merely sampling error.

A summary of the population densities and biomasses discussed in the previous pages is shown in table 67.

Table 67. Estimated population densities and biomasses of grayling in the River Dee.

site	Density (no/m^2)	95% C.L.	Biomass (g/m^2)	95% C.L.
a	0.024	0.021–0.028	2.586	2.263–3.017
c	0.143	0.087–0.499	15.421	9.382–53.811
h	0.057	0.032–0.252	5.760	3.233–25.467
m	0.050	0.030–0.079	7.764	4.658–12.267

(iii) The relative numbers of grayling, trout and juvenile salmon in the River Dee.

Attempts were made to assess the approximate densities of fish and the proportions of different species in the upper reaches of the River Dee (sites a and c) and at Corwen, by means of density indices (Gulland, 1955) based on seine net catches.

Netting was carried out in sites a and c by myself (see Chapter 4), and at Corwen on two occasions (September 1969, May 1971) by the Dee and Clwyd River Authority, using a net very similar to the one I used. Assuming that the netting efficiency was approximately the same in the two series of nettings, and that the fish caught were approximately representative of the actual proportions of the different species present, then considerable differences can be seen between the populations of fish at Corwen and at Bala. These differences are depicted in table 68.

Table 68. The species composition of catches of fish from different parts of the River Dee.

Site	No. of net hauls	No. of fish caught			Density index		
		salmon parr	trout	grayling	salmon parr	trout	grayling
Corwen	11	188	54	44	1709	491	400
Bala	8	9	50	165	113	625	2063

These results suggested that grayling were much less abundant at Corwen than at Bala, that trout were present in similar numbers at both sites, and that salmon parr were more numerous at Corwen than at Bala. It was considered that the density index obtained for salmon parr at Bala was too low, since these fish mostly occupied the shallow riffle areas which were not netted. The density indices obtained for trout and grayling at Bala were considered representative and indicated that grayling outnumbered trout by more than 3:1.

The habitat netted at Corwen consisted mostly of flats of more or less uniform depth, and the nettings at this site may have given a better representation of all three species. Salmon parr greatly outnumbered both trout and grayling at Corwen, and trout were equally as abundant as grayling. Some of the main spawning grounds of salmon are located on the flats at Corwen, and large numbers of salmon parr would therefore be expected in this area.

Whilst grayling densities may have always been much higher at Bala than at Corwen, evidence from anglers and River Authority reports (chapter 2) indicates that the numbers of fish have increased considerably throughout the area, and most especially in the upper reaches. Some increases in the numbers of grayling have been recorded in other British rivers in recent years (Hellawell, 1969a; Fisheries Liaison Group meeting, Birmingham, 1971), possibly as a result of natural cycles of abundance and scarcity. It is considered unlikely that such a natural cycle would have had so pronounced an effect on the numbers of fish and the size composition of the stocks, as has been recorded in the River Dee. It is thought much more likely that the stabilizing effects of regulation will have contributed to the observed increases.

Regulation is likely to have more effect on grayling than on trout and salmon, not only because of differences in breeding habits (chapter 9) but also because stabilization of river conditions favours those fish which prefer such habitats, rather than those which are characteristic of flashy mountain streams. From this point of view, regulation is likely to have an even more marked effect on coarse fish in the lower and middle reaches of the Dee.

C. The grayling population of Llyn Tegid

(1) Population structure.

The total catches of grayling in Llyn Tegid are given in table 69.

Table 69. Catches of grayling in Llyn Tegid, October 1968 to October 1970.

Site	Number of fish	Number of samples
A	40	15
B	149	13
C	94	9
D	122	15
E	53	16
F	167	15
G	78	9
H	183	22
I	0	0
J	138	10
Total	1014	124

The age composition of the catches is shown in table 70;

Table 70. Age composition of the Llyn Tegid grayling catches.

Age	0+	1+	2+	3+	4+	5+
No. of fish in each age group	155	570	219	55	14	1
Percentage of fish in each age group (excluding 0+ group)	-	66.3	25.5	6.4	1.6	0.1

The O+ group was represented to a greater extent in Llyn Tegid catches than in River Dee catches, forming 15.3% and 7.2% of the total catches respectively. This difference was chiefly accounted for by the capture of young fry in Llyn Tegid during July. This group of fish was caught less efficiently than older fish and has therefore been excluded from the percentage figures given in table 70, and also from the population estimates given in section 2C,ii. The age and length composition of the Llyn Tegid grayling stocks can also be seen in Figure 18 (chapter 5) and the sex ratios were given in chapter 9.

The age composition of grayling in Llyn Tegid was similar to that of grayling in the Llandrillo area of the River Dee and lower survival rates were indicated than those at Corwen. The percentage composition of the age groups in the catches of grayling made in Llyn Tegid by Jones (1953) was 1+ : 66.2%, 2+ : 18.9%, 3+ : 11.2%, 4+ : 3.0%, and 5+ : 0.7%. The main difference between the two groups of data being the higher survivals in older age groups during the 1950-53 period, which may be a reflection of the lower population densities at that time (see section 2C,iii).

(ii) <u>Present population densities of grayling in Llyn Tegid.</u>

Seasonal changes in the density of grayling in the Llyn Tegid shore zone were discussed in section 1C,iii and are shown in figure 89. In view of these changes it was decided that population estimates would best be carried out at the time when maximum numbers of fish were in the shore zone, i.e. during the winter months. Although large numbers of fish were also caught during May and early June (see table 23, chapter 5), it was considered that the many movements which occurred at that time (see section 1 C,ii) would unduly complicate attempts at estimating the numbers of fish present.

The loss of tagged fish by emigration was almost entirely eliminated by using data from those months in which few or no movements were recorded. Assuming seine netting to be a random sampling method for fish older than 1 year of age, then the catchability of grayling in Llyn Tegid, unlike that of grayling in the River Dee, should remain constant. This was reflected in the much higher rate of multiple recaptures in Llyn Tegid, 2 individual fish being recaptured on 5 separate occasions. In addition, all fish which had lost their tags were identifiable as "home" or "away" recaptures owing to additional marks placed on the fish in the manner described in chapter 4. These fish could therefore be included in the estimates, and increased the amount of data available. The number of tag losses recorded was 14, which amounted to 11.0% of the total recaptures.

Since the 0+ age group was not efficiently captured, and to rule out the possibility of error being introduced through recruitment to the catchable stock, all such fish were excluded from the estimate procedures. The population density estimates given in the following pages thus refer only to fish older than 1 year of age.

The estimates were made over relatively short periods of time, when the populations of grayling were more or less static. Because of this , and because of the elimination of many of the errors inherent in the River Dee data, it was considered unnecessary to apply any corrections to the material used in the estimates. It later appeared that a small correction should have been applied to the results for site H, where the rising population estimate may have reflected some movement out of the area by tagged fish towards the end of the study period. In addition, some differential mortality of marked and unmarked fish may have occurred, but no direct evidence of this was found.

Tagging data suitable for use in population estimates was obtained from site H between January 21st, 1969 and May 5th, 1969, from site D between November 19th, 1969 and February 16th, 1970, and from site F between December 15th, 1969 and January 12th, 1970. Schnabel (Chapman modification) estimates and Schumacher & Eschmeyer estimates were used on the data from sites H and D, and the results are shown in table 71. No fish were removed from the population during the study period.

Site H estimates rose slightly between April 24th and May 5th, probably as a result of the emigration of tagged fish. The proportion of recaptures of fish tagged on February 4th fell by 6.3% between the April and May samples. The first recorded movements of site H grayling occurred on June 3rd. The density of fish at site H was calculated from the April 24th Schumacher estimate, since this estimate was probably unaffected by emigration of tagged fish,

Table 71. Population estimates of grayling in Llyn Tegid.

Site	Sampling date	Mt	Ct	$\Sigma(CtMt)$	$(\Sigma Rt)+1$	$\hat{N}_1$	$\Sigma(MtRt)$	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% confidence limits
H	21st Jan.'69	-	1	-	-	-	-	-	-	-
	4th Feb.	1	24	24	0	-	0	24	-	-
	24th Apr.	25	22	550	10	55	225	13774	61	54 - 71
	5th May	33	10	880	14	63	357	24664	69	55 - 96
D	19th Nov.'69	0	7	0	0	-	0	0	-	-
	15th Dec.	7	8	56	2	28	7	392	56	-
	12th Jan.'70	14	19	322	8	40	91	4116	45	40 - 53
	16th Feb.	27	3	403	10	40	145	6303	43	39 - 49

$\hat{N}_1$ = Schnabel (Chapman modification) estimate. $\hat{N}_2$ = Schumacher & Eschmeyer estimate.

and because of the small confidence limits and high CtUt product at that time. The measured length of the shore line at site H which was sampled by seine netting was approximately 250 metres, indicating a density of 0.244 grayling/metre of shore line (95% confidence limits 0.216–0.284/metre), and a biomass of 4.731 g/metre (95% confidence limits 4.188–5.507).

The December 15th estimate for site D was considered unreliable since no confidence limits could be attached to it. The estimates on January 12th 1970 and February 16th 1970 were reliable, the confidence limits being small, and the values obtained being almost identical. No detectable change occurred in the R/C value in successive samples, and no movements of fish were recorded during the study period. The length of shoreline netted at site D was measured as approximately 120 metres, giving a population density on 16th February, from the Schumacher estimate, of 0.358 grayling/metre of shoreline (95% confidence limits 0.325–0.408 /metre), and a biomass of 7.853 g/metre (95% confidence limits 7.129–8.950 g/m). These values are somewhat higher than at site H, and may reflect a preference of grayling for sheltered habitats.

The population density of grayling at site F was estimated from the results of a single census. Grayling were tagged and released on December 15th 1969, and recaptures were made 28 days later on January 12th 1970. Since little or no emigration of tagged fish occurred at this time, and since the time between release and recapture was short, errors involving the numbers of marked fish at large were small. The estimate method used was the Bailey (1951) modification of the Peterson formula which is given by :

$$\hat{N} = \frac{M\,(C + 1)}{R + 1}$$

where $\hat{N}$ = estimated population size

M = number of marked fish at large

C = total catch

R = number of recaptures of marked fish.

This formula gives an almost unbiased estimate of N and its use was discussed by Ricker (1958). Approximate confidence limits were obtained from the charts of Clopper & Pearson (1934) using R as the entering variable in the manner described by Ricker (1958) and Cuinat (1970). The results obtained for site F are shown in table 72.

Table 72. Population estimate of grayling in Llyn Tegid at site F.

Census date	C + 1	M	R + 1	$\hat{N}$	95% C.L.
12.1.70	17	28	11	43	32–80

The measured length of shoreline netted at site F was 160 metres, giving a density of 0.269 grayling/metre of shoreline (95% confidence limits 0.200–0.500/metre) and a biomass of 4.988 g/metre (95% confidence limits 3.709–9.271 g/m). These results were very similar to those obtained at site H, and the general similarity of the results from all sites suggests that the estimates were fairly reliable. A summary of the results are shown in table 73.

Table 73. Estimated population densities and biomasses of grayling in Llyn Tegid.

Site	Density (no/m)	95% C.L.	Biomass (g/m)	95% C.L.
D	0.358	0.325-0.408	7.853	7.129-8.950
F	0.269	0.200-0.500	4.988	3.709-9.271
H	0.244	0.216-0.284	4.731	4.188-5.507

It is rather difficult to assess the total number of grayling in Llyn Tegid from these figures, but multiplying the mean number per metre from table 73 by the total length of the Llyn Tegid shore line (taken as 14,000 metres) gives a rough estimate of 4060. The distribution around the shoreline, however, is unlikely to be uniform, and the general lack of grayling in the shore zones of the central region has already been mentioned (section 1C,i). In addition, there are large areas of shallow water at each end of the lake which undoubtedly contain grayling, but which cannot be sampled by seine netting.

As an alternative the grayling caught at any one site could be assumed to occupy a certain area, in this case the littoral zone (0-3metres), and the approximate size of this area may be calculated. This procedure was most easily carried out at site H, where, with reference to figure 11 (chapter 3) the littoral zone extended a mean distance of 27 metres from the shore. The area occupied by the estimated site H population was therefore 6750 m^2, and from the total area of the littoral zone in the lake

(0.649 sq.Km, chapter 3) the estimated number of grayling in the lake was 5865.

The two estimates given for the total number of grayling in Llyn Tegid are only very approximate, but they may provide a useful value for comparison with future studies. Of the two estimates, that employing the total length of the Llyn Tegid shoreline is considered to be the easiest to duplicate. It should be remembered that the estimates of population size represent the maximum population, i.e. that present during the winter months, and during the summer the population size is very much reduced.

(iii) Changes in the numbers of grayling in Llyn Tegid since regulation.

Increasing catches of grayling per unit effort have been reported in Llyn Tegid by workers from the University of Liverpool during the last 10 years, and a comparison of net catches, expressed as density indices (Gulland, 1955), since 1950 are shown in table 74.

Table 74. Changes in the density of Llyn Tegid grayling since regulation.

Year	Density index
1950 - 51	83
1957 - 59	92
1968 - 70	296

The data for the 1950-51 period were provided by Dr. J.W. Jones, and the data for the 1957-59 period by Dr. J.C. Chubb. Only data from seine net captures between October and June were used to compile this table, so that comparisons between different years would be unaffected by summer emigrations.

The results obtained show that there has been a very large increase in the grayling population since 1959, and that very little change occurred between 1951 and 1959. It should be noted that the methods used by Dr. Jones and Dr. Chubb were almost identical to those I used as were the lake stations they sampled.

Svardson (1962, quoted in Jankovic, 1964) stated that whilst the numbers of trout may diminish in lakes which are converted to reservoirs, the abundance of char and grayling remains relatively unchanged or even increases. There appears to have been little or no increase in the grayling population in the first few years after Llyn Tegid was converted to a storage reservoir, possibly because of the large level fluctuations which occurred at that time (Hunt, 1970). In more recent years, however, the population has apparently trebled in size!

No indication of the number of grayling per haul was given by Siddiqui (1969), but his catch of 422 grayling from weekly seine net samples over a 13 month period was not very different from mine. He considered that his comparatively large catches of grayling may have been a result of the Bala regulation scheme, and gave four possible reasons for the apparent increase in the stocks. These were :

(1) The lowered lake level in the winter enabled netting of the previously unnettable sub-littoral zone to be carried out.

(2) Regradation of the River Dee may have made it easier for grayling to move into the lake.

(3) Grayling may swim upstream through the Bala sluices, but not downstream through the sluices, and are thus trapped in the lake.

(4) The Bala scheme may have increased the grayling territories in the lake.

The first of Siddiqui's (op.cit.) suggestions implies that grayling are normally residents of the sub-littoral zone, but this is not generally borne out by observations on the lake. His second and third suggestions do not fit in with the observed results of my tagging programmes, in which larger numbers of Llyn Tegid grayling were caught in the River Dee than vice versa. Only the last of his suggestions seems to show any correlation with the results I have obtained. It was suggested in chapter 9 that survival in the early stages of life might be enhanced by the summer lake level rise providing increased territories and food supply for the fry when they first enter the lake. The overall grayling territory however, will have been reduced as a result of the lowering of the mean lake level (see chapter 3, section C2b).

It is considered unlikely that the increase which has occurred in the numbers of Llyn Tegid grayling is merely the result of a natural population fluctuation because of the magnitude of the increase. The only major change which has affected the lake during the last 20 years has been regulation, and it seems reasonable to conclude that the increase in grayling stocks is a result of regulation. In the absence of any alternative theory which fits the data collected, it is suggested that the increase has been brought about by improved survival rates in the early stages of life.

3. Summary

(1) Approximately 85% of River Dee grayling were found to occupy restricted home areas, and 15% of the population moved, both upstream and downstream, mostly within 1Km. of the release point. Displaced fish showed a strong tendency to "home" and a high degree of territoriality was suggested.

(2) Movements of River Dee grayling increased slightly in the summer, possibly as a result of the influx of Llyn Tegid grayling. Some movement of fish into small tributary streams occurred during the winter. No long distance spawning migrations of River Dee grayling were recorded.

(3) Llyn Tegid grayling were mostly found in the littoral zone (0-3 metres) but a few were also caught in the sub-littoral region. The main concentrations of grayling occurred at each end of the lake where relatively large areas of shallow water were present.

(4) Llyn Tegid grayling moved very little during the winter

probably because of low activity at that time. Extensive movements of grayling occurred, in an apparently random manner, during spring and early summer. Displaced fish showed no tendency to "home", and it was suggested that grayling in lakes lose their aggressive territorial habits and adopt a more shoal-like behaviour pattern.

(5) Nearly all Llyn Tegid grayling disappeared from the shore zone during the summer, and the few remaining fish were located at river inlets. No grayling were caught in deep water at this time, but tagged lake fish were caught in the feeder streams and in the River Dee. It was therefore concluded that grayling left the lake during the summer. The Bala sluices and small weirs did not appear to hinder these migrations in any way.

(6) Possible reasons for the summer departure of grayling from Llyn Tegid may be high temperatures, low oxygen concentration and the influx of other species into the shore zone. Grayling returned to the lake from the feeder streams and the River Dee during the autumn, but the motivating force for this return was unknown.

(7) The 1+ age group of grayling dominated all catches, but the proportions of older age groups, and consequently survival rates, varied in different parts of the River Dee and between the River Dee and Llyn Tegid. Survival rates generally increased in a downstream direction in the River Dee, and the dominance of young fish in the upper reaches suggested overcrowding.

(8) Estimated densities of grayling in the upper Dee, using the methods of Schnabel and Schumacher & Eschmeyer, ranged from 0.024 to 0.143/m^2, which represented biomasses of 2.586 - 15.421 g/m^2. Most of the estimates were considered unreliable.

(9) Density indices (Gulland, 1955) suggested that grayling greatly outnumber trout in the upper reaches of the River Dee, but that trout and grayling were equally as abundant at Corwen. Salmon parr were very numerous at Corwen, where they outnumbered both trout and grayling.

(10) Estimated densities of grayling in Llyn Tegid, using the methods of Schnabel, Schumacher & Eschmeyer and Bailey, ranged from 0.244 to 0.358/metre of shoreline, representing biomasses of 4.731 - 7.853/m. The approximate number of grayling in Llyn Tegid was given as 4060 or 5865.

(11) The grayling population in Llyn Tegid was found to have greatly increased in size since the 1950-51 and 1957-59 periods, and it was considered that this increase resulted from regulation, possibly because of increased survival in the early stages of life.

CHAPTER XI

STUDIES ON THE POPULATIONS OF SALMON PARR AND TROUT IN THE LLYN TEGID FEEDER STREAMS

A. Introduction

Aspects of the population dynamics of brown trout and juvenile Atlantic salmon such as movements, population densities and production, have received much attention from fishery scientists, particularly in recent years (Schuck, 1943; Allen, 1951; Stefanich, 1952; Stuart, 1957; Kalleberg, 1958; Le Cren, 1958, 1969; Horton, 1961; Ball & Jones, 1962; Keenleyside & Yamamoto, 1962; Onodera, 1962; McFadden & Cooper, 1962; Mills, 1964, 1969; Saunders & Gee, 1964; Egglishaw, 1967, 1970; Horton et al., 1968; Shetter, 1968; Vickers, 1969; Jones, 1970).

Detailed studies on the populations of trout and juvenile salmon are being made in small streams in the Welsh Dee area by other workers from the University of Liverpool, as part of the Water Resources Board research programme, and investigations are also being carried out in the adjacent Gwynedd River Authority area for comparative purposes.

The data presented in this chapter are principally intended to give additional information on the general conditions in such streams, and to give some indication of the densities of fish present. Those aspects of population studies being dealt with in detail elsewhere, such as movements of fish, have only been considered in general terms.

Sampling in the Llyn Tegid feeder streams was carried out mainly in order to obtain some information on the age and growth of salmonids in the streams (see chapter 6), and many fish were removed for dietary studies and assessments of feeding relationships (M.A. Rahim). Some material was available for use in tagging programmes, and both trout and salmon were tagged in a number of the streams. The main tagging experiments were conducted in the Afon Glyn, where the largest numbers of fish were caught.

B. Population structures

Details of the catches of salmon parr and trout from the Llyn Tegid feeder streams are shown in tables 75 and 76, together with the numbers of fish tagged at each site and the numbers subsequently recaptured. The total numbers of fish shown in these tables are higher than those in tables 32 and 33 (chapter 6) because not all of the fish used in tagging experiments were used in the age studies. Not included in table 75 are the taggings of salmon smolts caught in the early months of the 1969 sampling period. These were as follows : Afon Llafar (site 2) 13; Afon Dyfrdwy (site 2) 3; Afon Lliw (sites 1-4) 19; Afon Glyn (site 1) 100. Some of these smolts were recaptured in Llyn Tegid after their descent from the feeder streams (see chapter 12).

Tables 75 and 76 also show the numbers and proportions of the different age groups in the samples from each river. The data on which these figures were based excluded that from samples affected by emigrations. The large spring emigrations of both

Table 75. Catch statistics for salmon parr in the Llyn Tegid feeder str[illegible]s.

River	Sampling site	Total catch	Number of samples	Number of fish tagged	Number of recaptures	Date	0+ – 1	1+ – 2	2+ – 3	3+ – 4
							(Number) of salmon caught and the percentage representation of each age group.			
A. Twrch	1	88	5	26	2					
	2	19	2	11	0		(27)	(221)	(40)	(2)
	3	43	5	16	1	May–March				
	4	44	4	22	1		–	84.0	15.2	0.8
	5	7	1	0	0					
	Total	201	17	75	4					
A. Llafar	1	94	8	0	0					
	2	20	3	0	0	May–March	(23)	(25)	(11)	–
	3	65	4	0	0					
	4	21	2	0	0		–	91.9	8.1	–
	Total	200	16	0	0					
A. Dyfrdwy (upper)	1	34	3	11	2	May–March	(38)	(134)	(18)	(1)
	2	61	7	25	8		–	87.6	11.7	0.7
	3 & 4	164	9	84	14					
	Total	259	19	120	24					
A. Dyfrdwy (lower)	5	49	4	0	0	May–October	(6)	(4[illegible])	–	–
	6	14	2	0	0		–	100.0	–	–
	Total	63	6	0	0					
A. Lliw	1	115	9	32	11		(40)	(173)	(28)	(1)
	2	26	3	5	0	July–March				
	3	125	6	48	13		–	85.6	13.9	0.5
	4	83	6	37	5					
	Total	349	24	121	29					
A. Glyn	1	376	13	157	51					
	2	179	9	86	71		(62)	(628)	(21)	(3)
	3	308	12	140	104	June–March				
	4	10	9	7	2		–	96.3	3.2	0.5
	5	53	10	31	4					
	Total	931	53	421	232					
Total for all rivers		2003	135	737	289	May – March	(196)	(1330)	(113)	(7)
							–	91.4	8.1	0.5

Table 76. Catch statistics for trout in the Llyn Tegid feeder streams.

River	Sampling site	Total catch	Number of samples	Number of fish tagged	Number of recaptures	Date	0+ – 1	1+ – 2	2+ – 3	3+ – 4	4+ – 5	5+ – 6
						(Number)of salmon caught and the percentage representation of each age group.						
A.Twrch	1 & 2	57	7	9	2	May–March	(7)	(25)	(34)	(8)	(1)	–
	3	28	5	0	0		–	36.8	50.0	11.8	1.4	–
	4	10	4	0	0							
	5	3	1	0	0							
	Total	98	17	9	2							
A.Llafar	1	37	7	0	0	May–March	(11)	(35)	(30)	(5)	–	–
	2	19	3	0	0		–	50.0	42.9	7.1	–	–
	3	45	4	10	1							
	4	20	2	0	0							
	Total	121	16	10	1							
A.Dyfrdwy (upper)	1 & 2	211	10	63	18	May–March	(78)	(90)	(32)	(21)	(2)	–
	3 & 4	178	9	25	7		–	62.0	22.1	14.5	1.4	–
	Total	389	19	88	25							
A.Dyfrdwy (lower)	5	22	4	0	0	May–October	–	(10)	(8)	(8)	(1)	–
	6	9	2	0	0		–	37.0	29.6	29.6	3.8	–
	Total	31	6	0	0							
A.Lliw	1	133	9	25	6	July–March	(14)	(69)	(46)	(5)	(3)	(1)
	2	30	3	0	0		–	55.6	37.1	4.1	2.4	0.8
	3	97	6	45	4							
	4	37	6	3	0							
	Total	297	24	73	10							
	1	153	13	29	9	June–March	(62)	(249)	(104)	(16)	(4)	–
	2	237	9	45	32		–	66.7	27.9	4.3	1.1	–
	3	141	12	53	52							
	4	166	9	40	23							
	5	216	10	54	34							
	Total	915	53	221	150							
Total for all rivers		1851	135	401	188	May–March	(172)	(472)	(254)	(63)	(1)	(1)
							–	59.2	31.5	7.9	1.4	0.1

trout (Ball & Jones, 1962) and salmon smolts obviously had a large effect on the age composition of the stocks at the time of migration, and only data obtained after the migration periods were considered representative of resident populations. The tables also indicate that the 0+ age group of both salmon and trout was less efficiently caught by electrofishing than were the older age groups. Catches of 0+ fish were therefore considered unrepresentative and were excluded from the age group percentage calculations shown in the tables.

The proportions of each age group shown in tables 75 and 76 reflect ages at emigration, rather than survival rates. The figures thus indicate that most salmon parr leave the streams as smolts at 2 years of age, and most trout descend to Llyn Tegid at 2 or 3 years of age. Ball & Jones (1962) estimated that 20% of the trout migrating to Llyn Tegid from the feeder streams were 1 year olds, 60% were 2 year olds and 20% were 3 year olds.

Variations in the proportions of the age groups in the Llyn Tegid feeder streams probably reflected differences in sampling site characteristics rather than in the populations of the streams. The younger fish, in both the trout and salmon parr populations, tended to inhabit shallow riffle areas, whereas older fish were more commonly found in pools, deeper riffles and in the vicinity of shelter such as boulders and tree roots. The latter types of habitat were particularly extensive in the Afon Twrch sampling sites, and the relatively high proportion of older fish in the Twrch samples may have resulted from this factor.

The age and length composition of the stocks are also shown in figure 45 (chapter 6) and sex ratios were given in chapter 9.

C. Movements of fish

1. General movements

The raw recapture data for salmon parr and trout in the Llyn Tegid feeder streams are shown in table 77. Those data were further analysed in those streams where density estimates were made (see section C2). Tagging experiments were carried out after the spring migration periods.

Table 77. Movements of tagged salmon parr and trout in the Llyn Tegid feeder streams.

Percentage and (number) of recaptures

Fish species	Distance moved downstream (m)			Home	Distance moved upstream (metres)					
	150-100	100-50	50-0	Section	0-50	50-100	100-150	150-200	200-250	250-300
Salmon parr	-	2.1 (6)	5.2 (15)	82.3 (238)	6.9 (20)	2.5 (7)	-	-	0.7 (2)	0.3 (1)
Trout	1.1 (2)	2.1 (4)	3.7 (7)	87.8 (165)	3.2 (6)	1.6 (3)	0.5 (1)	-	-	-

All trout were batch marked according to their site of origin, in the manner described in chapter 4 (section A2b). Salmon parr in the Afon Glyn sites 1 to 3 were also batch-marked by fin clipping, but at all other sites parr over 9cm. fork length were individually tagged. Trials with pan-jet innoculation techniques (Hart & Pitcher, 1969) using indian ink were carried out in conjunction with fin clipping methods. Marks were difficult to detect after 2 months in the summer rapid growth period, but lasted well during the winter period. The use of such techniques in long term experiments was considered unsatisfactory, and trials were discontinued.

Assuming marked fish behaved in the same manner as unmarked fish, then table 77 shows that the large majority of salmon parr and trout remained within the site in which they were caught and released. Some movements occurred both in upstream and downstream directions, and nearly all of these movements were within 150 metres of the release site.

The differences between the proportions of fish moving upstream and downstream, and between the proportions of salmon parr and trout remaining in the "home" site, were not significant (χ^2 test, $p > 0.05$).

Evidence of restricted movements amongst salmon and trout populations are numerous in the literature. Saunders & Gee (1964) recaptured most of the salmon parr they tagged in a 328 metre stretch of the Waweig River close to the sites at which they were released, and in addition they observed some "homing" of displaced fish from distances of up to 213 metres. Le Cren (1958) found that most trout remained in 30 metre sections in the small streams he studied. Schuck (1945) recaptured 42 of the 46 trout he tagged in Crystal Creek in their original sections, which were 214 ft (65 metres) long. Shetter (1968) working on brown trout over 7 inches long in the Au Sable River system, found that 56-85% remained within 1 mile of the release point, although some of the larger fish moved many miles. Stefanich (1952) recorded little movement of trout in 300 feet (91 metre) or 600 feet (183 metre) sections of Prickly

Pear Creek, but those that did move generally did so in a downstream direction.

Many other examples exist in the literature, but the apparent lack of published work on short distance movements has led to the detailed studies being made by other workers from the University of Liverpool (see section A). Furniss (pers. comm.), for example, finds that most of the recorded movements of trout and salmon parr in a small tributary of the River Dovey, occur within a range of 10 metres or less of the release site. Such short distance movements may be more indicative of the general behavioural relationships of salmonids than the long distance movements previously studied. Many of these short distance movements will not have been recorded in studies where relatively long river sections were used.

Although the demonstration of restricted home areas does not in itself mean that territoriality occurs (Gerking, 1953), this phenomenon has been observed amongst trout and young salmon both in the field (Keenleyside & Yamamoto, 1962) and in the aquarium (Kalleberg, 1958). These authors considered the territories of salmonids to be primarily feeding territories, and stressed the importance of territoriality to optimum growth and survival, and to the efficient utilization of the food supply. Kalleberg (1958) found that the size of the territory depended on both the size of the fish and the topography of the river bed. Territories were most abundant where a high degree of visual isolation occurred. Some evidence of high population densities of trout and salmon in river sections containing an abundance of boulders, rocks and other shelter is given in section D.

2. Movements of fish in specific streams

(a) Introduction

In order to make use of the tagging data for estimating population densities it was necessary to apply corrections to the value given for the number of marked fish at large (Mt) in relation to the observed movements of fish (see section D). It was therefore considered desirable to analyse the raw recapture data shown in table 77 in more detail for those rivers where estimates were made.

Williams (1965) and Stott (1967) pointed out that raw recapture data may not reflect the true tendency of marked fish to migrate. The number of "home" and "stray" recaptures depend on the number of fish marked in a particular section, the number of times the section is sampled and the degree of intensity of sampling in the section. The first factor can be partly allowed for by dividing the recaptures by the number of marked fish released previously (M), but this will cause some bias against fish being recaptured in their home section as a result of emigration reducing the true value of M. Some allowance can be made for the number of samples taken by further dividing the recaptures by the number of times the section, in which the recapture was made, was sampled (S) up to and including the one in which the recapture was made (Stott, op.cit.).

The recapture data for trout and salmon parr in the Afon Glyn, trout in the Afon Dyfrdwy and salmon parr in the Afon Lliw, were weighted by a factor of $^1/MS$ in the manner proposed by Stott (1967). Each section was, as far as possible, fished to an equal intensity and fishing efficiency was considered to be approximately the same at all sites, except at sites 1 and 3 in the Afon Glyn. At these sites stunned fish were often trapped in the cracks between the gabion blocks and could not be extracted. In addition, site 1 was difficult to sample during low summer flows (see chapter 4, section A1a).

(b) Afon Glyn

The percentage recapture figures, weighted by a factor of $^1/MS$, for salmon parr and trout in each section of the Afon Glyn are shown in table 78. The combined results for all sites are given in table 79. From this material it was apparent that some migration of fish out of the study area could have occurred, thereby giving some negative bias in the data towards zero movement. Permission for sampling the area of river above my sampling sections could not be obtained, and the loss of fish upstream out of the study area could not be directly assessed. An approximate figure for such movements was estimated, however, from the material shown in table 79.

Very few salmon parr were caught and tagged in sections 4 and 5 (see table 75) and movements of fish out of these areas did not affect density estimates which were only made for salmon parr in sections 1-3. It was considered, from the available data, that no loss of salmon parr from sites 1-3 occurred in an upstream direction out of the study area. The loss of fish in a downstream direction

Table 78. Movements of tagged fish in the Afon Glyn, sites 1 to 5.

Site	Fish species	Percentage of recaptures in each site 1	2	3	4	5
1	Trout	79.3	8.9	8.9	-	2.8
	Salmon	70.6	17.6	11.8	-	-
2	Trout	-	91.2	4.4	4.4	-
	Salmon	4.2	81.9	13.9	-	-
3	Trout	6.3	7.9	82.9	0.7	1.4
	Salmon	2.8	12.2	84.0	-	1.0
4	Trout	1.5	-	6.3	87.7	4.5
	Salmon	-	-	-	100.0	-
5	Trout	-	-	-	5.5	94.5
	Salmon	-	-	-	-	100.0

Table 79. Combined movements of tagged fish in the Afon Glyn.

Percentage of recaptures in each site

Fish species	Downstream sites 4	3	2	1	Home site	Upstream sites 1	2	3	4
Trout	-	0.2	1.8	4.4	87.5	3.1	2.6	-	0.4
totals		6.4			87.5		6.1		
Salmon	-	-	2.6	6.0	81.0	7.2	3.2	-	-
totals		8.6			81.0		10.4		

into Llyn Tegid was considered negligible since only 1 tagged salmon parr from the Afon Glyn was caught in the lake at the river inlet, and very few salmon parr were ever recorded in the lake (see chapter 3).

Some movement of trout upstream out of the study area from sites 4 and 5 could be expected from the results shown in table 79, but such losses from sites 1-3 were considered negligible. Some loss of tagged trout may have occurred downstream into Llyn Tegid but no such fish were caught in the lake outside of the spring migration period. Ball & Jones (1962) found that 18% of the feeder stream migrants descended into Llyn Tegid between September and March, and 82% between April and May. The latter group of fish did not affect my results because the experiments were carried out after May, but autumn and winter migrations may have reduced the number of tagged trout available in the Afon Glyn. Such losses could not be assessed from the data collected, and the density estimates given in section D may therefore be slightly too high. The amended values for the percentage movements of trout tagged at sites 4 and 5, in accordance with estimated upstream losses (from table 79) are shown in table 80.

Table 80. Amended values for the movements of trout tagged in the Afon Glyn sites 4 and 5.

	Percentage of recaptures in each site					Estimated percentage lost
Site	1	2	3	4	5	upstream
4	1.5	-	6.1	85.2	4.4	2.8
5	-	-	-	5.3	89.8	4.9

Table 78 suggests that some differences occurred in the movements of fish from different sites. The greatest degree of movement apparently occurred amongst fish from site 1. The difference between the movement of trout from site 1 and the movement of trout from other sites was not significant, however ($\chi^2 = 5.65$ with 4 d.f. $p > 0.05$). The movement of site 1 salmon was significantly different from that of other salmon parr at the 5% level ($\chi^2 = 9.01$, with 2 d.f. $p < 0.05$). No significant difference existed between the movements of trout from any of the Afon Glyn sites, and no difference existed between site 2 and site 3 salmon parr. The numbers of salmon parr recaptured in sites 4 and 5 were too few on which to base any assumptions.

There was no significant difference between upstream and downstream movements, nor between the movements of salmon parr and trout (table 79). The actual numbers and distributions of recaptures were not very different from the weighted results shown in table 79, and this reflected the relatively even application of fishing effort throughout the sampling area. The raw recapture data for trout in the Afon Glyn was 132 (88.0%) home, 10 (6.7%) downstream and 8 (5.3%) upstream recaptures, and for salmon parr, 191 (82.3%) home, 18 (7.8%) downstream and 23 (9.9%) upstream recaptures. A greater degree of movement might be expected for salmon parr than for trout, as a result of the trout's superiority with regard to aggressive territoriality (Kalleberg, 1958), but the differences in movements found in the Afon Glyn study were not significant (χ^2 test, p>0.05).

The relatively high degree of movement of salmon parr from site 1 needs further comment. During low summer flows the area of site 1 was very much diminished, the river becoming reduced to trickles between the gabion blocks (see chapter 4, section A1a). Such a reduction in space may have led to increased competition amongst the fish and a greater degree of movement than usual. In addition the summer level of Llyn Tegid was sometimes raised so high that much of site 1 became "flooded" by the lake water, and flows decreased accordingly. Salmon parr may have migrated upstream out of these slack-water conditions. Some evidence for such movements was obtained from the seasonal trends that were apparent amongst "home" and "away" recatpures. Thus, between July and September, 14 site 1 salmon parr were recaptured in site 1, and 13 were recaptured elsewhere. These 13 salmon parr accounted for 31.7% of the total movements recorded for all sites combined. Some evidence was found of a return to site 1 in the autumn and winter by fish which had gone upstream during the summer. Thus 3 of the 13 site 1 salmon parr caught elsewhere in the summer were recaptured back at site 1 between October and March.

The combined data on those salmon parr which moved showed that of 13 subsequent recaptures, 8 were in the sites to which they had first moved, 4 had returned to their site of origin, and 1 went elsewhere. Three of those salmon parr which returned to their site of origin were the site 1 fish discussed above, and the results obtained suggest that some salmon parr may temporarily adopt a secondary home area when conditions become unfavourable in the first. No evidence for the existence of a small continuously mobile portion of the population (Stott, 1967) was found.

Some migrationsof salmon parr associated with spawning activities (Jones & King, 1949) were recorded. Salmon spawning appeared to have taken place in the Afon Glyn in early December (see chapter 9) and redds were first seen on December 12th at site 5. The December sample of salmon parr included 5 fish which had moved up from site 2 to site 3, and 1 which had moved up from site 3 to site 5. These parr were all running-ripe males. In addition a large influx of untagged salmon parr occurred into site 5 during December, mostly comprising ripe males. Catches during other months never exceeded 5 salmon parr in site 5, but 24 were caught there on December 12th in the vicinity of the spawning gravels. Fifteen of these fish were tagged but none were subsequently recaptured. It appeared that they had moved out of site 5 after December, but where they went to was unknown. They were not recaptured in any of the lower sections and it seems possible that they moved upstream out of the sampling area.

No seasonal trends were found in the movements of trout and no spawning migrations of river fish were recorded. Two spent lake trout (as identified from their scale structures; Ball & Jones, 1960) were caught in site 5 on December 12th, and one was caught at site 1 on January 20th.

It should be noted that assessments of fish movements are affected by the arbitrary allocation of site boundaries which probably have little correlation with the actual territories of the fish (Gerking, 1953), and the Glyn results are no exception to this limitation. The small scale experiments being carried out elsewhere in the area may partly overcome this problem. In addition the Glyn results may be affected by the artificial restrictions to movements imposed by the gabion weirs, and the extent of this restriction is unknown.

(c) Afon Dyfrdwy and Afon Lliw

Estimates of the movements of tagged fish were also made for Afon Dyfrdwy trout and Afon Lliw salmon parr, for use as correction factors in density estimates (section D). Using Stott's (1967) weightings and allowing for possible emigration out of the study area, the percentage of fish remaining at each site was estimated at 80.9% for trout in the Afon Dyfrdwy, and 86.2% for salmon parr in the Afon Lliw.

The higher percentage of "home" recaptures in the Afon Lliw may have been a result of the long distances between the sampling sites (see figure 9, chapter 3). The Afon Dyfrwdy sites, like those in the Afon Glyn, were contiguous. The areas between the sampling sites in the Afon Lliw comprised relatively deep, slow flowing water which salmon parr did not generally inhabit. The errors introduced into the movement assessments by not sampling these areas were therefore likely to have been small.

No significant difference (χ^2 test, $p > 0.05$) was found between the proportions of trout moving upstream and downstream in the Afon Dyfrdwy (10.0% and 9.1%) respectively, but only upstream movements were recorded for salmon parr in the Afon Lliw. The latter movements occurred during the winter months and may have been associated with spawning activities.

D. Population densities

1. Methods

The data obtained from tagging experiments on salmon parr and trout provided an opportunity for estimating the density of these fish in some of the Llyn Tegid feeder streams. The material most suitable for such estimates was that from the Afon Glyn, but some estimates were also made for trout in the Afon Dyfrdwy and salmon parr in the Afon Lliw for comparative purposes.

Since the fish in the Afon Glyn were nearly all batch marked according to their site of origin, and not individually tagged, population estimate methods requiring information on individual fish, or on batches of fish from one marking session (e.g. Fisher & Ford, 1947; Jolly, 1965), were not suitable. The same methods were therefore used as for grayling, that is the Schnabel (Chapman modification) estimate and the Schumacher & Eschmeyer estimate (see chapter 10, section 2B,ii).

The main errors which occurred resulted from mortalities during the study period, and the emigration of tagged fish from their "home" sites. The first factor results in Schnabel-type estimates which are initially too low and finally too high (Ricker, 1958; see chapter 10, section 23,ii). To reduce such errors the mean values for those estimates made during the study period, to which confidence limits could be attached, were used for density calculations.

The errors caused by the emigration of tagged fish were allowed for by reducing the value of the marked fish at liberty (Mt) according to the observed movements described in section C2. Stott (1967) used this correction on his data for River Mole fish, and pointed out that such corrections were only satisfactory where no immigration of marked fish occurred. This objection was overcome in my studies, where immigration did occur, by excluding the recapture of such fish from estimate calculations, only "home" recaptures being used for this purpose.

Large errors could have arisen in the estimates from the recruitment of young fish into the catchable population. The 0+ age group of fish was less efficiently caught by electrofishing than were the older age groups (see section B), and errors resulting from recruitment were eliminated by excluding all 0+ fish from the estimate procedures.

Some errors may have been introduced into individual estimates as a result of assuming a constant emigration rate when correcting Mt values, but such errors were probably reduced when using the mean value of the population size estimates for density calculations. Errors in the value of Mt may also have arisen from possible migrations of tagged trout into Llyn Tegid (see section C2b).

Assuming electrofishing to be a random sampling method for all fish over 1 year of age in these streams, then no further serious errors should have occurred. Little or no angling is carried out on the sections of the rivers studied, and nearly all of the trout present are below the angler's takeable size limit of 8 inches.

In addition to the Schnabel and Schumacher estimates, one DeLury estimate was carried out in section 1 of t.e Afon Glyn for comparative purposes. This method has been described by DeLury (1947), Seber & Le Cren (1967), Cuinat (1970) and many others. In the DeLury estimate a series of sampling runs are made at one particular site and the fish caught on each run are removed and counted. Each sampling run is considered as a unit of effort, and catch per unit effort is plotted on the y-axis against cumulative catch on the x-axis. The regression line formed by the decreasing catch per unit effort as the population becomes reduced in successive samples, is extrapolated to the x-axis and the intercept gives an estimate of the original population size. When two sampling runs only are carried out (which is permissible when catches are large with respect to the population), the most probable population can be estimated by the formula

$$p = \frac{m^2}{m - n} \quad \text{(Cuinat, 1970)}$$

where m and n are the numbers of fish caught during the first and second sampling runs. The main drawback of the method is that it assumes constant sampling efficiency, which is often not so.

2. Results

(a) Afon Glyn

The results of the Schnabel and Schumacher estimates, and relevant details used in the calculations, are shown in tables 81 to 85. No estimates were obtained for salmon parr in sites 4 and 5, or for trout in site 1, because of the small numbers of fish caught and tagged in those sites.

Differences in the monthly estimates may partly reflect seasonal changes in movements, which were assumed to be constant for purposes of computation. It was noted in section C2b that some seasonal changes in movements did occur amongst the salmon parr population, but not apparently amongst the trout. The larger fluctuations in the salmon parr estimates than in the trout estimates may result from these changes.

The general upward trend in the estimates in successive samples towards the end of the study period, is contrary to what one would expect. The numbers of fish shouldhave been reducing as a result of natural mortalities. Such discrepancies are inherent in Schnabel-type estimates (Ricker, 1958) and were discussed in section D1.

The DeLury estimate carried out at site 1 on 12th April 1969 gave values of m = 38 and n = 17 for salmon parr, with the most

Table 81. Population estimates of salmon parr in the Afon Glyn site 1.

Sampling date	Mt	Ct	$\sum(MtCt)$	$(\Sigma Rt) + 1$	$\hat{N}_1$	$\sum(RtMt)$	$\sum(CtMt^2)$	$\hat{N}_2$	95% C.L.	No. of fish removed
8.3.69	0	27	-	-	-	-	-	-	-	8
12.4.69	13.4	21	281.4	5	56	53.6	3771.6	70	58 - 88	2
12.5.69	18.8	16	582.2	8	63	110.0	9426.0	86	56 - 189	3
12.6.69	13.4	31	997.6	11	91	150.2	14993.6	100	67 - 200	12
7.7.69	20.7	16	1328.8	16	83	253.7	21849.6	86	62 - 141	2
11.8.69	18.1	8	1473.6	22	67	362.3	24470.4	68	38 - 345	0
10.9.69	12.7	6	1549.8	25	62	400.4	25438.2	64	28 - 200	2
8.10.69	10.4	14	1695.4	28	61	431.6	26953.0	62	39 - 147	0
18.11.69	15.2	3	1741.0	28	62	431.6	27646.0	64	41 - 143	0
9.12.69	13.3	0	1741.0	28	62	431.6	27646.0	64	42 - 132	0
20.1.70	9.4	37	2088.8	30	70	450.4	30916.8	69	46 - 139	0
24.2.70	42.5	6	2343.8	32	73	535.4	41754.6	78	51 - 169	0
10.3.70	29.9	37	3450.1	38	91	714.8	74332.6	105	67 - 244	0

$\hat{N}_1$ = Schnabel (Chapman modification) estimates. $\hat{N}_2$ = Schumacher & Eschmeyer estimates.

Table 82. Population estimates of salmon parr in the Afon Glyn site 2.

Sampling date	Mt	Ct	Σ(MtCt)	Σ(Rt) +1	$\hat{N}_1$	Σ(RtMt)	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% C.L.	No. of fish removed
7.7.69	0	44	-	-	-	-	-	-	-	7
11.8.69	30.3	33	999.9	14	71	393.9	30297.3	77	-	0
10.9.69	36.3	37	2343.0	33	71	1083.6	79052.2	73	65 - 83	3
8.10.69	37.0	15	2898.0	45	64	1527.6	99587.2	65	47 - 107	0
18.11.69	31.1	1	2929.1	46	64	1558.7	100554.4	65	49 - 95	0
9.12.69	24.8	18	3375.5	50	67	1657.9	111624.4	67	51 - 97	0
20.1.70	30.1	13	3766.8	54	70	1778.3	123402.4	69	55 - 95	0
24.2.70	32.0	4	3894.8	55	71	1810.3	127498.4	70	60 - 85	0
10.3.70	27.1	13	4247.1	60	71	1945.8	137045.6	70	57 - 91	0

$\hat{N}_1$ = Schnabel (Chapman modification) estimate. $\hat{N}_2$ = Schumacher & Eschmeyer estimate.

Table 83. Population estimates of salmon parr in the Afon Glyn site 3.

Sampling date	Mt	Ct	$\Sigma(MtCt)$	$(\Sigma Rt) + 1$	$\hat{N}_1$	$\Sigma(RtMt)$	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% C.L.	No. of fish removed
12.5.69	0	8	-	-	-	-	-	-	-	0
12.6.69	6.7	15	100.5	2	50	6.7	673.5	101	-	0
7.7.69	5.6	42	335.7	3	112	12.3	1992.3	162	69 - ∞	0
11.8.69	39.1	41	1938.8	20	97	677.0	64673.1	95	82 - 114	7
10.9.69	47.2	39	3779.6	46	82	1904.2	151557.3	79	65 - 99	3
8.10.69	45.5	16	4507.6	57	79	2404.7	184682.1	77	65 - 93	0
18.11.69	39.9	11	4946.5	60	82	2524.4	202194.1	80	66 - 101	0
9.12.69	35.2	46	6565.7	70	94	2876.4	259188.1	90	74 - 125	0
20.1.70	54.8	23	7826.1	80	98	3424.4	328257.1	96	76 - 130	5
24.2.70	46.1	9	8241.0	83	99	3562.7	347383.9	97	78 - 128	0
10.3.70	41.0	18	8979.0	90	100	3849.7	377641.9	98	80 - 127	0

$\hat{N}_1$ = Schnabel (Chapman modification) estimate. $\hat{N}_2$ = Schumacher & Eschmeyer estimate.

Table 84. Population estimates of trout in the Afon Glyn.

Site	Sampling date	Mt	Ct	Σ(MtCt)	(ΣRt) + 1	$\hat{N}_1$	Σ(RtMt)	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% C.L.	No. of fish removed
	10.9.69	0	49	-	-	-	-	-	-	-	6
	8.10.69	37.4	31	1159.4	17	68	598.4	43362.8	72	68 - 76	0
	18.11.69	34.1	1	1193.5	18	66	632.5	44525.6	70	46 - 147	0
2	9.12.69	31.1	23	1908.8	29	66	974.6	66771.2	69	54 - 94	0
	20.1.70	28.4	5	2050.8	30	68	1003.0	70804.2	71	56 - 96	0
	10.3.70	26.1	4	2155.2	31	69	1029.1	73529.0	71	59 - 92	0
	7.7.69	0	29	-	-	-	-	-	-	-	2
	11.8.69	24.1	21	506.1	10	51	216.9	12196.8	56	-	1
	10.9.69	29.1	17	100.8	26	39	682.5	26592.4	39	21 - 278	0
3	8.10.69	25.2	20	1504.8	33	46	858.9	39292.4	46	27 - 149	0
	18.11.69	31.8	2	1568.4	34	46	890.7	41314.8	46	31 - 93	0
	9.12.69	27.5	14	1953.4	39	50	1028.2	51903.0	50	35 - 91	0
	20.1.70	23.8	4	2048.6	40	51	1052.0	54168.6	51	35 - 86	0
	10.3.70	19.2	11	2259.8	46	49	1167.2	58223.2	50	37 - 77	0

$\hat{N}_1$ - Schnabel (Chapman modification) estimate. $\hat{N}_2$ - Schumacher & Eschmeyer estimate.

Table 85. Population estimates of trout in the Afon Glyn.

Site	Sampling date	Mt	Ct	$\Sigma(MtCt)$	$(\Sigma Rt) + 1$	$\hat{N}_1$	$\Sigma(RtMt)$	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% C.L.	No. of fish removed
	10.9.69	0	28	-	-	-	-	-	-	-	0
	8.10.69	23.8	16	380.8	7	54	142.8	9062.4	63	-	0
	18.11.69	21.2	9	571.6	10	57	206.4	13107.0	63	-	0
4	9.12.69	23.2	19	1012.4	16	63	345.6	23332.8	67	60 - 76	0
	20.1.70	20.6	10	1218.4	19	64	407.4	27576.8	68	63 - 74	0
	10.3.70	21.7	7	1370.3	21	65	450.8	30873.1	68	63 - 73	0
	11.8.69	0	32	-	-	-	-	-	-	-	2
	10.9.69	26.9	29	780.1	11	71	269.0	20984.4	78	-	0
	8.10.69	24.0	32	1548.1	20	77	485.0	39416.4	81	79 - 83	1
5	18.11.69	35.8	8	1834.5	22	83	556.6	49669.2	89	80 - 101	0
	9.12.69	36.6	9	2163.9	26	83	703.0	61725.6	88	81 - 96	1
	20.1.70	35.4	12	2588.7	31	83	880.0	76764.[illegible]	87	81 - 93	0
	10.3.70	28.3	12	2928.3	36	81	964.9	86374.8	89	83.- 96	0

$\hat{N}_1$ = Schnabel (Chapman modification) estimate. $\hat{N}_2$ = Schumacher & Eschmeyer estimate probable number of fish present, p = 69. This estimate compares favourably with the Schnabel and Schumacher estimates for salmon parr shown in table 81.

No Schnabel or Schumacher estimates were obtained for salmon parr at sites 4 and 5, or for trout at site 1. During the DeLury estimate at site 1, 13 trout were caught on the first sampling run, and 4 on the second run, giving a probable population, p = 19 . This figure represents a density of about 0.1 trout/metre^2. The numbers of salmon parr were very low in sites 4 and 5, particularly in site 4 (see table 75), and the densities of salmon parr were probably about 0.05/m^2, and certainly less than 0.1/m^2.

The mean values for the estimates shown in tables 81 to 85 were calculated as described in section D1, and the density of fish at each site was estimated with reference to the site areas given in table 5 (chapter 3). The mid-year biomasses represented by these densities of fish were calculated from the mean mid-year weights for each age group (see chapter 6). The proportions of each age group were given in tables 75 and 76. The results obtained are shown in table 86.

Table 86. Density and biomass of salmonid fishes over 1 year of age in the Afon Glyn.

Fish species	Site	mean no. of fish present	mean density no/m^2	95% C.L.	mean biomass g/m^2	95% C.L.
Salmon	1	76	0.386	0.249–0.883	4.964	3.202–11.355
	2	68	0.412	0.327–0.564	5.302	4.208–7.259
	3	89	0.382	0.313–0.493	4.915	4.028–6.345
Trout	2	71	0.430	0.345–0.612	9.879	7.925–14.064
	3	47	0.202	0.133–0.554	4.641	3.056–12.731
	4	68	0.329	0.300–0.362	7.560	6.894–8.319
	5	87	0.259	0.241–0.230	5.933	5.538–6.434

(b) Afon Dyfrdwy and Afon Lliw

The population size estimates for Afon Dyfrdwy trout and Afon Lliw trout, calculated in the same way as for Afon Glyn fish, are shown in table 87.

Table 87. Estimated numbers of salmonids in the A. Dyfrdwy and A. Lliw.

Fish species	Trout	Salmon	Salmon
River	Dyfrdwy	Lliw	Lliw
Site	3 + 4	3	4
Mt	33.4	38.4	22.0
Σ(MtCt)	2129.6	1941.4	693.5
Σ(Rt) + 1	20	12	8
$\hat{N}_1$	113	162	87
Σ(RtMt)	546.3	368.6	156.5
Σ (CtMt^2)	60038.2	65105.4	15199.7
$\hat{N}_2$	110	167	97
95% confidence limits	94–132	120–380	70–156

$\hat{N}_1$ = Schnabel (Chapman modification) estimate

$\hat{N}_2$ = Schumacher & Eschmeyer estimate

Only the final estimates are shown in table 87, confidence limits on earlier estimates being unacceptable. The final estimates are for fish present in March 1970 after 4 sampling sessions at each site. No fish older than 1+ were killed during the census period, and younger fish were excluded from the estimates. Emigration rates were assumed to be constant, as with the Glyn estimates, and the possibility of pre-spring movements of trout to Llyn Tegid was neglected. Tagging data at other sites, and in other streams, was unsuitable for use with population estimate procedures.

Densities and biomasses of the estimated populations were calculated in the same manner as described for Afon Glyn fish, and the results are shown in table 88.

Table 88. Density and biomass of salmonids over 1 year of age in the Afon Dyfrdwy and Afon Lliw.

Fish species	River	Site	Density no/m²	95% C.L.	Biomass g/m²	95% C.L.
Trout	Dyfrdwy	3+4	0.230	0.197-0.276	6.046	5.179-7.256
Salmon	Lliw	3	0.373	0.268-0.848	5.358	3.850-12.181
Salmon	Lliw	4	0.144	0.104-0.232	2.068	1.493-3.331

(c) Variations in the densities of salmon parr and trout

Variations in the densities of salmon parr and trout at different sites in the Llyn Tegid feeder streams appeared to be chiefly correlated with the types of habitat present at those sites.

Salmon parr were most abundant in turbulent water, in deep riffle areas, and at sites containing extensive cover such as boulders and rocks. Sites 1-3 in the Afon Glyn, and site 3 in the Afon Lliw were characteristic of such habitats. The importance of a broken river bed topography in increasing the number of visually isolated territories was mentioned in section C1, and Gilson (1961) stated that "the capacity of a river to produce trout depends not only on the food supply, but often to a greater extent on the number of nooks and crannies where fish can lie."

Salmon parr were least abundant in pools, such as those in the Afon Glyn site 4, and were scarce in shallow, exposed riffle areas, such as in the Afon Glyn site 5, except during the spawning season (see section C2b). Site 4 in the Afon Lliw contained both pools and riffles. The riffles were of moderate depth, but far less cover was available for fish than was present at site 3. The cover at Afon Lliw site 3 mainly comprised blocks used to strengthen the river banks for flood prevention purposes.

Trout, like salmon parr, were most dense in sites containing large numbers of visually isolated territories, but, unlike salmon parr, they were more abundant in pools than in riffle areas. They were most numerous in the Afon Glyn in the pool at the lower end of site 2, and in the pools in site 4. The pool in site 2 was shallower than those in site 4, and contained numerous rocks. Trout were also numerous in the pools in the Afon Dyfrdwy, and in the vicinity of overhanging banks.

Trout were least numerous in the shallow riffle areas of the Afon Glyn site 5, although they were abundant in pools at that site. They were less common than salmon parr in the turbulent riffle areas of sites 1 and 3 in the Afon Glyn.

These results indicate that whilst a considerable degree of overlapping occurs between the habitats of salmon parr and trout, certain differences exist, particularly with regard to the occupation of pools or riffle areas, which may decrease the effects of competition between the two species.

The Afon Twrch sites 1 and 2 (see plate 8, chapter 3) contained many deep water areas, and an abundance of cover in the form of boulders, undercut banks and tree roots. These sites appeared to be well suited as a habitat for trout, but were very difficult to sample because of the uneven nature of the river bed. Many trout were seen whilst electrofishing, and a very dense population of trout was indicated. The high density of trout may have accounted for the slow growth rates recorded in this river (see chapter 6).

The fry of trout and salmon, not included in the density estimates given in this section, were more common in shallow, exposed areas than were older fish.

3. Discussion

Some comparative figures for the densities and biomasses of salmonids over 1 year of age in a number of British rivers are shown in table 89. A number of the authors quoted in this table also give figures for the density and biomass of 0+ fish, as does Le Cren (1958).

The results obtained for salmonids in the Llyn Tegid feeder streams were within the ranges found by most workers in similar types of rivers in other parts of the British Isles. The figures given by Mills (1964) were lower, but his figures were obtained from a river system which had only recently been opened up to

Table 89. Density and biomass of salmonids, 1+ and older, in British rivers.

Source	River	Salmon parr	Trout
Egglishaw (1967)	Shelligan Burn Scotland	$0.15–0.53/m^2$ $2.7–6.0\ g/m^2$	$0.21–0.42/m^2$ $5.3–11.7\ g/m^2$
Egglishaw (1967)	River Almond, Scotland	$0.37–0.58/m^2$ $3.6–5.5\ g/m^2$	$0.12–0.26/m^2$ $3.5–7.1\ g/m^2$
Jones (1970)	River Teify & tributaries, S. Wales.	$0.04 - 0.49/m^2$ $0.6 - 6.6\ g/m^2$	$0.07–0.41/m^2$ $6.5–29.1\ g/m^2$
Vickers (1969)	Lough Erne feeder streams, N. Ireland	$0.03 - 0.83/m^2$	$0.02 - 0.23/m^2$
Nott & Beale (1966)	River Dart, Devon	up to $0.36/m^2$	up to $0.48/m^2$
Nott & Beale (1968)	River Exe, Devon	up to $0.66/m^2$	up to $0.25/m^2$
Horton et al. (1968)	Walla Brook, Devon	-	$0.30 - 0.58/m^2$
	River Yarty, Devon	-	$0.05 - 0.08/m^2$
	West Webburn, Devon	-	$0.14 - 0.50/m^2$
Mills (1964)	River Bran & tributaries, Scotland	$0.05 - 0.18/m^2$	-
Woolland (1972)	Llyn Tegid feeder streams	$0.144–0.386/m^2$ $2.068–5.358\ g/m^2$	$0.100 - 0.412/m^2$ $4.641–6.046\ g/m^2$

migratory fishes, and in which the salmon fishery had been started by fry plantings.

Vickers (1969) and Jones (1970) both found considerable variations in the densities of salmonids at different sites within the same rivers, and between different rivers within the same areas. Similar variations were evident even in the short stretch of the Afon Glyn which I studied, and such variations indicate that results from one particular area are unlikely to be representative of the river as a whole.

Vickers (1969) thought that the comparatively low densities of trout he found in the Lough Erne feeder streams resulted from the migration of trout out of the streams into Lough Erne. Low densities of trout were not found in the Llyn Tegid feeder streams despite similar migrations, but the biomass of trout was relatively low as a result of these migrations. Jones (1970) generally found much higher biomasses of trout in the River Teify system , where no such migrations took place.

Horton et al. (1968) found higher population densities of trout in acid streams (Walla Brook and West Webburn) than in the alkaline stream (River Yarty) which they studied. They correlated high densities of fish and poor food supply with the low growth rates of trout in the acid streams. In addition they recorded that the acid streams contained a much greater quantity of suitable spawning gravel than did the River Yarty, and that there was some evidence of overgrazing of the available food supply by the very large fry population which resulted from the favourable breeding conditions.

The relatively slow growth rates of salmonids in the Llyn Tegid feeder streams (see chapter 6) probably result from much the same factors as those described by Horton et al. (1968), the feeder streams being typical acid mountain streams containing abundant spawning gravel and high population densities of fish. Data on the benthic fauna of the streams and feeding relationships (M.A. Rahim) are not yet available, but it seems likely that food is a limiting factor for the growth of fish in these streams.

E. Summary

(1) The results obtained on population structures indicated that most salmon parr migrated as smolts at 2 years of age, and that most trout descended into Llyn Tegid from the feeder streams at 2 or 3 years of age. The 0+ age group of fish was less efficiently caught by electrofishing than were older fish.

(2) Most salmon parr (82.3%) and most trout (87.8%) remained within a restricted "home" area. The remainder moved, equally upstream and downstream, over distances not generally exceeding 150 metres. No significant difference existed between upstream and downstream movements, or between the movements of salmon parr and trout.

(3) Adjusted values (Stott, 1967) for "home" recaptures of fish in the Llyn Tegid feeder streams ranged between 70.6% and 86.2% for salmon parr, and between 79.3% and 89.8% for trout. Some seasonal trends in movements correlated with adverse summer

conditions and spawning activities, were recorded for salmon parr, but not for trout.

(4) Mean densities of salmon parr (over 1 year of age) in the Afon Glyn and the Afon Lliw ranged between $0.144/m^2$ and $0.412/m^2$, corresponding to mid-year biomasses of 2.068 g/m^2 to 5.302 g/m^2. A rough estimate of the density of salmon parr in sites 4 and 5 of the Afon Glyn was $0.05/m^2$.

(5) Mean densities of trout in the Afon Glyn and Afon Dyfrdwy ranged between $0.202/m^2$ and $0.430/m^2$, corresponding to mid-year biomasses of 4.641 to 9.879 g/m^2. An approximate density of 0.1 trout/m^2 was obtained in the Afon Glyn site 1 from a DeLury estimate.

(6) Variations in population densities reflected differences in the types of habitat at each site, the densest populations of salmonids being found where visual isolation (Kalleberg, 1958) was most extensive. Trout generally preferred pool areas, in contrast to salmon parr which more frequently occupied deep, turbulent riffles, and such differences may have reduced the effects of competition between the two species.

(7) The results of density and biomass estimates for salmonids in the Llyn Tegid feeder streams compared favourably with those found in other, similar British rivers. Biomasses of trout in the Llyn Tegid feeder streams were reduced as a result of emigrations to Llyn Tegid.

(8) High population densities of both salmon parr and trout, together with poor food supplies and abundant spawning gravel, probably contribute to the relatively poor growth of fish in acid, mountain streams.

CHAPTER XII

SALMON SMOLTS IN LLYN TEGID

A. Introduction

Small numbers of salmon smolts have been caught in Llyn Tegid in previous years by other workers from the University of Liverpool (Dr. J.W. Jones, pers.comm.) but details of these catches were not recorded. Following the capture of 586 smelts in the spring of 1969 whilst sampling for grayling, it was decided to carry out some observations on these fish.

During the spring of 1970 a further 753 smolts were caught in Llyn Tegid. These smolts were caught by shore seine netting, as were the 1969 smolts. Some factors which may have influenced the time of smolt descent into Llyn Tegid were investigated, and predation on smolts by pike in the lake and in the upper Dee, was assessed.

Recaptures of smolts tagged as parr in the feeder streams were recorded in both the 1969 and 1970 catches, and data from these recaptures were used to estimate the numbers of smolts which had descended into Llyn Tegid. In addition, most of the smolts caught during 1970 were marked and released back into the lake, providing further material for use in population estimate procedures.

Although many studies have been made on the descent of salmon smolts in rivers and from lakes, information on smolts in lakes is scanty. Allen (1944) and Mills (1964) found that the migration of smolts through lakes was slower than in rivers, possibly because smolts followed indirect routes along the shorelines of lakes (Allen, op.cit.). Investigations have been made into predation on smolts in lakes, and Mills (op.cit.) found that pike fed extensively on smolts in three Scottish lochs.

Studies have been made on the acclimatisation to salt water and the age, growth and sex ratios of River Dee smolts by Jones (1947, 1949), and Jones (1939, 1950a, 1950b, 1951, 1953b) also assessed the proportions of the different smolt age groups in the River Dee from the scales of incoming adult salmon. Further detailed investigations into the River Dee smolt runs are being carried out as part of the Water Resources Board research programme.

B. Material

The numbers of smolts caught in Llyn Tegid, together with details on the date and place of capture, are shown in table 90.

Most of the smolts were captured near to river inlets (sites B,E and H) during a period of about 3 weeks, from late April to Mid-May. The main smolt run occurred about one week earlier in 1970 than in 1969. Smolts were still present in the Afon Glyn on May 12th 1969, but large numbers of these fish were caught in Llyn Tegid on May 13th.

C. Population structure

(1) Age composition

The age composition of the 1969 and 1970 smolt runs are

Table 90. Catches of salmon smolts in Llyn Tegid.

Date	Site	No. of smolts caught
1969		
April 22nd	A,H	2, 9
April 29th	B,C	6, 70
May 5th	H	72
May 13th	D,E	53, 371
May 20th	J	0
May 27th	B	2
June 3rd	E	1
Total for 1969		586
1970		
April 14th	H	1
April 20th	D	14
April 27th	E	101
April 28th	E,H	11, 40
April 29th	E,G,J	4, 1, 2
May 5th	E	258
May 6th	B,E,	18, 179
May 11th	E,F,H	16, 12, 7
May 12th	E,H	6, 45
May 13th	B,E,H	27, 3, 5
May 14th	E	2
May 18th	E	1
May 19th	B,E,H	0
Total for 1970		753

shown in table 91.

Table 91. Age composition of Llyn Tegid smolt catches

	(Number) and percentage of smolts in each age group.			
Date	1 year	2 year	3 year	4 year
1969	(9) 1.5	(555) 94.7	(22) 3.8	-
1970	(8) 1.1	(702) 93.2	(41) 5.4	(2) 0.3

The age composition of River Dee smolts found in previous investigations is given in table 92.

Table 92. Age composition of River Dee smolts.

		Percentage of smolts in each age group		
Source	Material	1 year	2 year	3 year
Jones (1949)	1938 smolts 1939 smolts	7.0% 3.5%	89.8% 89.5%	3.2% 7.0%
Jones (1939, 1950a,b, 1951, 1953b)	Adult scales 1937 - 1951	4.5% (1.6-7.8)	93.3% (88.5-97.0)	2.2% (0.8-6.3)

The main difference found between my results (table 91) and those of Jones (table 92) was the lower proportion of one year smolts in the Llyn Tegid catches. This may be a reflection of the slow growth rates of young salmon in the Llyn Tegid feeder streams (see chapter 6), the age at which salmon migrate as smolts being correlated with size (see section E1). One year old smolts may be generally scarce in the headwaters of the Dee, but may be more common in lowland areas. Two year old fish clearly dominate the smolt runs of the River Dee.

Osterdahl (1969) and Mills (1964) found that older smolts migrated earlier in the run than younger fish, and some evidence of a similar migration pattern was found in the Llyn Tegid catches. Thus all three year old smolts were caught before and during the main runs (May 13th, 1969; May 5th & 6th, 1970), whereas all one year old smolts were caught during and after the main runs.

(2) Size composition

The main lengths (and S.D. of lengths) of each smolt age group at the time of capture are shown in table 93.

Table 93. Size composition of Llyn Tegid smolts.

	Mean length (± S.D.) in cms. of each age group			
Date	1 year	2 year	3 year	4 year
1969	11.9(±1.7)	13.8(±1.2)	15.9(±0.9)	-
1970	11.0(±0.6)	13.7(±0.8)	15.1(±1.9)	16.7(±0.4)

A comparison with figure 47 (chapter 6) shows that the mean length of each age group had increased since the end of the previous year's growth in the Llyn Tegid feeder streams.

(3) Sex ratios

The sex ratios of 35 smolts removed from Llyn Tegid during 1969 and 1970 were determined and are shown in table 94, together with the results recorded by Jones (1949) for River Dee smolts. The results I obtained were very similar to those of Jones (1949), who correlated the variation in the sex ratios of different age groups with the spawning activities of male parr (see chapter 9, section B

Osterdahl (1969) also associated the predominance of females in his smolt catches with sexual maturation in male parr.

Table 94. Sex ratios of Llyn Tegid smolts.

Age group	No. of males	No. of females	Proportion of males to females 1969-70	Jones (1949)
1 year	1	0	1 : 0	1.04:1
2 year	10	21	0.48 : 1	0.65:1
3 year	2	1	2 : 1	2.07:1

D. Population size

The recapture of smolts in Llyn Tegid, which had been tagged as parr in the feeder streams, presented an opportunity of estimating the total production of smolts in the feeder streams.

In 1969 13 such recaptures were made in the total catch of 586 smolts. The number of pre-smolts tagged in the feeder streams in the early months of 1969 was given in chapter 11 (section B) as 135. Twenty two of these were tagged in January, 5 in February, 51 in March and 57 in April. The numbers of smolts which descended into Llyn Tegid from the feeder streams during 1969 was estimated from these data using Bailey's modification of the Peterson method, described in chapter 10 (section 2C,ii). The results of this estimate are shown in table 95.

Table 95. Estimated number of smolts in Llyn Tegid during 1969.

M	C + 1	R + 1	$\hat{N}$	95% confidence limits
135	587	14	5660	4820 - 6750

This may be an overestimate since mortalities of tagged pre-smolts in the streams, between January and April, were not taken into account. Such mortalities were probably not a serious source of error, however, since most tagging was carried out during March and April, and the time elapsing between then and recapture as smolts in Llyn Tegid was relatively short.

Larger numbers of smolts were available for recapture in Llyn Tegid during 1970, since 737 parr had been tagged in the feeder streams (table 75, chapter 11) between the 1969 and 1970 smolt runs. Excluding losses from natural mortality, the numbers of tagged parr which would have migrated to Llyn Tegid as smolts in 1970 were reduced by two main factors. Firstly, a small percentage of salmon would not have migrated as smolts at 2 years of age (table 91, section C), and secondly, a total of 49 tagged fish were killed whilst sampling in 1969-70. An estimated 30 fish were lost as a result of the first factor, and the maximum number of tagged smolts available for recapture in Llyn Tegid during 1970 was therefore taken as 658. Recaptures of these fish in the lake totalled 41 in a catch of 753 smolts.

A Bailey's estimate carried out on these data, in the same way as for the 1969 data, gave an estimated population $\hat{N}$ = 11,813 (95% confidence limits 10,976-12,889). This is obviously an overestimate, because natural mortalities would hage removed many of the tagged fish from the population between 1969 and 1970, and the value of M used in the Bailey estimate was therefore too high. Survival rates in the Llyn Tegid feeder streams may have been even less than the 34.7-59.0% quoted by Horton et al. (1968) for 1-2 year old salmon parr at relatively low population densities. Losses of this magnitude would have greatly reduced the value of $\hat{N}$ obtained from the 1970 data, if they had been taken into account.

Since such losses could not easily be assessed, a further experiment was carried out whereby all smolts captures in Llyn Tegid from 27th April 1970 onwards were marked (see chapter 4, section A2,b) and released. Subsequent recaptures of these fish were used for estimating the total number of smolts present in the lake. Estimates were made using the methods of Schnabel (Chapman modification) and Schumacher & Eschmeyer (see chapter 10, section 2B,ii). Recapture data were obtained on seven occasions from April 28th to May 13th, and the final multiple census estimates are shown in table 96. No further recaptures were made after 13th May.

Table 96. Estimated number of smolts in Llyn Tegid during 1970.

Mt	Σ(CtMt)	(ΣRt)+1	$\hat{N}_1$	Σ(RtMt)	$\Sigma(CtMt^2)$	$\hat{N}_2$	95% C.L
700	208475	29	7189	13058	93286721	7144	4545-16670

$\hat{N}_1$ = Schnabel (chapman modification) estimate
$\hat{N}_2$ = Schumacher & Eschmeyer estimate.

The results obtained compared favourably with the 1969 Bailey estimate (table 95), but were considered to be an overestimate because of handling mortalities. Some efforts were made to reduce these mortalities (see chapter 4, section 1b), but many smolts were seen to swim erratically across the lake surface after release. Such fish may have been very exposed to predation, especially by gulls (see section G).

A summary of smolt recaptures in Llyn Tegid is shown in table 97. The table includes those smolts tagged in the lake.

Table 97. Recaptures of tagged salmon smolts in Llyn Tegid.

Year	Lake site at which caught	Number caught	Place of origin
1969	D	1	A. Lliw
	E	12	A. Glyn
1970	B	1	A. Dyfrdwy
	D	1	A. Lliw
	E	28	A. Glyn
	E	4	A. Lliw
	E	3	A. Dyfrdwy
	H	2	A. Lliw
	H	2	A. Dyfrdwy
1970	B	5	Llyn Tegid
	E	15	Llyn Tegid
	F	1	Llyn Tegid
	H	7	Llyn Tegid

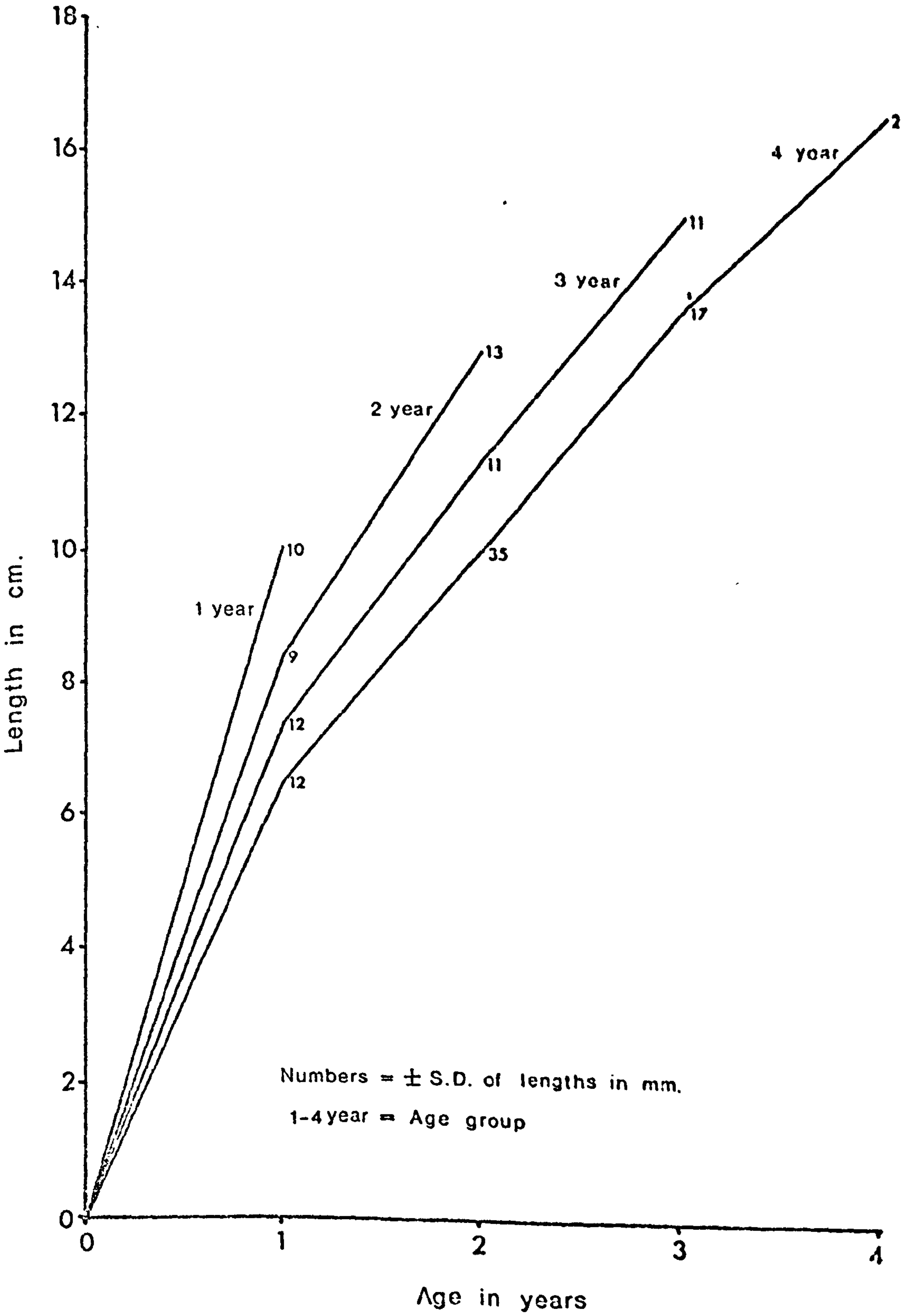
E. Growth of smolts

(1) Growth in length

The calculated growth rates (see chapter 6, section 3b) of each smolt age group caught in Llyn Tegid during 1969 and 1970 are shown in figure 91. Figure 91 clearly illustrates the general tendency for more rapidly growing fish to migrate at an earlier age

FIGURE 91

Calculated Lengths of Llyn Tegid Salmon Smolts



than slower growing fish (Allen, 1944). Jones (1939, 1949) considered that the rate of growth was probably the most important factor governing the age at which smolts migrate. Other workers (e.g. Went, 1938; Frost & Went, 1940; Pyefinch & Mills, 1963; Mills, 1964; Went, 1964) have recorded similar variations in the growth rates of different smolt age groups.

(2) Scale growth

Went (1940, 1942) and Went & Barker (1943) separated the smolts of the Shannon , Erne and Waterville Rivers into "Type A" and "Type B" smolts, according to their pattern of scale growth. Type A smolts showed no + growth (summer growth) at the scale margin, but Type B smolts did show + growth at the scale margin. Similar growth patterns have been recorded by other workers (Pentelow et al., 1933; Jones, 1939, 1949; Nall, 1939; Allen, 1944; Vibert, 1950) and attempts have been made to relate this growth to the time of smolt migration.

Pentelow et al. (1933), Went (1940, 1942) and Went & Barker (1943) considered that it was necessary for smolts to attain a physiological condition associated with size. They suggested that the growth made by Type B smolts (Went, op.cit.) enabled such fish to achieve a minimum necessary size for migration. Allen (1944) and Jones (1939, 1949) agreed with this view but found that it did not apply to all cases, and Allen (op.cit.) thought that, although there was a close relationship between size and time of migration, there was no critical size at which all smolts migrated. Nall (1939) and Vibert (1950) rejected the view that attainment of a minimum size was a critical factor because the parr population was so heterogenous in that respect.

The catches in Llyn Tegid comprised 40.7% Type A smolts, and 59.3% Type B smolts. Went (1964) stated that Type B smolts formed 75% or more of the smolt populations in most Irish rivers. Harris (1970) found a higher proportion of Type A sea trout smolts than Type B, and suggested that this was because his smolt catches were made at a long distance from the sea. He thought that more + growth may have occurred during the descent from the upper reaches to the sea, and the same may be true for Llyn Tegid salmon smolts. Jones (1939, 1949) found 2+ salmon smolts in the lower reaches of the River Dee which had apparently grown as fast or faster than some of the 2 year old migrants which had no third summer rings on their scales. He considered that these fish may have been migrants from the upper reaches of the river which became 2+ fish by the addition of third summer rings on their scales following intensive feeding during their long downstream migration.

(3) Condition.

The weights of smolts were not measured in the field because of the large inaccuracies which occurred (see chapter 4), and to reduce handling mortalities. The data available for assessing the condition (K) of smolts were therefore limited to the few fish that were killed and brought back to the laboratory. The mean weights for each age group of these fish are shown in table 98.

Condition factors were calculated for these fish in the manner described in chapter 5 (section 3a,iv). The 1970 smolts shown in table 98 were caught between April 14th and April 27th, and the mean condition factor remained at 0.98 throughout this period. The 1969 smolts shown in table 98 were caught over a longer period of time and changes which occurred in the mean condition factor are given in table 99.

Table 98. Mean weights of Llyn Tegid smolts.

	Mean weight (± S.D.) in gms. of each age group).			
Date	1 year	2 year	3 year	4 year
1969	16.0	24.0(±4.2)	36.8	-
no. examined	1	18	1	-
1970	-	22.1(±3.4)	33.8(±5.8)	43.0
no. examined	-	13	3	1

Table 99. The condition of Llyn Tegid smolts during 1969.

Date	Mean condition factor (K)
April 22nd	0.97
May 13th	0.91
May 27th	0.80
June 3rd	0.80

The condition of smolts decreased as the migration period progressed, at the same time as the condition of salmon parr in the feeder streams was rising. The K values for 2 year old salmon parr in the feeder streams were 0.96 in April, 1.07 in May and 1.21 in June (see chapter 6, section 3a,iv).

This decline in the condition of salmon smolts has been recorded by a number of workers (Hoar, 1939; Allen, 1944), and has been related to the physiological changes which occur during the smolt transformation process.

F. The descent of smolts into and through Llyn Tegid

(1) Time of descent

The time of descent of smolts into Llyn Tegid was shown in table 90, and was noted in section B.

Sampling was continued at weekly intervals after the dates shown in table 90, by myself in 1969, and by other workers from the University of Liverpool in 1970. No further catches of smolts were recorded. An electrofishing survey in the Afon Glyn on May 19th 1970 indicated that all the smolts had left that stream. No evidence of summer, autumn or winter runs of smolts (Calderwood, 1906; Pyefinch, 1955) was found.

(2) Factors affecting the time of descent

Many suggestions have been put forward concerning the factors which control the time of smolt transformation and migration, and the influence of size on these phenomena was mentioned in earlier sections. The smolt transformation is undoubtedly controlled by neuro-endocrinological response (Hoar et al. 1951; Hoar, 1953; Fontaine, 1954), possibly initiated by photoperiodism (White, 1940; Hoar, 1953), but Osterdahl (1969) considered that if smolt migration was only attributable to such factors then a dome shaped migration curve would be expected. In fact he found marked short-term fluctuations superimposed on a general dome shaped curve, and considered that at least one phase in smoltification, the change in territoriality and rheotaxis (Kalleberg, 1958), was influenced by some environmental factor which could fluctuate from day to day.

Environmental factors which have been considered by workers in this field include rainfall and water flows (Bull, 1931a, 1931b; Berry, 1932, 1933; Allen, 1944; Pyefinch & Mills, 1963), changes in water temperature (Berry, op.cit; Allen, op. cit; White, 1940; Mills, 1964), weather conditions (Berry, op.cit.) and solar radiation (Osterdahl, 1969). Allen (op.cit.) thought that the passage of actively migrating smolts may influence other smolts to start migrating, and considered it likely that susceptibility to migration producing stimuli and smolt livery commence to develop together. Susceptibility to migration producing stimuli increases with time, smolts which have delayed their departure react to smaller stimuli than smolts which migrate early in the run (Jones, 1959).

Water temperatures (taken at midday on each sampling occasion), weather conditions and river flows were recorded during the 1969 and 1970 Llyn Tegid smolt runs, and the relation between some of these factors and the numbers of smolts caught are shown in figures 92 and 93. River flow details were not available for spring 1969 (see chapter 3, section C1), but those in the 1970 smolt migration period closely followed fainfall fluctuations. Weather conditions during the main smolt runs were

FIGURE 92

Environmental Conditions During the 1969 Llyn Tegid Salmon Smolt Run

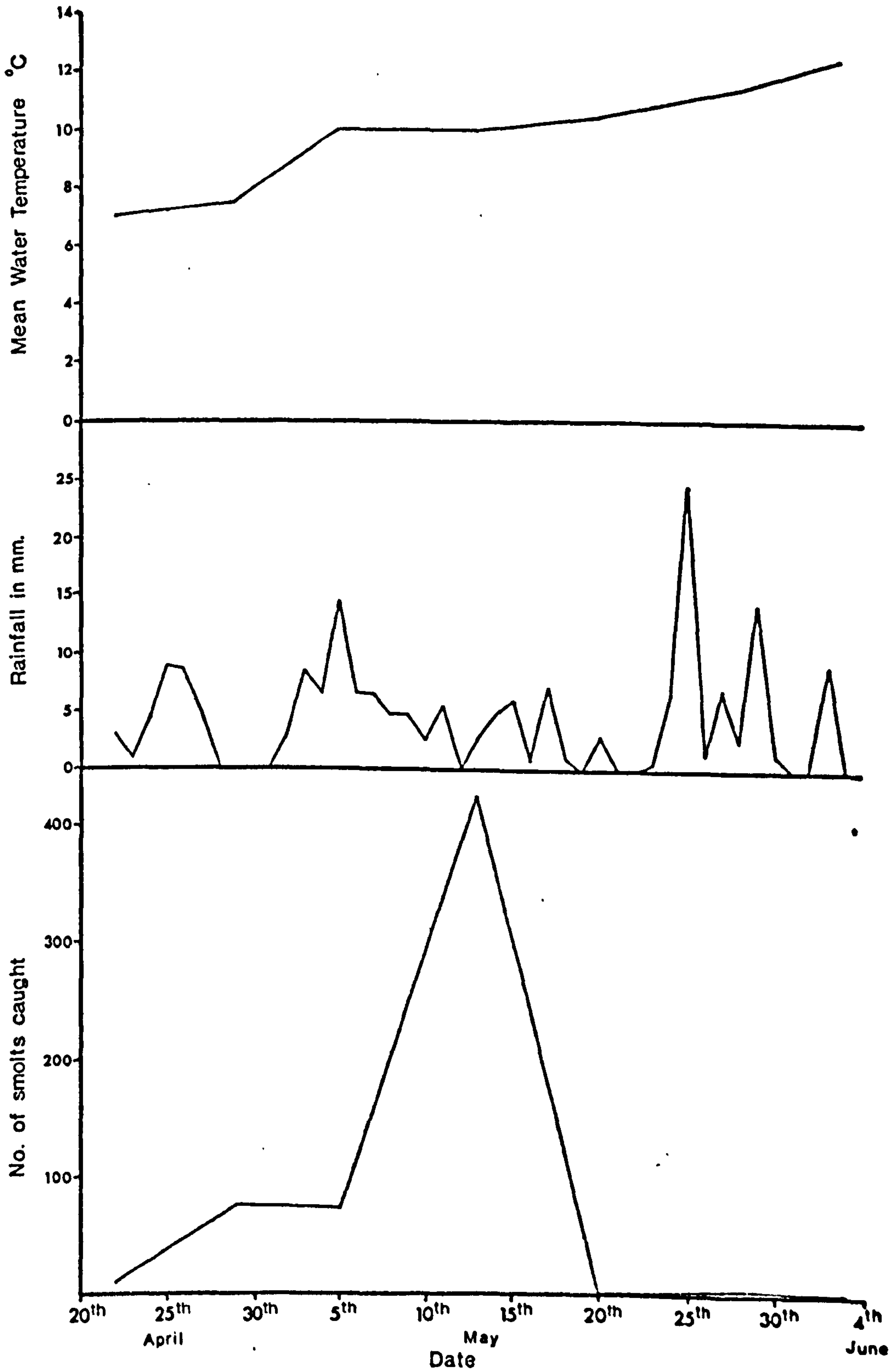
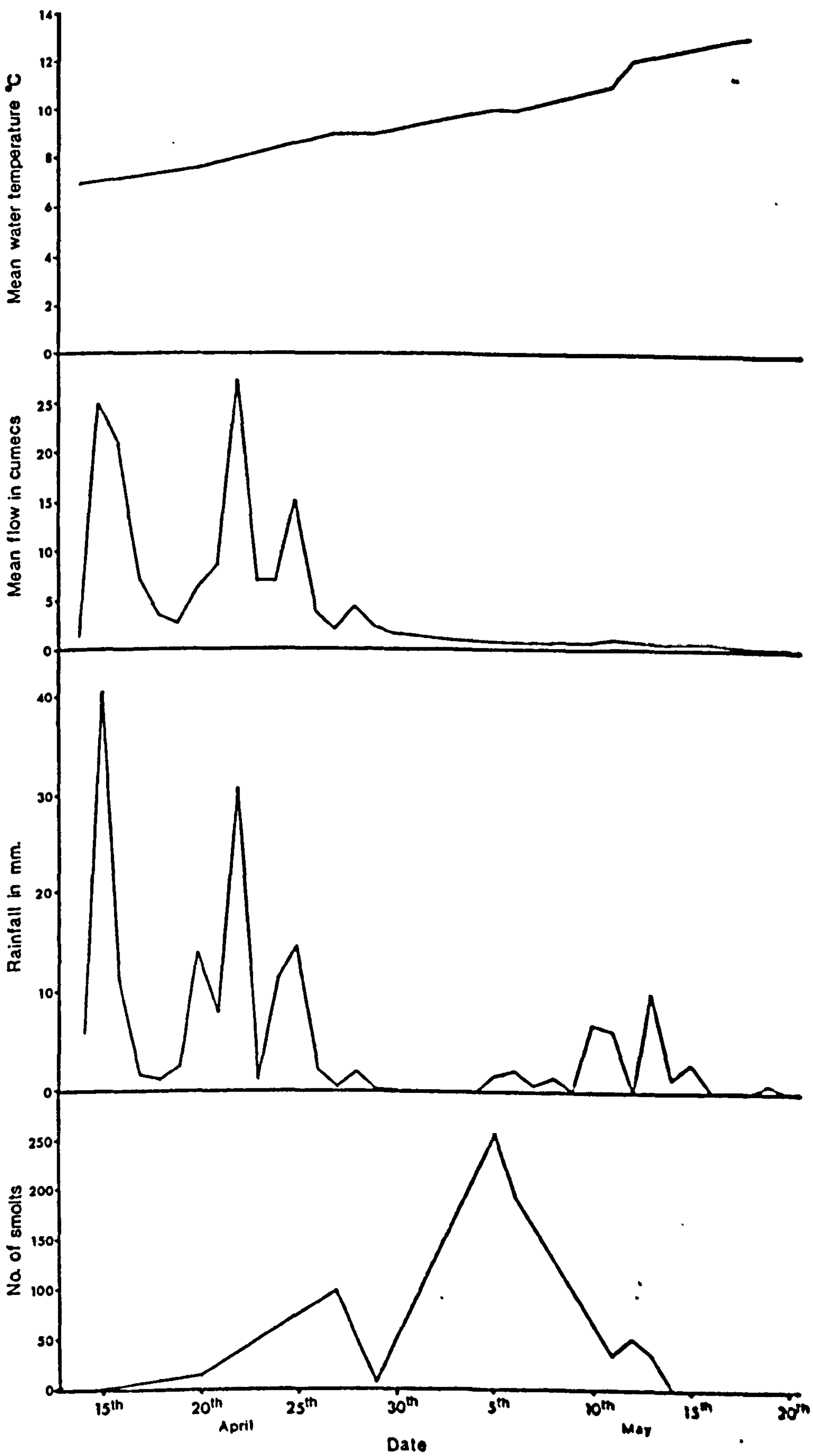


FIGURE 93

Environmental Conditions During the 1970 Llyn Tegid Salmon Smolt Run



similar in both years. Mild conditions persisted, winds were light (south, southwest or west) and rainfall was low.

There appeared to be little correlation between rainfall, river flows and the size of the smolt run (figures 92 and 93), although some of the early runs may have been influenced by these factors. Bull (1931a) considered that a local rainfall of only 0.1 inches could initiate the migration of smolts, and White & Huntsman (1938) also considered rainfall to be an important migration producing stimulus. Berry (1932) and White (1940), however, found that major runs of smolts passed observation points during times of low water flow.

The timing of the main smolt runs during 1969 and 1970 appeared to be more closely correlated with water temperatures than with rainfall or river flows. In both years the largest numbers of smolts were caught in Llyn Tegid at a time when water temperatures were approximately 10°C. Mills (1964) and Osterdahl (1969) also found that the main smolt runs occurred when the water temperature rose to 10°C or above, but the latter author considered that this may have been a coincidence, not a direct causal connection.

Allen (1944) thought temperature was an important factor in determining the time of smolt migration, but found that the large stimulus derived from a rapid rise in water level could more than offset the effect of low temperature. Several large increases in river flows occurred in the Llyn Tegid feeder streams between 15th April and 25th April 1970, when water temperatures were 7.0 to 8.5°C, but these did not give rise to large smolt runs.

Osterdahl (1969) recorded that during the early stages of the run most smolts migrated at night, but later on daytime migrants predominated. During the 1970 Llyn Tegid smolt run a seine net was left overnight around the Afon Glyn inlet in water less than 1½ metres deep (see chapter 4, section Alb). The net was drawn in just before dawn and the recorded catches are shown in table 100.

Table 100. Overnight catches of smolts in Llyn Tegid during 1970.

Date	Number of smolts caught
20th April	11
29th April	2
5th May	258
12th May	3
13th May	3
Total	277

The Glyn seine net "trap" accounted for 36.8% of the total catch in 1970, and it seems probable from these results that most smolts descended into Llyn Tegid at night.

(3) Movements through Llyn Tegid

Movements of smolts through Llyn Tegid took place in shallow water close to the shore. Smolts were never seen in mid-lake areas, but they were frequently observed near to the lake surface in the littoral zone during periods of calm weather. Gulls were often seen preying on the shoals of smolts (section G) in the littoral zone.

From the location of recaptured fish (see table 97) it was apparent that smolts from the Afon Dyfrdwy and Afon Lliw migrated along both the north and south shores of the lake, although most of the recaptures occurred on the south shore. Afon Glyn smolts were only recaptured on the south shore, and never in a more southwesterly position than the Glyn inlet. This suggests that smolts orientate themselves towards the River Dee outlet immediately on entering the lake. The means by which they do this is not known. No smolts from the Afon Llafar or Afon Twrch were recaptured in Llyn Tegid.

(4) Movements out of Llyn Tegid

Movements of smolts out of Llyn Tegid were not investigated, but some observations were made by the staff of the Dee and Clwyd River Authority at the Bala sluices.

Large numbers of smolts were seen in slack water above the Bala sluices on May 11th, 1970. The flow in the River Dee at that time was low (2.5 cumecs). At 6.00 p.m. on May 11th the River Authority at Chester ordered an artificial flood of 11 cumecs to be released from the lake for a 48 hour period, to dilute the effects of a pollution in the lower reaches of the Dee. The smolts which were above the sluices were seen to pass through the sluices on this flood. The river flow had returned to its previous level by May 14th.

Mills (1964) quoted a newsletter from the Atlantic Sea Run Salmon Commission which mentioned that some smolts took as long as 14 days to negotiate the 2.5 miles (4 Km) from the inlet to the outlet of Beddington Lake, Maine, and suggested that the lake may have slowed migration. This may also be true of Llyn Tegid where in 1970, for instance, smolts entered the lake from April 14th onwards, but were not observed leaving the lake in large numbers until May 11th. In this instance, however, some of the delay may have been attributable to a reluctance to pass through the Bala sluices during periods of low river flow.

On May 20th, 1970, a smolt was captured at Corwen which had been tagged as a parr in the Afon Twrch. Assuming this fish left Llyn Tegid on, or about May 11th, then its speed of migration was approximately 2.4 Km. per day. Allen (1944) recorded smolt migration rates of 0.14 - 5.94 Km/day in the Thurso River system, and Mills (1964) recorded rates of 0.86 - 2.04 Km/day in the River Bran.

G. Predation on smolts

Pike were caught in Llyn Tegid whilst sampling for smolts and the stomachs of these fish, together with those from pike caught at the same time in the upper Dee (see chapter 4, section A1c), were examined. In addition, small numbers of pike caught in Llyn Tegid and the upper Dee at other times of the year were examined. The results of these analyses are given in tables 101 and 102.

The results obtained indicated that very little predation

Table 101. The food of pike in Llyn Tegid

	1969 April 22nd to May 27th	1970 April 14th to May 13th	Total for 1969-1970 smolt migration periods	1968-1970 June - March
No. of stomachs examined	15	25	40	34
Percentage of stomachs empty	53.3	84.0	72.5	41.2
Percentage of stomachs containing :				
Salmo salar (juv.)	6.7	-	2.5	-
Salmo trutta	20.0	8.0	15.0	8.8
Perca fluviatilis	6.7	8.0	7.5	17.6
Rutilus rutilus	-	-	-	2.9
Coregonus clupeoides	6.7	-	2.5	32.4
Phoxinus phoxinus	-	8.0	5.0	-
Gobio gobio	-	-	-	2.9
Anguilla anguilla	6.7	-	2.5	-
Lampetra planeri	6.7	-	2.5	5.8
Invertebrates	-	-	-	-

(range of size of pike = 30 - 92 cm.)

Table 102. The food of pike in the River Dee.

	1969 April 14th to May 11th	1970 April 28th to April 30th	Total for 1969-70 smolt migration periods	1969-1970 June to March
No. of stomachs examined	28	15	43	36
Percentage of stomachs empty	75.0	93.3	81.4	58.3
Percentage of stomachs containing:				
Salmo salar (juv.)	7.1	6.7	4.6	2.8
Salmo trutta	10.7	-	9.2	13.9
Phoxinus phoxinus	7.1	-	4.6	19.4
Esox lucius	7.1	-	4.6	2.8
Invertebrates	7.1	-	4.6	2.8

(range of size of pike = 13 - 85 cm.)

on smolts by pike in Llyn Tegid and the upper Dee occurred during 1969 or 1970. All of the pike caught during the smolt runs were running ripe, spending or newly spent, and the very high incidence of empty stomachs was probably associated with a preoccupation with spawning activities. The pike caught in the upper Dee at this time were captured as they entered backwaters to spawn, but many of these in Llyn Tegid were caught amongst the smolt shoals. Frost (1954) recorded the lowest percentage of feeding pike during the spawning period, and the highest after this time.

Pike preyed to a greater extent on small trout in Llyn Tegid than on smolts. The reasons for this were not known, since both species were of similar size and similar abundance in the littoral zone during April and May. Trout were also slightly more common in the stomachs of River Dee pike than were smolts.

Other workers have recorded extensive predation by pike on smolts (e.g. Mills, 1964), and the results found in the Llyn Tegid study may be attributable to the late spawning of pike following the severe winters of 1969 and 1970. Spawning may occur earlier in milder years, and pike may be feeding intensively at the time when smolts begin to descend. Predation by pike could be a serious factor if smolts were allowed to pass through the lake formed by the estuary barrage scheme (see chapter 1), since pike may spawn earlier in the milder conditions which persist at lower altitudes, and may thus recommence feeding before those in the upper reaches.

At other times of the year (see tables 101 and 102) pike in Llyn Tegid fed mostly in deep water, and the fish most commonly found in the stomachs were gwyniad and perch. Minnows and trout formed the main food of River Dee pike, and pike under 25 cm. ate some invertebrate food (mostly *Asellus meridianus*).

No predation on smolts by other fish in Llyn Tegid was recorded. Only small trout (10-20 cm.) were caught during the smolt runs, and perch caught at this time were mostly less than 15 cm. in length. No smolts were found in a sample of 20 perch stomachs which were examined, but the stomach of one very large perch (41 cm.) contained a 12 cm. trout. Ball (1961) and Graham & Jones (1962) found no salmon smolts in the stomachs of the Llyn Tegid trout which they examined, but Mills (1964) found that large trout in the River Conon ate many smolts. Piggins (1958) recorded extensive predation on salmon parr and smolts by 9-13 inch trout in the Burrishoole River system.

Predation on smolts by birds was not investigated but gulls (Larinae) were frequently seen preying on the shoals of smolts in Llyn Tegid, and indeed the shoals were often located by observing the behaviour of such birds. Cormorants (*Phalacocorax carbo*), which occur in small numbers in Llyn Tegid, may also feed on smolts. Predation on smolts by birds has been dealt with by other workers and the chief predators in the British Isles appear to be goosanders (*Mergus merganser*) and red-breasted mergansers (*Mergus serrator*). Mills (1962) investigated the predation of these species on salmon in Scotland, and reviewed the British, European and North-American literature on this subject. Mills (1965) also investigated the feeding habits of cormorants in Scottish inland waters and considered that they were not serious predators of young salmon. Other birds recorded as being predators of salmon smolts in the British Isles include common and black-headed gulls (Berry, 1936; Hardy, 1951), herons (Berry, op.cit; Piggins, 1958) and terns (Berry, op.cit). Berry (op.cit.) gave an extensive list of birds which occasionally eat young salmon.

H. Summary

(1) Investigations of the salmon smolt runs of the Llyn Tegid feeder streams were made following the capture of 586 smolts in Llyn Tegid during the spring 1969. A further 753 smolts were caught in the lake in spring 1970.

(2) Smolts were caught in Llyn Tegid between April 22nd and June 3rd 1969, and between April 14th and May 18th in 1970. The main smolt runs occurred about May 13th in 1969, and May 5th and 6th in 1970.

(3) Two year old smolts dominated all catches, forming 94.7% of the 1969 catch and 93.2% of the 1970 catch. Some evidence of older smolts migrating before younger smolts was recorded.

(4) Female smolts were more common in the 2 year age group than males. This difference may be correlated with the sexual maturation of the male parr.

(5) The numbers of smolts in Llyn Tegid were estimated from

recaptures of fish tagged as parr in the feeder streams, and as smolts in the lake. The estimates were 5660 in 1969, and 7144 in 1970. These may have been overestimates (particularly in 1970) because of mortalities of tagged fish.

(6) Calculated growth rates of smolts clearly illustrated the connection between size and age at migration. "Type A" and "Type B" smolts (Went, 1938) comprised 40.7% and 59.3% of the catches respectively.

(7) The condition (K) of smolts fell as the migration period progressed. This decline is related to physiological changes which occur during the smolt transformation process.

(8) The time of descent of smolts into Llyn Tegid appeared to be more closely correlated with water temperature than with rainfall or river flows. Most smolts probably descended into the lake at night.

(9) Movements of smolts through Llyn Tegid took place in shallow water close to the shore. On entering the lake, smolts apparently orientated themselves towards the outflow and did not wander about the lake searching for an outlet.

(10) Smolts were seen passing out of Llyn Tegid through the Bala sluices on May 11th 1970 during an artificial flood of 11 cumecs. The sluices may delay the smolt run when river flows are low.

(11) Little predation on smolts by pike was recorded, the pike being preoccupied with spawning at the time of smolt descent.

Some predation on smolts by gulls was observed. Between June and March pike ate mostly gwyniad and perch in Llyn Tegid, and minnows and trout in the River Dee.

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The studies presented in this thesis were carried out under the supervision of Dr. J.W. Jones, O.B.E. at the University of Liverpool, as part of a long-term investigation into the effects of river regulation on aquatic organisms in the Welsh Dee. The studies, sponsored by the Water Resources Board, were designed to obtain information on the ecology, population dynamics and interspecific relationships of salmonid fishes in the upper Dee area.

The research undertaken was principally concerned with studies on grayling (Thymallus thymallus L.) in the upper reaches of the River Dee and in Llyn Tegid. The age, growth, population structure, feeding habits, sexual maturation and fecundity of grayling were determined, and mark-recapture experiments were conducted to assess population movements and densities. The feeding relationships of grayling, brown trout (Salmo trutta L.) and juvenile salmon (Salmo salar L.) in the River Dee were examined, and observations were made on the spawning habits of grayling. The distribution of grayling was considered and recent changes in stock sizes were assessed from River Authority records and previous research in the area.

Differences in the growth rates of grayling in Llyn Tegid and the River Dee were correlated with population densities and food supplies. Interspecific and intraspecific competition for food occurred within the populations of salmonid fishes in the River Dee and this competition was reflected in the growth rates of fish.

High population densities of grayling were found in the upper Dee and increases in Llyn Tegid grayling catches since regulation were demonstrated. It was suggested that stabilization of river flows and alterations in lake levels may have contributed to the present abundance of grayling.

A high degree of territoriality was demonstrated in River Dee grayling, but Llyn Tegid grayling did not occupy definite home areas. Extensive seasonal movements of grayling occurred between Llyn Tegid and the River Dee, and such movements were apparently unimpeded by the Bala regulation scheme installations.

Studies were also made on the growth rates, population structures, population densities, biomasses and movements of trout and juvenile salmon in the unregulated Llyn Tegid feeder streams for comparison with researches in progress elsewhere in the Dee watershed. Density and biomass estimates compared favourably with those in other similar British rivers, although trout biomasses were relatively low because of migrations of older fish to Llyn Tegid.

Variations in the population densities of trout and salmon were associated with differences in the types of habitat present, and differences in the niches occupied by the two species may have reduced the effects of interspecific competition. Few movements occurred in the populations except during the spring and during the spawning season.

Growth rates of trout and salmon in the streams were low, probably because of high population densities and poor food supplies. The growth of trout and salmon in the River Dee was also assessed and was found to be significantly faster than in the Llyn Tegid feeder streams.

The age and size composition of the 1969 and 1970

Llyn Tegid salmon smolt runs were investigated together with factors influencing the time of smolt descent, the passage of smolts through the lake and predation on smolts by pike (*Esox lucius* L.). The main smolt runs, which consisted mostly of 2 year old migrants, occurred in early May and the time of migration appeared to be chiefly correlated with water temperatures. Little predation on smolts by pike occurred, the pike being occupied with spawning activities at the time of smolt descent. The numbers of smolts produced in the Llyn Tegid feeder streams were estimated from mark-recapture experiments.

SUMMARY

of

Studies on Salmonid Fishes in Llyn Tegid and the Welsh Dee

by

J. V. Woolland