Aspects of the biology of the twaite shad, *Alosa fallax fallax* (Lacépède), in the Rivers Severn and Wye

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

By

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Frontispiece

The Severn Bore, at Newnham.

ABSTRACT

Biological studies were carried out on the twaite shad (*Alosa fallax fallax* (Lacépède)) in the Rivers Severn and Wye between October, 1978 and September, 1981.

The visible structure of the scale surface is described. The use of scales for age determination and reconstruction of the fish's growth history were validated. Scales also provided information on the number of previous spawnings. The coefficients of the Von Bertalanffy growth equation were determined, and the growth curve obtained agrees closely with that determined from back calculation. Similar growth rates were exhibited by both sexes up to age three, after which the growth rate of the females exceeds that of the males.

The adults enter the Severn estuary during the middle of April, the upstream migration continues over a nine week period, reaching a peak in the middle of May. Environmental factors were implicated in affecting their movement through the estuary. Temporal and spatial variation in the sex ratio, age and size structure, the relationship between total weight/-, somatic weight/-, and gonad weight/fork length for the adult population during the migration were investigated. The spawning areas are described and factors affecting the extent of the migration upriver are discussed. For females returning to the estuary following spawning, somatic weight loss ranged from a maximum of 10.3% (300 mm. fl.) to 25.7% (390 mm. fl.) and somatic fat levels were approximately 50% of pre-spawning levels.

The majority of the males mature at age three or four and females at four or five. Significant differences in the mean age at maturity for the females existed between sample years and appears related to growth rate. No significant difference was found for males.

Two size classes of eggs were present in the ovaries, the larger (0.44 - 1.61 mm. in diameter) were spawned. The relationship between fecundity and fork length, total weight, somatic weight, gonad weight and age was calculated. Multiple regression analysis indicated that total weight and age were the most important variables. Egg size was found to increase with ovary weight.

For those fish that survive, spawning is an annual event, once the fish reach maturity. Males were found to spawn as many as five times and females four. Changes in the proportion of repeat spawners of both sexes between sample years was investigated. Growth rate declined following maturation and the effect of reproduction on future 'fecundity' and survival was investigated.

The eggs and larval stages are described. In July and August, juveniles were found in freshwater stretches of the River Wye, few were caught after periods of high freshwater discharge. The majority of the juvenile population in the River Severn was present in the inner estuary from the end of July onwards. Final emmigration from the inner estuary occured between October and November. The juveniles reappeared in the estuary during the spring and remained until the following August. Large fluctuations in juvenile abundance were recorded between 1979 and 1981 and possible causative factors were investigated.

The diet is described for adult and juvenile populations from freshwater, estuarine and marine sites. The adults did not feed actively while in freshwater. Feeding recommences after spawning and the main dietary items in the estuary were mysids, gammarids and shrimps. The larvae and juveniles in freshwater fed mainly on simuliids, chironomid larvae and pupae and ephemeropteran nymphs and in the estuary copepods, mysids and gammarids predominated.

The change in diet with size of juvenile is discussed as well as the differential distribution of juveniles in the Severn and Wye which may be related to available food items.

Information on parasites was also obtained.

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CHAPTER ONE

INTRODUCTION

Introduction

The aim of the research was to investigate aspects of the biology of *Alosa fallax fallax* (Lacépède), the results of which are presented in this thesis. This species (plate 1.1) is an anadromous member of the family Clupeidae and its life cycle is shown in figure 1.1. The study was carried out on the Rivers Severn and Wye, from October 1978 to September 1981.

A. Historical

In the British Isles there are three members of the genus *Alosa*. Two of the species are anadromous, *Alosa alosa alosa* (Linnaeus, 1758) (now referred to as *A.alosa*), *Alosa fallax fallax* (Lacépède 1803) and one that is landlocked *Alosa fallax killarensis* (Regan, 1916) in the lakes of Killarney, south west Ireland (Regan, 1916, Trewavas, 1938).

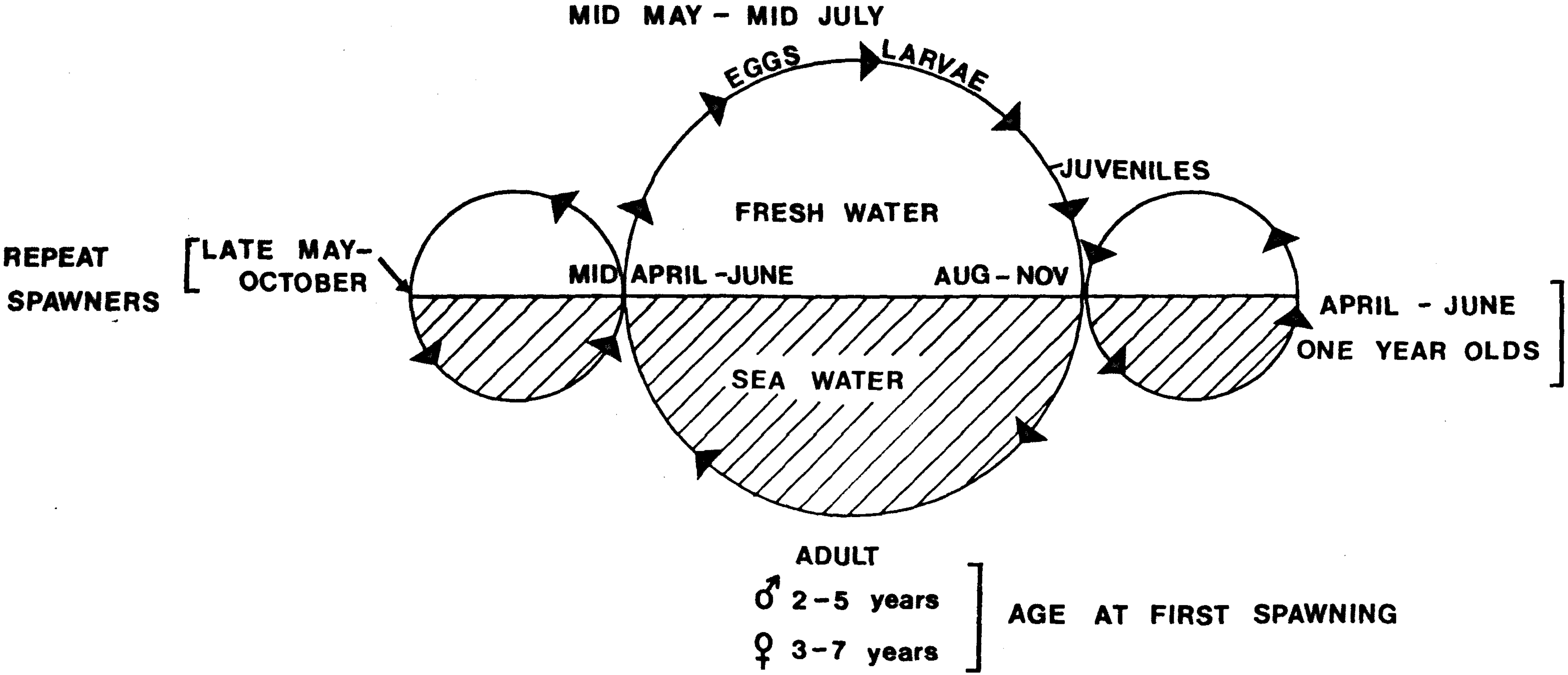
The first recorded written record of the shad was made by Giraldus Cambrensis who undertook extensive travels throughout the British Isles during the twelfth century. Of the Irish rivers he wrote, "The rivers and lakes, also, are plentifully stored with sorts of fish peculiar to those waters and especially three species: salmon and trout, muddy eels and oily shad . . ." Wright (1905).

The Shad, along with the salmon and the lamprey, was one of the principal kinds of fish sent from the River Severn to the court of Henry III and many references are made to shad in the Calender of Liberate Rolls.

In 1800, Gmelin (1800) wrote of *A.alosa* "The Severn produces the shad in higher perfection than any other British river . . .

Plate 1.1, Twaite shad, Alosa fallax fallax (Lacépède).

LIFE HISTORY OF THE TWAITE SHAD (*ALOSA FALLAX*) FIG 1·1



About Gloucester the shad is esteemed a great delicacy, it is caught in nets and sold at a price as high as that of salmon". A.fallax fallax was never so highly thought of and he reports the following - "There is a variety in the Severn near Gloucester called the twaite which is equally disesteemed as the Thames shad". A.alosa and to some degree A.fallax fallax were of considerable economic importance to the fishermen of the Severn. It was common for shad to make up as much as one third of their income from a fishery. However, in some instances, when there had not been a good run of salmon the shad would have brought in a lot more (Her Majesties Stationery Offices, 1861). About this time (1860) A.alosa was selling for between 9^d and 1/- per pound, A.fallax fallax for 3^d each and salmon 1/6 per pound (H.M.S.O. 1861). The importance of A.fallax fallax to the fishermen of the River Severn is further substantiated by a petition sent to the Severn Fishery District in 1888 against the proposed banning of the smaller meshed net $2^3/4$" diameter (1.75 cms knot to knot). This net was used principally for catching freshwater fish and ". . . much loss would be caused by the prohibition of netting for twaite . . ." However, it appears that A.fallax fallax was not included in the bye-law (Severn Fishery District, 1888).

In the River Wye, Kissak (1978) mentions that during the sixteenth century, shad were bought at Monmouth to relieve the poor during Lent. By the middle of the nineteenth century, however, shad did not appear to contribute greatly to the value of the fishery (H.M.S.O., 1861).

Since the middle of the nineteenth century there has been a decline in the abundance of the two anadromous species. The best documented evidence exists for A.fallax fallaxfrom the River Thames and for A.alosa from the River Severn. This decline has been mainly attributed to the construction of navigation weirs and to pollution. Yarrell (1836) mentions that ". . . Twaite shad appear during these three months (April - June)in abundance in the Thames from the first point of land below Greenwich, opposite the Isle of Dogs, to the distance of a mile below and great numbers were taken every season . . . Formerly great quantities were caught with nets opposite the present penitentiary at Millbank, Westminster. Above Putney bridge was another favourite spot for them; but the state of the water it is believed prevents the fish ascending the river in the same manner as in former years and comparatively few are taken . . ." Yarrell (1836) reports that A.fallax fallax were ". . . in little repute as food, their muscles being exceedingly full of bones and dry . . .". Wheeler (1979) mentions that shad bones have been found in several medieval archaeological sites in London indicating that they may have been an important food fish in the past.

The decline of the shad population in the River Thames coincided with that of Salmo salar, (Linnaeus) Platichthys flesus (Linnaeus) and Osmerus eperlanus (Linnaeus). Mr. Henry Farnell (Secretary to the Thames Angling Preservation Society) in 1860, blamed the decline on the increase in the numbers of steamers stirring up great amounts of ". . . frightfully offensive stuff . . ." (H.M.S.O., 1861). The decline was also recorded by Buckland and Walpole (1879) who quote a Gravesend 'Whitebait' fisherman as saying that ". . . only a few shad were caught now" (1877) their numbers having decreased. However, Murie (1903) claims that shad were still abundant and mentions captures at Queenborough,Swale, the Blyth sands Leigh, Hadleigh Ray and Southend. Robbins (1962) does mention that in Autumn, A.fallax fallax were abundant in the outer Thames estuary at Leigh-on-Sea. This does not appear to be the case today and A.fallax fallax in the River Thames must be regarded as exceedingly rare

(Andrews pers. comm., Wheeler 1958, 1979).

On the River Severn, navigation weirs were constructed at Gloucester, Tewkesbury, Worcester and Shrewsbury around 1842, and were thought by Day (1890) to partly explain their decline. The weirs at Worcester and Shrewsbury were probably the main factors in preventing A.alosa reaching their spawning grounds. Evidence given at the enquiry into salmon fisheries (England and Wales) in 1860 indicates that A.alosa used to migrate as far as Welshpool to spawn (H.M.S.O., 1861). Pennant (1810) mentions that they were known to occur in the River Vyrnwy during the spring. At the same time as the weirs were installed there was a considerable amount of road building taking place and construction engineers removed large amounts of gravel from many of the fords. This activity may also have enhanced the decline as it is on these gravel fords that a large proportion of the spawning takes place, (chapter four). It is interesting to note that as a result of the decline in the fishery for A.alosa in the Severn, fishmongers in Stroud (Gloucestershire) were importing A.alosa from as far away as Norway (Whitchell and Strugnall, 1892).

B. Distribution of Alosa fallax in the British Isles (figure 1.2)

At the present time a spawning population of A.fallax fallax is known to exist in the Rivers Severn and Wye. Around the majority of the United Kingdom, this species is only rarely seen Blacker (1969), Maitland (1972), Rae and Lamont (1962 a + b, 1963), Rae and Pirie (1969), Rae and Wilson (1952, 1953, 1956 a + b) and Wheeler and Blacker (1972) Wheeler et al. (1975).

In the past a number of authors have recorded their presence around the coast. Day (1880-1884) mentions their occurence along the east coast between Banff and Yarmouth. Sim (1903) reported

Figure 1.2 The distribution of *Alosa fallax* in the British Isles

Rivers	
1	Tyne
2	Colne
3	Thames
4	Axe
5	Exe
6	Teign
7	Dart
8	Clyde
9	Cree
10	Mersey
11	Dee
12	Ogwen
13	Dovey
14	Tywi
15	Taf
16	Loughor
17	Usk
18	Wye
19	Severn
20	Slaney
21	Barrow
22	Nore
23	Suir
24	Blackwater
25	Lee
26	Bandon
27	Ilen
29	Foyle

Lakes	
28	Lakes of Killarney


Banff
Oban
Firth of Forth
Eyemouth
8
1
9
Wigtown Bay
29
Dundalk Bay
Clogherhead
Howth
Blackpool
Formby
10
Anglesey
12
11
21
22
23
20
Barmouth
13
Cardigan Bay
Yarmouth
Dingle Bay
28
24
25
26
27
15
18
19
14
16
17
2
3
London
5
4
6
7
Isle of Wight

their occasional occurence off the east Scottish coast. Rae and Lamont (1964) reported that in 1962, a large number were caught off Eyemouth during the winter. Relatively large numbers were also caught in 1956 (Rae and Wilson, 1961) and in 1957 (Rae and Lamont, 1961). Parnell (1831-1837) found that they were ". . . tolerably abundant" in the Firth of Forth between July and August. Meek (1916) mentions the occurence of a specimen from the Tyne and Lowe (1901), recorded occasional catches off the coast of East Anglia. Paget (cited by Day 1880-1884) mentioned that at Yarmouth they were not uncommon. Laver (1903) mentions that A.fallax fallax were sometimes quite common in the River Colne.

Boulenger (1900) reported their occasional occurence off the south coast, at Hampshire and the Isle of Wight whilst Cunningham (1906) who recorded their presence in Devon, and more recently reports of their occasional occurence have been recorded in the Anglers Mail (1972, 1974, 1978) and the Angling Times (1974). Couch (1877) reported that large numbers were frequently taken by drift nets off the Cornish coast. In the south west rivers this species is comparatively rare though a few are caught by the commercial salmon netsmen in the Rivers Axe, Exe, Dart and Teign (Davis, pers. comm.) Kennedy (pers. comm.) has obtained reasonable numbers from the River Exe and this suggests that they may be slightly more abundant in this region. However, the commercial fishermen in the Exe have noticed a decline in the numbers being caught over the last decade (Kennedy pers. comm.).

Along the west coast they have been reported from Oban (Gordon pers. comm.) and from the Clyde (see review by Bagenal, 1965). Gordon (1921) mentions that they were not uncommon in the nets operating in Wigtown Bay and that they spawned in the River Cree. Glastone (1912) also mentions that they were common in this region.

However, Hutchinson (pers. comm.) has recently carried out extensive netting in the River Cree and has only recorded a single specimen. There are occasional records of their occurence off the Cumberland coast (MacPherson, 1901; Day, 1880-1884), the Duddon estuary (Stewart cited by Ellison and Chubb, 1962) from Blackpool and Formby (Herdman and Dawson, 1902; Johnstone, 1906), the river Mersey (Johnstone, 1906) and ". . . sometimes in the Dee . . ." (Walker, cited by Johnstone, 1910; O'Hara, 1976).

Along the North Wales coast, Professor White (cited by Herdman and Dawson, 1902) believed that a spawning population existed in the River Ogwen. They have also occasionally been caught off the coast of Anglesey (Gosling cited by Forrest, 1907) and in Cardigan Bay at Barmouth (Lister cited by Forrest, 1907). In recent years a number of adults have been caught in the Rivers Dovey and Mawddach during the spring (Lewis pers. comm.; Shaw, 1977) and it is possible that a small spawning population exists in these rivers. During late September early October this species may be caught in inshore stake nets in Cardigan Bay. These may be fish leaving west Wales rivers on their over-wintering migration or members of the Severn and Wye populations. A spawning migration occurs in the spring in the Rivers Tywi and Taf, south Wales (Neville-Jones, 1972) and reports from the Loughor (Shaw, 1977) and in the River Usk (Lambert pers. comm.; Shaw, 1977) where they are known locally as 'Scatsyn'.

In Ireland the species is known locally as 'Boney Horseman', 'Alewife' and 'Chops' (Farran, 1946). Spawning populations are known to exist in most of the rivers on the south coast notably the Barrow, Suir, Nore and Blackwater (Bracken and Kennedy, 1967; Went, 1953). Specimens have also been caught in the Rivers Ilen, Bandon, Lee and Slaney (Went, 1963). They have only occasionally been caught around the rest of the Irish coast at Howth (O'Riordan, 1965), Clogherhead (Minchin and Molloy, 1978) in Dundalk Bay, the

Irish Sea and Dingle Bay (Bracken and Kennedy, 1967). During the summer of 1980 a number were taken in the Foyle estuary by the commercial salmon netsmen (Johnston pers. comm.).

A landlocked population A.fallax killarensis is found in the lakes of Killarney, south west Ireland and is locally known as the 'Goureen' (Gibson, 1956; Regan, 1916; Trewavas, 1938; Twomey, 1958).

Numbers of specimens have occasionally been caught in trawls made in the English Channel and the Irish Sea (Bowers pers. comm.; Bruce et al., 1963, Jenkins, 1942; Marine Biological Association Plymouth, 1957 and Wallace pers. comm.).

C. European Distribution of Alosa fallax

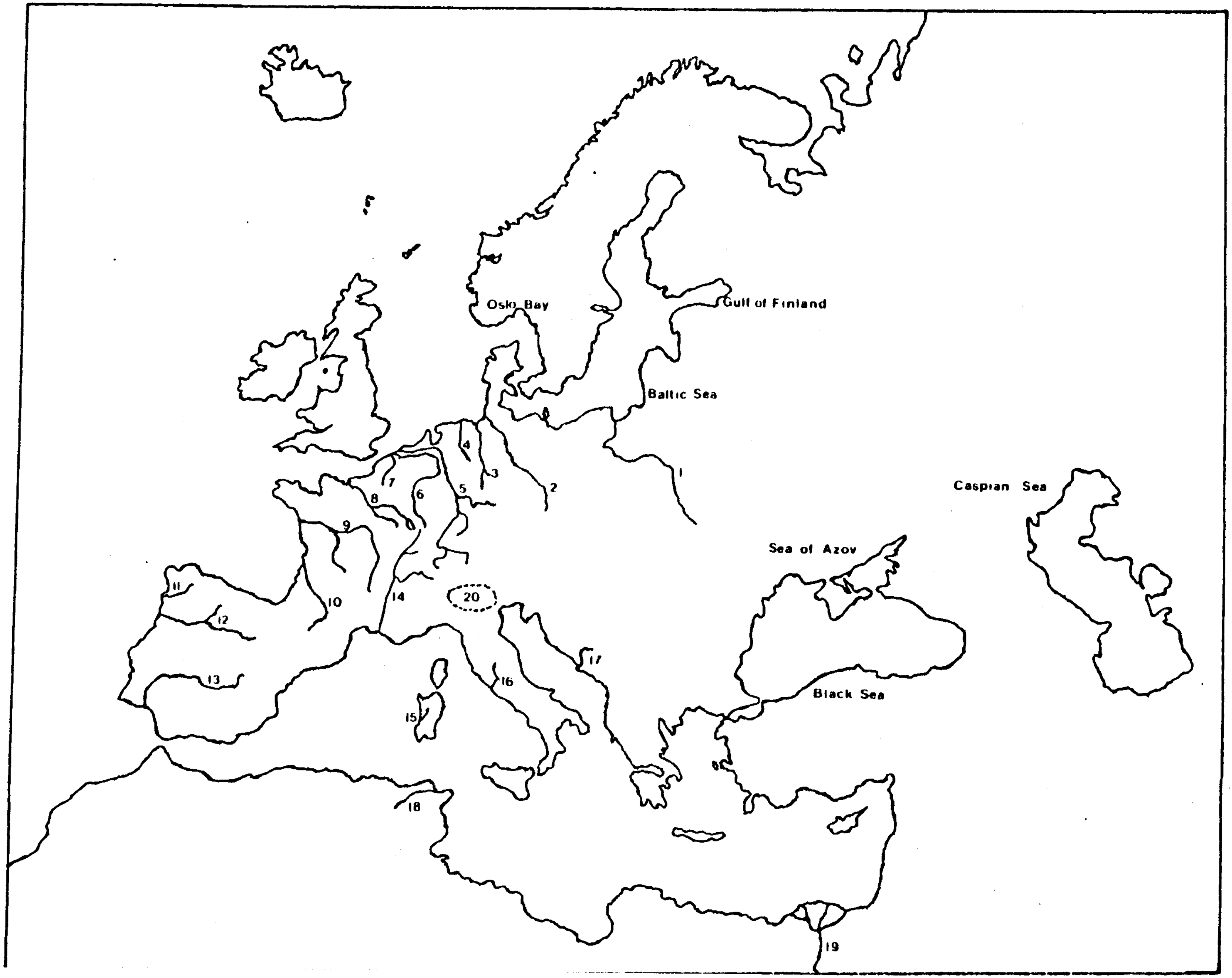
According to the taxonomic study of Quingard and Kartas (1977) there exists four anadromous species of A.fallax; Alosa fallax fallax (Lacépède, 1803), Alosa fallax rhodanensis (Roule, 1924), Alosa fallax algeriensis (Regan, 1916) and Alosa fallax nilotica (Geoffroy Saint-Hilaire, 1808). There are also two landlocked populations; Alosa fallax killarensis (Regan, 1916) and Alosa fallax lacustris (Fatio, 1890).

The main areas of distribution presently discussed are taken from Lelek (1980) and are shown in figure 1.3. A.fallax fallax (from now on referred to as A.fallax) has been recorded as far north as Iceland (Saemundsson, 1949). In northern Europe the sub-species has been reported from Scandinavia by Couch (1877) (citing a report by Nilsson) and Seeley (1886), their most northerly occurence appearing to be the Bay of Oslo. They are also present in the Baltic Sea, the limit of their distribution on the northern shore ends level with Stockholm and on the southern shore, the Gulf of Finland. In Poland, on the southern shore of the Baltic Sea, Chmielewski (1965) records their presence in the lower reaches of the River Vistula.

Figure 1.3 European Distribution of *Alosa fallax*

Rivers

1	Vistula
2	Elbe
3	Weser
4	Ems
5	Rhine
6	Meuse
7	Escaut
8	Seine
9	Loire
10	Garonne
11	Mino
12	Douro
13	Quadiana
14	Rhone
15	Tirso
16	Tiber
17	Neretva
18	Miliane
19	Nile
20	Lakes of:
	Como, Garda, Iseo, Lugano and Maggiore


Oslo Bay
Gulf of Finland
Baltic Sea
Caspian Sea
Sea of Azov
Black Sea
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

In West Germany, a spawning population is known to exist in the River Elbe (Hass, 1965) it is also known to be abundant in the Rivers Weser and Ems (Svetovidov, 1963). A spawning population was also known to exist in the Rhine (Hoek, 1900; Redeke, 1938; Regan, 1911) and in the Meuse River, (Cunningham, 1891-1892, citing work by Metger and Hoek). This population may now not be as abundant as a result of the construction of a barrage (Poll, 1947). Very few are now recorded from around the Dutch coast and the decline may be attributed to the construction of dams preventing the fish from reaching their spawning grounds, Steinmetz (pers. comm.). Along the coast of Belgium a spawning population was found to exist in the River Escaut and its major tributaries, the Rivers Rupel and Durme (Poll, 1947).

In France A.fallax have been recorded in the Seine (Roule, 1922) the Loire (LeClerc, 1941) and in the Garonne (Quignard and Kartas, 1977). On the north west coast of Spain spawning populations were reported from the River Mino (Steindachner, cited by Seeley 1886) and in Portugal, spawning populations are known to exist in the River Douro and Guadiana (Eiras, 1980). The southern limit of their distribution appears to be in Morocco (Lahaye, 1962; LaHaye et al., 1963).

In the Mediterranean, they have been recorded off the coast of Algiers (Bounhiol, 1917). This may, however, be the sub-species A.fallax algeriensis, Quignard and Kartas (1977) found this sub-species along the coast of North Africa ranging from Tunisia to Morocco. Populations have been recorded from the River Miliane, Tunisia Pellegrin (1921) (cited by Quignard and Kartas, 1977). Cottiglia (1963, 1969) recorded a spawning population in the River Tirso, Sardinia, that is also probably a member of this sub-species.

The sub-species A.fallax rhodanensis also found in the Mediterranean was recorded as spawning in the Rivers Rhone and Saône, France by Roule (1933). The population in the Rhone has since declined due to the construction of dams along the system (Ramaye et al., 1976). D'Ancona (1928) recorded a population of A.fallax nilotica spawning in the River Tiber, Italy but according to Quignard and Kartas (1977) this sub-species is more likely to be A.fallax rhodanensis.

In the eastern half of the Mediterranean, the sub-species A.fallax nilotica is found in the Adriatic in the River Neretva and the Lakes Skadarsko and Bacinska, Yugoslavia (Vukovic, 1961; Pavlovic and Pantic, 1975), the sea of Marmara and the Black Sea (Kerch Strait) Svetovidov (1963). This sub-species has also been recorded from the River Nile, Egypt (Boulenger, 1907).

A number of landlocked populations have also been recorded. The sub-species A.fallax lacustris in the Lakes Lugano and Maggiore (Fatio, 1890) as well as Lakes Como, Garda and Iseo, Italy (Lelek, 1980). A landlocked population of A.fallax nilotica has been reported from Lake Skuta, Albania (Lelek, 1980, Maitland, 1979), there is also a non-anadromous population in Sardinia (Cottiglia, 1969).

CHAPTER TWO

STUDY AREA AND FIELD METHODS

A.1 Severn River Basin

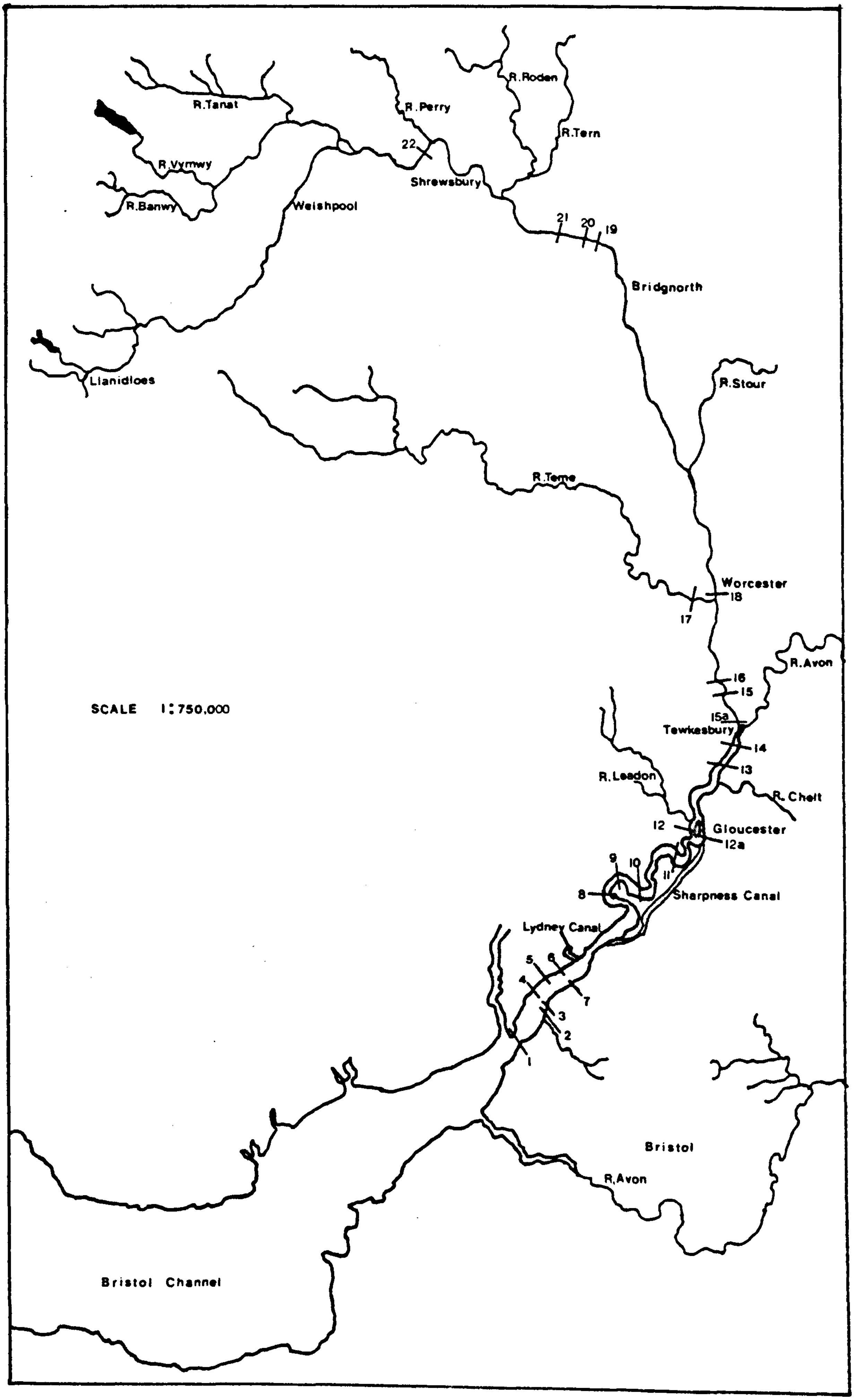
The Severn River basin (figure 2.1) is the largest in Great Britain, covers an area of 11,404.5 square kilometres and is roughly shaped like the letter 'Y' with a mean run-off of 115.7 cumecs. It reaches from Rugby in the east to Lake Vyrnwy in the west and the Bristol Channel in the south. The human population situated along the river is approximately ten times greater than that of the Wye basin and the major towns are Shrewsbury, Bridgnorth, Tewkesbury and Gloucester.

The source of the River Severn is on the slopes of Plynlimon, a height of 739.2 metres above sea level. The river flows from there in a north easterly direction to Shrewsbury. There are many tributaries joining the Severn in this region including the Banwy, Vyrnwy and Tanat. By the time the river reaches Montford it has fallen to 52.4 metres above sea level. Here is is joined by the Perry, Roden and Tern and from here on the river follows a southerly course to the Bristol Channel. Some 19.2 kilometres below Shrewsbury the river enters the Ironbridge Gorge, one of the early industrial areas of Coalbrookdale, Ironbridge and Coalport. The heavily industrialized area of Wolverhampton, Dudley, Stourbridge and Kidderminster drains into the Severn via the polluted and discoloured tributary the Stour. At this point the river is 17.4 metres above sea level.

The area to the west of Shrewsbury and Worcester is mostly rural with rich fertile lowlands, particularly in the Teme Valley. The Teme joins the Severn just below Worcester and this river, with its tributary the Clun, flows through country which is heavily

Figure 2.1 Severn River Basin

22	Montford
21	Coalbrookdale
20	Ironbridge
19	Coalport
18	Diglis Weir
17	Powic Weir
16	Upton-on-Severn
15a	Upper Lode weir
15	Saxons Lode
14	Deerhurst
13	Wainlode
12a	Maisemore Weir
12	Llanthony Weir
11	Elmore
10	Framilode
9	Broadoak
8	Newnham
7	Hayward Rock putchers
6	Lydney putchers
5	Guscars Rocks
4	Pillhouse Rocks
3	Oldbury Power Station
2	Narlwood Rocks
1	Severn Bridge (division between inner and outer estuary)


R.Tanat
R.Roden
R.Perry
R.Tern
22
R.Vymwy
Shrewsbury
R.Banwy
Welshpool
21
20
19
Bridgnorth
Llanidloes
R.Stour
R.Teme
Worcester
18
17
R.Avon
16
15
SCALE 1:750,000
15a
Tewkesbury
14
13
R.Leadon
R.Chelt
12
Gloucester
12a
9
10
11
8
Sharpness Canal
Lydney Canal
5
6
4
7
3
2
1
Bristol
R.Avon
Bristol Channel

cultivated for hops and soft fruits.

At Tewkesbury the river is approximately 13.7 metres above sea level and is joined from the east by another major tributary the Avon. This river includes the towns of Rugby, Coventry, Warwick and Stratford-on-Avon situated along its length and runs through the fertile Vale of Evesham. This area around Tewkesbury is the most densly populated in the Severn basin.

The section between Tewkesbury and Gloucester is tidal and navigable. Here it is joined by the Leadon and the Chelt. The area below Gloucester is subject to the effects of the greatest tidal range in the United Kingdom, there is a difference of some 10.4 metres between low and high tide levels. The division of the river and the weirs at Gloucester break the force of the bore (a wall of water produced by the flood tide) and prevent all but the high spring tides passing the town but, with exceptions, the effect of the tides pass up as far as Tewkesbury.

Below this area the receding tide leaves deep mud. When the river flow is low, high tides cause a reversal of flow in the river and water, pumped from the river into Gloucester Docks to supplement the water in the Sharpness Canal, stirs up large quantities of mud and silt.

The first part of the estuary is the Nooze a wide expanse of mud and sandbanks exposed at low water leaving a channel fed by tributaries or pills, the preponderance of these from the Forest of Dean. The disposition of the channel is influenced by the inflow of water from the Sharpness and Lydney Canals and the various pills as well as the interception of the Guscar, Pillhouse and Narlwood rocks. The last major tributary entering the inner estuary before the Severn Bridge is the Olbury Pill, a little lower the main channel is directed through the 'shoots', a channel cut through rock by the combined Severn and Wye, across to join the Avon and thus reach the outer estuary.

2. Geology

The geology of the Severn hydrometric area is complex. It is underlain by rocks ranging in age from Pre-Cambrian to Jurrassic and there are extensive Pleistocene glacial drift deposits throughout the region. These vary in thickness by locality.

Describing the area from north to south, the source in the Welsh highlands flows over Ordovician and Silurian rocks which are relatively poor aquifers and on down over drift deposits in the valley between Llanidloes and Montford. There are local 'spreads' of sand and gravels and areas of Carboniferous and Silurian limestone are exposed along the river bed. The gradient at this point prevented the deposition of alluvial silts and muds. Carboniferous rocks underlay most of the Shropshire flood plain covered by extensive Glacial drift deposits and there are large areas of sands and gravels termed the 'Buildwas sands' between Ironbridge and Coalbrookdale.

The Ironbridge Gorge is of recent origin and was formed when the glacial 'Lake Lapworth' overflowed through Ironbridge thus diverting the River Severn which had previously flowed northwards towards the watershed of the Welsh River Dee. The bedrock of the gorge is composed of clean unsilted Triassic and Carboniferous limestone sands. Between Ironbridge and Bridgnorth extensive Carboniferous rocks and a few Old Red Sandstone intrusions and Triassic 'Bunter Pebble' beds underly the river. These are exposed in places and known as 'fords'.

Below Bridgnorth there are further 'fords' appearing through patchy gravel drift deposits which overlay lower Keuper Sandstone down as far as Worcester. The Worcester area down to Tewkesbury is characterised by Rhaetic and Keuper Marl. It is bound to the west by the Malvern Hills representing some of the oldest known material in the British Isles, Granatoid rocks and to the east by a large area of lower lias. The Keuper marl of the Severn Vale is a series of red and green, slightly calcareous mudstones and sandstones. It is these Keuper rocks which give rise to the characteristic red soils of the Severn Valley. Terrace gravels are found throughout the area and are a result of rivers transporting and redepositing material of glacial origin as terraced river deposits.

Below Tewkesbury and down the length of the inner Severn estuary to Severn Bridge, the surrounding land, geologically speaking, is not very well documented. Patches of thin drift are found over much of the area with occasional deposits of Millstone grit and carboniferous limestone.

Information presented in the previous two sections was taken from publications by the following authors: Adlam (1974), Ellis (1909), H.M.S.O. (1948, 1960, 1961 and 1971), North (1955), and Rodgers (1947).

3. Description of the Sites

River Severn

Outer Estuary - Below Severn Bridge, Beachley Point to Aust Cliffs. River width 2.6 km. (Plate 2.1).

On the Beachley side the shore is a continuous mud bank backed by salt marsh. The Aust side is a steeper mud bank, fringed with salt marsh along the top and backed by sandstone cliffs. The outer estuary narrows at this point to 2.6 km. wide creating the neck to the funnel shaped estuary.

Adults - Salmon drift net.

Juveniles - Sampled using Otter Trawl and Beam Trawl.

Plate 2.1, Severn Bridge, looking from Beachley Point
to Aust cliffs.

Plate 2.2, Severn estuary at Newnham.

Inner Estuary

Oldbury - Power Station. Grid reference ST 604945. River width 3.7 km.

An artificially created reservoir surrounded by natural and artificial rocky outcrops or ledges. The shore is composed of steep mud cliffs dropping right down to the low water mark and the rest of the estuary is filled with extensive sandbanks usually cut off from land, even at low water, by deep channels. Salt marshes occur along both banks.

Adults and Juveniles - Sampled from Power Station cooling water intake using 'Micromesh' cone nets.

Newnham - Grid reference SO 693100. River width 600m. (Plate 2.2)

Situated on a large loop of the river, one bank is a high cliff of sandstone followed closely by the deep water channel the other a gently sloping bank leaving large sandbanks exposed at low water with occasional patches of soft mud.

Adults - Sampled using Salmon seine net and 85.2 m seine net.

Juveniles - Sampled using 20 m 'micromesh' seine net and large 'fry' seine.

Framilode - Grid reference SO 742107. River width 350 m.

A narrower more riverine site with lower banks, tree lined on one side. A large sandbank exposed at low water and more residual mud than at Newnham.

Adults - Sampled by Salmon seine net.

Juveniles - 20 m 'micromesh' seine net.

Elmore - Grid reference SO 792163. River width 100 m. (Plate 2.3)

At this point the sand gives way to steep mud banks protected on the sharper bends by boulders to stop erosion by the force of the tidal bore. The banks are topped by meadow land and the river edge lined by shrubs and trees.

Adults - Sampled by Salmon seine net.

Plate 2.3, Severn estuary at Elmore, with the Severn bore approaching.

Plate 2.4, River Teme at Powic weir, looking downstream. Shallow gravel areas along the right hand side utilized for spawning.

Juveniles - Sampled using 20 m 'micromesh' seine net.

Wainlode - Grid reference SO847258. River width 100 m.

The site sampled was at the base of a small sandstone cliff with a gradually shelving beach of bedrock and fine silt. The far bank where the main channel runs is lined with overhanging willow trees and shrubs.

Adults - Sampled by electrofishing from a boat.

Juveniles - Samples using 20 m 'micromesh' seine net.

Deerhurst - Grid reference SO 858292. River width 100 m.

At this point the river bed cross section is more  shaped with tree and shrub lined banks and muddy shelving beaches. The bottom is gravel covered with layers of fine silt and mud. Land on either side of the river consists of water meadows frequently subject to flooding.

Juveniles - Samples using 20 m 'micromesh' seine net.

Eggs and larvae - Sampled using fine mesh cone nets set to catch drift.

Upton-on-Severn - Grid reference SO 864397. River width 75 m.

A very similar site to Deerhurst though there is a much thicker covering of shrubs and overhanging trees on both banks. River bottom silty. Once again surrounding area water meadows subject to flooding.

Juveniles - Samples using 20 m 'micromesh' seine net.

Diglis Weir - Grid reference SO 847534. River width 75 m.

This weir constructed for navigation purposes, forms an effective barrier to the upstream migration of *A.fallax* on the Severn. The area downstream of the weir acts as a large holding pool and salmon fishermen catch numbers of *A.fallax* in late May and June.

Adults - Sampled for using rod and line.

River Teme

Powic Weir - Grid reference SO 832524. River Width 50 m. (Plate 2.4)

The site, immediately downstream of Powic Weir, is bounded by banks of between five and six metres in height above river bed level. The Teme, when the main river is full is caused to pond back upstream. The weir is breached in part and has an open fish ladder which does not act as an obstruction to the upstream movement of A.fallax but the fish tend to congregate in a pool just below the weir. There are extensive gravel fords, which are utilized for spawning, stretching downstream to the junction with the Severn.

Adults - Sampled for using Rod and line and Electric fishing.

Eggs - Sampled for using FBA net.

Larvae - Sampled for using 20 m 'micromesh' seine net.

B.1 Wye River Basin

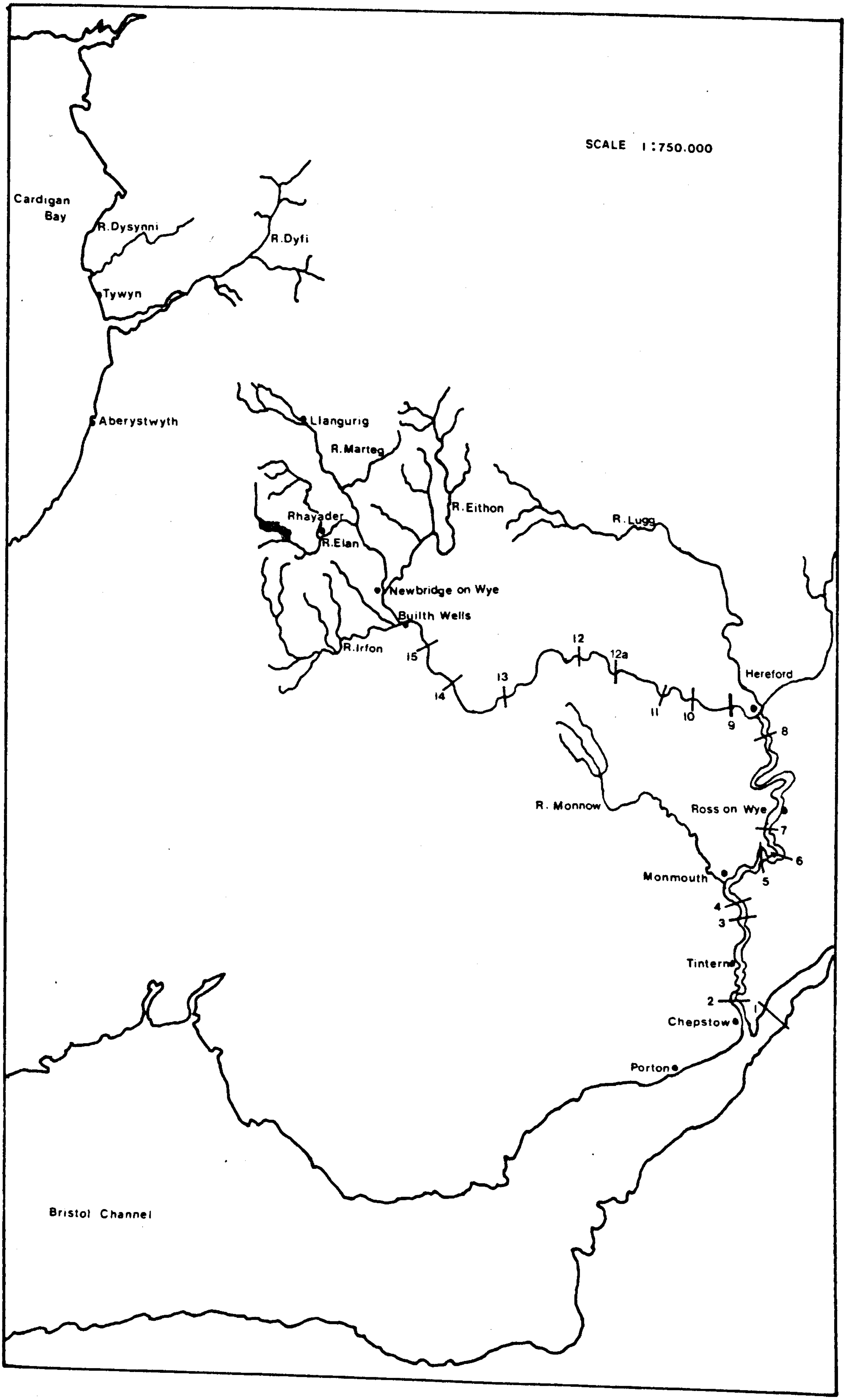
The area lies to the west of the Severn Basin with which it has many similarities. These two large rivers both rise on the shoulders of Plynlimon but whereas the river Severn takes a wide sweep to the north east before entering the Severn estuary, the River Wye takes a south east course to the same estuary, figure 2.2.

The superficial area of the River Wye basin is 4,183 square kilometres and is very sparsely populated when compared to the Severn basin. The principle towns along the 250.5 Kilometre length of the river being Rhyader, Builth Wells, Hereford, Ross-on-Wye, Monmouth and Chepstow.

The source or sources of the River Wye are on the slopes of Plynlimon at an altitude of approximately 677 m above sea level. It is soon joined by a number of small tributaries and by the time it reaches Llangurig it is already a sizeable river. Large

Figure 2.2 Wye River Basin

15	Erwood
14	Pipton
13	Glasbury
12	Winforton
12a	Brobury
11	Byford
10	Bridge Sollars
9	Belmont
8	Holme Lacey
7	Hillcourt
6	Courtfield
5	Symonds Yat
4	Redbrook
3	Bigsweir
2	Longhope Reach
1	Slime Road Putchers


SCALE 1:750.000
Cardigan Bay
R.Dysynni
R.Dyfi
Tywyn
Aberystwyth
Llangurig
R.Marteg
R.Eithon
Rhayader
R.Elan
R.Lugg
Newbridge on Wye
Builth Wells
R.Irfon
15
14
13
12
12a
11
10
9
Hereford
8
R. Monnow
Ross on Wye
7
6
5
Monmouth
4
3
Tintern
2
1
Chepstow
Porton
Bristol Channel

tributaries come in from other valleys in the rugged and mountainous country such as the Marteg, Elan, Ithon and Irfon which in turn increase the volume and size of the Wye to an average of 34.2 cumecs by the time it reaches Builth Wells.

Below Builth Wells the river drops down through Erwood to Glasbury where it takes a left hand bend and emerges from the valley into a richly agricultural plain meandering past Hereford where it is joined by the River Lugg and its tributaries. The river continues on through orchard lands past Ross-on-Wye to Symonds Yat through a series of gorges and on down to Monmouth where it is joined by the last big tributary, the River Monnow. Below Monmouth the river cuts its way through into a massive gorge winding past Tintern and finally the sheer cliffs at Chepstow and enters the Severn estuary 2.06 kilometres further south. A peculiarity of the mouth of the Wye is the long narrow Beachley peninsula with its sheer drop to the Severn in the east. The river near Chepstow has a buried channel cut 16.45 m deep which is filled with alluvium.

The tidal limit is about 1.6 kilometres below Redbrook and by this time the average discharge has increased to 71.56 cumecs.

2. Geology

Although complex in detail the geology of the Wye hydrometric area can be much simplified in broad outline. The Wye above Erwood and the upper part of the Lugg both drain Lower Palaeozic rocks which are relatively impermeable and only hold small volumes of ground water in storage. Silurian rocks of the Woolhope dome crop out east of the confluence of the Lugg and the Wye. The remainder of the hydrometric area is underlain by Old Red Sandstone strata except for an outcrop of Carboniferous rocks along the south-eastern margin and a restricted outcrop of Triassic and Jurassic strata near Chepstow.

The solid rocks are covered by widespread superficial deposits consisting of alluvium and gravel along the bottom of most of the river valleys, head deposits on the valley sides and glacial boulder clay over much of the country north west of Hereford, frequently overlain by layers of peat on high ground.

Information presented in the previous two sections was taken from publications by the following authors: Brown (1959), H.M.S.O. (1961, 1965, 1970, 1971), North (1955), Rodgers (1947) and Searle (1970).

3. Description of the Sites

Chepstow - Long Hope Reach - Priors Reach.

Grid reference ST 535943/538968. River width 300 m. (Plate 2.5)

This site, approximately 6 kilometres in length consists of a series of meanders cut through sheer Carboniferous Limestone cliffs some 91.4 metres above sea level. The reach is heavily wooded on both sides and at low water large banks of tidal mud are exposed.

Adults - Sampled using a Trammel net.

Monmouth - Grid reference SO 514121. River width 150 m. (Plate 2.6)

The main feature at this site was a crib or croy made of concrete which creates a deep pool behind it with a slight current apparent during summer flow. The rest of the river is a series of runs and pools with a large gravel shoal on the opposite bank. The surrounding land is river meadows and a dense wood on the cribside.

Adults - Sampled for using rod and line.

Juveniles - Sampled using 20 m 'micromesh' seine.

Eggs and Larvae - Sampled using fine mesh cone nets and F.B.A. net.

Courtfield - Grid reference SO 584173. River width 100 m. (Plate 2.7)

A large gravel shoal extending two thirds across the river bed was the main feature of the site. The bank where the main channel

Plate 2.5, Wye estuary, looking down Long Hope Reach.

Plate 2.6, River Wye at Monmouth, shallow gravel areas along the right hand side utilized for spawning.

Plate 2.7, River Wye at Courtfield, gravel shallows in foreground utilized for spawning. 'Kick' and drift sampling for eggs, in progress. Two grey cone nets can be seen.

Plate 2.8, River Wye at Pipton.

runs was steep and heavily wooded with overhanging trees. The gravel shoal was backed by a shallower bank, lightly shrubbed and topped by cultivated fields.

Adults - Sampled for by rod and line.

Juveniles - Sampled for using 20 m 'micromesh' seine net.

Eggs and Larvae - Sampled using fine mesh cone nets and F.B.A. net.

Hillcourt - Grid reference SO 566218. River width 100 m.

Situated on a bend in the river with steep banks on either side, one heavily wooded, agricultural land on the other. There are a series of gravel shoals culminating in a deep pool and back eddy.

Juveniles - Sampled for using 20 m 'micromesh' seine net.

Eggs - Sampled using fine mesh cone nets to catch drift and F.B.A. net.

Holme Lacy - Grid reference SO 565328. River width 100 m.

A site very much like Courtfield with a large gravel shoal extending half way across the river. The bank where the main channel runs is very steep. The surrounding land is used for grazing.

Eggs - Sampled for using F.B.A. net.

Byford - Grid reference SO 399426. River width 100 m.

The site consisted of a very long shallow gravel ford averaging half a metre or less in depth of water. Both banks shallow and overhung with Willow trees.

Juveniles - Sampled for using 20 m 'micromesh' seine net.

Eggs - Sampled for using F.B.A. net.

Winforton - Grid reference SO 293462. River width 150 m.

A loop on the river consisting of two gravel fords with a deep pool of slack water in between. Banks steep and topped with grazing land.

Adults - Sampled for using rod and line.

Juveniles - Sampled for using 20 m 'micromesh' seine net.

Eggs - Sampled for using F.B.A. net.

Glasbury - Grid reference SO 181394. River width 150 m

A very shallow gravel run with large areas exposed under low flow conditions. One bank is very heavily undercut producing a deep pool. Surrounding land used for grazing.

Adults - Sampled for using rod and line.

Juveniles - Sampled for using 20 m. 'micromesh' seine net.

Eggs - Samples for using fine mesh cone nets to catch drift and F.B.A. net.

Pipton - Grid reference SO 163382. River width 75 m. (Plate 2.8)

Areas of bed rock show through the gravel shoals at this site. There is a deep pool under one bank. Overhanging trees and shrubs on both banks backed by cultivated farmland.

Juveniles - Sampled for using 20 m 'micromesh' seine net.

Eggs - sampled for using F.B.A. net.

Builth Wells - Grid reference SO 043513. River width 200 m.

Shallow site, mostly bed rock and fairly large boulders with small amounts of gravel on the river bed. Shallow shelving banks with a few shrubs and trees, surrounding land used for grazing. This site just on the outskirts of the town.

Eggs - Sampled for using F.B.A. net.

C. Cardigan Bay

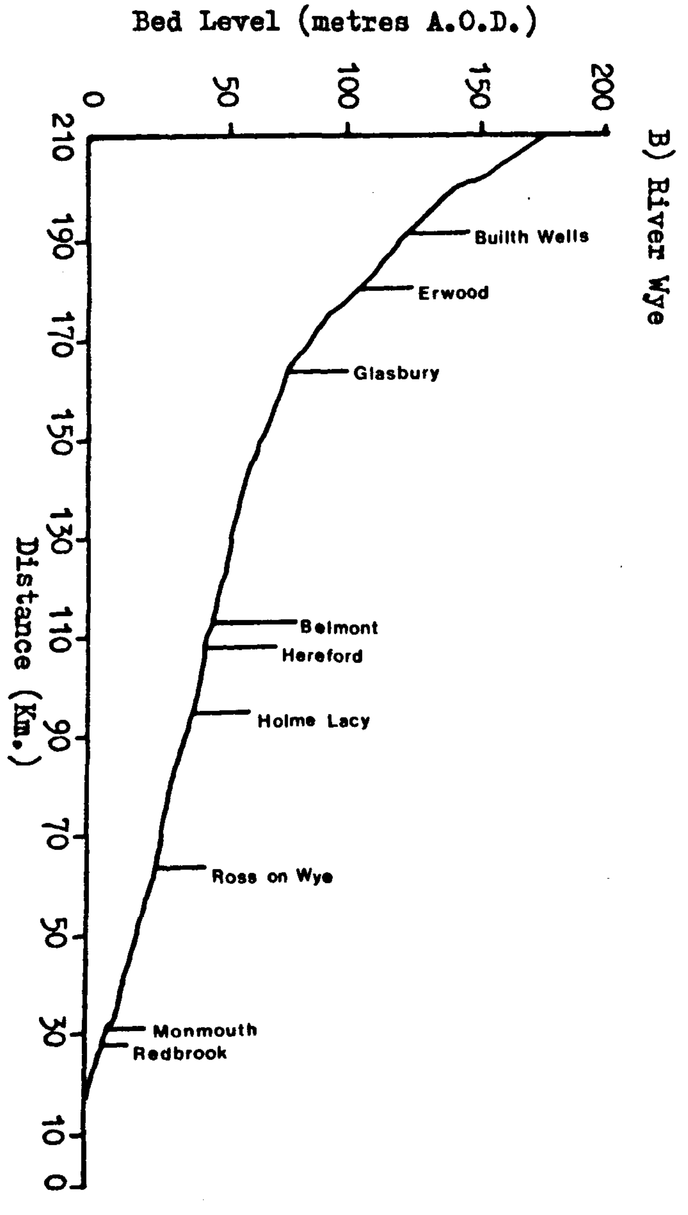
Tywyn

A shallow shelving stoney beach.

Adults - Sampled for using a stake net.

D. Bed Profile

A longitudinal profile of the river bed is shown in figure 2.3 A + B for the River Severn, from Newnham to Worcester, and


Bed Level (metres A.O.D.)
0
50
100
150
200
B) River Wye
210
190
170
150
130
110
90
70
50
30
10
0
Distance (Km.)
Builth Wells
Erwood
Glasbury
Belmont
Hereford
Holme Lacy
Ross on Wye
Monmouth
Redbrook

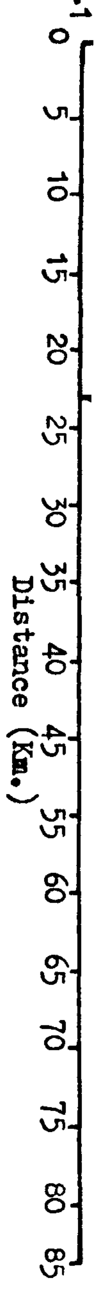
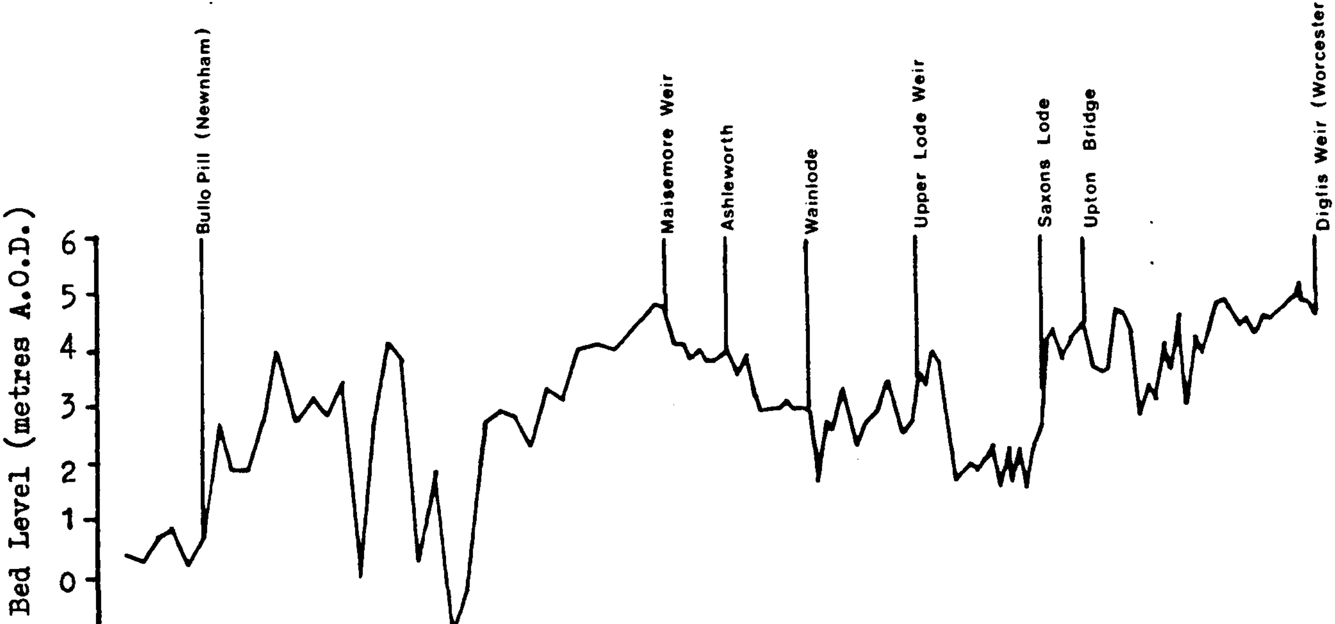

-1
0
5
10
15
20
25
30
35
40
45
55
60
65
70
75
80
85
Distance (Km.)

Figure 2.3, A & B, Bed profile for the rivers Severn and Wye.

A) River Severn



for the River Wye, from its mouth to Builth Wells. These profiles were obtained from the Severn Trent and Welsh Water Authorities, respectively.

The height of the weirs on the River Severn at Llanthony, Maisemore, Upper Lode and at Diglis were; 6.0, 6.5, 8.04 and 10.4 metres above ordnance datum, respectively, (British Water Ways Board, pers. comm.).

E. Water Quality

According to the National Water Council (1981) the quality of the River Wye upstream of Brobury (grid reference SO 345436) has been designated '1A', the dissolved oxygen saturation being greater than 80%, the biochemical oxygen demand does not exceed 3 mg./L., and the ammonia level is not greater than 0.4 mg./L. The River Wye below Brobury to the estuary, and the River Severn from Worcester (limit of the study area) to Gloucester are of quality '1B'. The dissolved oxygen content being greater than 60%, biochemical oxygen demand not exceeding 5 mg./L., and ammonia levels not greater than 0.9 mg./L. Thus the water quality may be regarded as 'good'.

Some chemical parameters were obtained from the Welsh and Severn and Trent Water Authorities for the two river systems, these are presented in tables 2.1 and 2.2. These are given for three sites from April to September, covering the area and time that *A.fallax* might be expected to be present in each river system. The chemical characters measured by the two authorities were different and presumably depended on their respective requirements. Where possible the same characters have been compared.

The estuary of the Wye and the greater majority of the inner Severn estuary down to the mouth of the Wye, may be regarded as 'good' in quality (N.W.C., 1981). The outer Severn and a small portion of

Table 2.1 Some chemical components of the water from three sites on the River Wye, from April to September 1979 and 1980

1979	Builth Wells						Bridge Sollars						Monmouth					
	A	M	J	J	A	S	A	M	J	J	A	S	A	M	J	J	A	S
Ph		7.7	7.1	7.1	7.1	7.1	7.9	7.8	7.7	8.3	7.4	7.6	7.8	8.2	8.2	9.0	8.2	8.0
Dissolved Oxygen mg/l		12.0	11.4	11.1	10.6	10.9	10.9	11.7	10.6	10.4	10.0	9.3	11.1	11.5	11.2	12.8	10.9	11.0
Conductivity micsm		102.5	120.0	94.0	66.0	72.7	13.0	190.0	185.0	232.5	115.5	155.0	240.0	335.0	325.0	395.0	280.0	297.5
Alkalinity mg/l		20.0	25.0	20.0	22.0	13.3	35.0	51.5	51.0	72.0	29.5	38.0	70.0	106.0	104.0	143.0	88.5	98.0
Hardness (total CaCo$_3$ mg/l		36.0	38.0	26.0	32.0	21.0	48.0	74.0	71.0	127.0	94.0	54.7	114.0	147.0	141.0	190.0	171.5	122.0
Othophosphate mg/l		0.06	0.02	0.23	0.06	0.08	0.07	0.05	0.15	0.13	0.05	0.04	0.11	0.12	0.25	0.20	0.17	0.17
B.O.D.$_5$ A.T.U. mg/l		2.86	2.02	1.43	2.14	2.26	0.6	1.79	1.67	3.21	5.59	2.14	2.38	1.55	1.07	2.38	3.81	2.26
Solids G.F.C. filtered mg/l		5.0	5.6	10.0	11.5	7.3	57.0	15.1	21.8	6.3	54.0	18.0	79.0	7.4	19.6	11.5	18.5	2.8
Chlorides mg/l		13.0	12.0	13.0	7.0	7.7	11.0	18.0	14.5	13.0	8.5	9.3	16.0	19.5	22.0	25.0	16.5	15.5
Ammonia as N mg/l		0.12	0.02	0.05	0.02	0.02	0.04	0.1	0.03	0.09	0.04	0.02	0.09	0.07	0.04	0.03	0.02	0.03
Nitrite as N mg/l		0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.02	0.02	0.03	0.02	0.04	0.02	0.02	0.03	0.02	0.02
Nitrate as N mg/l		1.11	0.5	0.5			3.1	1.9	1.8	0.5			4.7	3.5	3.6	3.8		

1980	Builth Wells						Bridge Sollars						Monmouth					
	A	M	J	J	A	S	A	M	J	J	A	S	A	M	J	J	A	S
Ph	7.7	7.2	7.3	8.0	7.5	7.4	7.4	7.7	7.4	7.7	7.5	7.5	8.0	8.5	7.7	8.1	7.7	8.0
Dissolved Oxygen mg/l	12.4	11.6	11.6	11.2	10.0	11.2	11.2	11.4	10.3	9.6	9.3	10.0	14.6	12.1	9.3	10.4	8.5	9.8
Conductivity micsm	115.0	125.0	82.0	110.0	120.0	87.5	217.5	247.5	120.0	145.0	155.0	135.0	115.0	415.0	220.0	267.5	245.0	225.0
Alkalinity mg/l	27.5	26.0	12.0	26.0	20.0	21.0	75.0	86.0	30.0	38.0	43.5	40.7	144.0	148.0	60.0	85.0	68.0	73.0
Hardness (total) CaCo$_3$ mg/l	36.0	42.0	22.0	38.0	44.0	28.0	96.0	107.0	46.0	54.0	59.5	51.0	188.0	190.0	85.0	111.0	108.0	116.0
Orthophosphate mg/l	0.02	0.1	0.12	0.07	0.07	0.08	0.04	0.06	0.04	0.14	0.08	0.07	0.25	0.11	0.12	0.17	0.18	0.21
B.O.D.$_5$ A.T.U. mg/l	1.79	1.43	1.31	7.79	2.5	2.14	1.07	2.62	1.67	4.64	1.9	1.31	2.62	2.62	2.14	3.69	1.9	6.07
Particulate solids mg/l	10.6	0.8	5.2	0.4	66.0	3.9	5.6	4.8	12.0	4.0	9.8	7.0	21.6	4.8	16.8	2.8	13.0	30.4
Chlorides mg/l	8.5	12.0	3.0	11.0	7.0	7.5	11.5	15.0	5.0	13.0	9.0	8.7	21.0	23.0	7.0	16.6	12.0	12.5
Ammonia as N mg/l	0.02	0.04	0.02	0.02	0.03	0.03	0.02	0.03	0.02	0.03	0.02	0.02	0.02	0.02	0.03	0.02	0.06	0.02
Nitrite as N mg/l	0.02	0.02	0.02	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.07	0.02	0.02	0.02	0.02
Nitrate as N mg/l		0.48	0.05	0.05	0.52	0.36	3.6	1.6		0.8	1.01	0.72		4.4	2.28	1.5	1.9	1.8

Table 2.2 Some chemical components of the water from three sites on the River Severn, from April to September 1979 and 1980

1979	Worcester						Tewkesbury						Gloucester					
	A	M	J	J	A	S	A	M	J	J	A	S	A	M	J	J	A	S
Ph	7.7	7.8	7.7	7.9	7.8	7.9	7.9	7.8	8.0	8.1	7.7	7.9	7.9	7.9	8.1	8.1	7.8	7.9
Dissolved Oxygen mg/l	10.8	10.0	10.2	10.2	9.0	9.5	10.5	10.1	10.7	9.5	7.2	7.8	10.5	10.5	10.5	9.6	7.1	7.7
Conductivity micism	395.0	463.5	530.0	755.0	637.5	610.0	565.5	469.0	520.0	720.0	577.5	617.5	501.5	565.0	620.0	810.0	700.0	787.5
Alkalinity mg/l	94.0	122.5	125.0	157.5	127.5	117.5	141.5	139.5	130.0	155.0	125.0	132.5	139.0	146.0	157.5	170.0	142.5	155.0
Hardness (total) $CaCo_3$ mg/l	189.0	205.5	210.0	272.5	220.0	222.5	291.5	231.5	232.5	282.5	225.0	237.5	260.5	284.0	207.5	332.5	292.5	302.5
Orthophosphate mg/l	0.18	0.05	0.35	0.75	0.65	0.70	0.24	0.05	0.35	0.40	0.85	0.80	0.05	0.33	0.4	0.65	1.2	1.0
$B.O.D._5$ A.T.U. mg/l	3.2	3.4	3.3	3.9	3.1	2.1	2.9	3.6	3.0	4.5	2.7	1.8	3.6	4.5	4.4	5.2	2.9	3.2
Suspended solids mg/l	28.5	16.5	19.0	30.5	21.0	8.5	42.5	21.0	18.0	18.0	16.0	8.0	60.5	40.5	37.5	96.0	144.5	133.2
Chlorides mg/l	45.0	57.0	63.0	108.5	81.0	79.0	44.0	48.0	51.0	83.0	64.0	71.0	41.5	49.5	51.5	82.0	69.0	81.5

1980	Worcester						Tewkesbury						Gloucester					
	A	M	J	J	A	S	A	M	J	J	A	S	A	M	J	J	A	S
Ph	8.1	8.5	8.6	7.6	7.7	7.8	8.1	8.4	8.0	7.8	7.6	7.6	8.1	8.6	8.0	7.9	7.6	7.7
Dissolved Oxygen mg/l	11.6	11.0	7.7	8.2	9.0	8.0	12.5	11.3	8.5	6.6	8.7	8.7	12.1	12.9	8.2	7.8	8.6	8.4
Conductivity micism	520.0	680.0	750.0	587.0	430.0	480.0	535.0	675.0	806.7	625.0	600.0	437.5	632.5	785.0	763.3	720.0	620.0	585.0
Alkalinity mg/l	125.0	155.0	145.0	93.6	73.0	165.0	132.5	165.0	158.3	135.0	135.0	84.0	157.5	185.0	166.6	150.0	145.0	125.0
Hardness (total) $CaCo_3$ mg/l	220.0	260.0	320.0	198.3	115.0	160.0	230.0	275.0	253.3	242.0	210.0	240.0	292.5	327.5	308.3	305.0	240.0	265.0
Orthophosphate mg/l	0.3	0.6	1.2	0.95	0.35	0.60	0.2	0.45	0.85	0.85	0.70	0.70	0.25	0.80	1.2	1.3	1.0	1.0
$B.O.D._5$ A.T.U.	3.2	5.5	5.3	2.1	1.7	1.6	4.4	6.1	2.7	1.3	2.1	1.9	4.4	8.1	3.5	1.7	2.1	1.9
Suspended solids mg/l	10.0	18.0	20.0	18.7	13.0	10.0	19.0	21.0	12.3	7.0	9.0	22.8	35.0	114.5	74.0	37.0	52.0	164.3
Chlorides mg/l	63.0	81.0	91.0	79.0	52.5	59.0	52.5	77.0	77.7	65.5	64.0	44.5	55.0	79.0	77.7	72.5	56.0	56.0

the inner estuary, between Gloucester and Newnham, are reported as being of 'fair' quality (N.W.C., 1981). In the region between Gloucester and Newnham low levels of dissolved oxygen have been recorded in the summer months, during periods of low river flows. This may be caused by fine solids, rich in organic matter, settling out during neap tides, then being resuspended during the following spring tides. This results in a rapid increase in the oxygen demanding microfauna in the water column, producing a reduction in the level of dissolved oxygen. During the spring tides the situation is compounded as the reduced oxygen levels have not completely recovered by the following tide. The effect over four or five successive tides can result in a body of water 20 km long with depressed oxygen levels, with in which, (over 10 km) the levels may approach zero (Severn Estuary Survey and Systems Panel, 1977).

F. Tidal Influence

The effects of the tide depend on the stage of the tidal cycle and the amount of freshwater discharge. On the Severn, the limit of freshwater back up is regarded as Upper Lode Weir (grid reference SO 882328) at Tewkesbury. In terms of salinity the limits are shown in figure 2.4, along with the rate of change in salinity that might be expected at various sites, these have been redrawn from Bassindale (1943). Figure 2.5 illustrates the salinity conditions in the Severn Estuary (S.T.W.A., pers. comm.).

On the Wye the upper limit of freshwater back up is taken to be Redbrook (grid reference SO 535101) (27.5 km. from the mouth of the Wye) and of salinity intrusions, Bigsweir (grid reference SO 538051) (22.0 km from the mouth).

Figure 2.4, The actual changes and the rate of change of salinity along the Severn estuary (redrawn from Bassindale, 1943).

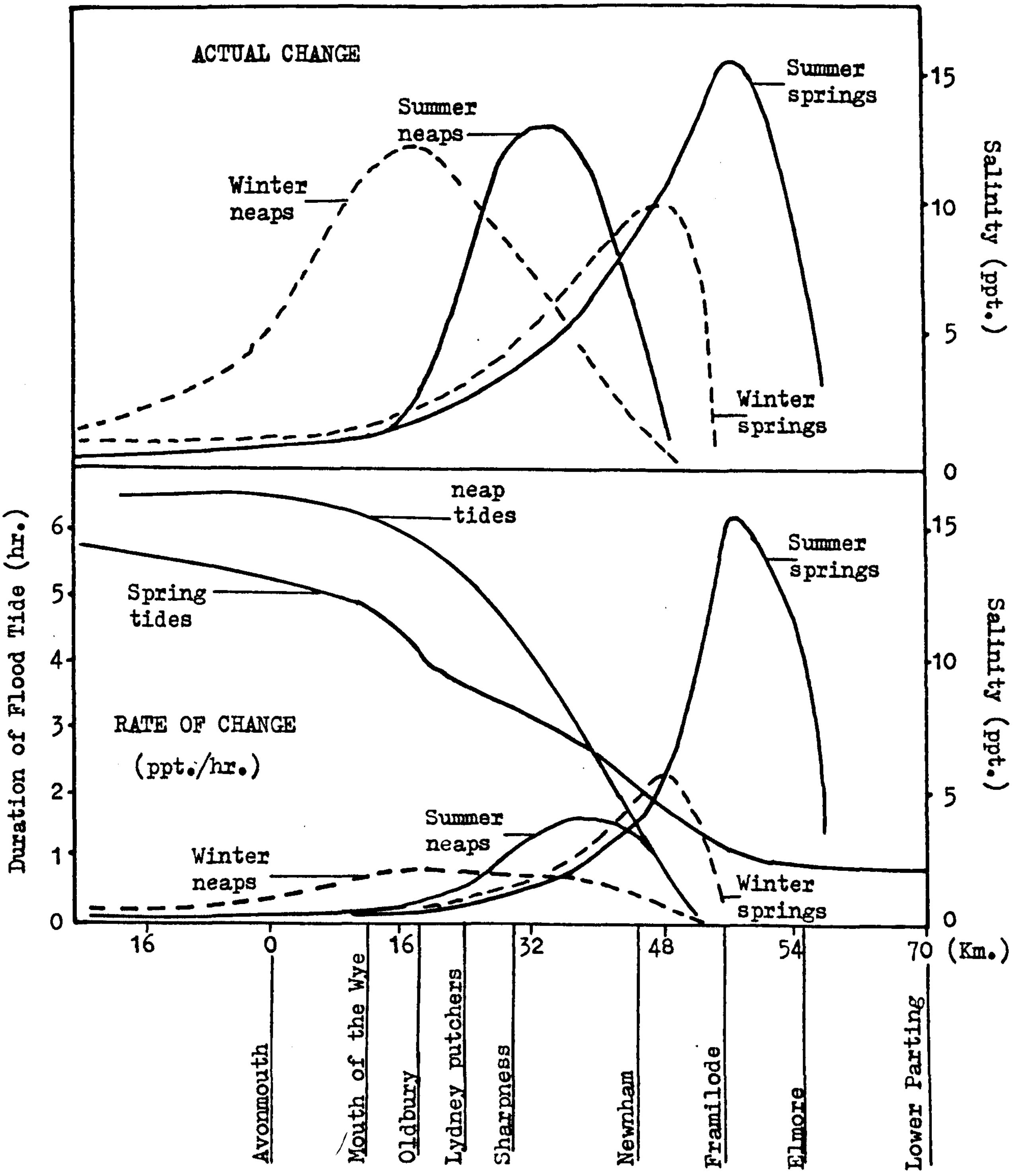
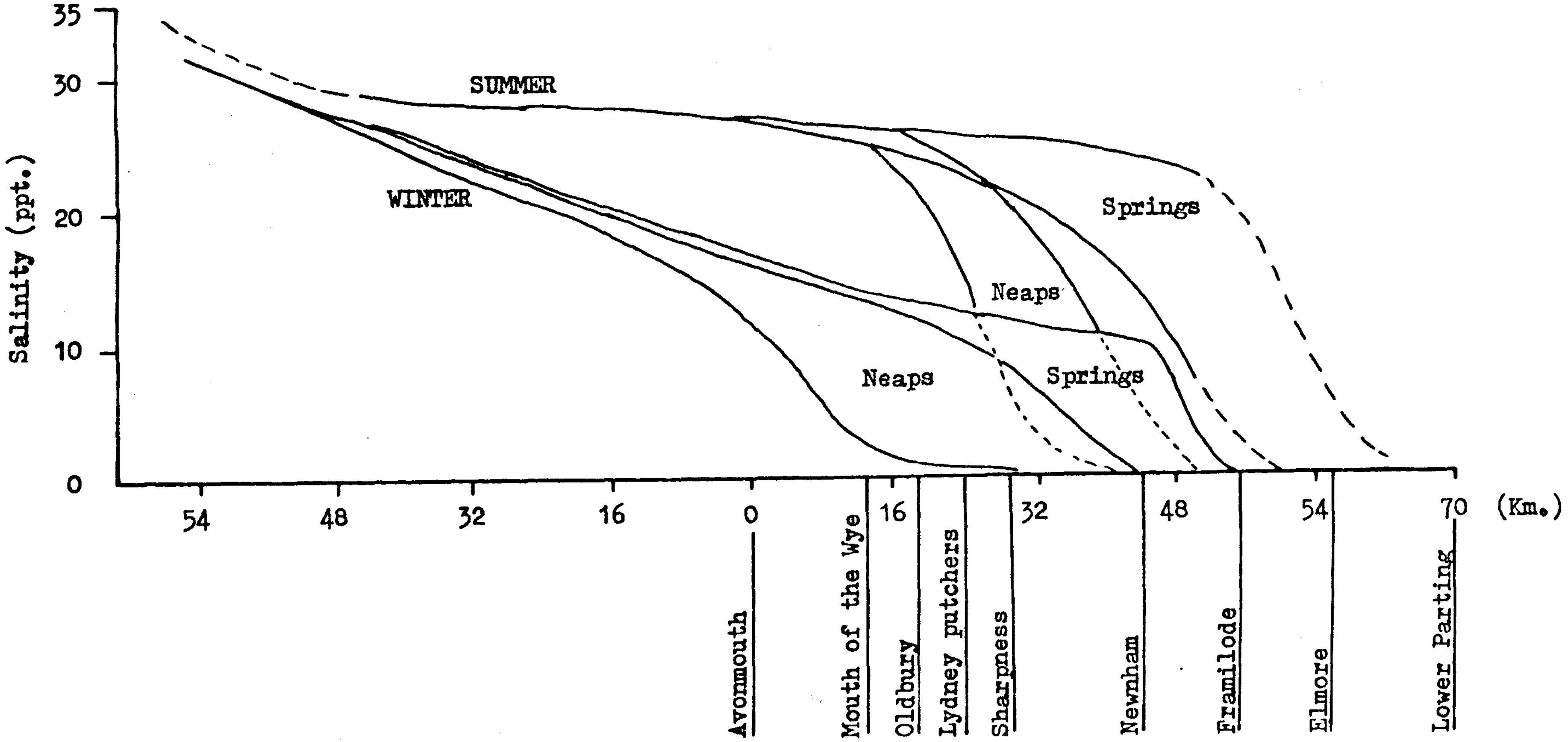


Figure 2.5, Salinity conditions in the Severn estuary. The upper limit of each zone represents the high tide salinity and the lower limit the low tide salinity.



G. Field Methods

1. Adults and Juveniles

Drift Netting

Two types of drift nets were used to obtain samples. In the outer Severn estuary A.fallax were caught using drift nets operated by the commercial salmon netsmen. These nets measured 274.1 m in length, 2.74 m deep and with a mesh size of 5.05 cm (measured from knot to knot).

In the inner estuary of the Wye, along Long Hope Reach, a trammel net was used. The net was 60 m long, 2 m deep. The inner wall of netting was 4.5 cm (knot to knot) and the outer wall measured 28 cm (knot to knot).

Fixed Engines

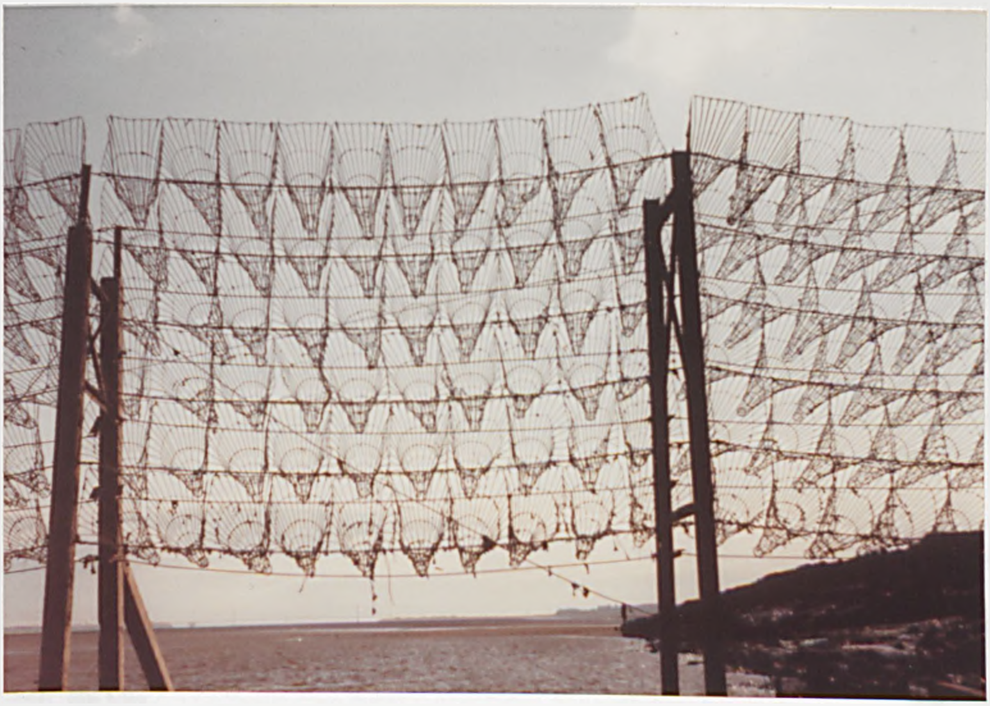
Two main types were used. In the Severn estuary fish were caught using putchers. These are conically shaped baskets set in 'weirs' and generally fish the ebb tide. The main putcher rank, at Lydney (plates 2.9 and 2.10) used in this study consists of 550 conically shaped baskets set in bays of 54 or 60 baskets. Each bay is 6 baskets high, the lowest basket fishes 2 m above the bottom. The putcher rank is completely covered by a 6.5 m tide, as recorded at Sharpness Dock. Each basket is 61 cm high, 71 cm wide and 1.73 m in length, and made from mild steel 0.635 cm bar set.

The rank fishes the ebb tide and fish, when caught, cannot escape because of the strong current and the fact that there is no room to turn around and swim out.

The traditional putcher baskets were woven using willow and hazel branches, but the more modern ranks are now constructed from mild steel or aluminium rods, sometimes dipped in P.V.C. or plastic coated.

Plate 2.9, Putcher rank at Lydney, Severn estuary.

Plate 2.10, Putcher rank at Lydney, a single bay of putchers.



As well as the rank at Lydney, samples were also obtained from Putcher ranks at Broad Oak, Hayward Rock, Slime Road and Porton.

The other type of fixed engine used to obtain samples, were staked nets, set in Cardigan Bay at Tywn. These nets fish intertidally and measure 54.8 m in length, 2.44 m deep and with a mesh size of 5.08 cm (knot to knot).

Rod and Line

Fish were angled for at a number of sites in freshwater. The main method was by spinning, plate 2.11. The lure used was a 2 cm trout spoon with a treble hook. When A.fallax were present this proved a very effective way of catching them.

Electrofishing

Sampling was carried out using an A.C. Erskine portable power generator, with an output of 230 volts, 6.9 amps, which was rectified. The circuit was completed by a stationary negative copper earth plate and a portable positive hand electrode. Fish within a radius of 2-3 m of the positive electrode were stunned and removed from the water by a hand net.

This method was used wading the pool below Powic weir, on the River Teme, and from a boat between Wainlode and Maisemore on the River Severn, in an attempt to sample the spawning population.

Seine Netting

In this study four different types of seine nets were used. Two for adult A.fallax and two for juveniles. The use of seine nets in rivers requires a different technique when compared with their use in lakes, to allow for the currents affect on the net. The commercial salmon fishermen of the River Severn have developed and perfected this technique which we in turn modified for the use of our own nets.

Plate 2.11, Rod and line fishing at Powic weir, river Teme.

Plate 2.12, Seine netting, with fry seine net, at Newnham, Severn estuary.

The dimensions of the nets were as follows:-

(a) Micromesh seine net - 20 m in length x 3 m deep with a mesh of 3 mm. The 3 mm mesh was made of knotless netting.

(b) Fry seine net - 69.5 m in length x 3 m deep with a mesh of 6.35 mm (knot to knot). The mesh was of knotless netting, (plate 2.12).

(c) Large mesh seine - 85.2 m in length x 3 m deep with a mesh of 3.2 cm (knot to knot).

(d) Salmon drift net - 160 m in length x 1.9 m deep at the centre tapering to either end, with a mesh of 5.08 cm (knot to knot).

Oldbury Power Station

Fish samples were collected from the cooling water intake screens. The water used for cooling the power station is taken from a large holding reservoir of 160 hectares, and is drawn through longitudinal screens of bars to prevent large items of trash entering the intake chamber. Large revolving drums approximately 12 m in diameter surfaced with mesh and retaining troughs at intervals, (plate 2.13) to collect the finer trash, also collects organisms, such as fish. These troughs are washed out by jets of water and the trash is carried along channels leading into a skip. Fine mesh cone nets 30 cm in diameter, 1.5 m in length and with a mesh of 3 mm were placed in these channels to intercept the flow before it reached the skip (plate 2.14). These nets were emptied and sorted as they filled.

Sampling was carried out on spring tides of approximately 8.0 m high (as recorded at Sharpness Dock) commencing two hours after high water and continued for six hours.

Plate 2.13, Oldbury Power Station, Severn estuary, the large revolving drum can be seen in the foreground. In the background the edge of the reservoir can just be seen.

Plate 2.14, Oldbury Power Station, sampling in the channel for 'rubbish' brought up by the revolving drum, on the left, using conical 'micromesh' nets.

Trawls

(a) Otter Trawl

The Otter Trawl used was based on the design by Ruppe and de Roche, (1960). It has a 3.6 m x 0.5 m mouth. The conical net of polypropylene made from knotless netting of mesh sizes graduating from 3.2 cm to 6.5 mm to a micromesh cod end of 3 mm. The otter boards measured 37 cms x 58 cms in size and were set 5.8 m from the net and had a bridle which was attached to the towing rope by a swivel. The non-rigid upper boundary to the mouth was made bouyant by polystyrene floats, and the lower boundary weighted with chain.

This trawl has been used successfully by Butterworth (1981), Coles (1977) and by Sewell (in prep.).

(b) Beam Trawl

The Beam Trawl used had a 2.44 m beam or span fitted to two iron heads or shoes 0.46 m high with a conical net of mesh size 10 mm graduating to a 3 mm micromesh cod end. A bridle, twice the length of the beam was shackled to the fore end of each head and was fitted with an eye piece for the attachment of the towing rope. The beam trawl was used without a tickler chain.

Trawling was carried out in the outer estuary of the Severn, in areas not accessible by the micromesh seine and in an attempt to fish a larger area.

2. Eggs

(a) Freshwater Biological Association (F.B.A.) net

An F.B.A. net measuring 20 cm wide, 25 cm high and with a mesh size of 47.2 meshes/cm was used to 'kick' sample the gravel shallows for the eggs. The net was placed downstream of the operator who then proceeded to dislodge the eggs from the river bed by kicking the gravel, (plate 2.7). The eggs drifted downstream with the current into the net.

A small representative sample of the invertebrates were taken using this method.

(b) Drift Samples

Cone shaped fine meshed net (meshes of 1.0 mm x 0.7 mm) 30 cm in diameter and 1.5 m in length, (plate 2.7).

H. Selectivity of the Methods Used to Sample the Adult Population

The sizes of adult A.fallax caught, in 1980, by the various methods is shown separately for females and males (figures 2.6 and 2.7 respectively), as the males mature at a smaller size than the females (see chapter five). Judging from the size range of fish caught, the selectivity of the methods increases in the following order; putcher rank at Lydney < rod and line < Salmon seine net < salmon drift net. (For the males the salmon drift net was excluded as only two fish were caught). It is evident that though the putcher rank at Lydney is the least selective of the methods used there were fish present in the spawning stock not sampled. Evidence of their presence in the population comes from the rod and line catches. Thus the smaller males may not be quantitatively sampled by the putcher rank, though this does not appear to be the case for the females. Similarly the lack of large fish caught using rod and line may be a function of the gear, or that they were not present.

Figures 2.6 and 2.7 only provide information on the relative selectivity of the various methods, for without knowing the size distribution of the population it is not possible to make an assessment as to which method gives the most accurate estimate of the length composition of the population.

Figure 2.6, Length frequency histograms for female <u>A.fallax</u> caught using various methods, in 1980.

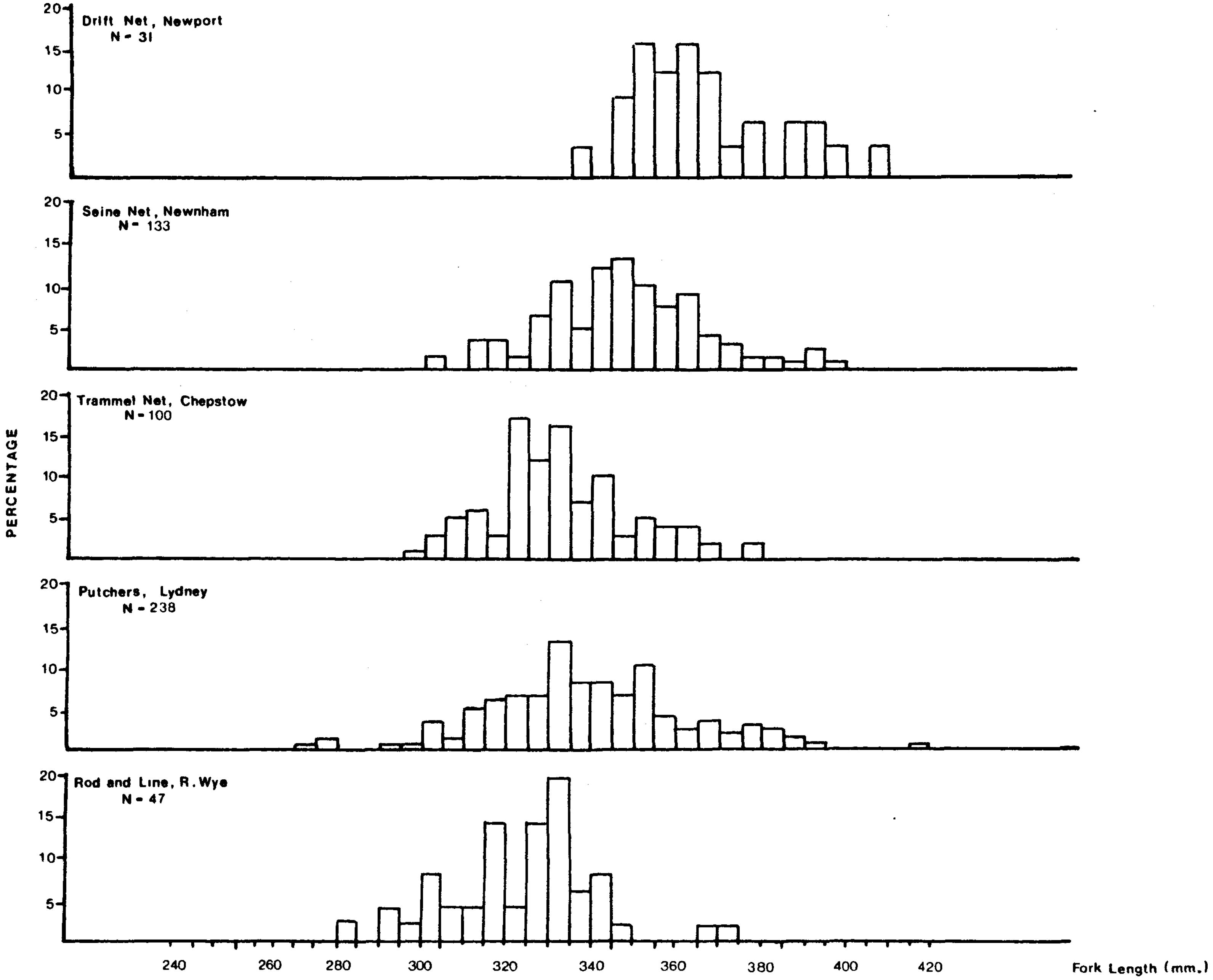
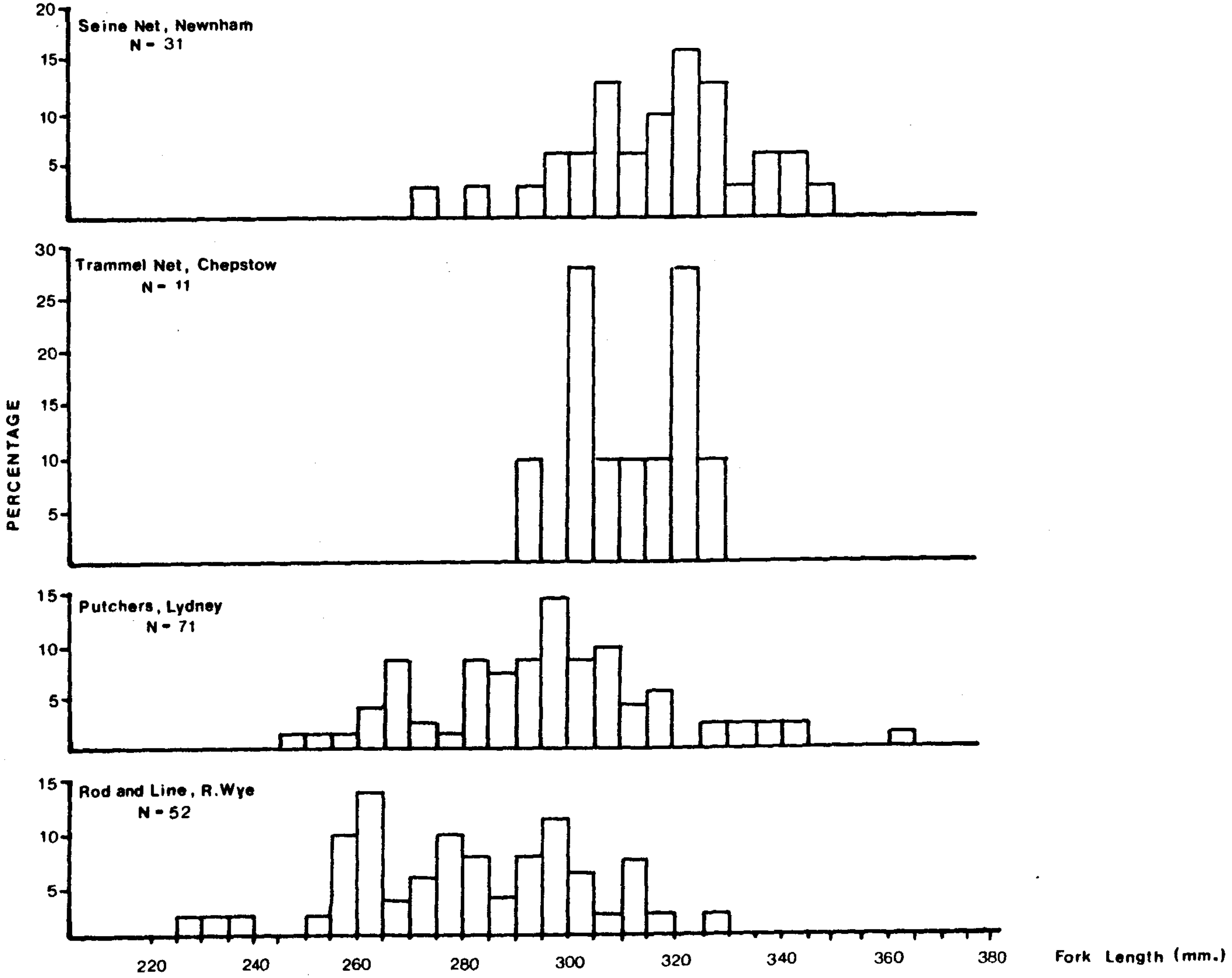


Figure 2.7, Length frequency histograms for male A.fallax caught using various methods, in 1980.



I. River Flow and Discharge, Temperature, Wind Direction and Tidal Height Data

While sampling in the field, river flow and temperatures were recorded. Flow recordings over the spawning gravels were made using a Braystoke current meter, taken just above the river bed and in water of 30 cms in depth. A set of 3/5 readings were made at each site and an average taken.

River discharge and temperature data at a number of different sites on the Wye and Severn River systems are regularly recorded by both the Welsh and Severn and Trent Water Authorities respectively. The data is in the form of average daily discharge in cubic metres per second and for the Wye was taken at Belmont (grid reference SO 485388) and for the Severn from Saxons Lode (grid reference SO 864390). Temperature data for the Severn was also taken from Saxons Lode but for the Wye was taken from Bridge Sollars (grid reference SO 413424). For the Severn estuary temperature data was also available from Oldbury Power Station, and from helicopter sampling carried out by the Severn and Trent Water Authority.

Wind directions were obtained from the meterological office at Innsworth (grid reference SO 866214), near Gloucester. Information on tidal height was taken from the 'Arrowsmith's Bristol Channel Tide Table' (published by J.W. Arrowsmith Ltd., Bristol).

CHAPTER THREE

AGE AND GROWTH

Introduction

The determination of age in fishes is one of the most useful approaches in fishery science. Carlander (1974) mentions a number of different types of information that might be obtained when ageing fishes notably, growth rate, age at maturity, number of spawnings, age at harvest, age composition of the catch, abundance of year classes, longevity and mortality rates. These data may be further used in relation to problems in fishery management. Ageing is generally carried out from examination of the various growth zones laid down in the bony structures of which scales, operculae and otoliths are the most commonly used. In this study, ageing has been determined using scales, as previous investigations by Chugunova (1963) and Judy (1961) have demonstrated their validity for use in determining age in anadromous alosids. Ageing is based on the determination of the number of annuli which are formed during periods of slow growth. The appearance of which, though differing between species and between habitats, in temperate climates is generally during early summer when faster growth resumes (De Bont, 1967).

The possibilities of errors arising in age determination are due to the development of false annuli (Coble, 1970; Hatch, 1961) and a number of causative factors have been suggested for their appearance (Chugunova, 1963; Hammer, 1942; Van Oosten, 1957). Errors may also arise when fish growth is extremely slow and the scales do not show an annulus (Buchholz and Carlander, 1963; Regier, 1962) or when fish mature and the annulus on their scales no longer forms, Aass (1972), though this may be due to the retardation in their growth. Environmental factors reducing their growth may also result in the failure of the fish to produce scales in their first year of life (Jensen and Johnsen, 1982). Spawning marks may also produce a source of error as they may interfere with or be incorrectly read as annuli. A number of methods have been suggested for reducing errors in ageing (Blacker, 1974; Carlander, 1974), but possibly the most important is experience. Some of the possible effects of errors in ageing have been reported by Brander (1974) on marine fishery modelling and by Le Cren (1974) for production studies.

Growth in fishes may be studied by two methods. The first and simplest is to plot the observed lengths with age, however, this depends upon obtaining a representative sample of the population. The other is by means of back calculation. Calculation of ages at previous length depends on two factors, 1) that a proportional relationship exists between the growth of fish and its scale and 2) that annulus formation is annual.

This chapter is mainly concerned with a description of the method of age determination from scales and in obtaining an accurate method of reconstructing their growth history.

A. Materials and Methods

Fish were sampled using the methods previously described in chapter two and their fork length was measured to the nearest millimetre. Scales were removed from the flanks just behind the origin of the dorsal fin and above the mid-line, as these scales were found to be the most symmetrical. Zamakhaev (1940) and Chugunova (1940) (cited by Chugunova, 1963) observed that scales from near the head and tail do not show spawning marks and have annuli indistinguishable from false annuli. Similar findings were observed for A.fallax where scales from around the head region were more difficult to age. Chugunova (1963) recommends using scales from around the median part of the body as the annuli and spawning marks on the scales are most clearly defined, in this region. The scales were cleaned of mucous and skin by rubbing them between the fingers when either fresh, or, having soaked them in a weak solution of trypsin. The scales were placed between two glass slides, examined and measured with the aid of a 'Projectina' micro-projector. All scales were read three times and only if the same reading was obtained on at least two occasions was that age attributed to the fish.

B. Description of Scale and Terminology

Plate 3.1 a + b, 3.2 a + b and 3.3 show typical A.fallax scales. Plate 3.1 a + b show scales from a maiden or virgin spawning fish (a fish spawning for the first time), plate 3.2 a + b show scales from fishes that have previously spawned and plate 3.3 is a regenerated or replacement scale. The terminology used in describing the visible markings on the scales are taken from Cating (1953) and are:

(1) ANNULI - These are lines on the surface of the scale and follow the contours of the periphery, through both the anterior and posterior portions of the scale. They are usually indicated by attenuation or slight waviness of the transverse grooves and striae.

(2) FALSE ANNULI - These are similar to true annuli, though nowhere near as definitive and usually not found encircling the whole anterior portion of the scale.

(3) SPAWNING MARKS - These are formed during the pre-reproductive period by lateral absorption and/or erosion of the scale, followed by rapid regenerative

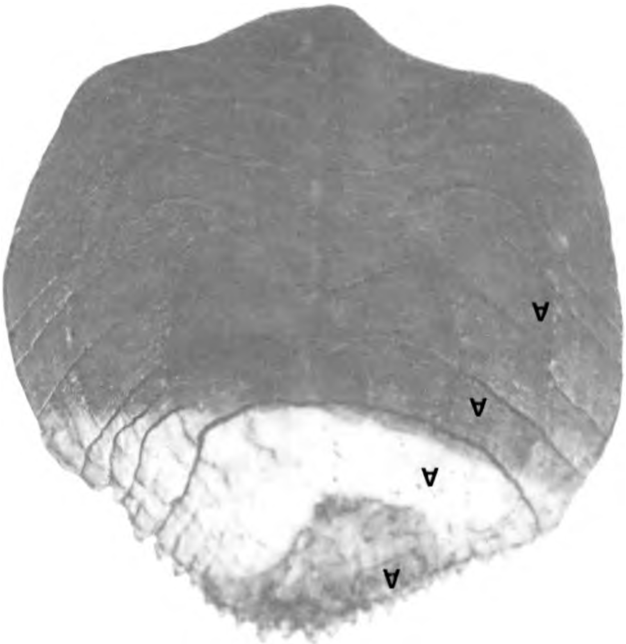


Plate 3.1a,

Scale from a four year old virgin spawner, caught at the start of the spawning migration, in the estuary. Three annuli (A) can be seen. Also note the smooth edge of the scale. X 10

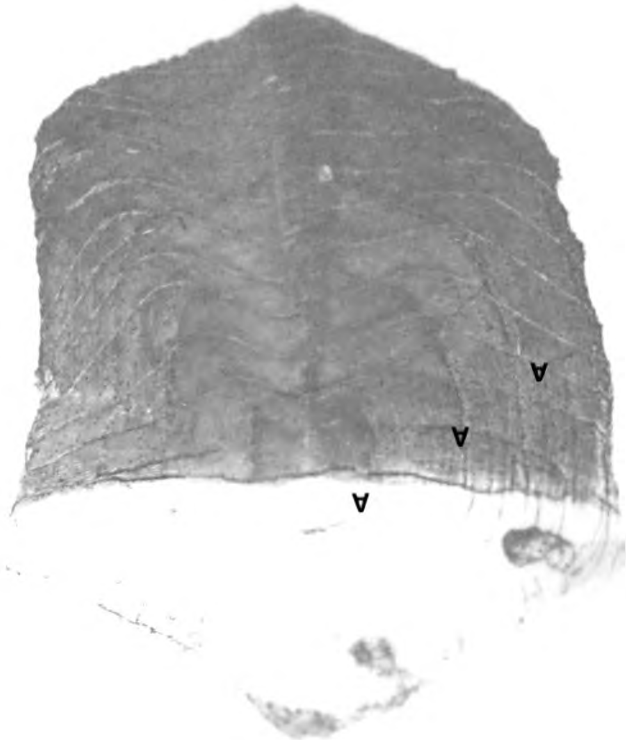


Plate 3.1b,

Scale from a five year old virgin spawner, caught on the spawning grounds. Four annuli (A) can be seen. Also note the severe erosion and/or absorbtion that has occured on the left hand side of the scale. X 10

A
A
A

A
A
A
A

Plate 3.1a,

Scale from a four year old virgin spawner, caught at the start of the spawning migration, in the estuary. Three annuli (A) can be seen. Also note the smooth edge of the scale. X 10

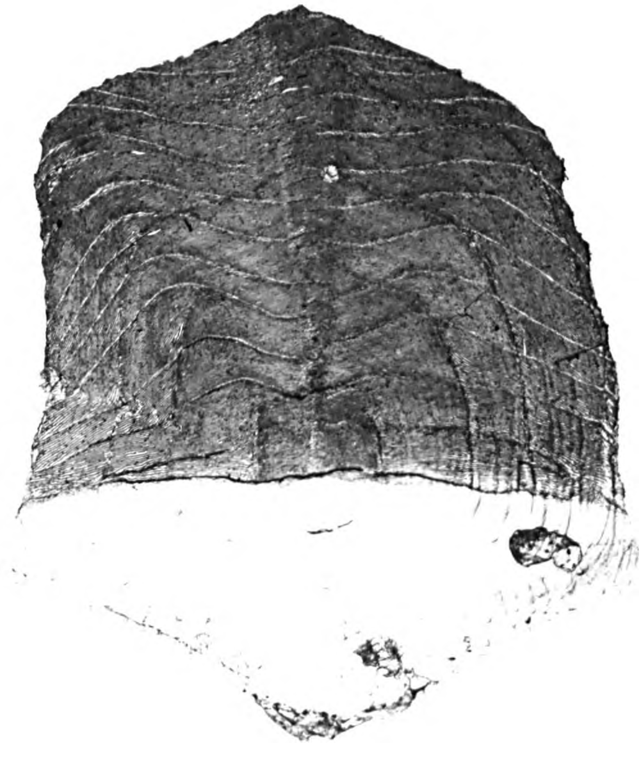


Plate 3.1b,

Scale from a five year old virgin spawner, caught on the spawning grounds. Four annuli (A) can be seen. Also note the severe erosion and/or absorbtion that has occured on the left hand side of the scale. X 10

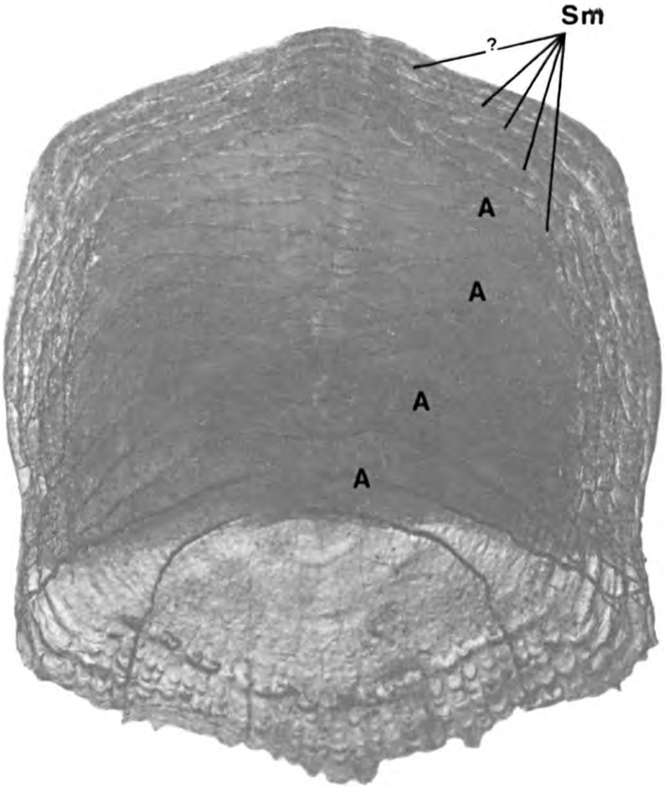


Plate 3.2a,

Scale from a fish that may be either nine or ten years old. Four annuli (A) can be seen followed by either four or five spawning marks (Sm). X 10

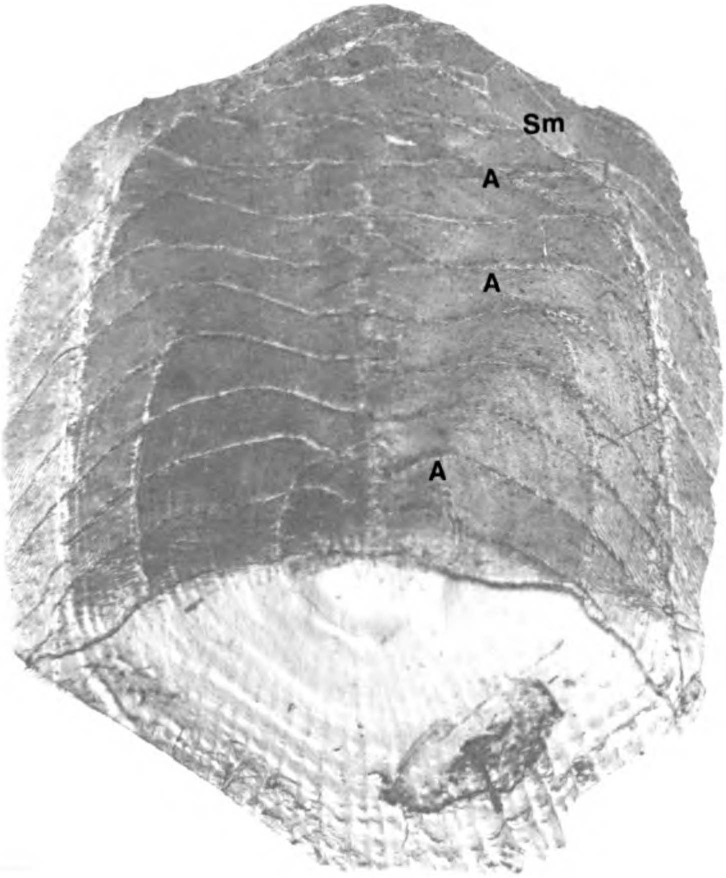
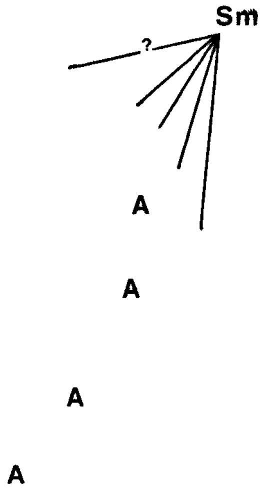


Plate 3.2b,

Scale from a five year old fish that spawned for the first time at age four. Three annuli (A) can be seen followed by a single spawning mark (Sm). Also note the relative positions of the third annulus and the spawning mark, around the scale. X 10


Sm
?
A
A
A
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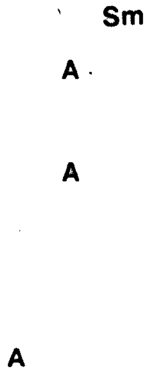

Sm
A
A
A

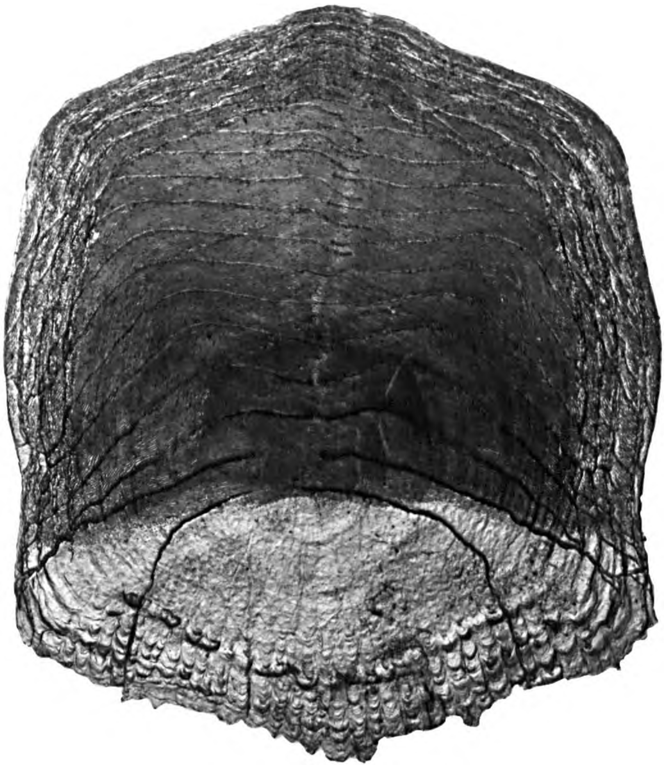


Plate 3.2a,

Scale from a fish that may be either nine or ten years old. Four annuli (A) can be seen followed by either four or five spawning marks (Sm). X 10

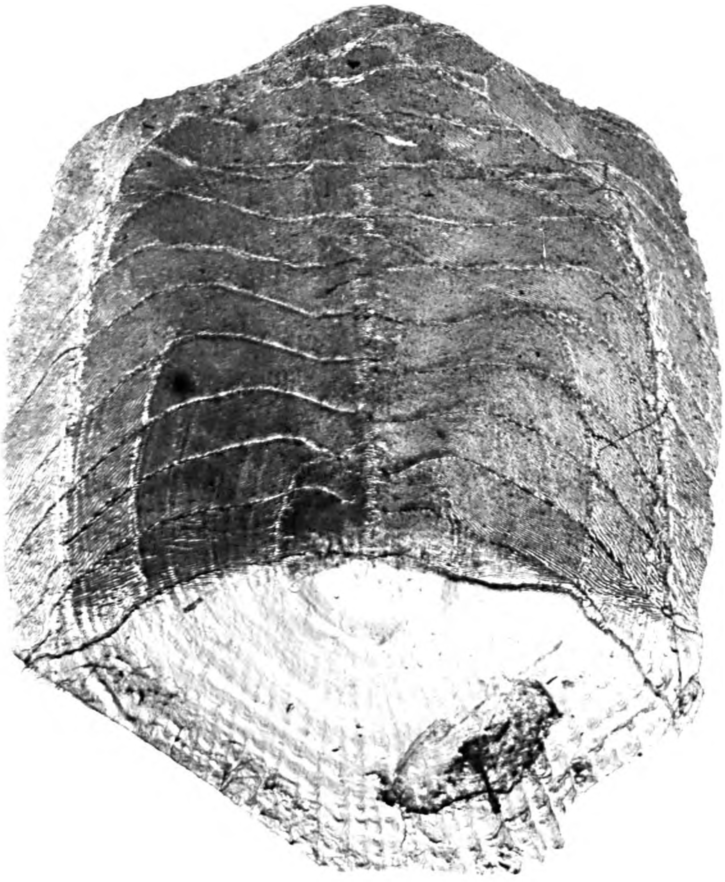


Plate 3.2b,

Scale from a five year old fish that spawned for the first time at age four. Three annuli (A) can be seen followed by a single spawning mark (Sm). Also note the relative positions of the third annulus and the spawning mark, around the scale. X 10

Plate 3.3,

A replacement or regenerated scale. X 10

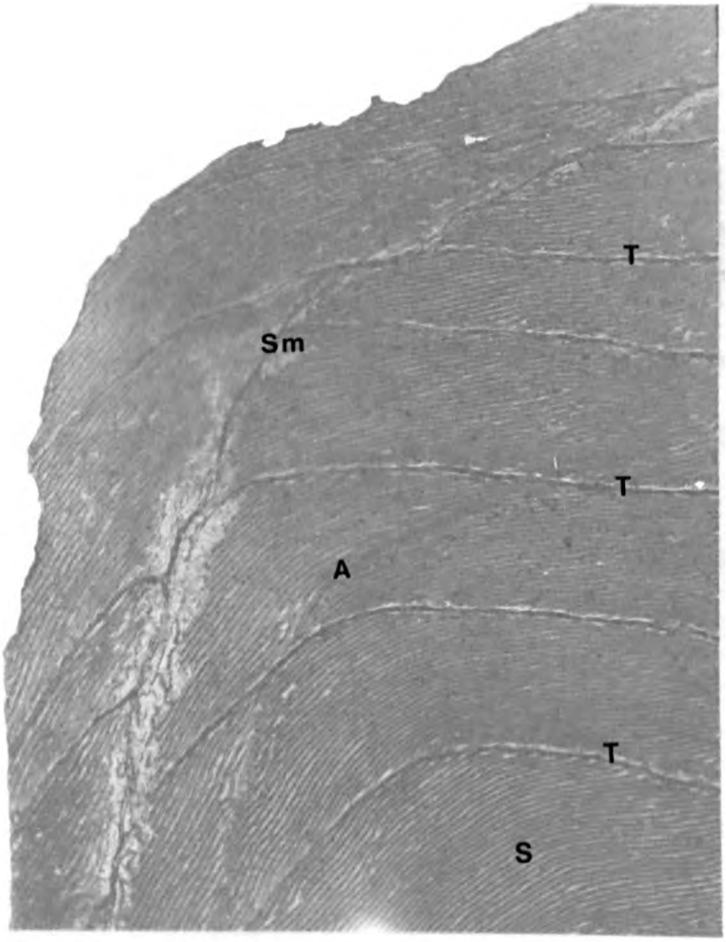


Plate 3.4,

Detailed picture of a scale taken from a fish caught on the spawning grounds, showing the annuli (A), spawning mark (Sm), transverse grooves (T), and stria (S). Also note erosion on the scale's edge. X 30

T

Sm

T

A

T

S

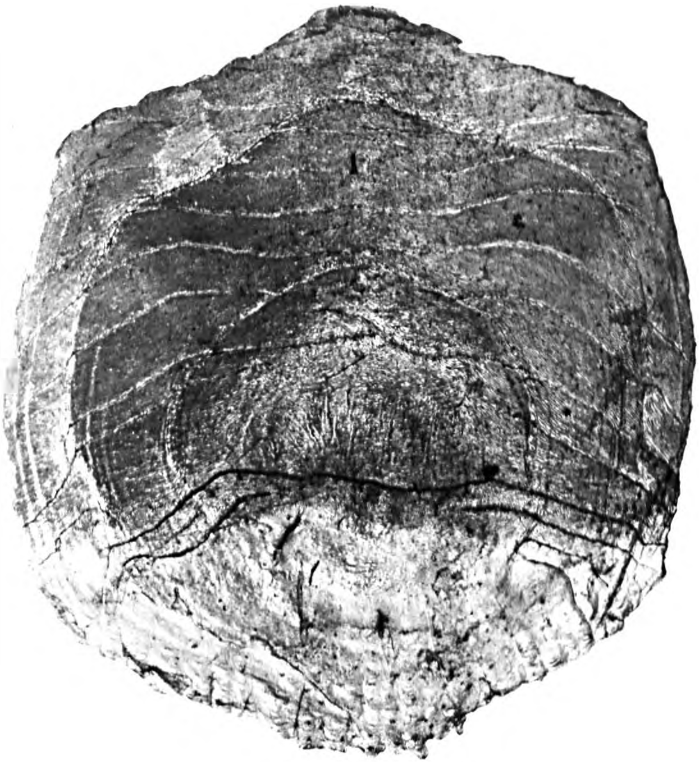


Plate 3.3,

A replacement or regenerated scale. X 10

Plate 3.4,

Detailed picture of a scale taken from a fish caught on the spawning grounds, showing the annuli (A), spawning mark (Sm), transverse grooves (T), and stria (S). Also note erosion on the scale's edge. X 30

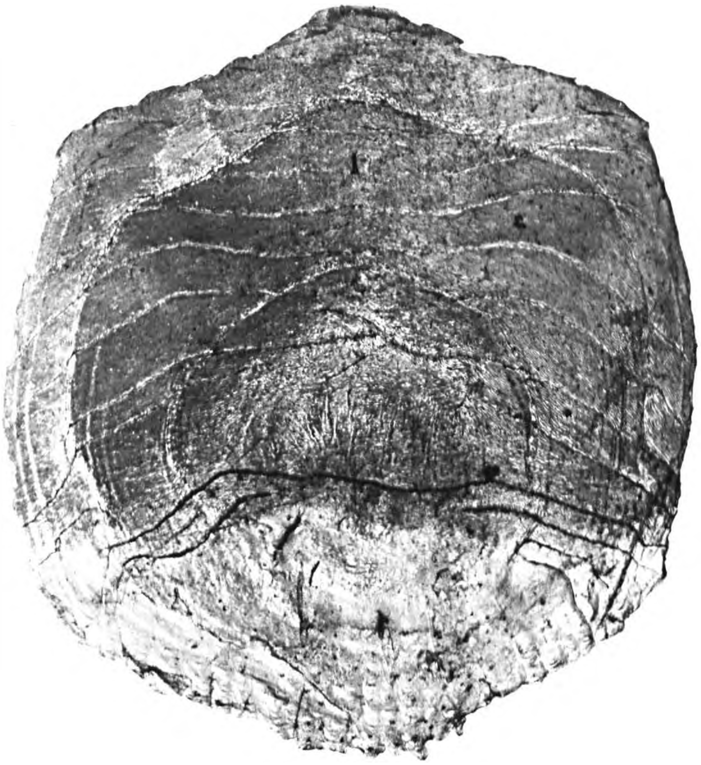


Plate 3.3,

A replacement or regenerated scale. X 10

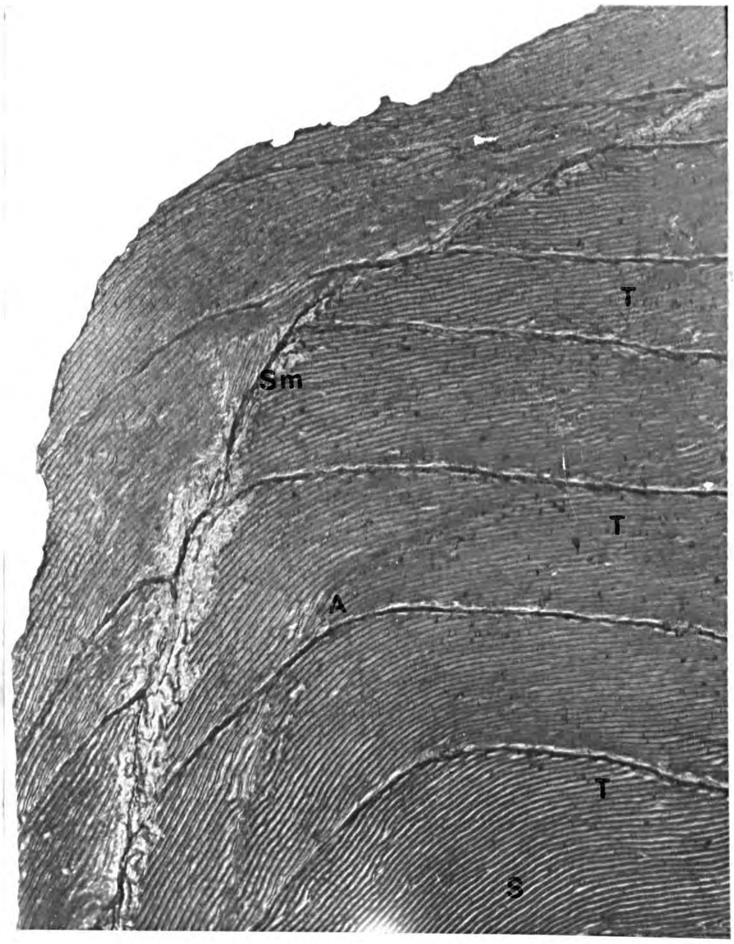


Plate 3.4,

Detailed picture of a scale taken from a fish caught on the spawning grounds, showing the annuli (A), spawning mark (Sm), transverse grooves (T), and stria (S). Also note erosion on the scale's edge. X 30

scale growth after spawning, leaving a characteristic scar.

(4) TRANSVERSE GROOVES - These are characteristic grooves running laterally across the surface of the anterior portion of the scale. The grooves are generally not continuous and may sometimes branch forming two lines.

(5) STRIAE - These are fine ridges covering the anterior portion of the scale, they lie very close together and run laterally across the scale.

(6) BASELINE - This has been taken as that line separating the anterior portion of the scale from the posterior portion.

A detailed picture of these structures is shown in plate 3.4.

C. Age determination

The first published information on the determination of age for A.fallax was by Jenkins (1902) using otoliths. Since then, except for the study by Claridge and Gardner (1978), few investigators have used otoliths for age determination. The scale method of ageing A.fallax has its advantages for, as well as indicating their age, it also provides information on their spawning history. Scales have been used for determining age of A.fallax by Bracken and Kennedy (1967), Hass (1965) and by Roule (1922) and of A.fallax lacustris by Berg and Grimaldi (1966 and 1967). Age determination has also been carried out by Bounhoil (1917), D'Ancona (1928) and Vukovic (1961).

Age determination for A.sapidissima (Wilson)was first carried out by Leim (1924) by counting annuli. Borodin (1925) presented a method which involved counting the number of transverse grooves and dividing by two, so establishing the age in years. Though Barney (1925), using otoliths, confirmed Borodin's method, Greeley (1937) (cited by Cating, 1953) found that the method produced misleading results. Cating (1953) describes a method of ageing based on counting the number of annuli and spawning marks and used counts of transverse grooves to separate true from false annuli. Once the fish had spawned, the spawning marks were subsequently used as annuli as the absorption and/or erosion of the lateral margins of the scale, associated with spawning, tend to obliterate the previous annulus. Similar characteristics are shown by the scales of other anadromous alosids, for example, A.kessleri kessleri (Grimm), A.kessleri volgensis (Berg) and A.caspia (Eichwald) (Chugunova, 1963), A.pseudoharengus (Wilson) and A.aestivalis (Mitchill) (Marcy, 1969), and freshwater forms A.fallax lacustris (Berg and Grimaldi, 1966 and 1967). Chugunova (1963) also observed that the spawning mark was more noticeable in the anadromous species, than in the marine ones, and of the anadromous species A.kessleri kessleri which migrate further up the Volga than either A.kessleri volgensis or A.caspia, shows a more distinctive spawning mark. However, in some species, the spawning mark does not completely obliterate the previous annuli, Chugunova (1963) reported this for the northern herring which spawns in the autumn thus producing two 'rings' per year, an annuli and a spawning mark. A similar situation exists for A.fallax lacustris which spawns during July, and at the time of spawning, the annulus may be clearly seen, most of the other species spawn between April and the end of June. The subsequent absorption and/or erosion around the lateral margins of the scale may obliterate the annulus from these regions but not from the apex where the annulus is still visible (Berg and Grimaldi, 1966 and 1967). Cating (1953), when ageing adult A.sapadissima entering freshwater to spawn, added a year for the scales' edge, as at the time of migration the annulus had not completely formed or was just at the edge of the scale and was about to be displaced by the spawning mark.

La Pointe (1958) using Cating's method validated the annulus as the true year mark and this was further confirmed by Judy (1961) who used annuli and spawning marks to determine the age of marked A.sapidissima. Methods of ageing freshwater populations by using annuli have been confirmed by Berg and Grimaldi (1966, 1967) for A.fallax lacustris, and for A.pseudoharengus by Norden (1967a) and Rothschild (1963).

The scale of A.fallax differs from other anadromous alosids by the absence of a 'freshwater zone', this has also been observed by both Bracken and Kennedy (1967) and Hass (1965). The 'freshwater zone' was first described by Hammer (1942) who observed that A.sapidissima lay down a false annulus when the juveniles migrate from fresh to saltwater during their first summer, when approximately three to five months old. A 'freshwater zone' has also been reported as occuring in anadromous A.pseudoharengus and A.aestivalis (Marcy, 1969). Chugunova (1963) reported the development of a false annulus during the first year of life for A.caspia as well as in some totally marine forms, for example, in A. saposhnikovi (Grimm) which is reported to have several juvenile 'false' annuli.

Evidence that no 'freshwater zone' is formed by A.fallax studied during this investigation comes from juvenile fish, caught during the summer months, in the Severn estuary. Figure 3.1 shows a length frequency histogram of juvenile A.fallax caught between June and October 1980. Two groups are apparent, one with no annulus on their scale (Plate 3.5), ranging in size from 20 mm. to 73 mm. (Fork length) and represent the O-group (or young of the year) fish. The other group has one annulus on their scale (Plate 3.6), and range in size from 66 mm. to 124 mm. and represent the one year olds.

Figure 3.1, A length frequency histogram for juvenile A.fallax, caught at Newnham, between June and October 1980.

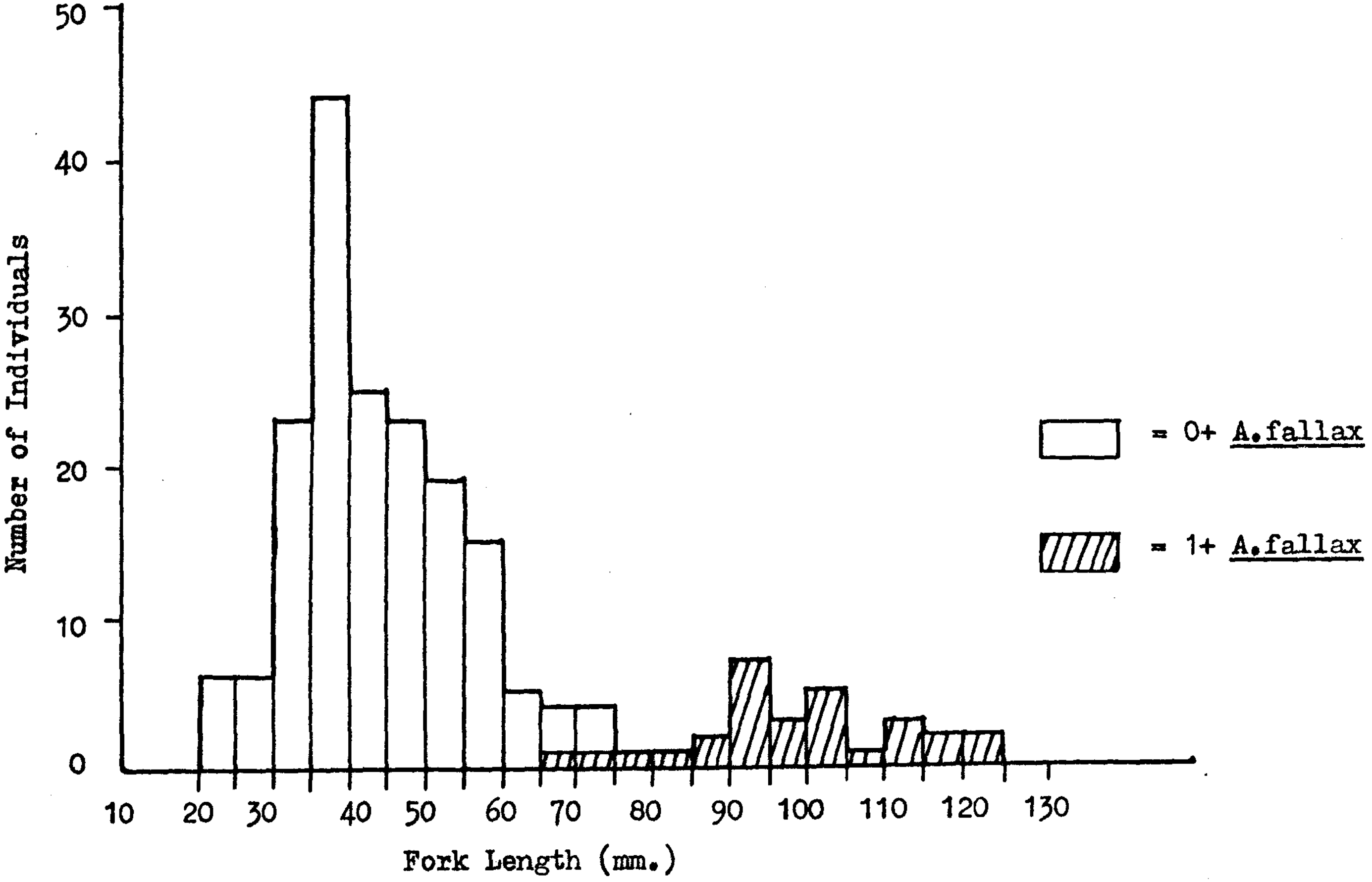
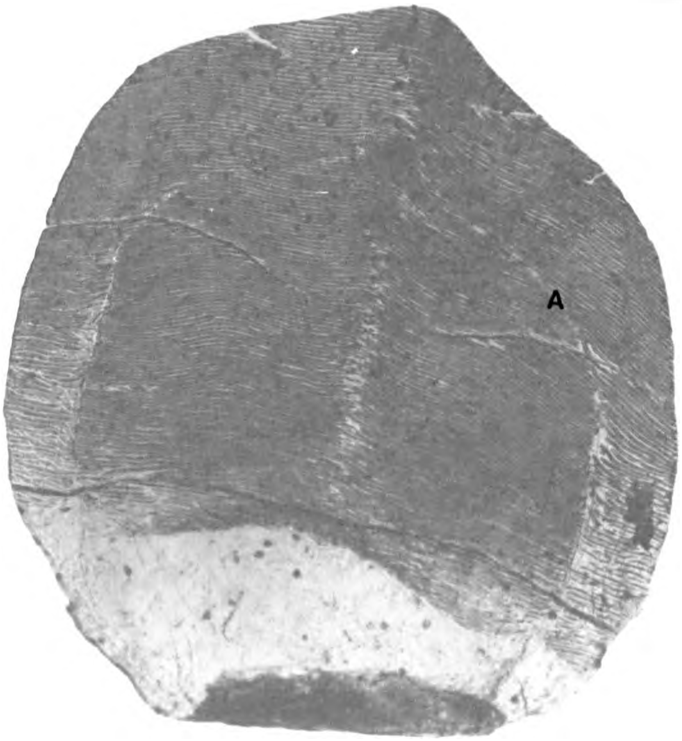


Plate 3.5, Scale from a 0+ fish. X 30

Plate 3.6, Scale from a 1+ fish. The annulus (A) can be clearly seen. X 30



A

Plate 3.5, Scale from a 0+ fish. X 30

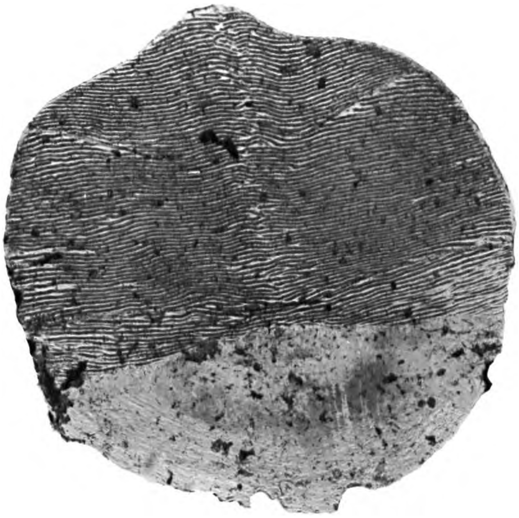
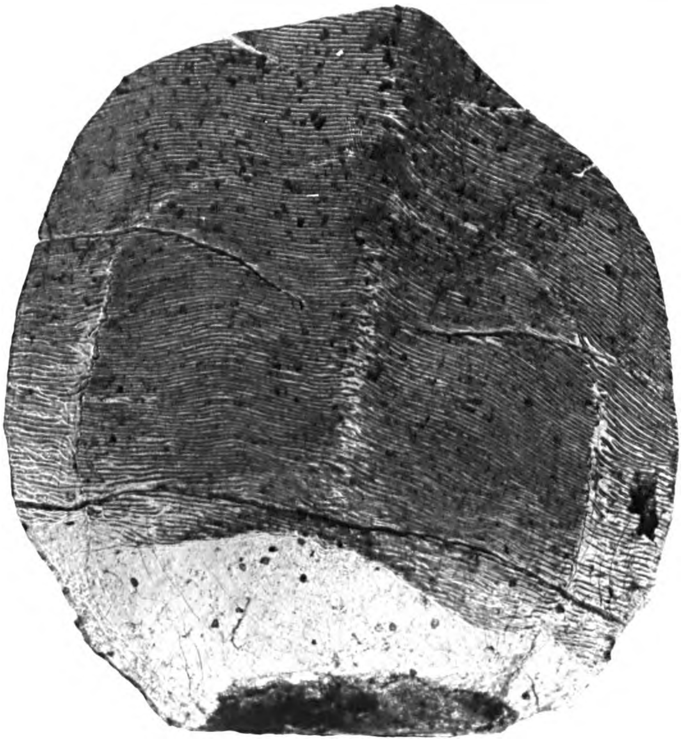


Plate 3.6, Scale from a 1+ fish. The annulus (A) can be clearly seen. X 30



This is very similar to the situation described by Bracken and Kennedy (1967) for A.fallax from the estuary of the Waterford river (Southern Ireland). There, they observed two separate groups, distinguishable by size as well as by the presence or absence of an annulus.

Therefore, in this study, ageing was carried out by summing the number of annuli and spawning marks, and for the adults adding a year for the scale's edge.

D. Accuracy of age determination from scale readings

Le Cren (1947) summarizes five criteria which may be used to substantiate the method of age determination, of these two are applicable to this study, and are:

1. Agreement between the number of length frequency modes and the number of annuli on the scales. (This has sometimes been referred to as Petersen's method.)
2. Variation in the relative abundance of year-classes, resulting in one particular year-class being recognizable over several years.

It has been mentioned, in the previous section, that juvenile A.fallax caught in the Severn estuary during the summer months constitute two groups. The length frequencies of the juveniles were shown in Figure 3.1 and the two modes are apparent. The larger group characterized by having one annulus on their scales, and the smaller group by having either no scales or no annulus on their scales. This seems to indicate that the distance between annuli or between the first annulus and the scale's focus represents approximately one year.

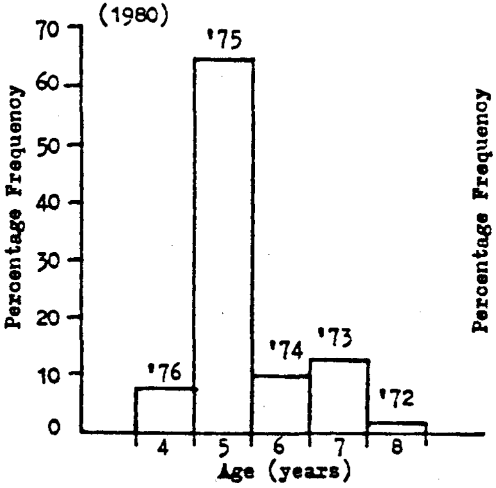
Evidence for the second criteria, combines this study with previous work done by Claridge and Gardner (1978). It is apparent from their catch data that the 1974 year-class was particularly 'poor' when compared to that of the 1975 and 1976 year-classes. Figure 3.2 shows the proportions of the various year-classes of the spawning migrants for the years between 1979 and 1981 inclusive. The expected 'poor' 1974 year-class, as well as the relatively 'good' 1975 and 1976 year-classes are evident. The 'good' 1976 year-class did not appear until 1981, due to the comparatively late maturation of the females of this year class. This is more fully discussed in chapter five.

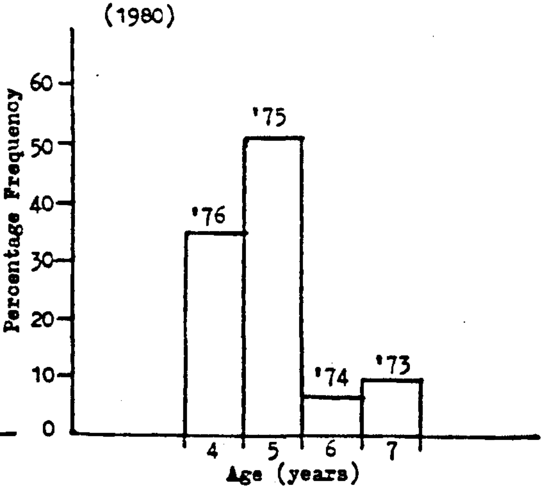
It therefore appears that A.fallax may be accurately aged from their scales using annuli and spawning marks, and in contrast to other member of the genus, which are anadromous, they do not lay down a 'freshwater zone' on their scales when migrating seaward.

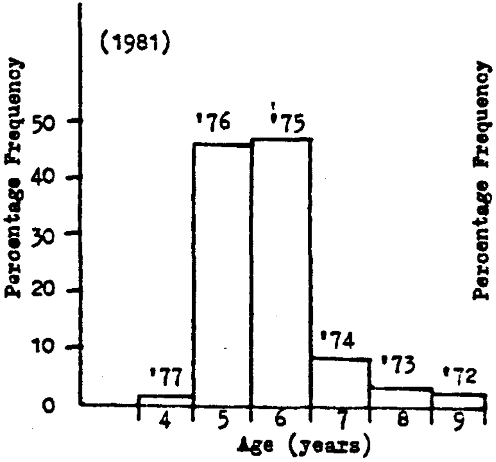
E. Back calculation of annual growth from scales

The method of back calculating length (or weight) at age from scales depends on the annual nature of the annulus, and that the relationship between the fishes size and its scale is directly proportional. The methods used for back calculations have been reviewed by Bagenal and Tesch (1978), Carlander (1981), and Duncan (1980). Back calculation of length at age has been carried out for A.sapidissima by Foote (1976), and La Pointe (1958), and for A.aestivalis by Scherer (1972).

It has already been mentioned that there is absorption and/or erosion of scale material during the spawning migration and it was therefore important to determine whether scales from fish that had previously spawned show the same relationship to fish size as do virgin or first time spawning fish. Figure 3.3 shows a plot of fork length against scale radius (measured to the scales apex), for virgin and repeat spawners. The regression was fitted by the method of


(1980)
Percentage Frequency
0
10
20
30
40
50
60
70
'76
'75
'74
'73
'72
4
5
6
7
8
Age (years)


(1980)
Percentage Frequency
0
10
20
30
40
50
60
'76
'75
'74
'73
4
5
6
7
Age (years)


(1981)
Percentage Frequency
0
10
20
30
40
50
'77
'76
'75
'74
'73
'72
4
5
6
7
8
9
Age (years)

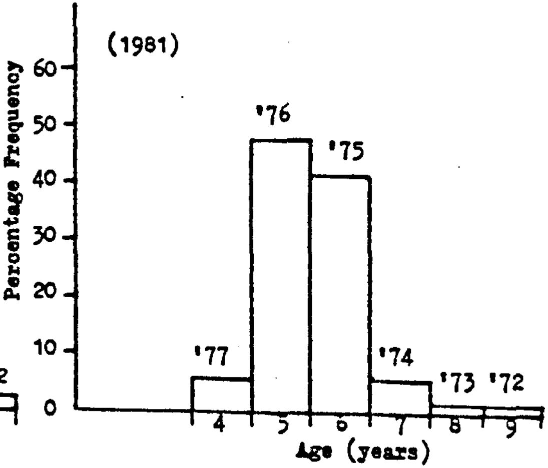

(1981)
Percentage Frequency
0
10
20
30
40
50
60
'77
'76
'75
'74
'73
'72
4
5
6
7
8
9
Age (years)

Figure 3.2, The percentage frequency of each year-class present in the spawning stock, as recorded at Lydney (Severn), for the years 1979, 1980 and 1981.

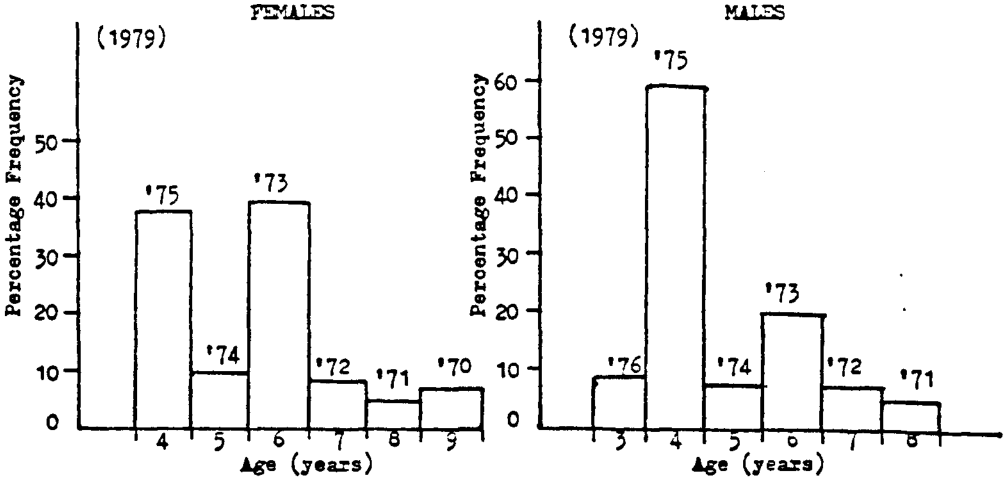


Figure 3.3, An arithmetic plot of scale radius against fork length.

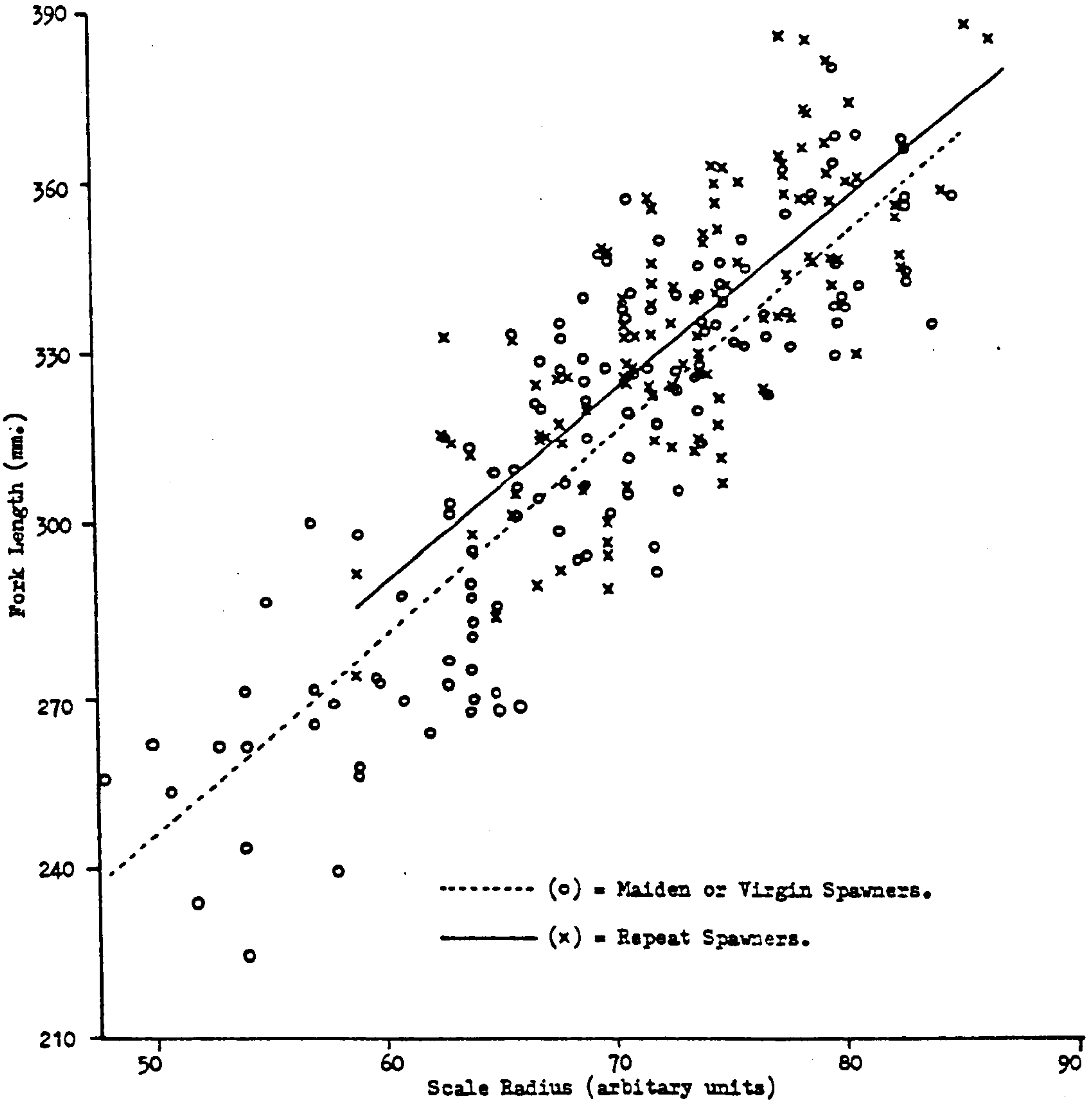


Table 3.1 Coefficients for the regression of scale radius against fork length

Source	N	Slope (b) ± 95% con. limits	Intercept (a)	Coefficient of determination (r^2)	F Value	Significance
Virgins	134	3.445 ± 0.345	73.75	0.7476	388.99	$P < 0.0005$
Repeats	110	3.326 ± 0.530	89.80	0.5888	154.67	$P < 0.0005$

Comparison of the regressions using the student t-test;
Between slopes: $t = 0.3707$, $df = 240$, $P > 0.50$
Between intercepts $t = 0.6171$, $df = 240$, $P > 0.50$

least squares and the coefficients are shown in Table 3.1. It is apparent that the scale radius for a given size of fish is smaller for repeat spawners than for virgins, and this may be associated with some absorption and/or erosion from the apex of the scale. However, student t-test analysis indicates that there is no significant difference between the regressions and so scales from both virgin and repeat spawning fish were used to obtain a relationship between scale radius and fork length.

An arithmetic plot of fork length against scale radius is shown in Figure 3.4 , for 304 sets of data. It may appear from the data that two regressions, one through the bottom cluster of points and one through the top cluster, would best describe the situation. It is quite apparent that insufficient data are available in the middle region. However, as the regression fitted through the points by the method of least squares produced a high value for the coefficient of determination ($r^2 = 0.9873$) it was felt that a linear regression of the form:

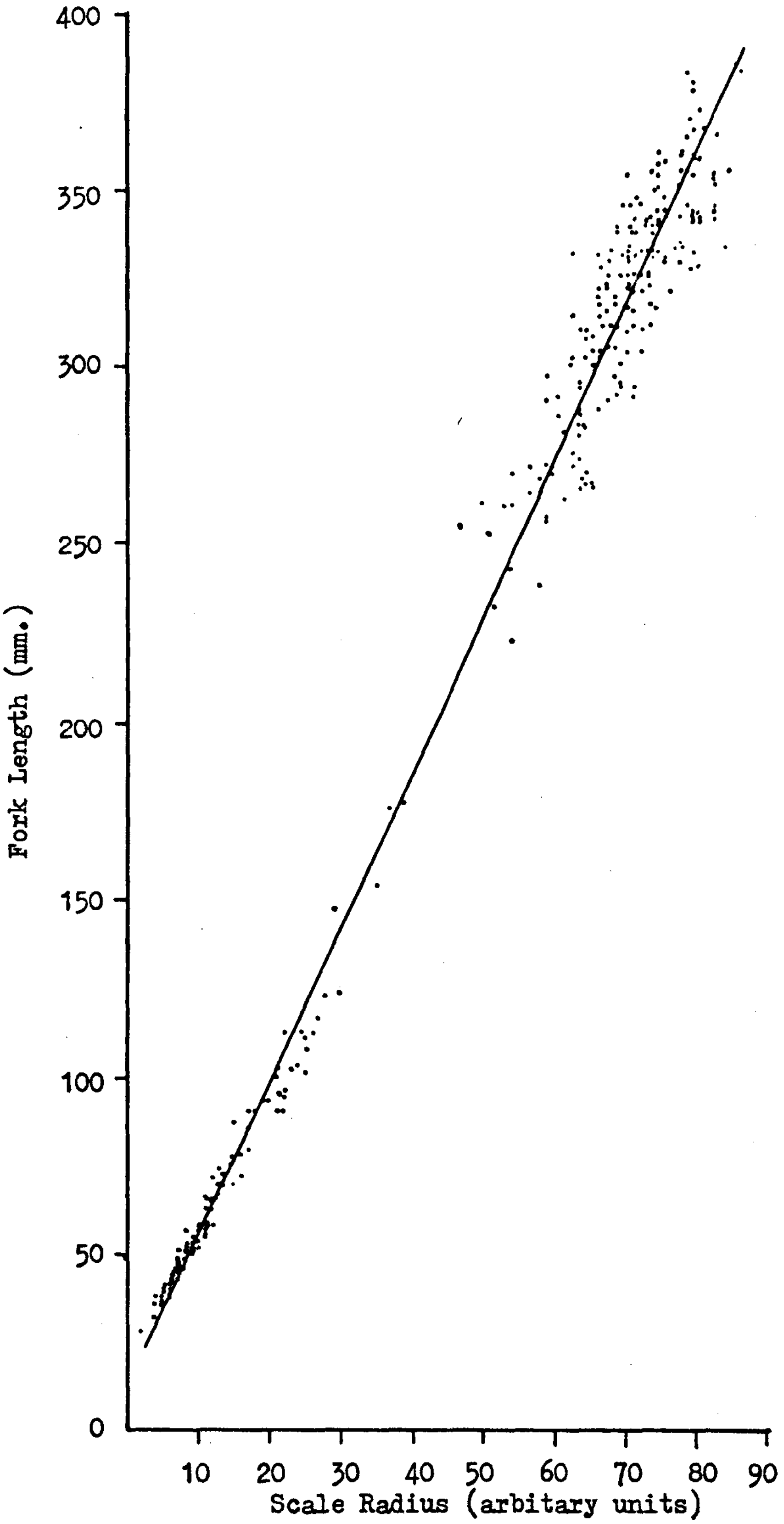
$$\text{Fork Length} = 4.312 \times \text{Scale Radius} + 14.5662$$

$$(F = 23627.75,\ df = 1,302;\ \ P < 0.0005)$$

adequately described the data for the practical purpose of obtaining a relationship to perform satisfactory back calculations.

Thus Figure 3.4 indicates that the growth of A.fallax is allometric in that the regression does not pass through the origin. Similar findings have been reported for A.fallax lacustris (Berg and Grimaldi, 1966), for A.sapidissima (La Pointe, 1958; Leim, 1924) and for A.pseudoharengus in lake Michigan (Norden, 1967a).

Figure 3.4, An arithmetic plot of fork length against scale radius.



Back calculations of the lengths of A.fallax at different ages were carried out using a modification of the direct proportion formula (Lee, 1920), so that:

$$Ln - A = \frac{Sn}{S} (L - A)$$

where

Ln = Length of fish when annulus 'n' was formed,

L = Length of fish when scale sample was obtained,

Sn = Scale radius of annulus 'n',

S = Total scale radius,

A = Intercept from the regression equation (14.5662).

Lengths, back calculated to the various annuli or spawning marks, for the various age groups sampled during the study period, are shown in Table 3.2 and 3.3, for females and males respectively. The overall mean for each age group is shown in the last row.

In any study involving back calculations it is important to investigate whether Lee's phenomenon exists (in Bagenal and Tesch, 1978), this is where, with increasing age, a fish will show a decreasing rate of growth in the back calculated values. Ricker (1975) outlines possible reasons for this. Examination of the back calculated values indicates no evidence of this phenomenon or the reverse situation which has been found in some fish populations (O'Hara, 1976; Wilkinson, 1974).

The mean fork lengths of the different age groups and year classes, caught during this study, are shown in Tables 3.4 and 3.5, for females and males respectively. (The data presented in these tables comes from fish collected using all methods and from both river systems so that an overall picture

Table 3.2 Growth (Mean fork length (mm.) ± 95% confidence limits) of female A.fallax as determined by back calculation from scales, number of individuals in brackets

Year Class	Age in Years							
	1	2	3	4	5	6	7	8
1979	69.13 ± 2.59 (31)							
1978	69.99 ±10.84 (3)	138.44 ±91.42 (3)						
1977								
1976	78.89 ± 2.22 (81)	150.37 ± 4.52 (81)	232.69 ± 5.11 (81)	298.47 ± 4.13 (81)				
1975	77.94 ± 2.65 (119)	179.01 ± 4.76 (119)	256.99 ± 5.45 (119)	314.84 ± 4.38 (119)	340.99 ± 3.05 (119)			
1974	73.52 ± 5.05 (31)	168.1 ± 9.50 (31)	253.36 ± 8.73 (31)	314.12 ± 7.82 (31)	342.7 ± 7.4 (31)	369.54 ±12.5 (10)		
1973	69.11 ± 3.65 (45)	153.93 ± 6.52 (45)	239.62 ± 8.41 (45)	298.17 ± 8.49 (45)	335.13 ± 6.14 (45)	352.88 ± 5.6 (45)	358.65 ±17.81 (9)	
1972	72.51 ± 4.25 (10)	164.43 ±14.9 (10)	243.53 ±17.77 (10)	312.82 ±14.74 (10)	348.39 ±13.03 (10)	364.8 ±11.96 (10)	378.75 ±23.42 (5)	377.2 (1)
1971	73.2 ±16.08 (5)	168.38 ±22.63 (5)	245.16 ±14.84 (5)	294.28 ±27.11 (5)	328.99 ±25.77 (5)	351.36 ±22.76 (5)	365.04 ±19.85 (5)	376.68 ±63.82 (3)
1970	63.6 ±18.65 (4)	143.39 ±37.05 (4)	217.34 ±56.68 (4)	284.88 ±28.75 (4)	327.29 ±28.6 (4)	355.34 ±25.94 (4)	370.58 ±24.6 (4)	383.28 ±24.75 (4)
Mean	71.988	158.256	241.241	302.511	337.248	358.784	368.255	379.053

Table 3.3 Growth (Mean fork length (mm.) ± 95% confidence limits) of male A.fallax as determined by back calculation from scales, number of individuals in brackets

Year Class	Age in Years							
	1	2	3	4	5	6	7	8
1979	69.13 ± 2.59 (31)							
1978	69.99 ±10.84 (3)	138.44 ±91.42 (3)						
1977	62.01 ± 7.26 (5)	136.88 ±11.27 (5)	225.07 ±20.97 (5)					
1976	77.23 ± 3.62 (56)	151.58 ± 8.56 (56)	230.71 ± 9.55 (56)	284.02 ± 6.27 (56)				
1975	73.81 ± 3.58 (48)	174.4 ± 8.95 (48)	248.80 ± 7.88 (48)	290.07 ± 5.89 (48)	308.31 ± 5.02 (48)			
1974	63.88 ± 4.88 (9)	162.68 ±10.54 (9)	254.41 ±14.34 (9)	299.34 ± 8.76 (9)	321.96 ±12.39 (7)	336.13 ±18.08 (4)		
1973	65.99 ± 3.74 (20)	145.0 ±11.04 (20)	228.79 ±10.51 (20)	276.14 ± 9.31 (20)	297.25 ±10.12 (20)	313.64 ±23.68 (7)	352.55 (1)	
1972	75.94 ±21.78 (4)	154.93 ±35.7 (4)	217.85 ±20.65 (4)	279.47 ± 4.07 (4)	306.97 ±10.73 (4)	321.27 ±22.82 (4)	321.98 ± 6.29 (2)	339.56 (1)
1971	65.26 (1)	159.97 (1)	234.85 (1)	292.12 (1)	309.74 (1)	325.15 (1)	344.98 (1)	
Mean	69.249	152.985	234.354	286.86	308.846	324.048	339.837	339.56

Table 3.4 Mean fork length (mm.) ± 95% confidence limits for each age group of female *A. fallax*, number of individuals in brackets

Year Class	Age in Years					
	4	5	6	7	8	9
1977	317.0 ±241.4 (2)					
1976	311.3 ± 4.8 (34)	339.2 ± 2.3 (140)				
1975	323.6 ± 5.3 (49)	338.2 ± 1.9 (290)	358.3 ± 2.3 (141)			
1974		421.2 ± 8.3 (17)	353.9 ± 7.2 (33)	378.7 ± 9.8 (12)		
1973			355.4 ± 4.6 (61)	367.5 ± 4.7 (44)	382.9 ±11.6 (7)	
1972				378.8 ±15.1 (8)	391.7 ±12.3 (7)	390.0 (1)
1971					383.8 ±24.3 (5)	395.2 ±25.6 (5)
1970						400.7 ±14.5 (6)
Mean	317.3	339.5	355.9	375.0	386.1	395.3

Table 3.5 Mean fork length (mm.) ± 95% confidence limits for each age group of male A.fallax, number of individuals in brackets

Year Class	Age in Years						
	3	4	5	6	7	8	9
1977		283.6 ±13.6 (5)					
1976	240.0 ±37.5 (3)	277.4 ± 4.4 (59)	310.3 ± 4.9 (58)				
1975		287.3 ± 7.1 (31)	308.2 ± 4.1 (62)	324.5 ± 5.0 (49)			
1974			311.3 ±28.8 (4)	326.4 ±19.5 (5)	345.7 ±17.4 (6)		
1973				309.4 ±12.8 (14)	320.7 ±30.1 (6)	361.0 (1)	
1972					351.5 ±69.9 (2)	329.0 (1)	348.0 (1)
1971						367.0 (1)	
Mean	240.0	282.8	309.9	320.1	339.3	352.3	348.0

of growth might be presented. It was not possible to compare sizes of fish in each age category from each system as the sampling methods were not comparable.)

F. Accuracy of the Back Calculations

This was carried out using a method suggested by Le Cren (1947) whereby the mean lengths of a sample of fish caught in one year can be compared with back calculated lengths of a sample of fish caught at a later date. This was carried out using females from the 1975 year-class. Members of the 1975 year-class caught in 1981 were used to obtain the mean lengths at ages four and five. These were then compared using a Student t-test with four year olds caught in 1979, and with five year olds caught in 1980. The results are shown in Table 3.6, no significant difference between the means at the 5% level of probability was apparent. This indicates that the method used for calculating the length of fish at previous ages produced reliable results, as well as helping to substantiate the method of age determination.

G. Von Bertalanffy Growth Model

Ricker (1975) described a number of models for representing growth in fishes, of which probably the most common and widely used is that of Von Bertalanffy, (Von Bertalanffy, 1938). Dickie (1978) suggests two main reasons for constructing growth models, firstly, to describe the general pattern of growth so that comparisons may be made within species and between species, Beverton and Holt, (1959) and Pauly, (1980). Secondly, it is important for investigating those factors which are important in studying growth.

The Von Bertalanffy equation is based on physiological considerations in that growth is depicted as the sum of anabolic

Table 3.6 Comparison of directly measured lengths (mm.) with that back calculated from their scales. (Source of material - Females of the 1975 year class)

Source of Material	Mean Fork length (mm.)	95% Confidence limits	N
4 year olds first time spawners sampled 1979	323.59	± 5.308	49
6 year olds - third time spawners sampled 1981 - length at 4th annulus or 1st spawning mark	328.77	± 3.5352	54
t - test	t = 1.5415	df = 101	$p > 0.10$

Source of Material	Mean Fork length (mm.)	95% Confidence limits	N
5 year olds - second time spawners - sampled 1980	342.76	± 2.8448	113
6 year olds - third time spawners sampled 1981 - length at 5th annulus or 2nd spawning mark	346.83	± 3.5352	54
t - test	t = 1.6901	df = 165	$p > 0.05$

Source of Material	Mean Fork length (mm.)	95% Confidence limits	N
5 year olds - first time spawners - sampled 1980	336.76	± 2.3725	172
6 year olds - second time spawners sampled 1981 - length at 5th annulus or 1st spawning mark	338.35	± 4.1405	60
t - test	t = 0.66902	df = 230	$p > 0.50$

profit and catabolic loss where each is a function of size, Von Bertalanffy (1938). However, Ricker (1975) questions whether these assumptions actually occur in nature.

The equation takes the form of:

$$Lt = Loo(I - e^{-k(t-to)})$$

where

Lt = length of fish at time 't',

Loo = The mathematical asymptote of the curve (often referred to as the 'final' or 'Maximum' size),

k = a measure of the rate the growth curve approaches the asymptote,

to = a parameter indicating the hypothetical time at which the fish would have been zero length if it had always grown according to the Von Bertalanffy equation.

The parameters of the equation were calculated separately for females and males, using the mean of the back calculated lengths at each age from all the year-classes. This was done so that a general description of growth was obtained.

Determination of the parameters were carried out by means of Walford plot (Ricker, 1975), for if the equation is rearranged so that,

$$Lt + I = L(I-e^{-k}) + Lte^{-k}$$

a linear relationship is recognizable between Lt and Lt + I. Solving the regression by the method of least squares so that the slope is equal to e^{-k} and the intercept is equal to Loo $(I - e^{-k})$ and therefore

$$Loo = \frac{Intercept}{(I - slope)}$$

A plot of the data is shown in Figures 3.5A and 3.6A for females and males respectively. The regression equations are:

$$Lt + 1 = 118.4356 + 0.7161\ Lt \qquad \text{(females)}$$

$$Lt + 1 = 118.3777 + 0.6747\ Lt \qquad \text{(males)}$$

From the equation, Loo is equal to 417.1 (mm.) for females and 363.86 (mm.) for males, and this agrees closely with the value which may also be obtained from the graphs, where Loo is taken as the length at which the regression line intercepts the 45° diagonal from the origin.

Ricker (1975) rearranges the equation by taking logarithims of the base e, so that:

$$Log_e\ (Loo - Lt) = (Log_e Loo + Kt_o) - Kt$$

which is a linear relationship between t and $Log_e(Loo - Lt)$, with a slope equal to -k and the intercept equal to $(Log_e Loo + kt_o)$. The regressions produced are shown in Figures 3.5 B and 3.6 B for females and males respectively, and take the form:

$$Log_e\ (Loo - Lt) = 6.1352 - 0.3275\ t \qquad \text{(females)}$$

$$Log_e\ (Loo - Lt) = 6.0133 - 0.3833\ t \qquad \text{(males)}$$

From these regressions t_o may be computed and is found to be 0.311

Figure 3.5 A, A Walford plot for female *A. fallax*.

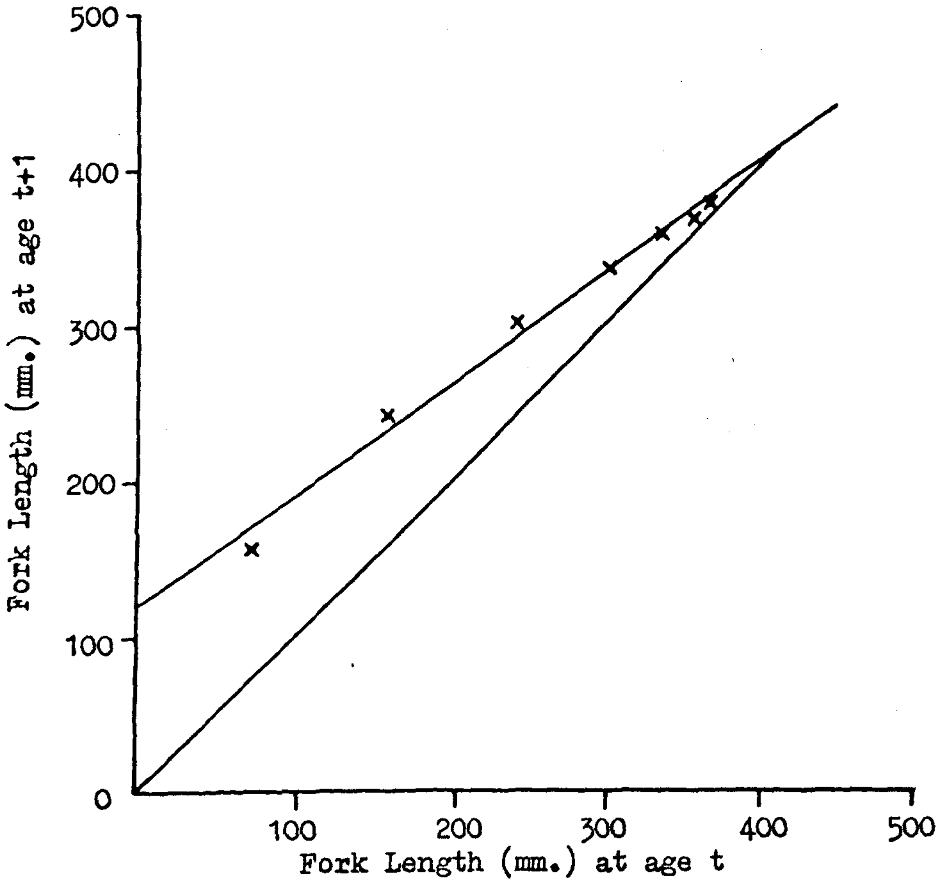


Figure 3.5 B, A plot of $\text{Log}_e(L_\infty - Lt)$ against age for female **A.fallax.**

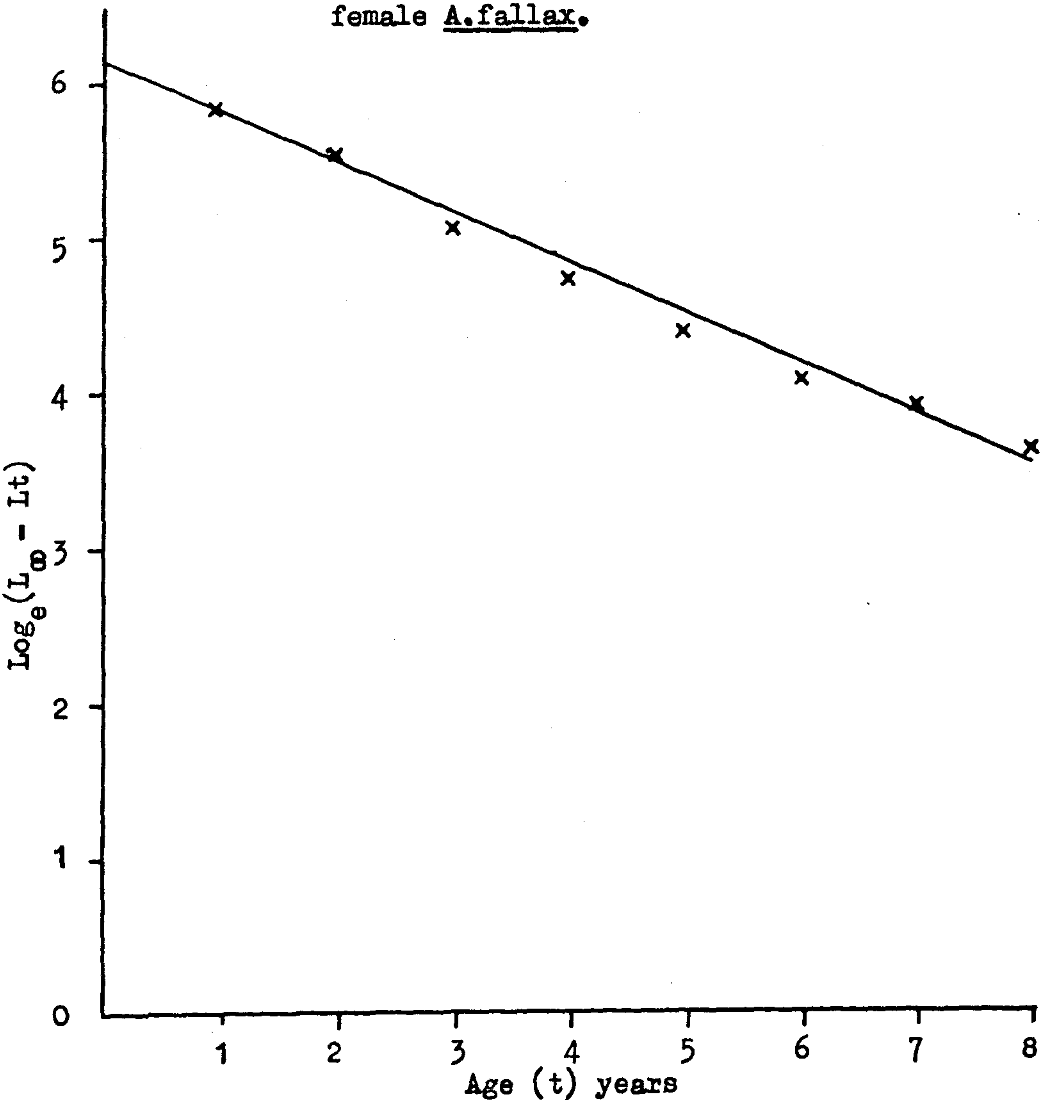


Figure 3.6 A, A Walford plot for male *A. fallax*.

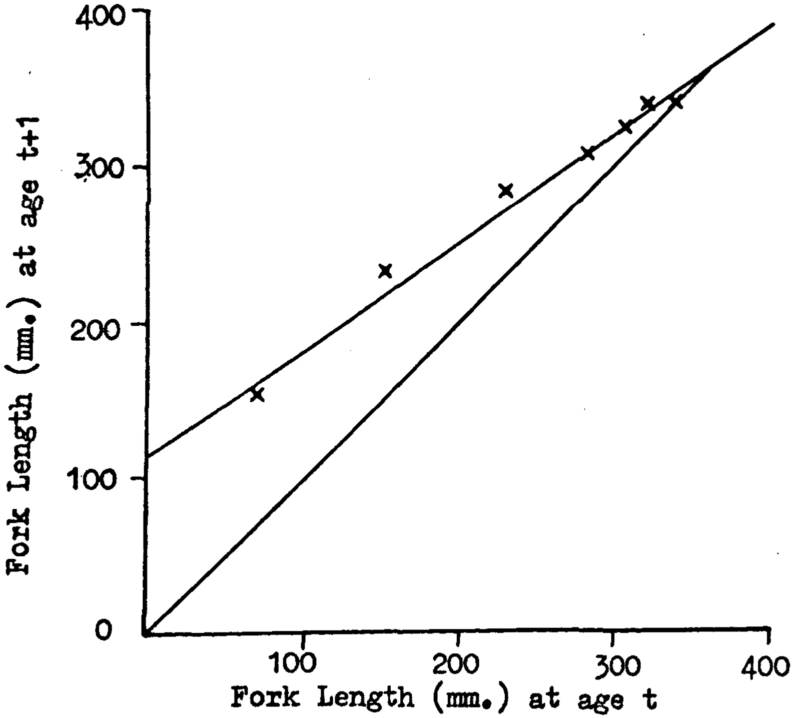
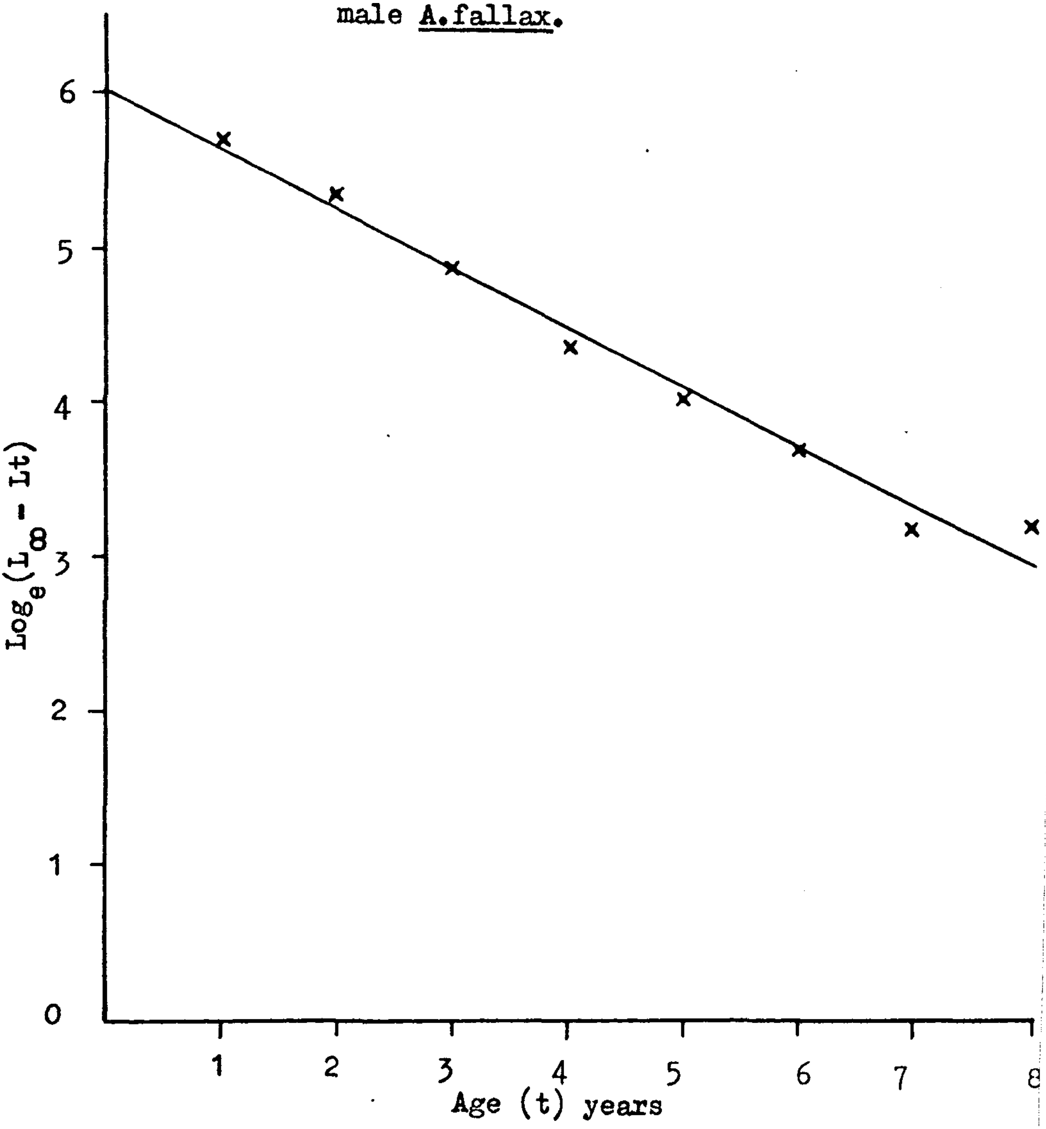


Figure 3.6 B, A plot of $Log_e(L_\infty - Lt)$ against age for male <u>A.fallax</u>.



year for females and 0.304 year for males.

Thus the constants for the Von Bertalanfry equation calculated from the data obtained during this study are;

Loo = 417.1 (mm.); k = 0.3275; t_o = 0.311 (year) (females)
Loo = 363.86 (mm.); k = 0.3833; t_o = 0.304 (year) (males)

Substituting these parameters into the Von Bertalanfry equation produced the predicted lengths at each age, and these are shown in Figures 3.7 A + B, for females and males respectively, together with the curve obtained from the back calculated values. The model appears to give a reasonable description of the data. However, the lengths computed at ages one and two may be regarded as slightly higher than expected.

From the data it appears that there is very little difference in the mean length at age for each sex, until the third year of life after which the absolute growth rate appears to slow down sooner for the males than for the females. This may be related to the fact that males generally mature earlier than the females, and the onset of sexual maturity is closely associated with a decline in the growth rate, (see chapter five).

H. Comparison with other populations

From the literature, it was possible to obtain some information on the growth of various populations of A.fallax. The data represented in Table 3.7 is presented in terms of fork length and it can be seen that some of the published information had to be converted so that comparisons could be made. The data was converted using the formulas presented in appendix one, it had to be assumed that all the populations had the same or similar standard: fork : total

Figure 3.7 A & B, The growth of female and male *A.fallax* determined by back calculation from scales, and by the Von Bertalanffy equation.

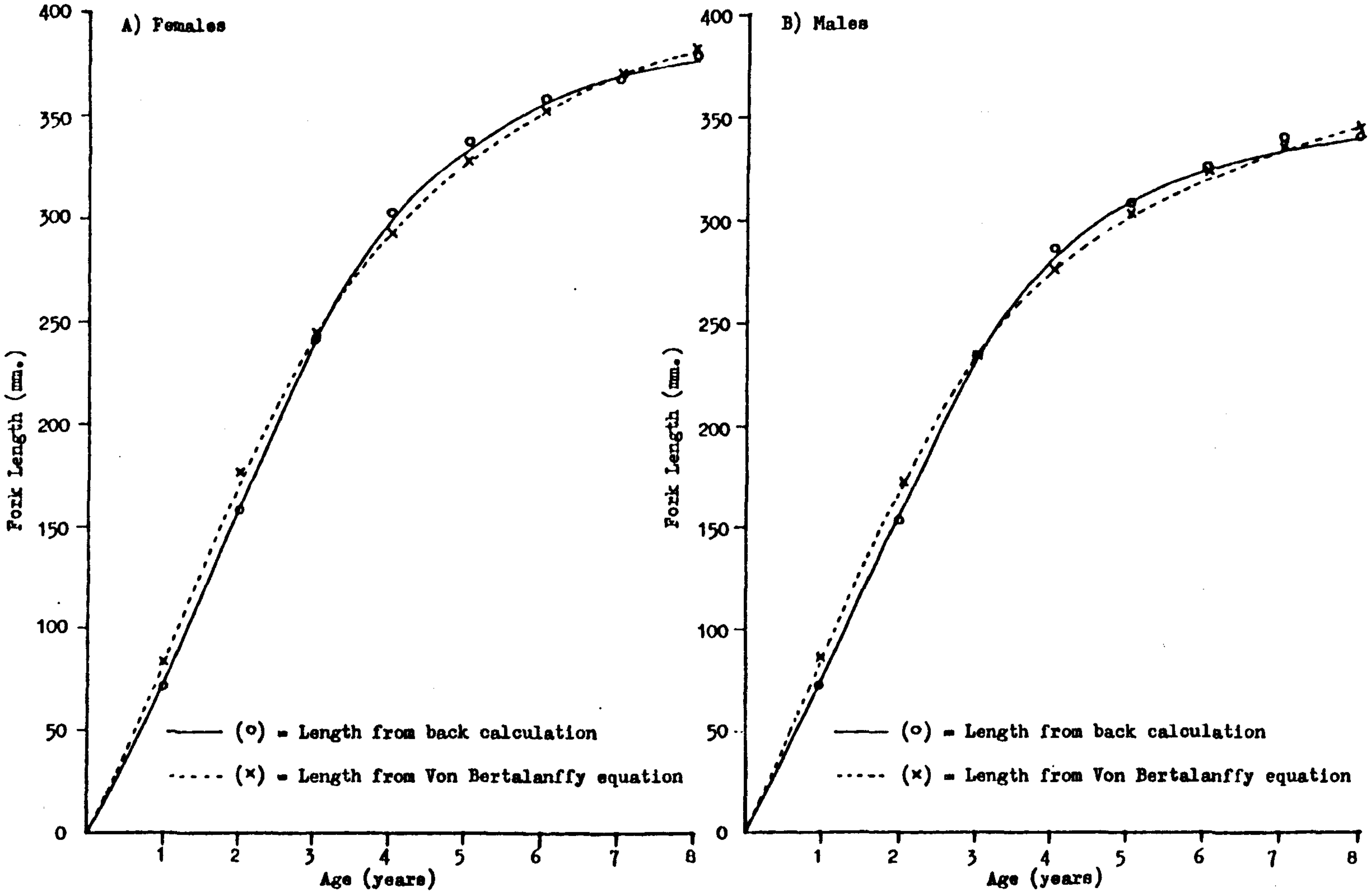


Table 3.7 The Growth of *A.fallax* from Various Sources

Source of Material	Alteration of Material	Sex	Mean Fork Length (mm.) at Age									Reference
			1	2	3	4	5	6	7	8	9	
R.Severn & R. Wye		M	69.3	153.0	234.4	286.9	308.8	324.0	339.8	339.6	(348.0)	This Study
		F	72.0	158.3	241.2	302.5	337.8	358.8	368.3	379.1	(395.3)	
Holland	Total length converted to fork length	M					305.5	322.0	332.8	340.6	345.0	This Study
		F				314.4	355.6	359.3	391.9	390.9	401.8	
R. Severn	Standard length converted to fork length	M			252.1	301.8						Claridge & Gardner (1978)
		F				322.2	347.9	361.6				
S.Ireland		com-bined	75.0	141.0	210.0	258.0	317.0	343.0	350.0			Bracken & Kennedy (1967)
R.Suir R.Blackwater (S.Ireland)		M							367.5	351.0	390.0	Went (1953)
		F				310.0		349.3	350.0		380.0	
R. Elbe (Germany)	Total length converted to fork length	M			277.0	305.7	332.6	336.4	350.5	347.1		Hass (1965)
		F			314.6	351.8	354.5	386.4	386.4	408.1		
R. Elbe (Germany)		M				303.3						Jenkins (1902)
		F				340.0	397.8					
Algiers		M	109.1	157.2	218.3	235.8	253.3					Bounhiol (1917) (species possibly *A.fallax algeriensis*)
		F	139.7	192.1	266.4	292.6	336.3					

A.fallax lacustris

L.Maggiore (Italy)	Total length converted to fork length	M	117.5	187.1	220.9	238.8						Berg & Grimaldi (1966)
		F	114.1	190.1	232.6	249.3						

length relationships. A further alteration was made to the data of Hass (1965) in that a year was added to the ages for Hass took their birthday to be the first of July. So that a fish caught during the spawning migration and referred to as four years old by Hass (four annuli visible on the scale and a considerable amount of 'plus' growth) would be considered as a five year old in this study. For the same reason a year was added to the data of Claridge and Gardner (1978).

The data obtained in this study agrees closely with that found by Claridge and Gardner (1978) and also with that from Holland (supplied, courtesy of Dr. Steinmetz, and presented in appendix two). It is interesting to note that the population from the Elbe (Hass, 1965; Jenkins, 1902) is larger for a given age when compared with other anadromous populations. Jones (1976) reported for some marine species, *Clupea harengus* (Linnaeus), *Gadus morhua* (Linnaeus) and *Melanogrammus aeglefinus* (Linnaeus), that differences in their growth rate exist throughout their geographical range. Temporal changes have also been shown to be apparent by Burd and Cushing (1962) for *C.harengus* and by Rollefsen (1953) for *G.morhua*, in both cases density dependent factors were implicated. Other possible reasons for these variations have been suggested by Jones (1976).

These differences may indicate that there exists several different stocks of *A.fallax*. It has been shown that *A.fallax* from different river systems exhibit variation in some of their taxonomic characters (Eiras, 1980; Quignard and Kartas , 1977). A similar situation is encountered with *A.sapidissima* where differences in meristic characters (Carscadden and Leggett, 1975b; Fischler, 1959; Hill, 1959; Nichols, 1966; Valdykov and Wallace, 1938; Warfel and Olsen, 1947) as well as reproductive characters (Carscadden and Leggett, 1975a; Glebe and Leggett, 1981b; Leggett, 1969; Shoubridge and Leggett, 1978; Walburg and Nichols, 1967) have been observed between populations from several Atlantic coast rivers. This would seem to indicate that isolated populations do exist so that heredity and environmental factors could play a part in affecting such factors as growth rate.

For comparison of growth rate with other members of the genus, an extensive synopsis of biological data on the American species is given by Carlander (1970) and for the species from the Black Sea, Sea of Azov and Caspian Sea by Svetovidov (1963).

I. Spawning Mark

In this chapter many references have been made to the development or presence of a spawning mark on the scales. Chugunova (1961) considers the spawning mark to be the result of an adaption of the scale covering to changes in the bodies' shape resulting from either the release of sexual products or to a decrease in food intake. This erosion enables the fish to maintain it's mobility. Zamakhaev (1940) made similar conclusions.

Absorption of scale material in association with spawning has also been attributed to the utilization of essential nutrients which must be obtained as the fish are not feeding actively during this period. Garrod and Newell (1958) observed a drop in the calcium content of the scales in association with the development of the ovaries. Mugiya and Watabe (1977) have found that calcium may be resorbed from the scales and that it is under the control of reproductive hormones. As well as a possible store of calcium, O'Grady (1981) has shown that scales may also be an important store of essential trace metals. O'Grady (1981) found a reduction of between 42% and 53% in the Zinc concentration of the scales of anadromous Salmo trutta (Linnaeus) just prior to spawning when compared with fish caught earlier in the season from the estuary and suggested that this may represent the utilization of stored nutrients for gonadal development and maturation.

An attempt to illustrate the amount of adsorption and/or erosion and from which part of the scale, was undertaken using a method suggested by Jones (1959). Scales were taken from females of the 1975 year-class, caught during 1980. A proportion of which had spawned for the first time at age four and were making their second spawning migration. The others which were spawning for the first time at age five, were taken to represent the 'normal' pattern of scale growth. The scales were measured from the focus point to the third annulus, fourth annulus or spawning mark , and to the scale's edge. The scale radii were taken at six different locations starting at the apex of the scale and rotating at 18^{o} intervals. The measurements were taken from both sides of the scale, averaged and related to fork length using a regression fitted by the method of least squares.

The regressions are shown in Tables 3.8 and 3.9 for five year old second and first time spawners respectively. The scale dimensions were calculated for a fish with a fork length of 350 mm. and these are shown in figures 3.8 A + B. The diagram shows that there is a considerable amount of absorption and/or erosion from the lateral regions of the scale in that the spawning mark nearly (and in some cases does) obliterate the third annulus.

The situation described here relates to the average amount of absorption and/or erosion for female <u>A.fallax</u> that have successfully spawned once and the situation may be worse for those fish which failed to survive. In salmonids the amount of absorption and/or erosion is associated with the length of time spent in freshwater (Crichton, 1935; Jones, 1959), the same situation probably applies to <u>A.fallax</u>,

Table 3.8 Coefficients for the regression of scale radius (arbitary units) against fork length (mm.) for females aged five spawning for the second time

Scale Edge

Position	N	Slope (b) ± 95% confidence limits	Intercept (a)	Coeff. of Determination r^2	F Value	Significance
1	66	3.373 ± 0.391	84.628	0.7803	233.06	$P \ll 0.0005$
2	66	3.212 ± 0.502	115.75	0.7183	163.176	$P \ll 0.0005$
3	66	2.966 ± 0.545	128.504	0.6491	118.388	$P \ll 0.0005$
4	66	2.695 ± 0.833	177.742	0.3952	41.817	$P < 0.0005$
5	66	2.2 ± 0.893	222.651	0.2752	24.298	$P < 0.0005$
6	66	2.074 ± 0.995	238.311	0.2132	17.346	$P < 0.0005$

4th Annulus/Spawning Mark

Position	N	Slope (b) ± 95% confidence limits	Intercept (a)	Coeff. of Determination r^2	F Value	Significance
1	66	3.182 ± 0.485	118.129	0.7289	172.077	$P \ll 0.0005$
2	66	3.12 ± 0.538	141.17	0.6769	134.112	$P \ll 0.0005$
3	66	3.037 ± 0.672	147.027	0.5605	81.602	$P \ll 0.0005$
4	66	2.634 ± 0.944	203.514	0.3269	31.081	$P < 0.0005$
5	66	2.519 ± 1.047	226.178	0.2651	23.083	$P < 0.0005$
6	66	2.116 ± 1.127	250.157	0.1803	14.072	$P < 0.0005$

3rd Annulus

Position	N	Slope (b) ± 95% confidence limits	Intercept (a)	Coeff. of Determination r^2	F Value	Significance
1	66	2.234 ± 0.604	209.135	0.4602	54.556	$P \ll 0.0005$
2	66	2.703 ± 0.58	191.959	0.575	86.582	$P \ll 0.0005$
3	66	2.701 ± 0.632	190.254	0.5321	72.788	$P \ll 0.0005$
4	66	2.072 ± 0.78	241.512	0.3057	28.174	$P < 0.0005$
5	66	2.401 ± 0.916	239.557	0.3002	27.461	$P < 0.0005$
6	66	2.292 ± 1.005	249.614	0.245	20.772	$P < 0.0005$

Table 3.9 Coefficients for the regression of scale radius (arbitary units) against fork length (mm.) for females aged five spawning for the first time

Scale Edge

Position	N	Slope (b) ± 95% confidence limits	Intercept (a)	Coeff. of Determination r^2	F Value	Significance
1	66	3.419 ± 0.323	78.674	0.8749	465.01	$P \ll 0.0005$
2	66	2.298 ± 0.474	171.114	0.6391	113.325	$P \ll 0.0005$
3	66	2.854 ± 0.431	131.263	0.6934	144.738	$P \ll 0.0005$
4	66	2.903 ± 0.63	156.439	0.57	84.846	$P < 0.0005$
5	66	2.762 ± 0.709	183.955	0.4861	60.539	$P < 0.0005$
6	66	2.536 ± 0.806	206.689	0.3818	39.518	$P < 0.0005$

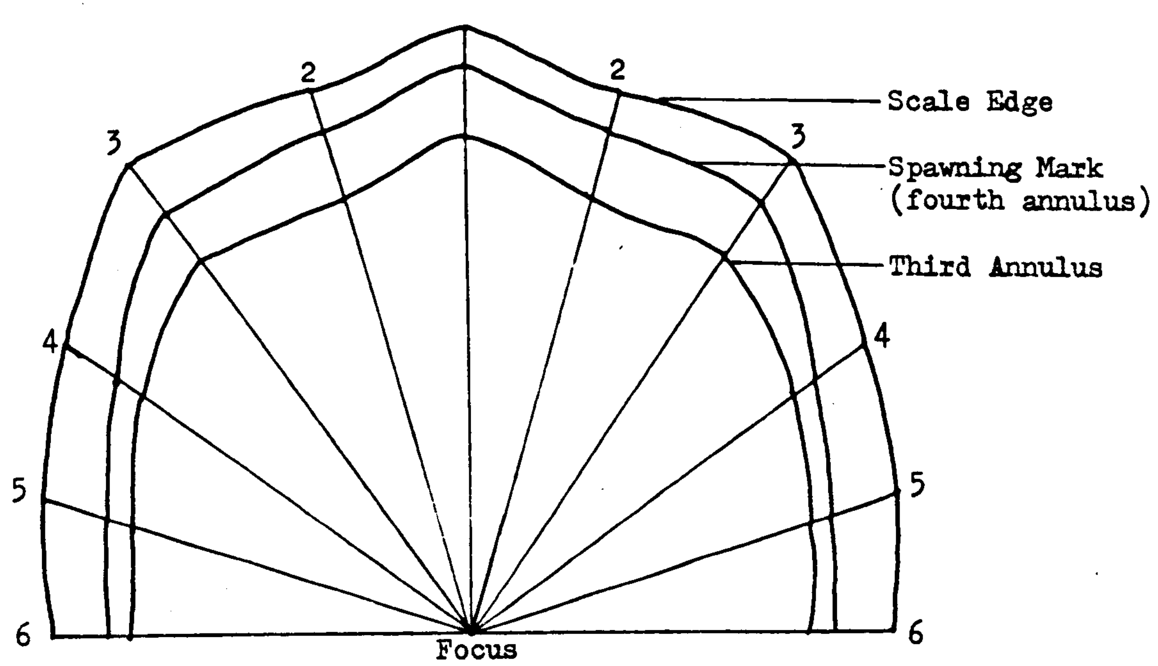
4th Annulus

Position	N	Slope (b) ± 95% confidence limits	Intercept (a)	Coeff. of Determination r^2	F Value	Significance
1	66	2.938 ± 0.363	142.664	0.8033	261.354	$P \ll 0.0005$
2	66	2.858 ± 0.466	160.58	0.7011	150.083	$P \ll 0.0005$
3	66	2.818 ± 0.551	159.277	0.6204	104.607	$P \ll 0.0005$
4	66	2.706 ± 0.692	190.142	0.4885	61.114	$P < 0.0005$
5	66	2.981 ± 0.863	193.583	0.4266	47.608	$P < 0.0005$
6	66	2.735 ± 0.884	213.43	0.3737	38.192	$P < 0.0005$

3rd Annulus

Position	N	Slope (b) ± 95% confidence limits	Intercept (a)	Coeff. of Determination r^2	F Value	Significance
1	66	1.897 ± 0.634	235.725	0.3585	35.765	$P \ll 0.0005$
2	66	2.235 ± 0.66	226.796	0.4168	45.731	$P \ll 0.0005$
3	66	2.154 ± 0.682	229.408	0.3832	39.76	$P \ll 0.0005$
4	66	1.759 ± 0.743	261.245	0.2591	22.385	$P < 0.0005$
5	66	2.134 ± 0.799	255.447	0.3078	28.455	$P < 0.0005$
6	66	1.974 ± 0.953	266.116	0.2109	17.103	$P < 0.0005$

A) Age five, one previous spawning.



B) Age five, virgin spawner.

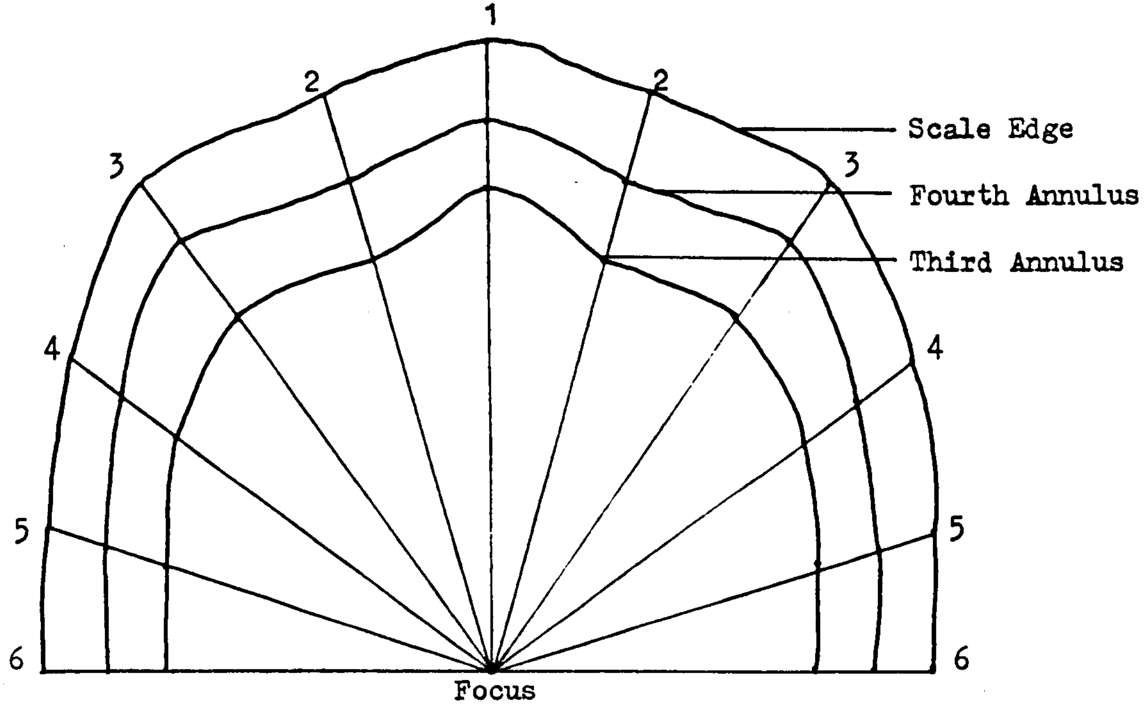


Figure 3.8, The relative positions of the annuli for female A.fallax that have previously spawned (A) and those which have yet to spawn (B). Measurements taken along numbered lines.

though not as definitively, as the length of time spent in freshwater is considerably less.

CHAPTER FOUR

SPAWNING MIGRATION

Introduction

Spawning migrations are undertaken by a vast number of fish species for the purpose of optimizing the survival of the eggs and larvae (Northcote, 1978). This is enhanced by an ability to home to the natal river system, or more specifically to spawning areas within a river system. This ensures the orderly arrival of mates in the correct physiological condition as well as the optimal utilization of spawning areas (Northcote, 1978). The precision of homing has been suggested to vary with the complexity of the situation which the fish have to overcome to complete their life history (Banks, 1969). However, homing that is too precise has its disadvantages, from the populations viewpoint, in that it does not allow for the exploitation of new and possibly more favourable spawning areas and that there is no insurance against the chance that the spawning area may be completely destroyed, thus some straying may be advantageous (Harden Jones, 1968; Northcote, 1967).

For some species these migrations involve travelling over vast distances and for the anadromous and the catadromous species, through to a different medium. For anadromous species entering freshwater on their spawning migration, except possibly for the initial transition from salt to freshwater, the change in medium should not cause an added increase in energy expenditure (Farmer and Beamish, 1969; Rao, 1968). During such migrations feeding generally stops or is reduced, and this has been found to be the case for *A.fallax* (chapter seven). Thus the fish must rely on stored energy reserves of which fats have been reported to be the most important (Cowey and Sargent, 1979). The optimum utilization of which may be beneficial in a number of ways, either by increasing egg size, and/or egg number, and/or post-spawning survival. Thus the study of fish behaviour during the migration period is important as it may be of adaptive significance. Certain behavioural changes in swimming speed as observed by Leggett and Trump (1978) and in the fishs' spatial distribution (Brett, 1965; Weihs, 1978) have resulted in a better use of energy reserves.

Some information on the spawning migration of A.fallax have been reported by Bounhoil (1917), Claridge and Gardner (1978), D'Ancona (1928), Day (1890), Ellison (1935), Gallois (1946-7), LaHaye et al. (1963), Hass (1965), Rameye et al. (1976) and Roule (1922 & 1933), though it is poorly understood when compared with other members of the genus. In this chapter the effects of some environmental factors on the spawning migration, the changes that occur during the upstream migration as a result of spawning, and the characteristics of the spawning areas have been investigated.

A. Materials and Methods

The fish were caught using those methods described in chapter two, measured to the nearest millimetre and weighed to the nearest gramme. The gonads were removed and weighed to the nearest 0.1 gramme. Somatic weight was calculated as total weight minus gonad weight. The fish were aged using scales as described in chapter three.

All measurements were carried out on fresh fish or on fish that had been kept under ice for no longer than 24 hours. In a few instances fish had to be frozen. In these cases approximately 20 fish were placed in a plastic bag and as much of the air as possible extruded, in an attempt to reduce dehydration. All frozen samples were processed within a month.

Fish taken for the determination of total lipids were caught at Newnham, using a seine net, and placed in plastic bags in groups of five. The air was extruded with the aid of a vacuum pump and the bags sealed, no leakage was observed. Total lipid extraction was carried out according to the method of Bligh and Dyer (1959). To a five gramme (wet weight) sample of muscle, 10 mls. of chloroform, 10 mls. of methanol and 4 mls. of distilled water were added and homogenized using a polytron blender for two minutes. A further 10 mls. of chloroform was then added and homogenized for 30 seconds. To this was then added 10 mls. of distilled water and homogenized for 30 seconds. The homogenate was then filtered using a Buchner funnel. The residue, when dry was further homogenized with 10 mls. of chloroform for two minutes and filtered. The residue was then washed with 5 mls. of chloroform. The filtrate was then placed into a separating funnel and the bottom layer (containing the lipids) was removed. The chloroform was then evaporated off, with the aid of compressed air, by placing the boiling tube in a water bath at 50°C. Two samples were analysed from each fish. Muscle used in the determination was taken from the flanks, and only white muscle was used in the analysis.

Water content of muscle was determined by drying two 5 gramme samples to constant weight at 60°C as proposed by Dowgiallo (1975).

B. Entry into Freshwater

There is some evidence that A.fallax home to their parent stream. It has been shown, that A.fallax from several different river systems exhibit differences in a number of their morphological characteristics, by Eiras (1980) and by Quignard and Kartas (1977). During this study the number of gillrakers from the right gill arch were counted, and the distribution is shown in table 4.1. The numbers range from 38 to 60, with a mean of 44.51 (95% confidence limits = ± 0.447). This is slightly higher than that found by Claridge and Gardner (1978) of

43.61 (95% confidence limits = ± 0.678) for adult <u>A.fallax</u> from the Severn.

Table 4.1 Variation in the total number of gill rakers of the first Branchial arch, on the right hand side (n = 189)

38	39	40	41	42	43	44	45	46	47	48	49	50	51	56	58	60
2	9	5	6	18	22	29	36	23	13	11	3	3	1	1	1	1

Furnestin and Vincent (1958) reported that for fish greater than 20 cms. in length, the number of gillrakers was not related to total length. However, Quignard and Kartas (1977) found a significant correlation between gillraker number and total length. A similar association was found for <u>A.fallax</u> from the Severn, figure 4.1 and table 4.2. (An association might be expected if the gillrakers were important in feeding). From the data presented by Eiras (1980) and by Quignard and Kartas (1977), it appears that <u>A.fallax</u> from different river systems exhibit variation in the number of gillrakers on their first gill arch. As differences in both the means and in the regressions were evident, it would appear that <u>A.fallax</u> spawning in the Severn may represent a separate stock.

A similar situation is encountered with <u>A.sapidissima</u> where populations from different river systems show differences in some of their meristic characters, (Fischler, 1959; Hildebrand and Schoeder, 1928; Hill, 1959; Nichols, 1966; Vladykov and Wallace, 1938; Warfel and Olsen, 1947) as well as within a river system (Carscadden and Leggett, 1975b). Variation in some meristic characters between different areas has also been reported for <u>A.pseudoharengus</u> (Messieh, 1977). Reproductive characteristics, for <u>A.sapidissima</u>, have also

Figure 4.1, The arithmetic relationship between the number of gillrakers on the first gill arch and fork length.

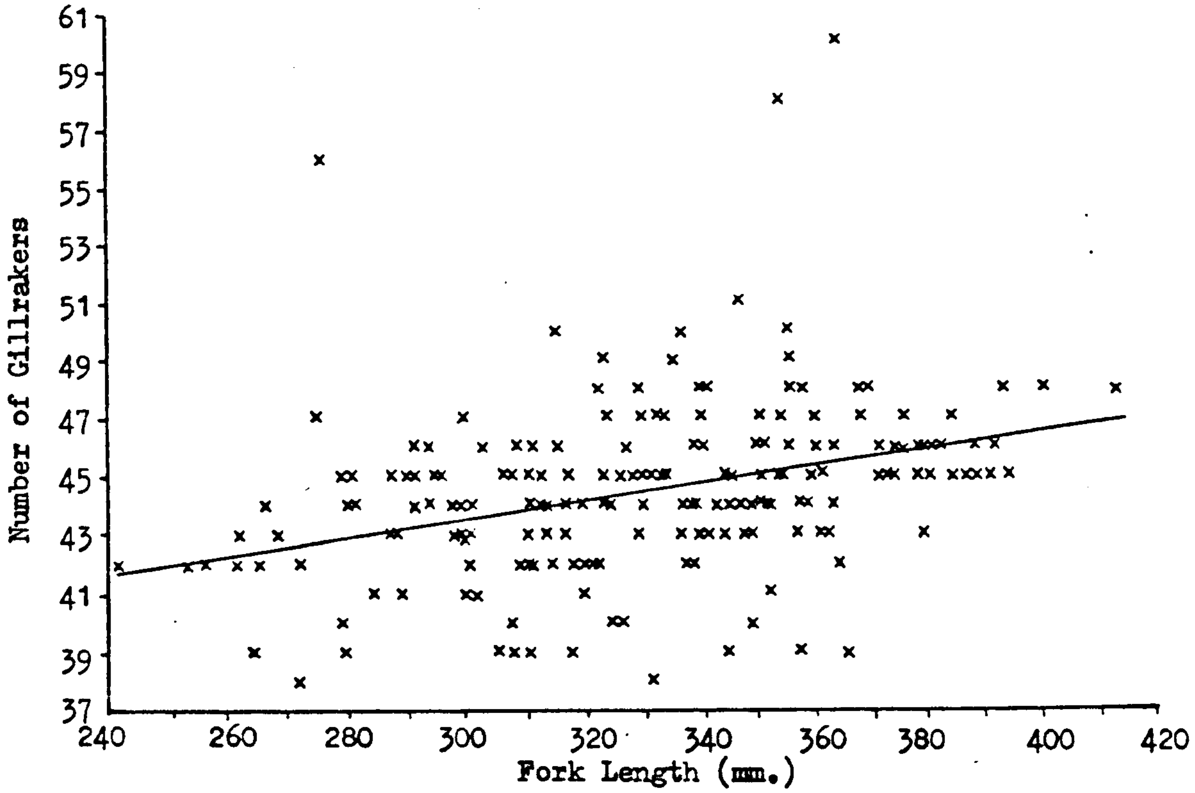


Table 4.2 Coefficients for the regression of gillraker number against length.

Independent Variable	Intercept	Slope (b) ± 95% confidence limits	Coefficient of Determination	F Value	Significance of F
Fork length	34.5826	0.0299 ± 0.0121	0.1155	23.7692	$P < 0.0005$
Total length	34.6756	0.02563 ± 0.0104	0.1142	23.4554	$P < 0.0005$

been found to vary between river systems (Glebe and Leggett, 1981b; Leggett, 1969; Leggett and Carscadden, 1978; Shoubridge and Leggett, 1978; Walberg and Nichols, 1967) as well as within a river system (Carscadden and Leggett, 1975a).

There is also evidence from the establishment of a spawning population from the stocking of mature A.pseudoharengus (Havey , 1961; Hildebrand, 1963), and from tagging studies with A.sapidissima (Nichols, 1961). Leggett (1977) reported that modification to the Holyoke Dam on the Connecticut River has allowed greater numbers of A.sapidissima to migrate upriver. Evidence for homing comes from the fact that the numbers arriving at the dam showed a four or five year periodicity which would be expected if the fish were homing. As the age at first spawning for the Connecticut River population is between four and five years old (Leggett, 1969). There also existed a difference in the proportion of repeat spawners in the spawning population above and below the dam which would not have arisen if the choice of spawning location was totally random. This would seemingly indicate homing to spawning areas within a river system.

The method used for selecting the parent stream may be similar to that described by Hasler (1971) for salmonids, of odour. Thunberg (1971) found that A.pseudoharengus can distinguish between homestream water and water from other sources, by olfaction.

A relationship between the onset of the spawning migration and temperature was mentioned by Pennant (1777) for A.alosa from the Severn. At Lydney on the River Severn the first A.fallax were recorded, for the years 1979, 1980 and 1981, during the middle of April when the temperature had reached 9.5°C, 10.2°C and 10.2°C. (It should be noted that in this region of the estuary sampling started on the 15th April. Thus in 1981 when fish were caught on the first tide indicates that the migration at Lydney may have started at a slightly lower temperature.) These temperatures are slightly lower than those found by Claridge and Gardner (1978) for the commencement of the spawning migration through the estuary (12°C) and may reflect differences in sampling efficiency.

On the Seine Roule (1922) reported an association between the onset of the spawning migration and temperature with the first A.fallax being seen at temperatures between 10°C and 11°C. Gallois (1946) on the Rhone found the migration started in mid-April when the temperature had reached between 11°C and 14°C. Rameye et al. (1976) also on the Rhone found that A.fallax commence their migration slightly earlier at the end of March, when the temperature had reached 10°C. Rameye et al. (1976) also reported that the time of entry may be severely affected by weather conditions, for example, in 1976 the spawning migration on the Rhone was delayed by a month presumably due to the cold spring. Similar observations were reported by Roule (1933). Around the coast of Algiers, Bounhoil (1917) found that A.fallax commence their migration in March. This is similar to the situation in Morocco where the onset of the migration for A.fallax occurs towards the end of March - start of April (LaHaye et al. 1963). A relationship between movement and temperature was also evident for landlocked populations of Alosa in Morocco, where upstream movement to the spawning areas was associated with a rise in temperature (Furnestin and Vincent, 1955).

For other members of the genus the suggestion that temperature plays a crucial role in controlling the timing of the migration was first reported for A.sapidissima by McDonald (1884) who found that favourable temperatures accelerated the run, with the converse also being true. Since then a number of investigators have reached similar conclusions for A.sapidissima notably Leggett and Whitney

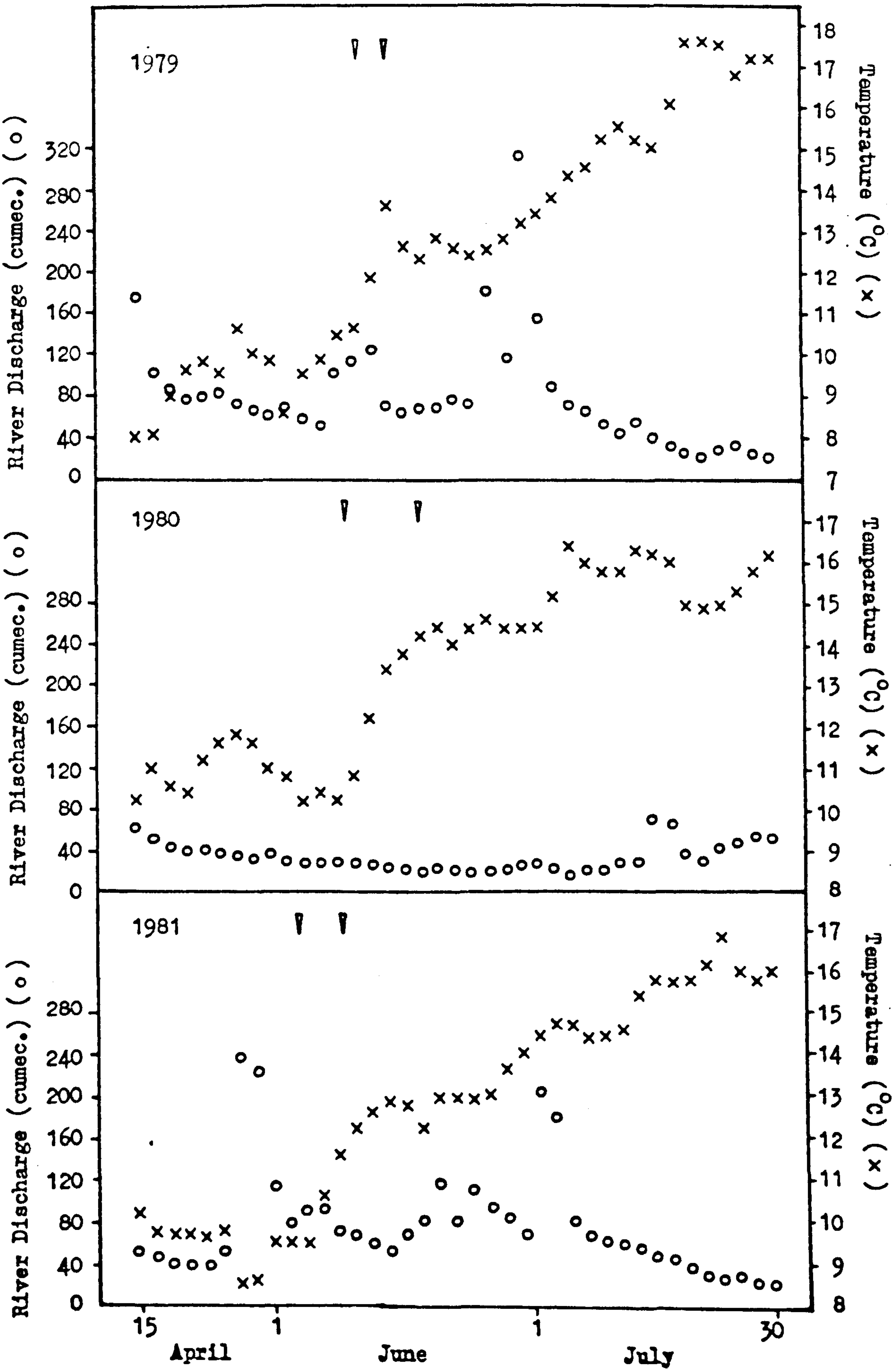
(1972), Leim (1924), Massman and Pacheco (1957) as well as for *A.pseudoharengus* by Beltz (1975), Cooper (1961), Dominy (1971), Kissil (1974), Libey (1976), Richkus (1974), Tyus (1974) and for *Alosa Kessleri pontica* (Eichwald) from the Danube (Moroz, 1969). Mogil'chenko (1977) as well as finding that the onset of the spawning migration of *A.kessleri pontica* was closely related to temperature also reported that fish of a specific size tend to migrate at a very specific temperature, with the larger specimens entering at lower temperatures.

As well as temperature, Talbot (1954) concluded that the amount of freshwater discharge also affected the time of entry of *A.sapidissima* into the Columbia River. Leggett and Whitney (1972) examined a further nineteen years of data from the Columbia River and found a significant correlation between the time of entry with both temperature and river flow. However, from the fact that *A.sapidissima* select the same temperature in different river systems and due to the large variation in discharges between the river systems, Leggett and Whitney (1972) concluded that *A.sapidissima* were unlikely to select a particular flow in a given river system. For *A.pseudoharengus*, Richkus (1974) found a significant positive correlation between movement and river discharge two or three days beforehand. Libey (1976) found that water temperature was the main factor governing the spawning migration of *A.pseudoharengus* and that tidal stage and river discharge were important modifying influences. Day (1890-8) reported "that the Allis shad (*A.alosa*) entered the Severn about the middle of April, but the time depends to a considerable extent on the condition of the water, as it does not appear to like to face the Severn floods, waiting until such have subsided."

The temperature and the amount of freshwater discharge for the River Severn during the upstream migration period for the years 1979, 1980 and 1981 are shown in figure 4.2. The upstream migration period of A.fallax lasted approximately nine weeks, with the peak at Lydney occuring during the middle of May. (The peak refers to the maximum number of fish caught during one tide, in the putcher rank at Lydney. It should be noted that the catch appears to have a tidal component, see figures 4.3 and 4.5. Thus the peak of migration will be associated with spring tides). The peak of migration appears closely associated with a sudden rise in temperature, occuring within the temperature range 10.7 - 13.5°C for 1979; 10.3 - 14.3°C for 1980 and between 9.5 - 11.8°C for 1981. There may also be some association between discharge and movement, for in 1979 the peak of migration occurred during a period of relatively high discharge levels, and in 1981 the peak followed such a period. However, in 1980 no such relationship was evident.

A close correlation with temperature may be associated with the advantage of increased swimming capacity. Beamish (1978) reported that within a species thermal range of tolerance prolonged swimming speeds generally increased with increasing temperature, up to an optimum and there after declined. An association would also have the effect of placing the maximum number of adults on the spawning grounds when temperatures were optimal for the survival of the eggs and young (Leggett, 1969). The survival of the early life stages has been found to be temperature dependent (Leggett, 1977; Marcy, 1976; Shoubridge and Leggett, 1978). This, however, does assume that either the temperature for optimal swimming and for spawning success are the same, or that after a period of delay required for final maturation of the gonads, the temperature is optimal for spawning. However, Shoubridge and Leggett (1978) have shown that overall adult mortality is positively correlated with the thermal regime of

Figure 4.2, Temperature (recorded at Oldbury power station) and the amount of freshwater discharge (recorded at Saxons Lode) for the river Severn from 15 April to the 30 June for the years 1979, 1980 and 1981. Interval between arrows indicates period of peak migration of A.fallax at Lydney.



the river during the upstream migration. This is in agreement with the findings of Glebe and Leggett (1981a) who found that the late migrants (migrating when the temperatures were higher) expend proportionally more energy than did early and peak migrants. This can be associated with the higher post - spawning mortality of the late migrants (Leggett, 1969). Thus the timing of the migration may be a balance between optimizing swimming capacity, juvenile survival and post-spawning survival.

In estuaries fish movement may be influenced by the tides. Changes in a fishs' position in the water column has been reported for some marine species (Creutzberg et al., 1978; de Veen, 1967 & 1978; Greer Walker et al. 1978 & 1980; Harden Jones et al. 1979), as well as for species migrating through (Creutzberg, 1961; Johnston, 1981) or maintaining station in (Graham, 1972) an estuary. The advantage of a strategy whereby the fish elect to change their position so that they might take advantage of the current, when running in a favourable direction and avoiding the reverse current, when compared with swimming continuously has been shown theoretically by Weihs (1978) of savings in terms of energy of 40% for adult Pleuronectes platessa (Linnaeus) and Solea solea (Linnaeus) and as much as 90% for juvenile fish migrating over a fixed distance. In this study no information could be obtained on the behaviour of A.fallax during the flood tide, however, some information could be obtained on their behaviour during the ebb tide and how this appears to be affected by environmental factors.

Mott (pers. comm.) has found that the catch of Salmo salar and A.fallax in the putcher rank, at Lydney, follows a tidal pattern. This is idealised in figure 4.3, high catches being associated with spring tides, the converse being true for neap tides. The drop in the catch at the peak of the spring tides is probably associated with

Figure 4.3, The relationship between tidal height and the number of fish caught in the putcher rank at Lydney.

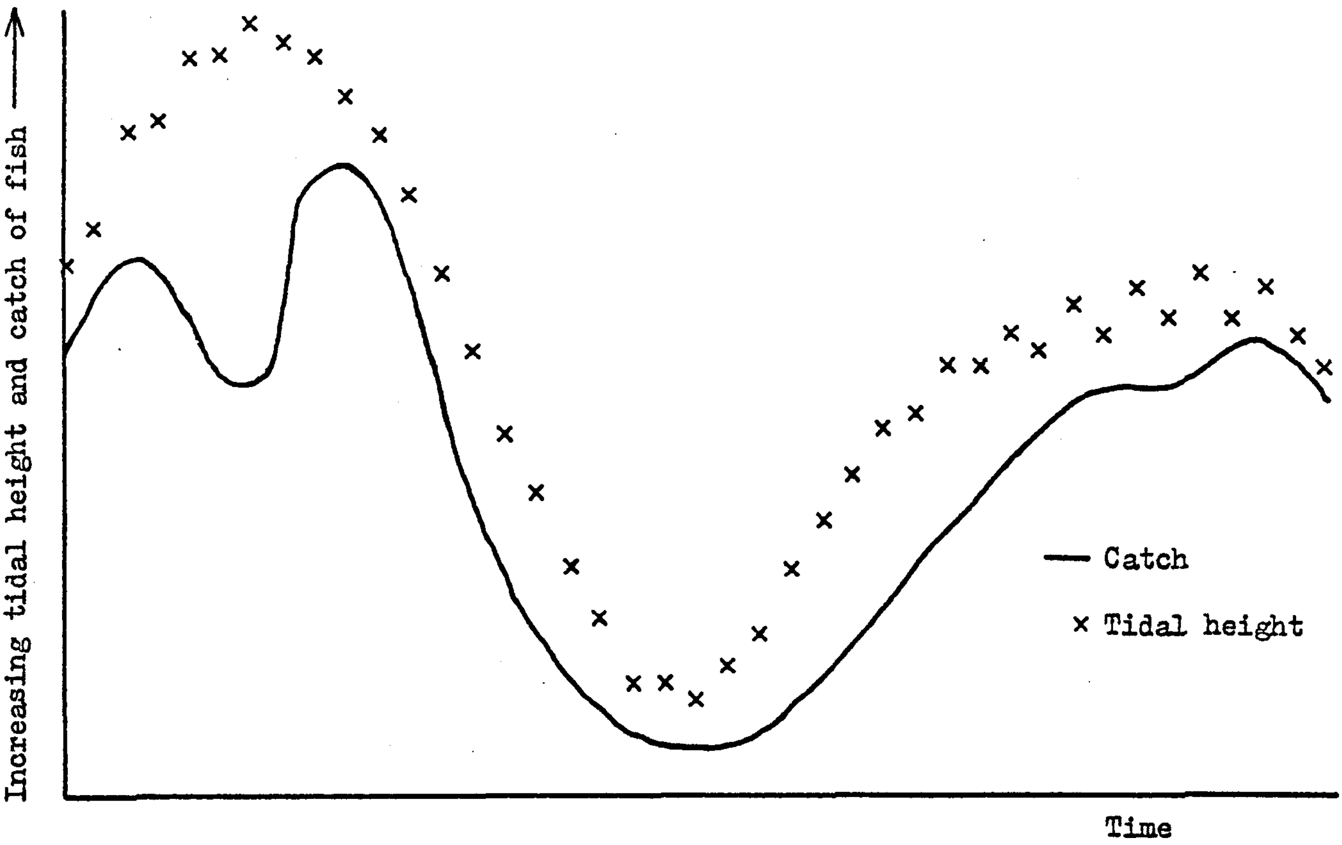
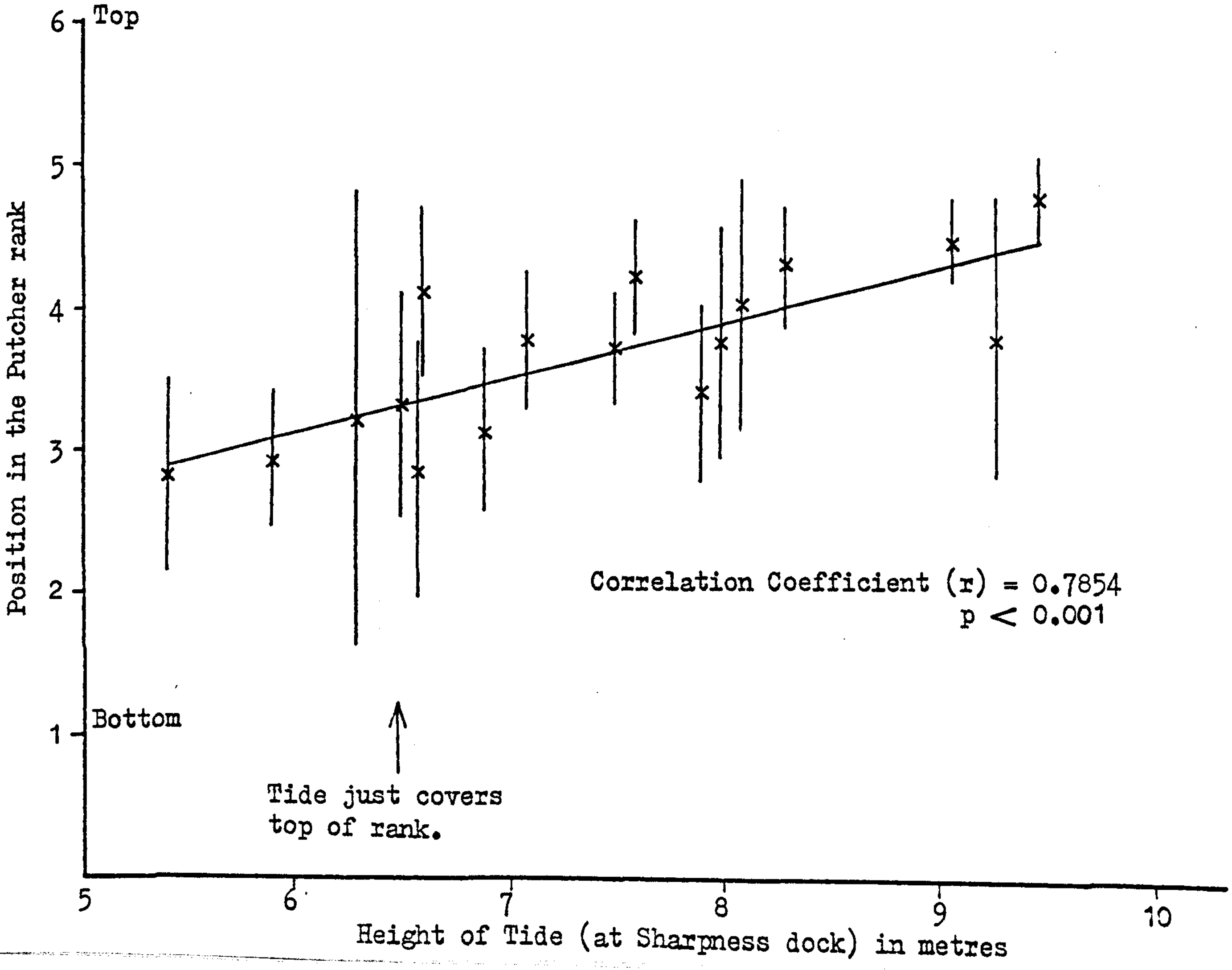


Figure 4.4, Position of <u>A.fallax</u> in the putcher rank, at Lydney, (mean row ± 95% confidence limits) in relation to the hight of tide.



the majority of the fish passing over the top of the putcher rank. Similarly part of the decline in numbers associated with neap tides may be as a result of fish passing beneath the rank. The relationship between the mean position of A.fallax in the putcher rank and tidal height is shown in figure 4.4. Though the actual fishing time for the putcher rank is only 15-30 minutes longer on spring tides when compared with neap tides, the amount of water 'filtered' or sampled is considerably greater and this may be in part the cause for the differences in the catch. On spring tides it is characteristic for the catch to be slightly higher when the tide is 'dropping back' (i.e. falling from spring to neap tides) as opposed to when the tide is 'shooting' (i.e. rising from neap to spring tides), on equivalent tidal heights.

The fish caught by the putcher rank are moving concurrently with the ebb current (i.e. moving downstream). As their ultimate aim is to migrate up river, for spawning, two possibilities exist for this behaviour. The first is that the current velocity is too great for the fish to make any headway against it, and secondly that they may not yet be physiologically adapted for life in freshwater.

Associated with an increase in tidal height is an increase in the velocity of the ebb current and if A.fallax are still to maintain headway upriver then there would have to be a corresponding increase in their swimming speed. Leggett (1976) has shown that A.sapidissima both in fresh and brackish water can increase their swimming speed in association with an increase in current velocity. However, in brackish water the current can exceed a velocity where A.sapidissima fail to compensate and no upstream progress is made, in relation to the bottom. Weaver (1965) concluded that flows in the range of 3.47 - 4.14 m/s may poise a barrier to A.sapidissima, if extending over several metres.

Thus under neap tide

conditions, when fewer A.fallax were caught, the fish may be able to stem displacement by the ebb tide or make upstream progress relative to the bottom. However, under spring tide conditions the velocity of the ebb current may exceed the maximum against which the fish can maintain station, resulting in their being displaced downstream. This may either be by active swimming or by passive drift, with the outcome being reflected in higher catches.

However, instead of trying to maintain a constant speed over the bottom, Trump and Leggett (1980) have proposed that the optimum strategy for a fish migrating through an estuary is to maintain a constant swimming speed through the water. This may mean some retrograde movement which would be expected when the velocity of the ebb current exceeds the swimming capacity of the fish.

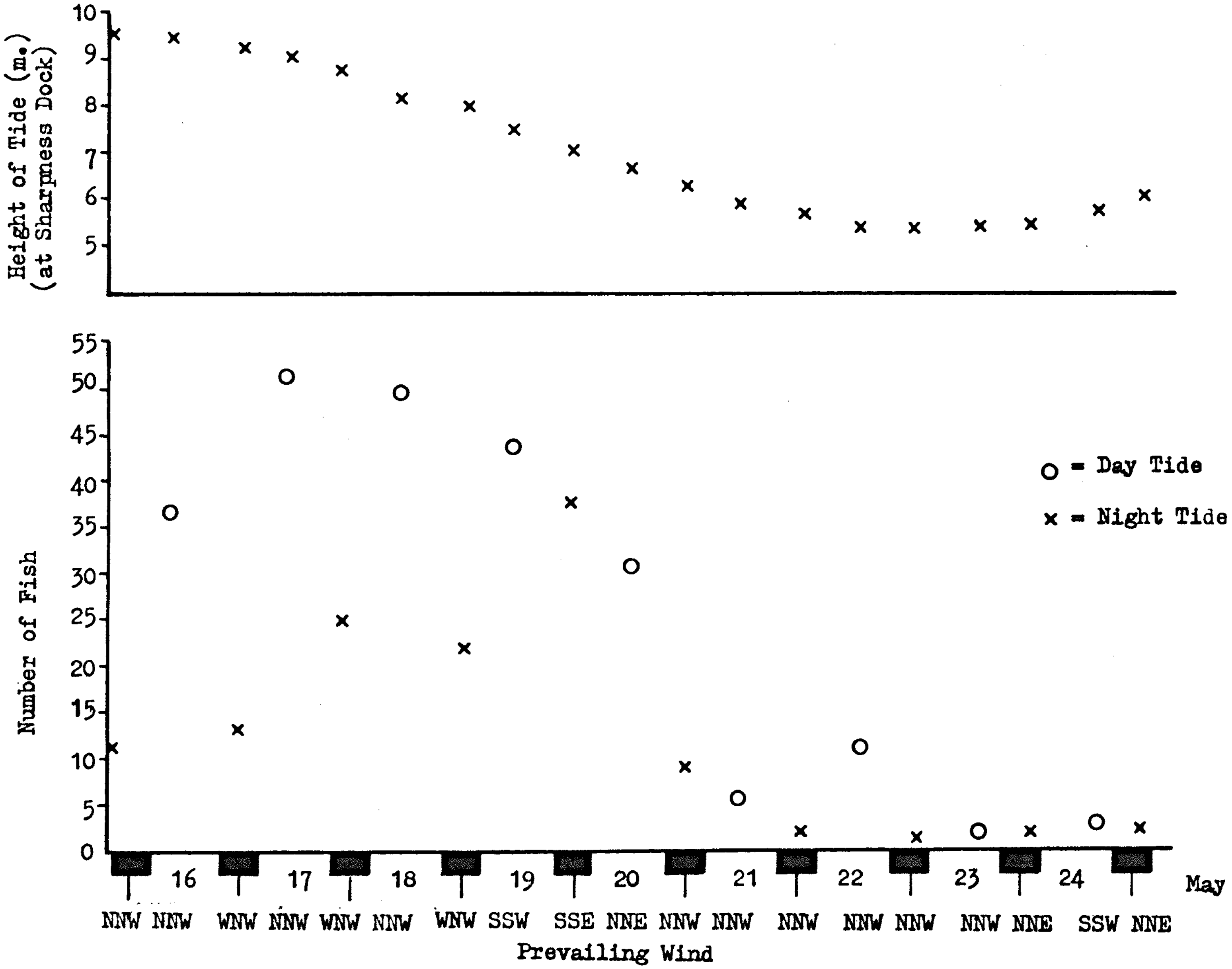
An alternative strategy of changing the effective current regime by altering where the fish swims, might also be adopted. A possibility would be for the fish to move closer into the bank where the current is generally less than in the middle or by swimming near the bottom where the counter current is weakest (Harden Jones, 1980). If the fish were to move in closer to the bank the result would be an increase in the catch associated with an increase in the velocity of the ebb current, i.e. under spring tide conditions. A similar behaviour response has been reported by Tesch (1977) for elvers migrating in the Severn, of moving closer inshore when the tide is ebbing. Brett (1965) on analysis of Idler and Clemens (1959) data concluded that Oncorhynchus nerka (Walbaum) actively seek out and swim in areas of reduced current, during their upriver migration. Stasko et al. (1973) found that S.salar move predominantly with the tidal influences, except when the fish are migrating upriver when they differ by stemming the ebb current.

A.sapidissima appear to need a period of acclimatization before entering freshwater. Tagatz (1961) has found that *A.sapidissima* exhibit between 30% and 50% mortality when transferred directly from salt to freshwater, at the same temperature. Leggett and O'Boyle (1976) concluded that *A.sapidissima* display considerable physiological stress when rapidly transferred from salt to freshwater. This stress may be significantly reduced if the transition time between salt and freshwater was increased. This could be achieved by adopting a meandering behaviour (Leggett and Trump, 1978) and thus increasing residence time in particular regions of the estuary. Meandering behaviour has been reported by Dodson et al. (1972) and by Leggett (1976) for *A.sapidissima* and by Groot et al. (1975) for *O.nerka*. Thus the downstream movement associated with spring tides may also reflect meandering behaviour in this region of the estuary. The period needed for adapting to freshwater life appears to be approximately one to two days for *A.sapidissima* (Dodson et al., 1972; Leggett, 1976).

Physiological changes that may be associated with survival in freshwater have been reported by Pavlovic and Pantic (1975) for *A.fallax* and by Eiras (1981) for *A.alosa* of an increase in activity of the prolactin secreting cells in the pituitary. Prolactin has been implicated as being important for the survival of a number of fish species while in freshwater (see review of Ensor, 1979).

In 1980 from 15th May to 25th May the catch of *A.fallax* for every tide was recorded and the results are shown in figure 4.5. As well as the characteristic tidal pattern to the catch, it appears that light intensity has an influence on the catch, more fish being caught during the day than during the night. This possibly indicates that *A.fallax* are more committed to migrating up river during the hours of darkness than they are during the hours of daylight.

Figure 4.5, The catch of A.fallax, in the putcher rank at Lydney, from 15 - 25 May 1980 in relation to tidal height and wind direction.



The movements of other members of the genus have been shown to be influenced by light. Svetovidov (1963) reported for *A.kessleri pontica* that the peak of migration occurred during the first half of the day (0700 - 1200), dropping during mid-day and afternoon, increasing towards the evening, with the run totally ceasing after sunset until dawn. Light intensity was also found to influence the horizontal distribution of *A.kessleri kessleri* and *A.kessleri volgensis*, during the day the fish would move closer to the banks travelling in the deeper parts of the river (Svetovidov, 1963). If a similar situation operated for *A.fallax* on the Severn, then this could explain the higher catches obtained during the day tides.

The movement of *A.pseudoharengus* has been found to be affected by light intensity (Beltz, 1975; Dominy, 1971; Kissil, 1974; Tyus, 1974), with temperature (Saila et al. 1972; Richkus, 1974) and degree of sexual maturity (Cooper, 1961) being important modifying factors. In general the upstream migration of *A.pseudoharengus* takes place during the day, at low light intensities. Upstream nocturnal movement has been reported by Richkus (1974) in association with high water temperatures, as well as by Tyus (1974), and downstream movement by Dominy (1971).

The observations could be accounted for if swimming speed was directly related to light intensity. Swimming speed has been found to follow a diel pattern for *Oncorhynchus tshawytscha* (Walbaum) (Johnson, 1960) and for *O.nerka* (Madison et al., 1972). Leggett (1976) has found that in freshwater *A.sapidissima* shows a diel pattern of activity, however, this pattern was not as pronounced in brackish water. Dodson et al. (1973 found no such diel periodicity of swimming speeds for *A.sapidissima* in coastal waters. Richkus and Winn (1979) reported diurnal activity cycles for *A.pseudoharengus*, and these were not affected by salinity or temperature. For juvenile *A.sapidissima*, Katz (1978) showed a diurnal pattern of swimming speeds with high levels during daylight hours changing to slow swimming speeds at night. Similar observations have been found by Godin (1981) that the swimming speed of juvenile Oncorhynchus gorbuscha (Walbaum) increased significantly with increasing light intensity.

A number of authors have suggested that wind direction and/or speed are important in influencing fish catches (Harden Jones and Scholes, 1980: Scholes, 1982) as well as the behaviour of salmonids (see review by Banks, 1969). Day (1890-8) mentions that S.salar in the Severn run mostly when there is a wind blowing up the estuary (south westerly). Nedoshivan (1929) and Kvintilianov and Popov (1925) (cited by Svetovidov, 1963) reported that A.kessleri pontica, in the Don and in the Dnieper, enter more easily when assisted by upstream winds, that accelerate the water current. Downstream winds that retard the water current and even occasionally cause a reversion of the current flow may produce a slowing down of the migration or it may cease entirely. The reverse situation seems to be the case for A.kessleri volgensis where offshore winds tend to favour upstream migration, while onshore winds tend to hold back the migration (Svetovidov, 1963).

In the Severn, putcher ranks on the north bank of the estuary, as is the case at Lydney, have their best catches on southerly winds (especially south westerlies), while for those on the south bank the opposite is true. Wind presumably has the effect of displacing the fish across the estuary. This could result from either wind affecting the mean circulation pattern (Dyer, 1979) or by affecting the fish's mechanism for orientation. This may explain why on the night tide of the 19th May the catch of A.fallax was higher than might be expected, as the prevailing winds changed from a northerly to a southerly direction.

It would therefore appear that the spawning migration of A.fallax through the Severn estuary may be influenced by a number of abiotic factors. However, considerably more data is required before an accurate understanding of the effect environmental factors have on their movement, is achieved.

C. The Spawning Stock

1. Age

The potential spawning stock, was recorded at Lydney for the years 1979, 1980 and 1981, are shown in tables 4.3 & 4.4, for females and males respectively. It is apparent that the males commence their spawning migration between the ages of two and five and the females approximately one year later. Similar findings were reported by Claridge and Gardner (1978) on the Severn, by Roule (1922) on the Seine, by Hass (1965) on the Elbe, by Redeke (1938) on the Rhine and by D'Ancona (1938) for A.fallax nilotica from the Tiber. Berg and Grimaldi (1966) found that both sexes of A.fallax lacustris spawn earlier than their anadromous counterparts, at age two.

The fact that the males may spawn at age two with the majority at three and/or at four; and the majority of the females at four and/or at five with a few at three, seems to be the case for most of the anadromous members of the genus. Similar findings have been documented for A.sapidissima (Chittenden, 1969; Leggett, 1969; Walburg and Nichols 1967); A.aestivalis (Messieh, 1977; Scherer, 1972); A.pseudoharengus (Graham, 1956; Havey, 1961; Messieh, 1977); A.alosa (Hoestlandt, 1958; LaHaye et al., 1963; the larger form of A.kessleri pontica (Moroz, 1969; Svetovidov, 1963); A.kessleri kessleri (Svetovidov, 1963); and A.kessleri volgensis (Demidova, 1951; cited by Svetovidov, 1963).

Table 4.3 Age composition of female A.fallax caught at Lydney during the spawning migration in 1979, 1980 and 1981

Age	Number of previous spawnings	1979		1980		1981		Combined 1979 - 1981 average percentage
		N	%	N	%	N	%	
4	0	31	36.47	18	7.56	2	0.66	14.9
4	1	1	1.18	-	-	-	-	0.39
5	0	5	5.88	93	39.08	122	40.13	28.36
5	1	2	2.35	59	24.79	18	5.92	11.02
5	2	-	-	3	1.26	-	-	0.42
6	0	1	1.18	5	2.1	14	4.61	2.63
6	1	12	14.12	8	3.36	67	22.04	13.17
6	2	19	22.35	14	5.88	60	19.74	15.99
6	3	-	-			1	0.33	0.11
7	0	-	-	1	0.42	-	-	0.14
7	1	-	-	2	0.84	1	0.33	0.39
7	2	6	7.06	24	10.09	4	1.32	6.16
7	3	-	-	6	2.52	5	1.62	1.38
8	2	-	-	1	0.42	2	0.66	0.36
8	3	3	3.53	3	1.26	4	1.32	2.04
8	4	-	-	1	0.42	3	0.99	0.47
9	3	3	3.53	-	-	-	-	1.18
9	4	2	2.35	-	-	1	0.33	0.89
Total		85	100%	238	100%	304	100%	100%

Table 4.4 Age composition of male A.fallax caught at Lydney during the spawning migration in 1979, 1980 and 1981

Age	Number of previous spawnings	1979		1980		1981		Combined 1979 - 1981 average percentage
		N	%	N	%	N	%	
3	0	2	6.45	-	-	-	-	2.15
4	0	12	38.71	23	32.39	6	5.0	25.37
4	1	6	19.35	2	2.82	-	-	7.39
5	0	1	3.23	3	4.23	18	15.0	7.49
5	1	1	3.23	15	21.13	28	23.33	15.90
5	2	-	-	17	23.94	11	9.17	11.04
5	3	-	-	1	1.41	-	-	0.47
6	1	1	3.23	-	-	4	3.33	2.19
6	2	4	12.9	3	4.23	26	21.66	12.93
6	3	1	3.23	1	1.41	17	14.17	6.27
6	4	-	-	-	-	2	1.67	0.56
7	2	2	6.45	1	1.41	1	0.83	2.90
7	3	-	-	4	5.63	2	1.67	2.43
7	4	-	-	1	1.41	3	2.50	1.30
8	4	1	3.23	-	-	-	-	1.07
8	5	-	-	-	-	1	0.83	0.27
9	5	-	-	-	-	1	0.83	0.27
Total		31	100%	71	100%	120	100%	100%

In other species of the genus some of the females may spawn at age two though predominantly at age three and/or four. For the anadromous forms this has been reported to be the case for Alosa mediocris (Mitchill) (Pate, 1972) and for A.caspia caspia (Makhmudbekov, 1947; Ostroumov, 1948 & 1949; cited by Svetovidov, 1963). This situation seems to be similar for other members of the sub-species A.caspia and Alosa brashnikovi (Borodin) as well as the species Alosa curensis (Suworow) (Svetovidov, 1963) which are all non-anadromous and inhabit the Black Sea, Sea of Azov and the Caspian Sea.

There is, however, one anadromous species that matures at one year old notably the smaller form of A.kessleri pontica (Belyy, 1970; Svetovidov, 1963).

There are some exceptions to the general pattern given above. Walburg and Sykes (1957) found that for A.sapidissima the majority of the males, in the Potomac River in 1952, spawned at four and five years old. La Pointe (1958) found that the majority of the males in the Susquehanna and Neuse Rivers spawn at age four, similar findings exist for the St. Johns River, New Brunswick (Leggett, 1969). Similar to landlocked populations of A.fallax, non-anadromous freshwater populations of A.pseudoharengus in Lake Ontario (Graham, 1956) and in Lake Michigan (Brown, 1972) mature and spawn a year earlier than their anadromous counterparts.

To investigate whether the age structure of the spawning stock changed through the upstream migration period, the spawning stock was divided up into five bimonthly periods starting from the 15th April. These results are presented in tables 4.5 a + b, for the females and males. Though fluctuations in the proportion of each age group do occur, during the migration period, there is little evidence of any trend. However, it is interesting to note that in

Table 4.5 The age structure of the spawning stock, caught at Lydney, on the 15th April

(a) Females (1980)

Age	Period 1		Period 2		Period 3		Period 4		Period 5	
	N	%	N	%	N	%	N	%	N	%
4	1	1.96	3	5.0	3	5.08	11	22.0	-	
5	28	54.9	42	70.0	34	57.64	35	70.0	16	88.89
6	11	21.57	8	13.33	7	11.86	1	2.0	-	
7	10	19.61	6	10.0	13	22.03	2	4.0	2	11.11
8	1	1.96	1	1.67	2	3.39	1	2.0	-	
9										
Total	51	100%	60	100%	59	100%	50	100%	18	100%

(b) Males (1980)

Age	Period 1		Period 2		Period 3		Period 4		Period 5	
	N	%	N	%	N	%	N	%	N	%
4	11	44.0	3	13.64	4	36.36	6	66.67	1	25.0
5	12	48.0	14	63.63	6	54.55	3	33.33	1	25.0
6	2	8.0	1	4.55	-				1	25.0
7			4	18.18	1	9.09			1	25.0
8										
9										
Total	25	100%	22	100%	11	100%	9	100%	4	100%

at bimonthly intervals during the upstream migration period, starting

Females (1981)

Age	Period 1		Period 2		Period 3		Period 4		Period 5	
	N	%	N	%	N	%	N	%	N	%
4							2	3.17		
5	23	45.1	39	56.52	38	46.92	23	36.51	17	42.5
6	22	43.14	28	40.58	38	46.92	34	53.98	20	50.0
7	3	5.88	1	1.45	3	3.70	2	3.17	1	2.5
8	3	5.88	1	1.45	1	1.23	2	3.17	2	5.0
9					1	1.23				
Total	51	100%	69	100%	81	100%	63	100%	40	100%

Males (1981)

Age	Period 1		Period 2		Period 3		Period 4		Period 5	
	N	%	N	%	N	%	N	%	N	%
4	3	13.04	1	1.79	1	4.17			1	9.09
5	11	47.83	30	53.57	12	50.0	2	33.33	2	18.18
6	8	34.78	22	39.29	9	37.5	4	66.67	6	54.55
7	1	4.35	1	1.79	2	8.33			2	18.18
8			1	1.79						
9			1	1.79						
Total	23	100%	56	100.02%	24	100%	6	100%	11	100%

1980 and in 1981 the majority of the females aged four entered the estuary during period four (1st - 15th June). There is also some indication that females aged six and older had a tendency to migrate during the earlier part of the run, in 1980.

2. Sex ratio of the spawning migrants

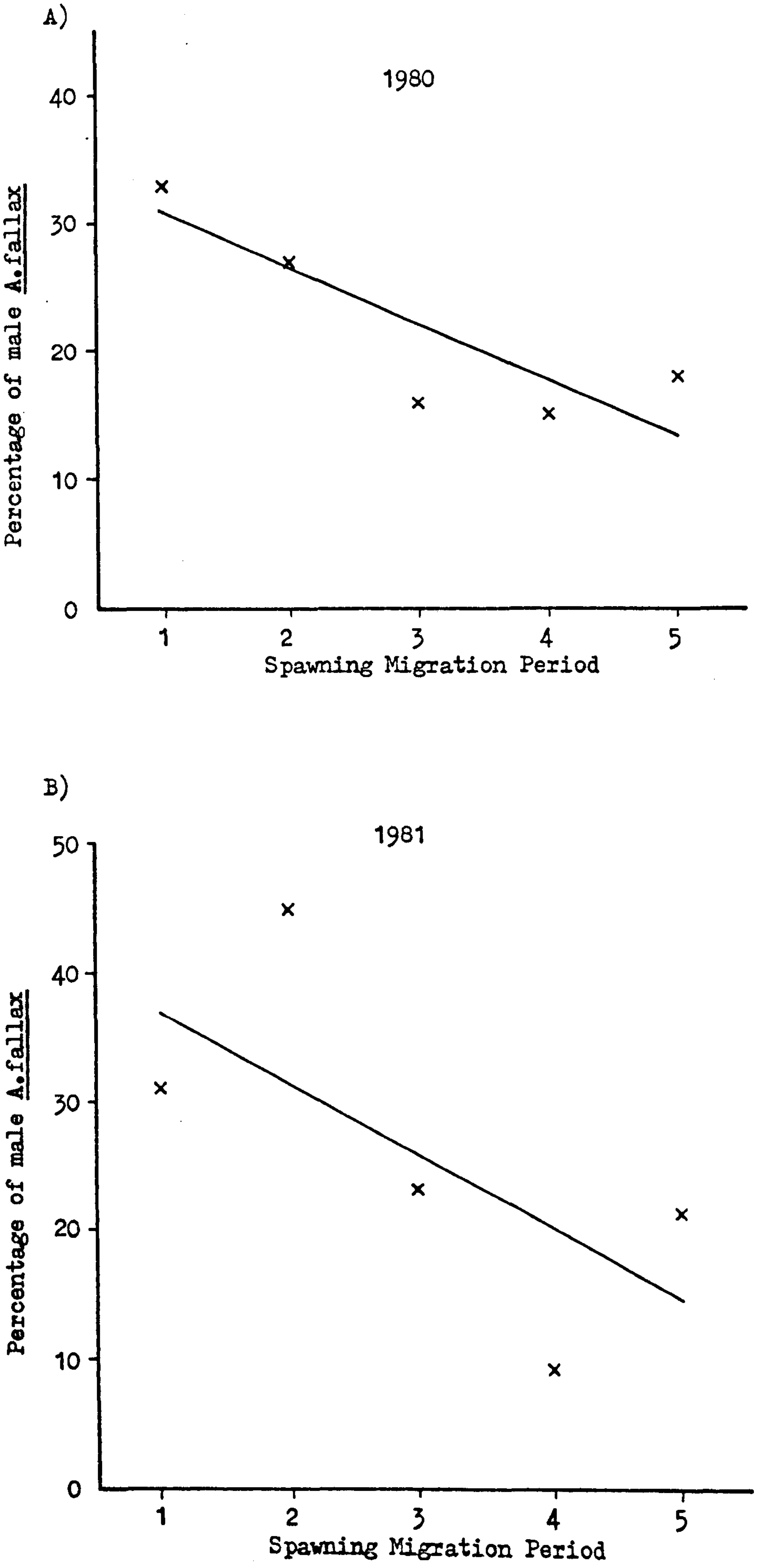
The number of male and female A.fallax, caught at Lydney during 1980 and 1981, are shown in tables 4.5 a + b. The change in the sex ratio, shown by the proportion of males in the catches are illustrated by figures 4.6 a + b, a trend line has been included.

Analysis of the numbers of males and females in the catches suggests that there was no significant change between the various time intervals, in 1980 (Chi-square = 9.2783; df = 4; $p > 0.05$). However, in 1981 there existed a highly significant difference in the sex ratio of the spawning migrants during the upstream migration period (Chi-square = 32.7909; df = 4; $P < 0.001$). It was apparent, from the analysis, that the numbers of males was higher than expected during the first two periods and lower during periods three, four and five; the reverse being the case for the females.

Claridge and Gardner (1978) found that male A.fallax appeared approximately a week or two before the first female, at Oldbury on the River Severn. Similar findings were obtained by Hass (1965) on the Elbe, Roule (1922) on the Seine, by Rameye et al. (1976) for the anadromous population on the Rhone and by D'Ancona (1928) for those in the Tiber.

Analogous observations have been reported for A.alosa (Day, 1890-8; Hoestlandt, 1958); for A.aestivalis (Loesch, 1968); A.kessleri kessleri (Svetovidov, 1963); for A.sapidissima (Chittenden, 1969; Davis, 1980; Walburg and Nichols, 1967), and for A.pseudoharengus (Cooper, 1961; Tyus, 1971), however, no change in their ratio was reported by Havey (1961). Glebe and Leggett (1976) found that peak

Figure 4.6, Sex ratio of the spawning migrants, in 1980 and in 1981, at bimonthly intervals during their upstream migration, starting on the 15 April.



migration of male A.sapidissima into the Connecticut River occurred approximately nine days earlier than that of the females. In the Don River, Svetovidov (1963) stated, for A.kessleri pontica, that males predominated at the beginning of the migration, the percentage of females increased through the run, though at the end, the proportion of males increased again. The ratio of males to females was also reported to undergo diurnal changes with the proportion of females increasing towards evening with a peak between 1700 - 1900 hours.

For the non-anadromous freshwater population of A.pseudoharengus in Lake Ontario, the females were found to be the first to leave the deeper water and make the inshore spawning migration (Graham, 1956).

3. Size of the spawning migrants

(a) Females

Length frequency histograms of fish caught at bimonthly intervals during the upstream migration period are shown in figures 4.7 a + b. It appears that the larger femaleswere the first to arrive in the estuary, with a gradual trend (during the first four time periods) towards the smaller ones. The final set of migrants are slightly larger than might be expected from the trend and this may reflect those females that are not in 'prime' spawning condition leaving entry until the last possible moment. This probably depends more on weight for length, and thus energy reserves, than on length alone.

This trend may infer a change in the age structure or spawning histories of the migrants. Therefore to avoid bias produced by such factors, the mean length of various groups of the same age and spawning histories were determined, and these are shown in figure 4.8. Analysis of variance (table 4.6) indicates that there were significant differences between the mean lengths within each category, (Bartlett's test indicated no significant difference in the variances within each

Figure 4.7 A, Length frequency histograms of female A.fallax, caught at Lydney, at various times during the upstream phase of their spawning migration, in 1980.

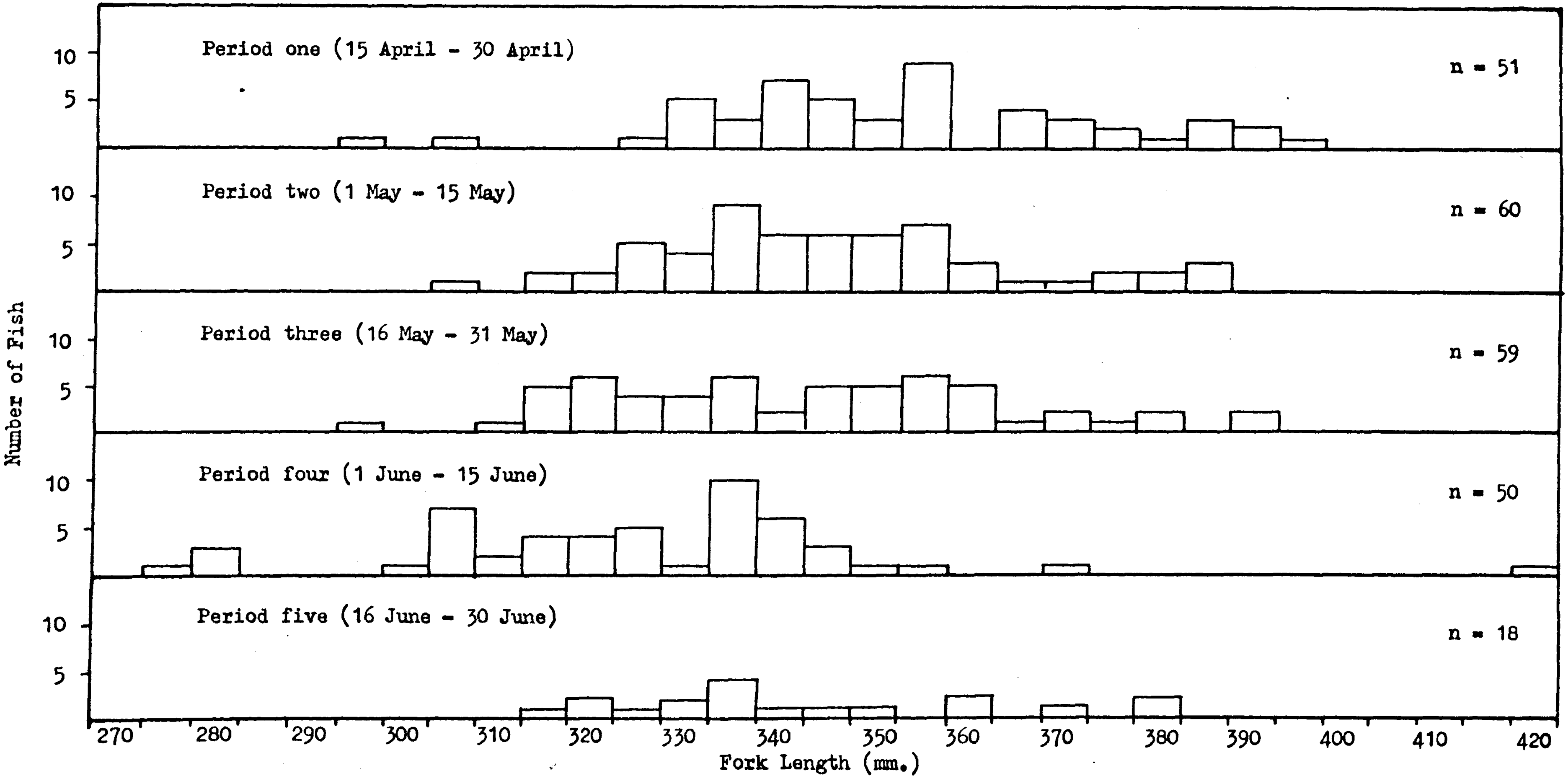


Figure 4.7 B, Length frequency histograms of female *A.fallax*, caught at Lydney, at various times during the upstream phase of their spawning migration, in 1981.

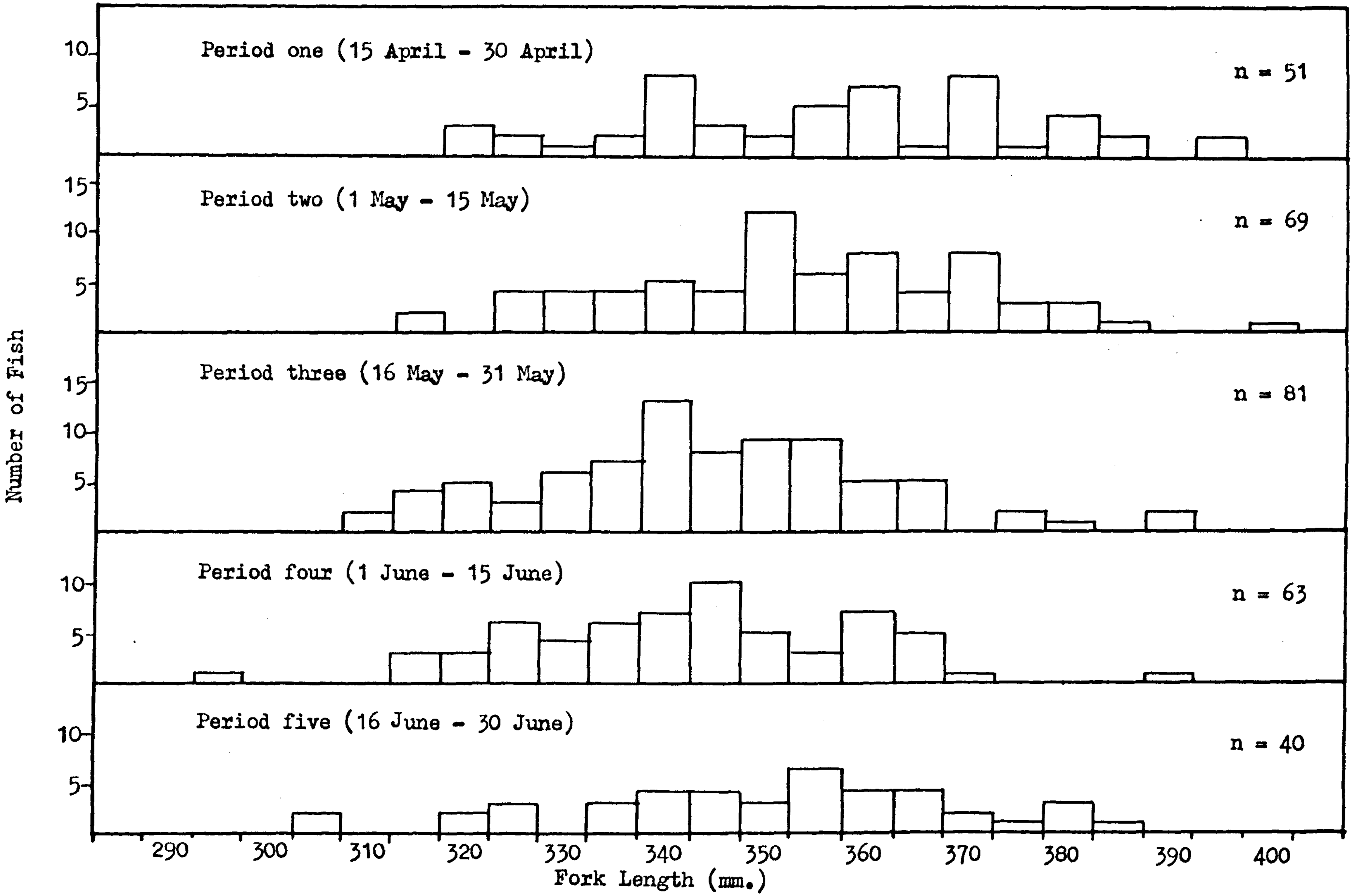
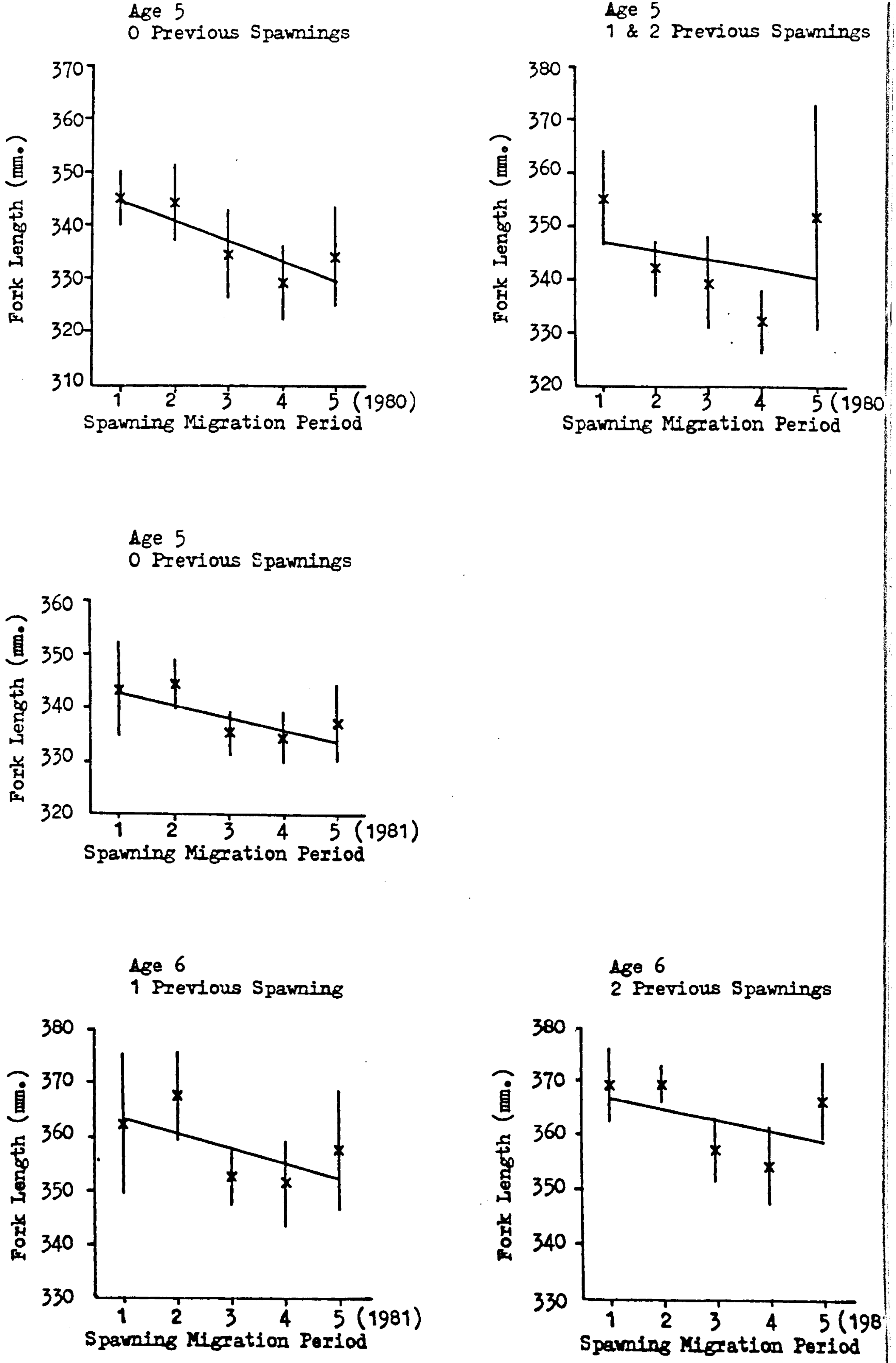


Figure 4.8, Size (mean ± 95% confidence limits) of female A.fallax, of various ages and spawning histories, at bimonthly intervals during their upstream migration, starting on the 15 April.



category). There exists within each of these categories a similar pattern of the larger females predominating at the start of the migration period.

Table 4.6 Results of analysis of variance and Newman - Keuls multiple range test on the sizes of female A.fallax of different ages and spawning histories, caught at Lydney, at bimonthly intervals during the upstream migration period in 1980 and 1981, starting on 15th April.

Age	Number of Previous Spawnings	Sample Year	F Value	Significance	Multiple Range Test
5	0	1980	3.96	$P<0.01$	1 5 2 3 4
5	1 + 2	1980	5.22	$P<0.0025$	1 2 5 3 4
5	0	1981	2.77	$P<0.05$	2 1 5 3 4
6	1	1981	3.49	$P<0.01$	2 1 5 3 4
6	2	1981	12.24	$P<0.0005$	1 2 5 3 4

Cooper (1961) reported a similar situation for A.pseudoharengus where the mean length dropped by just over two centimetres, by the end of the migration period. Tyus (1971), for the same species, observed no trend in the size of either sex during the upstream migration. Though during the nineth week of a ten week migration period, in 1970, the average length dropped markedly, and may reflect the occurrence of a larger proportion of a younger year-class. This feature was not, however, evident during the 1971 spawning season. For A.kessleri pontica, Mogil'chenko (1977) found that the largest individuals entered first, and that this was associated with a particular temperature. Loesch (1968) found no variation in the size of A.aestivalis during the migration. Similar findings were reported by Davis (1980) for A.sapidissima from the St. Johns River (Florida) of the absence of any trend. Though in an earlier study Walburg (1960) observed a decrease in mean length through the migration period.

(b) Males

Length frequency histograms for the males caught at fortnightly intervals during the spawning migration are shown in figures 4.9 a + b. It is evident that the pattern is different to that found for the females Rameye et al. (1976), for A.fallax, on the Rhone mentioned that the first migrants were always the small males. On the Severn A.fallax appear to show the same pattern but because of low numbers it was not possible to compare the mean lengths within a particular category. However, when all the categories were pooled, a comparison was made between the first two time periods in 1980 and the first three in 1981. These are shown in table 4.7. Though the mean length of the first migrants, in both years, was approximately one centimetre smaller than the second group, this difference was not significant in 1980. However, in 1981 analysis of variance indicates a significant difference between their means. Where this difference lies was not indicated by the multiple range test, (Zar 1974, mentions that this sometimes does occur). In both cases no significant differences were found between their variances.

From the results it must be assumed that there is no trend in the size distribution of the males during the spawning migration. However, as already mentioned (chapter two) the smaller males may not be quantitatively sampled, though their presence in the spawning population is indicated from the angling catches.

Figure 4.9 A, Length frequency histograms of male A.fallax, caught at Lydney, at various times during the upstream phase of their spawning migration, in 1980.

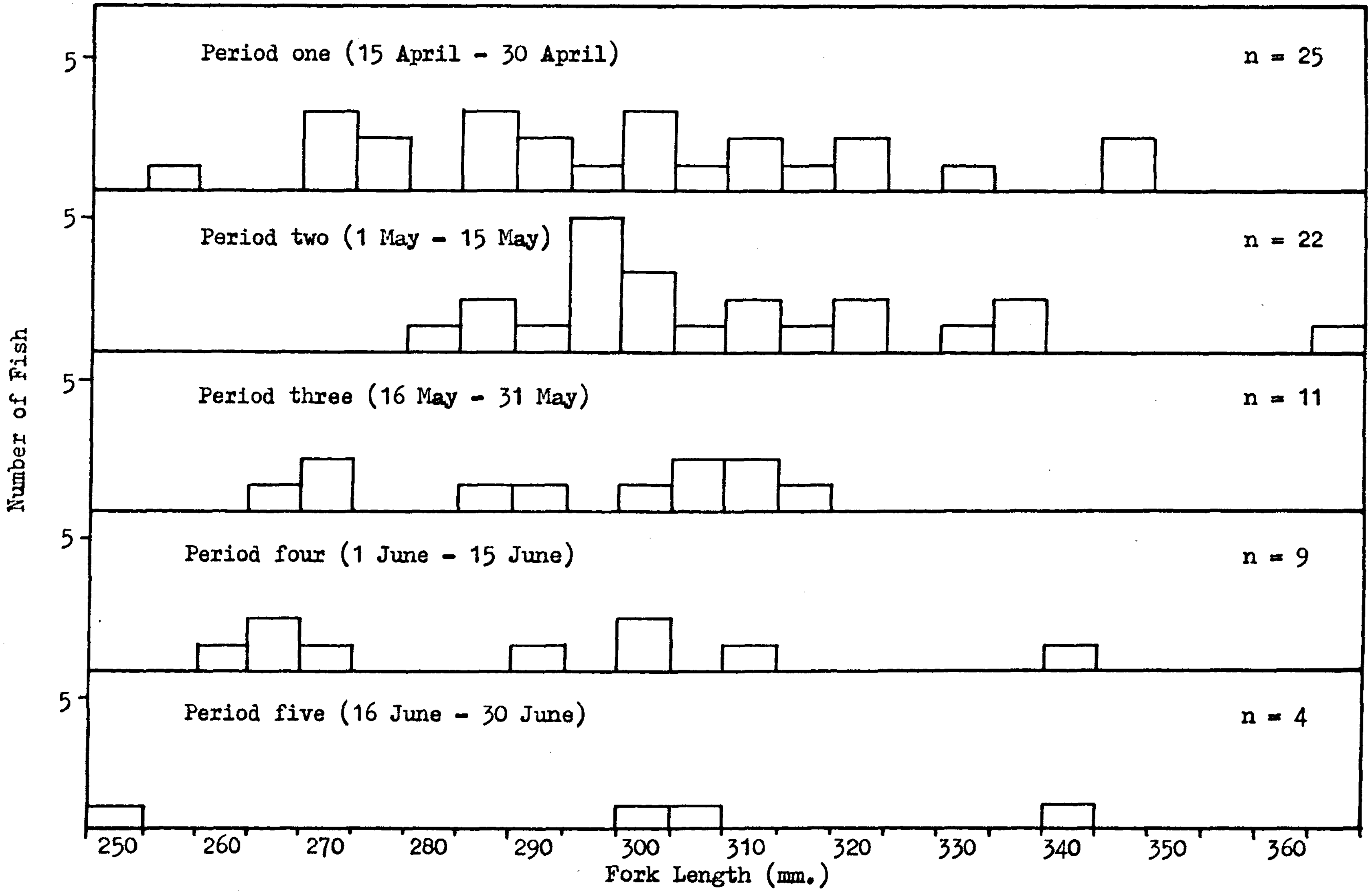


Figure 4.9 B, Length frequency histograms of male A.fallax, caught at Lydney, at various times during the upstream phase of their spawning migration, in 1981.

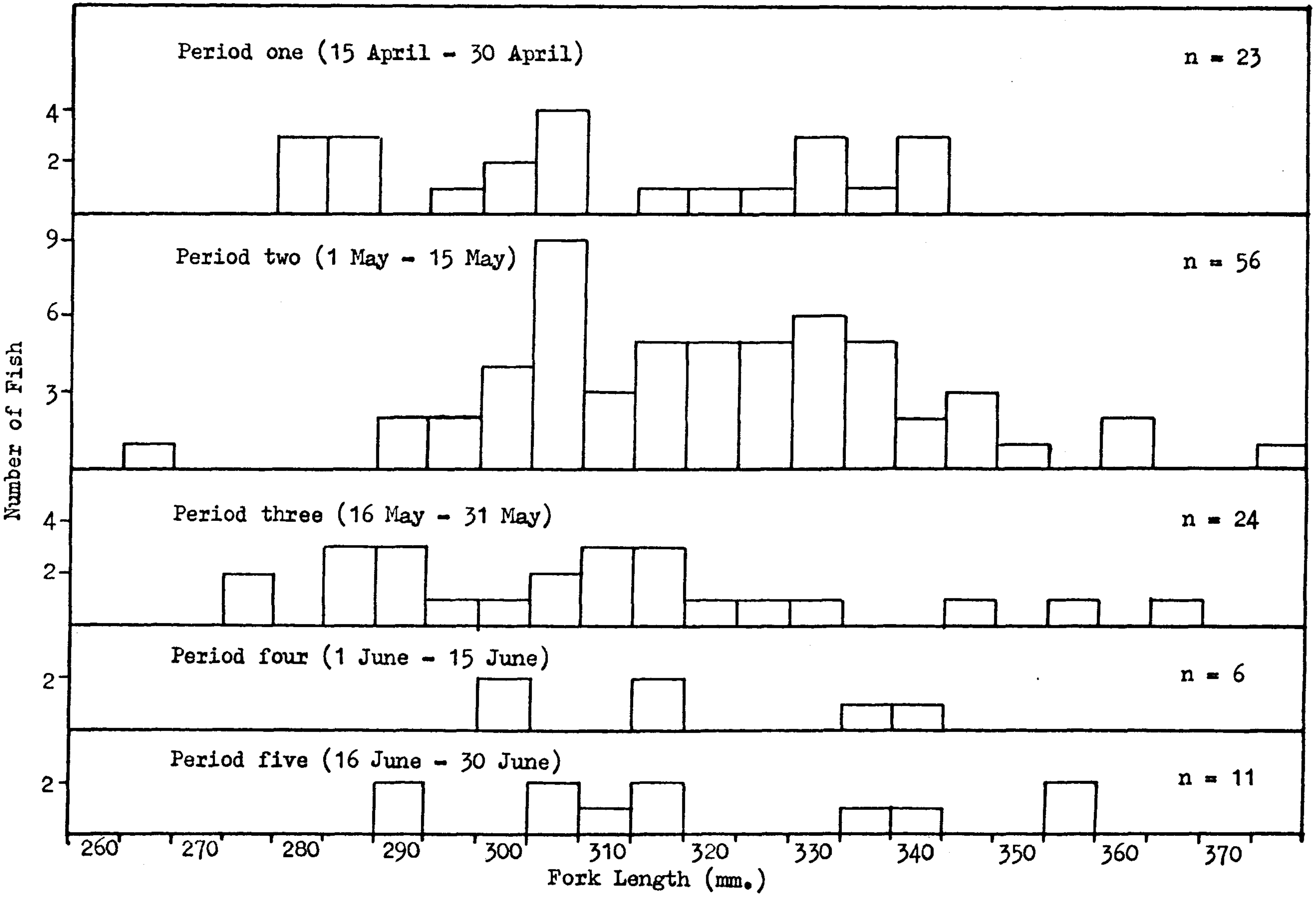


Table 4.7 Size of male, <u>A.fallax</u> caught at Lydney at bimonthly intervals, starting on the 15th April

1980

Period	N	Mean cms.	± 95% Conf. limits
1	25	29.97	± 0.9957
2	22	30.93	± 0.9192
t-test	t = 1.4688, df = 45, $P > 0.10$		

1981

Period	N	Mean cms.	± 95% Conf. limits
1	23	31.16	± 0.9168
2	56	32.2	± 0.5338
3	24	30.99	± 0.9916
ANOV	F = 3.7042, df = 2,100 $P < 0.05$		
Multiple range test	$\underline{1 \quad 2 \quad 3}$		

In other populations of alosids Walburg (1960) and Davis (1980) both found that large male A.sapidissima predominated at the start of the migration. Cooper (1961) showed that the mean length of male A.pseudoharengus fell by just over two centimetres during the spawning migration period. However, Tyus (1971) observed no such trend for A.pseudoharengus. Similar findings were reported for A.aestivalis by Loesch (1968) of no trend in their size during the migration.

4. Length to weight relationships of the spawning migrants

The length to weight relationship, in fishes, may be represented by the equation:

$$\text{Weight} = a \times \text{length}^{b} \qquad \text{(Bagenal and Tesch, 1978)}$$

where a and b are constants. A logarithmic transformation produces a straight line. When considering total weight the regression coefficient 'b' usually lies between two and four, (Bagenal and Tesch, 1978). Bagenal and Tesch (1978) mention in their review that variation in the regression coefficient is thought mainly to be associated with major changes in the species biology, such as smoltification for salmonids or the onset of maturation. Variation in 'a' is often associated with changes within a particular environment, which may be caused by seasonal, diurnal or some other factors.

Values of the coefficients are given for total weight/-, somatic weight/-, and for gonad weight/fork length, for each of the time periods, in tables 4.8 a + b & 4.9 a + b, for females and males. The regressions are illustrated in figures 4.10 & 4.11, for females and males. Analysis of covariance was used to test for statistical significance between the slopes and if homogenous the analysis was continued to test for differences between the intercepts. If significant differences existed then the Newman - Keuls multiple range test was used to determine where the difference lay. (The multiple range test is not as strong as the analysis of covariance, (Zar, 1974) and some of the differences were not picked up. This in fact was the case for the intercepts of the regressions of total weight/fork length (1980), somatic weight/fork length (1980) and gonad weight/fork length (1981), for the males).

(a) Females

Analysis indicates that there were significant differences in the regression coefficients of the spawning migrants, entering the estuary. For both 1980 and 1981 there existed significant differences in all the groups, except for the regression coefficient for the regression of somatic weight/fork length in 1981. Significant differences in both years concerned periods three and four. In 1980 a low value of 'b' was followed by a significantly higher one, while in 1981 a high value of 'b' was followed by a significantly lower one.

Significant differences in the regression coefficients were unexpected as all the migrants should be undergoing similar changes associated with maturation. This, however, does assume that all the migrants are commited to spawning, though in some anadromous species, notably Salmo trutta this may not be the case (Mills, 1971). The presence of precocial fish in the spawning run has been reported by Foerster and Goodbred (1978) who also cite personnal communications by Loesch and Richkus of immature A.pseudoharengus present in the spawning migration. For A.fallax none were found with underdeveloped gonads and thus it was presumed that all the fish were committed to spawning.

There appears to be no real explanation as to why these differences do occur. Glebe and Leggett (1981a) show that there were changes in

Table 4.8a Coefficients for the regressions of total weight/-, somatic weight/-, and gonad weight/fork length for female *A.fallax*, caught at Lydney at bimonthly intervals during the upstream migration period in 1980, starting on the 15th April.

$\log_{10}$ Total weight = $\log_a$ + b $\log_{10}$ Fork length

Period	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
1	51	- 4.5087	2.8778 ± 0.5174	0.7271	125.23	$P < 0.0005$
2	60	- 3.8107	2.5949 ± 0.444	0.7025	136.93	$P < 0.0005$
3	59	- 2.4773	2.0647 ± 0.3508	0.7095	139.22	$P < 0.0005$
4	50	- 5.9643	3.4375 ± 0.43	0.8408	258.71	$P < 0.0005$
5	18	- 3.4321	2.4217 ± 1.2069	0.5307	18.10	$P < 0.001$

Analysis of covariance:
Between slopes F = 6.1163; df = 4,228; $P < 0.0005$
multiple range test $b_3\ b_5\ b_2\ b_1\ b_4$

$\log_{10}$ somatic weight = $\log_a$ + b $\log_{10}$ Fork length

1	51	- 4.1676	2.7203 ± 0.5014	0.7172	119.17	$P < 0.0005$
2	60	- 3.7364	2.5392 ± 0.4452	0.6921	130.38	$P < 0.0005$
3	59	- 2.5508	2.065 ± 0.3523	0.7075	137.84	$P < 0.0005$
4	50	- 5.375	3.1757 ± 0.3888	0.8462	269.61	$P < 0.0005$
5	18	- 3.5228	2.428 ± 0.8652	0.6887	35.39	$P < 0.0005$

Analysis of Covariance:
Between slopes F = 4.513; df = 4,228; $P < 0.005$
multiple range test $b_3\ b_5\ b_2\ b_1\ b_4$

$\log_{10}$ gonad weight = $\log_a$ + b $\log_{10}$ Fork length

1	51	- 8.0705	3.9247 ± 1.032	0.5547	58.54	$P < 0.0005$
2	60	- 5.6121	2.9688 ± 1.0859	0.3406	29.96	$P < 0.0005$
3	59	- 2.8897	1.9027 ± 1.0907	0.1764	12.21	$P < 0.001$
4	50	- 10.5167	4.909 ± 1.2696	0.5521	60.4	$P < 0.0005$
5	18	- 1.8256	1.4572 ± 4.889	0.0243	0.399	$P > 0.25$

Analysis of Covariance:
Between slopes F = 5.9567; df = 3,212; $P < 0.001$
multiple range test $b_3\ b_2\ b_1\ b_4$

Table 4.8b . Coefficients for the regression of total weight/-, somatic weight/-, and gonad weight/fork length, for female A.fallax caught at Lydney at bimonthly intervals during the upstream migration period in 1981, starting on the 15th April

$\log_{10}$ Total weight = $\log_a$ + b $\log_{10}$ Fork length

Period	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
1	51	- 4.662	2.9257 ± 0.4979	0.7401	139.5	$P < 0.0005$
2	69	- 3.9061	2.6296 ± 0.4358	0.6842	145.17	$P < 0.0005$
3	81	- 5.5918	3.294 ± 0.3904	0.7813	282.21	$P < 0.0005$
4	63	- 3.1093	2.302 ± 0.4811	0.6002	91.59	$P < 0.0005$
5	40	- 4.0584	2.6625 ± 0.6637	0.6274	65.66	$P < 0.0005$

Analysis of Covariance:
Between slopes F = 2.7074; df = 4,294; $P < 0.025$
multiple range test $\underline{b_4\ b_2\ b_5\ b_1}\ b_3$
$\underline{}$

$\log_{10}$ Somatic weight = $\log_a$ + b $\log_{10}$ Fork length

1	51	- 3.7034	2.5294 ± 0.4659	0.7129	119.2	$P < 0.0005$
2	69	- 3.0659	2.275 ± 0.43	0.6289	111.83	$P < 0.0005$
3	81	- 5.0724	3.068 ± 0.3694	0.7759	273.46	$P < 0.0005$
4	63	- 3.1636	2.3 ± 0.4456	0.6398	106.58	$P < 0.0005$
5	40	- 3.7487	2.515 ± 0.6161	0.6362	68.19	$P < 0.0005$

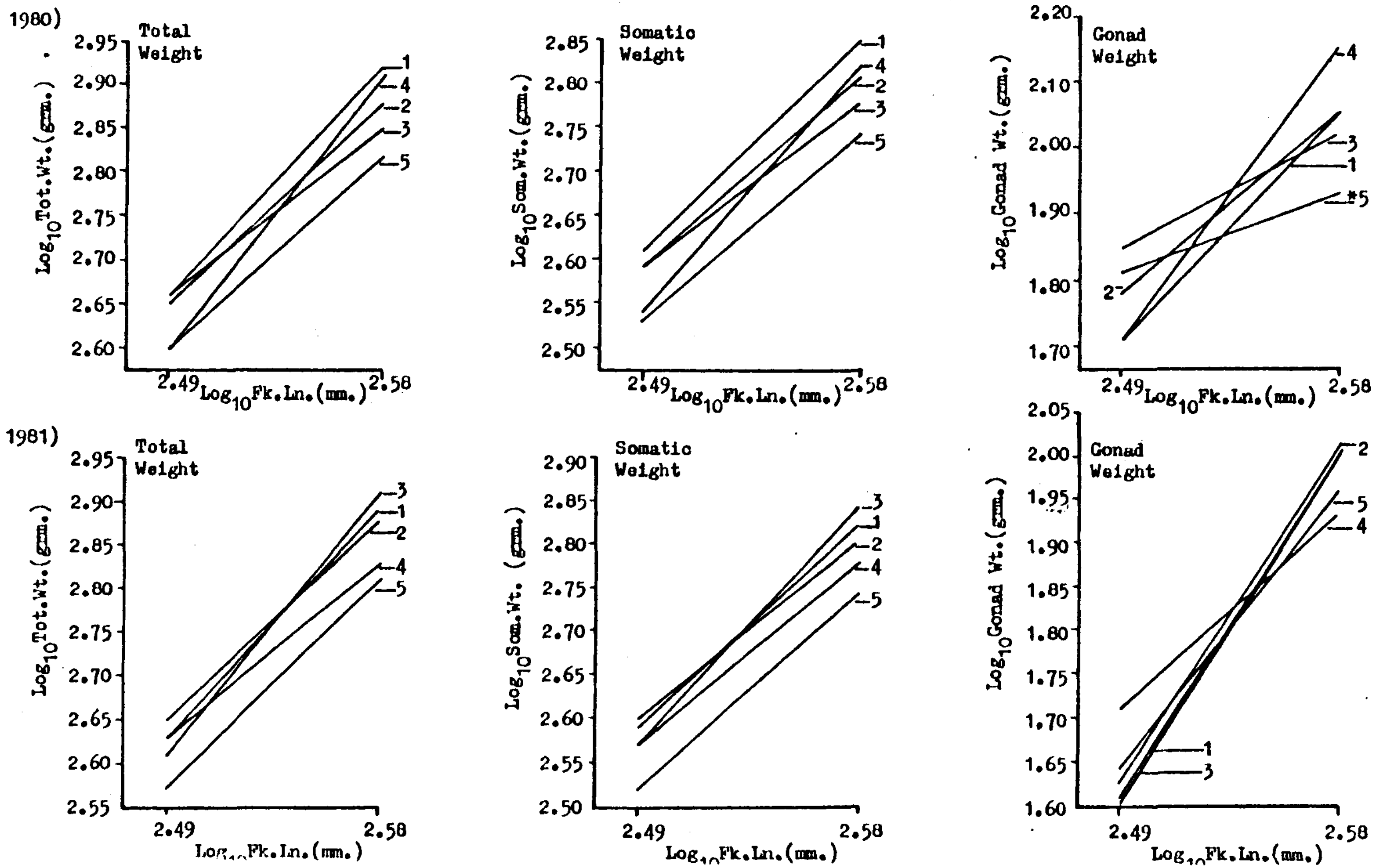
Analysis of Covariance:
Between slopes F = 2.3476; df = 4,294; $P > 0.05$
Between intercepts F = 37.8127; df = 4,294; $P < 0.0005$
multiple range test $\underline{a_2\ a_4\ a_1}\ a_5\ a_3$
$\underline{}$

$\log_{10}$ Gonad weight = $\log_a$ + b $\log_{10}$ Fork length

1	51	-10.1114	4.7039 ± 1.3597	0.5021	48.4	$P < 0.0005$
2	69	-11.0826	5.0998 ± 1.06	0.5829	92.24	$P < 0.0005$
3	81	-10.4609	4.8432 ± 1.0059	0.5374	91.90	$P < 0.0005$
4	63	- 4.5399	2.5097 ± 1.3883	0.1789	13.07	$P < 0.001$
5	40	- 7.5273	3.6787 ± 2.3069	0.2106	10.41	$P < 0.005$

Analysis of Covariance
Between slopes F = 2.6278; df = 4,294; $P < 0.05$
multiple range test $\underline{b_4\ b_5\ b_1}\ b_3\ b_2$
$\underline{}$

Figure 4.10, Regressions of total weight/-, somatic weight/-, and gonad weight/fork length of female *A.fallax*, caught at Lydney at bimonthly intervals (indicated by the numbers, starting on the 15 April) during the upstream migration period in 1980 and in 1981. Asterisk indicates the regression was not significant at the 5% level.



the regressions of somatic weight/-, visceral weight/ and gonad weight/ length for female A.sapidissima entering the Connecticut River at various times after the start of the spawning migration. Significant differences in the regression of somatic weight/length resulted from the fact that the peak migrants had significantly greater somatic reserves than either the early or late migrants. The same situation does not appear to apply for A.fallax on the Severn.

Variations in the regression coefficients do occur, however, most studies have been concerned with the whole population with the coefficients being determined on a monthly basis, and most of the variation being associated with spawning. There are a few studies which have been solely concerned with one particular category or stage of a fishs' life history. Notably by Le Cren (1951) who found that regression coefficients of immature Perca fluviatilis (Linnaeus) did vary between months, but this was not significant. Bagenal (1957) found significant variation in the regression coefficients, which showed a seasonal trend, for Hippoglossoides platessoides (Fabricius). Pedley (1975) and Diamond (in prep.) found that regression coefficients for immature S.trutta and Rutilus rutilus (Linnaeus), respectively, varied monthly, but were homogenous for the winter and summer months. However, Sewell (in prep.) has found significant variation in the regression coefficients for immature Platichthys flesus in the Ribble, and that no trend was apparent. Therefore it seems that significant changes in the regression coefficients do occur which appear not to be attributable to major changes in their life history.

(b) Males

One of the problems associated with the analysis was the very low numbers obtained, particularly during the last three periods of 1980 and the last two of 1981. Though some of the regressions were significant, the small sample sizes does not allow too much emphasis to be placed on them.

Table 4.9a Coefficients for the regressions of total weight/-, somatic weight/-, and gonad weight/fork length for male <u>A.fallax</u> caught at Lydney, at bimonthly intervals during the upstream migration period in 1980, starting on the 15th April.

Log_{10} Total weight = $\log_{10} a + b \log_{10}$ Fork length

Period	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
1	25	- 4.933	3.037 ± 0.435	0.9052	210.02	$P < 0.0005$
2	22	- 3.9644	2.6401 ± 0.7383	0.7358	55.71	$P < 0.0005$
3	11	- 5.359	3.1957 ± 1.5373	0.7627	25.93	$P < 0.001$
4	9	- 4.1444	2.6922 ± 1.267	0.783	25.25	$P < 0.0025$
5	4	- 4.1053	2.6672 ± 2.2759	0.9272	25.43	$P < 0.05$

Analysis of Covariance:
Between slopes F = 0.3934; df = 4,61; $P > 0.25$
Between Intercepts F = 72.4859; df = 4,61; $P < 0.0005$
Multiple range test $\underline{a_2\ a_5\ a_4\ a_1\ a_3}$

$\log_{10}$ Somatic weight = $\log_{10} a + b \log_{10}$ Fork length

1	25	- 4.7749	2.9566 ± 0.4381	0.8991	195.87	$P < 0.0005$
2	22	- 4.2704	2.7453 ± 0.6849	0.7757	69.91	$P < 0.0005$
3	11	- 5.5239	3.2453 ± 1.1907	0.8086	38.00	$P < 0.0005$
4	9	- 4.3485	2.7589 ± 1.0704	0.8414	37.16	$P < 0.0005$
5	4	- 3.9113	2.5785 ± 1.754	0.9524	40.01	$P < 0.025$

Analysis of Covariance:
Between slopes F = 0.3559; df = 4,61; $P > 0.25$
Between Intercepts F = 5.4967; df = 4,61; $P < 0.001$
Multiple range test $\underline{a_2\ a_5\ a_4\ a_1\ a_3}$

$\log_{10}$ Gonad weight = $\log_{10} a + b \log_{10}$ Fork length

1	25	- 8.3748	4.0 ± 1.3077	0.6265	58.89	$P < 0.0005$
2	22	- 2.6006	1.6807 ± 1.8959	0.146	3.42	$P > 0.05$
3	11	- 7.8249	3.7606 ± 6.4502	0.1619	1.35	$P > 0.25$
4	9	- 3.0192	1.80 ± 3.9432	0.1427	1.17	$P > 0.25$
5	4	-10.7879	4.8431 ± 14.4069	0.5112	2.09	$P > 0.25$

Table 4.9b Coefficients for the regression of total weight/-, somatic weight/-, and gonad weight/fork length for male A.fallax, caught at Lydney, at bimonthly intervals during the upstream migration period in 1981, starting on the 15th April

$\log_{10}$ Total weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Period	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
1	23	- 5.3212	3.1737 ± 0.6472	0.8321	104.04	$P < 0.0005$
2	56	- 5.1369	3.1037 ± 0.4249	0.7989	214.53	$P < 0.0005$
3	24	- 4.623	2.8855 ± 0.6066	0.8156	97.34	$P < 0.0005$
4	6	- 6.6584	3.6976 ± 2.1905	0.8458	21.96	$P < 0.01$
5	11	- 3.3394	2.3463 ± 0.8669	0.8064	37.48	$P < 0.0005$

Analysis of Covariance:
Between slopes $F = 0.9208$; df = 4,110; $P > 0.25$
Between Intercepts $F = 13.3416$; df = 4,110; $P < 0.0005$
Multiple Range test $a_5 \; \underline{a_3 \; a_2 \; a_1 \; a_4}$

$\log_{10}$ Somatic weight = $\log_{10}$ a + b $\log_{10}$ Fork length

1	23	- 4.7104	2.9141 ± 0.6614	0.80	83.99	$P < 0.0005$
2	56	- 5.1196	3.0804 ± 0.4329	0.7937	203.97	$P < 0.0005$
3	24	- 4.5393	2.8381 ± 0.5872	0.8203	100.47	$P < 0.0005$
4	6	- 4.8839	2.9742 ± 2.244	0.7719	13.54	$P < 0.025$
5	11	- 3.2864	2.3118 ± 0.7944	0.8281	43.34	$P < 0.0005$

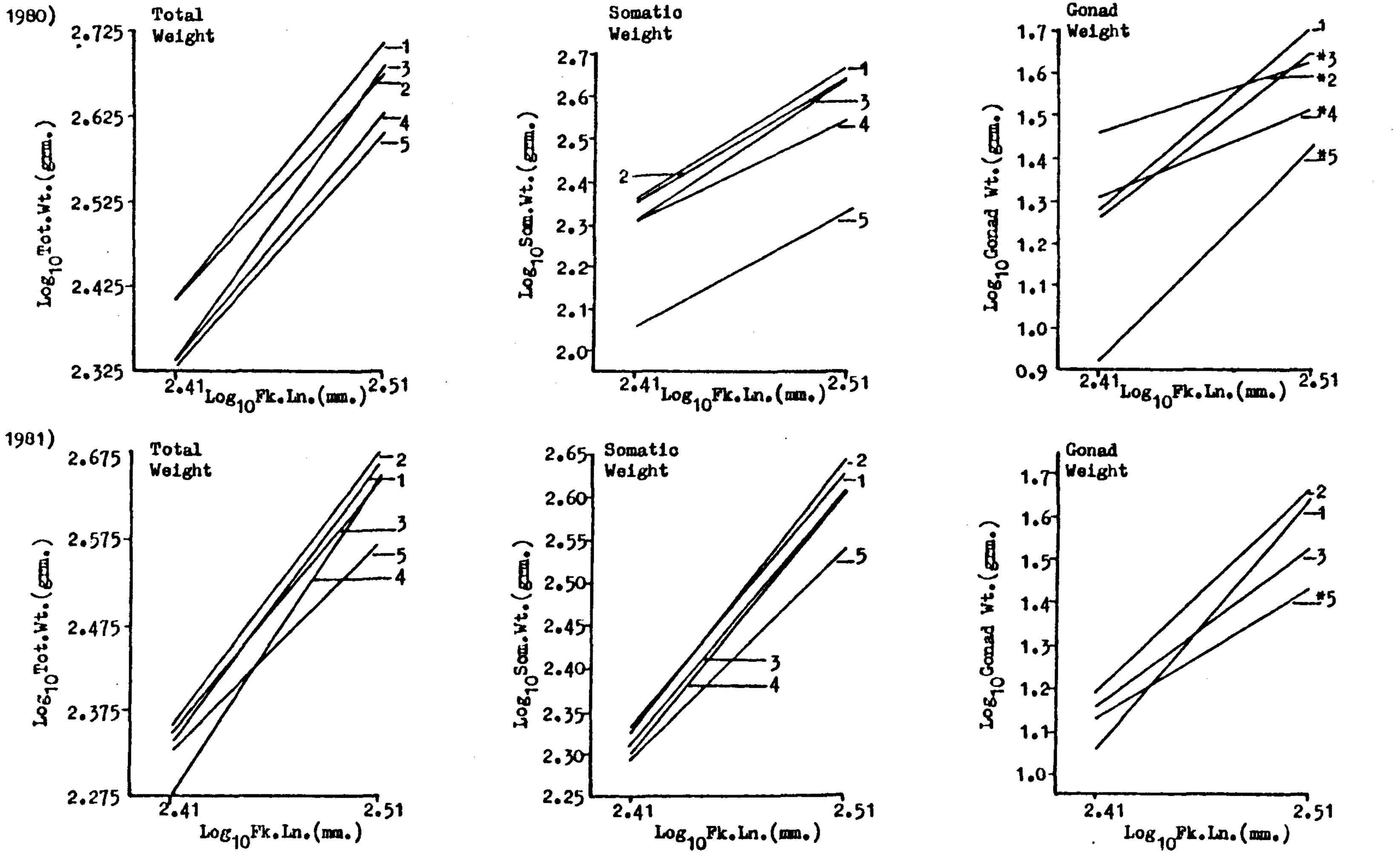
Analysis of Covariance:
Between slopes $F = 0.6929$; df = 4,110; $P > 0.25$
Between Intercepts $F = 13.2088$; df = 4,110; $P < 0.0005$
Multiple Range test $a_5 \; \underline{a_3 \; a_1 \; a_4 \; a_2}$

$\log_{10}$ Gonad weight = $\log_{10}$ a + b $\log_{10}$ Fork length

1	23	-12.4033	5.5741 ± 1.9682	0.623	34.7	$P < 0.0005$
2	56	- 9.5775	4.4599 ± 1.0473	0.5796	73.05	$P < 0.0005$
3	24	- 7.3767	3.5353 ± 1.8774	0.4095	15.25	$P < 0.001$
4	6	-30.4884	12.7603 ± 8.6688	0.8068	16.7	$P < 0.025$
5	11	- 5.874	2.8991 ± 3.5941	0.2701	3.33	$P > 0.10$

Analysis* of Covariance:
Between slopes $F = 1.6453$; df = 2,97; $P > 0.10$
Between Intercepts $F = 6.0492$; df = 2,97; $P < 0.005$
Multiple Range Test $\underline{a_3 \quad a_2 \quad a_1}$

Figure 4.11, Regressions of total weight/-, somatic weight/-, and gonad weight/fork length of male **A. fallax**, caught at Lydney at bimonthly intervals (indicated by the numbers, starting on the 15 April) during the upstream migration period in 1980 and in 1981. Asterisk indicates the regression was not significant at the 5% level.



The analysis indicates that the regression coefficients for total weight/, and somatic weight/fork length were homogenous during the upstream migration through the estuary, in both 1980 and 1981. In 1980 only one of the regressions of gonad weight/fork length were significant, while in 1981 there were four significant regressions. The coefficients of the regression gonad weight/fork length from period four in 1981 should be regarded with some caution, and has been ignored for the purpose of analysis. As found for the females, Glebe and Leggett (1981a) showed that male A.sapidissima migrating at the peak of the migration period had significantly more somatic reserves than did the early or late migrants. An analogous situation exists for A.fallax in the Severn for the final group of migrants, from the 1981 season (period 5), were significantly lighter for a given length when compared with those of the previous four periods.

5. Entry of maiden or virgin fish

In chapter three it was mentioned that information on the spawning history of A.fallax may be obtained from their scales. The spawning migration causes resorbtion and/or erosion of scale material and after spawning when feeding recommences, rapid scale growth ensues thus producing an easily distinguishable 'scar' or spawning mark.

(a) Females

The numbers of virgin and repeat spawners for the whole sampled population, at Lydney are shown in table 4.10 a + b, and proportions illustrated in figure 4.12 a + b, for 1980 and 1981. During the 1980 spawning migration there was a significant increase in the proportion of virgin spawners through the migration period, (Chi-square = 18.64; df = 4; $p < 0.005$). However, in 1981 analysis showed there to be no significant difference in the proportion of virgin to repeat spawning fish during the migration (Chi-square = 5,395; df = 4; $p > 0.10$), the pattern taking the form of a parabola.

Table 4.10 a + b The number of virgin and repeat spawning female *A.fallax* caught at Lydney at bimonthly intervals during the upstream migration in 1980 and 1981, starting on the 15th April

(a) 1980

Period	Number of Virgin Spawners	Number of Repeat Spawners
1	18	33
2	26	34
3	25	34
4	37	13
5	11	7
Total	117	121

(b) 1981

Period	Number of Virgin Spawners	Number of Repeat Spawners
1	22	29
2	36	33
3	41	40
4	26	37
5	13	27
Total	138	166

Table 4.11 The numbers of virgin and repeat spawning female *A.fallax*, age five, caught at Lydney during 1980 at bimonthly intervals during the upstream migration period, starting on the 15th April.

Period	Number of Virgin Spawners	Number of Repeat Spawners
1	16	12
2	20	22
3	20	14
4	26	9
5	11	5
Total	93	62

Figure 4.12 a & b, The percentage of virgin spawning female A.fallax caught at Lydney during 1980 and 1981, at bimonthly intervals starting on the 15 April.

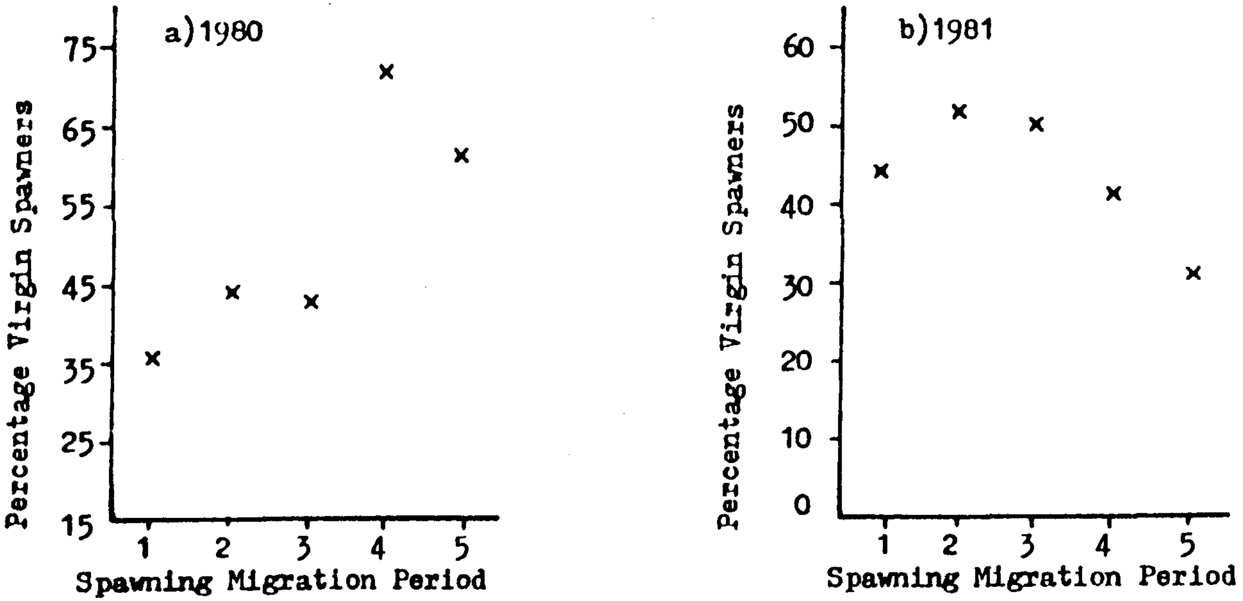
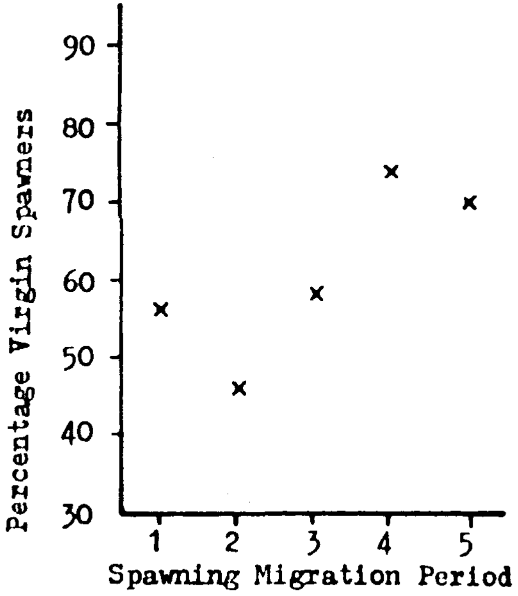


Figure 4.13, The percentage of virgin spawning female A.fallax age five caught at Lydney during 1980, at bimonthly intervals starting on the 15 April.



In 1980, there was enough five year olds (1975 year-class) to examine whether this trend existed within a particular age group. From table 4.11 and figure 4.13, it appears that the proportion of virgin fish to repeat spawning fish does increase towards the end of the migration. Though analysis shows that this was not statistically significant (Chi-square = 6.248; df = 4; $p > 0.10$). The same analysis could not be conducted for the 1981 data as very few of the 1976 year-class matured at age four, resulting in low numbers of repeat spawners.

(b) Males

The number of virgin and repeat spawners for the whole sample population are shown in table 4.12 a + b, and the proportions illustrated in figures 4.14 a + b, for 1980 and 1981. As a result of the low number of observations, chi-square analysis was carried out on the first three periods of 1980 and not at all on the 1981 data. There was no significant difference in the number of virgin to repeat spawning fish during the first three time periods in 1980, (Chi-square = 3.062; df = 2; $p > 0.10$).

Though analysis was not conducted on the 1981 data it is interesting to note that the proportion of virgin spawners during the first period was nearly twice that when compared with the other periods. This ties in with the observation that a proportion of small males appeared at the start of the spawning migration.

D. Spawning and Spawning Grounds

Spawning areas were determined by the collection of eggs or from the observations made by fishermen and water bailiffs. The spawning grounds are characterized by fairly fast moving water over sandy - gravel shallows, closely situated to an area of deep water. Reports indicated that the small males are the first to arrive in these deeper pools, where the fish form a shoal. This is similar to

Table 4.12 a + b The number of virgin and repeat spawning male <u>A.fallax</u> caught at Lydney at intervals during the upstream migration in 1980 and 1981

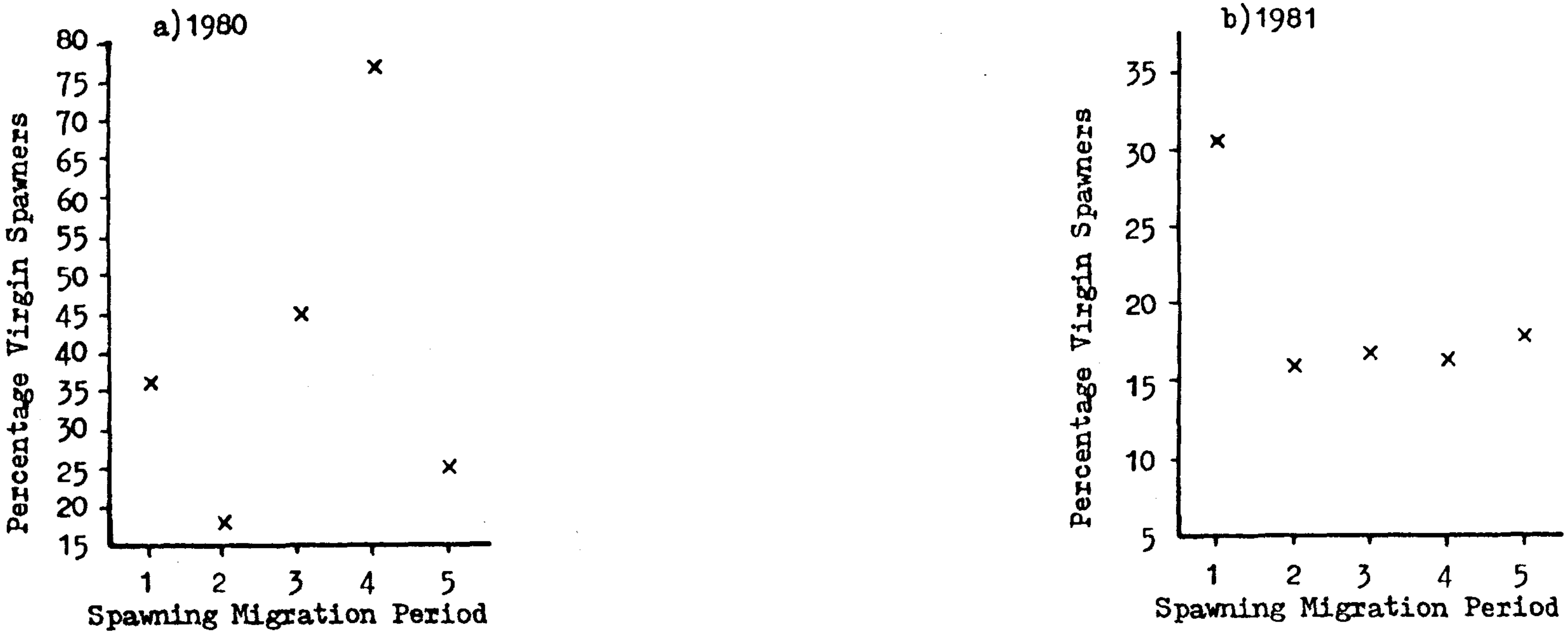
(a) 1980

Period	Number of Virgin Spawners	Number of Repeat Spawners
1 (15-30 April)	9	16
2 (1-15 May)	4	18
3 (16-31 May)	5	6
4 (1-15 June)	7	2
5 (16-30 June)	1	3
TOTAL	26	45

(b) 1981

Period	Number of Virgin Spawners	Number of Repeat Spawners
1 (15-30 April)	7	16
2 (1-15 May	9	47
3 (16-31 May)	4	20
4 (1-15 June)	1	5
5 (16-30 June)	2	9
TOTAL	23	97

Figure 4.14 a & b, The percentage of virgin spawning male A.fallax caught at Lydney during 1980 and 1981, at bimonthly intervals starting on the 15 April.



the situation reported for *A.kessleri pontica* by Svetovidov (1963). During the day the shoals of *A.fallax* mill about in the pool. This behaviour becomes very obvious when angling for the fish as the frequency of the catch periodically rises and falls as the shoal passes the fishing point. Towards evening/dusk the adults move out from the deeper water onto the shallows. The spawning act is characterised by a considerable amount of commotion, the fish splashing and flashing.

These observations on the characteristics of the spawning grounds are similar to those described by Ellison (1935) for alosids on the Wye, who further added that these species prefer a stoney and gravelly bottom in water about one metre deep, and situated at the tail of a pool, which has a good current flowing through it. Rameye et al. (1976) reported for *A.fallax* from the Rhone that the gravel must be clean for if covered by mud the eggs would be asphyxiated. From the study of Auld and Schubel (1978) it appears that the hatching success of a number of *Alosa* species was not significantly affected by suspended solid levels up to 1000 mg/l (the limit of their study). However, the larvae stages were more vulnerable and survival of *A.sapidissima* larvae were significantly reduced by suspended solid levels equal to or greater than 100 mg/l.

Several investigators have reported on the daily timing of the spawning act. The situation for *A.fallax* is very similar to that described by Chittenden (1969) for *A.sapidissima* in the Delaware River. Leim (1924) reported that spawning commences in the evening and continues until midnight or later. Similarly Leach (1925) mentions that spawning occurs between 5 p.m. and 10 p.m. Similar findings were recorded for *A.alosa* by Hoestlandt(1958) who found that the fish prefered to spawn on gravel in a water depth of between 0.5 m and 1.5 m. Frantsuzov (1941) (cited by Svetovidov, 1963) observed that A.kessleri kessleri and A.kessleri volgensis spawn mainly in the evenings between 1600 and 2200 hours. However, not all reports are of nocturnal spawning, Massman (1952) concluded that A.sapidissima spawn at all hours although most intensively between noon and midnight.

Not all of the genus elect to spawn on shallow gravels, Loesch (1968) reported that A.aestivalis selected to spawn in deep pools, depositing their eggs over a rocky bottom, with a preference for fast flowing water. Cooper (1961) reported that A.pseudoharengus, which spawn in ponds, deposit their eggs in shallow water over detritus, though occasionally over a hard sandy bottom, where there was little or no current.

Temperature appears to be an important factor in determining the onset of spawning. Gallois (1946-7) mentions for A.fallax, from the Rhone, that the temperature must exceed 17°C for the gonads to complete maturation. Rameye et al. (1976) reported that spawning commences at temperatures above 16°C, with most occuring between 18°C and 24°C. Similar findings were also reported by Roule (1922) and by D'Ancona (1928). The importance of temperature on the eggs' hatching success has been shown for A.sapidissima by Bradford et al. (1968) and for A.pseudoharengus by Edsall (1970), as well as on the survival of young A.sapidissima while in the river system (Leggett, 1977; Marcy, 1976; Shoubridge and Leggett, 1978).

The distribution of eggs on the spawning grounds is shown for two sites on the Wye, figure 4.15, this distribution agrees closely with what might be expected from the fishes reported spawning behaviour. The lack of eggs at Courtfield at a depth of 15 cms. may be attributed to the fact that there was little if any current in this area. (This investigation was only intended to be a pilot investigation, and one of the main problems was that only three

Figure 4.15, The mean density of eggs, of A.fallax, on the spawning grounds in relation to water depth.

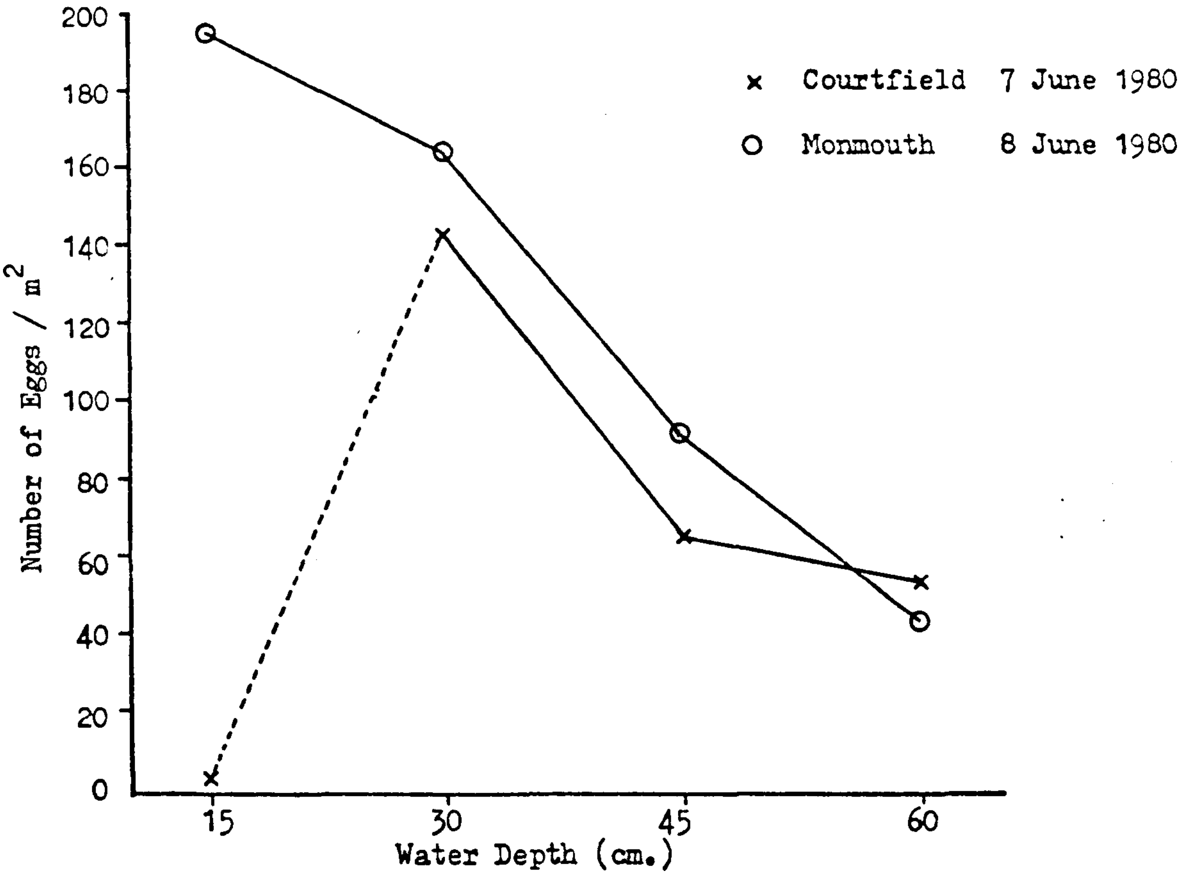
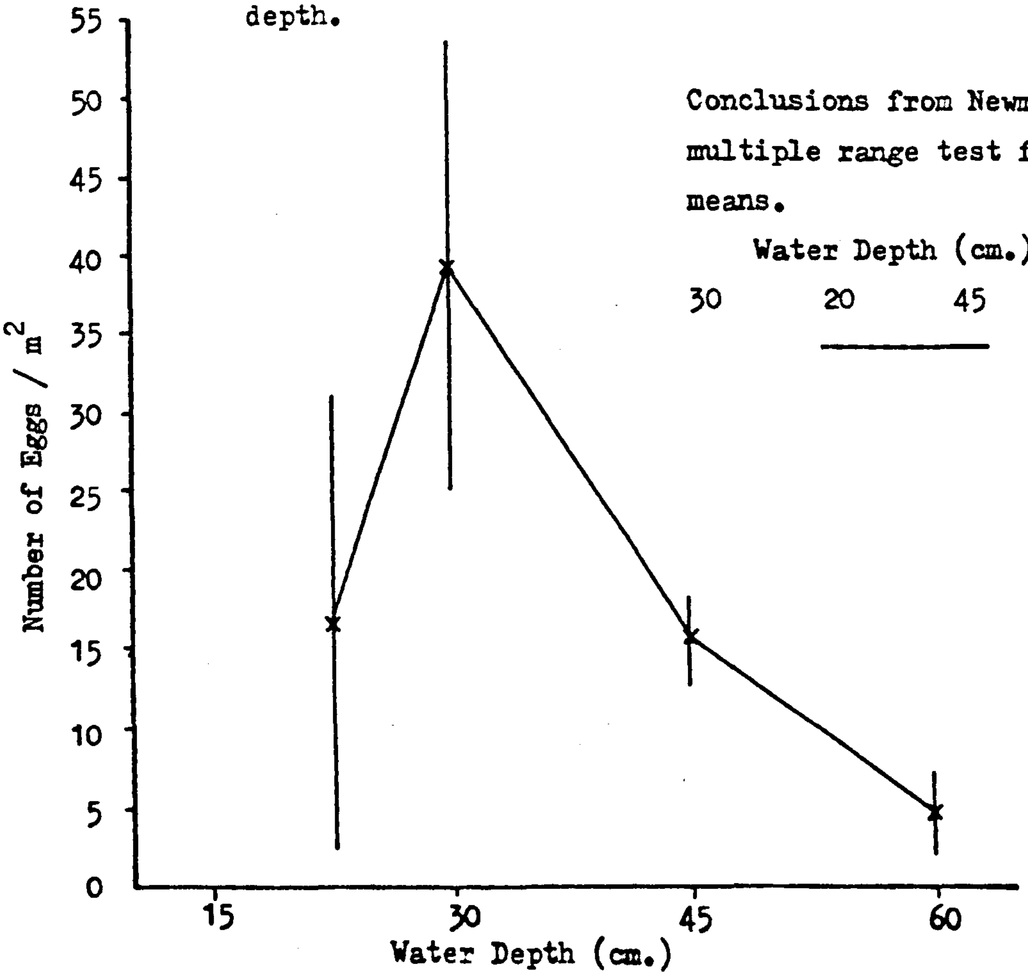


Figure 4.16, The density (mean ± 95% confidence limits) of eggs, of A.fallax on the spawning ground, at Courtfield, in relation to water depth.



Conclusions from Newman - Keuls multiple range test for homogenous means.

Water Depth (cm.)

30 20 45 60

samples were taken at each depth, making any statistical analysis questionable. It had been hoped to repeat the investigation a week later, however, the river was heavily in flood and did not return to near the initial level for at least 15 days, and this may well have affected the distribution of the eggs.) Taking account of these difficulties, on the 22nd June, 1980, it was possible to take further samples at Courtfield and the distribution of eggs are shown in figure 4.16.

Analysis of variance shows that there is a highly significant difference between the mean number of eggs at each depth ($F = 13.3591$; $df = 3.24$; $p < 0.0005$). The multiple range test shows that the majority of the eggs are at a depth of 30 cms, at depths either side of this the numbers fell significantly. (It should be noted that Bartlett's test produced a significant difference between the variances; $Bc = 21.222$; $df = 3$; $p < 0.001$. However, according to Zar (1974), analysis of variance may still be used even if their is considerable heterogeneity of variances, as long as the number of observations in each group is equal or nearly equal.)

These types of shallows in close association with pools characterizes all of the spawning areas on the River Wye and River Teme, below Powic Weir. However, on the River Severn, considerable amount of spawning takes place in water that is approximately three metres deep, though spawning is still over gravel. Walburg and Nichols (1967) for _A.sapidissima_ reported that water depth during spawning could vary from one to ten metres, and has been as deep as 12.2 m in the Hudson River. A smaller variation in water depth at spawning was reported for _Alosa caspia caspia_ (Eichwald) by Svetovidov (1963) of mainly between one and three metres, but has been known to be as deep as six metres.

The eggs of _A.fallax_ are non-adhesive. The situation for

A.sapidissima is slightly confused, Chittenden (1969) found the eggs slightly adhesive, while Hildebrand (1963), Leim (1924) and Scott and Crossman (1973) report that the eggs are not adhesive. Mansueti (1956b) stated that the eggs of A.pseudoharengus were strongly adhesive after extrusion, but are essentially non-adhesive. Similar reports for A.pseudoharengus are given by Cooper (1961), Hildebrand (1963) and by Pate (1972). Pate (1972) found the eggs of A.mediocris to be slightly adhesive and the same has been reported for A.aestivalis by Bigelow and Schroeder (1953), Cianci (1969), Kuntz and Radcliffe (1918), Loesch (1968) and by Scherer (1972).

The eggs of A.fallax are thus susceptible to periods of drought as well as to floods. For at Courtfield during periods of relatively low flows (7th June, 1980; flow = 0.16m/sec) eggs were drifting down at a rate of 1.03 eggs/m^3, at a water depth of 30 cms. Hass (1968) on the Elbe found that the eggs of A.fallax were dispersed by the current and most were found in a layer between the bottom and a height of 2.5 m above it. Similar observations of eggs drifting down with the current have been reported for A.sapidissima by Barker (1965), Marcy (1972), Walburg and Nichols (1967) and by Williams and Bruger (1972). From the age of the eggs in the drift samples Marcy (1972) concluded that the eggs travel between 1.6 kms and 6.4 kms from where spawned, the current velocities ranged from 0.15 m/s and 0.61 m/s. Similar conclusions were reached by Barker (1965). Chittenden (1969) found that the eggs of A.sapidissima settle out after six seconds in water that was 0.355 m deep, after the eggs had travelled nearly two metres, the current velocity at the time was between 0.49 m/sec and 0.61 m/sec. He concluded, that under normal flow conditions, the eggs would not drift far from where they were released. However, if the eggs were not securely lodged in the gravel, they may be vulnerable to disturbance and swept downstream. This agrees with

Massman (1952) who found that the density of eggs in drift samples increased with increasing current velocity.

On the gravel beds the eggs are susceptible to predation. Though no quantitative assessment of the inverebrates were made, it appears that the eggs may be vulnerable to cyclopoid copepods which Vladimirov (1962) reported feeding on Alosa eggs before the eggs become water hardened. Of the species recorded present, other invertebrates which may cause egg mortality are: caddis larvae (Trichoptera) by Fox (1978b) planarians (Dugesia tigrina (Girard)) by Newburg (1974); oligochaetes by Briggs (1953); large stoneflies Perla spp. by Stuart (1953) as well as by fish (Edsall, 1964). The percentage of dead eggs collected from the spawning grounds in 1979 and in 1980 are presented in table 4.13. As a result of the small number of samples taken, no statistical analysis was performed. It is apparent that most of the observations lie below 10%, with a range between zero and 71.08%, (Monmouth 4th June, 1980, 15 cms depth). These results are similar to those of Watson's (1970) who found the egg mortality of A. sapidissima in the Connecticut River to be on average 20% and 12.82% in the years of study. Bradford et al. (1968) found for A. sapidissima that the mean mortality of control eggs during bioassays was 15.7%. Carlson (1968) found that the mortality of A. sapidissima eggs hatched in river boxes ranged from 33.5% to 55.7%. Leim (1924) found a mean mortality level of 33.54% for samples (greater than 30 in number) of A. sapidissima eggs. Massman (1952) found an exceptionally high mortality of almost 66% for eggs collected from various Virginia Rivers. This may either be due to the different criteria used to determine a dead egg. Massman (1952) considered an egg was dead if the yolk was coagulated or had adhered to the vitelline membrane instead of drifting free within. In this study an egg was considered as dead if it had turned completely opaque after preservation.

Table 4.13 The density and percentage mortality of eggs from various sites

Site	Date	Depth cms	Number of samples at each depth	Total No. of eggs	Mean % mortality	Number/ m^2	Temperature
<u>Kick Samples</u>							
R. Teme							
Powic weir	14.6.79	50 cms	1	35	17.14	87.5/m^2	16.0°C
	21.6.79	50 cms	1	164	21.02	164 /m^2	12.5°C
	29.6.79	50 cms	1	129	9.3	129 /m^2	13.0°C
	14.7.79	50 cms	1	159	7.55	79.5/m^2	16.0°C
	19.5.80	50 cms	1	79	13.92	19.8/m^2	18.0°C
	20.5.80	50 cms	1	20	10.0	20 /m^2	14.0°C
	1.6.80	50 cms	1	43	4.54	21.5/m^2	13.5°C
R. Wye							
Pipton	2.6.80	50 cms	1	33	6.06	19.8/m^2	15.0°C
Winforton	23.5.80	25 cms	1	68	7.35	85 /m^2	14.0°C
	31.5.80	25 cms	1	46	6.52	23 /m^2	16.0°C
Holme Lacey	23.5.80	50 cms	1	46	8.70	15.3/m^2	15.0°C
Courtfield	4.6.80	50 cms	1	275	25.45	275 /m^2	17.5°C
	7.6.80	15 cms	3	12	0	4 /m^2	
		30 cms	3	430	9.77	143.3/m^2	18.0°C
		45 cms	3	198	9.60	66 /m^2	
		60 cms	3	161	8.08	53.6/m^2	
	22.6.80	20 cms	7	116	6.03	16.6/m^2	
		30 cms	7	275	6.91	39.3/m^2	14.5°C
		45 cms	7	110	3.18	15.7/m^2	
		60 cms	7	31	6.45	4.4/m^2	
Monmouth	20.5.80	25 cms	1	40	10.0	100 /m^2	17.5°C
	25.5.80	25 cms	1	137	8.76	342.5/m^2	16.5°C
	4.6.80	15 cms	1	83	71.08	83 /m^2	18.0°C
		30 cms	1	30	13.33	30 /m^2	
		60 cms	1	34	23.53	34 /m^2	
	8.6.80	15 cms	3	590	4.75	196.7/m^2	16.5°C
		30 cms	3	494	9.11	164.7/m^2	
		45 cms	3	277	9.03	92.3/m^2	
		60 cms	3	130	8.46	43.3/m^2	
<u>Drift Samples</u>						<u>Number/ m^3</u>	
Courtfield	7.6.80	0-25	2	250	10.8	1.03	
	17.6.80	30-60	2	29	3.57	0.06	16.5°C
	22.6.80	5-35	2	69	8.55	0.12	
Monmouth	8.6.80	0-30	1	78	7.69	2.36	
		30-60	1	35	0	0.63	

Another possible explanation of the high mortality figures is that Massman's (1952) samples were based on drift samples and as dead eggs have been found to be lighter than live eggs (Chittenden, 1969, Massman, 1952), this, in theory, would produce higher mortality figures. However, in this study, from the few samples taken, it does not appear that the percentage mortality of the eggs in the 'drift' samples were any different to those of the 'kick' samples.

E. Extent of the Spawning Grounds

The fact that eggs from some species of *Alosa* do drift down with the current has been used by a number of investigators to determine the extent of the spawning grounds as well as times, notably by Marcy (1972), Massman (1952), Pate (1972), Scherer (1972), Street (1970), Walburg and Nichols (1967), Watson (1970) and by Williams and Bruger (1972). This method could not be used in this study due to the problem of leaving equipment unattended and where it may get in the way of the major recreational interests, fishing and canoeing. The extent of the migration hdd to be determined from the collection of eggs and/or the sighting of adults.

Various studies have reported changes in the distribution of the spawning areas from year to year. Williams and Bruger (1972) concluded that this may be due to a change in water levels and currents. Marcy (1972) suggested that water temperature acting on the development of the ovaries may affect the distribution of the spawning areas, as the ovaries develop more slowly at lower temperatures (Mansueti and Kolb, 1953), and thus the fish would tend to migrate further before spawning. Similar conclusions were reached by Watson (1970). Svetovidov (1963) reported that the spawning grounds of *A.kessleri volgensis* were not permanent and tended to change.

In the River Severn catchment the uppermost spawning site found during this study was at Powic Weir on the River Teme (adults have been caught above the weir, but extremely rarely). In 1979 a larger spawning population was found to exist at Powic, than in 1980. The differences were reflected in the rod and line catch of 6 fish/ person/hr. in 1979 in contrast to the situation in 1980 of 0.5 fish/ person/hr. The relatively smaller spawning population at Powic in 1980 was also reflected in the lower egg densities, table 4.13. (It should be noted that though no quantitative estimates of the spawning stock was made, it was thought that the spawning stock in 1980 was larger than that of 1979). To reach the spawning grounds at Powic the fish must pass two weirs either at Maismore or at Llanthony and at Tewkesbury. The weirs at Maismore and at Llanthony do not present any real obstruction to the migrants as these weirs are covered by tides of 7.33 m and 7.83 m (as recorded at Sharpness dock) respectively. In a typical tidal cycle from peak spring to peak spring tides these levels are reached by approximately 62% and 51% of the tides respectively. The weir at Tewkesbury is only slightly affected by the tides and may pose some restriction to their migration. There is, however, a lock around the weir but personal observations and opinions seem to indicate that it was not used to any great extent by the migrants to circumvent the weir.

The mean daily discharge and temperature for 1979 and 1980 are shown in figures 4.17 and 4.18. It seems that both water level and temperature may play an important role in determining the extent of the spawning migration. In 1979 the amount of discharge was considerably greater than in 1980 and this would make any such barrier more surmountable. The water temperature in 1979 was consistently lower than in 1980, until the middle of June and may prolong the final stages of maturation and ovulation (Gallois, 1946-7; Mansueti and

Figure 4.17, Mean daily discharge at Saxons Lode, river Severn, from 15 April to 30 June 1979 and 1980.

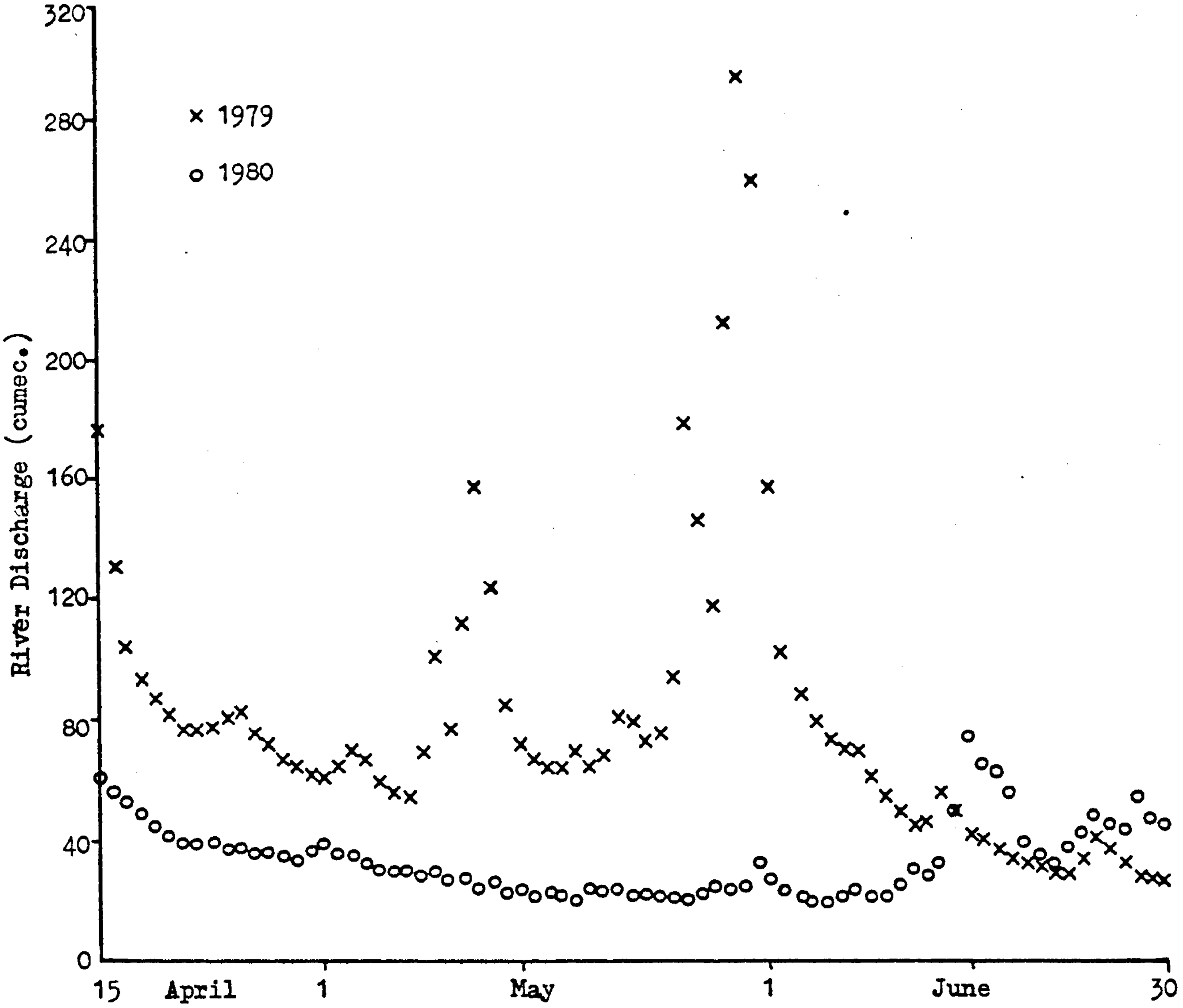


Figure 4.18, Mean daily river temperature at Saxons Lode, river Severn, from 15 April to 30 June 1979 and 1980.

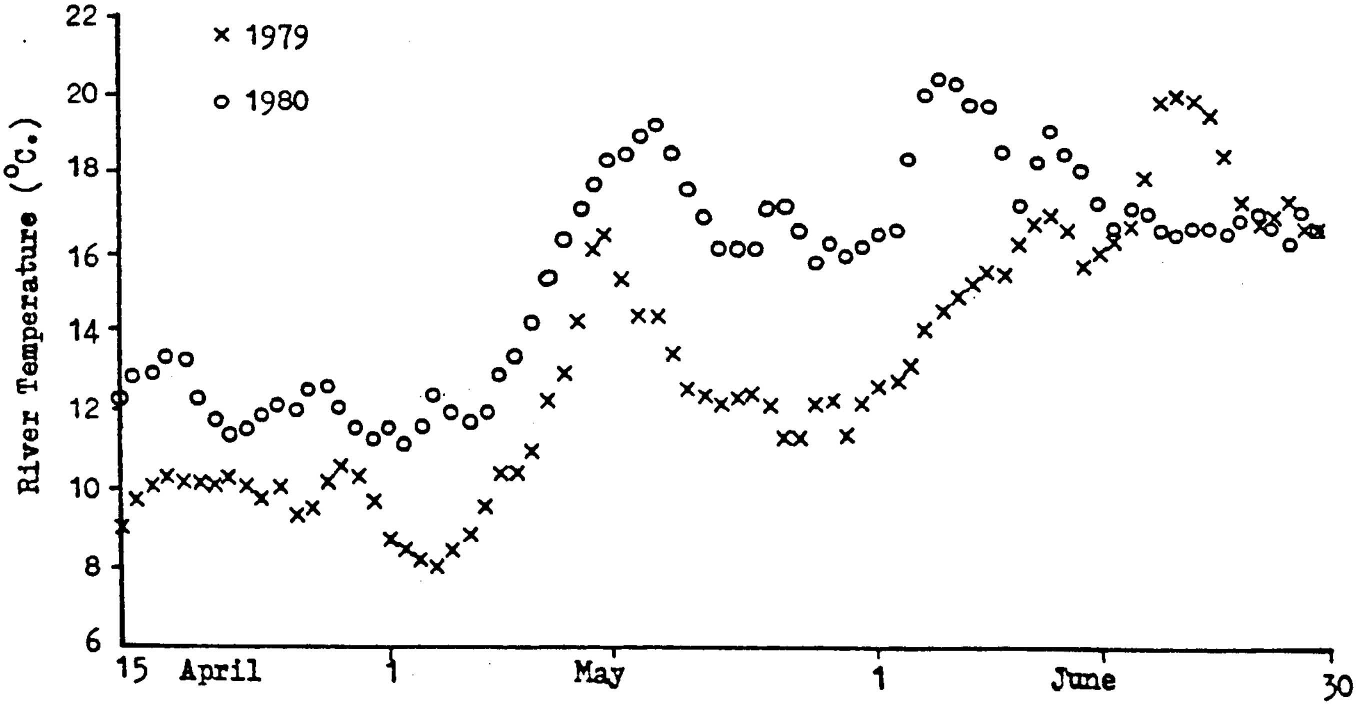


Figure 4.19, Mean daily discharge at Belmont, river Wye, from 15 April to 30 June 1979 and 1980.

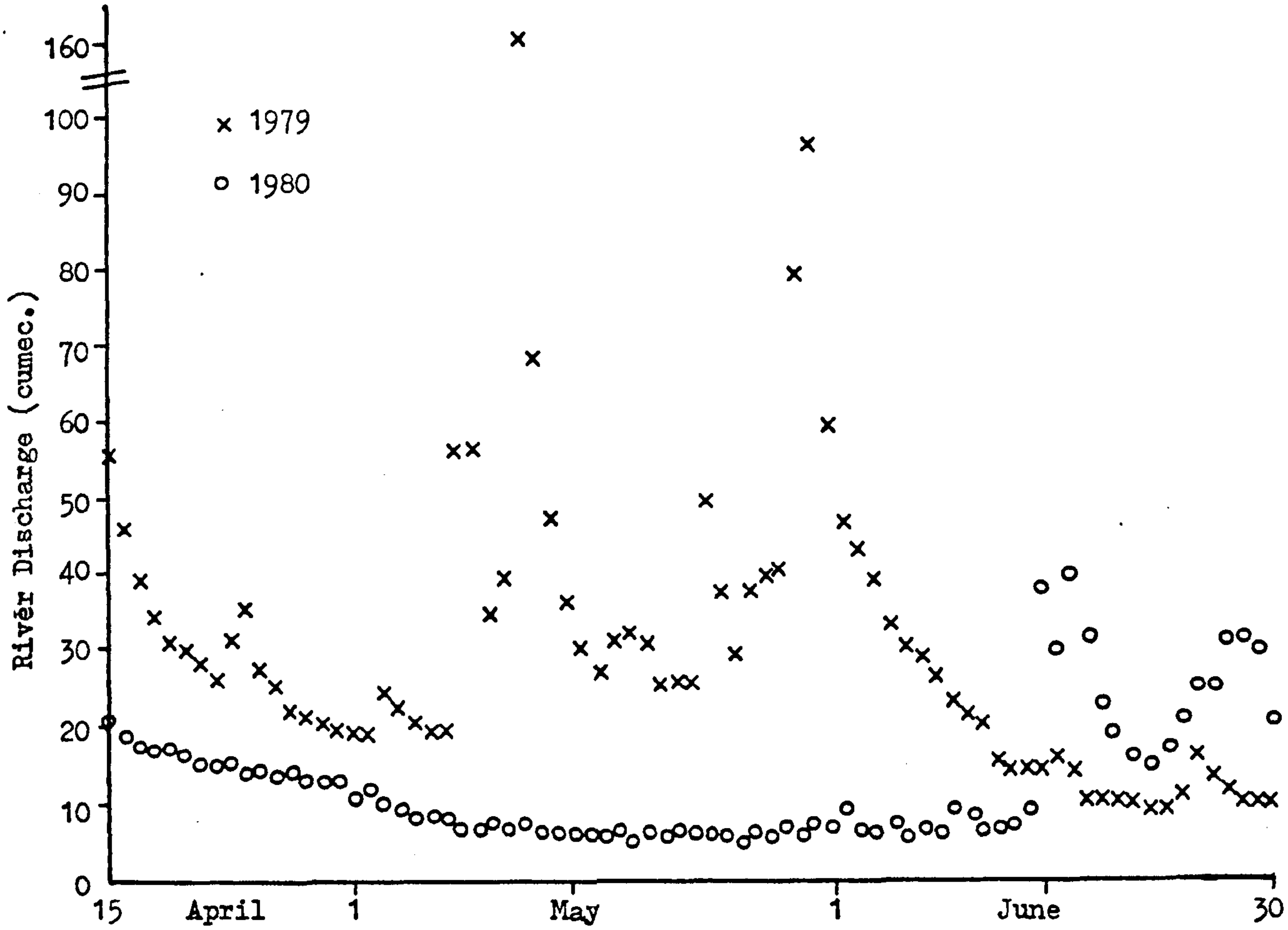
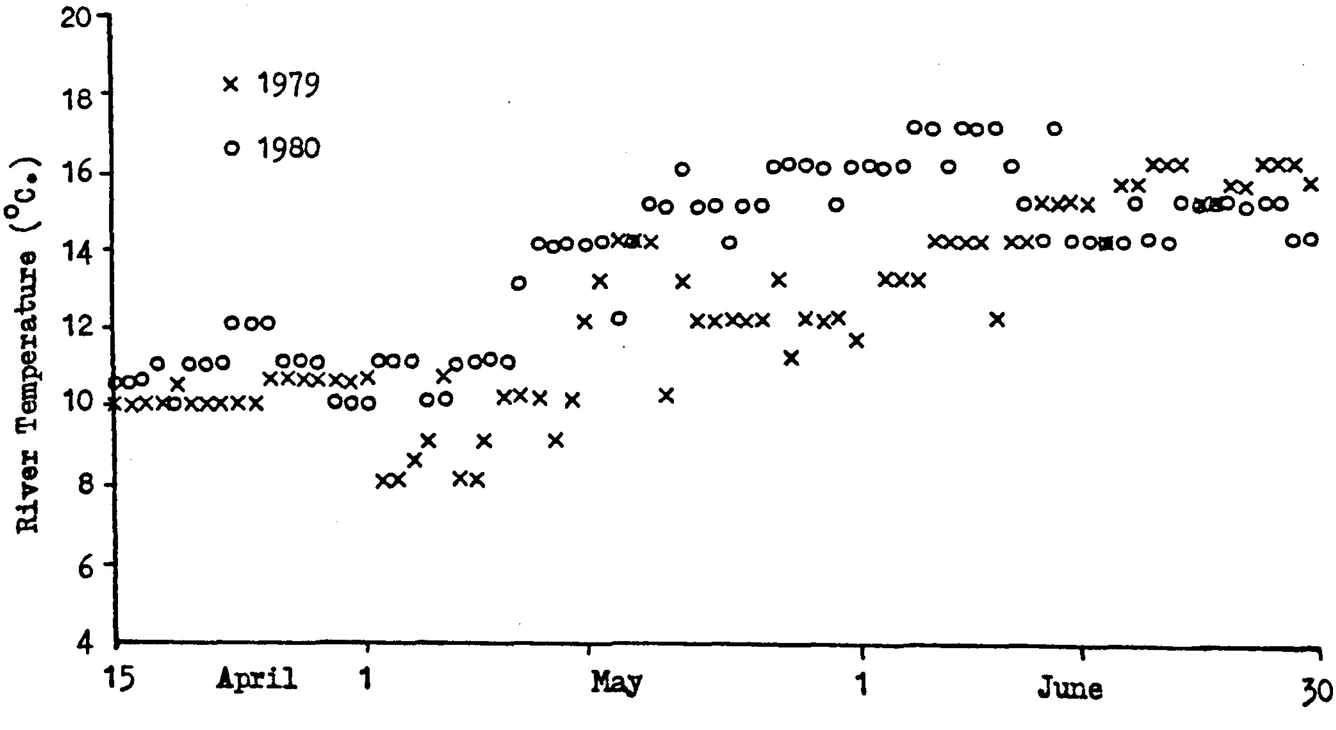


Figure 4.20, Mean daily river temperature at Belmont, river Wye, from 15 April to 30 June 1979 and 1980.



Kolb, 1953). However, Stacey et al. (1979) has shown that aquatic vegetation was important in triggering the final stages of gonad maturation and ovulation, for Carassius auratus (Linnaeus). Thus it is possible that factors other than temperature and discharge are important in determining the extent of the spawning area for A.fallax.

On the Wye the upstream limit of the spawning migration has been found to be Builth Wells (Welsh Water Authority Annual Reports, for the Wye, 1962-1981), though they have been reported as far upstream as Newbridge on Wye (Ellison, 1935). In 1979 large numbers of A.fallax were caught at Builth Wells, (river km = 192.5) while in 1980 none were seen, and no eggs were obtained. In 1980 the adults were found to penetrate upstream as far as Tyrcelyn (nr. Erwood) (grid ref. SO 074456 river km = 184), however, eggs were not found as far upstream, their limit appeared to be at Pipton (river km. = 170). As in this region of the river system the gradient starts to rise rapidly (see chapter two), then similar to the situation on the Severn the higher flows in 1979 when compared to 1980 (figure 4.19) may have facilitated the fishs' penetration upriver. The clear cut distinction in water temperature between the two years, for the Severn, was not so apparent for the Wye (figure 4.20). Though in general the temperatures were higher in 1980 than in 1979.

F. Fish on the Spawning Grounds

1. Size

In 1980, it was possible to obtain samples of the spawning stock during the last week in May (26th - 31st May) from three locations on the River Wye at Monmouth (30.5 km from river mouth) Courtfield (50.0 km) and Winforton (149.0 km). All the samples were obtained by rod and line fishing.

The mean length, for each sex, at each of the sites is shown in table 4.14. The females showed no significant difference in length between the three sites. A different pattern is evident for the males, the fish at Monmouth being significantly smaller than those at the two sites further upstream (Courtfield and Winforton). (No significant differences existed between variances) this may have arisen because the small males do not have sufficient energy reserves to migrate further upriver for successful spawning. In the Volga, Shteinfeld (1945) (cited by Svetividov, 1963) observed that the larger members of *A.kessleri kessleri* were encountered further upstream.

2. Length to weight relationships of fish on the spawning grounds

(a) Females

Regression equations were produced for total weight/-, somatic weight/-,and gonad weight/fork length and the coefficients are shown in table 4.15, and illustrated in figure 4.21. All the regressions, except for those representing gonad weight/length at Courtfield and Winforton were significant. This may be because the spawning stock at these sites consists of fish that have partially but not yet completed spawning and those which are still fully gravid. Ramaye et al. (1976) reported that *A.fallax* from the Rhone release their eggs in a number of separate layings. Hoestlandt (1958) found that *A.alosa* normally lay between 10,000 and 23,000 eggs at one time. Similar observations were reported for *A.kessleri pontica* by Tonhikh (1937) (cited by Svetividov 1963) who reported that eggs were laid in several portions over a wide area within the river. The last portion of eggs being deposited during the descent of the fish. Canfield (1937) (unpublished manuscript cited by Walburg and Nichols 1967) reported that the eggs developed gradually in the ovaries as the temperature of the water increased and that spawning occurred

Table 4.14 The size (mean length ± 95% confidence limits) of female and male *A.fallax* from three sites on the River Wye, caught between 26th-31st May, 1980

Females

Site	Mean cms.	95% Confidence limits	N
Monmouth	32.456	± 0.881	18
Courtfield	32.3	± 0.97	10
Winforton	33.568	± 0.895	19

Single factor analysis of variance:

$F = 2.5946$

$df = 2,44$

$p > 0.05$

Males

Site	Mean cms.	95% Confidence limits	N
Monmouth	27.504	± 0.963	24
Courtfield	29.3	± 1.061	8
Winforton	29.375	± 0.924	20

Single factor analysis of variance:

$F = 5.2877$

$df = 2,49$

$p < 0.01$

Newman - Keuls multiple range test

Monmouth Courtfield Winforton

Intermittently as the eggs ripened. Shoubridge and Leggett (1978) concluded that eggs must be shed in several batches, if not, the body cavity of A.sapidissima would have to increase in volume by two to four times in order to accommodate all the eggs if they reached full maturity and were spawned simultaneously.

There was no significant difference between the regression coefficients for the relationship between total weight/fork length though the intercepts differed significantly. Though between which sites this difference lay could not be detected, using the Newman - Keuls multiple range test. This may be related to their spawning behaviour of not releasing their eggs at one time. This is reinforced by the fact that there is no significant difference in the regression equations for somatic weight/fork length at the three sites. It may also imply that the females will migrate as far as their energy reserves will allow. It was evident that the somatic reserves of females entering the Severn differed between times of entry. Assuming that the same situation occurs on the Wye, then the strategy would appear to be four those fish with greater somatic energy reserves to migrate further upriver until a critical level was reached.

This strategy would have the effect of increasing the spawning areas as well as optimizing the chance of a repeat spawning assuming that the critical level is high enough to allow the fish to return to the estuary and recommence feeding.

(b) Males

The regression equations for total weight/-, somatic weight/-, and gonad weight/fork length were computed and the coefficients are shown in table 4.16 and illustrated in figure 4.21. The situation

Table 4.15 **Coefficients for the regressions of total weight/-, somatic weight/-, and gonad weight/fork length for female <u>A.fallax</u> from three sites on the River Wye, caught between 26th-31st May 1980.**

Log_{10} Total weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Site	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
Monmouth	18	- 4.6512	2.9274 ± 0.7853	0.796	62.46	$P < 0.0005$
Courtfield	10	- 5.0795	3.0852 ± 2.6278	0.4782	7.33	$P < 0.05$
Winforton	19	- 3.2255	2.3443 ± 1.007	0.5866	24.13	$P < 0.0005$

Analysis of covariance:
Between slopes F = 0.5004; df = 2,41; $P > 0.25$
Between intercepts F = 3.7821; df = 2.41; $P < 0.05$

$\log_{10}$ Somatic weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Site	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
Monmouth	18	- 3.8057	2.5558 ± 0.629	0.7737	70.45	$P < 0.0005$
Courtfield	10	- 3.1259	2.2763 ± 1.7948	0.5167	8.55	$P < 0.025$
Winforton	19	- 3.6203	2.4742 ± 0.7895	0.7201	43.72	$P < 0.0005$

Analysis of covariance:
Between slopes F = 1.2434; df = 2,41; $P > 0.25$
Between intercepts F = 1.5695; df = 2,41; $P > 0.10$

$\log_{10}$ Gonad weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Site	N	Log_{10} Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
Monmouth	18	-10.6786	5.0273 ± 2.8132	0.4729	14.35	$P < 0.0025$
Courtfield	10	-15.4807	6.9408 ± 9.8504	0.2709	2.97	$P > 0.10$
Winforton	19	- 1.4646	1.3009 ± 4.4612	0.0218	0.38	$P > 0.25$

Table 4.16 Coefficients for the regressions of total weight/-, somatic weight/-, and gonad weight/fork length for male <u>A.fallax</u> from three sites on the River Wye, caught between 26th-31st May 1980

$\log_{10}$ Total weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Site	N	$\log_{10}$ Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
Monmouth	24	- 4.8174	2.9678 ± 0.3734	0.9251	271.67	$P < 0.0005$
Courtfield	8	- 4.7529	2.9389 ± 1.4775	0.798	23.69	$P < 0.005$
Winforton	20	- 4.6618	2.8958 ± 0.6034	0.8495	101.67	$P < 0.0005$

Analysis of covariance
Between slopes $F = 0.0246$; df = 2,46; $P > 0.25$
Between intercepts $F = 1.96$; df = 2,46; $P > 0.10$

$\log_{10}$ Somatic weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Site	N	$\log_{10}$ Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
Monmouth	24	- 4.7027	2.9029 ± 0.3273	0.939	338.4	$P < 0.0005$
Courtfield	8	- 4.8129	2.9453 ± 1.4093	0.8134	26.15	$P < 0.0025$
Winforton	20	- 4.597	2.8551 ± 0.525	0.8789	130.56	$P < 0.0005$

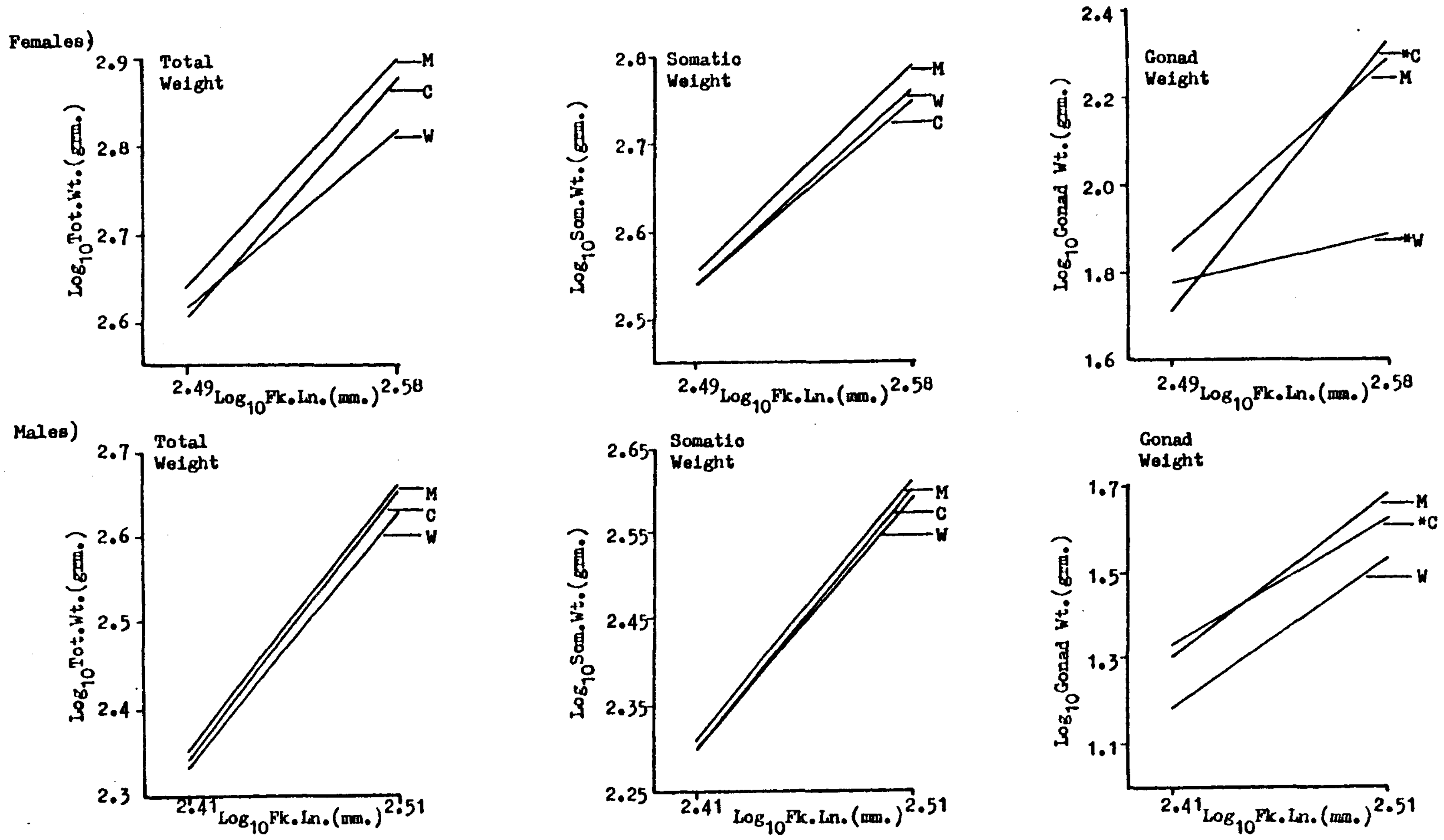
Analysis of covariance
Between slopes $F = 0.0188$; df = 2,46; $P > 0.25$
Between intercepts $F = 0.8407$; df = 2,46; $P > 0.25$

$\log_{10}$ Gonad weight = $\log_{10}$ a + b $\log_{10}$ Fork length

Site	N	$\log_{10}$ Intercept	Slope b ± 95% Confidence limits	Coefficient of Determination r^2	F Value	Significance
Monmouth	24	- 7.5502	3.6662 ± 1.264	0.6219	36.19	$P < 0.0005$
Courtfield	8	- 5.5536	2.8518 ± 3.0349	0.4684	5.29	$P > 0.05$
Winforton	20	- 6.9078	3.3498 ± 2.7297	0.2697	6.65	$P < 0.025$

Student t test
Between slopes $T = 0.239$; df = 40; $P > 0.50$
Between intercepts $T = 4.9669$; df = 41; $P < 0.001$

Figure 4.21, Regressions of total weight/-, somatic weight/-, and gonad weight/fork length of female and male *A.fallax* from three sites on the river Wye, Winforton (W), Courtfield (C) and Monmouth (M) between 26 - 31 May 1980. Asterisk indicates the regression was not significant at the 5% level.



for the males is very similar to that for the females. The regression equation of gonad weight/fork length at Courtfield was not significant though this was not the case at Monmouth and Winforton. The latter two sites showed no significant difference in the regression coefficients, however, they did show highly significantly different intercepts. The overall result being a general fall in the expected gonad weight for length and this may have arisen from partial spawning as already mentioned for the females. There was no significant difference between the regressions for total weight/-,and somatic weight/fork length at any of the sites indicating that the same strategy is used by both the females and the males.

3. Age and spawning histories

The age and spawning histories of the fish caught at Monmouth, Courtfield and Winforton are presented in table 4.17 a + b, for the females and males. Though the numbers of individuals in the samples were small, some differences do appear to exist between the sites. At Monmouth there appears a predominance of first time spawners, of age five for the females and four for the males. At the other two sites the percentage of repeat spawners was found to be at least 50%. Analysis shows, for the females, that the number of repeat to virgin spawners at each of the sites was not homogenous (Chi-square = 12.0195; df = 2; $p < 0.005$). Comparison between individual sites indicates that the number of repeat spawners at Winforton is significantly higher than expected, when compared with Monmouth, (Chi-square = 11.5649; df = 1; $p < 0.001$). Comparisons between the observations at Courtfield and the other two sites were not carried out due to the small sample size. Similarly, for the males, analysis did not include Courtfield, a significant difference was found between Monmouth and Winforton (Chi-square = 9.564; df = 1; $p < 0.005$).

This would seem to indicate that virgin fish do not migrate

Table 4.17 The age and spawning histories of female and male A.fallax from three sites on the River Wye

a) Females

Age	Number of previous spawnings	Monmouth		Courtfield		Winforton	
		N	%	N	%	N	%
7	2					2	10.53
6	2			1	10.0		
6	1			1	10.0		
5	1	1	5.56	3	30.0	9	47.37
5	0	14	77.77	2	20.0	4	21.05
4	0	3	16.67	3	30.0	4	21.05
Total		18	100	10	100	19	100
Percentage repeat spawners		5.56		50		57.89	

b) Males

Age	Number of previous spawnings	Monmouth		Courtfield		Winforton	
		N	%	N	%	N	%
6	2	1	4.17				
5	2	1	4.17	3	37.5	5	25.0
5	1	1	4.17	3	37.5	4	20.0
5	0					1	5.0
4	1					2	10.0
4	0	21	87.5	2	25.0	8	40.0
Total		24	100	8	100	20	100
Percentage of repeat spawners		12.51		75		55	

as far up river when compared to fish which have spawned previously. Though this may be more directly related to size and the energy reserves, as virgin fish are generally smaller than repeat spawners from the same year-class (see chapter five). Comparison of the mean lengths of the four year old males at Monmouth and Winforton indicates that distance migrated may be size dependent. The mean length of four year old virgin males at Monmouth (269.7 mm, 95% confidence limits = ± 8.54 mm) was significantly smaller than those at Winforton (285.6 mm, 95% confidence limits = ± 10.81 mm) ($t = 2.2026$; $df = 27$; $p < 0.05$).

However, these differences may also reflect homing to specfic areas within a river system, similar to that reported by Carscadden and Leggett (1975a) for A.sapidissima, for which the size at age and the proportion of repeat spawners was found to vary between sites.

4. Sex ratio of adults on the spawning grounds

Information on the sex ratio of adults was obtained for one site in 1979 (Powic Weir, River Teme) and for three sites in 1980 (Monmouth, Courtfield and Winforton on the River Wye) table 4.18. At none of these sites was there a significant departure from a 1:1 ratio.

Table 4.18 The sex ratio of A.fallax from four sites

Site	Males	Females	Chi-squared for 1:1 ratio	Significance
Powic 1979 River Teme	23	30	0.92453	$P > 0.25$
Monmouth 1980 River Wye.	24	18	0.85714	$P > 0.25$
Courtfield 1980 River Wye	8	10	0.22222	$P > 0.50$
Winforton 1980 River Wye	20	19	0.02564	$P > 0.75$

G. Post Spawning

In 1980, spent A.fallax could be caught in the Severn estuary from the end of May onwards. Adult fish were present in the estuary until the end of October, when they presumably left for their over-wintering grounds. Very few fish were obtained, and these were mostly females. The reason for this is probably related to the loss of 'condition' associated with spawning the fish having used up some of their energy reserves were now 'thin' and not as readily caught by the gear. It is also possible that they move into the main channel where the downstream current is greatest and are thus not as available to the gear. Regression equations for spent fish caught between May and the start of July 1980 of total weight/, somatic weight/, and gonad weight/fork length are shown in table 4.19. Data for males caught during 1980 and females during 1981 were not included because the regression equations were not significant.

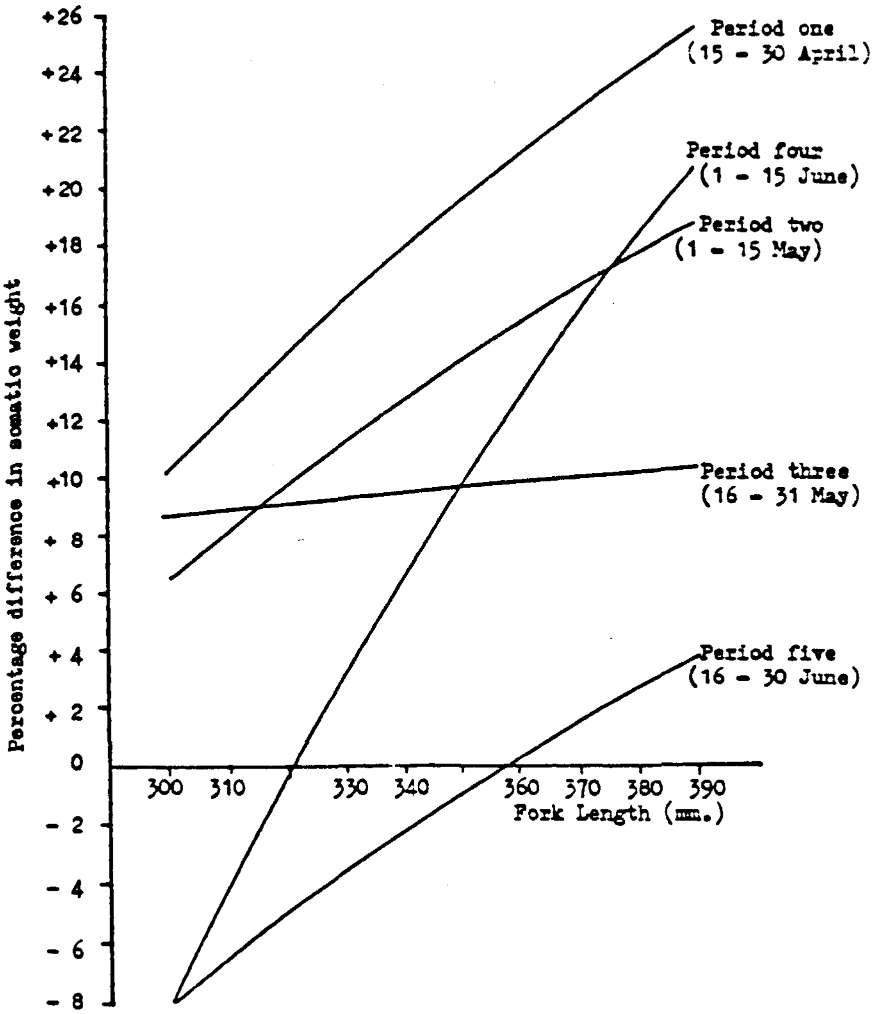
The main change in the regression of total weight/fork length when compared with that for fish entering the estuary is due to the loss of their gonad products. Some change must also be related to the energy expended during the migration as the fish do not feed actively while in fresh water (chapter seven). If the somatic weight/fork length regression of the spent fish is compared with that of the upstream migrants, then it is evident that the first migrants experience the greatest somatic weight loss, of approximately 10% for the smaller fish rising to 25% for the largest, figure 4.22. The upstream migrants from period two and three did not show such a large percentage somatic weight loss and probably reflects a shorter period of residence in freshwater.

When the spent fish are compared with the migrants of period four and five it appears that the smaller migrants were entering the estuary with less somatic reserves than fish which had already completed spawning. It should be noted that the majority of the

Table 4.19 Coefficients for the logarithmic regression of total weight/-, somatic weight/- and gonad weight/fork length for post spawning female A.fallax caught in the Severn estuary from late May to Early July, 1980

Dependent Variable	N	$\log_{10}$ Intercept (a)	Slope (b) ± 95% Con. limits	Coeff. of Determ. (r^2)	F Value	Significance
Total wt	21	- 3.663	2.4865 ± 1.1367	0.5245	20.9601	$P < 0.0005$
Soma wt	21	- 2.4298	1.9997 ± 1.5819	0.3645	7.4552	$P < 0.025$
Gonad wt	21	25.416	-9.5712 ± 7.0963	0.395	8.4875	$P < 0.01$

Figure 4.22, Percentage difference in somatic weight of pre-spawning female A.fallax caught at Lydney during various periods of the upstream migration (table 4.8a) when compared with post spawning females caught between late May and early July,1980 (table 4.19).



post spawning migrants (70%) were caught during period four (1st - 15th June). Thus the regression of somatic weight/fork length for the spent fish should only be compared with the upstream migrants from the first three time periods.

The fact that 70% of the spent fish were caught during the first half of June may indicate a higher post spawning survival of the early and peak migrants when compared with the late migrants. This may have resulted from the level of somatic reserves of these late migrants, being in fact lower when compared with some fish that have already completed spawning. Indications of higher post spawning mortalities of the late migrants have been reported for A.sapidissima by Leggett (1969).

This low percentage of spent fish caught after the middle of June may also have arisen from the fact that the late migrants being generally smaller than early and peak migrants may not be equally available to the sampling methods, once spawning has been completed.

Chittenden (1976) found that the average somatic weight loss for female A.sapidissima ranged from 38% (421 mm FL.) to 56% (531 mm), and for males from 24% (359 mm) to 46% (493 mm), in the Delaware River. This is associated with a migration of between 266 and 403 kilometres to the spawning grounds, (these distances are measured from just above the transition between brackish and freshwater). Leggett (1972) found that the somatic weight loss for female A.sapidissima averaged 45%, and for males 44% (Age IV) and 51% (Age V). This reflects energy expended over a 40-100 day period and a migration of 105 kilometres from the river mouth to the spawning grounds of the Connecticut River. Glebe and Leggett (1981a) reported a somatic weight loss of between 30%-40% for both male and female A.sapidissima in the Connecticut River for a complete journey of 265 kilometres (or 137.5 km to the spawning grounds). Glebe and Leggett (1981b) in the St. John River Florida, observed a somatic weight loss of between 20%-35% for males and 40%-50% for females over a distance of 370 kilometres to the spawning grounds. For both sexes of A.pseudoharengus, Cooper (1961) found a decrease of approximately 13.5% in their somatic weight over the spawning period.

These journeys are considerably longer than those undertaken by A.fallax in the Severn. The maximum extent of the migration is to Powic weir on the Teme and Diglis weir on the Severn which reflects a journey of 92 and 91 kilometres respectively from Lydney. However, considerable spawning takes place between Maisemore and Tewkesbury weirs which are subjected to tidal freshwater on approximately 16 days per month and represents a distance of between 50 and 66 kilometres respectively from Lydney. In the River Wye the distance migrated may be much greater, being 192.5 kms from the mouth of the river to Builth Wells.

This reduction in somatic weight was similarly reflected in a fall in the lipid content of muscle. Analysis was only carried out on the females as so few spent males were caught. The sample of pre-spawning females was taken just prior to the peak of the migration (10th May) and the post-spawning or spent females during June and early July. Table 4.20 shows the percentage of lipid in terms of wet weight and dry weight as well as moisture content. Love (1970) reported an inverse relationship between lipid and moisture content, with the joint content being somewhere near 80% which compares closely with that found by Atwater (1888) (cited by Jacquot 1961) of between 78.7 and 80.6%. The same was shown by Eiras, (1981), Glebe and Leggett (1981a) and by Perkins and Dahlberg (1971) for A.mediocris. However, in A.sapidissima, Perkins and Dahlberg (1971) found lipid and moisture content to be directly related.

Table 4.20 Level of lipid and water in the muscle of female A.fallax caught at Newnham on the 10th May, 1980 (pre-spawning) and during June and early July, 1980 (post-spawning)

Condition of fish	Percentage wet weight of lipid ± 95% conf. limits	Percentage dry weight of lipid ± 95% conf. limits	Percentage moisture ± 95% conf. limits	N
Pre-spawning (fish entering estuary)	3.664 ± 0.834	15.797 ± 3.280	77.12 ±1.10	19
Post-spawning (fish leaving estuary)	1.498 ± 0.374	7.525 ± 1.712	80.3 ± 0.83	15

The pre-spawning level of lipids in A.fallax were considerably lower than those given for American populations of shads. Gabriel et al. (1976) found lipid levels of 15.67% (wet weight) for females and 17.25% for males in the body of A.sapidissima entering the Connecticut River. In the St. Johns River (Florida) they found levels of 17.98% and 18.74% for females and males respectively and in the St. John River (New Brunswick), the levels were 21.96% for females and 18.91% for males. Perkins and Dahlberg (1971) found levels of 9.3% (wet weight) and 11.9% for female and male A.sapidissima and 8.4% and 7.3% for female and male A.mediocris in the Altamaha River. In the Altamaha River A.sapidissima have to travel 368 kms and A.mediocris 216 kms from the river mouth to their respective spawning grounds. For A.alosa, Eiras (1981) reported lipid levels of between 8.2% (wet weight) and 11.3% for fish entering the river system on their spawning migration. Nikolsky (1961) reported levels of 16.22% for A.kessleri kessleri, 8.71% for A.kessleri volgensis, and 7.48% for A.caspia caspia (though whether these are in terms of percentage dry or wet weight was not made clear).

The lipid levels in the muscle were significantly lower in spent fish when compared with those in fish entering the estuary at the peak of the migration ($U = 251.5$; df = 15.19; $p < 0.001$, for wet weight; and $U = 246.0$; df = 15.19; $p < 0.001$, for dry weight). (In this case the Mann - Whitney test was used to test for statistical significance, as significant differences were found between the variances, $F = 6.6295$; df = 18.14; $p < 0.001$, for wet weight; and $F = 4.8859$; df = 18.14; $p < 0.005$, for dry weight). These differences represent a mean drop of 59.12% (in terms of wet weight) and 52.36% (in terms of dry weight) when compared to pre-spawning lipid levels. For A.sapidissima, Gabriel et al. (1976) found a drop of 29.1% and 85.48% for females from the Connecticut River and from the St. Johns River (Florida), respectively, over the spawning period. For the males, the reduction in the level of lipid were 54.78% and 83.62% in the two river systems. Glebe and Leggett (1981a) reported similar findings for A.sapidissima in the Connecticut River, early and peak migrants consuming approximately 40% of their total somatic fat reserves to reach the spawning grounds and an additional 10 - 30% on the return journey. Late migrants, however, needed to utilize 60% of their total somatic fat reserves in reaching the spawning grounds. For both sexes of A.sapidissima from the St. Johns River (Florida) exhibit a decline of between 50 - 60% in their somatic fat content by the time the fish had reached the spawning grounds with an additional loss of approximately 36% during or immediately after spawning (Glebe and Leggett, 1981b). Perkins and Dahlberg (1971) found for female A.mediocris and for female A.sapidissima that the fat content did not decrease significantly with distance migrated upstream, however, a significant decline in fat content was found for male A.sapidissima. Eiras (1981) found that female A.alosa, from the River Douro (Portugal) utilized between 15% and 52% of their somatic fat reserves and males between 20% and 48%, by the time the fish had reached their spawning grounds, a distance of approximately 70 kms. Similar to the situation for A.sapidissima (Glebe and Leggett, 1981a) the amount of lipid utilized was greater for those entering the river system at the end of the upstream migration period when compared to those entering at the start. For a freshwater population of A.pseudoharengus, Travis (1966) reported a decline in their fat content, associated with spawning.

As well as body fat, visceral fat may also be utilized as an energy source during the migration. For A.sapidissima, Glebe and Leggett (1981a) found that 70%-80% of the visceral fat was utilized by both males and females. Gabriel et al. found for female A.sapidissima that 64.67% and 96.69% of their visceral fat was utilized for the migration in the Connecticut River and in the St. Johns River (Florida) respectively. The reduction for the males was 58.08% and 88.99%, in the two river systems. Though there is an extremely high loss in percentage terms, the actual amount, a maximum of 12 grammes is relatively small when compared with a somatic weight loss of 150 grammes (Glebe and Leggett, 1981 a + b). The liver may also provide an important source of energy. Eiras (1981) found for both sexes of A.alosa a reduction of approximately 26% in the lipid content of the liver by the time the fish had reached the spawning grounds.

However, for A.fallax macroscopic observation suggests that an important component of their energy reserves may come from their visceral fat. The pre-spawning fish have large amounts of fat deposited around the stomach and especially around the pyloric caecae, this, however, is not the case for spent fish.

During the spawning migration, O.nerka show a similar decline in their fat reserves, the main source of which comes from the head, skin, bones and tail (trimmings) (Idler and Bitners, 1959). Other sources of fats are derived from the muscle (Idler and Bitners, 1958) as well as from the alimentary cannal (Idler and Bitners, 1960). Gilhousen (1980) found that fats provided between 72.5% and 81% of the energy expended in the upstream migration, and spawning. The main source of fat was derived from the muscle and trimmings, with slightly more comming from the muscle.

As well as lipids, proteins may provide an energy source. Glebe and Leggett (1981a) found a reduction of approximately 45% in visceral protein over the entire migration period for both sexes of A.sapidissima. Protein loss from the soma averaged between 14% and 30% for the females and between 24% and 37% for male A.sapidissima. Similarly Eiras (1981) found for both sexes of A.alosa on the spawning grounds significant declines in the protein content of the soma and of the liver when compared with those at the mouth of the river system. Protein was also found to be an important energy source for O.nerka (Gilhousen, 1980).

However, this decline in fats and protein may not be totally due to energy expenditure but may also be associated with gonadal development. Glebe and Leggett (1981b) found that in the case of the female population of A.sapidissima from the St. Johns River (Florida) part of the fat reserves were incorporated into the ovaries, the ovarian fat levels increasing by 35% by the time the fish had reached the spawning grounds. The protein content of the ovaries was also found to increase. However, for the males the pre-spawning levels of testicular fat and protein remained fairly constant. In contrast the levels of fat and protein in the ovaries remain virtually constant, until spawning, for the population of A.sapidissima from the Connecticut River (Glebe and Leggett, 1981a). For A.alosa, Eiras (1981) found a decline in the fat content and an increase in the protein content of both the ovaries and the testes by the time the fish had reached the spawning ground. For O.nerka fat and protein were also found to be utilized for development of the gonads, proteins were also found incorporated into the trimmings for the development of secondary sexual characteristics (Gilhousen, 1980; Idler and Bitners, 1959 & 1960).

It appears from the study of Glebe and Leggett (1981b) that an iteroparous species, such as the population of A.fallax in the Rivers Severn and Wye, must utilize less than 60% of their total energy reserves for the upstream migration, spawning and their return to the sea. Species or different populations of the same species may utilize a larger percentage of their total energy reserves, with the consequence of complete spawning mortality, if this exceeds 70%.

CHAPTER FIVE

REPRODUCTIVE BIOLOGY

Introduction

Fishes are known to have evolved a wide range of life history strategies to ensure that the maximum number of progeny, summed over the parents life time, reach sexual maturity, Mann and Mills (1979). The key biological traits, have been outlined by Stearns (1976) and are fecundity, size of offspring, age, distribution of reproductive effort, the interaction of reproductive effort with adult mortality and the variation of these traits amongst an individual's progeny. The mechanism involved in the selection of these traits, depends on the organism having finite time and energy resources and natural selection will tend to adjust the reproductive effort at every age, so that the overall fitness of the life history is maximized (Cody, 1966).

The options open to an individual, depend on changes in time and energy resources allocated to one function influencing the quantity of resources allocated to others, Shoubridge and Leggett (1978). Hence a high reproductive effort may endanger future spawning by increasing the probability of post - breeding mortality through diverting resources away from maintenance and somatic growth.

In the allocation of resources for maximum survival of the progeny, there are two conflicting selection pressures, the parent may either increase the number of eggs, or increase the size of eggs. If egg size is correlated to larval size then increasing larval size may be advantageous in reducing predation, as proposed by Mann (1979), and Mills (1982). It may also increase growth efficiency by increasing the size of potential food items, according to Palaheimo and Dickie (1966) (assuming food supply is not limiting). As well as increasing their swimming capability and thus their ability to withstand floods, for lotic populations. Another factor which may be implicated arises from the work carried out by Anokhina (1960) (cited by Nikolsky, 1962) who found that egg size may also be influenced by the fat content of the female. The resultant distribution of egg sizes and fecundity may be considered as a compromise which, through natural selection, is best related to optimize larval survival.

Variation in some of these life history traits have been found within a species from different localities; notably by Bagenal (1966), Baxter (1959), Blaxter and Hempel (1963), Leggett and Carscadden (1978), Nagasaki (1958), Pope et al. (1961), Schaffer and Elson (1975), Schopka and Hempel (1973), Shoubridge and Leggett (1978), Withler (1966), see also review by Foerester (1968) and may be of adaptive significance, or represent the effects of different abiotic and biotic factors. In this chapter some of the reproductive characteristics of A.fallax in the Rivers Severn and Wye are determined.

A. Fecundity

In this study fecundity has been defined as the number of ripe eggs in the ovaries prior to the next spawning period, (Bagenal and Braum, 1978). The first record of egg production for alosids was based on the number of eggs extruded during stripping, for artificial rearing, of A.sapidissima, and was generally believed to be in the region of 30,000, however, it was realised that this did not represent total egg production (U.S. Commission of Fish and Fisheries, 1898). Estimates of total egg production were first made for A.sapidissima by Lehman (1953). The ovaries were damped dry and approximately one gramme samples were taken from the anterior, central and posterior regions of each ovary. The number of mature eggs in each subsample were counted and the fecundity computed from the mean. Norden (1967b) used the same method to estimate fecundity for A.pseudoharengus. Samples were taken from three regions of the ovary to compensate for the fact that the mean number of mature eggs decreased slightly from anterior to posterior. Similar findings were reported by Davis (1957) who further concluded that total estimates could be made, just as accurately, using one count from the central portion of each ovary. Since then the latter method has been used by Nichols and Massman (1963) and by Walburg (1960) for A.sapidissima, Loesch (1968) for A.aestivalis, and by Huber (1978) for A.pseudoharengus.

Street (1970) modified the method by using 0.1 gram samples instead of 1 gram. samples to compute total egg production for A.mediocris and A.aestivalis. This revised method was also used by Scherer (1972) for A.aestivalis.

Another method was used by Hass (1965) for A.fallax where the ovaries were placed in Gilsons' fluid to liberate the eggs from the ovarian tissue. The eggs were then placed into a solution of sodium chloride, to prevent them from settling too quickly, and five subsamples were taken and fecundity computed. A similar method was used by Pate (1972) for A.mediocris where, instead of volume, dry weight was used to estimate fecundity.

Leggett (1969) devised yet another method for calculating fecundity. After liberating the eggs in modified Gilsons' fluid, they were then washed through a series of sieves which separated the eggs into the following size categories; larger than 1.0 mm., 1.0 - 0.7 mm., 0.7 - 0.5 mm., and 0.5 - 0.25 mm. in diameter. A sample of 1,000 eggs was then taken from each size category and together with the main sample, dried to a constant weight, the total egg production was then computed. This method has since been used by Carscadden and Leggett (1975a), Leggett and Carscadden (1978) and by Shoubridge and Leggett (1978).

1. Materials and Methods

Fish were caught using the methods described in chapter two, lengthed to the nearest millimetre and weighed to the nearest gramme. Fish were aged using scales, as described in chapter three. The ovaries from each fish were removed, damped dry, weighed to the nearest 0.1 gram split longitudinally and preserved in Gilsons' fluid as modified by Simpson (1951). The ovaries were shaken periodically to help free the eggs from the ovarian tissue which was later removed. The method used to determine egg diameter was similar to that described by Hancock (1979) for Barbus barbus (Linnaeus). The Gilsons' fluid was decanted and replaced by 70% Alcohol so that the total volume was 400 mls. The eggs were stirred continuously and a 2 mL subsample was taken using a wide mouth dip sampler. The maximum diameter of all eggs was measured using a Wild microscope and graticule with a 12x magnification. The reliability of this method has been shown by Hancock (1979). Prespawning data on intraovarian egg size was obtained from ten fish entering the estuary at the peak of the migration period in 1979. None of the samples were from spent or partially spawned fish. Egg frequency data from each fish was combined and divided by ten and the data plotted as size frequency histograms, figure 5.1. The distribution of egg diameters in the pre-spawning population are divisible into two modes. These modes correspond to the ripening eggs, which are yellow with yolk and range in size from 0.44 mm. to 1.61 mm. in diameter, and eggs which may be regarded as "recruitment stock" (Bagenal, 1978), which are white, irregularly shaped and less than 0.44mm. in diameter. That the larger size of eggs are shed during spawning was evident from examination of the ovaries of seven spent fish taken from the estuary in June, 1979, figure 5.2. Similar modes have been found by Street (1970) for A.mediocris and A.aestivalis by Lehman (1953) for A.sapidissima, and by Huber (1978) for A.pseudoharengus. For A.caspia and A.kessleri

Figure 5.1, Pooled size frequency distribution of interovarian eggs present in ten fish caught at Lydney (R.Severn), 11 May 1979.

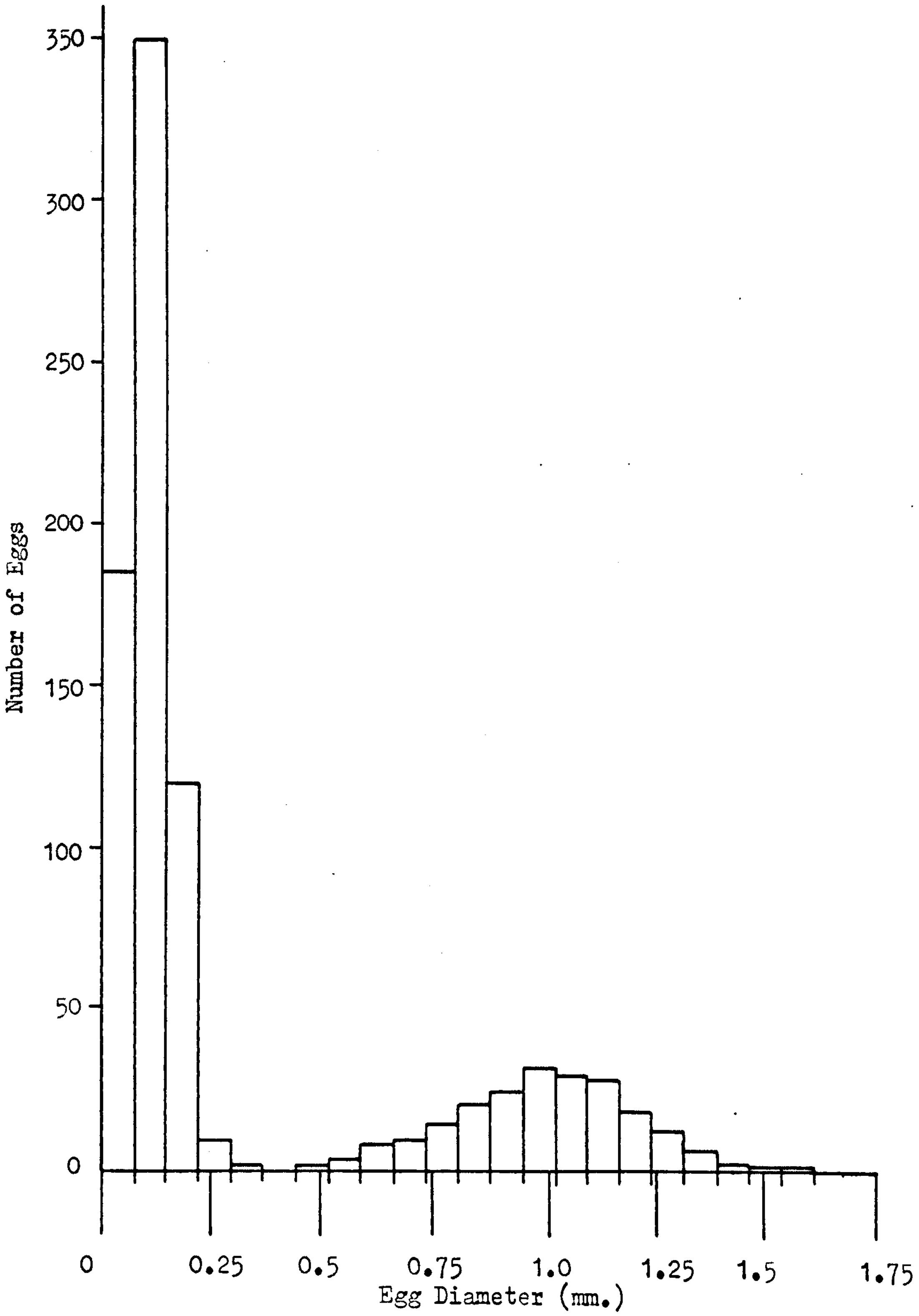
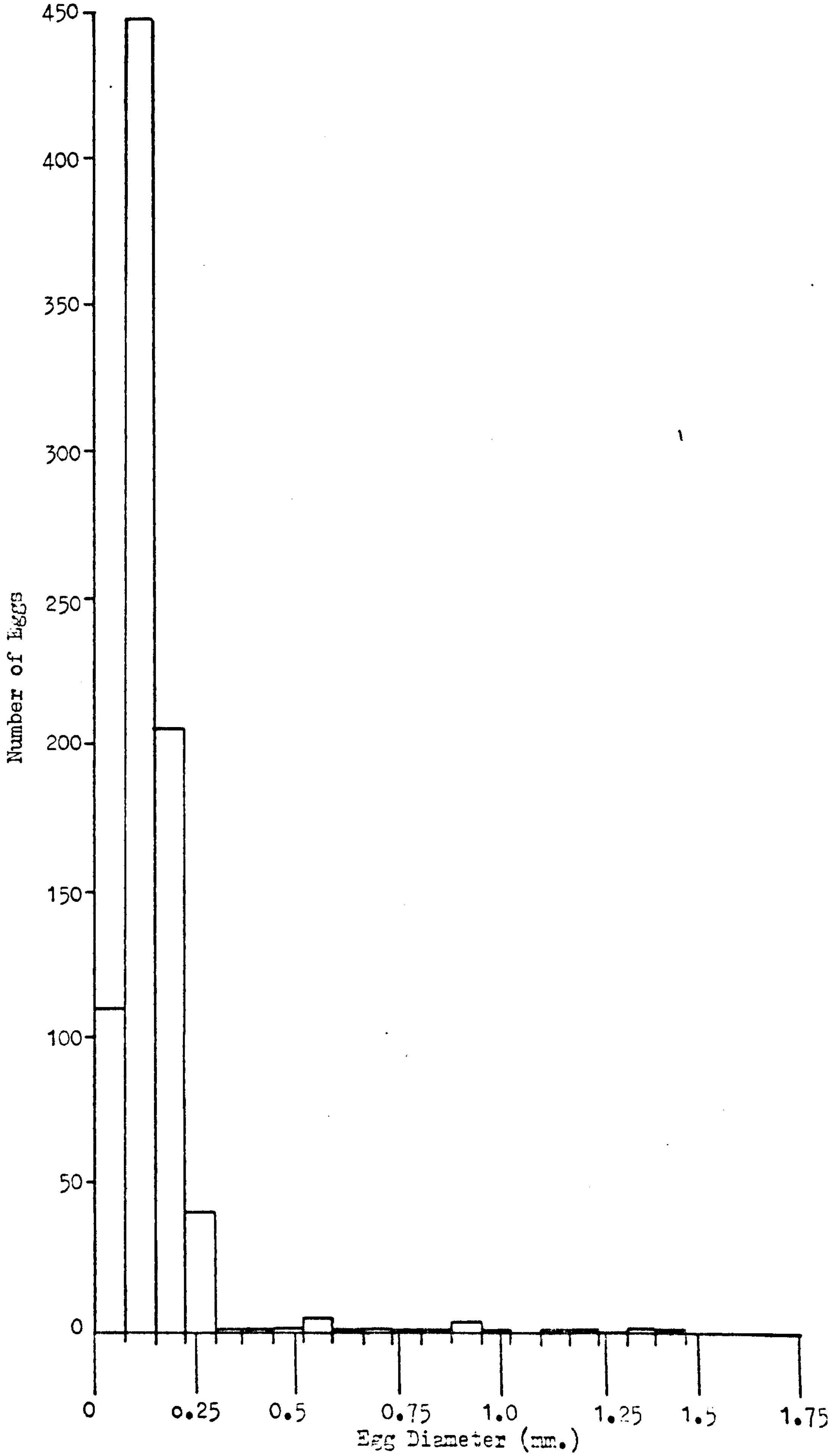


Figure 5.2, Pooled size frequency distribution of interovarian eggs present in seven fish caught at Framilode and Newnham (R.Severn), during late June 1979.



volgensis, Kisselevitch (1923) reported 3 size classes of eggs. The modal diameter of 1.022 mm. for maturing eggs is in close agreement with that found by Lahaye (1962) and Lahaye et al. (1963) for A.fallax from Morroco.

It appears from examination of figure 5.1 that, except for approximately 0.5%, the mature eggs of A.fallax are completely represented by the first three size categories described by Leggett (1969). Thus, for fecundity estimates, the smallest sieve was dispensed with and the eggs were gently washed through sieves with pores of 1.0, 0.7, and 0.5 mm. in diameter. The first sieve had the effect of taking out most of the ovarian tissue, which was removed by forceps and/or by decanting. Four lots of 250 eggs were taken, in the same manner as already described for interovarian egg size, from each size category (Bagenal and Braum (1978) suggest it is better to take a few replicate samples rather than one large one). The subsamples along with the main samples were dried to constant weight at 60°C and weighed to the nearest 0.1 mg., on a Mettler H/10W balance. The number of eggs in each size category were computed using the mean weight of the four subsamples, using the equations;

$$Na = \frac{na\ (wta + Wta)}{wta}$$

Where:

Na = total number of eggs in size category a

na = number of eggs in subsample (250)

wta = mean weight of eggs in subsample, of size category a

Wta = weight of eggs in sample, of size category a

The total number of eggs per fish were calculated by summing the number of eggs in each size category. Fecundity estimates were carried out on thirty-five fish selected, using random numbers, from fish caught during the upstream migration between May 11th - 23rd, 1979, using all methods of capture. None of these fish were spent or partially spent.

2. Sampling Error

Calculation of the estimated error caused by weighing was carried out in a similar manner to that used by Leggett (1969). Ten samples of 250 eggs from each size category were taken at random from one ovary, dried to a constant weight, and weighed to the nearest 0.1 mg.. The true weight of 250 eggs will then lie within 2.262 x standard error of the mean sample weight (with a probability of 0.95). Therefore, in 95% of the samples the percentage error in estimating the weight of 250 eggs will be less than or equal to:

$$\frac{(2.262 \times \text{standard error})}{\text{mean}} \times 100$$

These results are shown in table 5.1 and are slightly higher than those reported by Leggett (1969), who found percentage errors of between 1.3 and 1.8%.

Table 5.1 Mean weight per 250 eggs, standard error and percentage weighing error by egg size category from a single specimen.

Egg size in mm.	No. of samples	Sample mean in gram	Standard error	% error
1.0	10	0.07343	9.0946×10^{-4}	2.799%
1.0 - 0.7	10	0.01618	3.4635×10^{-4}	4.842%
0.7 - 0.5	10	0.0057	1.5776×10^{-4}	6.261%

In this study the percentage error has been taken as 6.26%, the highest in estimating any of the size categories. It was assumed that since all eggs were sized prior to weighing that the estimated error from each size category would be constant between specimens.

3. Fecundity Relationships

Both the arithmetic and logarithmic relationships between fecundity and fork length, total weight, somatic weight, ovary weight and age are shown in figures 5.3 a + b, 5.4 a + b, 5.5 a + b, 5.6 a + b, 5.7 a + b and tables 5.2 a + b. Bagenal and Braum (1978) have concluded that the relationship between fecundity and these variables is best expressed by the equation:

$$\text{Fecundity} = a\ (\text{independent variable})^{b}$$

OR

$$\text{Log}_{10}\ \text{Fecundity} = \log_{10} a + b \log_{10}\ (\text{independent variable})$$

However, some investigators have used a linear relationship of the form:

$$\text{Fecundity} = a + b\ (\text{independent variable})$$

to represent the relationship, and it is for this reason that both regressions are presented here. However, using the Coefficient of Determination (r^2) as a guide to whether the data is best fitted by a curvilinear or by a linear equation, it appears that a larger percentage of the total variation in fecundity could be accounted for by the curvilinear regression rather than by the linear regression, in all cases, tables 5.2 a + b. The regressions were fitted by the method of least squares.

Table 5.2 a + b Coefficients for the arithmetic and logorithmic regressions between fecundity and fork length, total, somatic, and ovarian weight and age.

(a) Arithmetic relationship $\text{fecundity} = b.x + a$

Independent variable (x)	Intercept (a)	Slope ± 95% confidence limits (b)	Coefficient of determination r^2	F Value	Significance of F
Fork length (mm.)	-130146.87	620.43 ± 231.57	0.47391	29.7271	$P < 0.0005$
Total weight	18037.68	110.15 ± 37.82	0.51562	37.8187	$P < 0.0005$
Somatic weight	14797.83	132.27 ± 47.02	0.49825	32.7701	$P < 0.0005$
Ovarian weight	43366.43	547.92 ± 194.1	0.50083	32.8912	$P < 0.0005$
Age	57224.08	5770.83 ± 6521.59	0.08947	3.2426	$P < 0.05$

Logarithmic relationship $\log_{10} \text{fecundity} = b \log_{10} x + \log_{10} a$

(b)

Independent variable (x)	Intercept $\log_{10} a$	Slope (b) ± 95% confidence limits	Coefficient of determination r^2	F Value	Significance of F
Fork length (mm.)	-2.6495	2.9736 ± 1.0113	0.52035	35.8	$P < 0.0005$
Total weight	2.2560	0.9559 ± 0.2656	0.6191	53.6304	$P < 0.0005$
Somatic weight	2.1676	1.0085 ± 0.2874	0.60713	50.9985	$P < 0.0005$
Ovarian weight	3.8177	0.590 ± 0.1775	0.581	45.7681	$P < 0.0005$
Age	4.5356	0.5327 ± 0.48	0.1339	5.1017	$P < 0.05$

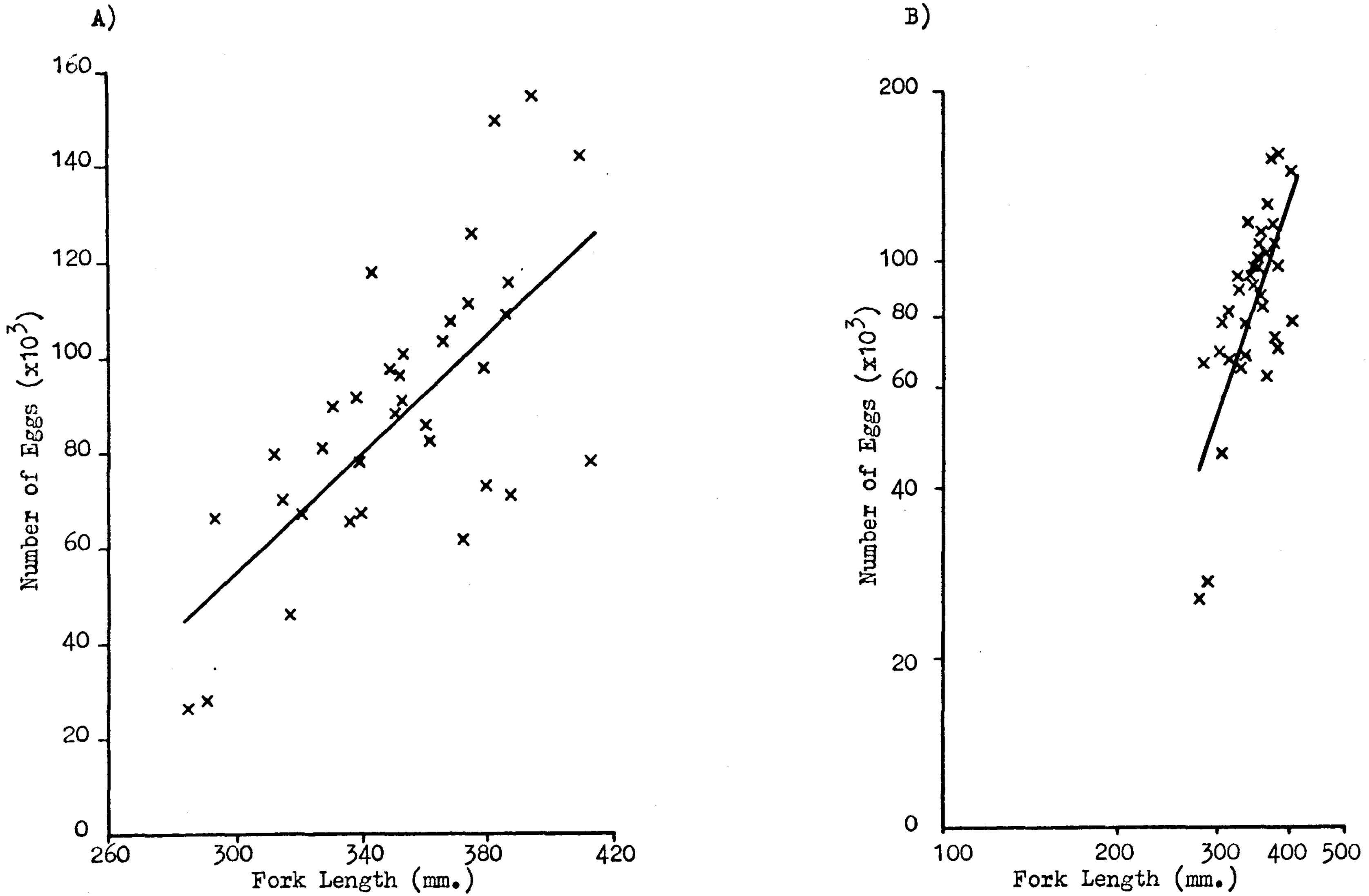
Fecundity has been related to length by many authors, (see review by Bagenal, 1978) and in the case of A.fallax, is best described by a curvilinear equation, figure 5.3 a + b, table 5.2 a + b. Hass (1965) showed similar results for A.fallax from the Elbe, and quotes typical examples for fish of 400, 450 and 500 mm. total length. These have been converted to fork length using the formula in appendix one and the results compared with those predicted from this study, table 5.3.

Table 5.3 Comparison of the Fecundity of A.fallax from the Rivers Elbe and Severn.

Fork length in mm.	Number of Eggs Elbe	Severn
354	71,000	85,156
398	119,000	120,646
441	191,000	163,682

Though care should be taken in the interpretation of these results as fecundity relationships have been found to vary between years, (Bagenal, 1973), it does seem that the regression coefficient (b) for the Elbe stock will be greater than that for the Severn population. A number of factors causing variation in fecundity have been reviewed by Bagenal (1978) and Wootton (1979), and other than the possibility of racial differences the main one appears to be food supply. In other members of the genus, linear relationships have been shown by Leggett (1969) for A.sapidissima, Loesch (1968) for A.aestivalis, Street (1970) for A.mediocris and A.aestivalis and Pate (1972) who determined the total number of eggs found in the ovaries of A.mediocris.

Figure 5.3 A & B, Arithmetic (A) and Logarithmic (B) relationships between fecundity and fork length.



The regression coefficient (b) for the curvilinear equation is usually about three when fecundity is related to length (Bagenal and Braun 1978). Student "t" test suggests that there is no significant difference between the regression coefficient (2.974) and 3.0 ($T = 0.05313$, $df = 33$, $p > 0.50$). Wootton (1979) found the modal class of some published information on values of 'b' for both marine and freshwater species, to lie between 3.250 and 3.749.

Likewise fecundity has been related to weight, figure 5.4 a + b and 5.5 a + b. Weight, however, has its disadvantages when compared to length due to changes as the spawning season approaches. Also the variables (weight and fecundity) will be slightly compounded because a more fecund fish will weigh slightly more than a less fecund fish due to the weight of extra eggs (Bagenal 1978). Bagenal and Braun (1978) state that when considering the correlation between fecundity and weight, the regression coefficient for the curvilinear equation should be close to one. Student t-test analysis indicates that the regression coefficient for total weight (0.9559) and for somatic weight (1.0085) were not significantly different from one, $t = 0.3376$ ($df = 33$; $p > 0.50$) and $t = 0.0602$ ($df = 33$; $p > 0.50$) respectively. This implies that as well as the relationship between fecundity and weight being linear, it is also isometric, in that fecundity is directly proportional to weight.

Linear relationships have been shown by Scherer (1972) for A.aestavalis, who found higher coefficients of determination for untransformed rather than for transformed data. Similar relationships have been shown by Leggett (1969) and Walburg (1960) for A.sapidissima and by Pate (1972) for A.mediocris and A.aestivalis. However, for one population of A.sapidissima, Roy (1969) observed that the quantity of eggs did not appear to depend on the length or weight of the parent.

Figure 5.4 A & B, Arithmetic (A) and Logarithmic (B) relationships between fecundity and total weight.

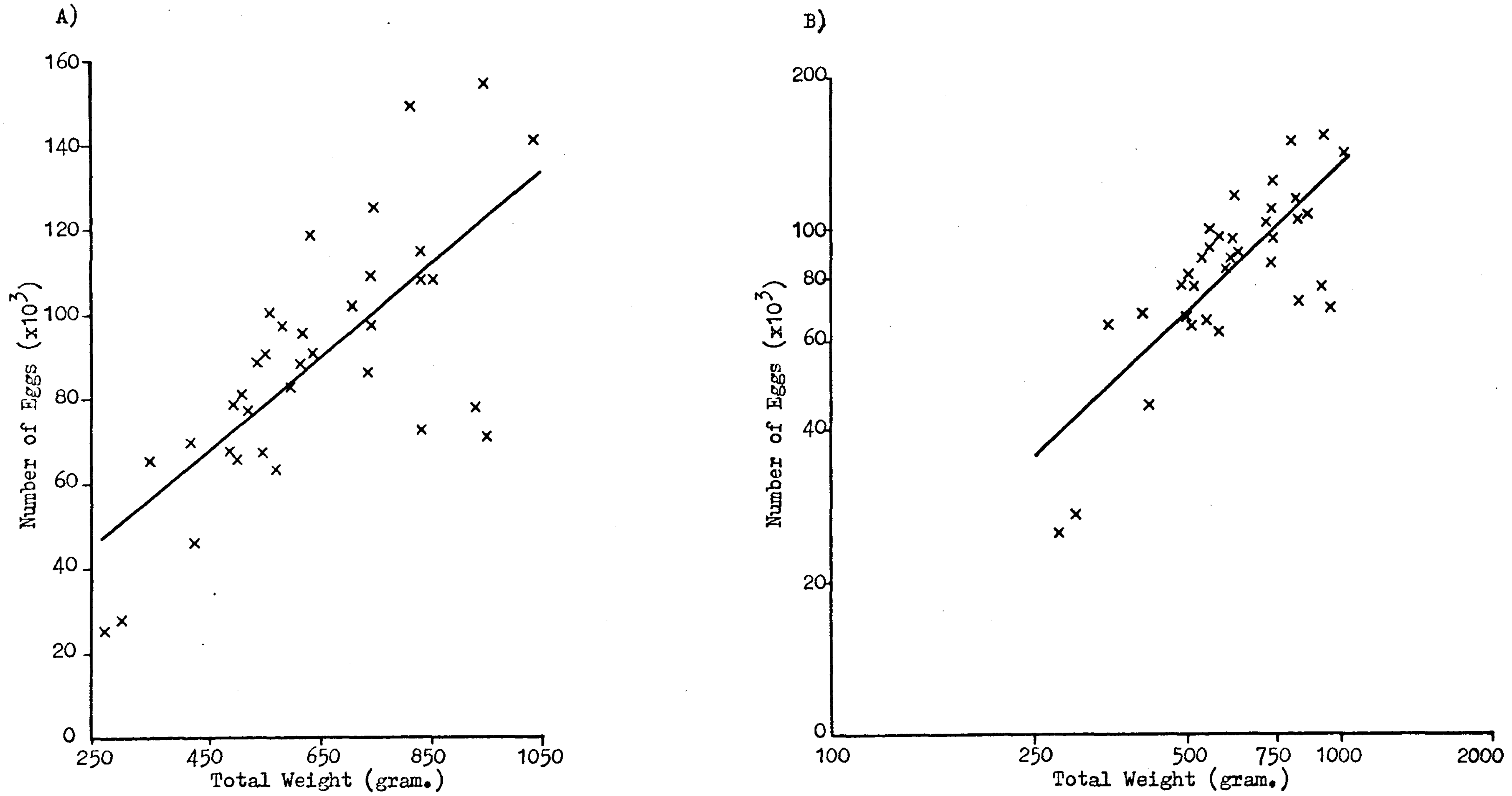
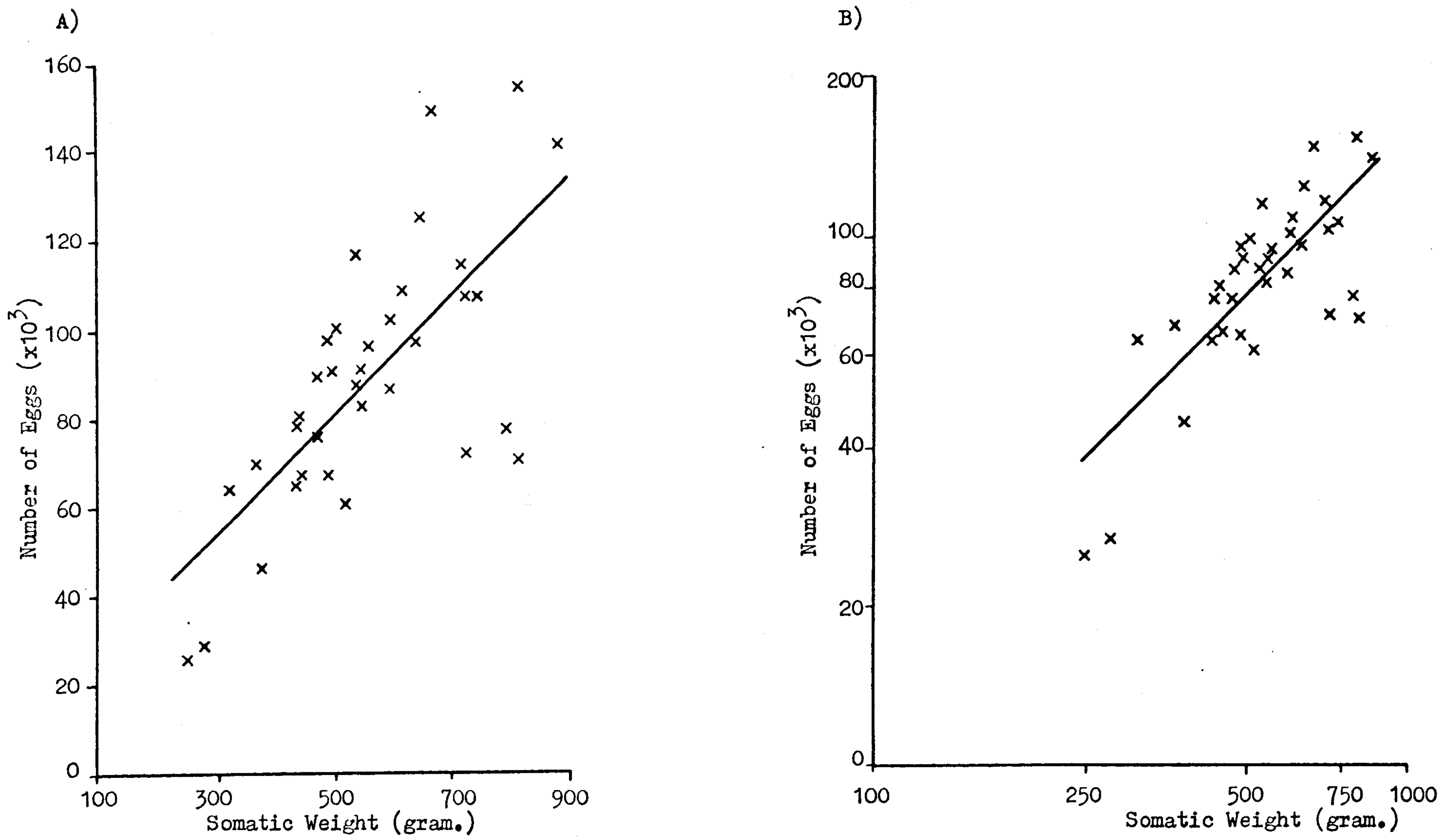


Figure 5.5 A & B, Arithmetic (A) and Logarithmic (B) relationships between fecundity and somatic weight.



The relationship between fecundity and ovarian weight (figure 5.6 a + b), which accounted for most of the variation, is similarly curvilinear (table 5.2 a + b), the student t-test shows that the regression coefficient of the curvilinear equation (0.59) is significantly different from one, ($t = 4.701$, $df = 33$; $p < 0.001$). Thus an increase in ovarian weight did not produce a proportional increase in fecundity. Bagenal (1978) suggested two possible reasons for this; firstly that heavier ovaries produce proportionally larger and fewer eggs than smaller ones and secondly that ovarian connective tissue may increase disproportionally in larger ovaries. Hancock (1979) showed that in Barbus barbus the mean diameter of ripening eggs is positively, curvilinearly correlated to ovary weight. Mann and Mills (1979) found for Leuciscus leuciscus (Linnaeus), egg size increased with size (or age). Kazakov (1981) found that the egg size in Salmo salar was directly related to the sea age of the parent. Similar correlations were found by Bilton (1970), Buchley (1967), Pope et al. (1961) and Schopka & Hempel (1973). However, in Gadus Morhua, no such correlation was found by Oosthuizen and Daan (1974).

An approximate guide as to whether there is an increase in egg size with ovary weight may be obtained by examining the relationships between the proportion of eggs from the largest size category and ovarian weight, an arithmetic plot is shown in Figure 5.8. The resultant regression is significant, suggesting that egg size does in fact increase with ovary weight. A possible advantage of varying egg sizes within a population was suggested by Mann and Mills (1979) which assumes that egg size is directly related to larvae size. This variation in size of newly hatched larvae would increase the size range of appropriate food organisms available and thus reduce interspecific competition. Bilton (1970) found the mean length and

Figure 5.6 A & B, Arithmetic (A) and Logarithmic (B) relationships between fecundity and ovarian weight.

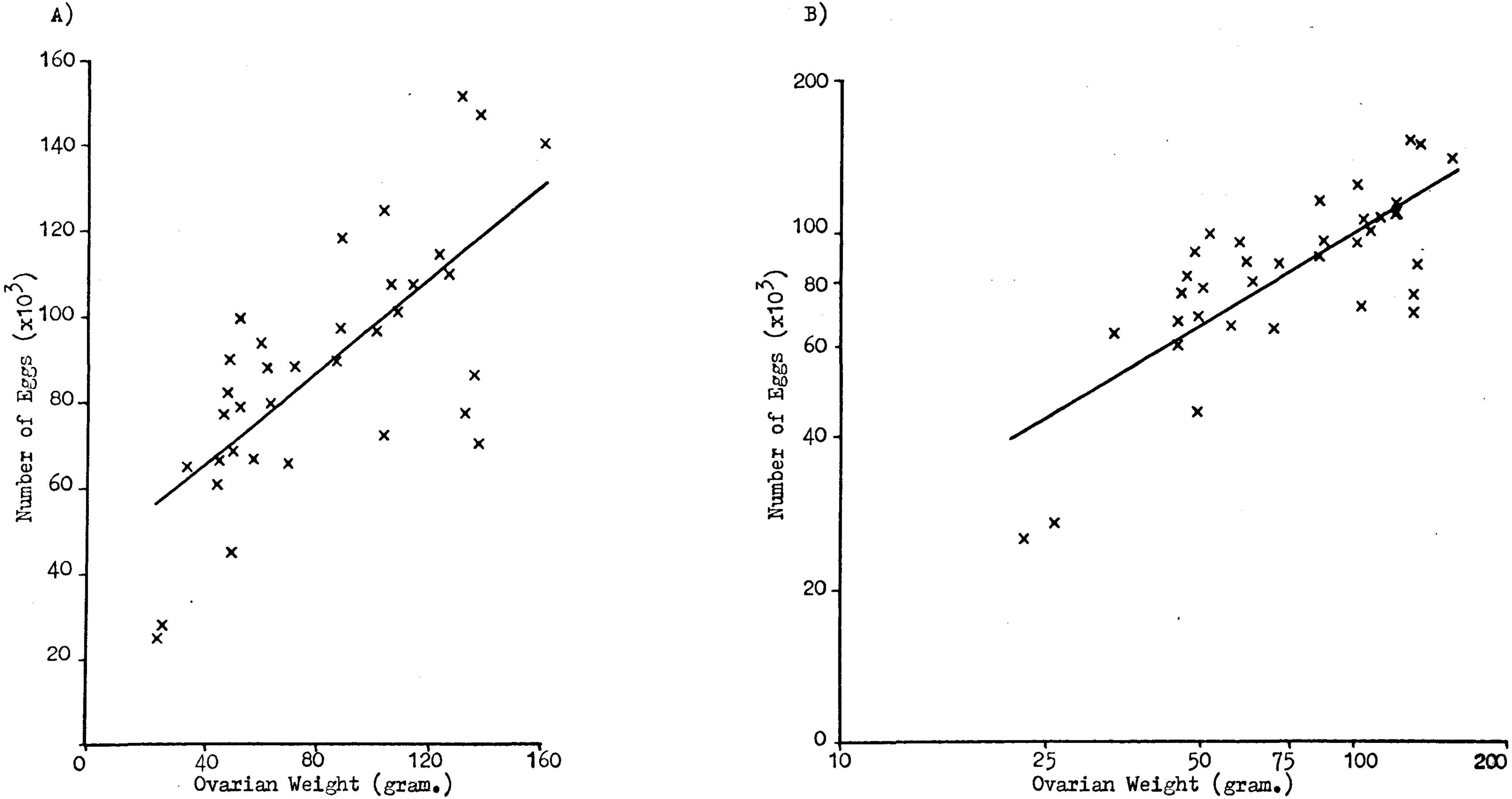
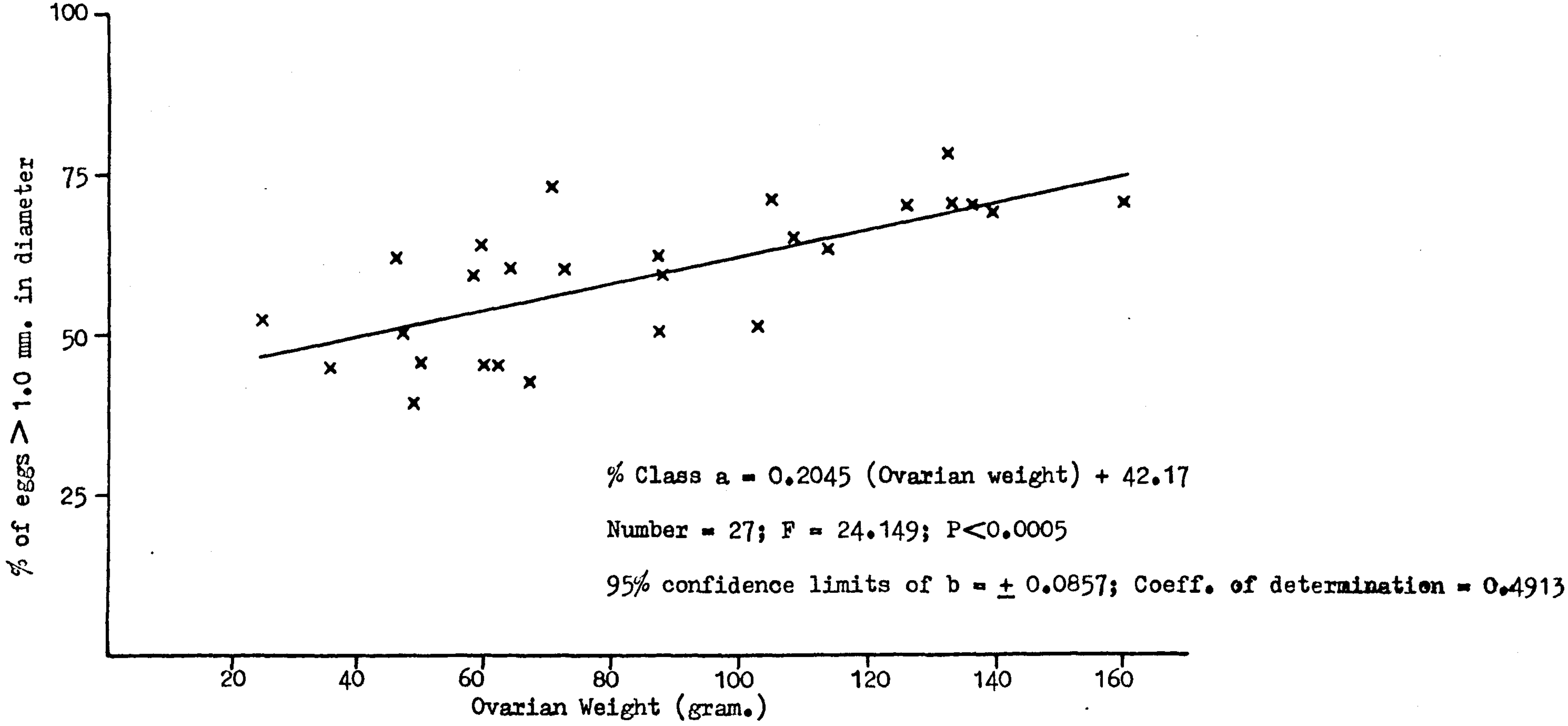


Figure 5.8, An arithmetic plot of the proportion of eggs greater than 1.0 mm. in diameter (class a) from fish sampled 11 May 1979 against ovarian weight.



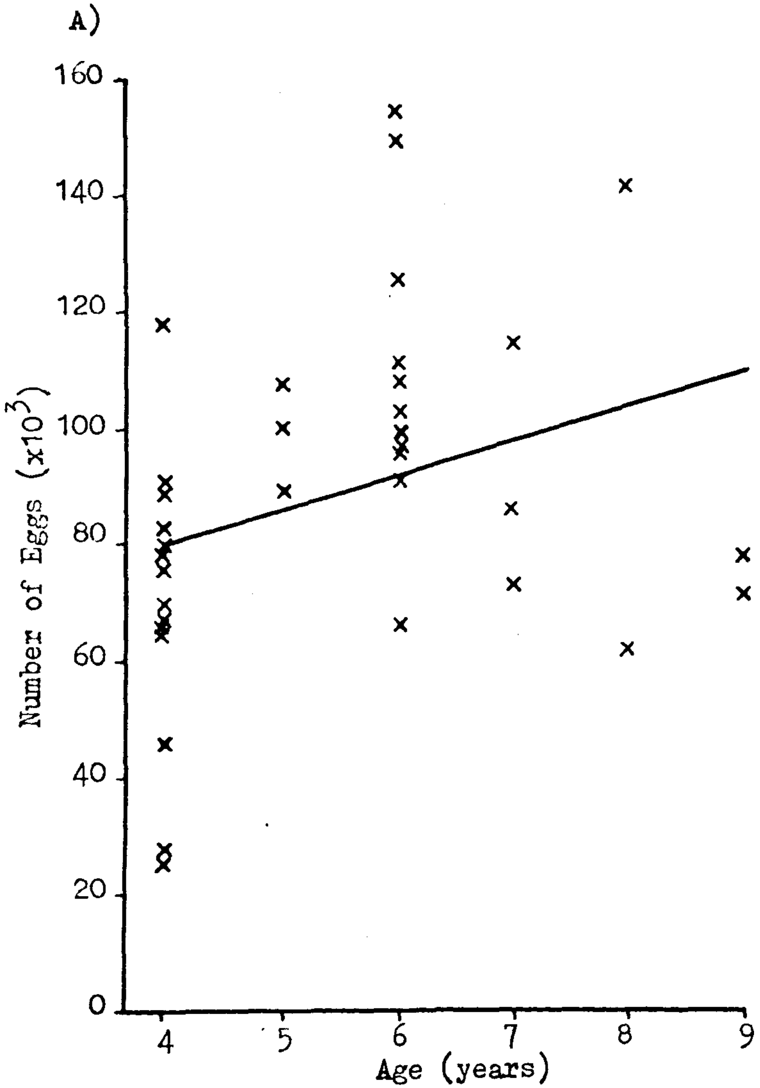
weight of O.nerka three months after hatching was significantly correlated with egg weight. Similarly Kazakov (1981) found that the size of eggs of Salmo salar was positively associated to embryo and alevin size. This was also reported to be the case for Clupea harengus by Blaxter and Hempel (1963). Loesch (1968) examined the fecundity of each ovary from A.aestivalis and found a significant correlation between fecundity and the left ovary but not the right.

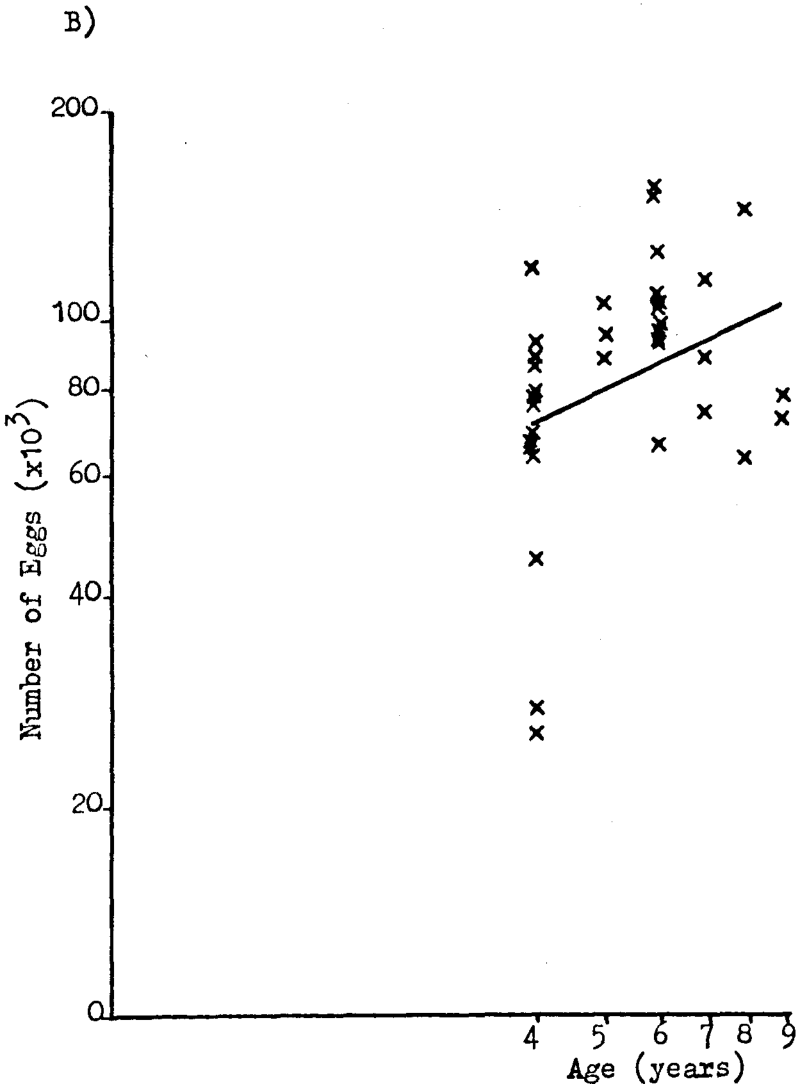
Bagenal (1978) reviews the literature on the relationship between fecundity and age. It seems that some authors, notably Bagenal (1957), Pitt (1964) and Simpson (1951) have shown no effect of age on fecundity, while others, for example, Raitt (1933) and De Silva (1973), have shown an increase in fecundity with age, within a length group and Bridger (1961) within a weight group.

In the case of A.fallax, it appears that there is a significant curvilinear relationship with age, figures 5.7 a + b, but this may only have arisen due to the correlation between age and another of the independent variables, notably size. However, even though they may be closely related, multiple correlation analysis has shown that in some cases, for example, Alburnus alburnus (Linnaeus) (Mackay and Mann, 1969) and Mallotus villosus (Müller) (Winters, 1971) fecundity is more closely related to age. While for Leuciscus leuciscus, Wilkinson and Jones (1977) found ovary weight the most important variable followed by age.

The possible effects of senility on fecundity were mentioned by Woodhead (1979) who found that in a number of studies, the weight of ovaries increased with age at a rate more rapid than that of fecundity, there being no corresponding increase in egg size. Hickling (1940) concluded that with increasing age and presumably with an increase in the number of spawnings, the amount of connective tissue would increase disproportionally as a result of the large seasonal changes in the volume of the ovaries, with a concomitant reduction in the proportion

Figure 5.7 A & B, Arithmetic (A) and Logarithmic relationships between fecundity and age.





of germinal epithelium. However, Woodhead (1979) concludes that this has yet to be verified histologically.

To assess the relative importance of the independent variables a stepwise multiple regression was performed of fecundity against the five independent variables. Multiple regressions were performed on both untransformed and $\log_{10}$ transformed data. Analysis of variance was used to test the significance of the overall regression and two-tailed t-tests for the relevance of each partial regression coefficient relating fecundity to each independent variable. The method used by the computer to construct the multiple regression has been outlined by Nie et al. (1970). The first step involves choosing a single variable which gives the best prediction, the second independent variable which is added to the regression is the one which gives the best prediction in conjunction with the first variable. This recursive process continues until either all the independent variables have been incorporated into the regression equation or the addition of another variable does not significantly contribute to the equation.

The results are shown in table 5.4 for untransformed data and table 5.5 for $\log_{10}$ transformed data. In both cases total weight was the most important of the independent variables followed by age. The addition of a third variable in the case of untransformed data was fork length, while for $\log_{10}$ transformed data the variable was $\log_{10}$ somatic weight, and in both cases the addition of a third variable did not significantly improve the multiple regression.

Thus it seems that accurate estimates of fecundity can be made using total weight and age in the following relationships;

$$\text{Fecundity} = 186.09\ (\text{total weight}) - 12391.92\ (\text{age}) + 36491.94$$

$$\log_{10}\ \text{Fecundity} = 1.4492\ (\log_{10}\ \text{total weight}) - 0.793\ (\log_{10}\ \text{age}) + 1.4512.$$

Table 5.4 Coefficients for the stepwise multiple regression (untransformed date) between fecundity and the independent variables

1. First variable

Independent variable	Slope (b)	95% confidence limits of (b)	t Value	Significance
Total weight	110.15	± 37.82	5.92688	$P < 0.001$

Fecundity = 110.15 (total weight) + 18037.68

Coefficient of Determination = 0.51562

Analysis of variance : F = 37.8187, df 1,33 $P < 0.0005$

2. Second variable

Independent variable	Slope (b)	95% confidence limits of (b)	t Value	Significance
Total weight	186.089	± 48.2769	7.8518	$P < 0.001$
Age	-12391.92	± 6090.2226	-4.1447	$P < 0.001$

Fecundity = 186.09 (total weight) - 12391.92 (Age) + 36491.94

Coefficient of Determination = 0.68641

Analysis of variance : F = 35.0227, df 2,32; $p < 0.0005$

3. Third variable

Independent variable	Slope (b)	95% confidence limits of (b)	t Value	Significance
Total weight	109.515	± 96.9	2.3056	$P < 0.05$
Age	-14414.89	± 6297.888	-4.6692	$P < 0.001$
Fork length (mm)	548.789	± 608.92	1.8386	$P > 0.05$

Fecundity = 109.52 (total weight) - 14414.89 (Age) + 548.79 (Fork length) - 97065.53

Coefficient of Determination = 0.7173

Analysis of variance : F = 26.21205, df 3,31; $P < 0.0005$

Table 5.5 Coefficients for the stepwise multiple regression ($\log_{10}$ transferred data) between fecundity and the independent variables

1. First variable

Independent variable	Slope (b)	95% confidence limits of (b)	t Value	Significance
Total weight	0.9559	± 0.2656	7.3238	$P < 0.001$

$\log_{10}$ Fecundity = 0.9559 ($\log_{10}$ total weight) + 2.2560

Coefficient of Determination = 0.6191

Analysis of variance : F = 53.6304, df 1,33; $P < 0.0005$

2. Second variable

Independent variable	Slope (b)	95% confidence limits of (b)	t Value	Significance
Total weight	1.4492	± 0.3294	8.9628	$P < 0.001$
Age	-0.793	± 0.397	-4.0688	$P < 0.001$

$\log_{10}$ Fecundity = 1.4492 ($\log_{10}$ total weight) - 0.793 ($\log_{10}$ Age)
+ 1.4512

Coefficient of Determination = 0.7511

Analysis of variance : F = 48.2942, df 2,32; $P < 0.0005$

3. Third variable

Independent variable	Slope (b)	95% confidence limits of (b)	t Value	Significance
Total weight	3.585	± 2.7377	2.6714	$P < 0.02$
Age	-0.8529	± 0.3956	-4.3987	$P < 0.001$
Somatic weight	-2.2428	± 2.8548	-1.6027	$P > 0.10$

$\log_{10}$ Fecundity = 3.585 ($\log_{10}$ total weight) - 0.853 ($\log_{10}$ Age)
- 2.243 ($\log_{10}$ Somatic weight) + 1.6633

Coefficient of Determination = 0.7702

Analysis of variance : F = 34.6305, df 3,31; $P < 0.0005$

B. Sexual Maturity

The age at which an organism becomes sexually mature, may be regarded as an adaption for optimizing their reproductive potential, Cole (1954). Bell (1976) mentions that the age at first spawning will depend on the ratio of juvenile to adult survival and on the rate fecundity increases with age, to these Bell (1980) added another factor, the energetic cost of reproduction. Bell (1980) refered to this as the potential fecundity cost and represents the possibility that the fecundity of an individual which has previously reproduced, may be lower at a given age than that of an individual of the same age which has not reproduced. Differences in the age at maturity have been shown for various populations of A.sapidissima by Leggett (1969), Carscadden and Leggett (1975a), Leggett and Carscadden (1978) and by Shoubridge and Leggett (1978) and for Salmo salar by Schaffer and Elson (1975). Alm (1959) and Gardner (1976) concluded from their studies that the age at maturity may be considered to be under the control of both hereditary and environmental factors.

1. Materials and Methods

The fish were collected using the methods described in chapter two and measured to the nearest millimetre. The fish were aged, spawning histories determined and growth pattern obtained through back calculation with the aid of the methods described in chapter three. In the literature, two methods have been used for determining the age at first spawning for alosids and thus both methods have been used in this study to allow comparisons to be made. The first method which has been used by Carscadden and Leggett (1975a), Leggett (1969), Leggett and Carscadden (1978) and by Shoubridge and Leggett (1978) involves the calculation of the mean age at maturity. This method gives consistently higher estimates of age at maturity than the second method which involves calculation of the point when 50% of the population have matured, using cumulative frequency and has been used by Messieh (1977).

2. Onset of Sexual Maturity

In the Severn and Wye river systems it was observed (chapter four) that male A.fallax mature mainly at age three or four and females at four and five years old. The mean age at maturity and the point at which 50% of the population of Alosa fallax have matured in the River Severn, for each sample year, are given in table 5.6 for females and table 5.7 for males. The column entitled 'combined material' represents the mean percentage for each of the years, i.e. all the years were equally weighted. Values for females and males caught during 1980 from the River Wye are given in tables 5.8 a + b. Two main methods were used to obtain the samples from the Wye, however, these did not produce significantly different results, for either sex, and the samples were combined.

For four Atlantic coast populations of A.sapidissima, Leggett (1969) found that the mean age at maturity for males ranged between 3.8 and 4.3 years and for females between 4.3 and 4.8 years; similar findings were reported by Carscadden and Leggett (1975a). Shoubridge and Leggett (1978) found that populations from the Pacific coast matured earlier at between 3.3 and 3.8 years for males and between 4.0 and 4.5 years for females; similar findings were reported by Mullen (1973) for some Oregon rivers. Mayo (1974), (cited by Libey, 1976), found that the mean age of maturity for anadromous A.pseudoharengus from the Parker River (Mass.) was 3.71 years for males and 4.01 years for females. (The 50% maturity point was 3.16 years for males and

Table 5.6 Age at first spawning (River Severn)

Females

Age	1979		1980		1981		Combined material
	N	%	N	%	N	%	
3	1	1.18	3	1.26	1	0.33	0.92
4	52	61.18	98	41.18	88	28.95	43.77
5	28	32.94	128	53.78	198	65.13	50.62
6	4	4.70	8	3.36	17	5.59	4.55
7	-	-	1	0.42	-		0.14
Total	85	100 %	238	100 %	304	100%	100 %
Mean	4.412		4.61		4.76		4.59
± 95% Conf. limits	± 0.1302		± 0.0769		± 0.062		
50% Maturity Point	3.8		4.15		4.3		4.1

Single factor Analysis of variance $F = 13.99724$

$df = 2,624$

$P < 0.0005$

Newman-Keuls multiple range test:

1979 1980 1981

Table 5.7 Age at first spawning (River Severn)

Males

Age	1979		1980		1981		Combined material
	N	%	N	%	N	%	
2	-	-	1	1.41	2	1.67	1.03
3	9	29.03	21	29.58	32	26.67	28.43
4	18	58.06	45	63.38	63	52.5	57.98
5	4	12.91	4	5.63	23	19.16	12.56
Total	31	100 %	71	100 %	120	100 %	100 %
Mean	3.84		3.73		3.89		3.82
± 95% Conf. limits	± 0.2327		± 0.1383		± 0.13		
50% Maturity Point	3.35		3.3		3.42		3.35

Single factor analysis of variance $F = 1.26941$

df 2,219

$P > 0.25$

Table 5.8 Age at first spawning (River Wye) 1980

(a) Females

Age at First Spawning	Source of Material				Combined Material	
	Trammel net		Rod and line			
	N	%	N	%	N	%
4	45	49.45	24	51.06	69	50.0
5	43	47.25	23	48.94	66	47.83
6	3	3.5			3	2.17
Total	91	100 %	47	100 %	138	100 %
Mean	4.54		4.49		4.52	
± 95% Confidence limits	± 0.1175		± 0.1484		± 0.0914	
Student t-test	t = 0.5107; df = 136; P> 0.50					
50% maturity Point	4.03		3.95		4.0	

(b) Males

Age at First Spawning	Source of Material				Combined Material	
	Trammel net		Rod and line			
	N	%	N	%	N	%
3	2	18.18	11	21.15	13	20.63
4	8	72.73	40	76.92	48	76.19
5	1	9.09	1	1.93	2	3.18
Total	11	100 %	52	100 %	63	100 %
Mean	3.91		3.81		3.83	
± 95% Confidence limits	± 0.3624		± 0.1238		± 0.1156	
Student t-test	t = 1.41541; df = 61; P> 0.10					
50% maturity Point	3.45		3.37		3.40	

3.50 years for females.) Messieh (1977) found that the 50% maturity point for A.pseudoharengus from St. Johns River (New Brunswick) was much higher being 4.4 years for males and 4.8 years for females; and for female A.aestivalis was 3.8 years. From data produced by Scherer (1972) the mean age at maturity for male A.aestivalis from the Connecticut River was 3.45 years, and 4.04 years in females (the 50% maturity point was 2.85 years and 3.52 years for males and females respectively). For A.aestivalis from the Cape Fear River system (N. Carolina) Fischer (1980) found that the mean age at maturity for the male was 4.24 years and for the females was 4.53 years, (the age at which 50% of the population had matured occured at 3.71 years for the males and 3.83 years for the females).

Leggett (1969) found intra-population variation in the mean age of maturity for A.sapidissima to be 0.2 years in 70% of the cases, but may be as high as 0.5 years (for females in the River York, Virginia). Generally the annual variation was of a lesser magnitude amongst males. This also seems to be the case for A.fallax on the Severn. Analysis of variance shows that there is a significant difference in the mean age at maturity for females between 1979 and 1981 (inclusive) and the resulting multiple range test indicated that none of the sample years have homogenous means (table 5.6). A different situation was encountered for the males, there being no significant difference in their means (table 5.7). As already mentioned, males mature approximately one year earlier than females, Mann - Whitney and t-test analysis comparing the mean age at maturity of each sex, for each of the sample years, indicated highly significant differences (table 5.9 a + b). During 1980, samples were also obtained from the Wye and these did not show any significant difference in the mean age at maturity from those in the Severn; females $t = 1.4535$ ($df = 374$, $p > 0.10$); males $t = 1.091$ ($df = 132$,

Table 5.9 Comparison of the mean age at maturity between female and male , A.fallax, caught on the Rivers Severn (at Lydney) and Wye (all sites) between 1979 and 1981

(a) Student t-test

Year	t-value	Degrees of freedom	Significance
R. Severn 1979	4.4347	114	$P < 0.001$
R. Severn 1980	11.4265	307	$P < 0.001$
R. Wye 1980	8.7509	199	$P < 0.001$

(b) Mann-Whitney test

Year	U-value	Z statistic	Degrees of freedom	Significance
R. Severn 1981	29305	11.4912	304,120	$P < 0.05$

$p > 0.20$), (table 5.8 a + b). (In nearly all the cases no significant differences were found between the variances, allowing analysis of variance and student t-test to be performed. However, when the variances of the females and males, caught during 1981, were compared, there was found to be a significant difference ($F = 1.7148$; df = 119,303; $P < 0.0005$). In this case the Mann-Whitney test was performed to test for a significant difference between their means.)

The intra-population differences evident amongst the females seems to have resulted from a shift in the proportion coming to maturity, from age four to age five. This is especially evident for the 1976 year-class, and possibly the 1977 year-class as well. If mortality between years is assumed to be constant, then a comparison between the spawning histories of the various year-classes may be made. The numbers of females from the 1973, 1974 and 1975 year-classes, aged six and maturing at different ages are shown in table 5.10 chi-squared analysis between these six year olds (those maturing at three and six years old have been excluded due to the low number of observations, Zar, 1974) shows that there is no significant difference in the proportions of females coming to maturity at age four and five for these year-classes (Chi-squared = 3.35, df = 2, $p > 0.05$). However, analysis of the five year olds table 5.11 (1979 data, corresponding to females of the 1974 year-class have been excluded due to low numbers) shows that there is a highly significant proportion of the 1976 year-class maturing at age five rather than at age four, (Chi-squared = 25.25, df = 1, $p < 0.001$), when compared with the 1975 and presumably 1974 and 1973 year-classes as well.

It appears that the upward trend in the mean age of maturity evident amongst the females has resulted from the comparatively later maturation of the 1976 year-class. Ricker (1972) in his review of the factors affecting various characteristics of certain salmonid

Table 5.10 Number of female <u>A.fallax</u> from the 1973, 1974 and 1975 year-classes maturing at age four and five. (Data taken from fish caught at Lydney between 1979 and 1981)

Year-Class	Age at First Spawning	
	4	5
1973	19	12
1974	14	8
1975	60	67

Table 5.11 Number of female <u>A.fallax</u> from the 1975 and 1976 year-classes maturing at age four and five. (Data taken from fish caught at Lydney, River Severn during 1980 and 1981)

Year-Class	Age at First Spawning	
	4	5
1975	59	93
1976	18	122

populations found that age at maturity was affected by hereditable and environmental factors. In Salmo salar both Elson (1973) and Piggins (1974) found that a genetic component exists in the determination of sea age, similar conclusions were reported by Naevdal et al. (1978 a + b), and for S.gairdneri by Naevdal et al. (1981). However, Piggins (1974) mentioned that the environment may influence the hereditable factor and in the case of S.salar suggested artificial rearing was the cause.

3. Relationship Between the Onset of Sexual Maturity and Growth Rate and/or Size

Alm (1959) observed, from a vast number of experiments, that within a particular age group encountering the same environmental conditions, growth rate and the reaching of a certain size were the most decisive factors determining the onset of sexual maturity. Alm (1959) concluded that a population of one species which from the beginning exhibited a good growth rate would mature earlier when compared with a population where the growth rate was slower. Similar observations have been made by Parker and Larkin (1959) for anadromous Salmo gairdneri, by Bagenal (1969) for Salmo trutta, by Kato (1975) and by Naevdal et al. (1979a) for S.gairdneri. In the latter case the difference in growth rate between those which were going to mature and those which were not could be traced back a year before maturation. For Salvelinus fontinalis (Mitchill) Wydoski and Cooper (1966) found that within a particular age group the percentage maturity for both males and females increased with an increase in total length.

For anadromous populations of *Salmo salar* similar observations to those already described have been found by Jones (1959), by Naevdal et al. (1979b) by Shearer (1966) where maturity was regulated by rate of parr growth. Shearer (1973) found that in general, the largest smolts from a particular brood year and with identical parr lives, matured first. For *Oncorhynchus nerka*, Foerster (1968) observed that maturity could be correlated with growth during the first sea year, but not with growth in fresh water, so that those returning as grilse exhibited the best growth rate. Similarly Bilton (1970) found that juvenile growth both in freshwater and at sea was inversely related to age at maturity, for *O.nerka*.

However, the converse situation for *S.salar* exists where a fast growth rate indicates late maturation. This has been shown to be the case by Ritter (1972) for hatchery reared smolts. Schaffer and Elson (1975) found that high marine growth rates in fish which did not spawn as grilse, were correlated with a high mean age at first spawning. The situation where neither case seems to exist, there being no apparent relationship between growth and/or size and maturity, has been reported by Naevdal (1978a).

The effect of size alone has been shown by McPhail (1977) in determining the onset of sexual maturity for female *Gastrosteus aculeatus* (Linnaeus). A genetic component was indicated from rearing ten populations under similar laboratory conditions and the high correlation between the size at which the laboratory populations matured, with the size at maturity found in the wild, suggested an inherent component for the minimum size at maturity.

To examine whether any relationship existed between growth rate and/or size and the onset of sexual maturity, the back calculated lengths of fish from the same year-class, but with different spawning histories were compared. The results are shown in table 5.12 and illustrated in figures 5.9, 5.10 a + b for females of the 1975 year-class and males from the 1975 and 1976 year-classes (caught during 1981 at Lydney). It appears that in both sexes, growth rate and/or size, has a marked effect on the timing of maturity, with those members of a group having the fastest growth rate, maturing earlier. Thus a possible reason as to why the majority of the 1976 year-class matured at five, may be related to their slower growth rate. Figure 5.9 also shows the growth curve for the five year old virgin spawners from the 1976 year-class, and assuming that maturity is related to size, then the majority had not reached the critical size which must be obtained before maturation commences. For A.fallax the critical size for the males appears to be in the region of 270mm. (fork length), those members of the 1975 and 1976 year-classes maturing at age three had mean lengths of 269.06 mm. and 271.41 mm., respectively. For the females the critical size seems to be around 330 mm. (fork length). This relation to growth rate and/or body size may be correlated with the energy reserves needed for successful reproduction.

Glebe and Leggett (1981b) showed that the mean size at maturation for both male and female A.sapidissima increases with latitude from south to north, and believed that this increase is correlated with the increased current velocities in the northern rivers during the upstream migration period. Similar observations were shown by Schaffer and Elson (1975) who found a significant positive correlation between river length (as a measure of river harshness and thus an indication of the energetic cost of the upstream migration) with age and size at first spawning for S.salar. The seasonal pattern of entry of S.salar (Jones, 1959) is further indicative of relating size to the difficulty of the upstream migration. In general fish which migrate in the spring and autumn are the largest

Table 5.12 Mean (± 95% confidence limits) back-calculated length, at age, for female and male A.fallax from the 1975 and 1976 year-classes

Females 1975 Year-Class

Total Age	Number of spawnings	Age at first spawning	Mean fork length at annulus ± 95% confidence limits (mm)						Number
			1	2	3	4th Annulus/ Spawning mark	Spawning mark	Scales edge	
6	1	5	73.21 ± 3.48	166.93 ± 5.67	243.76 ± 6.07	305.92 ± 5.39	338.35 ± 4.14	356.23 ± 3.59	60
6	2	4	83.5 ± 3.6	194.76 ± 5.56	274.78 ± 6.67	328.77 ± 4.19	346.83 ± 3.54	364.83 ± 3.08	54

Females 1976 Year-Class

5	0	5	78.89 ± 2.22	150.37 ± 4.52	232.7 ± 5.11	298.47 ± 4.13		339.75 ± 3.14	81

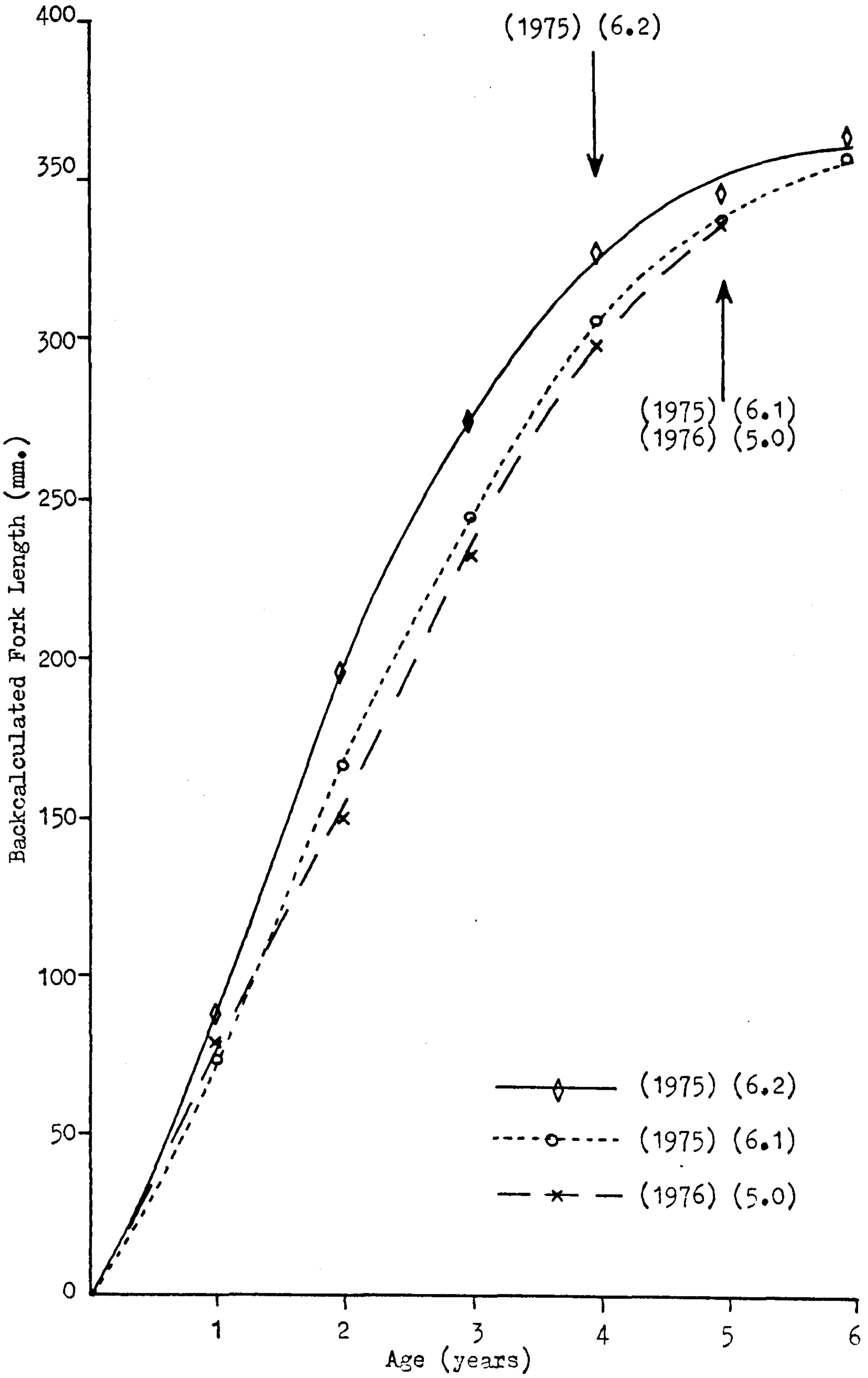
Males 1975 Year-Class

Total Age	Number of spawnings	Age at first spawning	Mean fork length at annulus ± 95% confidence limits (mm)						Number
			1	2	3rd Annulus/ spawning mark	4th Annulus/ spawning mark	Spawning mark	Scales edge	
6	2	4	69.45 ± 3.53	161.47 ± 8.88	239.72 ± 9.44	287.63 ± 7.41	306.59 ± 6.72	324.24 ± 7.18	25
6	3	3	80.45 ± 7.32	194.64 ± 15.42	269.06 ± 10.45	300.02 ± 9.72	315.02 ± 8.69	330.71 ± 7.37	17

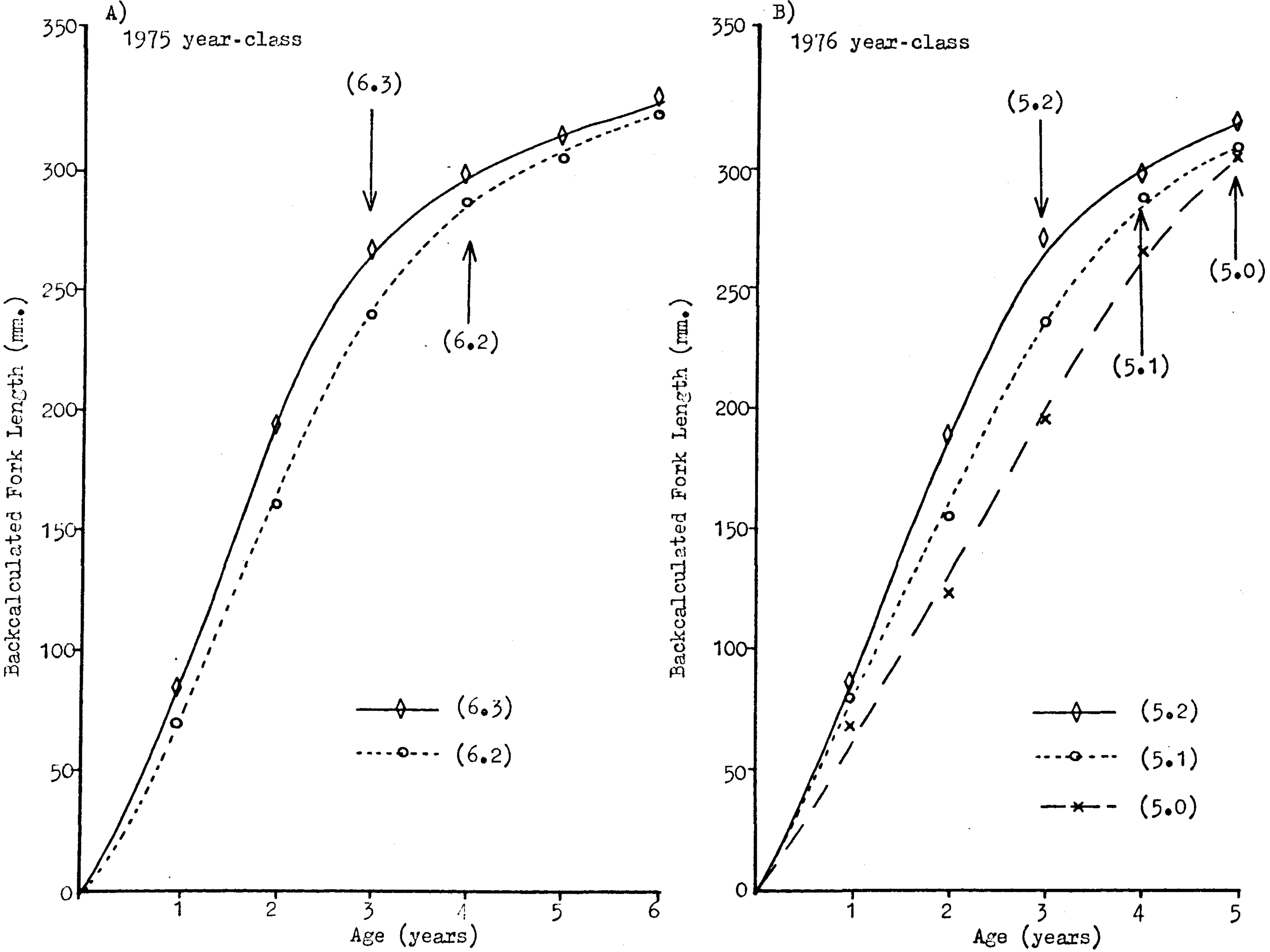
Males 1976 Year-Class

5	0	5	66.95 ± 3.73	122.99 ± 6.7	196.53 ± 8.43	265.45 ± 8.55		305.44 ± 7.26	18
5	1	4	80.63 ± 5.13	155.07 ± 9.41	236.91 ± 11.21	289.90 ± 8.58		309.67 ± 8.22	27
5	2	3	85.77 ± 8.84	189.81 ± 18.13	271.41 ± 13.42	299.95 ± 11.59		320.64 ± 11.6	11

Figure 5.9, Growth curve of females from the 1975 and 1976 year-classes (mean ± 95% confidence limits), arrows indicate onset of maturity for the (year - class) (age. number of previous spawnings).



igure 5.10, Growth curve of males from the 1975 and 1976 year-classes (mean ± 95% confidence limits), arrows indicate onset of of maturity (age. number of previous spawnings).



and at the same time river run off and river levels are greatest. On the other hand grilse migrate during the summer when current velocities are lowest.

This difference in growth rate between members of the same year class may depend on genetic and/or environmental factors. Weatherly (1976) mentions three factors that indicate genetic control of growth, (1) that growth rate of a species has a limit and therefore must be an inherited condition, (2) many species show intersexual differences in growth rate, and (3) some interspecific hybrids grow more rapidly than either parent under the same environmental conditions. Kincaid et al. (1977) showed a significant improvement in growth rate of S.gairdneri over three generations. Reintz et al. (1978) found marked differences in growth rate between four strains of hatchery reared S.gairdneri. Similar observations were shown by Gjedrem (1976) who demonstrated significant geographical differences in growth rate of S.salar.

Purdom (1980) found no differences in basic metabolic rate of S.gairdneri from two separate strains. Brown (1946) suggested that the difference in size in experiments with S.trutta depended on the development of a social hierarchy, similar findings were reported by Moav and Wohlforth (1973) for C.carpio. From laboratory experiments on Pleuronectes platessa x Platichthys flesus hybrids Purdom (1974) concluded that in natural populations the greater part of growth rate variation arose from behavioural interactions (aggression) which are essentially environmentally induced (crowding).

Due to the large dispersal of discrete spawning and nursery areas of A.fallax (see chapters four and six), some areas may produce more favourable conditions for growth than others. Then, at least in the early stages of life, a better growth rate may result. It has been shown by some authors that the size reached during the first year of life has a marked effect on size at subsequent ages, (Haskell and Griffiths, 1956; Hobbs, 1953; Parker and Larkin, 1959; Van Oosten, 1938).

The onset of sexual maturity is generally regarded as having an inhibitory effect on growth rate (Purdom, 1980), in that energy obtained, instead of being utilized in the production of soma, is partitioned off into the production of gonadal material, as well as physiologically adapting the body for reproduction. For *Merlangius merlangus* (Linnaeus) Hislop (1975) has calculated the theoretical increase in somatic weight had the fish not matured and spawned, which amounted to 0.03% of body weight per day in the smallest fish rising to 0.40% for the largest. However, in a study of the growth of female triploid (sterile) *Pleuronectes platessa* x *Platichthys flesus* hybrids and normal diploid *P.platessa* x *P.flesus* hybrids, Lincoln (1976) observed a cessation of growth in length in the diploids on approaching spawning, while the triploids continued to grow. However, after spawning the now smaller diploids put on a spurt of growth and caught up the triploid sibs.

In the case of *A.fallax* additional energy may also need to be expended in swimming to the spawning grounds. The situation is further complicated by the fact that the fish do not feed actively during the spawning period (see chapter seven), and this may last for approximately six to eight weeks. The effect of maturity on growth is illustrated by figures 5.9 and 5.10 a + b. It does seem that those members of a group that mature first slow down their growth rate following maturation in relative terms compared with the slower growing members. Thus the latter are able to catch up, as their growth rate has not been so severly affected. So that by the end of their life span there exists a smaller difference in their sizes than might be expected from examination of their growth curves at an earlier stage.

C. Repeat Spawning

The proportion of repeat spawners in a population has been shown to be closely associated with a particular river system (Leggett and Carscadden, 1978; Shoubridge and Leggett, 1978; Walburg and Nichols, 1967), and more specifically within a particular river system (Carscadden and Leggett, 1975a) for *A.sapidissima*. A number of authors have found that *A.fallax* is capable of spawning more than once, notably Roule (1922) on the Seine, Hass (1965) on the Elbe, and by Bracken and Kennedy (1967) for those population spawning in the rivers around the south coast of Ireland. The presence of repeat spawners in the population was evident in the material sent from Holland (see appendix two). Similar observations have been found for the landlocked population *A.fallax lacustris* (Berg and Grimaldi, 1966).

Other anadromous members of the genus are known to have a proportion of repeat spawners present amongst the spawning migrants. This has been shown to be the case for *A.caspia caspia* (Makhmudbekov, 1947; Ostroumov, 1948 and 1949; cited by Svetovidov, 1963; Zamakhaev, 1940), *A.kessleri kessleri* (Svetovidov, 1963), *A.kessleri volgensis* (Svetovidov, 1963; Zamakhaev, 1940), *A.mediocris* (Pate, 1972), *A.aestivalis* (Fischer, 1980; Joseph and Davis, 1965; Scherer, 1972) *A.pseudoharengus* (Joseph and Davis, 1965), as well both forms of *A.kessleri pontica* (Belyy, 1970; Svetovodov, 1963). Of the non-anadromous marine species *Alosa brashnikovi kisselevitshi* (Bulgahov) (Zamakhaev, 1949; cited by Svetovidov, 1963) has the ability to spawn more than once.

Once maturity has been reached, spawning takes place annually. However, in the case of the smaller form of A.kessleri pontica this may not necessarily be the case (Belyy, 1970; Svetovidov, 1963).

1. Materials and Methods

Fish were collected using the methods described in chapter two. Scales were used to determine the number of previous spawnings (see chapter three).

2. Proportion of Repeat Spawners

In the River Severn the proportions of repeat spawning A.fallax are shown in table 5.13 a + b for both females and males in each of the years sampled. The combined material represents the mean percentage occurence of each group. The females show no significant difference in the proportion of repeat spawners (chi-squared = 11.65, df = 6, $p > 0.05$), fish which had spawned three or more times were pooled together due to low numbers, with a long term mean of 54.0%. However, for the males there exists a significant difference in the proportions of repeat spawners, between the sample years (chi-squared = 16.032, df = 6, $p < 0.025$).

If each of the sample years are compared, analysis shows that there is no significant difference in the proportion of repeat to virgin spawning males for the years 1979 and 1980 (chi-squared = 1.9169, df = 3, $p > 0.50$). However, the proportions evident in 1981 were significantly different to those in 1979 (chi-squared = 12.0902, df = 3, $p < 0.01$) and in 1980 (chi-squared = 8.4956, df = 3, $p < 0.05$).

This appears to have resulted from a large number of older, repeat spawning fish still in the population, which in turn seems to have arisen from 'strong' 1975 and 1976 year-classes. Relatively few younger fish appeared in the population in 1981 and this may

Table 5.13 Spawning history - River Severn

(a) Females

Number of Previous Spawnings	1979		1980		1981		Combined 1979 - 1981 mean Percentage
	N	%	N	%	N	%	
0	37	43.53	117	49.16	138	45.39	46.03
1	15	17.65	69	28.99	86	28.29	24.98
2	25	29.41	42	17.65	66	21.71	22.92
3	6	7.06	9	3.78	10	3.29	4.71
4	2	2.35	1	0.42	4	1.32	1.36
Total	85	100 %	238	100 %	304	100 %	100 %
Percentage Repeat Spawners	56.47		50.84		54.61		53.97

(b) Males

Number of Previous Spawnings	1979		1980		1981		Combined 1979 - 1981 mean Percentage
	N	%	N	%	N	%	
0	15	48.38	26	36.62	24	19.99	35.0
1	8	25.81	17	23.94	32	26.67	25.47
2	6	19.35	21	29.58	38	31.67	26.87
3	1	3.23	6	8.45	19	15.83	9.17
4	1	3.23	1	1.41	5	4.17	2.94
5	-		-		2	1.67	0.55
Total	31	100 %	71	100 %	120	100 %	100 %
Percentage Repeat Spawners	51.62		63.38		80.10		65

be due to a 'poor' 1977 year-class. It may be though that a large proportion of the 1977 year-class have yet to mature, not having attained the critical size, which may control the timing of maturity, and may migrate next year (1982) as five year olds. If the situation found for males in 1981 is due to a 'poor' 1977 year-class, the same should arise for females in 1982 as they mature approximately one year later.

Large intra-population variation in the proportion of repeat spawners has also been shown by Leggett (1969) for A.sapidissima in the Connecticut and York Rivers and was considered to have resulted from a 'dominant' year-class passing through the population. Part of the variation may also be explained in terms of energetic cost. Shoubridge and Leggett (1978) have shown that the proportion of repeat spawners in the Connecticut River is strongly negatively correlated with average water temperatures during the migration period, one year earlier. The indication being that increased water temperature, probably acting through increased metabolism, causes an increase in spawning mortality. Glebe and Leggett (1981a) have shown that late migrants consume a larger proportion of their metabolic reserves than do early or peak migrants and this may have resulted in the low number of tag returns from late migrants (Leggett, 1969). The mean temperature at intervals during the migration period, are shown in table 5.14. It would seem that if temperature was having a significant effect on the percentage of repeat spawners, the high temperatures prevalent during the 1980 migration period would reduce the number of repeat spawning fish in 1981 when compared with those in 1979 and 1980. However, no significant difference existed among the females and the males showed an increase in their proportion. It would therefore appear that in the years of study, any variation in the percentage of repeat spawners can be mainly attributed to fluctuation in year-class strength and/or possibly due to reduced growth rate rather than temperature during the spawning migration.

Table 5.14 Mean Temperature (± 95% confidence limits) at Saxons Lode on the River Severn at bimonthly intervals during the upstream migration period for the years 1979 to 1981.

Date	Mean Temperature °C (± 95% Confidence Limits)		
	1978	1979	1980
15 April - 31 April	8.75 ± 0.56	9.82 ± 0.21	12.14 ± 0.33
1 May - 15 May	8.81 ± 0.41	10.28 ± 1.32	13.16 ± 1.22
16 May - 31 May	15.09 ± 1.65	12.58 ± 0.80	16.91 ± 0.65
1 June - 15 June	18.07 ± 1.01	14.47 ± 0.87	18.23 ± 0.80
16 June - 30 June	16.21 ± 0.53	17.38 ± 0.80	16.35 ± 0.14

The proportion of repeat spawning males was generally higher than for females, significant differences between their spawning histories existed in 1980 (chi-squared = 9.3432; df = 3; $p<0.05$) and in 1981 (chi-squared = 42.3678; df = 3; $p<0.001$), though this was not the case in 1979 (chi-squared = 1.9644; df = 3; $p>0.50$). Similar findings were obtained for A.sapidissima by Leggett (1969) and Carscadden and Leggett (1975a). Part of the differences may be due to the selectivity of the Putcher rank, the smaller males not being quantitatively sampled so the results would tend to be biased towards the older, larger and more probably, repeat spawning fish. If this is the case then one might expect that fish caught using rod and line, which are generally smaller than ones caught in the putcher rank, to show a lower percentage of repeat spawners. The mean fork length of males caught at Powic Weir in 1979 was 290.3 mm. (95% confidence limits = ± 9.475 mm.) which was not significantly smaller than those at Lydney 302.0 mm. (95% confidence limits = ± 11.608 mm.) ($t = 1.5576$, df = 55, $p > 0.05$). However, the females at Powic Weir were significantly smaller 335.5 mm. (95% confidence limits = ± 7.574 mm) compared with 352.8 mm. (95% confidence limits = ± 5.979 mm.) at Lydney ($t = 3.2949$, df = 119, $p < 0.002$). No significant differences were found between variances for both males and females. The percentage of repeat spawners is shown in table 5.15.

Table 5.15 Spawning history of male and female <u>A.fallax</u> caught at Powic Weir (River Teme) 1979.

Number of Previous Spawnings	Males		Females	
	N	%	N	%
0	7	26.92	13	36.11
1	10	38.46	13	36.11
2	8	30.77	10	27.78
3	1	3.85		
Total	26	100	36	100
% Repeat	68.18		64.52	

There was a greater percentage of repeat spawners at Powic Weir (table 5.15) than were found at Lydney (table 5.13 a + b). Those fish which had spawned two or more times were pooled together because of low numbers and analysis shows that there was no significant difference in the proportions of fish of varying reproductive histories entering the river system at Lydney in 1979 (table 5.13 a + b) and at Powic Weir (table 5.15). For the females chi-squared = 4.9372 (df = 2, $p > 0.05$) and for the males chi-squared = 2.7813 (df = 2, $p > 0.10$). Thus it appears that the differences between the spawning histories of males and females obtained at Lydney may not be a result of the selectivity of the putcher rank.

At Powic Weir there existed no significant difference in the spawning histories of male and female *A.fallax* (chi-squared = 0.6479, df = 2, $p > 0.50$), similar to the situation observed at Lydney in 1979.

Though the difference in the spawning histories of *A.fallax* caught at Powic Weir when compared to the spawning stock sampled entering the river, at Lydney, was not statistically significant the difference may still be of biological importance. For a significant difference may exist if the spawning histories of the population at Powic had been compared with those from another spawning population on the river system. It has been shown by Carscadden and Leggett (1975a) and mentioned by Leggett (1977) that populations of *A.sapidissima* spawning in different areas of a river system differ in a number of their reproductive characteristics of which the percentage of repeat spawners is one. Thus there exists the possibility that *A.fallax* may be homing to specific areas within a river system.

It appears that *A.fallax* has selected for iteroparity. According to Charnov and Schaffer (1973) the tactic selected for will depend on age specific mortality and that iteroparity will be favoured when adult survival rates are high relative to juvenile rates. Stearns (1976) produced some evidence to support the theory of Charnov and Schaffer but concluded, that due to the large amount of scatter, other forces than mortality have influenced the data. However, Roff (1981) found no correlation between brood success and reproductive lifespan in the

Pleuronectidae nor in the Clupeidae when additional data was added to that of Murphys' (1968). Roff (1981) assumed that reproductive lifespan is a correlate of another life history parameter such as, age at maturity, fecundity and/or pre-reproductive survival rate. If the intrinsic rate of increase is equal to or greater than zero, any change in the reproductive lifespan which alters the intrinsic rate of increase to below zero will be associated with a change in at least one of the other parameters, so that the intrinsic rate of increase becomes at least equal to zero. For the Pleuronectidae, reproductive lifespan was found to be closely correlated with age at maturity, (Roff, 1981). For A.sapidissima Leggett and Carscadden (1978) found no correlation between reproductive lifespan and age at maturity but did find one between repeat spawning and fecundity.

Therefore the adaptive significance of iteroparity in isolation would appear obscure, however, when other life history traits such as age at maturity and fecundity are taken into account, certain patterns emerge. Information on a species reproductive characteristics from different areas has been produced, by Leggett and Carscadden (1978), Shoubridge and Leggett (1978) and by Walburg and Nichols (1967) for A.sapidissima along the Atlantic and Pacific coasts. Similarly for Cottus gobio (Linnaeus) information has been obtained from Crisp et al. (1975), Fox (1978a) and Mann (1971 & 1979). For both species, those populations which may be considered to be inhabiting the more 'unfavourable' environment, (in the case of A.sapidissima this applies to the northern rivers of the Atlantic coast, and for C.gobio the upland rivers as opposed to the lowland rivers); show 1) a longer reproductive lifespan, 2) lower actual fecundity, 3) older age at maturity, and in the case of C.gobio a large fluctuation in reproductive success. It has already been mentioned that the age at maturity may be influenced by growth rate or the attainment of a certain size. However, it appears that there is little difference in the growth rate of C.gobio from the two regions. In the case of A.sapidissima age and/or size at first spawning may depend on the energetic cost of the spawning migration.

Thus for these two species certain similar patterns do exist, and it is the adaptive significance of a combination of life history parameters maximizing the number of offspring, from an individual, reaching maturity, and not one in isolation, that may be important.

D. Effects of Repeat Spawning

According to Bell (1980) a reproductive cost such as reduced fecundity and/or growth and/or survival in repeat spawners, might be expected. From figures 5.9 and 5.10 a + b it is apparent that growth rate decreased following the onset of maturity. Libey (1976) calculated mortality figures for A.pseudoharengus and found an increase from 42.0% to 56.1% once the fish had matured and spawning commenced. This presumably being due to a combination of the large expenditure of energy associated with reproduction and that spawning migrants do not feed actively while in freshwater.

1. Materials and Methods

An attempt to investigate the effect of repeat spawning was undertaken indirectly by using ovarian weight as an indication of fecundity, and, so that size variation was taken into account the relationship between ovarian weight and fork length was used. The arithmetic relationship between ovarian weight and fork length was used. The arithmetic relationship was used because of the small size range involved, as well as producing higher values for the coefficient of determination (r^2) for the relationship between ovarian weight and fork length, when compared with Log_{10} transformed data. The regressions where fitted by the method of least squares.

Survival was assessed from the relative numbers of fish of different spawning histories from the 1975 year-class, caught in 1980 and in 1981, at Lydney on the River Severn.

All measurements were made on material that was either fresh or had been kept on ice, for no longer than 24 hours.

2. Effect of Repeat Spawning on 'Fecundity' and Survival

It has already been mentioned that females from the 1975 year-class exhibited a difference in the timing of the onset of maturity, a proportion of them maturing at age four as well as at five. The regressions of ovarian weight and somatic weight against fork length for both virgin and repeat spawners from the 1975 year-class, during periods two (1 May - 15 May) and three (16 May - 31 May) of the 1980 migration, are shown in table 5.16 a and in figures 5.11 and 5.12. When the regressions for the same dependent variable for virgin and repeat spawning fish from the same time period were compared, significant differences were found (table 5.16 b). The periods could not be combined due to significant differences between the regressions (table 5.17). The other three periods did not produce significant regressions.

From the large amount of variation interpretation of the regressions suggests that the situation is far from conclusive. In period two the repeat spawners have larger ovaries and are presumably more fecund and/or have larger eggs than virgin fish. However, in period three the virgin fish have heavier ovaries at the lower end of the size range, while at the upper end of the size range the reverse situation occurs. It would thus appear that a reproductive cost was not manifest in terms of reduced fecundity.

Table 5.16a Coefficients for the arithmetic regression of ovary weight and somatic weight against fork length (mm.), for virgin and repeat spawning females, from the 1975 year class, caught at Lydney during the 1980 spawning migration.

Period two 1980 (1 May - 15 May)

Dependent variable (Y)	Spawning history	N	Intercept (a)	Slope (b) ± 95% Confidence limits	Coeff. Determ. (r^2)	F Value	Significance of F
Ovary weight	Virgin	20	-184.2636	0.7816 ± 0.5236	0.3534	9.8365	$P < 0.01$
Ovary weight	Repeat	22	-143.8225	0.6787 ± 0.5824	0.2281	5.9092	$P < 0.025$
Somatic weight	Virgin	20	-831.7722	3.9506 ± 1.4587	0.6427	32.3768	$P < 0.0005$
Somatic weight	Repeat	22	-779.4021	3.735 ± 1.7376	0.5013	20.1056	$P < 0.0005$

Period three 1980 (16 May - 31 May)

Ovary weight	Virgin	20	-120.8162	0.6205 ± 0.3432	0.4449	14.4268	$P < 0.0025$
Ovary weight	Repeat	14	-354.5873	1.3164 ± 1.2754	0.2965	5.0582	$P < 0.05$
Somatic weight	Virgin	20	-912.2382	4.1299 ± 0.8759	0.845	98.1423	$P < 0.0005$
Somatic weight	Repeat	14	-828.2486	3.848 ± 1.4377	0.7392	34.0121	$P < 0.0005$

Table 5.16b Comparison of the regressions for Virgin and Repeat spawners in each period

Dependent Variable (Y)	Period	Slope			Intercept		
		t-value	df	Significance	t-value	df	Significance
Ovary weight	1	0.271	38	$P < 0.50$	5.7433	39	$P < 0.001$
Ovary weight	2	1.3963	30	$P < 0.10$	32.4579	31	$P < 0.001$
Somatic weight	1	0.1975	38	$P < 0.50$	4.2414	39	$P < 0.001$
Somatic weight	2	0.3632	30	$P < 0.50$	5.6698	31	$P < 0.001$

Table 5.17 Comparison of the regressions of ovary weight and somatic weight against fork length, for virgin and repeat spawners from the 1975 year-class, caught at Lydney in 1980, between those caught during period two (1 May - 15 May) and those caught during period three (16 May - 31 May)

Dependent variable (Y)	Spawning history	Slope			Intercept		
		t-value	df	Significance	t-value	df	Significance
Ovary weight	Virgin	0.5494	36	$P>0.50$	11.2804	37	$P<0.001$
Ovary weight	Repeat	1.0876	32	$P>0.20$	29.0454	33	$P<0.001$
Somatic weight	Virgin	0.2258	36	$P>0.50$	8.9791	37	$P<0.001$
Somatic weight	Repeat	0.1012	32	$P>0.50$	2.6332	33	$P<0.02$

Table 5.18 Number of female <u>A.fallax</u> caught during 1980 and 1981 at Lydney on the River Severn, and their spawning histories.

1980		1981	
Age and Number of Previous Spawning	Number	Age and Number of Previous Spawning	Number
5.0	93	6.1	67
5.1	57	6.2	60

Figure 5.11, Arithmetic relationship between ovarian weight and fork length for females aged five, spawning for the first time (virgins) and for the second time (repeats), caught at Lydney during period two (1 - 15 May) and three (16 - 31 May) of the 1980 upstream migration.

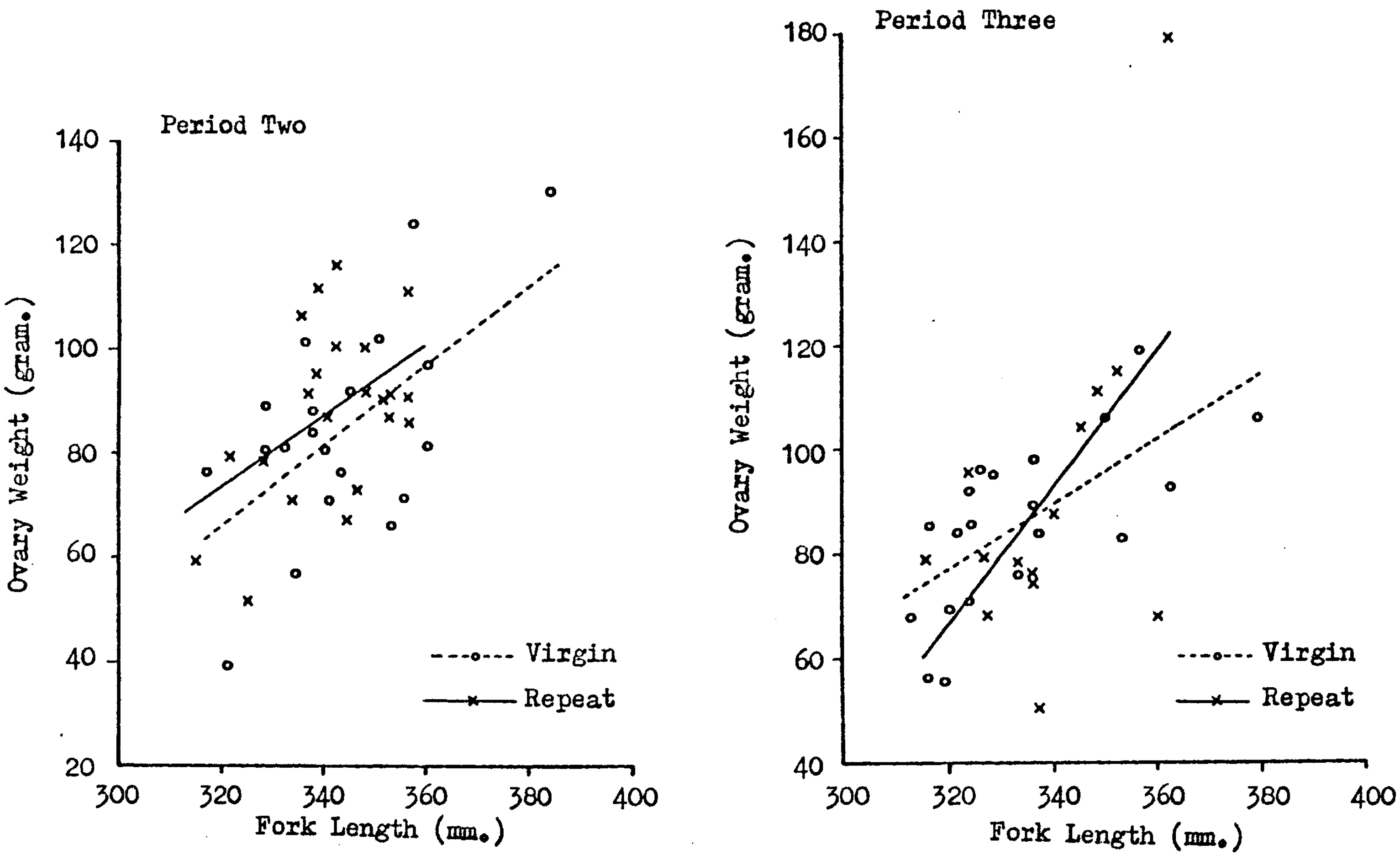
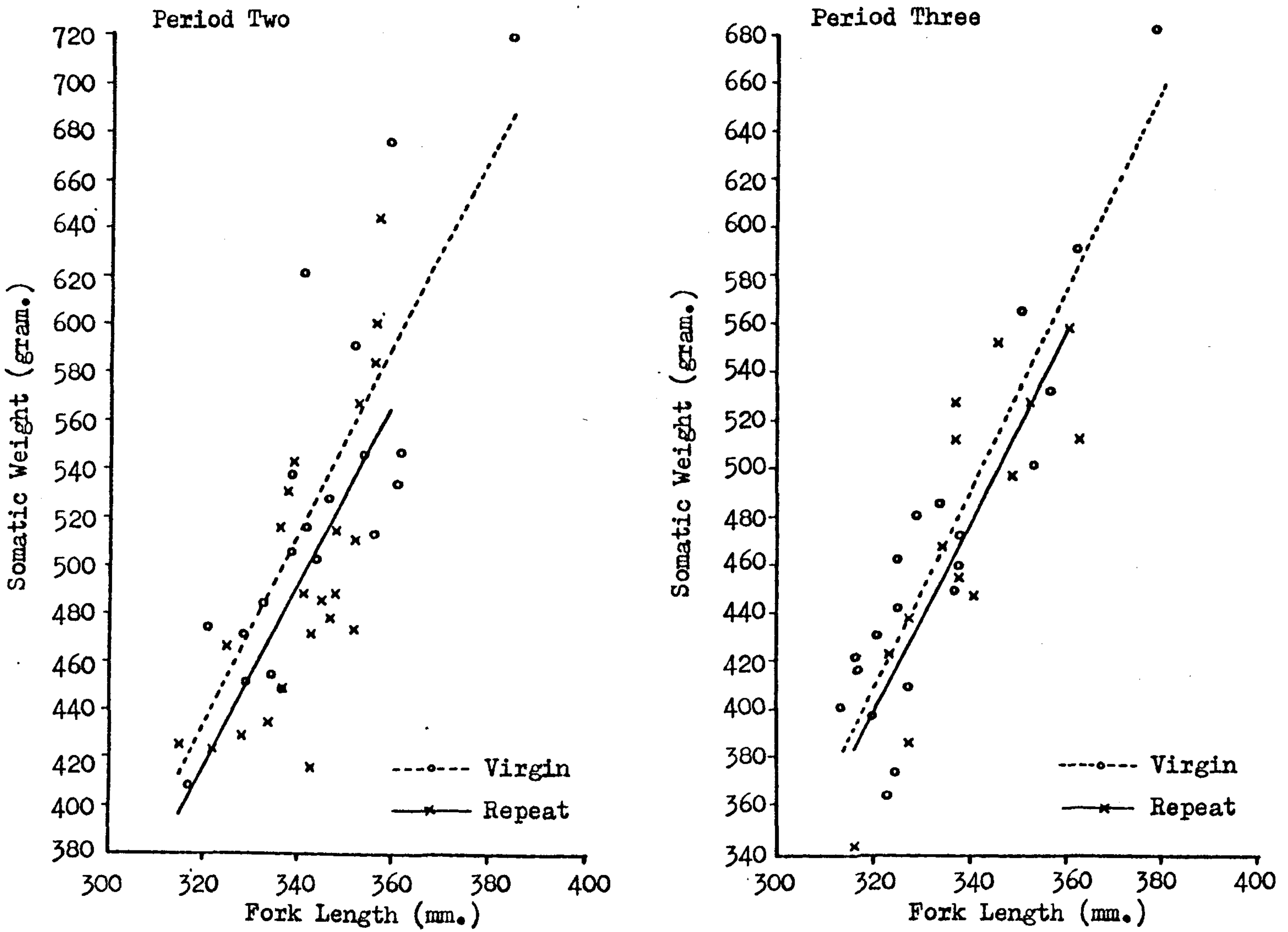


Figure 5.12, Arithmetic relationship between somatic weight and fork length for females aged five, spawning for the first time (virgins) and for the second time (repeats), caught at Lydney during period two (1 - 15 May) and three (16 - 31 May) of the 1980 upstream migration.



Bridger (1961) concluded that virgin spawning Clupea harengus from the North Sea and Clyde stocks were less fecund than repeat spawners. However, Schopka and Hempel (1973) studying a number of different stocks found no evidence to support this. The opposite was found by Anokhina (1963) for Clupea harengus pallasai maris-albi Var. B. Rabinerson, where in general virgin spawners were more fecund than repeat spawners. This was thought to have arisen as a result of insufficient time for the fish to accumulate enough energy reserves to both produce more eggs and survive the winter.

Another possibility exists where a reproductive cost has manifest itself in terms of reduced somatic reserves. From figures 5.12 it is apparent that in both of the periods virgin fish have greater somatic reserves than repeat spawners. Glebe and Leggett (1981b) have shown that the amount of energy reserves is very important in determining post spawning survival. They have shown that A.sapidissima in St. Johns River (Florida) (semelparous population) utilize a higher percentage of their energy reserves in gonadal development and migration to the spawning grounds when compared with an iteroparous population, as found in the Connecticut River. The average female, from the St. Johns River, allocated 16% of her energy reserves to reproductive products while those from the Connecticut River only 7%, the balance being used for a successful return to the sea. Therefore, assuming there is no difference in the allocation of energy reserves by virgin and repeat spawners, that virgin fish have slightly greater somatic reserves when compared with repeat spawners, and assuming the same distance migrated then one might expect that virgin fish have a higher chance of returning to spawn for a second time when compared to those that have spawned twice returning to spawn for a third time. Table 5.18 shows the number of fish caught from the 1975 year-class during 1980 and 1981.

It seems that the higher somatic reserves present in the virgin fish caught in 1980 did not produce a higher survival rate. It would therefore appear that a reproductive cost, associated with spawning, has not manifest itself in terms of reduced fecundity or survival. However, this is based on data from one year-class and only over a one year period and it may require a more detailed investigation of the effects of spawning on other year-classes before a detailed understanding of the effects of reproduction on post-spawning survival and future reproduction may be assessed.

CHAPTER SIX

EARLY LIFE HISTORY

Introduction

Aspects of the early life history of A.fallax are very poorly documented, though some information exists on their seaward migration (Day, 1890; Claridge and Gardner, 1978; Wheeler, 1969). In fishes, the survival from egg to adult is normally extremely small, Cherfas (1956) (cited by Nikolsky, 1963) found mortality rates varied from 99.42% to 99.994% (and were generally believed to be around 99.99%) for a number of fish species. Leggett (1977) estimated levels of mortality in A.sapidissima to be 99.99944% at the replacement level, and for maximum population growth, the level decreased to 99.99917%. For anadromous A.pseudoharengus mortality, from egg to completion of juvenile emigration was estimated to be 99.9987% by Kissil (1974) and 99.9976% by Huber (1978). Studies on the early life history are important as it is during the early stages of life that mortality is normally the largest, Le Cren (1961) as well as the most variable, Nikolsky (1963). Bannister et al. (1974) found mortality in Pleuronectes platessa, from the earliest egg stage to just prior to metamorphosis, was in excess of 99% in 'normal' years, occured within the first 130 days of life, but had been found to be as low as 92.66%. It has been suggested that spawning success and the subsequent survival of the young during the first year of life, is important in establishing year-class strength in fishes (Nelson et al., 1967).

An understanding of the factors affecting year-class strength is important in forcasting yields as well as for producing methods of controlling these fluctuations (Nikolsky, 1963). A number of factors have been implicated as important in determining abundance of fish, notably size of spawning stock (Leggett, 1976; Marcy, 1976), temperature (Le Cren, 1977; Mann, 1979; Marcy, 1976), river level and/or flow (Kuznetsov, 1975; Marcy, 1976; Marshall, 1982; Martin et al., 1981; Scarnecchia, 1981; Stevens, 1977) and pollution (Chittenden, 1969). Food supply at a particular time may also be important in determining future abundance (see review by May, 1974), for example, Nikolsky (1963) mentions that the strength of the year-class in P.platessa is at least partially determined by the food supply at the time the larvae are changing over from planktonic to benthic feeding.

A number of fish species show large scale migrations and/or movements, studies of which are important as they are often associated with production (Northcote, 1978). One of the main differences generally associated with anadromous species is the change from an hypo-osmotic to a hyper-osmotic medium, during the early stages of life. Except for the studies by Chittenden, (1972a & 1973), and Tagatz (1961), very little information exists on the osmoregulatory ability or tolerance of young alosids to various salinity conditions. Previous studies on salmonids, notably changes in morphology, behaviour and physiology, which have been reviewed by Hoar (1976), suggest this might be expected. A number of environmental factors have been implicated in initiating their seaward migration, of which, temperature (Chittenden and Westman, 1967; Jessop, 1975; Marcy, 1976; Richkus, 1975; Sykes and Lehman, 1957) and river discharge (Cooper, 1961; Huber, 1978; Kissil, 1974; Richkus, 1975; Sykes and Lehman, 1957) have been found to be important for anadromous alosids.

This chapter is mainly concerned with describing the early life stages of juvenile A.fallax, aspects of their ecology, seaward migration and possible environmental factors controlling it, as well as the effect of environmental factors on juvenile abundance.

A. Materials and Methods

Fish were caught using the methods described in chapter two. In 1979 and in 1981 sampling was carried out using the 20 m. 'micromesh' seine, (mesh size 3.0 mm.). However, in 1980, due to the low density of the juveniles, sampling at Newnham, starting in August, was carried out using the larger fry seine, with a mesh size of 6.35 mm.. At the other sites sampled in 1980 the 20 m. 'micromesh' seine was used. Fish were aged using scales, if developed, as described in chapter three. The eggs, larvae, and juveniles were preserved in a solution of:-

40% Formaldehyde	5%
Propylene glycol (Propane 1,2 diol)	5%
Propylene phenoxetol	1%
Distilled Water	89%

The solution was buffered to a pH = 7, using sodium acetate. This solution has been found satisfactory for the preservation of fish eggs and clupeid larvae, Nichols and Wood (1978). All measurements were made on material which had been preserved for at least six months. The eggs and prolarvae (larvae which had not completely absorbed the yolk sac) were measured using a Wild microscope and graticule, to the nearest 0.0365 mm.. The post-larvae and the juveniles were measured to the nearest millimetre. The sites sampled have been described in chapter two.

B. Description of Eggs and Larvae

The eggs (plates, 6.1, 6.2 + 6.3, 6.4) are spherical, have a single smooth transparent egg capsule with a large perivitelline space and numerous tiny oil globules scattered through a segmented yolk. The eggs, were non-adhesive, and generally found on fine gravel, in the absence of a current and may be considered demersal (though see chapter four). No pigmentation was present on the embryo or yolk sac, though in the later stages of development, the eye capsules become heavily pigmented. The mean diameter of the eggs collected were 2.668 mm. ranging in size from 1.971 mm. to 3.285 mm. These egg sizes were smaller than those observed by Hass (1968) who found a mean diameter of 3.85 mm. and by Maitland (1972) who reported that they ranged between 4.0 mm. and 5.0 mm. in diameter.

No estimate of the effects of the preservative on egg size was made during this study, but some estimate may be gained from the literature. Hiemstra (1962) estimated shrinkage, of pelagic eggs from marine species, to be approximately 7% in 4% formalin. Hancock (1976) found that eggs of Barbus barbus shrank by 1.45% when stored in 10% formalin with 10% W:V NaCl added.

The prolarvae can be seen in plate 6.5 and measure approximately 7.22 mm. (standard length) on hatching (range from 5.986 mm. to 8.906 mm.) (see appendix three). The yolk sac is slightly oval, with a number of small oil droplets scattered through it. The anus opens approximately four fifths of the way down the body, (appendix three). There is a very slight pigmentation of the ventral and posterior regions of the yolk sac as well as along the ventral region of the larvae. Measurements of various parameters were taken from twenty newly hatched larvae and these are presented in appendix three.

Plate 6.1, Eggs in the early stage of development, the yolk mass is of dense irregular granular consistency, with oil globules present, note wide perivitelline space. X 20

Plate 6.2, Embryo not well defined except for differentiation between the head, trunk and tail. X 20

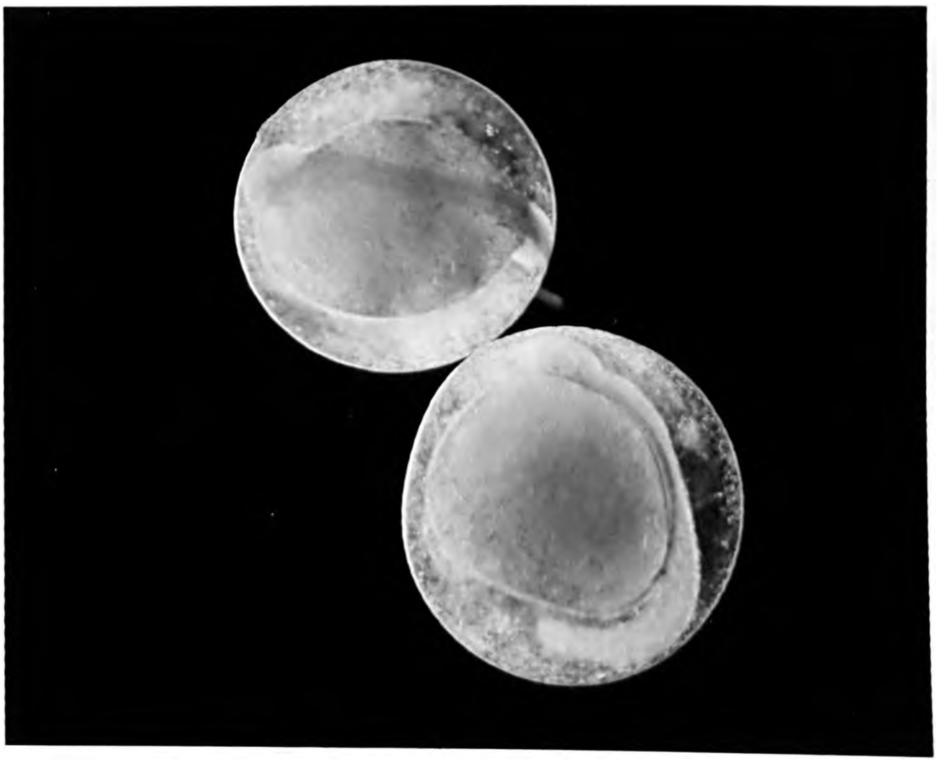


Plate 6.3, Somites of the embryo are visible and the tail is free from the yolk mass. X 20

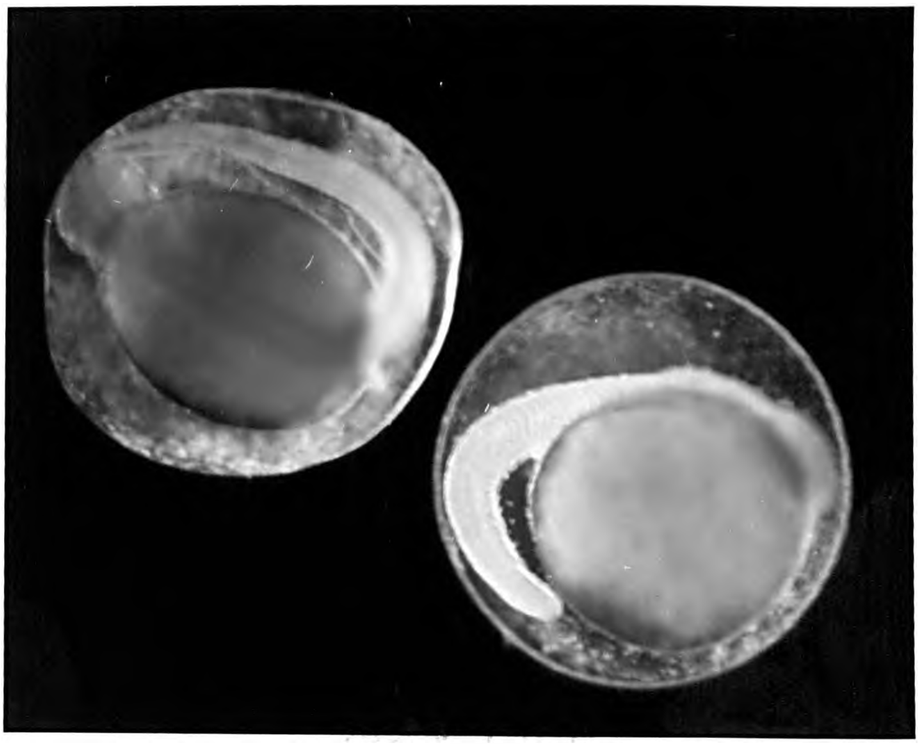


Plate 6.4, Embryo in an advanced stage of development, eyes heavily pigmented. Notocord, somites and other gross features are visible. X 20

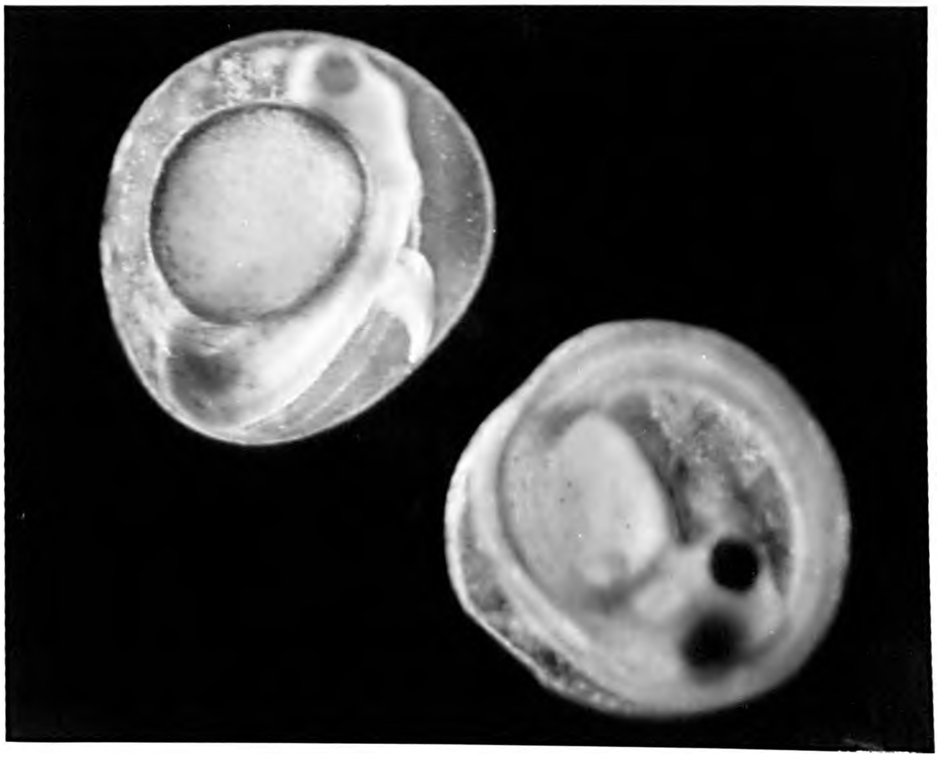


Plate 6.5, Prolarvae, primordial fin folds can be seen as well as the myomeres, also note the posterior position of the anus. In the upper specimen the heavily pigmented eye is visible. In the lower specimen a pectoral fin bud can be seen. X 12.5

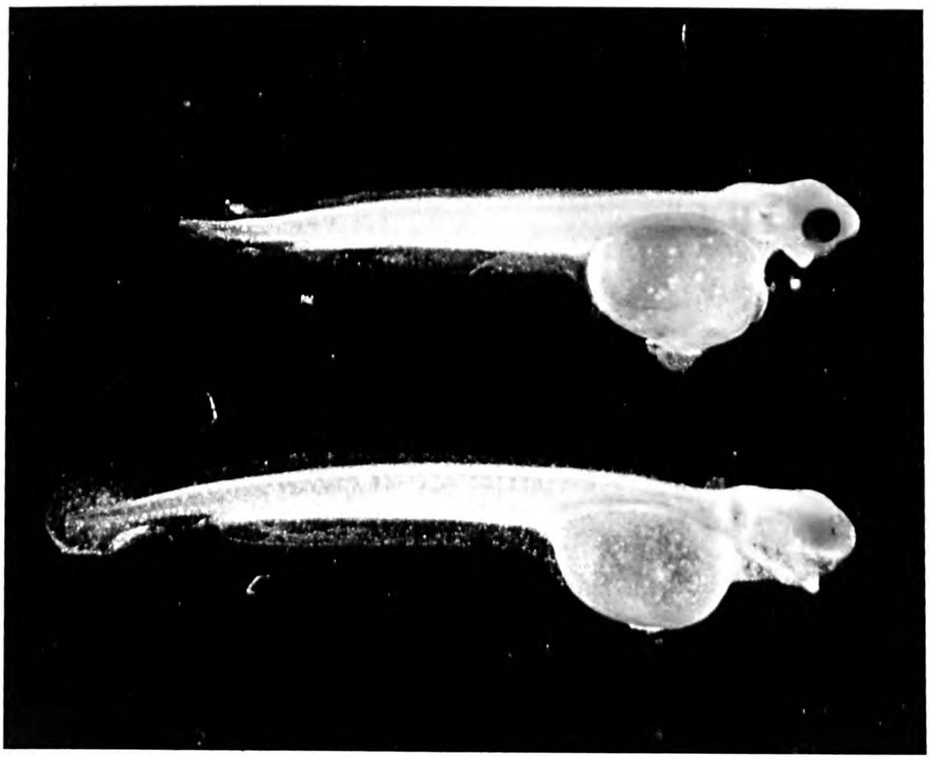


Plate 6.6, Post-larvae from the River Wye, note pigmentation on the dorsal surface. Scale in mm..

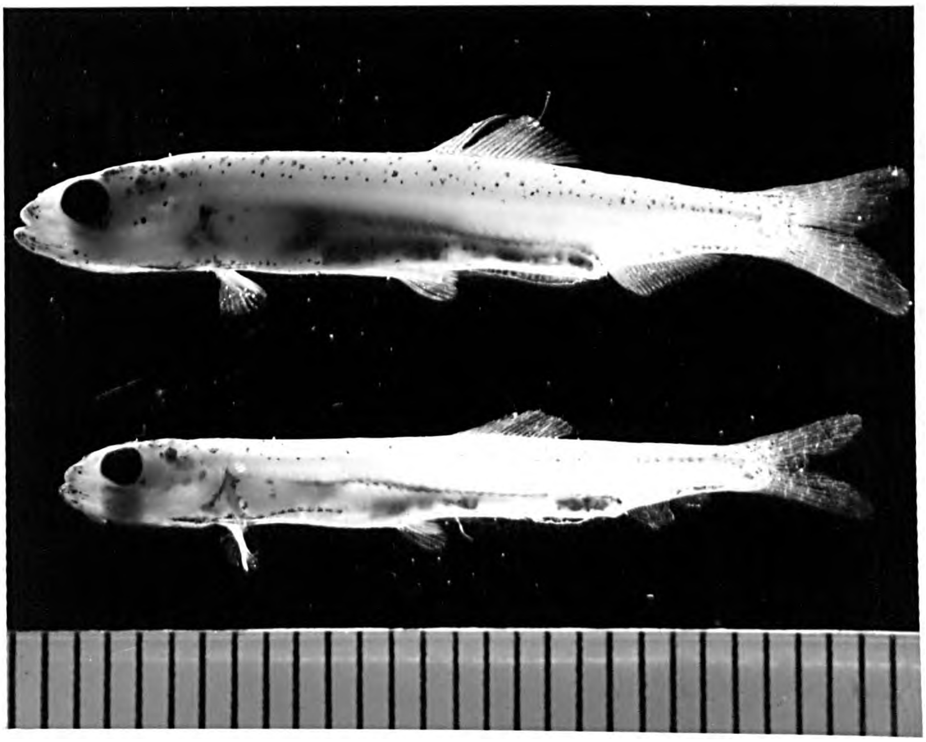


Plate 6.7, Post-larvae from the Severn estuary remnants of primordial fin still present along the ventral surface. Dorsal surface not markedly pigmented. Scale in mm..

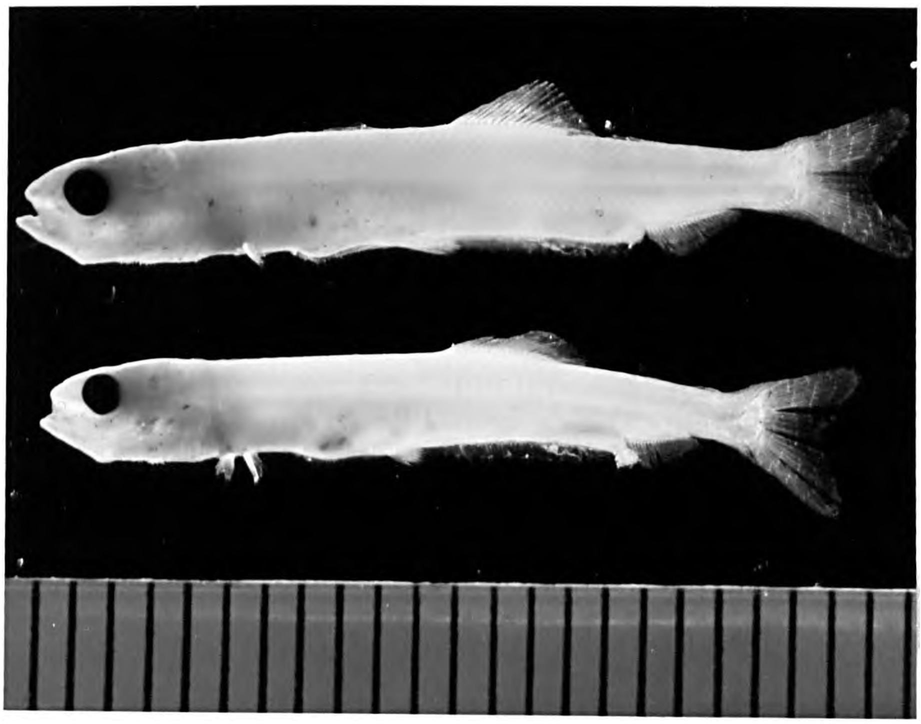
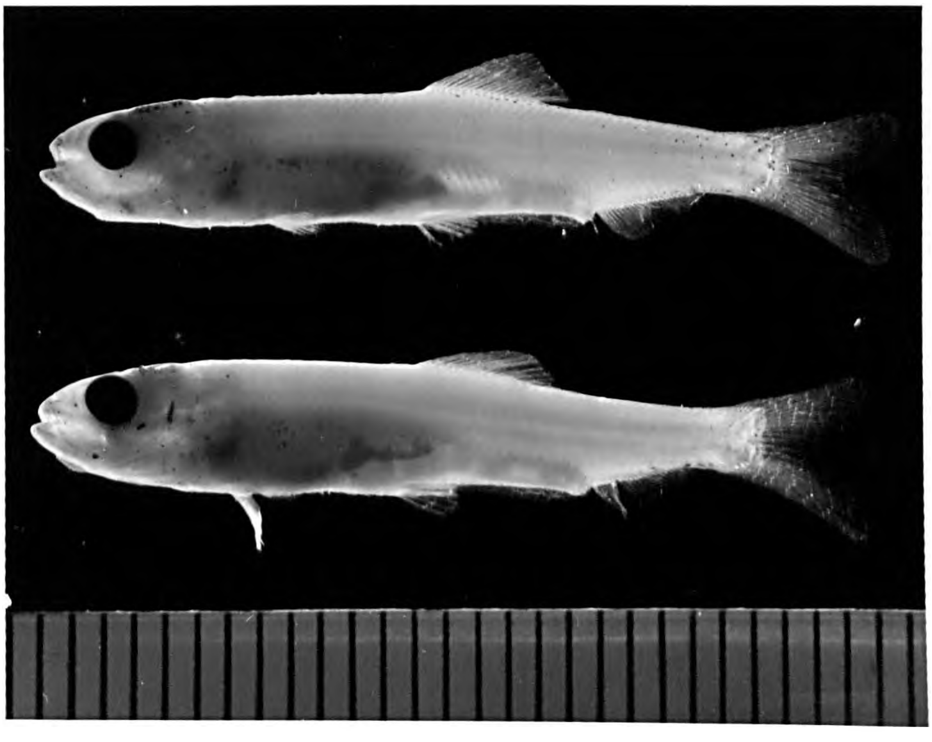


Plate 6.8, Post-larvae from the Severn estuary, note the dorsal fin and anus have migrated anteriorly. Scale in mm..



Plates 6.6, 6.7 and 6.8, show stages of development of post-larvae (larvae which have completely absorbed the yolk sac). A.fallax is typical of the clupeiformes (Russell, 1976) with the posterior origin of the dorsal fin and anus and their subsequent migration anteriorly, which occurs at between 25 mm. and 28 mm. (fork length), as the larvae transform into fry. There was a difference in pigmentation of the post-larvae between those caught in the River Wye and those from the upper Severn Estuary. This is illustrated in plates 6.6, 6.7 and 6.8 . The post-larvae in the River Wye were relatively heavily pigmented while those from the estuary had little or no pigmentation. This difference in pigmentation was also apparent in the fry and may possibly be attributed to the much higher turbidity in the estuary when compared to that in the river.

Blaxter (1962) estimated shrinkage in larval Clupea harengus to be about 10%, in later observations Blaxter (1971) found that shrinkage may be up to 20%; 15% immediately after capture in the net, and 5% by preservation in a 4% formalin-sea water solution. Farris (1963) observed a mean shrinkage of between 6.8% and 11.3% in larvae of different size classes of Sardinops sagax (Janyns) preserved for six weeks in borax buffered 3% formalin. Schnack and Rosenthal (1978) found for larvae of Clupea harengus pallasi Valenciennes fixed in a 10% formalin - sea water solution, a size dependent effect, with the newly hatched larvae shrinking by approximately 10% while the largest larvae (16-22 mm. S.L.) shrank by between 6-7% after storage for 1.5 years.

Chittenden (1969) found that the fry stage of A.sapidissima shrank on average by 1.9% after being preserved in 5% formalin for 3.75 years. For three species of salmonids, Parker (1963) reported shrinkage of between 3.2% and 5.4% following preservation in 3.8% formalin for 225 days. Lockwood (1973) found that Pleuronectes platessa (50 mm -

75 mm.) shrank by 2.62% when preserved in 4% neutral formalin for 420 days. Similar findings were reported by Lockwood and Daly (1975) for P.platessa (20 mm. - 75 mm.) with mean shrinkages of between 0.38% and 4.37%, after being preserved in 4% neutral formalin for a year. The smaller fish were found to shrink proportionally more. For Limanda limanda (Linnaeus) shrinkage was found to be 0.19% which was less than that found for P.platessa (2.7%), of the same size. Shrinkage was also observed to vary between preservative, with the least being found when formalin was diluted with distilled water.

Similar general features have been shown for A.sapidissima by Leim (1924), Maxfield (1953), Watson, (1968). For A.pseudoharengus by Chambers et al. (1976), Cianci (1969), Mansueti (1956b) and Norden (1967b). For A.aestivalis by Chambers et al. (1976), Cianci (1969) and Kuntz and Radcliffe (1918), for A.mediocris by Mansueti (1956a and 1962), for A.caspia caspia by Perceva (1939), and for various Alosa species in the Volga delta by Koblichkaoa (1966).

C. Distribution and Growth

1. River Wye

In 1979, sampling for juveniles was carried out at a number of different sites, between Monmouth (River Km. 30.5) and Pipton (River Km. 170). It appeared that the characteristics of the sites were an important factor determining whether larvae and/or juveniles were present. Generally, the young were found in deep pools close to the bank where the current was not so strong. This is very similar to the type of preferred habitat described for A.sapidissima by Chittenden (1969). This type of habitat was characteristic of the sites at Monmouth and Courtfield (River Km. 50), where large pools, created in the shelter of salmon cribs (Plate 6.9) were netted. Young were also caught at Hillcourt (River Km. 69.5) and

Plate 6.9, Seine netting at Monmouth, River Wye.

at Pipton where the sites in cross-section were characterized by a deep pool under one bank leading up onto a shallow area on the opposite side. All sampling was carried out from the shallow side. It became apparent that young A.fallax were only caught when the deep pool was netted, none were caught when only the shallows were sampled. The other sites sampled, at Byford (River Km. 131.5) and at Glasbury (River km, 166), were relatively shallow and fast flowing and no young were found. It was not possible to obtain quantitative estimates between sites due to differences in topography and thus netting efficiency.

In 1979 sampling for juvenile A.fallax started towards the end of July and from those caught there is some indication of a trend towards an increase in size down-stream, (Figure 6.1, Table 6.1). The samples taken were considered to be spaced too far apart in terms of time to justify a statistical analysis. However, there was a significant difference in size between those at Hillcourt and those at Courtfield, ($t = 3.1376$; $df = 41$; $P<0.002$), variances were found to be homogenous. For A.sapidissima, growth rate was found to vary between areas within a river system (Marcy, 1976; Watson, 1970) similar findings were also reported by Chittenden (1969) as well as observing a trend towards an increase in size seaward. This may be explained by either different environmental parameters such as temperature, water velocity, and/or biological conditions such as food supply as well as their relative densities and that of their competitors, affecting their growth rate at each of the sites. This trend may also have arisen from selective predation pressure on the smaller individuals further downstream. These differences could also have resulted from variation in the timing of spawning, or that the young have a tendency to migrate seaward as they grow (Chittenden, 1969; Marcy, 1976). For A.aestivalis, Scherer (1972)

Figure 6.1, The size (mean ± 95% confidence limits) of 0+ *A.fallax* from four sites in the river Wye, in 1979.

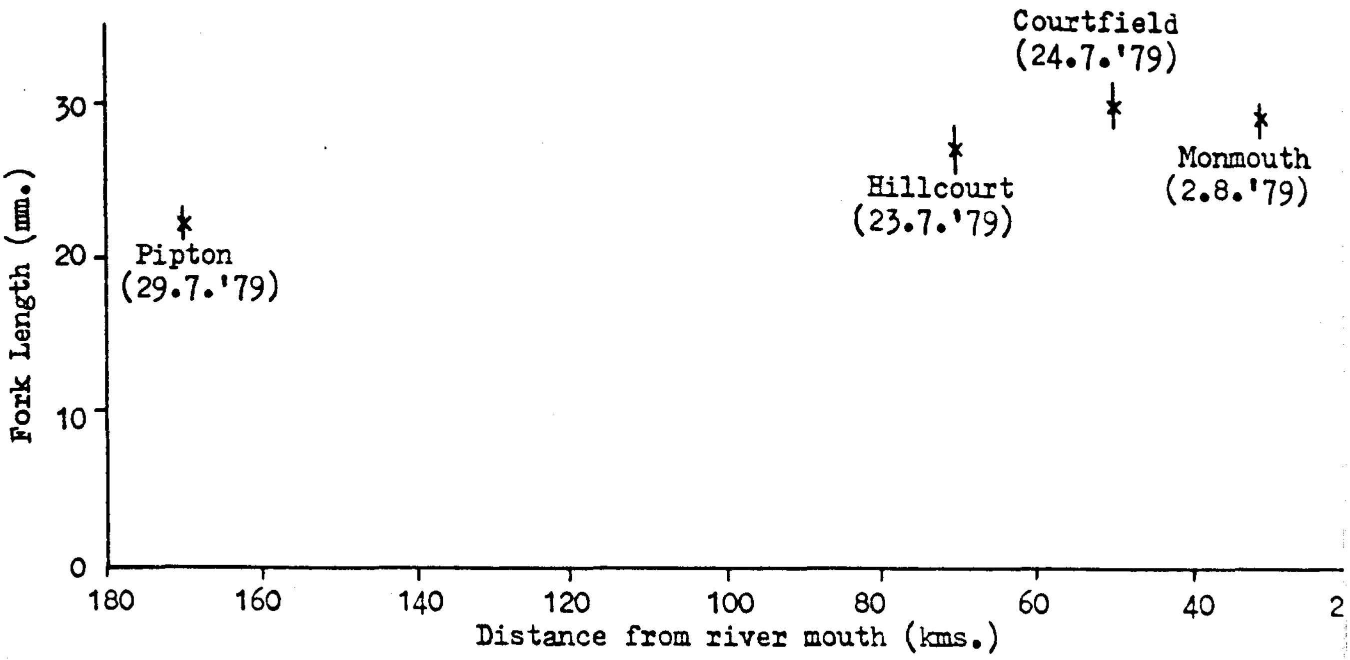


Table 6.1 The size of juvenile *A.fallax* from four sites in the River Wye in 1979

Site	Date	River km.	Mean fork length (mm) ± 95% confidence limits	N
Pipton	29.7.79	170	22.348 ± 0.745	23
Hillcourt	23.7.79	69.5	26.444 ± 1.15	27
Courtfield	24.7.79	50	29.375 ± 1.64	16
Monmouth	2.8.79	30.5	28.7 ± 0.80	80
	18.8.79		30.2 ± 2.56	10

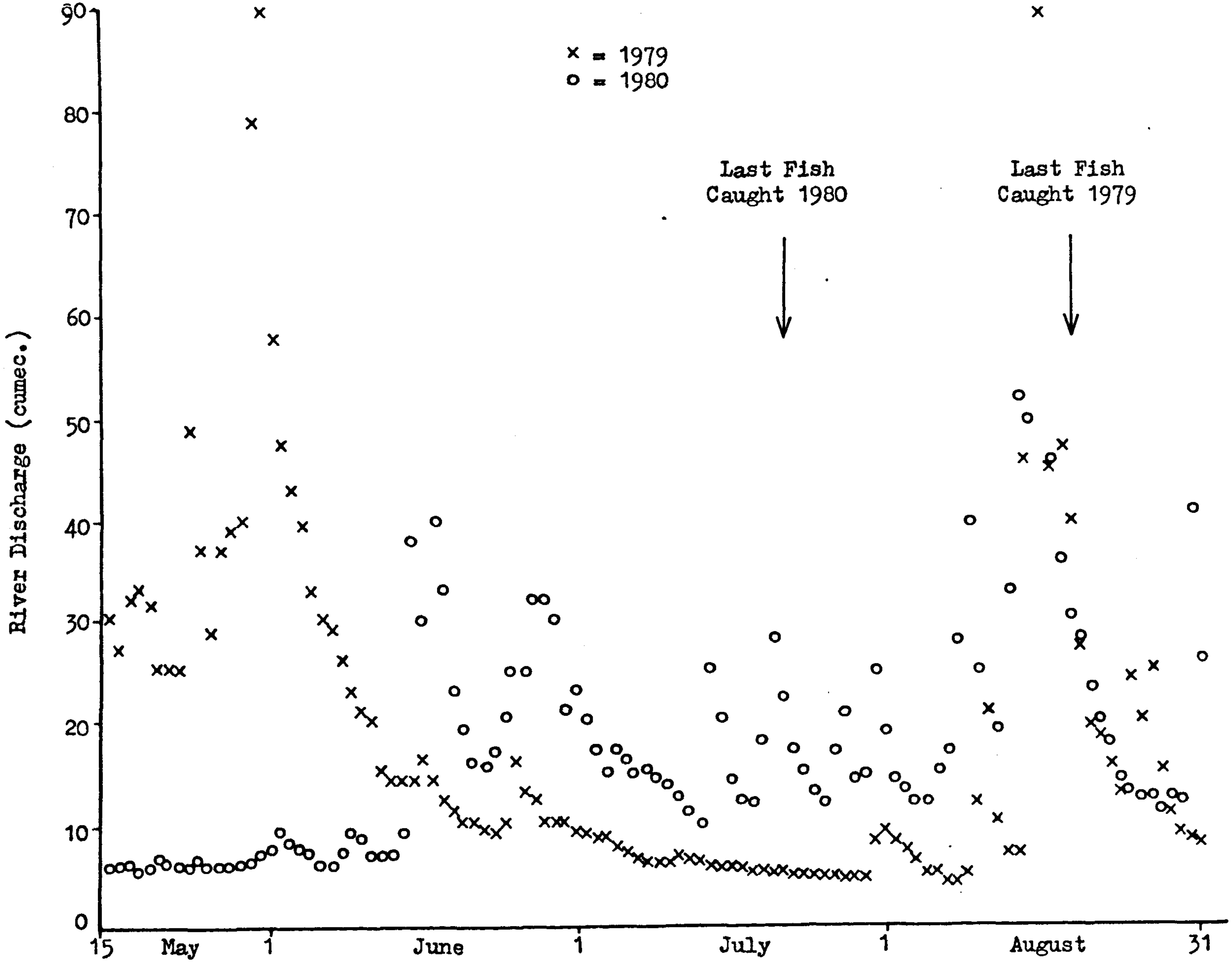
found that the fastest growing individuals had a tendency to disperse themselves upstream as well as downstream.

A similar situation has been found for catadromous species there being an increase in length of the juveniles with distance away from the natal area. This has been shown to be the case for Platichthys flesus (Johnston, 1981) and for two species of Anguilla (Jellyman, 1977 a & b). The establishment of such a gradient would exist if swimming speed was proportional to body size and that equal activity levels were exhibited amongst all the members, then, in time, the larger individuals would tend to have migrated further (Strubberg, 1923).

In 1980, sampling commenced at the start of July and except for the sample at Monmouth on 3rd July, very few juvenile A.fallax were found, Table 6.2. Those at Monmouth had a mean fork length of 22.52 mm. (95% confidence limits = ± 0.49, n = 60).

In both years no more young were found after periods of high discharges (Figure 6.2), which occured in mid August (1979) and in mid July (1980). These conditions may have initiated their seaward migration. Cooper (1961), Huber, (1978) and Kissil (1974) observed that the seaward migration of juvenile A.pseudoharengus normally accompanied high discharge levels and migration did not appear to be related to age or size. Similar findings were reported by Richkus (1975) who found that as well as increased water levels, seaward migration accompanied declining water temperatures. Similar conclusions were reported by Sykes and Lehman (1957) for A.sapidissima. This may be due to a change in their rheotaxic response. Brannon (1972) found for juvenile Oncorhynchus nerka that increasing the current velocity above a threshold level resulted in a change in orientation from positive to negative rheotaxis. However, another possibility exists where the young may have been displaced downstream by the high flows.

Figure 6.2, The mean daily discharge for the river Wye, at Belmont, from the 15th May to the 31st August 1979 and 1980.



Comparisons may be made between the two years (Table 6. 2), and the low numbers found during late July and August 1980, compared with 1979, probably reflects the consequences of the different flow regimes in the two years.

Table 6. 2 The relative density of juvenile A.fallax from various sites on the River Wye, during 1979 and 1980

Site	1979 Date	No.	No. of Drafts	1980 Date	No.	No. of Drafts
Pipton	29.7.79	23	3	4.7.80	0	2
				20.7.80	0	3
Hillcourt	23.7.79	27	3		0	2
Courtfield	24.7.79	16	1	7.7.80	2	1
Monmouth	2.8.79	80	1	3.7.80	60	1
	18.8.79	10	1	20.7.80	1	2
				6.8.80	0	2
				21.8.80	0	1

This difference in abundance is more fully discussed in Section E of this chapter.

2. River Severn

Juvenile A.fallax in the River Severn showed a different distribution when compared to those in the River Wye. In 1979, very few were found in freshwater at Deerhurst (1.16/1500m^2) and at Wainlode (1.75/1500m^2), and none at all in 1980. No freshwater sites were sampled in 1981.

In 1979, sampling started at the end of July and was carried out at all the sites described in chapter two. The majority of the population, at the end of July/start of August, was found in the upper estuary at Elmore ($166.8/1500m^2$) their density decreasing seawards, figure 6.3. During August, September and October there was a gradual trend for the population to shift down the inner estuary and by November none were caught at Oldbury the most seaward of the sampling stations, (until April, 1980). This seaward movement is illustrated in figure 6.3, together with their growth at each of the sites. In an attempt to determine their over-wintering areas sampling, with beam and otter trawls was carried out in the outer estuary just below Severn bridge, from October through to December. Only one juvenile A.fallax was caught. It therefore must be concluded that either the gear was not effective in their capture, (though it had been used successfully for the capture of young clupeids in the River Ribble estuary, Sewell pers. comm.); that the fish were in an area which we were unable to sample or that the juveniles had migrated further seaward.

In 1980 the densities recorded at all the sites were lower when compared to those found in 1979. At Elmore and Framilode maximum density was found to be less than $1/1500m^2$. The densities recorded at Newnham and at Oldbury are shown in figure 6.4, along with their growth, (The densities observed at Newnham in 1980, can not be directly compared with those found in 1979 and 1981, due to the different size of net used).

In 1981 sampling did not include Oldbury, and a slightly different pattern was evident in the upper estuary figure 6.5. The density at Framilode was lower than might have been anticipated if the gradual decline in density seaward, indicated by the 1979 data, was to be expected. However, the same pattern of movement seaward is still apparent, (figure 6.5).

Figure 6.3, The density and size (mean ± 95% confidence limits) (open circle represents a single individual) of 0+ *A.fallax* from four sites in the river Severn from July to October 1979.

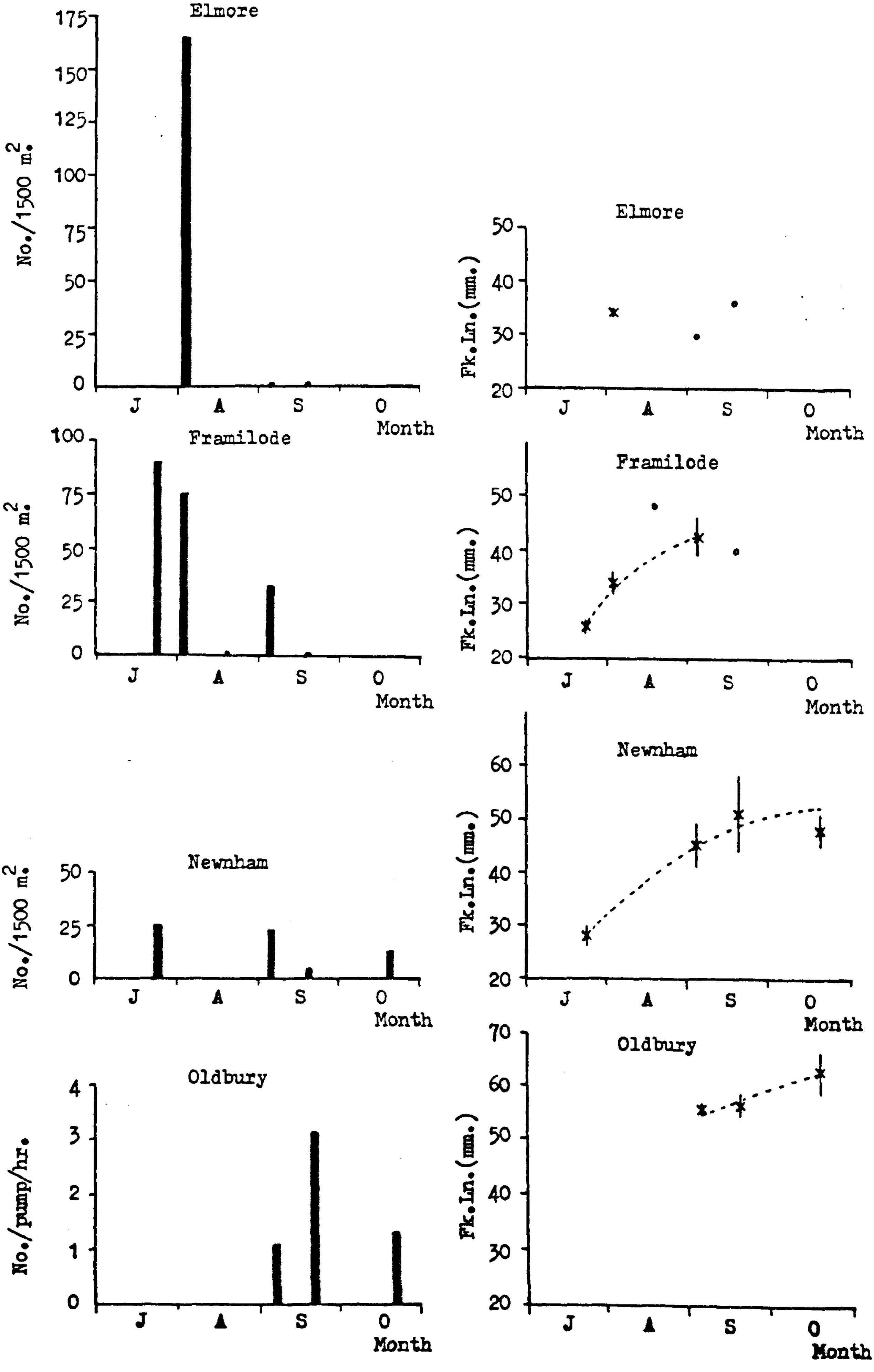


Figure 6.4, The density and size (mean ± 95% confidence limits) (open circle represents a single individual) of 0+ *A.fallax* from two sites in the river Severn, from July to November 1980.

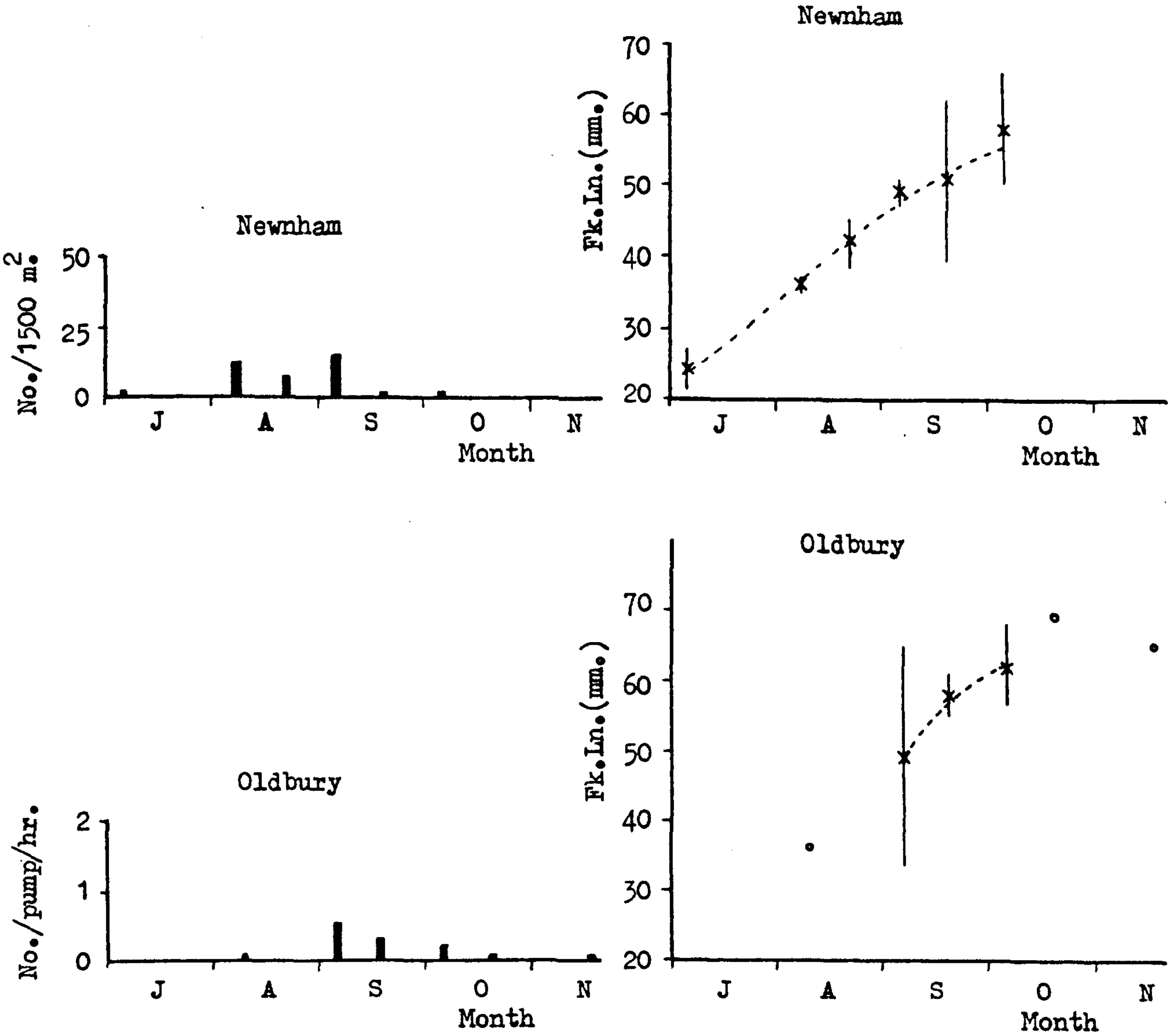


Figure 6.5, The density and size (mean ± 95% confidence limits) (open circle represents a single individual) of 0+ *A.fallax* from three sites in the river Severn, from July to September 1981.

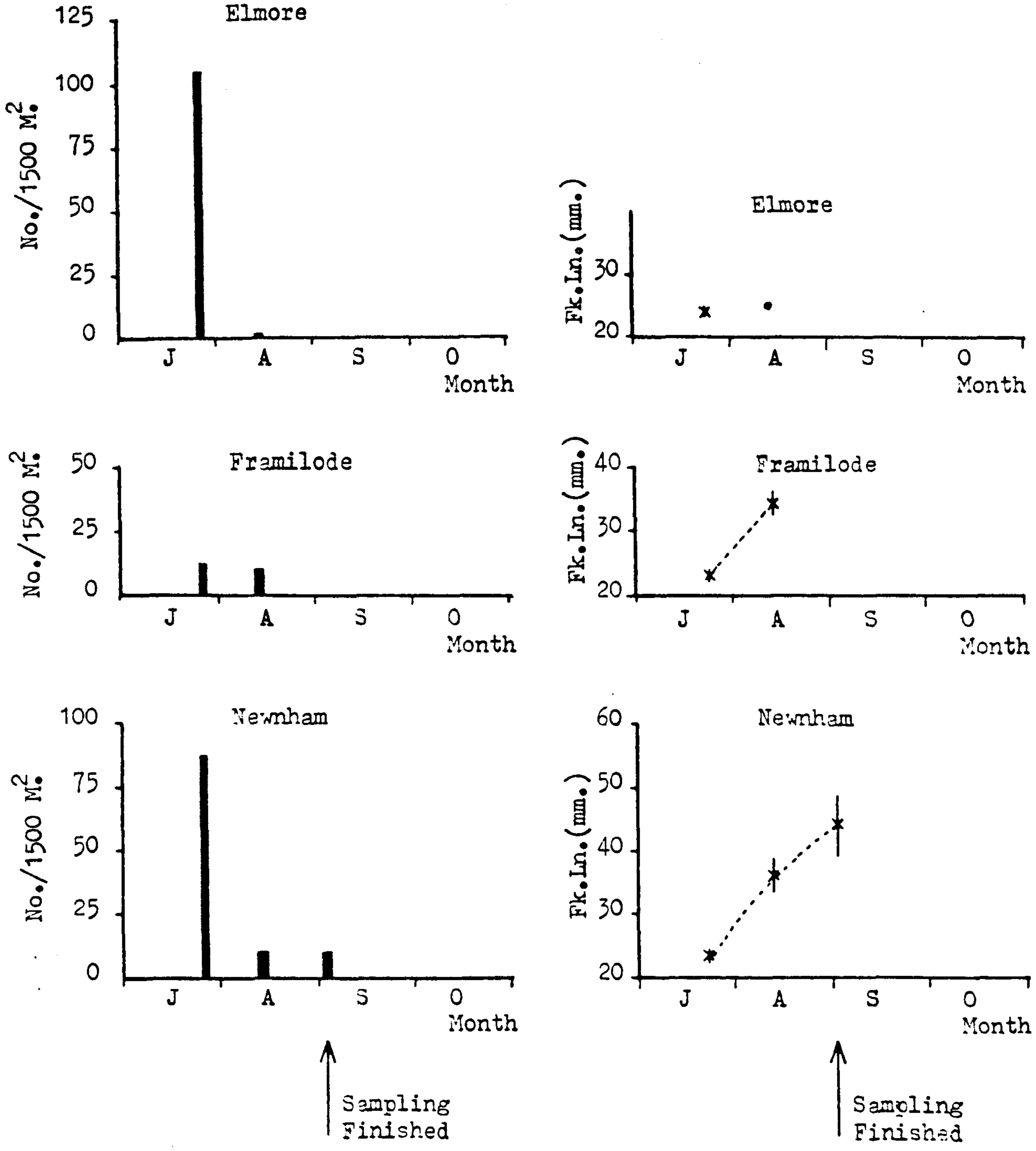


Table 6.3 Result of Newman-Keuls multiple range test on size of juvenile *A.fallax* at the end of July

Elmore Framilode Newnham

The mean size of the juveniles differed between the sites, in the upper estuary, in 1979 and in 1981, and also between the years. At the end of July (1979) the mean length at Framilode and Newnham was 26.1 mm. (fork length) (95% confidence limits = ± 0.82 mm, n = 105) and 27.7 mm. (95% confidence limits = ± 1.44 mm, n = 22), respectively. Thus showing a similar pattern to that on the River Wye, of an increase in length seaward, however, this difference was not significant ($t = 1.7544$; df = 125; $p > 0.05$), no significant difference was found between variances. During the summer (1979) there was a gradual upward trend in mean size, and by the time of peak migration past Oldbury they had reached a mean fork length of 56.4 mm. (95% confidence limits = ± 2.09 mm, n = 5), figure 6.3.

In 1980 juveniles were present at Newnham at the start of July when their mean length was 23.83 mm. (95% confidence limits = ± 3.08 mm, n = 6) and by the time of peak migration at Oldbury the young had reached a mean fork length of 49.4 mm. (95% confidence limits = ± 16.44 mm, n = 5). In both 1979 and 1980 their size at peak migration at Oldbury was smaller than that found by Claridge and Gardner (1978) (63.49 mm. fork length, 1976 year-class), the figure for mean length was obtained by converting the standard length given by Claridge and Gardner using the formula given in appendix one .

In contrast to the situation on the Wye and the upper estuary of the Severn in 1979 when there was some indication of an increase in size seaward, there existed in 1981 a gradual decrease in their mean size seaward. At the end of July the mean length of the juveniles at Elmore was 24.23 mm. (95% confidence limits = ± 0.54 mm, n = 61) thisdecreased to 23.57 mm. (95% confidence limits + ± 1.59 mm, n = 7) (at Framilode) and further to 22.75 mm. (95% confidence limits = ± 0.4 mm, n = 111), at Newnham. Single factor analysis of variance indicated that this was statistically significant ($F = 9.8509$; df = 2,176; $p<0.0005$). A Newman-Keuls multiple range test indicated that this difference lay between Elmore and Newnham and not between Framilode and the other two sites (table 6.3). (Bartletts test showed homogeneity of variances).

For A.sapidissima a pattern of peak juvenile abundance moving progressively down the river system, until final emmigration, was found by Marcy (1976). In conjunction with the observation that the larger fish are the first to leave the river system (Chittenden, 1969; Marcy, 1976), which may be similar to the situation observed in the Severn and Wye in 1979, but not in the Severn in 1981, may indicate that the larger or more rapidly growing fish were better adapted to more saline conditions.

For salmonids, Hoar (1976) has reviewed the literature on the changes in morphology, behaviour and physiology of parr to smolts. These changes are associated with adapting the species for a marine existence, of which one of the main problems is the change to a hyper-osmotic medium. The pattern of response to a hyper-osmotic medium has been found to vary within this group. For some species, resistance to higher salinities increases with increasing size. This has been found to be the case for S.salar (Farmer et al., 1978; Parry, 1960), for O.nerka (Bailey, 1971), for Oncorhynchus kisutch (Walbaum)(Conte et al., 1966) and for Salmo gairdneri Richardson (Conte and Wagner, 1965; Jackson, 1981; Landless, 1976). This may be related to the decline in the proportion of exposed surfaces with respect to mass, as the fish increases in size (Huntsman and Hoar, 1939), or to the development of an ability to regulate their internal salt concentrations. For other species notably Oncorhynchus tshawytscha, Oncorhynchus gorbuscha and Oncorhynchus keta (Walbaum) resistance to seawater is attained at an early stage in their life and for the latter two species is achieved through regulation of their internal salt levels (Weisbart, 1968). However, O.tshawytscha appears to rely more on tolerance to high internal salt levels, for survival. However, Wagner et al. (1969) concluded for O.tshawytscha that growth is important as the faster growing individuals seem to possess a regulatory system that is either more functional with respect to a given salinity gradient or capable of being initiated more quickly. Also Ewing et al. (1979) found in O.tshawytscha that size was important in regulating the activity of $Na^+:K^+$ Atpase, an enzyme important in regulating internal salt levels.

Therefore, if attainment of a specific size was important for the survival of alosids in seawater, this could explain their increase in size seaward as well as the timing of their seaward migration. However, the fact that in 1981 the mean lengths of juvenile A.fallax in the upper estuary of the Severn were significantly smaller as one progressed seaward, as well as the differences in the sizes of the migrants at Oldbury observed during this study when compared with the sizes found by Claridge and Gardner (1978), may indicate that this is not the case. It may be that different biological and/or environmental factors at each of the sites are involved.

Another possibility exists where survival in seawater may be under the control of environmental factors. For a number of the salmonids the levels of $Na^+:K^+$ Atpase has been found to increase at the time of their seaward migration and that this has been found to be under the control of temperature and photoperiod (Adams et al., 1975; Ewing et al., 1979; McCarty and Houston, 1977; Zaugg, 1981; Zaugg and Wagner, 1973). Thus the onset of the seaward migration of juvenile A.fallax, may occur after a period of exposure to certain temperature and photoperiod regimes, required to elevate the levels of Na^+:K^+ Atpase.

However, the young may be physiologically adapted for a marine existence and the fish do not undertake the migration because of certain favourable abiotic and/or biotic conditions in the upper estuary. The seaward migration only being undertaken when either some or all conditions become unfavourable. In laboratory experiments Chittenden (1973) has shown that juvenile *A.sapidissima* removed from freshwater reaches of the Delaware River can be successfully transferred from 5%o to 30%o salinity with 100% survival either directly or over a period of six days. In contrast, Tagatz (1961) found that juvenile *A.sapidissima* transferred rapidly from 0%o to 33%o salinity experienced mortalities of between 50% and 100% within 48 hours. The percentage mortality was reduced to between 50% and 70% when the fish were transferred over to 15%o and 8%o salinity. Gradual transfer from freshwater to 30%o - 32%o salinity produced lower mortalities when compared to those transferred directly. As Tagatz (1961) had mortalities in some of the control experiments, Chittenden (1973) suggested that variation in the levels of stress, especially from handling, may explain these differences in results. For *A.aestivalis*, Chittenden (1972a) found between 90% and 100% survival when juveniles were transferred directly from 5%o to 28%o salinity. Similar conclusions may be reached from the studies of Cooper (1961), Kissil (1974) and by Richkus (1975) who found that size was not an important factor in determining the onset of the seaward migration for juvenile *A.pseudoharengus*. This suggests that some members of the genus are tolerant to high salinities at an early stage in their life, and it may not be salinity that determines their distribution. For *A.kessleri pontica*, Zambriborshch and Chin (1973) found that the larvae survived for only 15-19 minutes in water of 3%o, and for 3-7 minutes in water of 9%o.

However, in freshwater the larvae only managed to survive for approximately an hour, which would seem to indicate that the larvae were severely stressed.

This apparent ability to live either in freshwater or seawater habitats may be advantageous in that it allows selection of optimum nursery areas. In the Wye this appears to be freshwater (and possibly the estuary as well, though this area was not sampled during this study) while in the Severn the upper estuary is favoured. The use of the upper estuary as a nursery area, during the summer, has been found for A.sapidissima (Chittenden, 1969; Leim, 1924; Marcy, 1976; Massman, 1963; Williams and Bruger, 1972), for A.aestivalis (Burbridge, 1974; Hildebrand, 1963) and for A.pseudoharengus (Davis and Cheek, 1966). In contrast, Mansueti (1962) concludes that the majority of juvenile A.mediocris leave the estuary during the early summer, though some do remain and may be caught throughout the year.

It is quite common for fish species to utilize estuaries and/or inshore waters as nursery areas, McLusky (1981). The advantages of such an area must be seen in terms of better growth and survival. This may result from a better food supply and/or a reduction in possible competitors and predators. In some estuaries the supply of suitable and sufficient food was found to be at least partially responsible for restricting the juvenile stages of some fish species to estuaries (Blaber, 1974; Blaber and Whitfield, 1977). Other species present in the upper estuary of the Severn that may be competitors were Dicentrarchus labrax (Linnaeus) and Leuciscus leuciscus fry as well as members of the Gobiidae and fry of the Mugilidae. At Elmore juvenile A.fallax, when present, were the most abundant followed by L.leuciscus, while at Framilode and Newnham the Gobiidae were dominant followed by A.fallax and D.labrax. Possible predators present in the sampling area were Anguilla anguilla, Platichthys flesus as well as piscivorous birds such as the cormorant (Phalacrocorax carbo (Linneaus)), and the heron (Ardea cinerea (Linneaus)). Blaber and Blaber (1980) found that the numbers of P.carbo were highest in areas where the water clarity was greatest and insignificant in turbid areas. Thus the turbid waters of the Severn estuary may provide some protection against predation from piscivorous birds.

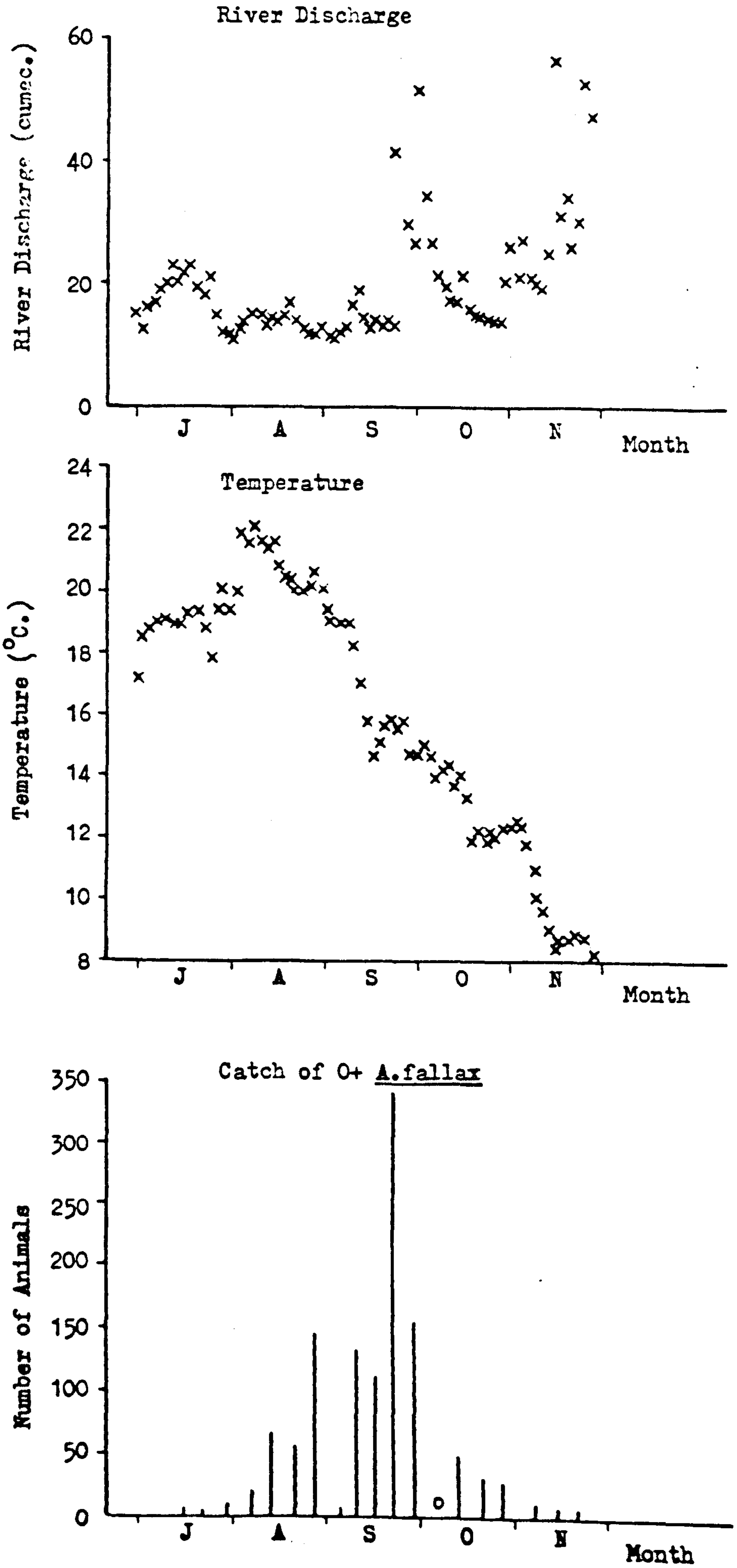
The seaward migration of juvenile A.fallax may possibly be associated with attaining a specific size, with an increase in the level of $Na^+:K^+$ Atpase, and/or with the onset of unfavourable abiotic and biotic conditions. The main environmental factor associated with the genus as initiating their seaward migration has been declining temperature. Claridge and Gardner (1978) associated peak migration of juvenile A.fallax at Oldbury with a decline in temperature below 19°C, with virtually no young being caught after the temperature had dropped to below 9°C, until the following spring. For A.sapidissima, Jessop (1975) found peak migration through non-tidal waters was reached when temperatures had fallen to below 15.5°C and that none were caught after the temperature had fallen to below 8°C to 9°C. Marcy (1976) found that peak migration of juvenile A.sapidissima occured at temperatures between 23°C. and 17.8°C, none were caught at temperatures below 6.6°C; and found that final emigration was also associated with high river discharge. Sykes and Lehman (1957) noted that juvenile A.sapidissima only move when the temperature has dropped to below 21°C and that the largest numbers migrate at temperatures less than 15.6°C. Chittenden and Westman (1967) found that juvenile A.sapidissima movement was almost complete when temperatures had fallen to below 8.3°C. Watson (1968) found that the migration of juvenile A.sapidissima started when the temperature had dropped to below 18.3°C, and there was some indication that the largest were the first to migrate. All the juveniles had left the study area when the temperature had dropped to below 10°C.

For A.pseudoharengus, Cooper (1961), Huber (1978) and Kissil (1974) found that seaward movement was normally associated with increasing water levels. Similar observations were reported by Richkus (1975) who also found that decreasing water temperature was important in the initiation of migration. It should be noted that A.pseudoharengus inhabit ponds rather than the main river at this stage of their life history. Thus one of the problems encountered by A.pseudoharengus will be detection of the outlet to the pond, Richkus (1975) proposes that this is facilitated at high discharge levels. Though for juvenile A.sapidissima, which are present in the main river, Sykes and Lehman (1957) mention that as well as decreasing temperature emigration may also be expedited by an increase in discharge.

It has already been mentioned that after periods of high discharge few if any juveniles were found in the Wye. To examine the effect of discharge on the seaward migration of the juveniles, the amount of freshwater discharge was plotted in relation to Claridge and Gardner's (1978) catch data. It was decided to use their catch data as it was much more comprehensive than that obtained during this study. The situation is illustrated in figures 6.6 and 6.7, and it appears that discharge levels do not seem important in initiating their seaward migration. In 1975 peak migration past Oldbury occured just prior to a spate, while in 1976 the discharge levels were fairly constant during the period of maximum movement. Thus, possibly, the reason for the absence of juveniles in the Wye, after periods of high discharge, may be as a result of their displacement.

Therefore, the autumn seaward migration may be designed to bring the juveniles into more favourable over-wintering areas, as the water temperature at sea is generally warmer than in the river or upper estuary, table 6.4. Their migration also has the effect of removing them from areas of high discharge.

Figure 6.6, River discharge, temperature as recorded at Saxons Lode on the river Severn and the catch of 0+ <u>A.fallax</u> at Oldbury (redrawn from Claridge and Gardner, 1978) for 1975.



(open circle indicates that no sample was taken)

Figure 6.7, River discharge, temperature as recorded at Saxons Lode on the river Severn and the catch of 0+ A.fallax at Oldbury (redrawn from Claridge and Gardner, 1978) for 1976.

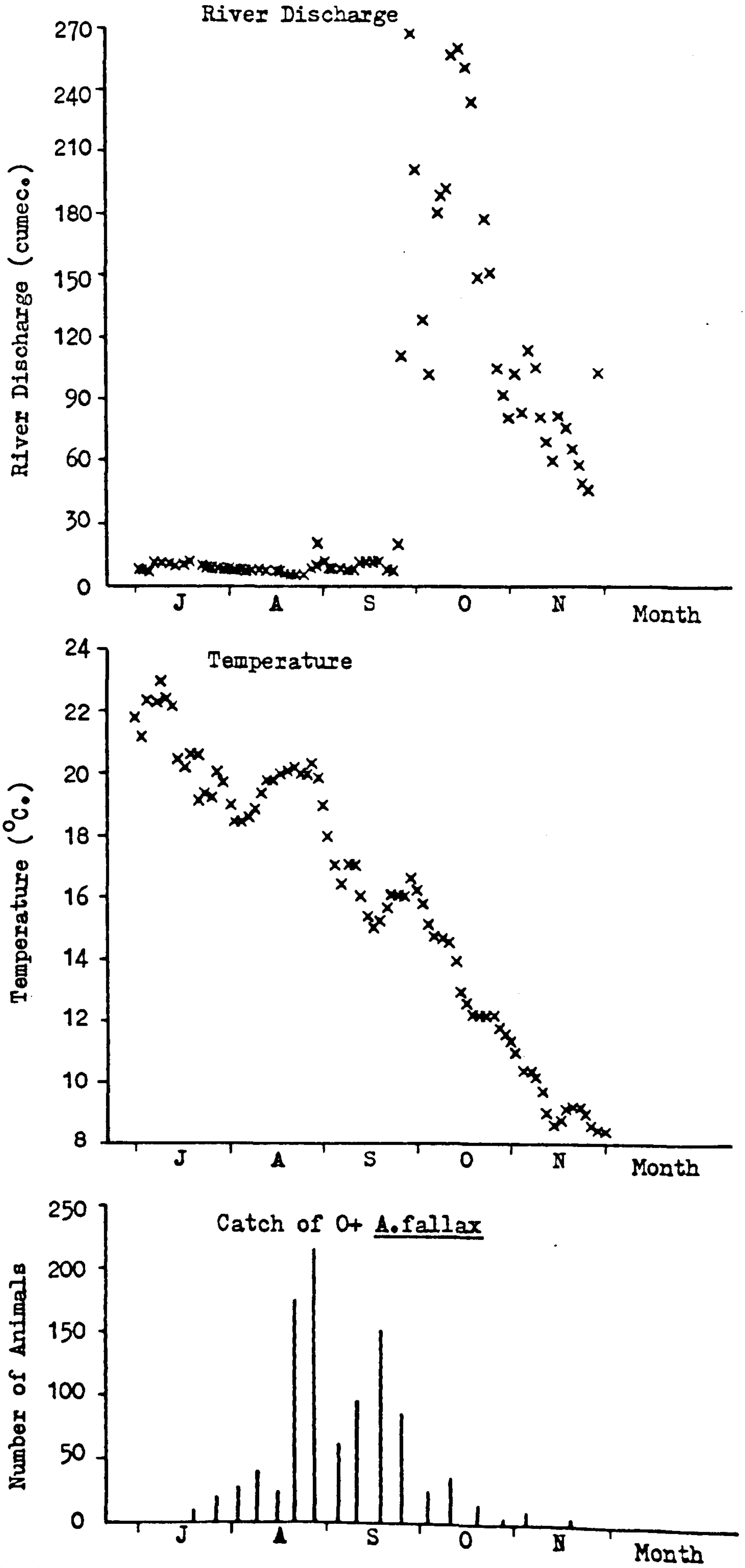
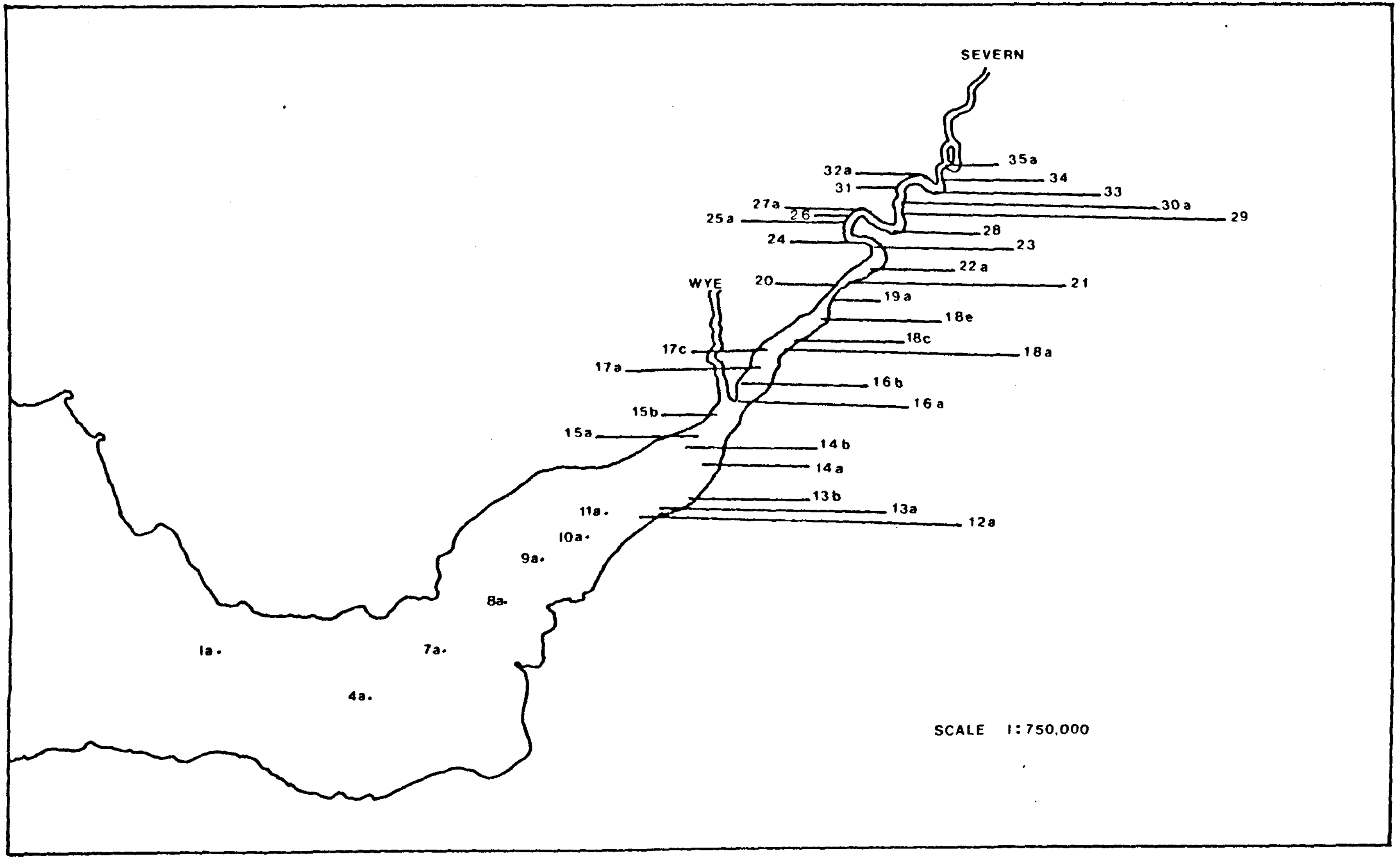


Table 6.4 Temperature (°C) at various sites (figure 6.8) in the Severn Estuary and Bristol Channel

SITE \ DATE	24.3 1976	16.4 1976	20.5 1976	14.6 1976	17.8 1976	27.10 1976	15.11 1976	9.12 1976	26.1 1977	28.2 1977	5.5 1977	20.6 1977	5.7 1977
1A	7.6	9.1	11.2	14.5	19.0	12.6	12.0	9.5	6.2	7.3	10.5	13.2	16.2
4A	7.6	8.9	10.6	14.6	19.0	13.0	11.7	8.9	5.2	7.1	10.2	13.0	15.8
7A	7.0	8.8	11.2	15.2	19.0	15.1	10.8	8.0	4.5	6.6	10.3	13.2	16.1
8A	7.0	8.8	11.3	15.0	19.0	15.2	10.7	7.8	4.2	6.7	10.2	13.4	16.1
9A	6.8	8.9	11.3	15.2	19.0	15.0	10.6	7.6	4.2	6.5	10.2	13.5	16.3
10A	6.8	8.9	11.6	15.5	19.0	14.8	10.5	7.4	4.1	6.5	10.3	13.5	16.3
11A	6.8	9.0	11.6	15.8	19.0	14.8	10.3	7.4	4.3	6.5	10.4	13.4	16.3
12A	6.7	9.1	11.8	15.8	19.0	14.9	10.2	7.0	4.2	6.4	10.5	13.4	16.5
13A	6.7	9.1	9.0	16.0	19.0	14.6	9.9	6.9	4.2	6.6	10.5	13.4	16.8
13B	6.75	9.2	11.8	16.0	19.1	14.4	9.8	6.6	4.5	6.6	10.9	13.4	
13C	6.75	9.2		16.0	19.4	14.2	9.8	6.5		6.5	10.7	13.2	17.4
14A	6.8	9.2	12.1	16.0	19.3	14.1	9.6	6.0	4.5	6.6	10.7	13.2	17.1
14B	6.8	9.2	12.0	16.0	19.2		9.6	6.0	4.5	6.5	10.8	13.2	17.2
15A	6.8	9.4	12.2	16.5	19.3	14.0	9.4	6.0	4.5	6.4	10.4	13.2	17.5
15B	6.8	9.4	12.2	16.5	19.2		9.2	5.8	4.5	6.2	11.0	13.3	17.5
16A	7.0	9.6	12.4	18.7	19.9	14.0	9.2	6.4	5.0	6.1	11.0	12.9	18.0
16B	7.0	9.6	12.3	17.6	19.5	14.0	9.2	6.0	4.9	6.2	11.0	13.2	17.8
16C	6.8	9.8	12.3	17.4	19.5	14.0	8.9	5.8	4.8	6.1	11.1	13.2	18.0
17A	6.8	9.8	12.8	17.2	19.7	14.0	8.8	5.8	5.2	6.1	11.2	13.3	17.8
17C	6.8	10.0	12.6	17.3	19.8	13.6	8.8	5.7	5.1	7.0	11.4	13.4	17.9
18A	6.8	10.0	12.5	17.3	19.9	13.9	8.7	5.6	5.6	6.0	11.3	13.3	18.1
18C	6.8	10.1	12.6	17.3	19.8	13.8	9.8	5.6	5.5	5.5	11.3	13.4	18.4
18E	6.8	10.1	12.7	17.6	20.0	13.8		5.5	5.5	7.0	11.3	13.5	18.9
19A	7.0	10.1	12.8	17.4	20.2	13.6	8.8	5.4	5.6	6.0	11.3	13.4	19.0
20	6.8	10.0	12.6	17.3	20.1	13.5	8.4	5.3	5.8	5.3			
21	6.9	10.0	12.6	17.2	20.1	13.6	8.4	5.0	5.6				
22A	6.8	10.0	12.8	17.4	20.2	13.3	8.4	5.0	5.8		11.1	13.2	18.4
23	6.6	10.0	12.8	17.5	20.1	13.4	7.7	4.6	5.7				
24	6.4	10.0	13.0	17.5	20.0	13.0	7.2	4.2	5.6				
25A	6.3	10.0	13.2	17.7	20.1	12.9	7.0	4.0	5.6		11.1	13.2	19.2
26	6.2	10.0	14.1		20.2	12.6	6.8	4.0					
27A	6.0	10.0	14.3	18.0	20.8	12.4	6.8	4.0	5.9		10.7	13.0	19.7
28		10.0		18.2	20.8	12.2							
29		10.0		18.4	20.7	12.2							
30A		10.0		18.8	20.6	12.2					10.3	12.8	20.9
31		10.0		19.6	21.4								
32A				19.8	20.9							12.7	20.2
33				19.8									
34				19.8									
35A				20.1								12.9	20.5

Figure 6.8, Sampling sites, for temperature, in the Bristol Channel and Severn estuary.



Chittenden (1972b) has shown that juvenile A.sapidissima are affected in their swimming ability, their ability to equilibrate themselves and their reaction to visual stimuli, when exposed to temperatures between 4^{o}C and 6^{o}C. Tagatz (1961) observed 100% mortalities when temperatures were dropped abruptly from 21.1^{o}C to between 12.8^{o}C and 7.2^{o}C, reduced mortalities were achieved by gradually decreasing the temperature. Abrupt transfers to an environment approximately 4.4^{o}C colder than the initial, resulted in between 30% and 40% mortality after 48 hours. Colby (1973) observed that at low temperatures (less than 3^{o}C) landlocked A.pseudoharengus exhibit signs of severe distress as well as mortalities. Similar findings were reported by Otto et al. (1976) of a lower lethal temperature of 3^{o}C with an incipient lethal temperature of between 6^{o}C and 8^{o}C. Stanley and Colby (1971) found that when A.pseudoharengus in fresh or saltwater experienced cold temperatures (3^{o}C) there was a shift in plasma sodium and calcium concentration towards that of environmental levels, i.e. a collapse of their osmoregulatory cabilities. Similar levels of mortality were present in both fresh and salt water indicating that salinity does not modify their ability to tolerate acute temperature stress.

The over-wintering areas of other anadromous alosids has been found to be in the outer estuary or in offshore areas. Hildebrand and Schroeder (1928) found juvenile A.aestivalis and A.pseudoharengus over-wintering in Chesapeake bay, a few A.sapidissima were also obtained. Milstein (1981) found juvenile A.aestivalis, A.pseudoharengus and A.sapidissima in an area just offshore of the Mullica estuary (New Jersey) from December to April, with virtually none being caught between May and November. Holland and Yelverton (1973) found that juvenile A.sapidissima could be caught offshore between December and February; A.pseudoharengus were mainly found in inshore areas and migrated to offshore areas where they were most abundant during January and February; A.aestivalis were present in offshore areas between December and April. From the survey by Haedrich and Haedrich (1974) there is some indication that juvenile A.aestivalis and A.pseudoharengus over-winter in the Mystic estuary. Mansueti (1962) observed that a small residue of A.mediocris could be found all year round in the estuary.

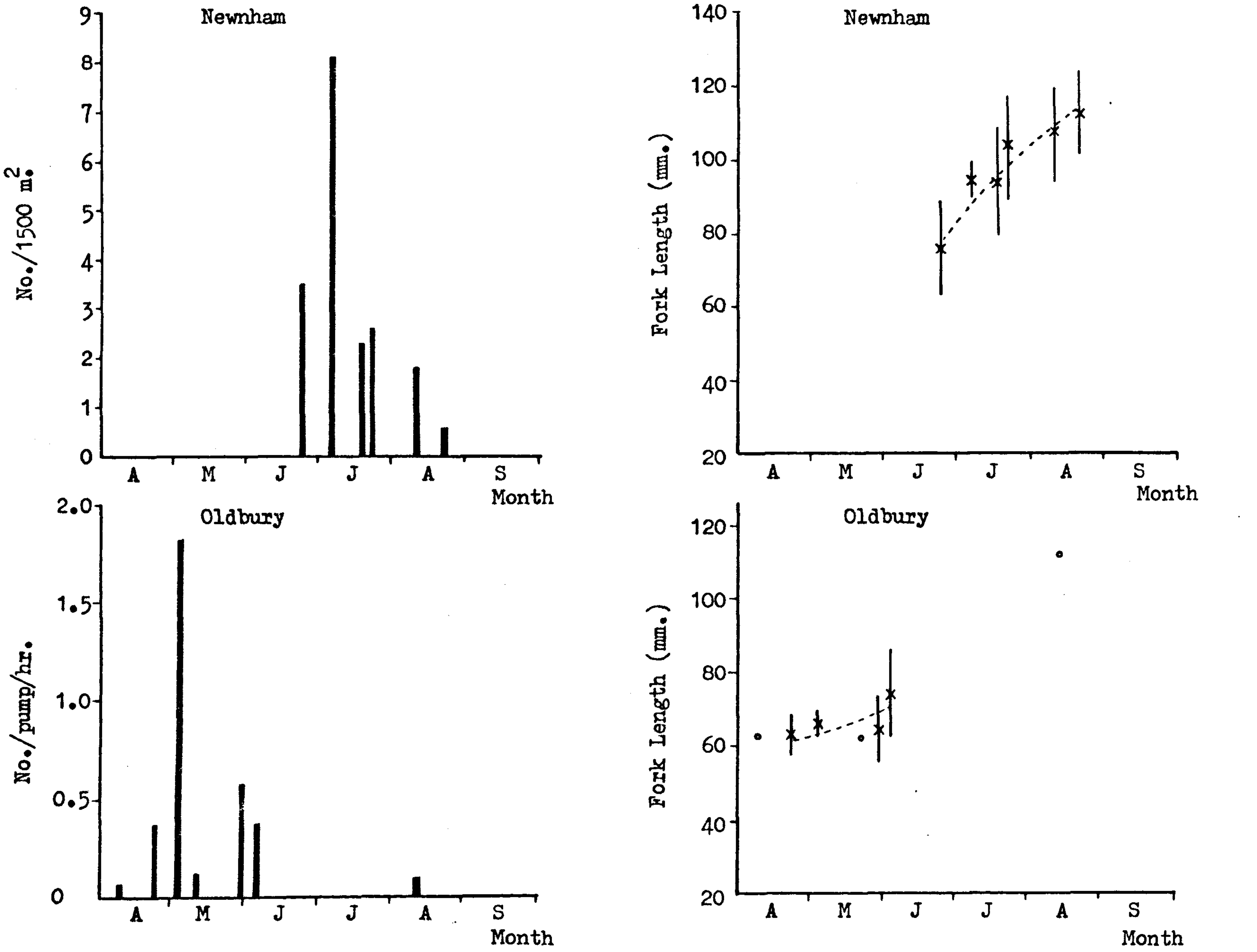
The response of landlocked A.pseudoharengus, from Lake Michigan, which migrate to deeper waters during the winter, where the temperatures are higher (Wells, 1968), may similarly be designed to place the fish into more favourable over-wintering areas.

D. One Year Old A.fallax

Towards the end of April (1980) the number of juvenile A.fallax (now nearly one year old) caught at Oldbury started to increase. They reached a peak during the start of May and then the numbers started to decline, figure 6.9. Further upriver at Newnham these one year olds were first caught towards the end of June (1980), and reached peak abundance in July. After July (1980) the numbers at Newnham declined until the middle of August, following which no more were caught at Newnham, figure 6.9. (It should be noted that in August, 1980, sampling was carried out using the large fry net, prior to which the 20 m. micromesh seine was used. Thus the densities are not strictly comparable.) From the catch data it would appear that juvenile A.fallax make an inshore migration during the spring - summer and may penetrate as far upstream as Elmore where a few were caught in July (1980).

It would therefore appear that the juveniles may over-winter in the outer estuary or in coastal waters and migrate into the

Figure 6.9, The density and size (mean ± 95% confidence limits) (open circle represents a single individual) of 1+ <u>A.fallax</u> from two sites in the river Severn, from April to September 1980.



inner estuary during the summer, similar conclusions were reached by Bracken and Kennedy (1967) for A.fallax. Hass (1965) observed in the Elbe the reappearance of one year olds during April. Cunningham (1891-92) reported observations by Metzger and Hoek from the Meuse estuary (Holland), of juvenile A.fallax present in the estuary during the spring. These fish ranged in size from 72 mm. to 92 mm. (total length) and were believed to be one year olds. Similarly, Hoek (1900) was able to obtain juvenile A.fallax of total length between 70 mm. and 150 mm. from the lower reaches of the Rhine in the spring. Claridge and Gardner (1978) found that juvenile A.fallax reappeared during the spring and associated this with a sharp rise in water temperature above 7°C. They concluded that a small portion of the 0 + group over-winter in the river and only start to migrate when the water temperature began to rise, this movement being aided by spring freshwater spates. However, their conclusions were based on samples taken from one point and thus cannot accurately assess direction of movement. However, as in this study they observed that the last of the one year olds had left the inner estuary by late summer. A similar inshore migration may exist for A.pseudoharengus in Chesapeake Bay. Kaufman et al. (1980) reported that, two distinct size classes of A.pseudoharengus could be caught during the summer. The smaller group were believed to represent the 0 + fish, and the larger the 1 + or older, and similar to the situation observed for A.fallax the larger group were the first to leave the area. However, a non-anadromous population of A.pseudoharengus have been found to exist in the northern part of Chesapeake Bay (Foerster and Goodbred, 1978), and it is possible that the larger group may represent members of this resident population.

The inshore migration of the one year olds may well be for the same reasons already mentioned for the 0 - group, namely increased growth and survival. The inshore areas are generally warmer during the summer months than offshore areas and increased temperature up to an optimum level increases feeding and growth rate, assuming other factors remain constant. Thus inshore areas would be more preferable than offshore areas, assuming no difference in food availability. Reckseik and McCleave (1973) observed that A.aestivalis, A.pseudoharengus and A.sapidissima, when present in the estuary, showed a tendency to be strongly associated with the warmest water.

Salinity may also be having an effect, Stickney and White (1973) found a beneficial effect of low salinity on growth of Paralichthys lethostigma Jordan and Gilbert, at high temperatures while Deubler (1960) found slightly better growth occured at high salinities in colder water. The reverse situation has been found by Kinne (1960) for Cyprinodon macularius Bair and Girard, where the optimal conditions for growth at high temperatures are at high salinities, and at low temperatures are at low salinities. Thus it is possible that a similar temperature - salinity interaction may be affecting the growth of juvenile A.fallax, which assuming selection for optimizing growth rate, could explain their offshore winter and inshore summer migration.

Only very few immature A.fallax exceeding one year old were caught in the estuary and thus it is presumed that these fish adopt a totally marine existance.

E. Year-Class Strength

The 1980 year-class in both the River Wye and Severn was poor in relation to those of 1979 and 1981 in the Severn, table 6.2 and figures 6.3, 6.4 and 6.5. Temperature, as one of the possible environmental factors influencing year-class strength, in fishes, has been shown to be important (Le Cren, 1977; Mann, 1979) as has river discharge (Marshall, 1982; Scarnacchia, 1981; Stevens, 1977).

The mean daily temperature, and the number of degree days greater than 14°C on the River Severn (at Saxons Lode) for the years 1979, 1980 and 1981 are shown in table 6.5. The temperature was taken from the 15th May, as this was thought to be the earliest time of spawning, until the end of August. The results shown in table 6.5 indicate that in 1980 the temperature was higher during the latter half of May and the whole of June, in July it was lower, and in August the mean lay in between that of 1979 and 1981. As low temperatures have been generally associated with 'poor' year-classes, then to explain the 'poor' 1980 year-class the critical month appears to be July.

For some members of the genus temperature has been found to affect juvenile survival. Shoubridge and Leggett (1978) found that 58% of the variation in year-class strength for A.sapidissima could be predicted from water temperatures during and shortly after spawning, thus indicating that the egg and larval stages represented the critical period. Bradford et al. (1968) have shown for A.sapidissima that the optimum temperature for hatching larvae lies between 15.56°C and 26.67°C. Above which the larvae showed increased amounts of crippling and below 10°C the larvae died quickly after hatching. Within this temperature range, varying the incubation temperature did not appreciably affect the viability of the larvae. Schubel and Auld (1972) showed that raising the temperature by 6°C from 18.5°C, in a matter of minutes, did not markedly effect hatching success. For A.pseudoharengus hatching occured between 6.89°C and 29.39°C with the optimum being 17.78°C. Below 10°C a large percentage of the larvae were deformed and the post-larvae had not developed a functional jaw, Edsall (1970).

However, assuming food supply unlimited and all other parameters remain equal then at higher temperatures (up to an optimum level) the young will grow faster and thus pass through the stage when they are

Table 6.5 Mean daily temperature ± 95% confidence limits, and the number of degree days greater than 14°C as recorded at Saxons Lode on the River Severn for the years 1979, 1980 and 1981

15th May to 31st May inclusive

	1979	1980	1981
Mean Daily Temp °C	12.77	16.98	14.34
95% Confidence limits	± 0.846	± 0.61	± 0.331
Degree days > 14°C	5.1	50.6	7.7

1st June to 30th June inclusive

	1979	1980	1981
Mean Daily Temp °C	15.93	17.29	16.5
95% Confidence limits	± 0.786	± 0.521	± 0.326
Degree days > 14°C	64.7	98.8	75.0

1st July to 23rd July and 30th & 31st July inclusive (recorder malfunction 1980)

	1979	1980	1981
Mean Daily Temp °C	18.91	17.2	19.57
95% Confidence limits	± 0.414	± 0.494	± 0.414
Degree days > 14°C	122.7	79.9	139.2

1st August to 31st August inclusive

	1979	1980	1981
Mean Daily Temp °C	16.87	18.55	20.21
95% Confidence limits	± 0.554	± 0.285	± 0.369
Degree days > 14°C	89.0	141.2	192.4

most susceptible to predation (Mann, 1979; Mills, 1982). Hiyama et al. (1972) found that large O.keta were not as susceptible to predation as smaller ones, on their seaward migration.

Large size has also been shown to reduce the effect of stressful environmental conditions. The over-winter survival rates of 0 + group Salvelinus fontinalis (Hunt, 1969) and some populations of Lepomis macrochirus Rafinesque and Micropterus salmoides (Lacépède), (Toneys and Coble, 1979) have been found to increase with increasing size. Similar findings have also been reported by Wandsvik and Jobling (1982) for Salvelinus alpinus (Linnaeus).

Temperature may also affect food supply, which for juvenile A.fallax in the Severn estuary was found to be dominated by copepods and mysids (chapter seven). For some copepods, development rate has been found to increase with increasing temperature (McLaren and Corkett, 1981; Sarvala, 1979). Thus under conditions of excess food and assuming that copepod size is unaffected by temperature then an increase in production would be expected with increasing temperature. However, studies by Lock and McLaren (1970) and by Sarvala (1977) have indicated a possible inverse relationship between copepod size and temperature.

If temperature has a significant effect on year-class strength at the egg and larval stage, as in the case of A.sapidissima then the critical time for A.fallax would be from the middle of May to the end of July. Thus, if temperature alone was significantly affecting year-class strength, then from the temperature regimes prevalent over the three year period of study (table 6.5) a 'good' 1980 year-class may have been expected. Thus it appears that temperature may not have been the main factor causing the 'poor' 1980 year-class.

It has also been shown that river discharge and level may be important in determining year-class strength. Kuznetsov (1975) found a strong correlation between the spawning of some Cyprinidae and water levels during the spawning period. Similar findings were reported by Martin et al. (1981) who found a significant increase in the abundance of a number of reservoir fishes, associated with an increase in the water level, suggesting that a flooded shoreline provided a more suitable substrate as well as protective covering for the early life stages. The results of an increase in abundance as a consequence of an increase in available habitat, occuring during periods of high river flows, have also been shown by Stevens (1977) for Roccus saxatilis (Walbaum). Similar findings were reported by Scarnecchia (1981) of a significant positive correlation between discharge and the catch of O.kisutch two years later.

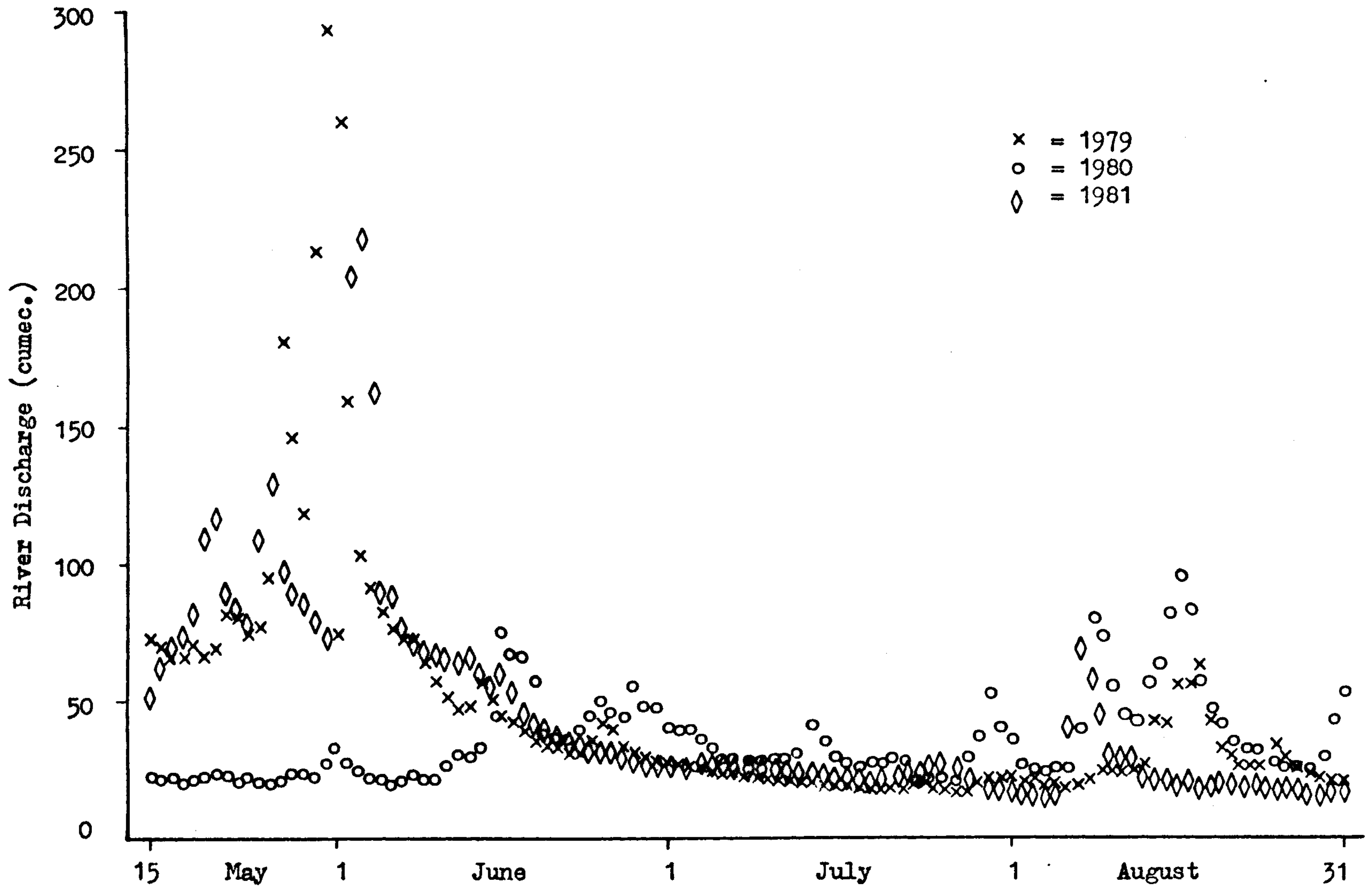
Increasing river flow, as well as having the advantageous effect of increasing the amount of available space, may, however, also have deleterious effects, causing displacement of the early life stages, contribute to their mechanical damage as well as causing the deposition of material after a period of high flows. For salmonids, Rulifson (1979) reported that if the percentage of silt and sand less than 3 mm. in diameter exceeded 20% mortality of eggs and fry increased sharply. This may be due to a reduction in the flow of water through the redd, and thus reduced oxygen supply leading to increased egg mortality (Coble, 1961). Crisp et al. (1975) have reported large fluctuations in the abundance of Salmo trutta, which may be associated with spates causing high mortality of the eggs and aelvins, Mann (1979). Similar conclusions have been reached by Seegrist and Gard (1972), Wickett (1958) and by Elwood and Waters (1969) who also reported a reduction in the invertebrate density which in turn caused a decrease in the growth rate of S.fontinalis. In marine fishes the availability of suitable food items, just after the yolk sac has been completely absorbed, has been considered one of the main factors in determining year-class strength, May (1974). In exceptional circumstances as observed by Hoopes (1975) 96% of the O-group of S.fontinalis was lost when normal summer flow levels were exceeded by 150 times. Other year-classes were also reduced but less drastically.

Decreasing river flow, as well as having the effect of reducing the amount of available habitat, may cause the drying up of the principal spawning areas. This was thought to be the cause of the 'poor' 1976 year-class for Esox lucius (Linnaeus) in the River Frome, Mann (1979).

The mean daily discharge on the River Severn (at Saxons Lode), for the three years of the study, are shown in figure 6.10, and for two years on the River Wye (at Belmont), in figure 6.2, from the middle of May until the end of August. It is evident that the river discharge from the middle of May until the middle of June was greater in 1979 and in 1981 than in 1980. These greater flows would increase the spawning area available. However, any early spawning might result in the displacement of the eggs and/or larvae into unsuitable environments, and/or in their damage. In 1979 and in 1981 the water temperatures were lower than in 1980 (table, 6.5) and thus spawning may have been delayed (see chapter four), so avoiding the deleterious effects of the floods. The level of discharge after mid-June 1979 and 1980, was low and relatively stable until the beginning of August. In contrast the discharge levels in 1980 after mid-June were continuously fluctuating as the river levels were heightened by a series of small spates during the rest of the summer.

The combination of high flows followed by low flows may have its disadvantages. It has already been indicated that A.fallax has a preference to spawn in shallow areas (chapter four) and in periods of low flow these may become exposed. However, it is not yet known if water velocities affect the timing of spawning and it may be that, under conditions of high flows, spawning would be delayed until more

Figure 6.10, The mean daily discharge for the river Severn, at Saxons Lode, from the 15th May to the 31st August 1979,1980 and 1981



favourable conditions prevail. In 1980, when low flows were followed by a series of spates there existed the possibility that the eggs and larvae may have been displaced and/or damaged.

Massman (1952) found for A.sapidissima that the density of eggs in the drift samples increased with increasing current velocity. Mills (1981) showed that the number of Leuciscus leuciscus eggs in the drift increased with an increase in discharge levels. Similar findings were reported for S.trutta by the Ministry of Agriculture Fisheries and Food and the National Water Council (1976) who reported that a large proportion of the egg population may be dislodged by bed water volocities of 0.5 m./s. During 1980 the flow over the spawning beds was recorded as 0.95 m./s. at Courtfield and 0.65 m./s. at Monmouth, on the 17th June. As these currents would cause the scouring out of S.trutta redds, then in the case of A.fallax where the eggs are not protected by being buried in the substrate, a large proportion of the eggs might be expected to be displaced. Ottoway and Clark (1981) found that juvenile S.trutta moved downstream in association with an increase in water volocity, though this movement could not be assessed as active or passive. They also found that the reaction to changes in water velocity altered with developmental stage. No downstream movement of fry in the yolk sac stage was observed and concluded that the fry evaded the increase in current by settling in the gravel. Once the yolk sac was absorbed and the fry were actively seeking food they became more vulnerable to current velocities and exhibited downstream movement in association with increasing flows.

It, therefore, seems possible that the 'poor' 1980 year-class resulted from the eggs and larvae being either damaged or displaced into unfavourable environments, such as areas of high salinity and high turbidity. Holliday (1969) reviewed the literature on the effects of salinity on the early developmental stages of fishes and it appears that in a number of species the most vulnerable stages are just prior to gastrulation and just after the larvae have hatched. For *A.caspia caspia*, Perceva (1939) reported that eggs could be successfully hatched in seawater as well as freshwater. For *A.sapidissima*, Leim (1924) found that salinities up to 15‰ did not effect hatching success, though the larvae at 15‰ started to show some deformities, however, this may have been a function of temperature. At a salinity of 22.5‰ hatching success had decreased markedly.

Auld and Schubel (1978) found that the hatching success of three species of *Alosa* were not significantly affected by levels of suspended solids up to 1000 $mg.L^{-1}$ (the limit of the study). However, the larvae of *A.sapidissima* were less tolerant and survival was significantly reduced by levels equal to or greater than 100 $mg.L^{-1}$.

Marcy (1976) found that 46% of the total variation in the production of juvenile *A.sapidissima* could be explained by river discharge, during June, though this was not significant at the 5% level of probability. However, a multiple regression relating juvenile abundance to both density independent and density dependent factors, which explained 86% of the total variation, found river discharge to be the most important variable, followed by temperature, and lastly by the number of adults returning to spawn. However, Leggett (1977) reported that of these three variables river discharge was the least important, explaining between 0.7% and 3% of the variation in juvenile abundance of *A.sapidissima*. (This difference in the result was caused by miscalculation of the data by Marcy (1976) (Leggett, pers. comm.).

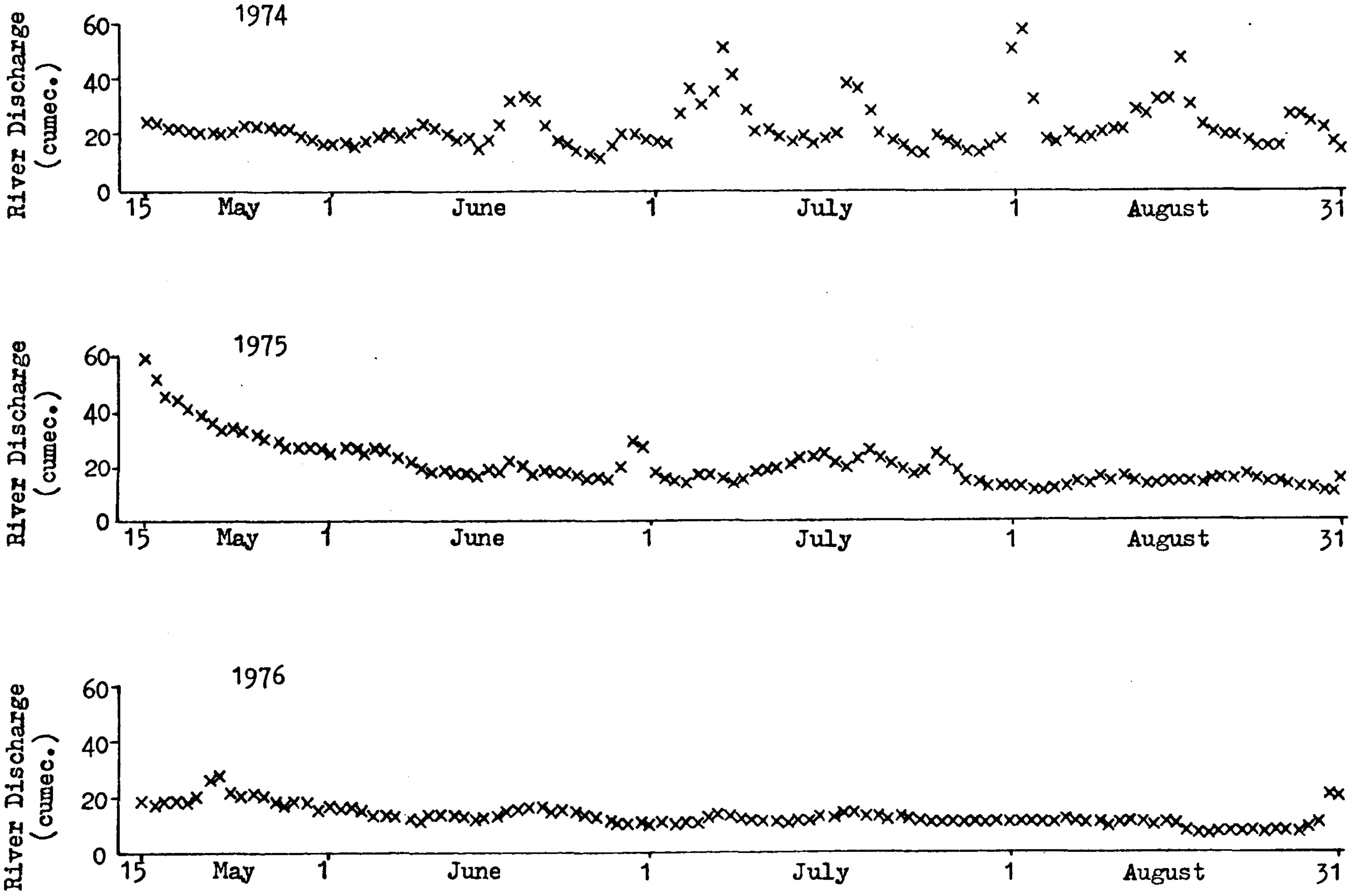
In the Delware River, Chittenden (1969) assumed that pollution was one of the main factors affecting year-class strength in *A.sapidissima*. As the failure of what appeared to be strong year-classes to later recruit to the fishery was attributed to 'catastrophic' losses of the young as they passed through the heavily polluted Philadelphia area, which had very low levels of dissolved oxygen.

As well as density independent factors Marcy (1976) found that 64% of the total variation in the abundance of juvenile A.sapidissima could be explained by the number of adults available to spawn. The role of density dependent factors regulating abundance, in A.sapidissima, was also demonstrated by Leggett (1977), where egg to adult survival decreased as the number of potential spawners increased. There was also a reduction in juvenile growth rate with increasing size of the spawning stock. Other factors that may be operating are differences in the level of competion and in the intensity of predation.

From the study by Claridge and Gardner (1978) and from data presented in chapter three and four, there should exist some relationship between river discharge and the relative strength of the 1974, 1975 and 1976 year-classes. The discharge levels for these three years are shown in figure 6.11. In none of the three years did the level of discharge between mid-May and mid-June reach the high levels of 1979 and 1981 and this may have limited their spawning areas. It is evident from figure 6.11 that the pattern of discharge in 1974 was very similar to that of 1980, though the first spate during the middle of June was not as large, the magnitude of the fluctuations in July were similar for both years. In contrast to the 1974 situation, the discharge pattern for 1975 and 1976 were relatively stable. Thus it appears that, as in 1980, the early stages of the 1974 year-class were displaced or damaged. Data on temperature (at Saxons Lode) was not available for the whole of 1974 and for 1975 until June.

It thus seems that spates occurring between mid-June and the end of July have a deleterious effect on year-class strength and such conditions produced 'poor' 1974 and 1980 year-classes.

Figure 6.11, The mean daily discharge for the river Severn, at Saxons Lode, from the 15th May to the 31st August 1974, 1975 and 1976



The prospect of total population collapse or large fluctuations in the total population from environmentally induced variations in reproductive success may be buffered by a strategy of repeat spawning (Ricker, 1954) or by a semelparous population (such as the genus *Oncorhynus*) maturing at different ages or a combination of both as is the case for the genus *Alosa* and *Salmo*. It is, however, doubtful that iteroparity has evolved so that large fluctuations in reproductive success of a population will be buffered, (Parker, pers. comm.) but it is a natural consequence of such a strategy.

CHAPTER SEVEN

DIET

Introduction

Comparatively little work has been specifically carried out on the food of anadromous populations of A.fallax. Most investigations have examined the diet of the spawning population in, or entering, freshwater (Bracken & Kennedy, 1967 Claridge & Gardner, 1978) and at sea (Bracken & Kennedy, 1967; Minchen, 1977; Rae and Lamont, 1961 & 1962a; Rae and Wilson, 1952, 1956a + b, 1961; Wheeler, 1969), no published information was found to exist on the diet of the larvae and young while in freshwater either in the rivers or the estuaries.

The majority of the published data on diet, exist for the American species, mainly the commercially important A.sapidissima (Atkinson, 1951; Bigelow & Schroeder, 1953; Chittenden, 1976; Domermuth 1976; Domermuth & Reed, 1980; Hildebrand, 1963; Holland & Yelverton, 1973; Leim, 1924; Levesque & Reed, 1972; Massman, 1963; Mitchell et al., 1925; Walburg, 1956; Watson, 1968; Williams & Bruger, 1972) as well as for landlocked populations of A.pseudoharengus (Edsall, 1964; Gannon, 1972; Janssen & Brandt, 1980; Kohler & Ney, 1980; Morsell & Norden, 1968; Norden, 1968; Rhodes & McComish, 1975; Rhodes et al., 1974; Webb & McComish 1974; Wells, 1980). The diets of the anadromous and non-anadromous species inhabiting the Caspian Sea, Black Sea and the Sea of Azov have been reviewed by Svetovidov (1963). Interest in the diet and feeding behaviour of A.pseudoharengus has resulted from its effect on the zooplankton community in lakes (Brooks & Dodson, 1965; Hutchinson, 1971; Vigerstad and Cobb, 1978; Warshaw, 1972; Wells, 1970). Laboratory based studies on feeding behaviour have been carried out on A.pseudoharengus by Janssen (1976, 1978 a + b) and

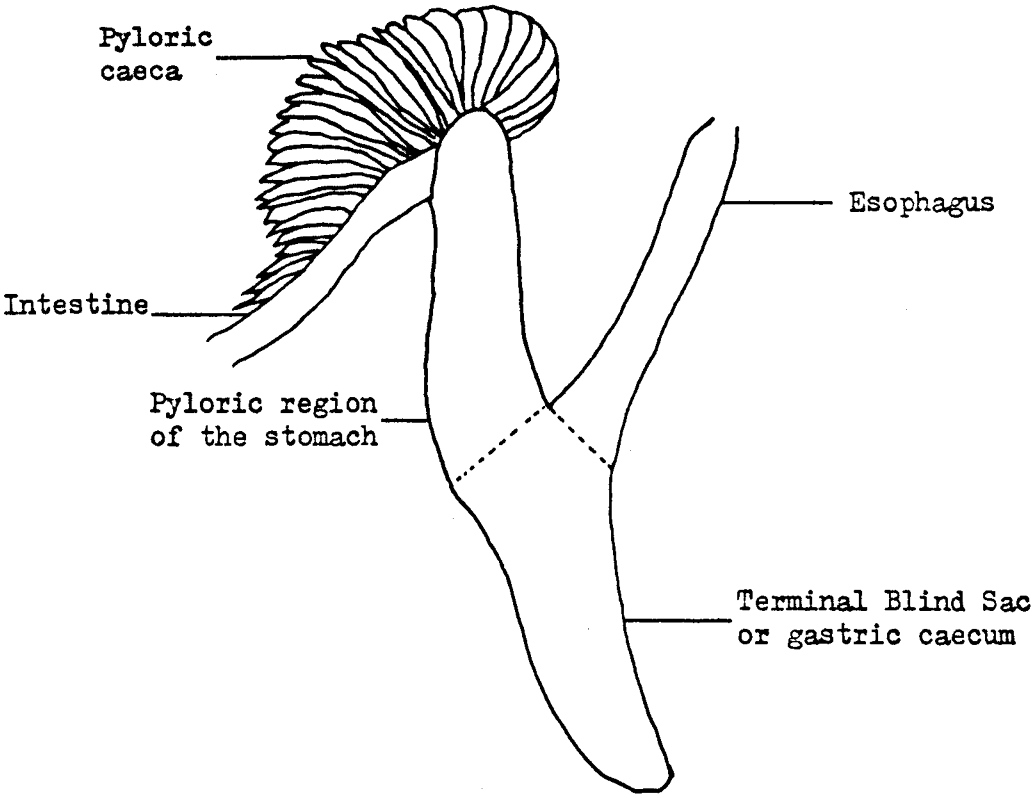
Hoagman (1974). Svetovidov (1953), cited by Nikolsky (1963), has demonstrated the correlation between the diet in various members of the species Alosa caspia and their morphology, with special reference to the number of gill rakers and pyloric caecae.

The purpose of this study was to investigate the freshwater feeding habit of the adult population, which is important in terms of their reproductive strategy. It has been shown that a considerable part of the population are repeat spawners and the source of energy required for post-spawning survival may either come from feeding during the migration, or from stored energy reserves, or a combination of both. The feeding habits of the young were also investigated to provide some information about their feeding niche in rivers, and where possible to compare A.fallax with other alosid populations. These objectives were tackled by analysing the stomach contents of fish caught at various sites, taken between April and October, 1979 and 1980.

A. Materials and Methods

The fish were caught using the methods described in chapter two. The juveniles were preserved as described in chapter six, and the stomachs of the adults in a 5% solution of formalin. The fish were aged as described in chapter three. The anatomy of the stomach of alosids has been described by Harder (1975) and is shown in figure 7.1. It is a Y shaped organ, consisting of two parts, a terminal blind sac or gastric caecum, thin-walled and presumably used for storage, which leads into the pyloric region of the stomach where the muscle wall is much thicker thus enabling food items to be crushed. In all cases, except for the larvae, the composition of the diet was analysed from the contents of the blind sac because these items were still fairly recognisable as opposed to those in the pyloric region of the stomach which had been crushed.

Figure 7.1, The stomach of Alosa fallax.



The organisms, where possible were identified to order and in some cases to species. The methods used in stomach analysis have been reviewed and discussed by many authors, notably Ball (1957), Berg (1979), Hynes (1950), Hyslop (1980), Sillah (1981) and Windell & Bowen (1978). In this study, the stomach contents were analysed using the occurrence, number and volume methods, as these would give the most complete picture of any one item's dietary importance. In summary, the occurrence method is qualitative, indicating the relative importance of a prey organism to the number of feeding fish and should be used in conjunction with a quantitative method. In this way one can see if the diet of any individual fish has greatly affected the overall result. Of the quantitative methods, both percentage number and percentage volume, have their limitations. The former over emphasizes small organisms while the latter tends to over emphasize large ones, as well as attempting to quantify amorphous material, thus both methods taken together provide a less biased picture. The volume of each category was measured, for large organisms, using volume displacement and for small organisms using a measuring slide devised by Chubb (1961). For the 0+ fish volumes of individual food categories were not taken but were estimated, from the total volume of the stomach contents.

An estimate of stomach fullness was made using the points method following that of Ball (1957), Pedley (1975), and Sillah (1981)

FULLNESS ESTIMATE	POINTS ALLOCATED
Empty	0
Trace	1
1/4 Full	2
1/2 Full	4
3/4 Full	6
Full	8
Distended	10

and where possible the mean and 95% confidence limits were calculated.

Most sampling took place during the day, though adults were also obtained during the night. Domermuth (1976) found that A.aestivalis and A.sapidissima fed mainly during daylight hours, with a peak during early and late evening respectively. Similar observations were recorded by Levesque and Reed (1972) and by Massman (1963). Sushkina (1939, 1940, 1942) cited by Svetovidov (1963) observed two feeding activity peaks for A.kessleri kessleri, a major one in the evening (1800-2000) and a minor one in the morning (0800). Janssen (1978b) showed that A.pseudoharengus were able to feed in the dark and the adaptiveness of this behaviour has been shown by Janssen and Brandt (1980). In the estuary, all samples for juveniles were taken at low water. In 1979 sampling was carried out on both neap and spring tides, while in 1980 only neap tides were sampled.

In those cases where the complete sample was not analysed, a random sample was taken using random numbers or using the method described by Coles (1977), T and F tests showed no significant difference between their mean lengths and their variances for those samples respectively. However, in 1980 the sample of spawning migrants consisted of the first thirty fish and visual inspection showed no change in feeding activity. In the one instance (August 1980, Newnham) when more than thirty fish were caught on both sampling occasions, equal numbers were taken from each sample and combined.

B. Adults

Pre-spawning A.fallax were collected from the Severn estuary (near Lydney) during the upstream migration period in both 1979 and 1980. The composition of their diet is shown in table 7.1 a + b. In general, the contents did not appear fresh and could possibly be considered to represent the more indigestible remnants of more active sea or estuarine feeding. In both years Gammarus species

Table 7.1a + b The composition of the diet of pre-spawning <u>A.fallax</u> caught in the Severn estuary (at Lydney) during April and May 1979 and 1980.

(a) 1979 Number examined = 30; Number empty = 10;

Fullness = 1.5 ± 0.56

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Actual	%
Mysidae	3	15	3	1.96	60	5.95
Gammaridae	16	80	138	90.2	673	66.77
Idoteidae	1	5	1	0.65	15	1.49
Decapoda	1	5	1	0.65	55	5.46
Eggs	6	30	10	6.54	8	0.79
Detritus	14	70			197	19.54
TOTAL			153	100	1008	100

(b) 1980 Number examined = 30; Number empty = 19;

Fullness = 0.88 ± 6.98

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Actual	%
Mysidae	1	9.09	122	65.24	635	50.8
Gammaridae	9	81.82	65	34.76	460	36.8
Detritus	6	54.55			155	12.4
TOTAL			187	100	1250	100

were the most frequent organisms encountered and in 1979 represented the most important food item both numerically and volumetrically. However, in 1980, mysids might be considered to be the most important food item though this can be attributed to just one fish which entered with its storage sac half full of mysids (74% numerically, 59.1% volumetrically, of the total sample), as well as Gammarids and detritus.

In their earlier study, Claridge and Gardner (1978) found only nereid jaws and small polystyrene spherules in the stomachs of upstream migrants, indicating that little, if any, feeding was taking place during the spawning migration. Kennedy (pers. comm.) found that A.fallax from the Rivers Severn and Exe contained only mysids. In the stomachs of A.alosa from the Rhine, Barfurth (1876) found only remnants of food organisms. Similar findings have been reported for A.sapidissima (Bigelow & Schroeder, 1953; Hildebrand, 1963), A.pseudoharengus (Bigelow & Schroeder, 1953, Cooper, 1961; Hildebrand, 1953), for A.mediocris (Pate, 1972) and for Alosa alabamae Jordan and Evermann (Hildebrand, 1963). Sirotenko (1969) found that the feeding intensity for A.kessleri pontica fell during the pre-spawning migration period.

The pre-spawning fish in the Severn had a slightly higher mean fullness index in 1979 (1.5) than in 1980 (0.88), with a corresponding lower percentage of empty stomachs 33.3% (1979) compared with 63.3% (1980). These results suggest that the adults, entering the estuary on their spawning migration, are not feeding actively.

In 1979 samples of adults from freshwater were taken by rod and line at Powic Weir on the River Teme, Diglis Weir on the River Severn and from a number of sites on the River Wye. No samples were taken for diet analysis during 1980. The contents of the 1979 sample are shown in tables 7.2 a, b and c and it is evident that the majority of the stomachs were empty. Of those fish from the River Teme which contained items in the gut, plant material and plastics constituted the majority of the items with relatively little animal material present. However, in the Wye, a relatively small amount of feeding on animal material, mainly emerging adult Trichoptera was evident. Similar findings were reported for A.fallax from the River Suir by Bracken and Kennedy (1967) who found that though stomachs were generally empty a few contained Ephemeroptera, winged Simulium species, Trichoptera (Hydropshyche species), plant material and/or shad spawn. Atkinson (1951) showed that spawning migrants of A.sapidissima kept under artificial conditions did feed and concluded that the reason for their empty stomachs whilst in freshwater was that the available food items were too small to be utilised by the fish. Chittenden (1976) found that the stomachs of adult A.sapidissima in freshwater frequently contained a few insects, occasionally a large number of Ephemeroptera and sometimes young A.sapidissima and Percina peltata (Stauffer). Svetovidov (1963) mentioned that little, if any, feeding is shown by A.kessleri kessleri during the spawning period. However, Chajanove (1940) cited by Atkinson (1951) observed that A.caspia caspia fed voraciously during the spawning period and similar findings were reported for A.kessleri volgensis (Tanasiichuk, 1948; cited by Svetovidov, 1963) and A.kessleri pontica (Belyy, 1970), with the latter feeding mainly on cladocerans and copepods.

It certainly appears from the results that the pre-spawning adult A.fallax do not feed actively while in freshwater. It seems that this species must rely on stored energy reserves or must suffer large post-spawning mortalities. The indications are that energy for the spawning migration comes from stored fat reserves, (see chapter four).

Table 7.2a, b + c The composition of the diet of Adult A.fallax while in freshwater

(a) Powic Weir - River Teme (1979) n = 62; empty = 43; (Fullness = 0.574 ± 0.27)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Actual	%
Ephemeroptera N.	1	5.26	1	25	5	0.56
Lymnaeidae	1	5.26	1	25	5	0.56
Alosa scales	1	5.26	2	50	2	0.22
Plastic material	4	21.05			148	16.63
Plant material	14	73.68			730	82.02
TOTAL			4	100	890	99.99

(b) Diglis Weir - River Severn (1979) n = 15; empty = 9;
(Fullness = 0.60 ± 0.459)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Actual	%
Eggs	4	66.67	13	100	7	4.61
Plant material	5	83.33			145	95.39
TOTAL			13	100	152	100

(c) River Wye (all sites, 1979) n = 25; empty = 0; (Fullness = 1.82 ± 0.962)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Actual	%
Trichoptera A.	4	26.67	37	77.1	235	42.96
Trichoptera L.	1	6.67	1	12.08	10	1.83
Ephemeroptera N.	4	26.67	7	14.58	32	5.85
Plecoptera N.	1	6.67	1	2.08	4	0.73
Chironomidae P.	1	6.67	1	2.08	3	0.55
Gammaridae	1	6.67	1	2.08	3	0.55
Plant material	12	80.0			260	47.53
TOTAL			48	100	547	100

A = Adults, L = Larvae, N = Nymphs, P = Pupae

There are a number of possible reasons as to why the spawning adults do not feed actively while in freshwater. Firstly, that A.fallax may not be morphologically or behaviourly suited for predation on freshwater invertebrates. Brooks (1968) has observed that A.pseudoharengus usually approach their prey from beneath, and this correlates with their slightly superior mouth position which would thus make benthic feeding extremely difficult. Similar observations were made by Janssen (1978a)who also found that it was possible to train A.pseudoharengus to take food off the bottom after six to eight weeks; however, only 10% of encounters were successful. The cessation of feeding would also allow considerably more space to be utilized by the gonads in the body cavity which in the case of the female may allow for either an increase in egg size and/or egg number.

Nikolsky (1961) mentions that cessation of feeding is an adaption that insures a sufficiently high osmotic pressure of the body fluids. Shehadah and Gordon (1969) have shown that if Salmo gairdneri are induced to drink while in freshwater, they will incur an added water load and an increased salt loss. However, these experiments were carried out using starved fish and for osmoregulation to be a valid reason for not feeding in freshwater, the urine flow rate would have to exceed the rate of endosmotic water gained so that drinking would accompany food intake, and that the subsequent loss of salts is not compensated for, from the food eaten.

Following spawning, the fish migrate back to the estuary where they recommence feeding. By comparison, the mean volume of food in the stomachs of the post-spawning fish is approximately fifty times that of the pre-spawning migrants, table 7.3 a + b. It must be noted that at this time the density of prey organisms has increased and there has been a rise in water temperature, which has

Table 7.3a + b The composition of the diet of post-spawning *A.fallax* caught in the Upper Severn Estuary (Framilode and Newnham) during June, July and August

(a) 1979 Total No. of stomachs 18, No. empty = 0, (Fullness = 5.72 ± 1.804)

Food Category	Occurence		Number		Volume (mm³)	
	Actual	%	Actual	%	Actual	%
Mysidae	17	94.4	7613	93.69	36923	83.21
Gammaridae	18	100	437	5.38	4245	9.57
Crangonidae	11	61.1	71	0.87	594	1.34
Pisces	1	5.6	3	0.04	65	0.15
Eggs	1	5.6	2	0.02	2	< 0.01
Detritus	14	77.7			2543	5.73
TOTAL			8126	100	44372	100.01

(b) 1980 Total No. of stomachs 18, No. empty = 2, (Fullness = 6.389 ± 1.732)

Food Category	Occurence		Number		Volume (mm³)	
	Actual	%	Actual	%	Actual	%
Mysidae	15	93.8	17862	94.93	95211	85.42
Gammaridae	16	100	705	3.75	6930	6.22
Crangonidae	11	68.8	236	1.25	1594	1.43
Pisces	1	6.3	4	0.02	40	0.04
Eggs	3	18.8	9	0.05	9	0.01
Detritus	13	81.3			7681	6.89
TOTAL			18816	100	111465	100.01

a direct effect on meal size up to an optimum value (Elliott, 1975; Grove et al., 1978) as well as increasing the evacuation rate (Elliott, 1972; Elliott and Persson, 1978; Grove et al., 1978). Post-spawning fish were only obtained from the upper estuary (at Framilode and Newnham), and due to low numbers, fish from all sites and for all months, were combined. The most important items found, using all three methods, were mysids (*Neomysis integer* (Leach) followed by gammarids (*Gammarus zaddachi* Sexton) and shrimps (*Crangon crangon* (Linnaeus)). Though occuring frequently in the diet, the gammarids and shrimps did not account for a large percentage of the overall diet in terms of volume and number.

The small proportion of shrimps and gammarids in the diet may reflect, in part, their low density in this region of the estuary. Bassindale (1942) mentions that this part of the estuary is unsuitable for the development of large populations of *Gammarus* because of the steep earth banks and the absence of stones or stable vegetation. As well as poor habitat, absence may also be due to physical factors. Girisch et al. (1974) have found that the survival rate of adult *Gammarus zaddachi* is affected by both salinity and temperature, with low salinity conditions being tolerated only at low temperatures. Thus, under summer conditions, a large population of *G.zaddachi* would not be expected in the upper estuary. This has been shown to be the case by Dennert et al. (1969) and by Girisch et al. (1974). However, gammarids may not be as readily available as prey when compared with other species. Moore and Moore (1976) observed that at least 50% of their collection, of this animal, was associated with weeds and other debris. Shrimps possess two behavioural features which may reduce their susceptibility as prey. Firstly, Moore and Moore (1976) mention that shrimps evade predation by *Platichthys flesus* by sharp movements of their tail which take them out of the predators field of view. Secondly, shrimps tend to remain buried during the day thus making themselves a difficult prey for a visual predator (Lloyd and Yonge, 1947).

The adults show the occasional occurence of piscivory with those species consumed represented by typical members of the estuarine fauna, namely P.flesus and Sprattus sprattus (Linnaeus) and members of the Gobiidae. Though 0+ A.fallax were abundant and present in the same region of the estuary as the adults, there was no evidence of cannabalism. Wheeler (1969) found mysid shrimps and the Isopod Corophium species in the stomachs of post spawning A.fallax from estuaries. Post-spawning estuarine feeding for A.pseudoharengus has been described by Bigelow and Schroeder (1953) who mention that they feed ravenously on shrimps.

Very little is known about the diet of A.fallax while at sea. Wheeler (1969) mentions that the adults ate Ammodytidae species, S.sprattus, young Clupea harengus (Linnaeus) and the euphausiids, Nyctiphanes couchii (Bell) and Meganyctiphanes norvegica (M.Sars). Similar findings were reported by Murie (1903), Rae and Lamont (1961 & 1962a) and by Rae and Wilson (1952, 1956 a + b; 1961). Of the material that could be identified, Bracken and Kennedy (1967) found mostly fish remains, which in some cases were S.sprattus. Minchen (1977) recorded that two A.fallax taken from the southern Irish Sea had both been feeding on euphausiids, and a small goby (Aphia minuta (Risso)) was found in one of the specimens. During this study some post-spawning A.fallax were caught inshore, in stake nets, from Cardigan Bay, where they were present for a two week period from the end of September to the start of October. Their diet is shown in table 7.4. The most important food item was the mysid Schistomysis spiritus (Norman), followed by fish which were 0+ clupeids. Mauchline (1967) mentions that S.spiritusoccurs inshore in sandy bays, and at high water during

Table 7.4 Composition of the diet of adult A.fallax caught during October 1979 from Cardigan Bay

n = 13; empty = 0; (Fullness = 5.92 ± 1.787)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Actual	%
Mysidae	13	100	3261	98.61	21149	66.61
Gammaridae	1	7.69	5	0.51	20	0.06
Idoteidae	1	7.69	1	0.03	5	0.02
Ostracoda	1	7.69	3	0.09	3	0.01
Decapoda	1	7.69	1	0.03	2	0.01
Crustacea L.	1	7.69	1	0.03	1	< 0.01
Mollusca	2	13.58	4	0.12	4	0.01
Pisces	2	13.58	31	0.94	8250	25.98
Detritus	8	61.54			2318	7.30
TOTAL			3307	100	31752	100.01

L = Larvae.

calm conditions the population is dispersed between the low and high water tide mark. Thus it appears that A.fallax move inshore, following the mysids, and are caught in the stake nets at high water.

Details of marine feeding for other members of the genus have been recorded by Cunningham (1895), Bigelow and Schoeder (1953), Hildebrand (1963), Holland and Yelverton (1973), Leim (1924), Rae and Wilson (1953), Sirotenko (1969), Svetovidov (1963) and Wheeler (1969).

C. 1+ A.fallax

The movements of O+ and 1+ A.fallax have been described in chapter six. It seems that some of the young after making their seaward migration in the autumn return to the inner estuary in the following spring - early summer. The diet of those migrants caught in May 1980 at Oldbury power station are shown in table 7.5. Though none of the stomachs were empty, the mean fullness index was low (mean 4.5) indicating that they had not been feeding actively at the time of capture. Gammarus species appeared the most important of the food items, followed by calanoid copepods; at this time mysids did not feature very strongly in the diet.

By June 1980 the 1+ fish had moved further upstream into the inner estuary and were being caught at Newnham, where they remained until August feeding actively, tables 7.6 a, b and c. The mysid Neomysis interger was the main component of the diet in the three months the juvenile fish were present. By August (1980) juvenile fish, S.sprattus, and members of the gobiidae made up a fifth of the diet in terms of bulk. Though 1+ A.fallax have been recorded returning to the inner estuary by Hass (1965) and by Bracken and Kennedy (1967), no observations on diet were made by them.

Table 7.5 The composition of the diet of immature (age 1+) <u>A.fallax</u> caught in the lower Severn Estuary (Oldbury) on the 3rd May, 1980

n = 20; empty = 0; Fullness = 4.5 ± 1.035

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Actual	%
Mysidae	2	10	1	0.07	1	0.28
Gammaridae	16	80	70	4.87	263	74.08
Calanoidea	10	50	156	10.86	10	2.82
Platyhelminthes	6	30	16	1.11	3	0.85
Trichoptera N.	1	5	1	0.07	2	0.56
Eggs	8	40	1192	83.01	2	0.56
Detritus	18	90			74	20.85
TOTAL			1436	99.99	355	100

N = Nymphs.

Table 7.6a, b + c The composition of the diet of immature (age 1+) A.fallax caught in the upper Severn Estuary (Newnham) during the summer of 1980

(a) June 1980

n = 6; empty = 0; (Fullness = 8.67 ± 1.084)

Food Category	Occurence		Number		Volume (mm³)	
	Actual	%	Actual	%	Actual	%
Mysidae	6	100	193	95.54	833	97.66
Gammaridae	3	50	7	3.47	19	2.23
Cladocera	1	16.67	2	0.99	1	0.12
TOTAL			202	100	853	100.01

(b) July 1980

n = 14; empty = 1; (Fullness = 6.01 ± 1.57)

Food Category	Occurence		Number		Volume (mm³)	
	Actual	%	Actual	%	Actual	%
Mysidae	13	100	429	93.87	1866	93.58
Gammaridae	6	46.15	26	5.69	83	4.16
Pisces	1	7.69	1	0.22	37	1.86
Terrestial Insecta (A)	1	7.69	1	0.22	1	0.05
Detritus	1	7.69			7	0.35
TOTAL			457	100	1994	100

(c) August 1980

n = 11; empty = 1; (Fullness = 3.45 ± 2.068

Food Category	Occurence		Number		Volume (mm³)	
	Actual	%	Actual	%	Actual	%
Mysidae	9	90.0	142	93.42	480	72.40
Gammaridae	3	30.0	5	3.29	15	2.26
Calanoidea	1	10	2	1.32	1	0.15
Pisces	1	10	2	1.32	147	22.17
Unidentified material	1	10	1	0.65	4	0.60
Detritus	2	10			16	2.41
TOTAL			152	100	663	99.99

A = Adults

D. Larvae

Samples of larvae, all of which had absorbed their yolk sac, were only obtained from the River Wye at Pipton (River Km. 170) in 1979 and at Monmouth (River Km. 30.5) in 1980. Because a large majority of the stomachs were empty and because the prey consumed were large in relation to the stomach volume of larval A.fallax, resulting in only a few organisms contained therein. It was decided to analyse the contents from the intestine as well so that a wider picture of diet could be obtained. The intestinal contents were still fairly intact, presumably because the stomach muscles had not fully developed or because the enzymes involved in digestion had not become fully operative.

Norden (1968) similarly found in larval A.pseudoharengus that it was possible to examine the contents of the intestime. The contents were likewise found to lie in a linear position along the digestive tract with the chitinous exoskeletons of the zooplankton undigested. The volume of the organisms were not measured as they were too small for accurate measurement.

The diet of larvae at two sites is shown in tables 7.7 a + b. It is evident that the same groups of organisms characterise both situations, namely chironomid larvae and pupae, larvae of simuliid species and ephemeropteran nymphs. However, the dominant organism differed at Pipton where chironomid larvae were the most important and at Monmouth where Simulium larvae were predominant.

In freshwater, Leim (1924) found that the dominant food items of larval A.sapidissima were chironomid larvae as well as other insect larvae including ephemeropteran nymphs. In tidal water, copepods predominated in the diet with amphipods occurring in the larger specimens. As well as chironomid larvae and pupae and other insects, cyclopoid copepods and cladocerans (especially the families Daphnidae,

Table 7.7a + b The composition of the diet of larval *A.fallax* from two sites on the River Wye

(a) Pipton (River Km. 170) July 1979, n = 23; empty = 0

Food Category	Occurence		Number	
	Actual	%	Actual	%
Chironomidae L.	23	100	578	60.33
Chironomidae P.	23	100	86	8.98
Simuliidae L.	22	96.5	100	10.44
Ephemeroptera N.	13	56.25	23	2.40
Trichoptera L.	1	4.35	1	0.10
Molluscan Eggs	3	13.04	170	17.75
TOTAL			958	100

(b) Monmouth (River Km. 30.5) July 1980,

n = 30; empty = 1.

Food Category	Occurence		Number	
	Actual	%	Actual	%
Chironomidae L.	17	58.62	42	8.24
Chironomidae P.	10	34.48	14	2.75
Simuliidae L.	29	100	439	86.08
Ephemeroptera N.	12	41.38	12	2.35
Cyclopoidae	2	6.9	2	0.39
Ostracoda	1	3.45	1	0.2
TOTAL			510	100.01

L = Larvae; N = Nymphs; P = Pupae

Bosminidae and Polyphemidae) have been found to be important components in the diet of larvel A.sapidissima by Domermuth (1976), Levesque and Reed (1972) and Mitchell et al. (1925). Other important items recorded have been nematodes (Domermuth 1976) and ostracods and the mussel Glochidia (Mitchell et al. 1925).

Maxfield (1953) found that larvae under semi-artificial conditions may take food before the yolk sac is completely absorbed; the main organisms taken were cladocerans (Bosmina species). Following absorption of the yolk sac, there was a trend towards a greater variety in the diet. In the older, transforming larvae, ostracods, chironomid larvae and pupae, and cyclopoid copepods become major food items, though cladocerans still predominated. Similar findings were reported by Norden (1968) who found that as larval A.pseudoharengus (from lake Michigan) increased in size their diet changed and became more diverse. Dietary changes with size were also reported by Levesque and Reed (1972) for A.sapidissima who found that the larger larvae 21 mm - 28 mm tl.) ate more chironomid larvae and less cyclopoid copepods than did the smaller larvae (19-21 mm tl.) in terms of volume, as well as showing signs of cannabalism. Domermuth (1976) found that chironomid larvae and pupae and terrestrial insects were only consumed by larvae of A.sapidissima greater than 18 mm total length. These larger larvae also showed selective feeding on the larger cladocerans (daphnids and polyphemids). Selective feeding behaviour by larval A.pseudoharengus has also been revealed by Norden (1968).

E. O+ Juveniles

1. Freshwater

Samples of juveniles from two sites on the River Wye, at Courtfield (River Km. 50) and Monmouth (River Km. 30.5) were used to examine diet and the results are shown in tables 7.8 a + b. The main

Table 7.8a + b The composition of the diet of juvenile (age 0+) A.fallax from two sites on the River Wye

(a) Monmouth, August 1979, n = 30; empty = 2, (Fullness = 5.83 ± 1.11)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Chironomidae (A)	4	14.29	6	2.61	3.06	4.24
Chironomidae L.	25	89.29	119	51.97	25.24	35.00
Chironomidae P.	10	35.71	11	4.8	6.88	9.54
Simuliidae L.	20	71.43	70	30.57	24.14	33.48
Ephemeroptera N.	14	50.0	19	8.3	9.82	13.62
Trichoptera L.	4	14.29	4	1.75	2.47	3.43
Detritus	1	3.57			0.50	0.69
TOTAL			229	100	72.11	100

(b) Courtfield, July 1979, n = 16; empty = 1; (Fullness = 7.13 ± 1.56)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Chironomidae (A)	2	13.33	4	0.86	2.60	5.46
Chironomidae L.	13	86.67	41	8.8	6.62	13.74
Chironomidae P.	12	80.00	55	11.80	26.03	54.04
Simuliidae L.	3	20.0	3	0.64	1.25	2.59
Ephemeroptera N.	7	46.67	8	1.72	8.84	18.35
Molluscan eggs	2	13.33	355	76.18	2.83	5.88
TOTAL			466	100	48.17	100

A = Adults; L = Larvae; N = Nymphs; P = Pupae food items are similar to those described for the larvae. At Courtfield the most important item was chironomid pupae, while at Monmouth both chironomid and Simulium larvae predominated. At both sites ephemeropteran nymphs may be regarded as an important food item constituting approximately 15% in terms of volume.

Walburg (1956) studied the feeding habits of juvenile A.sapidissima from a number of different locations and found that the food consisted mainly of insects and crustaceans and was fairly similar in all rivers sampled. Of the items which could be identified the main components were Hymenoptera, Diptera, Copepoda, Ostracoda and Cladocera. Similar findings were reported by Williams and Bruger (1972) for A.sapidissima from the St. Johns River, Florida. Mitchell et al. (1925) observed that the diet of juvenile A.sap dissima differed between four sites from the Connecticut River catchment. The most frequent organisms found were insects (chironomid larvae and damsel fly larvae), crustaceans (cladocerans-Bosmina spp., ostracods-cypris and cyclopoid copepods) and the mussel Glochidia. Davis and Cheek (1966), based on data from both non-tidal and tidal reaches of the Cape Fear River system (N. Carolina) found that the diet of A.sapidissima consisted mainly of cladocerans, copepods, ostracods and amphipods as well as aquatic insects (Hemiptera and Coleoptera) and terrestial insects (Diptera adults and Hymenoptera). In the same river system the diet of A.aestivalis differed in that it did not utilize terrestial insects. The main items in its diet were cladocerans, copepods, ostracods and nematodes, dipteran larvae though appearing frequently in the diet did not constitute a major portion of the total volume. For A.alabamae Jordan and Evermann, Laurence and Yerger (1966) found that juveniles fed mainly on Diptera and young fish. For A.pseudoharengus the dominant food items were found to be cladocerans, copepods, ostracods and chironomids

(Hutchinson, 1971; Jimenz, 1978; Vigerstad and Cobb, 1978).

Levesque and Reed (1972) found that the diet in juvenile A.sapidissima was dominated, in terms of volume, by Crustacea (34%) (mainly calanoid and cyclopoid copepods as well as cladocerans, chiefly Leydigia quadrangularis Schödler and Sida crystalline (O.F. Müller)), chironomid larvae (15%), chirnomid pupae (13%), Trichoptera larvae (Hydropsychidae, 13%) and adult insects (11%). The electivity indices calculated indicated that the young were actively selecting chironomid pupae and crustaceans whilst avoiding chironomid larvae and at two of the three sites sampled, hydropsychid larvae. Domermuth and Reed (1980) found that juvenile A.sapidissima and A.aestivalis fed mainly on Cladocerans of the families Daphniidae and Bosminidae with chironomid pupae and larvae constituting a large percentage of the volume. However, some differences in diet were evident between the two species, A.sapidissima consumed terrestial insects; while copepods and cladocerans of the family Sididae, also constituted a large proportion of the diet of A.aestivalis. Virtually no prey organisms are obtained from the benthos suggesting that the alosids feed mainly on plantonic and drift organisms. A.sapidissima were shown to strongly select for Daphniidae and moderately for Bosminidae (though in the study by Levesque and Reed (1972) these cladoceran families did not appear important.) A.aestivalis strongly selected for the Bosminidae and the copepoda and moderately for the Daphniidae. Both species rejected other cladoceran families (Chydoridae, Sididae, Macrothricidae) as well as chironomid pupae and larvae, and in the case of A.sapidissima copepods were also rejected. For landlocked A.pseudoharengus, Gannon (1976) reported strong selection for large cyclopoid copepods. Selective feeding on components of the zooplankton was also reported by Hutchinson (1971) and by Jimenez (1978) for A.pseudoharengus.

The American species show a considerable similarity in their dietry items which consist mainly of cladocerans, copepods, ostracods and chironomids; they also demonstrate a high degree of selectivity. These items were not utilized to any great extent by A.fallax in the Wye. A.fallax differed in their dietary habits in that larvae of Simulium spp. and ephemeropteran nymphs were of considerable importance. These differences may be due to differences in the fishes morphology and/or behaviour. They may also arise from differences in availability, which will be a function of each rivers' characteristics. Simulium larvae require fairly shallow, rapidly flowing water (Chutter and Noble, 1966) over a stony bottom, a situation very characteristic of places in the Wye, and may not like deep slow moving stretches of river. Similarly the latter situation would favour the development of a zooplankton community rather than in a fast flowing river.

2. Estuaries

Changes in the diet might be expected to exist between the different sites sampled in an estuary due to changes in the degree of physiological stress as well as to physical changes in the substrate. In 1979 it was possible to obtain samples from four different sites, tables 7.9, 7.10a, b + c, 7.11a, b + c; and 7.12. At Elmore, the furthest upstream of the four estuarine sites, the diet was found to consist mainly of harpacticoid copepods (mainly Tigriopus brevicornis, Müller, but also a few Tisbe spp.), Gammarus species and the cladocerans (families Daphnidae and Chydoridae). Moving 11.5 Kms. down the estuary, to Framilode, a similar diet was recorded. In July, however, mysids (Neomysis integer) constituted a major portion of the diet, but in August, none were recorded and harpacticoid copepods predominated. By September, mysids re-emerged as the dominant food item. A further 9 Kms. down the river at Newnham, the main food items were mysids with gammarids (Gammarus sp.)

Table 7.9 Composition of the diet of juvenile (age 0+)
A.fallax from Elmore on the River Severn

Elmore, August 1979.

n = 25; empty = 0; (Fullness = 8.16 ± 0.41)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Diptera (A)	5	20.0	9	0.03	8.43	2.80
Chironomidae L.	19	76.0	49	0.14	6.25	2.07
Chironomidae P.	7	28.0	10	0.0	4.56	1.51
Ephemeroptera N.	3	12.0	3	0.01	0.83	0.28
Gammaridae	16	64.0	142	0.41	45.32	15.04
Cladocera	23	92.0	301	0.87	31.30	10.39
Harpacticoidea	25	100.0	34150	98.3	197.84	65.66
Cyclopoidea	18	72.0	68	0.2	5.42	1.80
Ostracoda	5	20.0	10	0.03	0.87	0.29
Detritus	1	4.0			0.50	0.17
TOTAL			34742	100.02	301.32	100.01

A = Adults; L = Larvae; N = Nymphs; P = Pupae

Table 7.10a b + c   Composition of the diet of juvenile (age 0+) *A.fallax* from Framilode on the River Severn

(a) July 1979, n = 30; empty = 0; (Fullness = 7.033 ± 0.76)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Diptera (A)	1	3.33	1	0.02	0.5	0.53
Chironomidae L.	8	26.67	13	0.31	2.91	3.07
Mysidae	15	50.0	92	2.22	37.37	39.37
Gammaridae	10	33.33	26	0.63	5.15	5.43
Cladocera	17	56.67	65	1.57	3.83	4.03
Harpacticoidea	29	96.67	3903	94.09	40.68	42.85
Cyclopoidea	4	13.3	12	0.29	1.64	1.73
Calanoidea	12	40.0	36	0.87	2.85	3.00
TOTAL			4148	100	94.93	100.01

(b) August 1979, n = 22; empty = 0; (Fullness = 3.91 ± 1.04)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Chironomidae L.	1	4.55	1	0.02	0.08	0.12
Gammaridae	1	4.55	1	0.02	0.07	0.10
Cladocera	22	100.0	246	4.05	11.86	17.34
Harpacticoidea	22	100.0	5795	95.74	55.42	81.02
Cyclopoidea	3	13.64	4	0.07	0.45	0.66
Calanoidea	2	9.09	6	0.1	0.52	0.76
TOTAL			6053	100	68.40	100

(c) September 1979, n = 12; empty = 1; (Fullness = 4.5 ± 1.87)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Diptera (A)	3	27.27	3	0.73	7.26	6.82
Trichoptera N.	1	9.09	1	0.24	0.50	0.47
Mysidae	6	54.55	29	7.06	57.47	54.02
Gammaridae	3	27.27	7	1.70	15.91	14.96
Cladocera	6	54.55	19	4.62	3.51	3.30
Harpacticoidea	2	18.18	325	79.08	4.18	3.93
Calanoidea	6	54.55	23	5.6	1.60	1.50
Ostracoda	2	18.18	2	0.49	0.09	0.08
Pisces	2	18.18	2	0.49	15.86	14.91
TOTAL			411	100.01	106.38	99.99

A = Adults, L = Larvae, N = Nymphs

Table 7.11a, b + c Composition of the diet of juvenile (age 0+)

<u>A.fallax</u> from Newnham on the River Severn

(a) July 1979, n = 24; empty = 0; (Fullness = 7.67 ± 0.59)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Estimated	%
Chironomidae L.	4	16.67	4	0.44	2.39	0.86
Mysidae	24	100.0	410	45.05	216.89	77.75
Gammaridae	12	50.0	60	6.59	31.23	11.20
Calanoidea	20	83.33	436	47.91	28.45	10.20
TOTAL			910	99.99	278.96	100.01

(b) September 1979, n = 20; empty = 3; (Fullness = 4.0 ± 1.45)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Estimated	%
Diptera (A)	2	11.76	1	1.25	0.65	0.46
Mysidae	14	82.35	51	63.75	128.18	90.68
Gammaridae	2	11.76	3	3.75	2.21	1.56
Cyclopoidea	1	5.88	1	1.25	0.74	0.52
Corophiidae	1	5.88	1	1.25	4.55	3.22
Idoteidae	1	5.88	1	1.25	2.60	1.84
Eggs	8	47.06	22	27.5	1.0	0.71
Detritus	2	11.76			1.43	1.01
TOTAL			80	100	141.36	100

(c) October 1979, n = 11; empty = 0; (Fullness = 7.45 ± 1.91)

Food	Occurence		Number		Volume (mm^3)	
Category	Actual	%	Actual	%	Estimated	%
Mysidae	11	100.0	74	33.04	148.16	73.15
Gammaridae	4	36.36	70	31.25	49.34	24.36
Calanoidea	4	36.36	80	35.71	5.03	2.48
TOTAL			224	100	202.53	99.99

A = Adults, L = Larvae

Table 7.12 Composition of the diet of juvenile (age 0+) *A.fallax* from Oldbury on the River Severn

September, 1979

n = 20; empty = 4; (Fullness = 2.6 ± 1.34)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Mysidae	16	100.0	46	43.4	204.64	85.87
Gammaridae	8	50.0	8	7.55	22.76	9.55
Eggs	2	12.5	52	49.06	0.52	0.22
Detritus	2	12.5			10.4	4.36
TOTAL			106	100.01	238.32	100

and the calanoid copepod, Eurytemora spp. also being important during all three months. At Oldbury another 26 Kms. down the estuary, Juvenile A.fallax were caught in September on their seaward migration and mysids were found to predominate in the diet though the fish were not feeding actively at this time (mean fullness index 2.6).

Variation in salinity may affect the distribution of Neomysis integer, Green (1968) mentions that they can tolerate freshwater for a limited period of time. Elmore is predominatly tidal freshwater (Bassindale, 1943) and mysids may not penetrate this far upriver. This may also explain why the August sample at Framilode did not contain any mysids as the height of the previous tide was only 5.5 metres (recorded at Sharpness Dock). In July, when mysids were found in the diet, the height of the previous tide had been 7.6 metres. This difference in tidal height would have considerably altered the salinity regime experienced on the two dates and either the salinity regime in August was not favourable for N.integer or, assuming mysid distribution is affected by tidal velocity, then possibly a 5.5 metre tide is not strong enough to bring the mysids up to Framilode. The reverse situation may also be true for the harpacticoids.

The composition of the diet may also be influenced by the turbidity of the water which in turn will be related to tidal velocity and thus tidal height. Assuming visual prey selection, then increased turbidity may cause selection for the larger prey organisms and thus under high tide conditions for mysids (if present). This assumes that the relative abundance of prey organisms remains constant. For P.flesus, Moore and Moore (1976) found that increasing tubidity did enlarge the minimum detectable size of prey as well as reducing the detection distance. However, increasing turbidity also had the effect of increasing the percentage of unsuccessful encounters and the capture time. This would presumably make larger prey, which have greater escapability than smaller prey, less vulnerable under turbid conditions. However, Gardner (1981) found that increased turbidity, reduced feeding rate but did not affect prey size in Lepomis macrochirus. This situation may be further complicated depending at which state of the tide A.fallax are feeding as turbidity will change throughout the tidal cycle.

Substratum type may also play an important part because these species of harpacticoids are found in or on the mud (Hockin 1982) and in the estuary there exists a gradual change from extremely muddy sites (such as Elmore) to increasing portions of sand down the estuary.

In 1980 samples were only obtained at Newnham and it appears that though the main components are the same, the diet is more diverse, table 7.13 a, b + c. In 1980 harpacticoids occured more frequently and during August, were certainly the most numerous, while calanoid copepods (Eurytemora spp.) were a more important food item than they had been in 1979.

In tidal waters, Leim (1924) found that the major food items of juvenile A.sapidissima were copepods, with amphipods occuring in the larger specimens. Chironomid larvae also constituted a major food source. Similar findings were also reported by Williams and Bruger (1972) who found, that of the organisms that could be identified, ostracods, copepods and amphipods, as well as aquatic stages of dipteran larvae were the most important prey items. However, unidentifiable insect parts were the most frequent items encountered. In the tidal reaches of the Pumumkey and Mattaponi Rivers (Virginia), Massman (1963) found that the most important food item of juvenile A.sapidissima were insects, 71% of terrestial origin (mainly Hymenoptera) and 28% of aquatic origin (mainly Ephemeroptera and Hemiptera), but the importance of each constituent varied between

Table 7.13a, b + c The composition of the diet of juvenile (age 0+) *A. fallax* from Newnham on the River Severn

(a) August 1980, n = 38; empty = 0; (Fullness = 6.21 ± 0.79)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Chironomidae L.	1	2.63	1	0.03	0.39	0.13
Mysidae	29	76.32	256	8.60	179.57	57.88
Gammaridae	19	50.0	55	1.85	36.65	11.81
Cladocera	11	28.95	27	0.91	1.47	0.47
Harpacticoidea	21	55.26	1583	53.16	16.11	5.19
Cyclopoidea	1	2.63	2	0.07	0.04	0.01
Calanoidea	30	78.95	1053	35.36	61.89	19.95
Pisces	1	2.63	1	0.03	6.19	2.00
Detritus	4	10.53			7.93	2.56
TOTAL			2978	100.01	310.24	100

(b) September 1980, n = 25; empty = 0; (Fullness = 8.72 ± 0.63)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Diptera (A)	3	12.0	3	0.05	3.40	0.24
Ephemeroptera N.	1	4.0	1	0.02	4.55	0.33
Mysidae	25	100.0	1043	18.74	729.0	52.42
Gammaridae	23	92.0	107	1.92	116.18	8.35
Cladocera	1	4.0	1	0.02	0.05	< 0.01
Calanoidea	23	92.0	4407	79.16	479.45	34.47
Idoteidae	2	8.0	2	0.04	2.86	0.21
Pisces	2	8.0	3	0.05	51.35	3.69
Detritus	1	4.0			3.90	0.28
TOTAL			5567	100	1390.74	100

(c) Oxtober 1980, n = 8; empty = 0; (Fullness = 6.5 ± 2.14)

Food Category	Occurence		Number		Volume (mm^3)	
	Actual	%	Actual	%	Estimated	%
Diptera (A)	1	12.5	1	0.72	2	2.22
Mysidae	8	100.0	119	85.61	74	82.22
Gammaridae	2	25.0	19	13.67	13	14.44
Detritus	1	12.5			1	1.11
TOTAL			139	100	90	99.99

A = Adults, L = Larvae, N = Nymphs

locations. Davis and Cheek (1966) found that A.pseudoharengus consumed mainly cladocerans, copepods and ostracods. However, dipterans, nematodes and Hydracarina also occured frequently in the diet. Burbridge (1974) found that juvenile A.aestivalis fed mainly on planktonic organisms of which the most important were copepods and cladocerans. There was also evidence of selection for adult copepods, but little if any, for the cladocerans unless they were at very high densities, and none at all for copepod nauplii.

It appears that the diet of A.fallax in the Severn estuary is fairly similar to that for A.sapidissima, A.pseudoharengus and A.aestivalis except for the study by Massman (1963). Also A.fallax in the Severn predate heavily on mysids (Neomysis integer) and at some sites they represent the major food item. Mysids were not recorded as being utilized by either A.sapidissima, A.pseudoharengus or by A.aestivalis. This may be due to differences in morphology and/or behaviour, or that the sites in the respective estuaries are not comparable, mysids not even being present.

F. Possible Reasons for the Differences in the Diet and in the Distribution of Juvenile A.fallax in the Rivers Severn and Wye

The variation in the diet found for A.fallax may reflect differences in the abundance of available prey organisms present in the two river systems. The main dietary items for juvenile A.fallax in the Wye were benthic invertebrates, whilst in the Severn, at a similar stage of development, zooplankton species predominated.

The density of zooplankton is very much dependent on that of the phytoplankton and on detritus either suspended or on the surface of the sediment. Jones (in prep.) found levels of phytoplankton in stretches of the Wye, where juvenile A.fallax were found, comparable to those reported by Swale (1969) for the lower reaches of the Severn. Thus the density of zooplankton in the river systems might not be expected to be significantly different. Though phytoplankton concentrations appear similar between the river systems, the lower reaches of the Severn are considerably more turbid than stretches of the Wye, where juveniles were found. Increased turbidity has a deleterious effect on the phytoplankton due to its effect on photosynthesis and on the feeding mechanisms of the zooplankton (Rylov, 1940; cited by Hynes, 1970) as well as facilitating the settling out of the plankton under low flow conditions as suggested by Chandler (1937). However, Swenson (1978) found a significant positive correlation between zooplankton density and turbidity for planktonic rotifers and cladocerans, but not for cyclopoid and calanoid copepods. This may have resulted from the active migration of the zooplankton to the surface, due to reduced light penetration, or possibly to the increase in primary production resulting from the leaching of nutrients, from the particles.

Thus the predominance of zooplankton in the diet of juvenile A.fallax in the lower reaches of the Severn may either be due to increased levels of suspended solids, acting on the distribution of the zooplankton, or to the lack of benthic inverebrates. This assumes that benthic invertebrates are selected for in favour to the zooplankton species. Two of the main factors reviewed by Hynes (1970) affecting the occurence and distribution of benthic invertebrates are current, which is important in terms of feeding and respiration, and the nature of the substratum. The substratum differs markedly between the areas. The lower reaches of the Severn show little gradient with slow moving waters and consequently are a lot muddier with occasional stretches of gravel and bedrock. On the other hand the Wye has a steeper gradient with more pool and riffle habitat .

Feeding may be taking place in the deep pools where the fish were caught, and where there should be rich detritus. O'Connell and Cambell (1953) found chironomids nearly three times as abundant in pool areas when compared with riffle areas. Similar findings were reported by Minshall and Minshall (1977) and by Rabeni and Minshall (1977). However, Egglishaw and Mackay (1967) found no significant difference in the numerical density of chironomid larvae from pools and from riffles. Presumably, because of the large numbers of Simulium recorded in the diet, and because of the association between the abundance of Simulium and areas of fast flowing water (Chutter and Noble, 1966), the fish may leave the pools and feed in the riffle areas. Riffle areas have been found to support a higher density of Simulium species (Rabeni and Minshall, 1977) or approximately equal densities when compared with pool areas (Minshall and Minshall, 1977).

The survey of benthic invertebrates undertaken by the Severn and Trent Water Authority (1979) showed low species abundance and diversity in the lower Severn. They concluded that one of the main causes lay in the substratum conditions which ranged from thick mud to clay, which for non-burrowing species will not provide a refuge from predators and/or from physical factors (Macan, 1961). This region of the Severn is characterized by large amounts of unstable and shifting debris (S.T.W.A., 1979). Petran and Kothe (1978) found that in areas of high bedload transport there existed a reduction in species as well as the numerical density of the benthic invertebrates, except for the Oligochaete families Naididae and Tubificidae. Similarly Percival and Whitehead (1929) found a reduction in inverebrate density on loosely embedded stones, when compared to areas where the stones were firmly embedded. Benthic invertebrates in the Severn were only found in piles of debris that were relatively stable thus providing some degree of shelter. The suposition of unstable substrate affecting invertebrate abundance was tested by the use of artificial substrates. These contained much higher densities of animals, though the species diversity remained low. This work on artificial substrates was carried out by the Applied Hydrobiology Unit at Aston University. The lack of macrophytes in certain stretches of the River Teifi has been attributed to an unstable substratum (Jones, 1943). Morton (1976) found that decreasing the amount of macrophytes resulted in an increase in the number of burrowing invertebrates taxa, and these organisms may not be as readily available as food items for A.fallax. Thus the lack of benthic invertebrates in the diet of juveniles from the lower Severn may reflect their paucity, a consequence of unsuitable flow regimes and poor substrate, or that those present were not suitable as prey.

The characteristics of the diet of A.fallax while in the Severn is very similar to that of the American species where the diet is dominated by zooplankton, and may reflect similarities between the river systems. A.fallax, similar to A.sapidissima and A.pseudoharengus (Janssen, 1976) show a diversity in their feeding habits, using both particulate and filter feeding mechanisms. This diversity has the advantage of allowing the juveniles to exploit a number of different habitats as well as optimizing on any changes in available prey. Thus the distribution of the species is unlikely to be limited by the feeding requirements of the juveniles as it seems that they would be able to exploit some feeding niche in most rivers.

This, however, does not explain why so few juveniles were found in the riverine area of the Severn (see chapter six). It might have been expected from the diversity of their feeding mechanisms that the fish should have been able to exploit the resource. This distribution may, however, be related to the abundance of available prey organisms, which has been shown to increase downstream in other river systems. Greenberg (1964) found in the Sacramento River that the density of plankton increased seaward and this could be related to temperature, biological oxygen demand and to river flow. In the River Severn, Swale (1969) found an increase in the density of phytoplankton in the lower reaches when compared to the upper reaches. This was attributed to the slowing down of the current, so increasing the time available for the suspended algae to divide. Therefore, the movement downstream may be designed to optimize available prey, in relation to the fishes physiological tolerance, as estuarine areas are generally associated with high productivity (McLusky, 1981). Such a restricted distribution is not found in the Wye and may be related to a greater abundance of available prey organisms in the riverine area as opposed to those in the Severn between Worcester and Gloucester.

It is apparent that more work is required in this area to investigate whether the different distribution of the juveniles between the two river systems is related to food availability or to some other factors.

G. Effect of Size

A number of authors have found that planktivore fish select out larger prey (Brooks, 1968; Janssen and Brandt, 1980; O'Brien et al. 1976; Werner and Hall, 1974) and there is some evidence that diet changes with size. Comparison of the food items in the samples of 0+ and 1+ A.fallax caught at Newnham during 1980 (tables 7.6a, b + c and 7.13a, b + c) shows that none of the 1+ fish fed on the smaller members of the plankton (copepods and cladocerans). Brooks (1968) observed that A.pseudoharengus selected for the larger prey species as well as selecting for the largest individuals of each species. Morsell and Norden (1968) who studied A.pseudoharengus in Lake Michigan found that the amphipod Pontoporeia species did not occur in fish less than 119 mm in length. Similar results were reported by Wells (1980) who found that the proportion of Pontoporeia in the diet increased with predator size with a concomitant decline in the importance of zooplankton (measured as percentage volume). In the shallower areas, the larger A.pseudoharengus were observed to consume a greater proportion of immature midges (dipteran larvae) and less zooplankton. Brandt (1980) reported similar findings for A.pseudoharengus. The young of the year were found to feed mainly on cyclopoid and calonoid copepods as well as some cladoceran species. The adults similarly fed on these prey items, but also consumed larger organisms namely, Mysis relicta Lovén and Pontoporeia. However, Hutchinson (1971) found no difference in terms of percentage number in the composition of the diet of A.pseudoharengus aged 0+ and those of 1+ and older. Similar conclusions were reached by Rhodes and McComish (1975) for A.pseudoharengus ranging in size from 140 - 169 mm (tl) and 170 - 189 mm (tl). Berg and Grimaldi (1966) found no difference in the feeding habits of A.fallax lacustris within the size range of 15 - 30 cms (tl), though for those which exceeded this range, some feeding on fish did occur.

The advantages of seeking out larger prey items have been indicated by Palaheimo and Dickie (1966). They found that a higher growth efficiency was correlated with an equivalent weight of larger particles presumably associated with the decreased energy expended in foraging. A larger prey item would also seem advantageous in terms of surface area to volume ratio in that a larger number of small zooplankton would contain a greater amount of undigestable material than an equivalent volume of larger zooplankton. Though this may be energetically more efficient on a weight to weight basis to consume larger organisms, consideration should also be taken into account of the energy demands produced by foraging and handling which may be expected to be higher for larger prey.

Drenner and McComes (1980) have measured the probability of capture of a number of prey items, and found for Dorosoma cepedianum (Lesueur) (a planktivore) and for Menidia beryllina (Cope) that zooplankton escapability while filter feeding was the controlling factor regulating their feeding rate and selectivity. Thus, any change in the morphology and/or behaviour of the predator may have an effect on the escapability of the prey. The morphological constraint of mouth size and for planktivore species, the space between gill rakers, is important in determining the size of prey (Durbin, 1979). This has been shown to be true by Drenner and McComas (1980) who found that D.cepedranum is able to utilize particle sizes down to 100 µ with 100% efficiency, whereas M.beryllina with their more widely spaced gill rakers can only filter out particles down to 200 µ in diameter with 100% efficiency. Thus 1+ A.fallax, with greater spaces between their gill rakers than the 0+ may not be able to filter out the smaller members of the plankton which constitute the majority of the diet of the 0+ fish.

As well as the morphological constraints on small fish taking large prey (Wong and Ward, 1972) the fact that 0+ A.fallax consume a large proportion of small prey may be advantageous. It reduces the time taken for search (small organisms are usually more abundant than large ones), pursuit and capture (Schoener, 1971). Thus according to Leviten (1976) the minimization of foraging time is an appropriate strategy for small predators probably because increasing the time spent foraging, increases the chances of their predation.

This strategy of minimizing foraging time, has been shown by Griffiths (1975) to be utilized by several species of larval and juvenile vertebrates. Mittlebach (1981) has shown that the large size classes of Lepomis macrochirus (> 101 mm S.L.) were found to forage so as to maximize their energetic gains, switching habitats from vegetation to open water as the profitability of the various prey species changed. However, small size classes (< 100 mm S.L.) did not extensively use the open water habitat, except when large prey species were abundant near the vegetation; there exists a trade off between foraging profitability and the risk of predation. Thus for L.macrochirus, in which predation is directly related to body size, the small size classes show a reduction in foraging time. The pressure of predation also has the effect of reducing intraspecific competition by segregating the size classes into separate feeding niches.

H. Limitations of the Study

In this study certain aspects which are significant to an overall understanding of feeding ecology were not investigated. A number of studies have shown diel feeding behaviour as well as diel changes in diet (Grigorash et al. 1972; Hutchinson, 1971; Johnson and Johnson , 1981; Keast and Walsh, 1968; Northcote and Lorz, 1966; Robb 1981); these may be due to changes in available prey or in the fishes feeding mechanism. Holanov and Tash (1978) observed that Dorosoma petenense (Günther) could carry out filter feeding regardless of light conditions, and particulate feeding, at intensities greater than bright moonlight. Thus for an overall appraisal of an items dietary importance diurnal studies on feeding are essential.

In estuaries and in coastal waters there exists the possibility that the diet may be influenced either directly or indirectly by the tide. From the study on the diet of juveniles from the Severn estuary it seems that the distribution of the potential prey items may be influenced by the height of the tide. Similarly their diet may depend on the state of the tide at which the fish are feeding. Though no information was found on a change in diet throughout a tidal cycle, a number of investigators have shown that feeding activity, for some species, does have a tidal component, (Healey, 1971; Kuipers, 1973; Lockwood, 1980; Weisburg et al. 1981). Diet may also be influenced by spatial segregation. It has been found that juvenile flatfish feed intertidally and that their diet may be different from those that remain subtidally (Wells et al. 1973). Similarly Mittlebach (1981) found differences in the diet of L.macrochirus from different areas.

In the determination of the relative importance of dietary item, erroneous results may arise due to differences in the digestion rate of prey items (Gannon, 1976), and thus the more easily digestable components of the diet will be underestimated.

Comparisons of feeding activity during the season or day are complicated by factors affecting meal size such as temperature (Elliott, 1975) and gastric evacuation rate. The latter may be affected by meal size (Svenson and Smith, 1973) as well as temperature, food composition and period of food deprivation (Elliott, 1972; Elliott and Persson, 1978). Thus, to obtain an accurate assessment of diet and feeding intensity, a number of factors have to be taken into account.

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Appendix One

Regressions for the conversion of total and standard length to fork length.

'Dependent Variable' (mm)	Least Square Regression					Geometric Mean Regression	
	Intercept	Slope ± 95% Conf. limit	Coeff of Determ. r^2	F Value	Significance	Intercept	Slope ± 95% Conf. limit
Total length	9.4044	1.1299 ± 0.0259	0.9774	7525.3	$P < 0.0005$	4.4816	1.1446 ± 0.0226
Standard length	31.4005	0.8488 ± 0.0542	0.8422	1642.7	$P < 0.0005$	9.2629	0.9702 ± 0.0561

All conversions were made using Geometric mean regressions.

Measurements were taken from 197 adult fish caught at Lydney during the upstream migration period in 1981, from material that was either fresh or had been kept on ice for no longer than 24 hours. Fish were measured to the nearest millimetre.

Appendix Two

Size, Age and Number of previous spawnings of Female and Male A.fallax, from various sites in Holland (material supplied courtesy of Dr. Steimetz).

FEMALES

Date of Capture	Site	Total Length (mm)	Age	No. Previous Spawnings
24.5.60	Amer	365	4	1
9.6.60	Amer	370	5	1
9.6.60	Hellevoetsluis	375	5	1
9.6.60	Amer	375	5	0
9.6.60	Hellevoetsluis	380	5	1
9.6.60	Amer	380	5	1
9.6.60	Amer	380	5	1
12.5.60	Amer	385	5	0
23.5.60	Amer	385	5	1
9.6.60	Hellevoetsluis	385	6	1
9.6.60	Amer	385	5	0
23.5.60	Amer	390	5	2
9.6.60	Amer	390	5	1
23.5.60	Amer	395	5	2
24.5.60	Amer	395	5	1
3.6.60	Goereese Gat	395	5	2
9.6.60	Amer	395	5	1
12.5.60	Amer	400	5	0
12.5.60	Amer	400	5	0
23.5.60	Amer	400	5	2
24.5.60	Amer	400	5	1
24.5.60	Amer	400	5	1
9.6.60	Hellevoetsluis	400	5	0
9.6.60	Amer	400	6	1
9.6.60	Amer	400	5	1
9.6.60	Amer	400	5	1
9.6.60	Amer	400	6	2
9.6.60	Amer	400	6	2
12.5.60	Amer	405	5	2
24.5.60	Amer	405	5	1
9.6.60	Amer	405	5	1
12.5.60	Amer	410	5	1
12.5.60	Amer	410	5	1
23.5.60	Amer	410	5	1
24.5.60	Amer	410	5	1
9.6.60	Amer	410	5	1
9.6.60	Amer	410	5	1
12.5.60	Amer	415	5	0/1
12.5.60	Amer	415	5	1
12.5.60	Amer	415	5	1
12.5.60	Amer	415	5	1
23.5.60	Amer	415	5	1
23.5.60	Amer	415	5	1
9.6.60	Amer	415	5	1
12.5.60	Amer	420	5	1
23.5.60	Amer	420	5	1
23.5.60	Amer	420	5	1
24.5.60	Amer	420	5	2
24.5.60	Amer	420	5	1
9.6.60	Amer	420	7	3
24.5.60	Amer	425	7	2
12.5.60	Amer	425	5	1
12.5.60	Amer	425	5	2
24.5.60	Amer	425	5	1
7.6.60	Numansdorf	425	5	1
9.6.60	Amer	425	5	1
12.5.60	Amer	430	5	1
12.5.60	Amer	430	5	2
24.5.60	Amer	430	8	5
24.5.60	Amer	430	5	1
7.6.60	Numansdorf	430	6	2
9.6.60	Amer	435	5	1
9.6.60	Amer	440	6	2
12.5.60	Amer	445	5	1
12.5.60	Amer	445	5	2
12.5.60	Amer	445	5	1
12.5.60	Amer	445	5	2
12.5.60	Amer	445	5	1
12.5.60	Amer	450	5	1
12.5.60	Amer	450	5	1
12.5.60	Amer	455	5	2
12.5.60	Amer	460	6	2
12.5.60	Amer	465	5	2
12.5.60	Amer	465	9	5
12.5.60	Amer	475	8	5
9.6.60	Amer	480	7	3
9.6.60	Amer	490	7	3

MALE

Date of Capture	Site	Fork Length (mm)	Age	No. Previous Spawnings
3.6.60	Goereese Gat	295	5	2
24.5.60	Amer	315	5	1
3.6.60	Goeresse Gat	315	5	2
3.6.60	Goereese Gat	315	5	2
3.6.60	Goeresse Gat	315	5	1
3.6.60	Goeresse Gat	315	5	2
3.6.60	Goeresse Gat	325	5	2
12.5.60	Amer	330	5	2
12.5.60	Amer	335	5	1
12.5.60	Amer	335	5	2
9.6.60	Hellevoetsluis	335	5	1
23.5.60	Amer	340	5	1
23.5.60	Amer	340	5	2
12.5.60	Amer	345	5	2
23.5.60	Amer	345	6	2
23.5.60	Amer	345	5	2
9.6.60	Hellevoetsluis	345	5	2
12.5.60	Amer	350	6	3
23.5.60	Amer	350	5	2
12.5.60	Amer	355	5	2
12.5.60	Amer	355	5	2
12.5.60	Amer	355	5	1
23.5.60	Amer	355	5	1
23.5.60	Amer	355	5	1
12.5.60	Amer	360	6	3
12.5.60	Amer	360	5	2
23.5.60	Amer	360	5	2
23.5.60	Amer	360	5	1
24.5.60	Amer	360	5	2
3.6.60	Goeresse Gat	360	7	4
3.6.60	Goereese Gat	360	5	2
3.6.60	Goereese Gat	360	5	1
9.6.60	Amer	360	5	2
12.5.60	Amer	365	5	1
12.5.60	Amer	365	5	2
12.5.60	Amer	365	6	1
12.5.60	Amer	365	6	3
23.5.60	Amer	365	5	2
23.5.60	Amer	365	6	3
24.5.60	Amer	365	6	3
3.6.60	Goereese Gat	365	5	1
12.5.60	Amer	370	5	2
12.5.60	Amer	370	5	2
12.5.60	Amer	370	5	2
23.5.60	Amer	370	5	2
23.5.60	Amer	370	6	3
24.5.60	Amer	370	5	2
24.5.60	Amer	370	6	3
9.6.60	Amer	370	5	2
12.5.60	Amer	375	6	3
12.5.60	Amer	375	5	1
12.5.60	Amer	375	5	2
12.5.60	Amer	375	6	3
23.5.60	Amer	375	5	2
9.6.60	Amer	375	5	1
9.6.60	Amer	375	5	2
12.5.60	Amer	380	5	2
23.5.60	Amer	380	6	3
24.5.60	Amer	380	7	4
9.6.60	Amer	380	6	2
12.5.60	Amer	385	5	2
12.5.60	Amer	385	6	3
12.5.60	Amer	385	5	1
24.5.60	Amer	385	7	4
9.6.60	Amer	385	6	3
9.6.60	Amer	385	5	1
23.5.60	Amer	390	5	2
23.5.60	Amer	390	7	5
12.5.60	Amer	395	6	3
23.5.60	Amer	395	8	5
12.5.60	Amer	400	9	6
12.5.60	Amer	400	6	3
23.5.60	Amer	400	6	2
23.5.60	Amer	415	7	4

APPENDIX THREE

Measurements of Pro-larvae (larvae that have not completely absorbed their yolk sac) in millimetres

Total length	Standard length	Length to anus	Length to Anus as % of standard length	Yolk sac	Head length	Head length as % of standard length	Back of eye to snout	Eye diameter
6.205	5.986	4.891	81.71	1.387	0.803	13.41	0.438	0.365
6.497	6.351	5.183	81.61	1.825	0.511	8.05	0.475	0.219
6.497	6.351	5.256	82.76	1.533	0.803	12.64	0.511	0.329
6.789	6.570	5.402	82.22	1.533	0.876	13.33	0.475	0.380
6.862	6.643	5.402	81.32	1.387	0.876	13.19	0.475	0.350
6.862	6.643	5.402	81.32	1.825	0.73	10.99	0.526	0.365
7.154	6.862	5.329	77.66	1.752	0.913	13.30	0.548	0.365
7.373	7.227	5.840	80.81	1.606	0.949	13.13	0.621	0.329
7.592	7.3	5.913	81.0	1.314	0.949	13.0	0.511	0.378
7.592	7.373	6.132	83.17	1.679	0.986	13.37	0.526	0.365
7.665	7.446	6.059	81.37	1.533	1.022	13.73	0.489	0.365
7.665	7.446	6.132	82.35	1.570	1.022	13.73	0.475	0.402
7.738	7.373	6.132	83.17	1.752	1.037	14.06	0.511	0.365
7.738	7.519	6.132	81.55	1.825	0.913	12.14	0.657	0.438
7.811	7.592	6.169	81.26	1.46	1.022	13.46	0.548	0.380
7.811	7.592	6.205	81.73	1.606	0.986	12.98	0.584	0.402
7.884	7.592	6.351	83.65	1.752	1.095	14.42	0.73	0.402
8.03	7.665	6.205	80.95	1.606	1.022	13.33	0.584	0.438
8.249	7.957	6.242	78.45	1.606	1.095	13.76	0.584	0.402
9.198	8.906	7.227	81.15	1.533	1.168	13.11	0.511	0.365

All measurements made from preserved material.

Appendix Four

Parasites

During the course of this study, some information on the parasites of adult fish were obtained. The adult fish taken from the estuary were all from the pre-spawning phase of the migration. Those taken from freshwater were collected from Powic Weir, on the River Teme, Diglis Weir, on the River Severn, and from a number of sites on the River Wye. Fish from all the freshwater sites were pooled together. Two species of gill parasite were found, a monogenean Mazocraes alosae Hermann and a crustacean Clavellisa emarginata (Kroyer). The number of parasites from both branchial chambers were counted and pooled together. The incidence and level of infection for the whole population sampled are shown in tables Ap. 4.1 and Ap. 4.2, for females and males separately and for the estuarine and freshwater sites. The relationship of age, size and the number of previous spawnings against the incidence and level of infection with M.alosae are presented in tables Ap. 4.3 a + b; Ap. 4.4 a + b; Ap. 4.5 a + b; and with C.emarginata in tables Ap. 4.6 a + b; Ap. 4.7 a + b and Ap. 4.8 a + b. Some of the counts of gill parasites were made by Finlayson (Birmingham University) who is carrying out a study into the biology of M.alosae.

Two species of parasites were found in the blind sac of the stomach a trematode Hemiurus appendiculatus (Rudolphi), and a nematode Thynnascaris aduncum (Rudolphi) (formerly known as Contracaecum aduncum). These species were identified by Dr. Khalil, Commonwealth Institute of Helminthology. The incidence and level of infection of H.appendiculatus and T.aduncum in the population sampled in 1979 and 1980 are shown in tables Ap. 4.9 a + b and Ap. 4.10 a + b. The relationship of age, size and the number of previous spawnings against the incidence and level of infection with H.appendiculatus are shown in tables Ap. 4.11 a + b; Ap. 4.12 a + b; Ap. 4.13 a + b and with T.aduncum in tables Ap. 4.14 a + b; Ap. 4.15 a + b and Ap. 4.16 a + b.

Information on parasites in the intestine was collected by Kennedy (Exeter University) from material obtained during this study. Aspects of the biology of the cestode Eubothrium fragile (Rudolphi) have been published, Kennedy (1981). Data on the incidence and level of infection with the fellodistomid Pronoprymna ventricosa (Rudolphi) and the acanthocephalan Pomphorynchus laevis (Müller) from the Severn estuary and from freshwater in 1979, are presented in table Ap. 4.17, with permission of Dr. Kennedy.

Reference

Kennedy C.R. The occurence of Eubothrium fragile (Cestoda; Pseudophyllidae) in twaite shad, Alosa fallax (Lacépède) in the River Severn. J. Fish Biol. 19:171 - 177.

Table Ap. 4.1 The incidence and level (mean ± 95% confidence limits) of infection with *Mazocraes alosae* in Female and Male *A.fallax* from the estuary and from freshwater sites.

Sex	Estuary			Freshwater			Combined Estuary & Freshwater	
	N	% Infected	$\bar{x} \pm$ 95% Conf. L.	N	% Infected	$\bar{x} \pm$ 95% Conf. L.	% Infected	$\bar{x} \pm$ 95% Conf. L.
Female	75	80.0	15.6 ± 4.2	20	90.0	5.0 ± 2.9	82.1	13.4 ± 3.5
Male	25	68.0	7.0 ± 3.4	24	70.8	3.5 ± 1.6	69.4	5.3 ± 1.9
Combined Female and Male	100	77.0	13.5 ± 3.3	44	79.5	4.2 ± 1.5	77.8	10.6 ± 2.4

Table Ap. 4.2 The incidence and level (mean ± 95% confidence limits) of infection with *Clavellisa emarginata* in Female and Male *A.fallax* from the estuary and from freshwater sites, in 1979.

Sex	Estuary			Freshwater			Combined Estuary & Freshwater	
	N	% Infected	$\bar{x} \pm$ 95% Conf. L.	N	% Infected	$\bar{x} \pm$ 95% Conf. L.	% Infected	$\bar{x} \pm$ 95% Conf. L.
Female	75	32.0	2.5 ± 1.7	20	10.0	3.0 ± 5.5	27.4	2.6 ± 1.7
Male	25	36.0	3.6 ± 2.6	24	12.5	0.3 ± 0.4	24.5	2.0 ± 1.4
Combined Female and Male	100	33.0	2.8 ± 1.4	44	11.4	1.5 ± 2.4	26.4	2.4 ± 1.2

Table Ap. 4.3a The relationship between age and the incidence of infection with *Mazocraes alosae*.

Age	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
3						3	66.7	1	0.0	50.0	66.7	0.0	50.0
4	30	60.0	9	100.0	69.2	15	53.3	15	66.7	60.0	57.8	79.2	65.2
5	5	80.0	3	66.7	75.0	1	100.0	2	50.0	66.7	83.3	60.0	72.7
6	29	96.9	8	87.5	94.6	4	100.0	6	100.0	100.0	97.0	92.9	95.7
7	6	100.0			100.0	2	100.0			100.0	100.0		100.0
8	2	100.0			100.0						100.0		100.0
9	3	100.0			100.0						100.0		100.0

Table Ap. 4.3b The relationship between age and the level (mean ± 95% confidence limits) of infection with *Mazocraes alosae*.

Age	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	Combined $\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	Combined $\bar{x}$ ± 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
3						3	4.7 ± 16.0	1	0	3.5 ± 9.1	4.7 ± 16.0	0	3.5 ± 9.1
4	30	1.8 ± 1.3	9	1.4 ± 0.4	1.7 ± 1.0	15	5.1 ± 4.2	15	2.5 ± 1.9	3.8 ± 2.2	2.9 ± 1.6	2.1 ± 1.2	2.6 ± 1.1
5	5	8.2 ±19.3	3	2.3 ± 8.0	6.0 ±10.3	1	1.0	2	3.0 ±38.1	2.3 ± 8.0	7.0 ± 14.9	2.6 ± 3.9	5.0 ± 7.1
6	29	24.5 ± 6.8	8	10.0 ± 6.3	21.3 ± 5.8	4	13.3 ± 14.6	6	6.7 ± 3.3	9.3 ± 4.8	23.1 ± 6.2	8.6 ± 3.5	18.8 ± 4.8
7	6	28.3 ± 8.6			28.3 ± 8.6	2	16.0 ± 50.8			16.0 ±50.8	25.3 ± 7.7		25.3 ± 7.7
8	2	52.5 ±82.6			52.5 ±82.6						52.5 ± 82.6		52.5 ±82.6
9	3	30.7 ±63.5			30.7 ±63.5						30.7 ± 63.5		30.7 ±63.5

Table Ap. 4.4a The relationship between fish size and the incidence of infection with *Mazocraes alosae*.

Fork Length (mm)	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
240-259						2	50.0	1	100.0	66.7	50.0	100.0	66.7
260-279						3	66.7	8	50.0	54.5	66.7	50.0	54.5
280-299	2	0	2	100.0	50.0	7	57.1	7	71.4	64.3	44.4	77.8	61.1
300-319	11	45.5	5	100.0	62.5	7	57.1	6	83.3	69.2	50.0	90.9	65.5
320-339	13	69.2	4	75.0	70.6	4	100.0	2	100.0	100.0	76.5	83.3	78.3
340-359	19	89.5	9	88.9	89.3	2	100.0			100.0	90.5	88.9	90.0
360-379	18	94.4									94.4		94.4
380-399	10	100.0									100.0		100.0
400-419	2	100.0									100.0		100.0

Table Ap. 4.4b The relationship between fish size and the level (mean ± 95% confidence limits) of infection with *Mazocrae alosae*.

Fork Length (mm)	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
240-259						2	6.0 ± 76.2	1	2	4.7 ± 16.0	6.0 ± 76.2	2	4.7 ± 16.0
260-279						3	4.7 ± 18.0	8	2.9 ± 3.8	3.4 ± 3.4	4.7 ± 18.0	2.9 ± 3.8	2.9 ± 3.8
280-299	2	0	2	1.5 ± 6.4	0.8 ± 1.5	7	4.9 ± 8.4	7	2.4 ± 2.2	3.6 ± 3.7	3.8 ± 6.3	2.2 ± 1.6	3.0 ± 2.9
300-319	11	1.1 ± 1.3	5	3.0 ± 2.9	1.7 ± 1.1	7	7.3 ± 9.0	6	3.5 ± 3.2	5.5 ± 4.5	3.5 ± 3.3	3.3 ± 1.8	3.4 ± 2.1
320-339	13	2.9 ± 3.2	4	6.0 ±16.0	3.6 ± 3.3	4	8.3 ± 10.0	2	10.0 ±12.7	8.8 ± 5.2	4.2 ± 3.0	7.3 ± 8.5	5.0 ± 2.8
340-359	19	11.5 ± 6.6	9	6.4 ± 5.2	9.9 ± 4.7	2	16.0 ± 50.8			16.0 ± 50.8	12.0 ± 6.0	6.4 ± 5.2	10.3 ± 4.4
360-379	18	31.7 ± 9.8			31.7 ± 9.8						31.7 ± 9.8		31.7 ± 9.8
380-399	10	27.0 ±10.6			27.0 ±10.6						27.0 ± 10.6		27.0 ± 10.6
400-419	2	30.5 ±260.5			30.5 ±260.5						30.5 ±260.5		30.5 ±260.5

Table Ap. 4.5a The relationship between the number of previous spawnings and the incidence of infection with *Mazocraes alosae*.

No. of Previous Spawnings	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER		Combined % Infected	ESTUARY		FRESHWATER		Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
	N	% Infected	N	% Infected		N	% Infected	N	% Infected				
0	35	60.0	11	90.9	67.4	14	42.9	10	40.0	41.7	55.1	66.7	58.6
1	11	100.0	5	100.0	100.0	5	100.0	8	87.5	92.3	100.0	92.3	94.7
2	24	100.0	4	75.0	96.4	6	100.0	5	100.0	100.0	100.0	88.9	97.4
3	4	100.0			100.0			1	100.0	100.0	100.0	100.0	100.0
4	1	100.0			100.0						100.0		100.0

Table Ap. 4.5b The relationship between the number of previous spawnings and the level (mean ± 95% confidence limits) of infection with *Mazocraes alosae*.

No. of Previous Spawnings	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER			ESTUARY	FRESHWATER	Est. F.W.
	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.			
0	35	1.7 ± 1.1	11	1.3 ± 0.4	1.6 ± 0.8	14	1.4 ± 1.8	10	0.6 ± 0.6	1.0 ± 1.0	1.6 ± 0.9	1.0 ± 0.4	1.4 ± 0.6
1	11	21.4 ± 8.1	5	6.4 ± 4.0	16.7 ± 6.5	5	14.4 ± 7.6	8	5.0 ± 3.6	8.6 ± 4.1	19.2 ± 5.8	5.5 ± 2.3	13.1 ± 4.1
2	24	28.3 ± 7.4	4	13.5 ± 14.7	26.2 ± 6.7	6	14.2 ± 8.1	5	5.8 ± 3.9	10.4 ± 4.9	25.5 ± 6.3	9.2 ± 5.6	21.7 ± 5.4
3	4	39.5 ± 40.7			39.5 ± 40.7			1	8.0	8.0	39.5 ± 40.7	8.0	33.2 ± 32.6
4	1	39.0			39.0						39.0		39.0

Table Ap. 4.6a The relationship between age and the incidence of infection with *Clavellisa emarginata*.

Age	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER		Combined % Infected	ESTUARY		FRESHWATER		Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
	N	% Infected	N	% Infected		N	% Infected	N	% Infected				
3						3	66.7	1	0.0	50.0	66.7	0.0	50.0
4	30	33.3	9	0.0	25.6	15	46.7	15	6.7	26.7	37.8	4.2	27.5
5	5	40.0	3	0.0	25.0	1	0.0	2	50.0	33.3	50.0	20.0	27.3
6	29	31.0	8	25.0	29.7	4	0.0	6	16.7	10.0	27.3	21.4	25.5
7	6	0.0			0.0	2	0.0			0.0	0.0		0.0
8	2	50.0			50.0						50.0		50.0
9	3	66.7			66.7						66.7		66.7

Table Ap. 4.6b The relationship between age and the level (mean ± 95% confidence limits) of infection with *Clavellisa emarginata*.

Age	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER			ESTUARY	FRESHWATER	Est. F.W.
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.			
3						3	2.3 ± 6.3	1	0.0	1.8 ± 3.8	2.3 ± 6.3	0.0	1.8 ± 3.8
4	30	2.7 ± 2.0	9	0.0	2.1 ± 1.6	15	5.5 ± 4.2	15	0.1 ± 0.3	2.8 ± 2.2	3.4 ± 1.9	0.1 ± 0.2	2.2 ± 1.3
5	5	1.0 ± 2.1	3	0.0	0.6 ± 1.2	1	0.0	2	0.5 ± 6.4	0.3 ± 1.4	0.8 ± 1.7	0.2 ± 0.6	0.5 ± 0.8
6	29	2.6 ± 3.2	8	7.4 ±15.5	3.6 ± 3.7	4	0.0	6	0.7 ± 1.7	0.4 ± 0.9	2.2 ± 2.8	4.5 ± 8.1	2.9 ± 2.9
7	6	0.0			0.0	2	0.0			0.0	0.0		0.0
8	2	1.5 ±19.1			1.5 ±19.1						1.5 ±19.1		1.5 ±19.1
9	3	12.7 ±48.2			12.7 ±48.2						12.7 ±48.2		12.7 ±48.2

Table Ap. 4.7a The relationship between fish size and the incidence of infection with Clavellisa emarginata.

Fork Length (mm)	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
240-259						2	100.0	1	100.0	100.0	100.0	100.0	100.0
260-279						3	66.7	8	0.0	9.1	66.7	0.0	9.1
280-299	2	100.0	2	0.0	50.0	7	28.6	7	14.3	21.4	44.4	11.1	27.8
300-319	11	45.5	5	0.0	31.3	7	42.9	6	0.0	23.1	44.4	0.0	27.6
320-339	13	30.8	4	25.0	29.4	4	25.0	2	50.0	33.3	29.4	33.3	30.4
340-359	19	31.6	9	11.1	25.0	2	0.0			0.0	28.6	11.1	23.3
360-379	18	27.8			27.8						27.8		27.8
380-399	10	20.0			20.0						20.0		20.0
400-419	2	0.0			0.0						0.0		0.0

Table Ap. 4.7b The relationship between fish size and the level (mean ± 95% confidence limits) of infection with Clavellisa emarginata.

Fork Length (mm)	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
240-259						2	3.5 ± 19.1	1	2.0	3.0 ± 4.3	3.5 ± 19.1	2.0	3.0 ± 4.3
260-279						3	6.3 ± 27.2	8	0.0	1.7 ± 3.8	6.3 ± 27.2	0.0	1.7 ± 3.8
280-299	2	11.5 ± 132.8	2	0.0	5.8 ± 14.4	7	4.0 ± 7.1	7	0.1 ± 0.3	2.1 ± 3.2	5.7 ± 6.4	0.1 ± 0.3	2.9 ± 3.2
300-319	11	1.5 ± 1.4	5	0.0	1.0 ± 0.9	7	3.1 ± 5.2	6	0.0	1.7 ± 2.6	2.1 ± 1.9	0.0	1.3 ± 1.2
320-339	13	6.9 ± 8.0	4	1.5 ± 4.8	5.6 ± 6.1	4	3.5 ± 11.1	2	2.0 ± 25.4	3.0 ± 5.9	6.1 ± 6.1	1.7 ± 2.8	5.0 ± 4.5
340-359	19	0.7 ± 0.7	9	5.9 ± 13.6	2.4 ± 3.9	2	0.0			0.0	0.7 ± 0.6	5.9 ± 13.6	2.2 ± 3.6
360-379	18	0.5 ± 0.5									0.5 ± 0.5		0.5 ± 0.5
380-399	10	3.8 ± 7.9									3.8 ± 7.9		3.8 ± 7.9
400-419	2	0.0									0.0		0.0

Table Ap. 4.8a The relationship between the number of previous spawnings and the incidence of infection with *Clavellisa emarginata*.

No. of Previous Spawnings	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
0	35	37.1	11	0.0	28.3	14	42.9	10	10.0	29.2	38.8	4.8	28.6
1	11	27.3	5	20.0	25.0	5	60.0	8	12.5	30.8	37.5	15.4	27.6
2	24	20.8	4	25.0	21.4	6	0.0	5	20.0	9.1	16.7	22.2	17.9
3	4	50.0			50.0			1	0.0	0.0	50.0	0.0	40.0
4	1	100.0			100.0						100.0		100.0

Table Ap. 4.8b The relationship between the number of previous spawnings and the level (mean ± 95% confidence limits) of infection with *Clavellisa emarginata*.

No. of Previous Spawnings	Females					Males					Combined Males anf Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
0	35	2.2 ± 1.8	11	0.0	1.7 ± 1.4	14	4.3 ± 4.0	10	0.2 ± 0.5	2.6 ± 2.4	2.8 ± 1.6	0.1 ± 0.2	2.0 ± 1.2
1	11	4.0 ± 8.9	5	10.6 ±29.4	6.1 ± 8.7	5	6.0 ± 9.7	8	0.5 ± 1.2	2.6 ± 3.3	4.6 ± 5.9	4.4 ± 8.9	4.5 ± 4.8
2	24	1.1 ± 1.7	4	1.5 ± 4.8	1.2 ± 1.5	6	0.0	5	0.2 ± 0.5	0.1 ± 0.2	0.9 ± 1.3	0.8 ± 1.5	0.9 ± 1.0
3	4	1.5 ± 2.8			1.5 ± 2.8			1	0.0	0.0	1.5 ± 2.8	0.0	1.2 ± 2.0
4	1	35			35						35		35

Table Ap. 4.9a The incidence and level (mean ± 95% confidence limits) of infection with *Hermiurus appendiculatus*, in the blind sac of the stomach, in female and male *A.fallax* from the estuary and from freshwater sites in 1979.

Sex	ESTUARY			FRESHWATER			Combined Estuary & Freshwater	
	N	% Infection	$\bar{x} \pm$ 95% Conf. L.	N	% Infection	$\bar{x} \pm$ 95% Conf. L.	% Infection	$\bar{x} \pm$ 95% Conf. L.
Female	31	83.9	5.9 ± 3.9	22	77.3	7.0 ± 5.3	81.1	6.4 ± 2.8
Male	12	100.0	3.3 ± 1.4	11	72.7	3.7 ± 4.6	87.0	3.5 ± 2.1
Combined Female and Male	43	88.4	5.2 ± 2.8	33	75.8	5.9 ± 3.8	82.9	5.5 ± 2.2

Table Ap. 4.9b The incidence and level (mean ± 95% confidence limits) of infection with *Hermiurus appendiculatus*, in the blind sac of the stomach, in female and male *A.fallax* from the estuary in 1980.

Sex	ESTUARY		
	N	% Infection	$\bar{x} \pm$ 95% Conf. L.
Female	17	100.0	5.1 ± 2.1
Male	13	100.0	11.5 ± 5.5
Combined Female and Male	30	100.0	7.8 ± 2.7

Table Ap. 4.10a The incidence and level (mean ± 95% confidence limits) of infection with *Thynnascaris aduncum*, in the blind sac of the stomach, in female and male *A.fallax* from the estuary and from freshwater sites, in 1979.

Sex	ESTUARY			FRESHWATER			Combined Estuary & Freshwater	
	N	% Infected	$\bar{x} \pm$ 95% Conf. L.	N	% Infected	$\bar{x} \pm$ 95% Conf. L.	% Infected	$\bar{x} \pm$ 95% Conf. L.
Female	31	67.7	12.4 ± 10.2	22	9.1	0.3 ± 0.4	43.4	7.4 ± 6.1
Male	12	58.3	15.3 ± 28.0	11	18.2	0.5 ± 1.0	39.1	8.3 ±11.4
Combined Female and Male	43	65.1	13.2 ± 10.1	33	12.1	0.4 ± 0.4	42.1	7.6 ± 5.8

Table Ap. 4.10b The incidence and level (mean ± 95% confidence limits) of infection with *Thynnascaris aduncum*, in the blind sac of the stomach, in female and male *A.fallax* from the estuary in 1980.

Sex	ESTUARY		
	N	% Infected	$\bar{x} \pm$ 95% Conf. L.
Female	17	88.2	16.3 ± 7.7
Male	13	92.3	22.8 ±13.7
Combined Female and Male	30	90.0	19.1 ± 6.8

Table Ap. 4.11a The relationship between age and the incidence of infection with *Hemiurus appendiculatus*, in 1979

Age	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
3													
4	9	77.8	6	83.3	80.0	9	100.0	2	0.0	81.8	88.9	62.5	80.9
5	3	100.0	2	100.0	100.0			1	100.0	100.0	100.0	100.0	100.0
6	8	75.0	8	75.0	75.0	1	100.0	3	100.0	100.0	77.8	81.8	80.0
7	3	66.7			66.7	1	100.0			100.0	75.0		75.0
8													
9	1	100.0			100.0						100.0		100.0

Table Ap. 4.11b The relationship between age and the level (mean ± 95% confidence limits) of infection with *Hemiurus appendiculatus*, in 1979.

Age	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
3													
4	9	2.4 ± 1.5	6	2.8 ± 2.4	2.6 ± 1.1	9	4.0 ± 1.6	2	0	3.3 ± 1.6	3.2 ± 1.0	2.1 ± 2.0	2.9 ± 0.9
5	3	2.3 ± 2.9	2	38.0 ±152.5	16.6 ±26.5			1	1	1	2.3 ± 2.9	25.7 ±60.9	14.0 ±21.1
6	8	2.4 ± 2.5	8	6.5 ± 7.2	4.4 ± 3.5	1	1	3	10.7 ±28.7	8.3 ±16.9	2.2 ± 2.2	7.6 ± 6.1	5.2 ± 3.5
7	3	1.7 ± 5.2			1.7 ± 5.2	1	2			2	1.8 ± 2.7		1.8 ± 2.7
8													
9	1	50			50						50		50

Table Ap. 4.12a The relationship between fork length and the incidence of infection with Hemiurus appendiculatus, in 1979.

Fork Length (mm)	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infecter	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
220-239						1	100.0				100.0		100.0
240-259													
260-279						1	100.0	2	0.0	33.3	100.0		100.0
280-299	1	100.0	1	100.0	100.0	2	100.0	5	100.0	100.0	100.0	100.0	100.0
300-319	5	80.0	4	100.0	88.9	5	100.0	2	50.0	14.3	90.0	83.3	87.5
320-339	6	83.3	10	70.0	75.0	1	100.0	2	100.0	100.0	85.7	75.0	78.9
340-359	8	87.5	4	75.0	83.3	2	100.0			100.0	90.0	75.0	85.7
360-379	6	83.3	3	100.0	88.9						83.3	100.0	88.9
380-399	4	100.0			100.0						100.0		100.0
400-419	1	0.0			0.0						0.0		0.0

Table Ap. 4.12b The relationship between fork length and the level (mean ± 95% confidence limits) of infection with Hemiurus appendiculatus, in 1979.

Fork Length (mm)	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
220-239						1	5				5		5
240-259													
260-279						1	5	2	0	1.7 ± 7.2	5	0	1.7 ± 7.2
280-299	1	4	1	3	3.5 ± 6.4	2	2.5 ±19.1	5	2.4 ± 1.4	2.4 ± 1.2	3.0 ± 4.3	2.5 ± 1.1	2.7 ± 0.9
300-319	5	1.8 ± 1.6	4	3.5 ± 2.8	2.6 ± 1.3	5	4.2 ± 3.0	2	2.0 ±25.4	3.6 ± 2.3	3.0 ± 1.6	3.0 ± 2.1	3.0 ± 1.1
320-339	6	5.7 ± 8.2	10	9.4 ±11.6	8.0 ± 7.2	1	1	2	12.5 ±146.1	8.7 ±34.0	5.0 ± 6.8	9.9 ± 9.9	8.1 ± 6.3
340-359	8	6.8 ± 8.8	4	4.0 ± 5.7	5.8 ± 5.5	2	1.5 ± 6.4				5.7 ± 6.9	4.0 ± 5.7	5.2 ± 4.7
360-379	6	4.0 ± 6.8	3	10.3 ±35.9	6.1 ± 7.2						4.0 ± 6.8	10.3 ±35.9	6.1 ± 7.2
380-399	4	14.8 ±37.5			14.8 ±37.5						14.8 ±37.5		14.8 ±37.5
400-419	1	0			0						0		0

Table Ap. 4.13a The relationship between the number of previous spawnings and the incidence of infection with *Hemiurus appendiculatus*, in 1979.

No. of Previous Spawnings	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
0	11	81.8	6	83.3	82.4	7	100.0			100.0	88.9	83.3	87.5
1	3	66.7	4	75.0	71.4	2	100.0	4	50.0	66.7	80.0	62.5	69.2
2	9	77.8	6	83.3	80.0	2	100.0	2	100.0	100.0	81.8	87.5	84.2
3													
4	1	100.0			100.0						100.0		100.0

Table Ap. 4.13b The relationship between the number of previous spawnings and the level (mean ± 95% confidence limits) of infection with *Hemiurus appendiculatus*, in 1979.

No. of Previous Spawnings	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
0	11	2.7 ± 1.2	6	2.8 ± 2.4	2.8 ± 1.0	7	4.0 ± 2.1			4.0 ± 2.1	3.2 ± 1.0	2.8 ± 2.4	3.1 ± 0.9
1	3	3.3 ± 12.3	4	20.8 ± 35.6	13.3 ± 17.2	2	4.0 ± 12.7	4	6.3 ± 18.8	5.5 ± 9.7	3.6 ± 4.4	13.5 ± 14.1	9.7 ± 9.1
2	9	1.7 ± 1.2	6	7.5 ± 10.3	4.0 ± 3.7	2	1.5 ± 6.4	2	4.0 ± 0.0	2.8 ± 2.4	1.6 ± 0.9	6.6 ± 7.0	4.0 ± 2.8
3													
4	1	50			50						50		50

Table Ap. 4.14a The relationship between age and the incidence of infection with *Thynnascaris aduncum*, in 1979.

Age	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
4	9	55.6	6	0.0	33.3	9	44.4	2	50.0	45.5	50.0	12.5	38.5
5	3	100.0	2	0.0	60.0			1	0.0	0.0	100.0	0.0	50.0
6	8	75.0	8	0.0	37.5	1	100.0	3	33.3	50.0	77.8	9.1	40.0
7	3	33.3			33.3	1	100.0			100.0	50.0		50.0
8													
9	1	100.0			100.0						100.0		100.0

Table Ap. 4.14b The relationship between age and the level (mean ± 95% confidence limits) of infection with *Thynnascaris aduncum*, in 1979.

Age	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
4	9	18.8 ± 35.5	6	0	11.3 ± 20.0	9	2.8 ± 3.1	2	0.5 ± 6.4	2.4 ± 2.5	10.8 ± 16.3	0.1 ± 0.3	7.5 ± 11.1
5	3	30.7 ± 87.5	2	0	18.4 ± 37.3			1	0	0	30.7 ± 87.5	0.0	15.3 ± 29.3
6	8	4.9 ± 7.7	8	0	2.4 ± 3.6	1	155	3	1.7 ± 7.2	40.0 ± 487.3	21.6 ± 39.0	0.5 ± 1.0	10.0 ± 16.2
7	3	0.3 ± 1.4			0.3 ± 1.4	1	1			1	0.5 ± 0.9		0.5 ± 0.9
8													
9	1	33			33						33		33

Table Ap. 4.15a The relationship between fork length and the incidence of infection with *Thynnascaris aduncum* in 1979

Fork Length (mm)	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER		Combined % Infected	ESTUARY		FRESHWATER		Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
	N	% Infected	N	% Infected		N	% Infected	N	% Infected				
220-239						1	0.0			0.0	0.0		0.0
240-259													
260-279						1	0.0	2	50.0	33.3	0.0	50.0	33.3
280-299	1	0.0	1	0.0	0.0	2	100.0	5	0.0	28.6	66.7	0.0	22.2
300-319	5	40.0	4	0.0	22.2	5	40.0	2	0.0	28.6	40.0	0.0	25.0
320-339	6	66.7	10	20.0	37.5	1	100.0	2	50.0	66.7	71.4	25.0	42.1
340-359	8	87.5	4	0.0	58.3	2	100.0			100.0	90.0	0.0	64.3
360-379	6	66.7	3	0.0	44.4						66.7	0.0	44.4
380-399	4	75.0			75.0						75.0		75.0
400-419	1	100.0			100.0						100.0		100.0

Table Ap. 4.15b The relationship between fork length and the level (mean ± 95% confidence limits) of infection with *Thynnascaris aduncum*, in 1979.

Fork Length (mm)	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER			ESTUARY	FRESHWATER	Est. F.W.
	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	N	$\bar{x}$ ± 95% Conf. L.	$\bar{x}$ ± 95% Conf. L.			
220-239						1	0				0		
240-259													
260-279						1	0	2	0.5 ± 6.4	0.3 ± 1.4	0	0.5 ± 6.4	0.3 ± 1.4
280-299	1	0	1	0	0	2	7.0 ±50.8	5	0	2.0 ± 3.8	4.7 ±14.1	0	1.6 ± 2.8
300-319	5	2.8 ± 7.1	4	0	1.6 ± 3.3	5	2.2 ± 4.3	2	0	1.6 ± 2.8	2.5 ± 3.2	0	1.6 ± 2.0
320-339	6	29.7 ±58.0	10	0.6 ± 1.0	11.5 ±18.4	1	155	2	2.5 ± 1.8	53.3 ±218.8	47.6 ±64.0	0.9 ± 1.1	18.1 ±22.3
340-359	8	7.9 ± 7.8	4	0	5.3 ± 5.3	2	2.0 ±12.7			2.0 ±12.7	6.7 ± 6.1	0	4.8 ± 4.5
360-379	6	13.5 ±29.7	3	0	9.0 ±17.9						13.5 ±29.7	0	9.0 ±17.9
380-399	4	11.8 ±24.4			11.8 ±24.4						11.8 ±24.4		11.8 ±24.4
400-419	1	1			1						1		1

Table Ap. 4.16a The relationship between the number of previous spawnings and the incidence of infection with *Thynnascaris aduncum*, in 1979

No. of Previous Spawnings	Females					Males					Combined Males and Females % Infected		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	% Infected	N	% Infected	Combined % Infected	N	% Infected	N	% Infected	Combined % Infected	ESTUARY	FRESHWATER	Est. F.W.
0	11	63.6	6	0.0	41.2	7	42.9			42.9	55.6	0.0	41.7
1	3	100.0	4	0.0	42.9	2	50.0	4	50.0	50.0	80.0	25.0	46.2
2	9	55.6	6	0.0	33.3	2	100.0	2	0.0	50.0	63.6	0.0	36.8
3													
4	1	100.0			100.0						100.0		100.0

Table Ap. 4.16b The relationship between the number of previous spawnings and the level (mean ± 95% conficence limits) of infection with *Thynnascaris aduncum*, in 1979

No. of Previous Spawnings	Females					Males					Combined Males and Females (mean ± 95% confidence limits)		
	ESTUARY		FRESHWATER			ESTUARY		FRESHWATER					
	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	N	$\bar{x} \pm$ 95% Conf. L.	$\bar{x} \pm$ 95% Conf. L.	ESTUARY	FRESHWATER	Est. F.W.
0	11	17.3 ± 27.8	6	0	11.2 ± 17.4	7	2.0 ± 2.8			2.0 ± 2.8	11.3 ± 16.3	0	8.5 ± 12.1
1	3	24.3 ± 100.4	4	0	10.4 ± 24.7	2	5.5 ± 69.9	4	1.5 ± 3.8	2.8 ± 4.7	16.8 ± 38.0	0.8 ± 1.5	6.9 ± 11.8
2	9	4.2 ± 6.7	6	0	2.5 ± 3.9	2	78.0 ± 978.4	2	0	39.0 ± 123.0	17.6 ± 31.1	0	10.2 ± 17.2
3													
4	1	33			33						33		33

Table Ap. 4.17 The incidence and level (mean ± 95% confidence limits) of infection of _Pronoprymna ventriosa_ and _Pomphorhynchus laevis_ in adult _A.fallax_ from the Severn estuary and from freshwater at Powic weir, River Teme.

Site	Number	_P.ventriosa_		_P.laevis_	
		% Infected	$\bar{x} \pm$ 95% Conf. L.	% Infected	$\bar{x} \pm$ 95% Conf. L.
Estuary	20	95.0	*	10.0	0.25 ± 0.37
Freshwater	11	100.0	*	9.1	0.27 ± 0.61
Ext. & Fw.	31	96.8	*	9.8	0.26 ± 0.30

* not counted

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ASPECTS OF THE BIOLOGY OF THE TWAITE SHAD *(ALOSA FALLAX)* IN THE RIVERS SEVERN AND WYE

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INTRODUCTION

There is at present very little published information on the life history of the allis and twaite shad in the British Isles. From the literature it was apparent that the adult fish enter the estuary during April and May and spawn in freshwater. The juveniles migrate seaward in the autumn of their first year of life.

This study was aimed at increasing our knowledge of the biology of this species and some of the findings are presented here.

HISTORICAL ASPECTS

In the British Isles there are two species of shad, the allis *(Alosa alosa)* and the twaite *(Alosa fallax)*, (Figure 1), both species are anadromous. The twaite shad does possess a subspecies that is land locked and found in the lakes of Killarney in South West Ireland where it is locally known as the goureen *(Alosa fallax killarnensis)*, (Regan, 1916; Trewavas, 1938).

The shad was first recorded by Giraldus Cambrensis who made extensive travels through the British Isles during the twelfth century. A quotation (Wright, 1905) (concerning the Irish rivers) goes as follows:-

> "The rivers and lakes, also, are plentifully stored with the sorts of fish peculiar to those waters and especially three species: salmon and trout, muddy eels and oily shad".

The shad, along with the salmon and of course the lamprey, which was pre-eminent as a table delicacy, was one of the principal kinds of fish from the Severn sent to the Court of Henry III and many references are made to shad in the Calendar of Liberate Rolls.

The allis, and to some degree the twaite, were of considerable economic importance to the fishermen of the Severn. It was common for the shad to make up as much as one third of the income from the fishery. However, in some instances when there had not been a good run of salmon the shad would have brought in more money.

The twaite shad is more widespread in European coastal waters than the allis shad and both species are considered to be less abundant than previously (Maitland, 1979). The best documented evidence for this decline comes for the allis shad in the Severn and the twaite shad from the Thames. This decline in abundance is mainly attributed to the construction of navigation weirs (Day, 1890) and to pollution. On the Severn, navigation weirs were constructed around 1842, at Gloucester, Tewkesbury, Worcester and Shrewsbury. The weirs at Worcester and Shrewsbury were probably the main culprits in preventing the allis shad migrating to their spawning grounds. Evidence given at the enquiry into salmon fisheries (England and Wales) between 1860 - 65 indicates that allis shad used to go the whole way up to Welshpool to spawn. At the same time there was a considerable amount of road building taking place and the construction engineers removed large amounts of gravel from the fords and it is on small gravelly fords that the majority of spawning takes place.

In the Thames it was probably pollution that caused the shad population to decline, as well as the salmon, smelt and flounder populations. Mr. Henry Farnell (1860) (Secretary to the Thames Angling Preservation Society) blamed the decline on the increase in the number of steamers stirring up great amounts of 'frightfully offensive stuff'.

The current situation is that the allis shad must be regarded as exceedingly rare and likewise the twaite shad from the river Thames. However, in the rivers Severn and Wye there appears to be a healthy spawning population of twaite shad. They are also believed to be in other Welsh rivers, the Tyfi, Taff, Usk and occasionally in the Dyfi and Mawddach. There may be a small spawning population in some of the south west rivers namely the Dart, Teign, Exe and Axe (results from Questionnaire on present status of stocks). Also in Southern Ireland there are a number of rivers which have a healthy spawning population of twaite (Bracken and Kennedy, 1967).

MATERIALS AND METHODS

The study area is shown in Figure 2. The spawning migration of the twaite shad was monitored using the catch data from a rank of putchers situated just below Lydney, (Figures 3 and 4), and from a salmon draft at Newnham. The putcher rank at Lydney consists of 550 conically shaped baskets measuring 71 cm x 61 cm at the mouth, 1.73 m long and tapering down to a point. They are arranged to fish for approximately 3½ to 4 hours of the ebb tide (depending on tidal height). The rank is completely covered by a 6½ metre tide.

The draft net used at Newnham is 160 m long by 1.9 m deep at the centre and tapers to either end with a mesh size of 50 mm knot to knot. Fishing is mainly concentrated on neap tides as on the spring tides the ebb current runs too hard making fishing more difficult. The draft nets also have a week-end closed fishing period. In the freshwater region of the river, angling was the main method used to obtain samples of spawning adults.

Eggs were 'hich' sampled using a standard FBA net and 'drift' sampled using conical shaped nets, which were 1.1 m long with a mouth of 30 cm in diameter and a mesh size of 1.0 mm x 0.7 mm.

The larvae and juveniles were sampled with a seine net that measured 20 m long x 3 m deep with a mesh size of 5 mm. This net was mainly used in freshwater (Figure 4). In the Severn estuary at Newnham a seine net 69.5 m long, 3 m deep and with a mesh size of 6.35 mm knot to knot was used. Sampling for juveniles was also carried out at Oldbury power station where 5 mm mesh nets were used to intercept the rubbish brought up by the revolving screens (Figure 6). Sampling was carried out on eight metre tides, starting two hours after high-water for a period of six hours, this was found to be the time, during daylight, when most of the fish were caught.

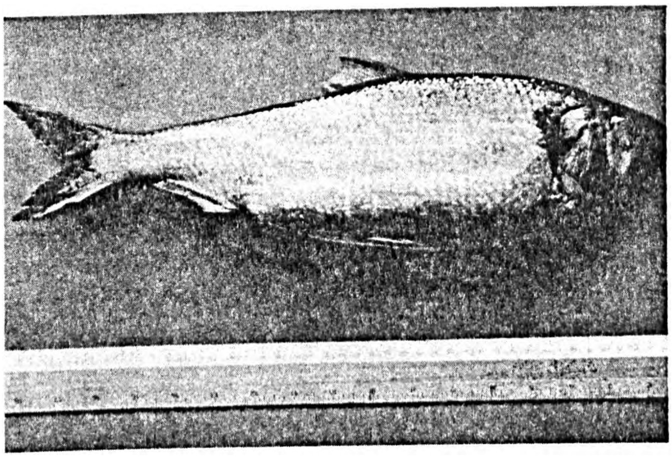

Fig. 1. A Twaite Shad *(Alosa fallax)*.

Fig. 2. The study area.

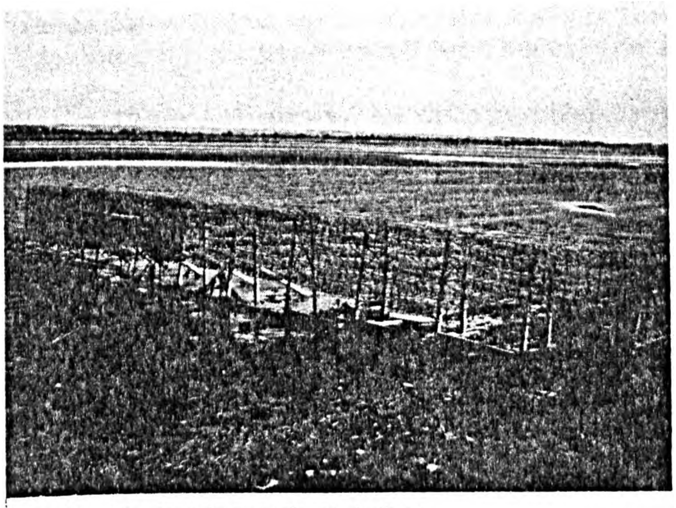

Fig. 3. The Putcher rank at Lydney.

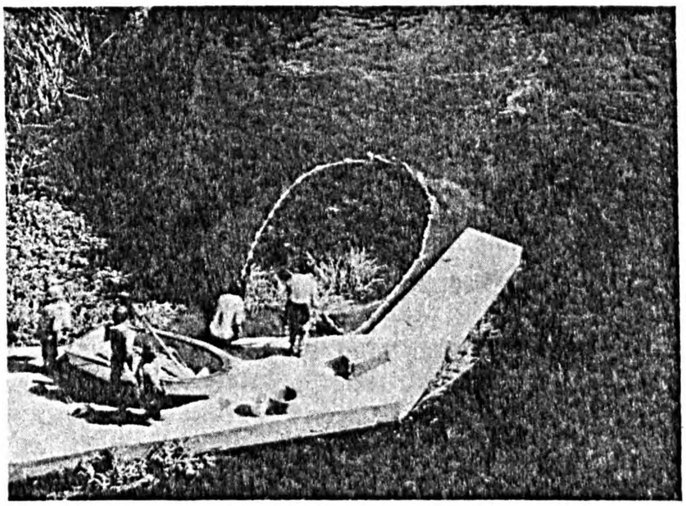

Fig. 4. Seine netting for the young at Monmouth on the river Wye.

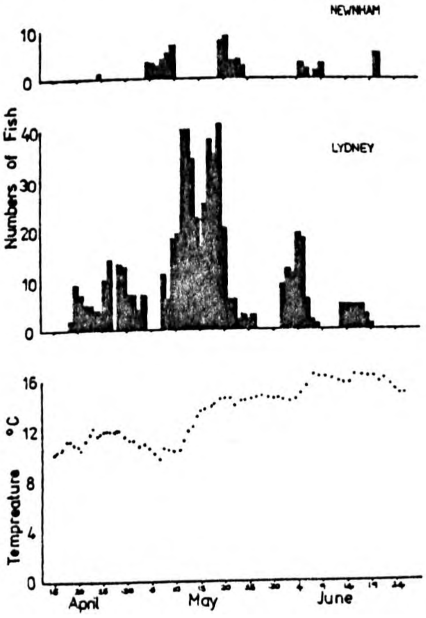

Fig. 5. The catch at Lydney (average number/tide/day), at Newnham (average number/draft/day) and temperature in degrees centigrade.

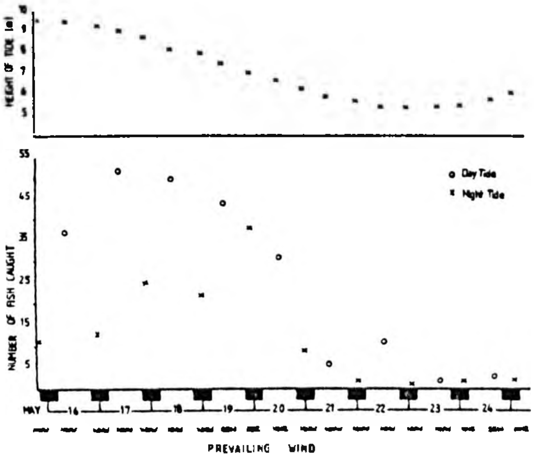

Fig. 6. The catch at Lydney between May 15 - 25 (1980) with height of tide in metres and wind direction.

RESULTS AND DISCUSSION

The first twaite were seen in the Severn estuary in mid April. They were being caught by the Newport drift netters about 10 days before the first ones started to appear in the rank at Lydney, when the temperature was 10°C. A number of workers have found a close correlation between temperature and the spawning migration, Cooper (1961), Leggett and Whitney (1972), Leim and Scott (1966). Claridge and Gardner (1978) found that the twaite's spawning migration in the Severn appeared to start when the temperature increased above 12°C. Figure 5 shows the catches of twaite at Lydney and Newnham and the temperature at that time. (The catch for the putcher rank at Lydney is the average catch per tide per day. Those for Newnham are the average catch per draft per day. The gaps in the data indicate that no sample was taken rather than that no fish were present). It is evident that the main part of the run did not enter the estuary until mid May when the temperature had started to rise sharply from 11°C to 14½°C. On close examination of the Lydney catch data it appears that there is a build up of numbers caught in the rank followed by a decline, followed by another build up in numbers and a subsequent decline.

Figure 6 shows, in detail, the catch for each tide between May 15 and May 25 (1980), with the corresponding tidal height and wind direction. One of the major features of the Severn is its immense tidal range, second largest in the world, and this must be taken into account when considering fish movement in the Severn. During the period in question the tidal height falls from 9.5 m to 5.3 m and there is a subsequent decline in the catch. Spring tides run much harder than neap tides, and it appears that the twaite are not as able to swim up river against the ebb current of spring tides as they are against neap tides; this is reflected in the catch data. This seems to indicate that as the current of the ebb tide falls below some critical velocity, the twaite are able to migrate up river against the ebb tide. The catch data may also represent periods of extensive meandering in the estuary as has been shown for the American shad by Dodson et al. (1972) and Leggett (1976). This behaviour allows time for the physiological adaptation associated with the transition from salt to fresh water. From Figure 6 it is also evident that more fish are caught during the day than during the night. As the rank of putchers catches twaite that are swimming downstream with the ebb current, it appears that the twaite are more committed to migrating up river during the night than during the day. It has been shown by Cooper (1961) for alewives and by Banks (1969) for salmonids, that patterns of movement of fish are influenced by light intensity and sometimes in conjunction with temperature (Richkus, 1974).

Wind is known to have an effect on catches (Harden Jones and Scholes, 1980) and on the behaviour of salmonids (Banks, 1969). Putcher ranks on the north bank have their best catches on southerly winds especially south westerlies, while for those on the south bank the opposite is true. It is evident that on 19th May the winds changed from northerly to southerly and this may have caused the higher than expected night catch, by displacing the fish towards the north banks.

Scales were used for ageing the fish, using the same criteria as described by Hass (1965) and Judy (1961). As well as age determination some information on spawning history may be determined from the scales. Spawning causes a considerable amount of resorption from the scales, producing a scar (spawning mark) after rapid scale growth has taken place, once spawning is completed. Most of the female twaite spawn for the first time at age four and five, the males mature and spawn a year earlier.

In 1980 the spawning migration past Lydney, lasted over nine weeks (from 18th April to 21st June) and certain changes in the composition of the migrants were evident through this period. Figure 7 shows the percentage of males plotted at weekly intervals through the run. It appears that the sex ratio is not constant, the early part of the run being characterised by a higher proportion of males. The same situation was found by Claridge and Gardner (1978) and also by Walburg and Nichols (1967) for the American shad and by Cooper (1961) for the alewife.

Figure 8 shows the percentage of female repeat spawners in the catch at weekly intervals, and it appears that the proportion declines through this period. Looking at their fork length distribution (Figure 9), it is apparent that the largest fish enter first and there is a gradual trend towards smaller fish coming in last; Cooper (1961) found similar results for alewives. There did not appear to be any gradual trend in the average age of the females at weekly intervals. Each group was dominated by the five year olds; however, in the seventh week a larger proportion of four year olds entered. In the ninth week the distribution had reverted back to large fish, these fish were not spent and may be fish that are not in prime spawning condition, waiting until the last moment to enter and thus saving on energy reserves.

The twaite, when they enter the estuary have remnants of food in their stomachs. However, by the time they have reached the spawning grounds their stomachs are completely devoid of food.

The spawning areas are widespread and depend to a large extent on the amount of water in the system, allowing them access to the upstream areas. In 1979 adults were found in larger numbers than for many years in the upper reaches of the Wye, around Bulith Wells (193 km from the mouth) (A. Gee, pers comm.) and near Worcester on the River Teme. On the river Teme in 1979, just over 6 twaite were being caught per person per hour; in 1980 the rate of catching fell by at least 12 times to half a twaite per person per hour. The same situation was evident in the upper reaches of the Wye. Examination of the flow data for the two years (Figure 10) indicates why this occurred, in 1979 there was approximately 3 times more water going down the river than in 1980.

After spawning, the twaite return immediately to the estuary and commence feeding, mainly on mysids, gammarids and shrimps.

This scarcity of twaite on the River Teme in 1980 was reflected in the egg densities which fell from 164 eggs/m^2 in 1979 to 21.5 eggs/m^2 in 1980. In the Wye the majority of the twaite eggs are found in the shallows on gravelly substrate. Their density falls off with depth; Figure 11 shows this for two sites on the River Wye, Courtfield (40 km from the river mouth) and Monmouth (26 km), and this may reflect preferred spawning depth. However, a lot of eggs do drift with the current and this pattern may also have arisen from distribution by the current, or a combination of both factors. In the Severn there is a considerable amount of spawning below Tewkesbury and mostly in water that is approximately 3 m deep, but still on top of gravel. The eggs measure 2 - 3 mm in diameter. The larvae at hatching are approximately 7 mm in length and are known as the yolk sac stage; these are shown in Figure 12 along with two slightly more advanced forms.

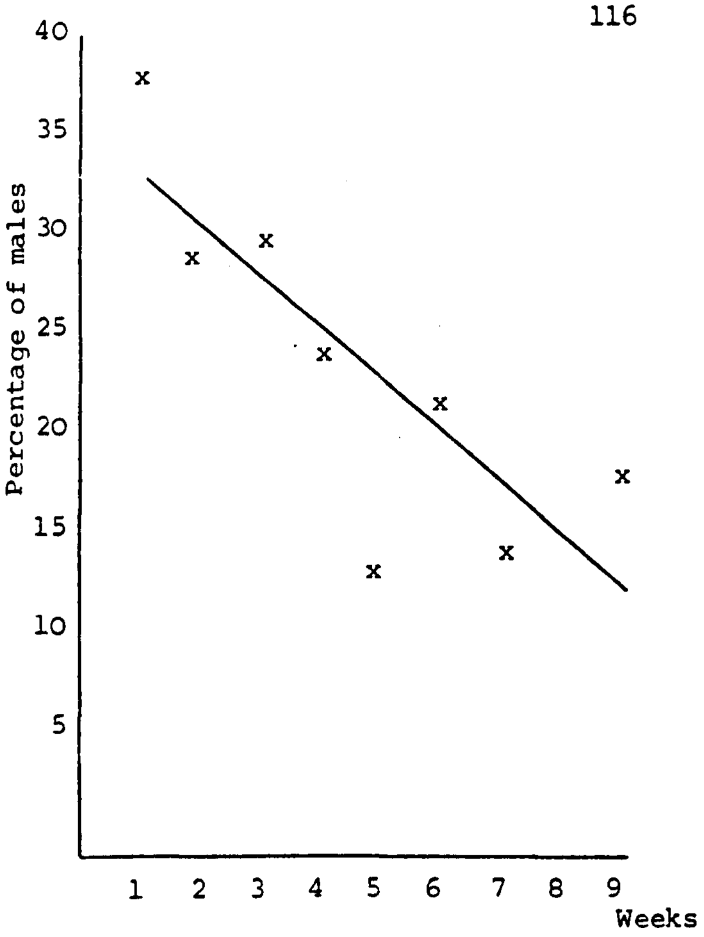

Fig. 7. Percentage of males caught at Lydney during the upstream migration period.

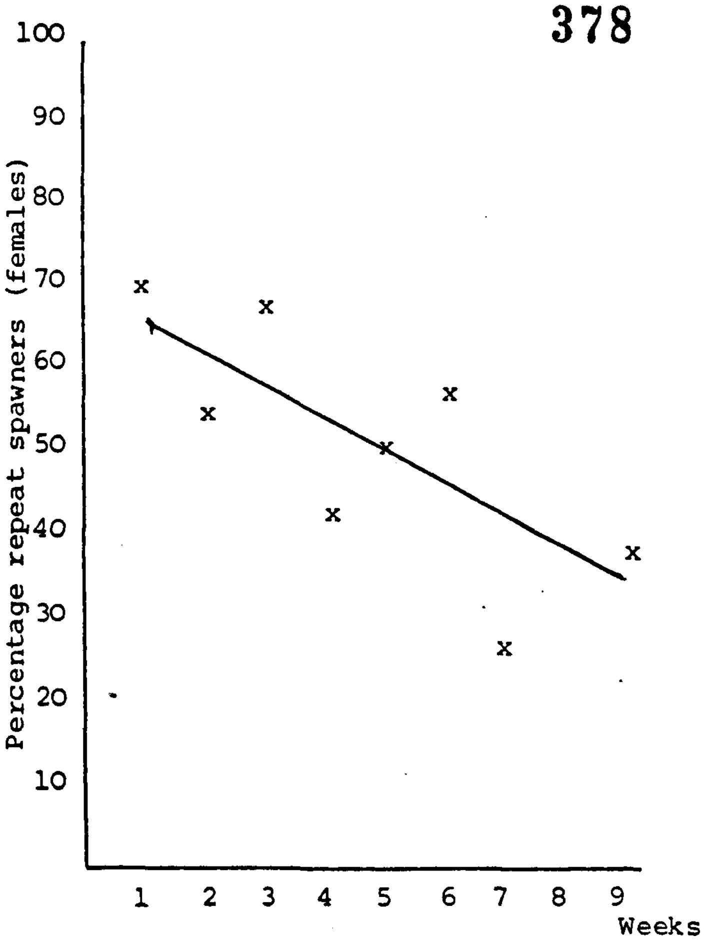

Fig. 8. Percentage of female repeat spawners caught at Lydney during the upstream migration period.

In the Wye, the majority of the larvae and juveniles are found in deep pools (Figure 4), similar observations were found for American shad young (Chittenden, 1969); virtually none were found in the shallows with the cyprinid fry. In late July - early August 1979, young could be found from the upper reaches (160 km) to just above tidal freshwater (26 km), their size increasing in mean length from 22.35 mm to 28.7 mm. In 1980 larvae were only found in the lower reaches. In the Wye the young appear to stay in freshwater until the first flood. In 1979 none were caught after mid-August and in 1980 none were caught after the start of July. It is not really understood how young shad respond to floods, they may use them in some way to facilitate their seaward migration, as has been shown to occur in alewives, Cooper (1961) and Richkus (1975). However, it is not really known at what stage they become physiologically adapted for their emigration, and if they are not yet adapted, are they behaviourally and/or morphologically suited to withstand high flows?

In the Severn, in 1979, a different distribution was evident when compared with the Wye, very few young were found in freshwater, the vast majority being in the inner estuary from Gloucester to Newnham. This may reflect some differences in the characteristics of the two rivers. Figure 13 shows the number of O+ and 1+ twaite at Newnham and Oldbury. It seems that the young arrive at Newnham during July at approximately 25 mm in length and finally leave the estuary in October when they have reached 50 - 60 mm in length. Claridge and Gardner (1978) related their emigration to temperature, the numbers at Oldbury declined rapidly during October and November, with virtually none recorded after the temperature had dropped below 9°C.

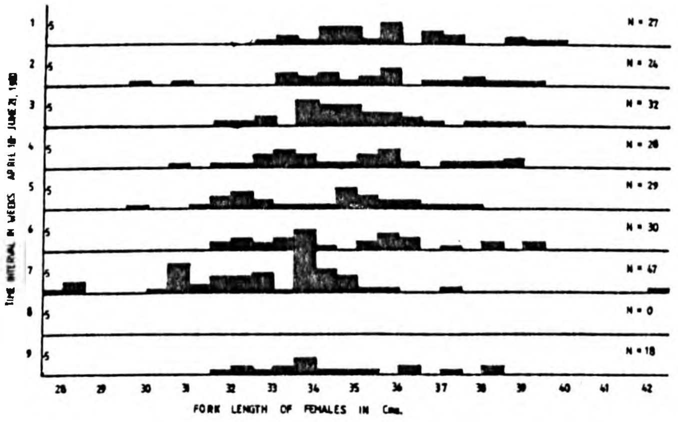

Fig. 9. The length distribution of females caught at Lydney during the upstream migration period.

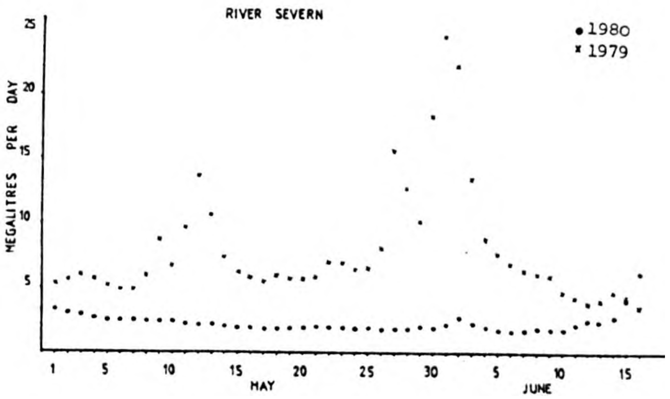

Fig. 10. Mean daily river flow at Saxons Lode, River Severn.

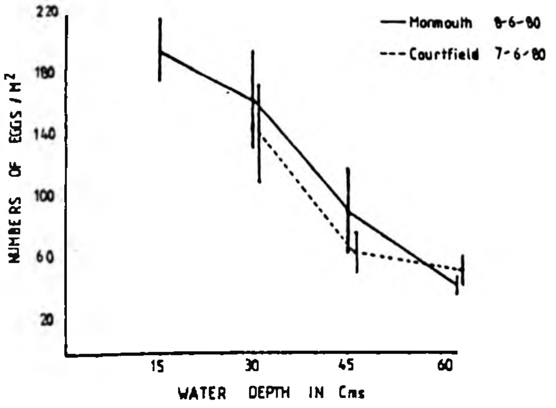

Fig. 11. Mean and standard deviation of the number of eggs in relation to water depth.

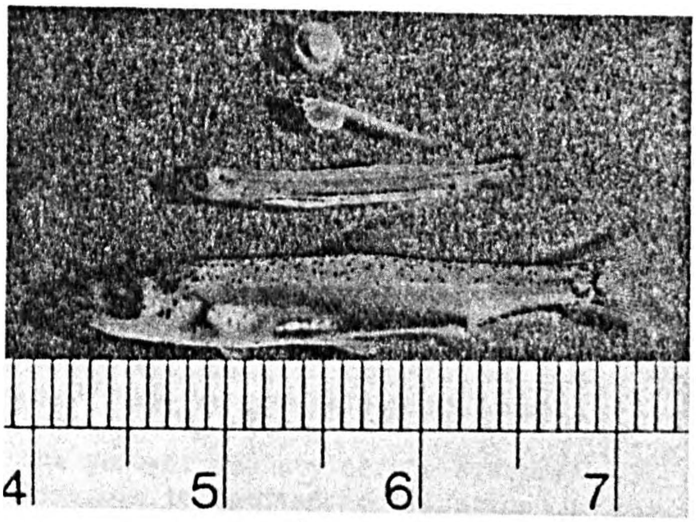

Fig. 12. Twaite egg and larvae.

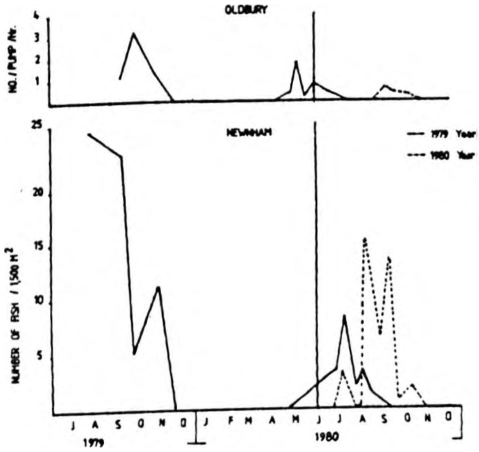

Fig. 13. Abundance of O+ group and 1+ group twaite in the Severn estuary.

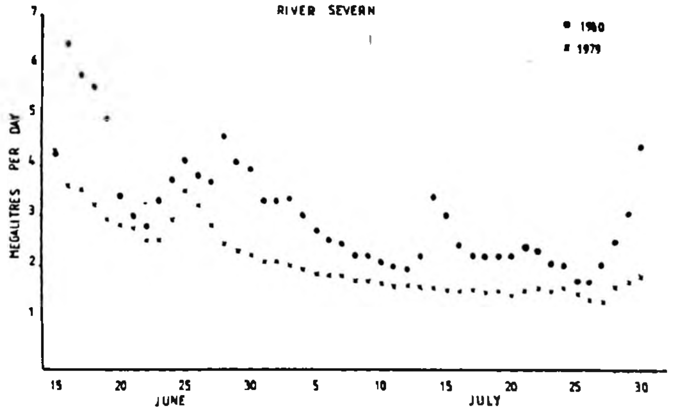

Fig. 14. Mean daily river flow at Saxons Lode, River Severn.

It is not until the end of April or beginning of May that the young (now nearly one year old) reappear in the inner estuary at Oldbury. By June these one year olds had moved up to Newnham and by mid-July were being caught in tidal freshwater just below Gloucester. These one year olds leave the inner estuary at the end of August. Thus it appears that the young may overwinter in the outer estuary moving back into the inner estuary during the summer; Bracken and Kennedy (1967) had similar findings.

It is apparent that in 1980 the density of fish caught at Newnham and at Oldbury was much lower than in 1979. However, the differences between these two years may be much more than Figure 14 illustrates, for in other areas sampled much larger differences in densities were obtained. This is thought to be mainly due to the flow conditions after mid-June (Figure 14). The summer of 1980 was characterised by a series of floods which was in complete contrast to the situation in 1979. This may have caused a large number of eggs and possibly larvae and juveniles to be washed into unsuitable environments. The effects of these floods will only start to become clear in three years time when the first males come into spawn, and in four and five years time when the females start their spawning migration.

It thus appears that floods may be one of the factors that plays an important role in determining year class strength. The optimal condition appears to be, high water in May and the early part of June, increasing the spawning area available, and low flows after mid-June preventing displacement of the eggs, larvae and juveniles. An area where they may be vulnerable to changes in the ecology that might be produced by a barrage is in the inner estuary between Newnham and Gloucester, where the fry remain for approximately two months. In 1979 they were easily the most abundant fish species present, there being very few coarse fish, the occasional goby, flounder, bass and mullet fry. Here in this nursery area there are virtually no competitors for the plankton on which they feed, and there are very few possible predators.

Shad may also be good indicators of the general quality of the system, as the genus appears to be particularly vulnerable to habitat modification (Walburg and Nichols, 1967) in both freshwater and in the estuary. Therefore the preservation of such a rare species can only be beneficial in that their protection can aid the wellbeing of species with similar requirements. The shad decline has coincided with or heralded the decline of other more commercially important species such as the salmon.

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