An Assessment Of The Current Status Of The Fish Communties In Loch Awe, Scotland, With Particular Emphasis On The Interactions Between Feral Rainbow Trout and Indigenous Brown Trout.

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I declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate I have acknowledged the nature, and extent of work carried out by others in this thesis.

Candidate William M. Duncan.

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Abstract.

This study investigated the interactions between feral rainbow trout and the native fish species of Loch Awe, Argyll, Scotland, with the relationship between rainbow trout and brown trout receiving particular attention.

Rainbow trout are found throughout Loch Awe but under normal circumstances they are only found in large numbers around the fish farms. The distribution of brown trout around the fish farms is only adversely affected when the rainbow trout to brown trout ratio exceeds a high but undefined threshold. Away from the fish farms rainbow trout are found in such low numbers that it is unlikely that they could have a significant impact on the native fish species. The highly localised distribution of the rainbow trout around the farms is related to the high dependency that they have on the uneaten pellets that pass through the cages. When they move away from the cages they consume large quantities of non-conventional prey items, this is due to the low repertoire of search prey images that they encounter in the fish farms. The native species largely consume conventional prey at and away from the fish farms depending upon its seasonal availability.

No evidence was found of rainbow trout spawning in the catchment. However on a small number of occasions sexually mature rainbow trout were found in the spawning burns, and their progeny were shown to survive at least to the alevin stage. In interspecific interactions in the first year of their life brown trout socially dominated the progeny of spring spawned rainbow trout.

An attempt was made to compare the present and historic catch per successful rod day (CPSR) on Loch Awe. This was complicated by differences in the recording systems, and the absence of information

on unsuccessful fishing days in the historic data set. Accepting this shortcoming, a comparison showed that the current CPSR is considerably lower than it was previously. It was suggested that this was due to the large increase in fishing effort that has occurred in recent years. The yield of brown trout to anglers is similar to that from other unstocked upland reservoirs. There was a marked decline in the catch of rainbow trout between 1987 and 1988. At present their is little evidence of the rainbow trout having a serious impact on the native species in Loch Awe.

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CHAPTER 1

INTRODUCTION

1. Introduction.

The rainbow trout Oncorhynchus mykiss (Walbaum) is a Pacific Salmonid, whose home range extends from Alaska to north Mexico. It has two main life history strategies. The anadromous steelhead spends part of its life at sea returning to freshwater to spawn. The freshwater rainbow or kamloops trout may also undertake a migration from the spawning streams to the lower parts of river systems, but remains in freshwater throughout its life cycle.

A degree of confusion existed regarding the classification of rainbow trout, it was originally known as Salmo gairdneri, Richardson, but recently this was changed to Oncorhynchus mykiss (Walbaum) (Kendall, 1988). The change of generic name occurred because new data suggested that all native Pacific-drainage trout were more closely related to Pacific salmon Oncorhynchus than to the Eurasian Salmo species. The specific name was changed because taxonomists now believe that rainbow trout and the "Kamchatkan" trout Salmo mykiss form a single species, for which mykiss has nomenclatural priority (Kendall, 1988). Prior to the change, different races were known by other specific names including irideus, kamloops and shasta (stonei). The irideus variant originated from the coastal streams of California whereas the shasta and kamloops came from more inland streams, the former from rivers running from Mount Shasta southwards in particular the McCloud river, and the latter from the Fraser and upper Columbia river areas of British Columbia. Until the late 1960's shasta and irideus were the names used for the autumn and spring spawning strains of rainbow trout. It is now generally accepted that the autumn spawning behaviour is a feature developed through selective breeding programmes in hatcheries, and that the ancestral form of rainbow trout spawned in the spring (Bromage & Cumaranatunga, 1988).

The species has been used extensively in Britain and other parts of the world in stocking programmes and by the aquaculture industry, largely due to a superior growth rate and tolerance of poorer environmental conditions compared to Britain's native salmonids.

Rainbow trout have been farmed continuously on Loch Awe since 1968. It has recently been claimed that the loch's brown trout fishery is in a state of severe decline and the role of escapee rainbow trout in this has been questioned. The aim of this study is to determine if the fishery is in decline, and to describe the ecological relationships between rainbow trout and the native fish species in the loch. This will be established by examining the distribution and feeding behaviour of feral rainbow trout and the native fish species in the loch. Also considered are the early life history interactions between brown trout and rainbow trout; and the current rod catches of brown trout are put into a historical perspective by comparing them with records from three hotels around the loch. The opportunity is also taken to present data on a variety of biological parameters collected from fish during the course of the study. This was done as the study was not intended to be an end in itself, but rather the start of a larger ongoing examination of the fish populations in Loch Awe.

Rainbow trout were first introduced to Britain in 1884, and to Scotland in the following year by Sir James R. G. Maitland at Howietoun fish farm (Worthington, 1941). The number of introductions increased slowly throughout the 1900's and more rapidly in the mid 1960's in response to the increased demands from angling. At about the same time, the potential for using rainbow trout in commercial fish farming was realised. Farming increased through the 1970's, and rose dramatically during the 1980's. Associated with this increase has been a rise in the number of escapes of farmed stock into the wild. Losses of 5t per annum (2.5% of total cage production) have been recorded (Phillips *et al*., 1985). Their potential for ranching in Scottish freshwater lochs has also been investigated by Phillips (1982).

By 1971, rainbow trout were present in 558 British and Irish waters (Frost, 1974), and although there are no current statistics on their distribution, it is generally accepted that it is considerably greater than the 1971 level. Evidence of sea run rainbow trout (steelhead) have been reported by Shearer (1975).

There are 3 fish farms currently operating on Loch Awe, one small land-based unit on the Clachan Dubh burn (a tributary entering the loch at Ford) and two larger cage farms at Braevallich and Tervine (See Figure 1). There have been small losses of farm stock since 1968 due to grading and other fish handling processes, and larger losses resulting from storm damage and vandalism. Munro *et al*. (1976) reported the earliest losses in the loch in 1970.

Recently fears have been raised that rainbow trout released in stocking programmes and those escaped from aquaculture installations may be having an adverse impact on our native salmonids. The fears are based on two premises:

1. That they are able to establish self-sustaining populations, and compete on the spawning grounds with native brown trout and Atlantic salmon *Salmo salar*. Linnaeus.
2. That they out-compete our native salmonids in feeding interactions, and thereby marginalise them.

In common with many species that have been introduced outside their home range, rainbow trout have been largely unsuccessful in establishing self-sustaining populations, particularly in Europe.

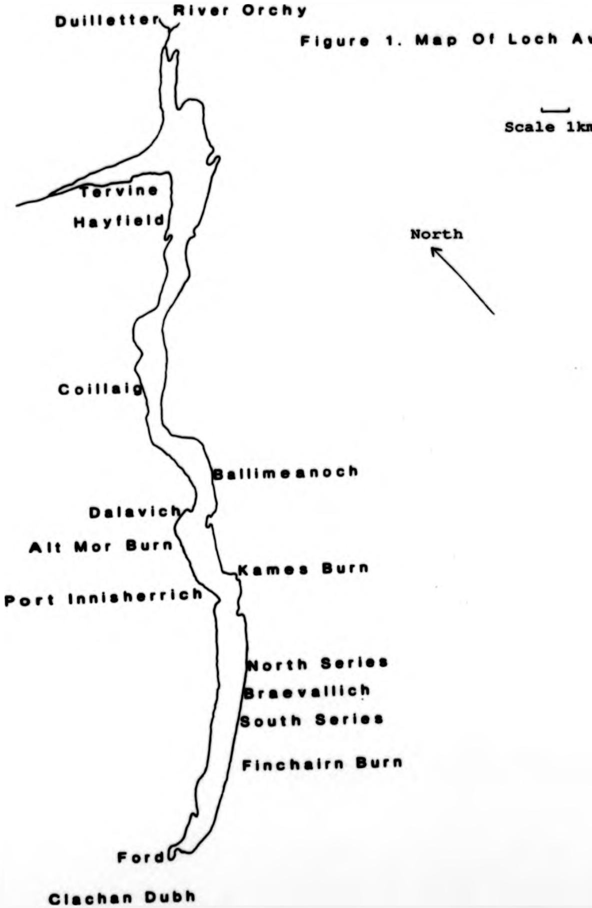


Figure 1. Map Of Loch Awe

Nilsson (1967) reported that in spite of thousands of introductions in Scandinavia they were only breeding successfully in two or three locations, similar findings were reported in France (Vivier, 1955). In Britain and Ireland, Frost (1974) reported that self-sustaining populations had only been established in five places. Other evidence of them breeding in the United Kingdom has been reported by Stuart (1967) in the Lake of Menteith, Lever (1977) in an Inverness-shire loch, by Brown and Diamond (1984) in a river in Wales and in Loch Fad (Phillips et al., 1984). Although the precise mechanism for this poor success rate is unknown, competition at the juvenile stage by earlier hatching brown trout has been implicated, with successful spawning occurring either where brown trout are not present or are found in low numbers (Frost, 1974; Lever, 1977; Phillips et al., 1984 & 1985). The lower survival of rainbow trout milt in acid waters such as that predominating in the Scottish uplands has also been implicated. Seamans & McMartin (1962) demonstrated that the survival of their milt was 50% lower in acid water than in the harder water that predominates in their home range. Despite this concern has now been raised about the deleterious effect that feral rainbow trout are having on indigenous British salmonids (Mills, 1982; Phillips et al., 1984 & 1985; Maitland, 1984; Mills, 1989). The continual release of adults from commercial fish farms, stocking programmes and potentially ranching, allows the establishment of an adult population without the need for successful reproduction in the wild.

Every species requires the use of a set of resources in order to survive (Grinnel, 1904). This idea was developed into the niche concept through a series of papers by Lotka (1932), Gause (1934), Elton (1946) and Hutchinson (1957). It became apparent, particularly in fisheries science, that individual species very often share the same resources (Forbes, 1914; Hartley, 1948; Starret, 1950; Nilsson, 1955;

Larkin, 1956), a phenomenon known as niche overlap. Further research highlighted the differences between a species fundamental niche (its potential niche) and its realised niche (that which it uses). Differences between them arise as a result of competition which increases as resources become limiting, described as interactive segregation by Nilsson (1978). He elegantly defined the concept as cohabiting species being forced by interaction to refine their virtues when resources are at a minimum (Nilsson, 1985). Competition only occurs when resources are limiting. Such competition was shown to have two components; interference, when two species harm one another in the process of securing a resource; and exploitation, resulting from one species having an innate behavioural or morphological advantage for utilising a resource. Due to natural selection these differences will develop between co-existing species or groups of sub-species. Although species initially segregate interactively by interference, successful co-existence requires fundamental differences to exist between their realised niches, differences that are reinforced by co-evolution. Therefore, when two closely related but geographically isolated species are brought into unnatural sympatry by man the potential for conflict is large. Such species may have considerable niche similarity but possibly not the mechanisms required to alleviate interspecific competition, as would have occurred with competitors in their native range (Hayes, 1984).

Nilsson (1985) outlined four possible outcomes when an exotic species is introduced to a community:

1. it is rejected because there is no vacant niche;
2. it hybridises with closely related stocks;
3. it causes the elimination of an ecological homologue;
4. it finds a vacant niche.

Such an example is the introduction of rainbow trout into waters holding brown trout in Britain. Wherever these species co-exist throughout the world examples of scenarios 1, 3 and 4 have been described. It is therefore clear that the interactions between the two species are complex, and that local environmental conditions will play a part in determining the outcome of any inter-specific interaction.

In the following chapters the study of theses interactions will be described and discussed.

CHAPTER 2

LOCH AWE AND ITS SURROUNDING CATCHMENT

2.1 Morphometry

Loch Awe at 40.99km long is the longest freshwater loch in Scotland. It lies to the west of Oban in Argyll on a NE, SW axis (See Figure 1). It is, however, an extremely narrow loch and in most places only about 1km in breadth. The mean breadth is only 2.3% of the length which is the lowest percentage observed in any of the 562 lochs surveyed by Murray and Pullar (1910). Its surface area is 38.5 km^2 which makes Loch Awe the third largest in Great Britain in this respect. It has a mean depth of 32.0m, a maximum of 93.6m and volume of 12.304 x $10^8 m^3$. In common with Loch Lomond, it has two main basins both of which are deeper than 30m, one occupies the northern arm (with two separate depressions) and the other occupies most of the long axis of the loch from the northern islands south (Maitland, 1981).

2.2 Recent and geological history.

The land forms in the Loch Awe area were created during the Caledonian mountain building period. The valley in which the loch sits was gouged out of the rocks during one of the three previous ice ages, and lies on a NE/SW syncline in a fault aligned valley. During the last ice age which ended 10,000 years ago, the ice extended down the major valleys present in Scotland, unlike previous ice ages when the whole of Scotland was covered in a massive ice sheet. In the valley now occupied by Loch Awe the ice cap only advanced as far as Ford (See Figure 1). Its forward movement was probably arrested by a series of basalt diorite dykes, which emanated from Mull, and ran perpendicular to the glacier's flow.

At the end of the ice age the glaciers went through a period of melting and re-advancement, before they completely melted. Once all of the ice had disappeared from the land there was a period of rapid uplifting which continued until around 5,000 years ago, when the rate of uplift decelerated. The west coast of Scotland is still in this uplifting mode. This resulted in Loch Awe emptying into the sea at the Ford end. However, as a result of a build up of glacial material at that end, the water in the loch ponded back until the watershed at Inverawe was breached, and the loch then flowed out to sea through the Pass of Brander and down the River Awe.

At that time the loch's surface area was considerably larger than it is today. Evidence of this is seen in the small raised beaches along the sides of the loch, whose height indicates that the water stretched as far back as Inverlochy in Glen Lochy. Since then the height of the loch has fallen by between 5-10m and continues to flow out to sea along the Pass of Brander.

In 1817 the Pass of Brander was blasted to make it deeper. This resulted in the depth of the loch being dropped, and the land at the north end of the loch being released for agriculture. In 1963 the Loch Awe barrage was constructed as part of the Ben Cruachan pump storage hydro electric scheme. This did not affect the mean level of water in Loch Awe but it has reduced the extremes in loch levels.

There is a marked contrast in the geochemistry of Loch Awe's four sub-catchments (see Table 2.1). The River Orchy catchment is very highland in character with a high mean altitude (392m and slopes 249m/km) and a base poor geology. The three other catchments, in contrast, are much lower in altitude (all with means of less than 250m) with gentler slopes (all less than 170m/km) and a much richer geology. Thus, it would be expected that the southern basin is richer than the northern one. This is borne out in the water quality and phytoplankton analysis performed by the Institute of Aquaculture's routine monitoring of the loch, (see Tables 2.1 and 2.2; site 1 and site 6 are at the S.W and N.E

Table 2.1 Analysis Of Loch Awe's Four Main Sub-catchments, (from Maitland, 1981).

Feature	Awe Sub-catchments.				Total
	Kames	Avich	Cladich	Orchy	
Area(km^2)	148	118	116	398	780
Mean Altitude(m)	234	199	245	392	307
Mean Slope(m/km)	140	163	147	249	198
Land Use(km^2)					
Rough	104.4	50.8	99.8	341.9	596.9
Water	2.7	5.2	2.2	4.4	14.5
Arable	4.2	1.8	3.8	2.7	12.5
Urban	0.5	0.4	1.2	0.8	2.9
Forest	36.2	59.4	8.6	48.3	152.5
Other	0.4	0	0	0	0.4
Rock(% Base Rich)	50	60	55	20	41
Aspect(% Composition)					
North	30	22	26	26	26
South	20	27	24	24	24
East	20	28	23	26	24
West	30	23	27	24	26
Lochs	74	28	10	44	156
Stream Junctions	196	157	95	801	1249
Waterfalls	1	1	2	3	7
Houses	102	87	122	96	407
Metalled Road(km)	41	38	36	58	173

ends of the loch respectively), and by George & Jones (1987) in their study of the spatial variation in phytoplankton production.

2.3 Water quality and ecology.

Both of the above studies have demonstrated that the nutrient status of the loch increases along its NE/SW axis (see Tables 2.2, 2.3 and Figure 1). There are two reasons for this difference:

1. the majority of the water that enters the northern arm of the loch from the main inflow (the River Orchy) is discharged through the loch's outflow which is also at the northern end (George & Jones, 1987), this results in the majority of the loch being short circuited;
2. the higher percentage of base rich rocks in the land surrounding the southern basin.

The results of the Institute of Aquaculture's routine monitoring of the water quality shows Loch Awe to be a typical mesotrophic type loch with above average productivity for Scottish freshwater lochs. The pH, alkalinity and conductivity measurements show that Loch Awe is slightly acid, with a relatively low buffering capacity typical of many freshwater lochs in the Scottish highlands. As with the nutrient status these parameters are higher at the south end of the loch compared with the north. The slight decrease in pH with depth is typical of stratified water and results from photosynthesis in the surface layer. The temperature profiles show that Loch Awe stratifies during the spring/early summer, and this is likely to remain for the whole summer. The implication of this is that water exchange is likely to be limited to the surface layers of the water column throughout the spring and summer. Dissolved oxygen was high at all sites and depths, indicative of well oxygenated water. Secchi disc depths were similar at all sites, with average turbidity for Scottish freshwater lochs.

Table 2.2 **Temperature, dissolved oxygen, and turbidity in Loch Awe on the 24/5/89 (from Institute of Aquaculture contract report, 1989).**

Site	1		2		3		4	
	T	DO	T	DO	T	DO	T	DO
Depth(m)	(°C)	(mg/l)	(°C)	(mg/l)	(°C)	(mg/l)	(°C)	(mg/l)
0	11.5	11.4	12.0	11.1	12.2	11.1	12.5	11.0
15	9.2	11.2	8.9	11.1	9.1	11.1	9.0	11.0
30	7.2	11.2	7.6	11.1	7.2	11.1	7.3	11.0
45	6.9	11.2	6.8	11.1	7.0	11.0	7.1	11.0
60	6.5	11.2	6.3	11.1				
Secchi Disc Depth(m)	3		3		3		3	

Site	5		6	
	T	DO	T	DO
Depth(m)	(°C)	(mg/l)	(°C)	(mg/l)
0	12.0	11.0	11.0	11.2
15	9.0	10.9	9.0	11.1
30	7.8	10.9	7.0	11.1
45	7.5	10.9	6.1	11.1
60				
Secchi Disc Depth(m)	3		3	

1. Site 1 is at the southern end of the loch, and site 6 is at the northern end.

Table 2.3 **Water Quality In Loch Awe On The 24/5/89 (from Institute of Aquaculture contract report, 1989).**

Site	1			2			3		
Depth(m)	0	30	75	0	30	90	0	30	45
pH	7.22	6.98	6.97	7.2	6.98	6.95	7.2	6.98	6.97
Alkalinity(meq/l)	0.2	0.17	0.19	0.2	0.19	0.19	0.2	0.18	0.18
Conductivity(uS/cm)	64	64	64	62	63	64	62	63	63
Total Ammoniacal Nitrogen(ug/l as N)	9	19	10	15	14	24	35	10	8
Nitrite(ug/l as N)	<1	<1	1.0	1.3	1.5	1.1	<1	<1	<1
Nitrate(ug/l as N)	122	121	137	88	-	130	-	182	-
Dissolved Reactive Phosphorus(ug/l as P)	<1	<1	<1	<1	<1	<1	<1	<1	<1
Total Dissolved Phosphorus(ug/l as P)	6.3	6.3	7.0	3.5	6.3	6.3	1.4	8.4	5.6
Total Phosphorus(ug/l as P)	15.8	15.8	15.8	16	15.8	15.8	16	-	16.3

Table 2.3 continued.

Site	4			5			6		
Depth(m)	0	30	45	0	30	45	0	30	45
pH	7.18	6.96	6.97	7.1	6.96	6.72	6.9	6.75	6.86
Alkalinity(meq/l)	0.17	0.18	0.18	0.2	0.16	0.12	0.1	0.14	0.16
Conductivity(uS/cm)	62	63	63	60	62	66	57	57	51
Total Ammoniacal Nitrogen(ug/l as N)	16	20	17	27	22	29	69	57	21
Nitrite(ug/l as N)	1.3	<1	<1	-	1.1	1.3	1.3	1.5	1.6
Nitrate(ug/l as N)	91	120	86	58	77	107	74	124	133
Dissolved Reactive Phosphorus(ug/l as P)	<1	-	<1	<1	<1	<1	<1	<1	<1
Total Dissolved Phosphorus(ug/l as P)	4.2	9.0	5.6	3.5	4.9	2.1	6.3	2.1	6.3
Total Phosphorus(ug/l as P)	16.9	15.8	18.0	17	14.1	16.9	19	12.5	11.4

1. Site 1 is at the southern end of the loch, and site 6 is at the northern end.

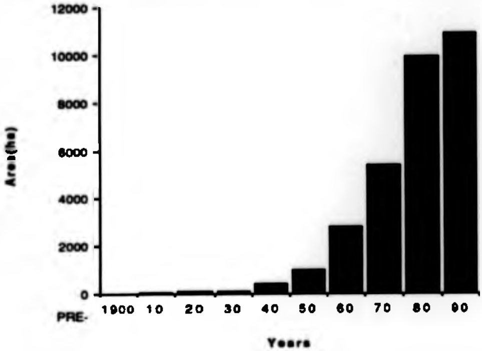
These results are in broad agreement with the findings of Maitland (1981). George & Jones (1987) were able to demonstrate improved mixing between the north and south basin after a storm that blew from the NE.

The following fish species are present in Loch Awe: Atlantic salmon Salmo salar Linnaeus 1758, brown trout Salmo trutta Linnaeus 1758, Arctic charr Salvelinus alpinus (Linnaeus 1758), rainbow trout Oncorhynchus mykiss (Walbaum), pike Esox lucius Linnaeus 1758, minnow Phoxinus phoxinus (Linnaeus 1758), eel Anguilla anguilla (Linnaeus 1758), three spined stickle back Gasterosteus aculeatus Linnaeus 1758; perch Perca fluviatilis Linnaeus 1758; brook lamprey Lampetra planeri (Bloch 1784) and roach Rutilus rutilus (Linnaeus 1758). Roach and brook lamprey were the only species not listed by Maitland (1981). A roach was taken in the course of the present research during some preliminary sampling. It is most likely that the species has been introduced to Loch Awe by pike anglers who use them as live bait, discarding them after their day's fishing. This is thought to be the source of the many coarse fish species found in Loch Lomond. It is likely that brook lamprey were present at the time of the earlier study but as it was restricted to the loch and the present study only found them in Loch Awe's tributaries it is not surprising that they were not listed. There are two types of Arctic charr in Loch Awe, the benthic and pelagic morphs. It has been demonstrated that clear ecological and morphometric differences exist between them. Early taxonomists originally classified Arctic charr into a number of distinct species, but through the 1900's this idea was rationalised. More recent studies have shown that there are indeed a number of distinct morphs of charr in Britain (Maitland et al., 1984; Partington & Mills, 1988; Walker et al., 1988).

2.4 Land-use.

Maitland (1981) described the various land use practices in the catchment (see Table 2.1). By far the largest percentage is rough grazing (76.5%), the second most important land use being forestry (19.6%). The exception to this pattern occurs in the Avich catchment where more than half of the catchment is under forestry. It is likely that the nutrient run-off from this will contribute to the greater concentration of nutrients found in the loch's southern basin. Water supply, arable land, urban area, and other uses are all below 2%. Forestry Commission figures show that planting of forestry increased through the 1900's with peaks occurring between 1951-55 and 1971-75 (see Figure 2.1) (D. Henderson pers. comm.).

Figure 2.1 The cumulative total area (ha) of new plantations in Loch Awe's catchment 1900-90 (pers. comm. D. Henderson, 1988)



CHAPTER 3

DISTRIBUTION AND GROWTH OF FISH IN LOCH AWE

3.1 Introduction

Fish farms have been shown to act as attractants to native fish populations in freshwater lochs. The aims of this chapter are:

1. to describe the distribution and population structure of rainbow trout and the native fish species in Loch Awe;
2. to study the growth rates of brown trout and rainbow trout at and away from the fish farms in the loch;
3. to examine the effect of fish farms on the distribution and growth rates of the fish populations.

This was achieved by a series of gill netting studies, following a pilot survey in 1986 which agreed with the findings of Phillips et al. (1985). The distribution of fish in each of the major habitat types was studied in 1987 to allow any seasonal variation to be determined, and in 1988 the area immediately adjacent to the fish farm at Braevallich was examined. Following storm damage in 1989 the opportunity arose to investigate the effect of a single large loss of rainbow trout on the loch's native fish species.

Conventional tagging studies in Loch Fad, a small Scottish loch, have shown that stocked rainbow trout rapidly distribute themselves throughout the water body after stocking, interacting with the indigenous fish population in the process Phillips et al. (1985).
By contrast the same authors demonstrated in larger lochs that the distribution of rainbow trout was highly localised around fish farm cages, and that the distribution of brown trout was unaffected
Attraction to cage sites has been noted in a number of instances. Collins (1971) described dense populations of blue gill sunfish Lepomis macrochirus Rafinesque near channel catfish Ictalurus punctatus (Rafinesque) cages in the USA. Loycano & Smith, 1976, Kilambi et al., 1978 and Hays, 1980 noted that many species of predatory and non

predatory fish were caught in greater numbers adjacent to channel catfish and rainbow trout cage farms.

Phillips et al. (1985) have demonstrated that the cage production of rainbow trout in two Scottish lochs increased the nutrient status of the water, and subsequently the growth of the fish in them. Munro (1961) demonstrated increased growth in brown trout following the fertilisation of Scottish lochs. In Canada a similar response was reported by Hyatt & Stockner (1985), and Mills (1986) in Pacific salmon and coregonids respectively.

3.2 Materials and methods.

3.2.1 Netting Sites.

Multimesh survey gill nets 55m long x 1.5m deep were used in the study. These consisted of eleven 5m panels, with knot to knot (bar) mesh (mm) sizes arranged in the following random order, 62, 21, 36, 84, 104, 66, 54, 16, 78, 48.

The above mesh sizes were selected for two reasons. It was anticipated that they would catch the size range of fish present in the loch. Using a variety of mesh sizes reduces the size selectivity inherent in gill net design (Hamley, 1975). As no record was made of whether the fish were caught by gilling, tangling or by their mouth, it was not possible to construct selectivity curves for brown trout or rainbow trout.

Due to Loch Awe's very steep sides and restricted littoral zone the nets at each site were set parallel to the shore. This was preferred to the perpendicular arrangement recommended by Craig (1977). The nets were set and lifted in the morning, after one night. The position of the gill netting sites are shown in Figure 1.

3.2.1.1 1987

In 1987 twelve sites were fished at monthly intervals in a variety of habitats at set distances from the fish farms for 24 hours. As only six nets were used, the netting was performed over two 24 hour periods with sites 1-6 being netted one day and sites 7-12 on the other, with 24 hours between each. The same habitat types were sampled in each period. There was approximately the same distance between Tervine, Hayfield, Coillaig, Ballimeanoch, Port Innisherrich and Braevallich. Details of the sites are given in Table 3.1.

Table 3.1 Sites And Habitats Sampled By Gill Netting In 1987.

Site No.	Name	Description	Position	Depth	N.G.R
1,12	Tervine, Braevallich	Fish Farm Littoral	Bottom	3m	NN 082262 NM 953076
2,11	Hayfield & Port Innisherrich Littoral	Littoral	Bottom	3m	NN 079236 NM 967111
3,10	Hayfield & Port Innisherrich Pelagic	Pelagic	*Surface	45m	NN 085230 NM 970110
4,9	Hayfield & Port Innisherrich Benthic	Benthic	Bottom	45m	NN 085230 NM 970110
5,8	Coillaig & Ballimeanoch Shallow	Littoral	Bottom	3m	NN 016196 NN 006154
6,7	Coillaig & Ballimeanoch Deep Littoral	Littoral	Bottom	10m	NN 016196 NN 006154

* The surface nets were set 2.5m below the surface to avoid interference from passing boats.

3.2.1.2 1988

In 1988 the nets were set for 24 hours in March, May, July and September. In March they were set at Braevallich in two series of five nets which were set in a line moving along the shore in a NE and SW direction from Braevallich. They were set parallel to the shore in 3m of water with at least 15m between each station. Due to the similarity in the catch from the north and south series it was decided only to fish the former in the remaining months.

3.2.1.3 1989

On the 27th February and 20th April 1989 gill nets were set at six sites to assess the distribution of rainbow trout lost from the farm at Tervine during a storm on 13th February 1989. On the 27th February 1989 Hayfield Littoral, Tervine and four other littoral sites between them were fished. On the 24th April 1989 site 4 was replaced by Port Innisherrich Littoral, to determine if there had been an increase in the abundance of rainbow trout throughout the loch as a result of the loss. All of the sites were fished for the standard 24 hours.

3.2.2 Fish processing

In 1987 and 1988 all fish were processed on the morning that they were landed, with the site of capture, species, fork length (mm), weight (g), mesh size (mm) captured in, sex, state of maturity, weight of gonads (g) and any visible signs of disease being recorded for each fish. For ageing studies the scales of rainbow trout and brown trout were removed from the area just above the lateral line on a line from the anterior edge of the anal fin to the posterior margin of the dorsal fin. They were stored in a scale packet prior to ageing. Due to the problems associated with scale reading a sub-sample of otoliths were also removed to cross check the ages determined by the above technique. The stomachs of all fish sampled were removed for feeding studies (see Chapter 4). In 1989 only the species composition at each site was recorded.

3.2.3 Statistics

3.2.3.1 Spatial variation in the distribution of species between shallow littoral and fish farm sites.

The variation in the distribution of species between sites was assessed by X^2. In 1987 this was performed on an annual basis and included data from the shallow littoral sites at Tervine, Braevallich, Hayfield, Ballimeanoch and Port Innisherrich. Coillaig was omitted from the analysis as the presence of pike resulted in an abnormal distribution of the salmonid species. In 1988 the analysis was made on a monthly basis and included all of the sites sampled. In 1989 both sampling sessions were analysed for all of the sites sampled.

3.2.3.2 The mean monthly catch of brown trout and rainbow trout at the littoral and fish farm sites.

In 1987 and 1988 the mean monthly catches (MMC) of rainbow trout and brown trout at the fish farm, and littoral sites were calculated. In order to calculate a mean value that was representative of the shallow littoral zone, only data from the shallow sites at Hayfield, Ballimeanoch and Port Innisherrich were used. The results from the two fish farms were analysed independently. As no gill netting was performed at Tervine in March 1987, the data from that month has been excluded from the other sites. As the variance exceeded the means in the experimental groups it was necessary to normalise the data. This involved a log 10 (x+1) transformation, the inclusion of the (x+1) component was necessary to allow transformation of the data in months when no fish were caught. The normalised means were then compared by one way analysis of variance (ANOVA).

3.2.3.3 Seasonal variation in fish abundance.

The seasonal variation in species abundance was measured by X^2. In 1987 this was done on a site basis. Due to the low monthly catch of some species in 1987 it was decided to pool the data into three time periods January until April, May until August and September until December. Owing to the proximity of the sites in 1988 it was decided to assess the variation by pooling the data, and no analysis was made on the data collected in 1989.

3.2.3.4 Seasonal variation in habitat use by juvenile and adult rainbow trout and brown trout.

Variation in the habitat use by juvenile and adult brown trout and rainbow trout was assessed by X^2. Age classes 0+ to 2+ were termed juveniles (age group A) and ages classes 3+ to 6+ were termed adults (age group B). In 1987 the habitats were classified as littoral and open water, the former being the pooled data from all of the littoral sites (including the fish farms) and the latter being the pelagic sites. In 1988 no open water sites were sampled and so the movement of fish was examined by considering changes in the proportion of juveniles and adults in March, May, July and September in the littoral zone only.

3.2.3.5 Sex ratios.

In 1987 and 1988 deviations from 1:1 sex ratios in brown trout, rainbow trout, Arctic charr and perch were tested by X^2. In the case of rainbow trout this analysis was performed as their sex ratio would have a bearing on their ability to establish a self-sustaining population. In the case of the other species it was performed to provide basic biological statistics about the fish in the loch.

3.2.3.6 Seasonal variation in habitat use by male and female brown trout, rainbow trout, Arctic charr and perch.

Seasonal variation in habitat use by male and females of the above species was assessed by X^2. In 1987 the habitats were classified as littoral and open water, as described in 3.2.3.4. For benthic Arctic charr the open water sites included the pelagic and benthic sites. In 1988 no open water sites were sampled so the movement of fish was examined by considering the changes in the littoral zone as described in 3.2.3.4.

3.2.3.7 Sexual maturity.

The age at which rainbow trout and brown trout first reached sexual maturity was considered, and the timing of maturity in brown trout, rainbow trout, and Arctic charr was examined by comparing their mean monthly gonad weight. Only data from 1987 were used, as this was the only year for which a complete data set existed. In the case of rainbow trout this analysis was performed to determine if those inhabiting Loch Awe spawned in the spring or autumn. In the case of the other species it was performed to provide basic biological statistics about the fish in the loch.

3.2.3.8 Growth.

The annual instantaneous growth rate was calculated using the back calculated lengths from the scales of the brown trout and rainbow trout caught in 1987 and 1988 using the formula described by Bagenal(1978):

$$G_o = \frac{\log L - \log L}{t} \times 100$$

G_o=Instantaneous Growth Rate, L= Length(mm) and t=Time.

The growth rate of brown trout and rainbow trout in Loch Awe was compared with that from other systems.

The length at capture of brown trout and rainbow trout in the same age class, caught at the fish farm and littoral sites in 1987 and 1988 were compared by the Mann-Whitney test. In order to maximise the number of fish in each experimental group, the variation in growth between male and female fish, and between the sites that comprised the habitats was measured using the Mann-Whitney test. Where no consistent significant difference existed between them the data were pooled. Only brown trout were examined in the littoral zone as there were insufficient rainbow trout to perform the analysis.

3.3 Results

3.3.1 Spatial distribution of the major fish species at the fish farm and shallow littoral sites in 1987.

3.3.1.1 Total annual catch.

It is shown in Figure 3.1 that the highest combined annual catch for all species was recorded at Tervine, followed by Braevallich, with lower but similar amounts being recorded at Hayfield, Ballimeanoch and Port Innisherrich. Table 3.2 shows that the variation in the annual catch between all of the sites, and between the two farm sites was highly significant at ($P< 0.001$ $X^2=231.6$) and ($P< 0.001$ $X^2=37.9$) respectively. There was no significant variation between the shallow littoral sites ($P> 0.05$ $X^2=4.9$). These results suggest that the fish farms act as an attractant to the fish in Loch Awe.

3.3.1.2 Annual catch of each species in 1987.

The highest annual catch of brown trout was recorded at Hayfield followed by Port Innisherrich, the next highest catch being recorded at Braevallich (Figure 3.1). The lower than expected catch at Ballimeanoch was probably due to the close proximity of the deep littoral net. When this result is combined with those from the shallow site a similar result to that recorded at Hayfield and Port Innisherrich is obtained. The lowest catch was recorded at Tervine. The variation between all of the sites, the two farms and all of the littoral sites was highly significant at ($P<0.001$ $X2= 54.7$), ($P<0.001$ $X^2=18.9$) and ($P<0.001$ $X^2=11.0$) respectively (Table 3.2). It is interesting to note that the variation between the sites excluding Tervine was only slightly higher than it was between the littoral sites on their own. Excluding Ballimeanoch less brown trout were caught at the fish farms than at the other littoral sites. This was most pronounced at Tervine where coincidentally the highest catch of rainbow trout was caught.

Figure 3.1 The annual catch, excluding March at the shallow littoral sites in 1987.

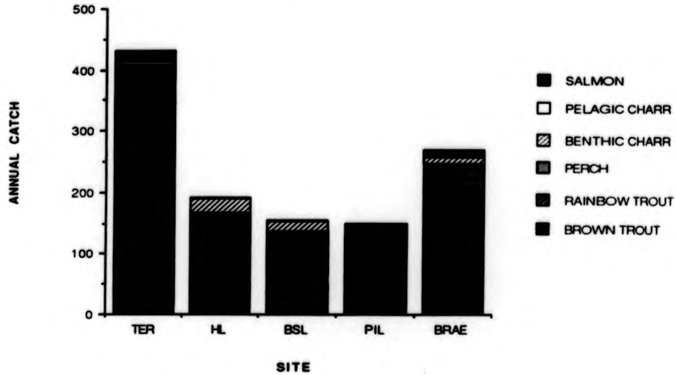


Figure 3.2 The site variation in the catch of each species in March 1988.

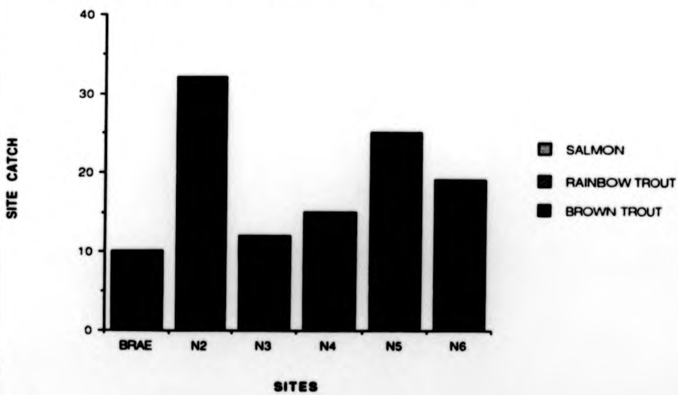


Table 3.2 The X^2 values and their significance for the variation in the distribution of, brown trout, rainbow trout, benthic Arctic charr, pelagic Arctic charr, perch and Atlantic salmon at the littoral sites at Tervine, Braevallich, Hayfield, Ballimeanoch and Port Innisherrich in 1987.

	All Sites	Sig	Tervine vs Braevallich	Sig	Littoral Only	Sig
Total	231.6	***	37.9	***	4.9	NS
Brown Trout	54.7	***	18.9	***	11.0	*
Rainbow Trout	314.0	***	96.0	***	5.7	NS
Benthic Charr	34.4	***	10.0	***	15.9	***
Pelagic Charr	STS		STS		STS	
Perch	18.8	***	1.9	NS	8.4	*
Salmon	41.4	***	1.7	NS	STS	

*=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant, STS=Sample too small.

The highest annual catch of rainbow trout was recorded at the fish farm sites, with considerably more being caught at Tervine than at Braevallich (P<0.001 X^2=96.0) (Figure 3.1 & Table 3.2). The annual catch at the littoral sites away from the farms was very low with the highest, 19, being recorded at Hayfield; the variation between them was not significant (P>0.05 X^2=5.7). The variation between all of the sites however was highly significant (P<0.001 X^2=314.0).

The low annual catch of benthic Arctic charr at the shallow littoral sites was restricted to Hayfield, Ballimeanoch and Braevallich, the highest catch of 22 being recorded at the former (Figure 3.1). The variation in catch between all of the shallow littoral sites, Tervine and Braevallich, and the littoral sites excluding the fish farms were all highly significant (P<0.001) with respective X^2 values of 34.4, 10.0 and 15.9 (Table 3.2).

Pelagic Arctic charr were caught in low numbers at each of the sites (Figure 3.1). The small sample size at each site precluded testing their distribution by X^2.

Perch were caught at each site with the highest number, 73, being recorded at Ballimeanoch (Figure 3.1). Their distribution was only marginally affected by the presence of the fish farms. The variation in catch between all of the sites was (P<0.001 X^2=18.8) (Table 3.2), which although being highly significant was the lowest recorded for all of the species that were examined. There was no significant difference in the catch between the two farm sites (P>0.05 X^2=1.9), and the variation in the catch at the sites excluding the fish farms was significant (P<0.05 X^2=8.4).

Atlantic salmon were only caught at the two farm sites and at Port

Innisherrich (Figure 3.1). Those at the latter were two spent adults and will not be considered further. The variation between the two farm sites was not significant (P>0.05 X^2=1.9) (Table 3.2). These results suggest that the juvenile salmon are attracted to the farm sites, however this is unlikely and there are probably different reasons for the catches at the two sites. The catch at Braevallich may be due to the farm's proximity to the Braevallich burn in which adult salmon spawn. The time that the young fish were caught coincides with the time that they start their migration to the sea. As the fish move from river to loch it is likely that some of them will be caught in the net which was set at Braevallich. It is the position of the site at Tervine which is responsible for the catch of young salmon. As the outflow from Loch Awe to the sea is approximately 2 km downstream from the fish farm every salmon smolt that migrates from the loch will have to pass the site at Tervine. This therefore increases the likelihood of catching migrating juvenile salmon.

3.3.2 Spatial variation in the monthly catch of each species. 1988.

As the specific aim of the 1988 gill netting was to examine the distribution of the fish species in relation to the fish farms, the data was examined on a monthly rather than an annual basis.

3.3.2.1 March

The 113 fish caught in March consisted of 94 brown trout, 17 rainbow trout, and 2 juvenile salmon caught at N3 (Figure 3.2). The highest catch was recorded at N2. In contrast to the pooled data from 1987 the lowest catch of all species was recorded at the fish farm site.

There was a large amount of variation in the numbers of brown trout caught at each site with the lowest and highest being recorded at

Braevallich and N2 (the site closest to Braevallich) respectively (Figure 3.2). The variation between all of the sites was highly significant ($P<0.001$ $X^2=31.2$), and at the sites excluding Braevallich it was only slightly lower ($P<0.01$ $X^2=18.1$) (Table 3.3).

Rainbow trout were caught at Braevallich, N3, N4, N5 and N6 with the highest catch being recorded at the fish farm, although this was lower than expected (Figure 3.2). The catch at the littoral sites away from the farm was similar to that recorded at littoral sites in 1987, therefore it appears that rainbow trout are only found in large numbers in the immediate vicinity of the fish farm. The sample was too small to perform statistical analysis.

3.3.2.2 May

The 149 fish caught in May consisted of 84 brown trout, 8 rainbow trout, 44 benthic Arctic charr, 13 perch, 1 pelagic Arctic charr and 1 stickleback (Figure 3.3). Contrary to the previous month the highest catch was recorded at Braevallich, and it declined with distance from the fish farm.

Brown trout were caught at each site with the highest catches being recorded at Braevallich and N2; although fewer were caught at the other sites there was no significant variation in the catch between them (Figure 3.3 and Table 3.3). In this instance it appears that the brown trout showed a slight preference for the sites closer to the fish farm.

The catch of rainbow trout was low, with the largest catch occurring Braevallich, and smaller numbers being recorded at N2 and N6 (Figure 3.3). The catch was too small to perform statistical analysis.

Benthic Arctic charr were caught at each site but showed a very strong

Table 3.3 The X^2 values and their significance for the variation in the distribution of brown trout, rainbow trout, benthic Arctic charr, pelagic Arctic charr, perch and Atlantic salmon at Braevallich, N2, N3, N4, N5, and N6 in March, May, July and September of 1988.

	March	SIG	May	SIG	July	SIG	September	SIG
Brown Trout	31.2	***	7.6	NS	20.8	***	8.6	NS
Rainbow Trout	STS		STS		STS		STS	
Benthic Charr	_		57.2	***	STS		STS	
Pelagic Charr	_		STS		_		STS	
Perch	_		STS		STS		STS	
Salmon	STS		_		STS		STS	

*=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant,
STS = Sample too small.

Figure 3.3 The site variation in the catch of each species in May 1988.

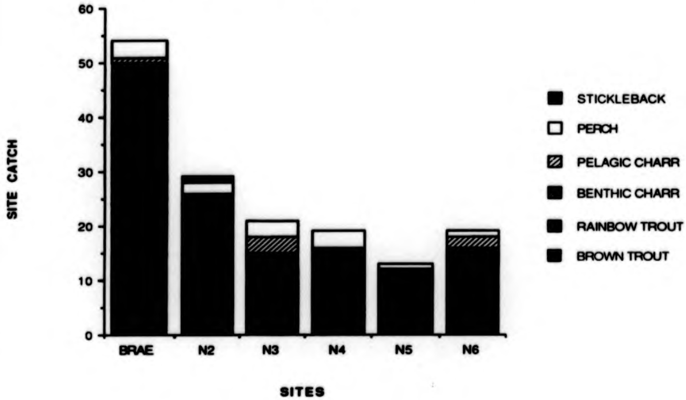
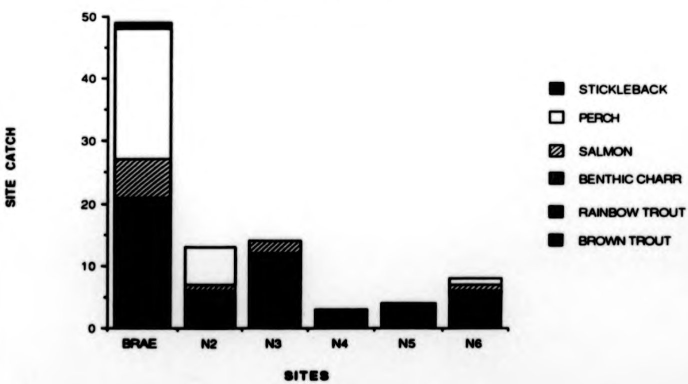


Figure 3.4 The site variation in the catch of each species in July 1988



preference for the fish farm (Figure 3.3). The variation between all of the sites was highly significant ($P<0.001$ $X^2=57.2$) (Table 3.3). Such a large movement into the littoral zone at this time of the year was unexpected, as the seasonal variation in 1987 showed that their movement into the littoral zone was largely restricted to slightly deeper water and occurred later in the year when they were spawning. Therefore the reason for the high catch in this month is unclear.

Pelagic Arctic charr were caught in small numbers at Braevallich, N3 and N6. Perch were caught in small numbers at each site showing no preference for the farm or littoral sites and sticklebacks were caught at N2.

3.3.2.3 July.

The 94 fish caught in July comprised 46 brown trout, 13 rainbow trout, 11 salmon, 22 perch, and 2 benthic charr (Figure 3.4). In common with the results from the previous month the highest total catch was recorded at Braevallich, with lower and similar catches being recorded at N2 and N3, and still lower catches being recorded at N4, N5 and N6.

The highest catches of brown trout were recorded at Braevallich, N2 and N3 (Figure 3.4). The most likely explanation for this is that these sites caught the summer migrants as they moved from the Braevallich burn to the loch, the size and age of the fish supports this. These sites are particularly sensitive to this migration as they are closest to the burn. The low catch at N4, N5 and N6 could be explained by the seasonal movement of adult brown trout from the littoral zone to the open water (see later section). The variation in the catch between the sites was highly significant ($P<0.001$ $X^2=20.8$) (Table 3.3).

Rainbow trout were caught in small numbers at Braevallich, N5 and N6, again the largest catch was recorded at the former (Figure 3.4). The sample of rainbow trout was too small to perform statistical analysis.

Atlantic salmon were caught at each site except N4 and N5, with the highest numbers being caught at the sites closest to the Braevallich burn (Figure 3.4). These sites will be sensitive to the lochward migration of juvenile salmon, similar to that described for juvenile brown trout. The sample was too small to perform statistical analysis.

The catch of perch was restricted to Braevallich, N2 and N6, with only a small number being caught at the latter (Figure 3.4). The highest catch was recorded at the fish farm, the reason for this being unclear. The sample was too small to perform statistical analysis.

Benthic Charr were caught in small numbers at N2, N3, N6 and a small number of sticklebacks were caught at Braevallich.

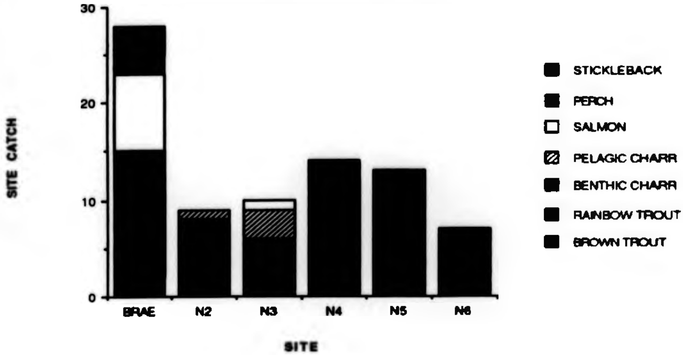
3.3.2.4 September

The 75 fish caught in September consisted of 40 brown trout, 20 rainbow trout, 10 salmon, 2 benthic charr and 4 perch (Figure 3.5). The distribution of the total catch between the sites was similar to that recorded in the two previous months, with the highest being recorded at Braevallich.

Brown trout were caught at each site with more being caught at the littoral sites than at the fish farm (Figure 3.5). This is in contrast to the results from the two previous months when more were caught at the farm, but in agreement with the results from March. The between site variation was not statistically significant ($P>0.05$) (Table 3.3).

Rainbow trout were caught at each site except N3. Although they were

Figure 3.5 The site variation in the catch of each species in September 1988.



only caught in small numbers, it is still clear that they showed a preference for the fish farm, with more being caught there than at the other sites combined (13 as opposed to 7)(Figure 3.5). The sample was too small to perform statistical analysis.

The catch of salmon was restricted to Braevallich and N3, with the highest catch being recorded at the latter. This catch of salmon coincides with the period of their autumn migration.

Perch were caught in small numbers at Braevallich and N5, this catch represents the small number of perch remaining in shallow water after the majority have migrated to the deeper water where they overwinter.

Pelagic charr were caught at N2 and N3, and the catch of benthic charr and sticklebacks was restricted to N5 and Braevallich respectively.

3.3.3 Distribution of rainbow trout after a large escape in February 1989.

On the 27th February 1989 the catch at each site was dominated by rainbow trout (Figure 3.6). The highest catch 98 was recorded at Tervine, it declined to site 3 where 31 rainbow trout were caught, with a similar number being caught at the remaining sites. The catch of rainbow trout at the fish farm and littoral sites was considerably higher than it had been in the two previous years. At the sites closest to the farms original position very few brown trout were caught, however, at site 5 and Hayfield Littoral the catch of brown trout was at a level one would have expected for that time of the year.

By the 20th April 1989 the catch of rainbow trout at each site was considerably lower than it had been during the previous netting (Figure 3.7). At Tervine it was lower than in the same month in 1987, and at

Figure 3.6 The site variation in the catch of each species on the 28/2/89.

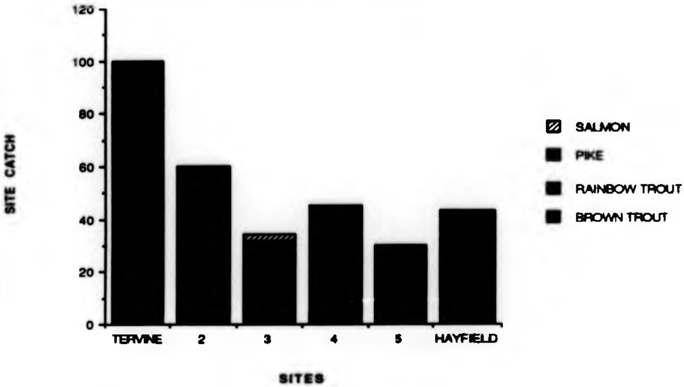
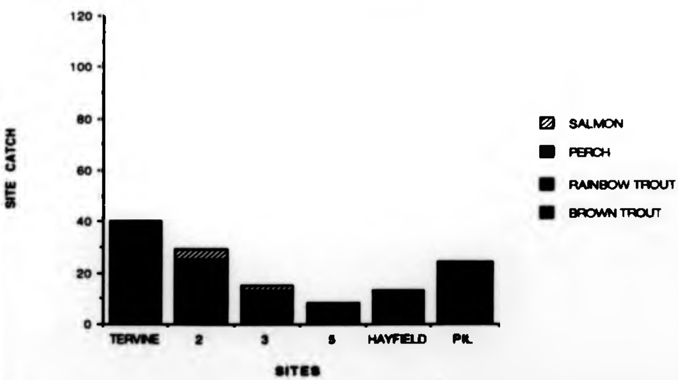


Figure 3.7 The site variation in the catch of each species caught on the 20/4/89.



sites 3, 5 and Hayfield Littoral the catch was as expected had there not been a large release of fish. At site 2, 21 rainbow trout were caught. This was higher than would have predicted from the 1988 results, but is probably due to the earlier loss of fish. It is also possible that the littoral areas around the site at Tervine have always held a higher number of rainbow trout, as then mean monthly catch of rainbow trout in 1987 at Tervine was higher than at Braevallich. As only one rainbow trout was caught at Port Innisherrich the site furthest from Tervine, it can be concluded that they did not spread through the loch in large numbers. The catch of brown trout at the littoral sites away from the fish farms was at the expected level had the loss of fish not occurred. Therefore it would appear that the distribution of brown trout had been adversely affected by the large numbers of rainbow trout that were present in the littoral zone immediately after the escape, but by April when their numbers had declined the brown trout distribution had reverted to its normal pattern.

3.3.4 Comparison of mean monthly catch of brown trout and rainbow trout at fish farm and littoral sites.

In 1987 the mean monthly catch (MMC) of rainbow trout was significantly higher than brown trout at Braevallich and Tervine ($P < 0.01$ and $P < 0.001$ respectively) (Tables 3.4-3.6), with more rainbow trout caught at Tervine than Braevallich ($P<0.001$), the opposite was true for brown trout ($P<0.01$). It is possible that the high number of rainbow trout around the farm site at Tervine caused the lower catch of brown trout. Further evidence of this is seen when the brown trout MMC at each farm site is compared with the MMC at the littoral sites away from the fish farms. The catch of brown trout at Tervine was significantly lower ($P < 0.001$) than at the littoral sites, whereas at Braevallich the difference was not significant. A comparison of the rainbow trout

Table 3.4 The mean monthly catches of brown trout and rainbow trout at the two fish farm and littoral sites in Loch Awe in 1987.

	Tervine	Braevallich	Littoral
Brown Trout	2.2	6.3	7.3
Rainbow Trout	32.2	12.3	1.2

Table 3.5 The statistical significance in the difference in the mean monthly catch of brown trout and rainbow trout at the two fish farm and littoral sites in Loch Awe in 1987, compared by one way ANOVA after a Log10(x+1) transformation.

	Tervine _vs_ Braevallich	Tervine _vs_ Littoral	Littoral _vs_ Braevallich
Brown Trout	**	**	N.S
Rainbow Trout	***	***	***

*=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant.

Table 3.6 The statistical significance in the mean monthly catch of brown trout compared to rainbow trout at Braevallich, Tervine and the littoral sites in 1987, the comparison was made by one way ANOVA after a Log 10(x+1) transformation.

	Braevallich	Tervine	Littoral
Rainbow _vs_ Brown Trout	**	***	***

*=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant.

MMC's at each of the fish farms, and the littoral sites shows that their distribution is highly localised. In both instances the rainbow trout MMC was significantly higher ($P<0.001$) at the fish farm sites. This is confirmed by comparing the brown trout and rainbow trout MMCs in the littoral zone. The difference was highly significant ($P< 0.001$), with a greater number of brown trout being caught.

The 1988 gill netting survey was designed to determine how localised the distribution of rainbow trout around the fish farm at Braevallich was. In common with the results from 1987 the rainbow trout MMC at Braevallich (the fish farm site) was significantly higher than at the littoral sites ($P<0.001$), 8.3 as opposed to 1.3. There was again no significant difference in the brown trout MMC between Braevallich and the littoral sites, 9.3 as opposed to 10.3; and the brown trout MMC in the littoral zone was significantly higher than the rainbow trout's ($P<0.001$), 10.9 as opposed to 1.3. The major difference between the two years was that there was no significant difference between the MMCs of brown trout and rainbow trout at Braevallich, 9.3 as opposed to 8.3. In the previous year the rainbow trout MMC had been significantly higher ($P<0.01$).

Therefore it is clear that rainbow trout are only found in large numbers in the immediate vicinity of the fish farms, and that they only adversely affect the distribution of brown trout when the rainbow trout: brown trout ratio is high. It was not possible to establish the threshold value beyond which this occurred.

3.3.5 Seasonal variation in the distribution of fish at each site in 1987.

3.3.5.1 Tervine

The 535 fish caught at Tervine comprised 24 brown trout, 354 rainbow trout, 4 pelagic Arctic charr, 19 juvenile salmon, 34 perch, 2 sea trout, 99 sticklebacks and one minnow (Figure 3.8).

The seasonal variation in the catch of rainbow trout, salmon, perch and sticklebacks was highly significant ($P<0.001$); brown trout also showed seasonal variation, but the significance was slightly lower ($P<0.01$). The other species were not caught in large enough numbers to perform statistical analysis (Table 3.7).

The highest numbers of brown trout were caught in the spring with only a few individuals being caught after that. There was considerable monthly variation in the catch of rainbow trout, but a seasonal trend was still apparent, with more being caught in the spring than in the summer. It was unclear if this pattern was related to food availability, or whether it was due to the pattern of losses from the fish farm.

The highest numbers of juvenile salmon were caught in July, with only a few being caught after that in August, November and December. The number of perch caught increased from 1 in May to a maximum of 10 in July and fell in the autumn. A small number were caught in the early winter months after the majority of the population had migrated back into the deeper water. Sticklebacks showed a bimodal distribution with peaks in early summer and November.

3.3.5.2 Hayfield Littoral

The 198 fish caught at Hayfield Littoral comprised 110 brown trout, 21 rainbow trout, 22 benthic charr, 44 perch and one juvenile salmon (Figure 3.9). The catch of brown trout, rainbow trout, benthic charr and perch all showed highly significant seasonal variation ($P<0.001$) (Table 3.7).

Figure 3.8 Monthly variation in the catch of each species at Tervine in 1987.

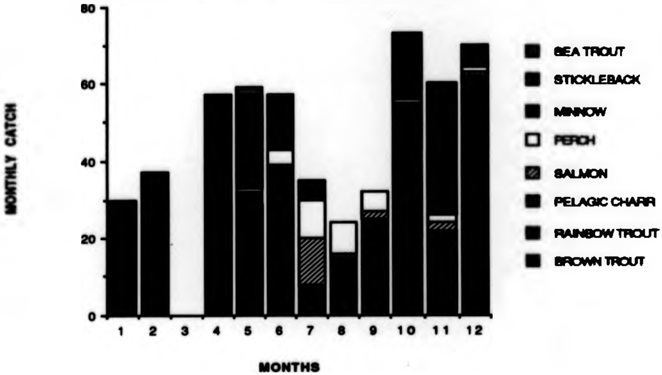


Figure 3.9 Monthly variation in the catch of each species at Hayfield Litteral in 1987.

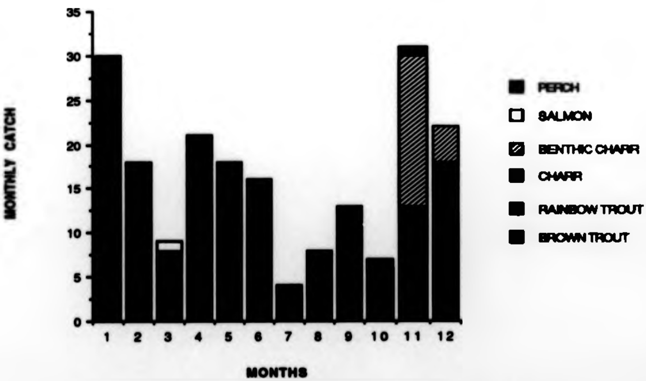


Table 3.7 The X^2 values and their significance for the seasonal variation in the catch of brown trout, rainbow trout, benthic Arctic charr, Atlantic salmon and Perch at all of the sites in 1987.

	Brown Trout	Rainbow Trout	Benthic Charr	Salmon	Perch
Tervine	9.7 **	31.5 ***	- -	14.4 ***	25.2 ***
Hayfield Littoral	38.9 ***	10.9 **	42.0 ***	- -	38.5 ***
Hayfield Pelagic	7.7 *	- -	STS -	- -	- -
Hayfield Benthic	STS -	- -	40.8 ***	- -	STS -
Coillaig Deep	STS -	STS -	STS -	- -	83.4 ***
Coillaig Shallow	STS -	STS -	STS -	- -	83.4 ***
Ballimeanoch Shallow	37.6 ***	STS -	STS -	- -	103.4 ***
Ballimeanoch Deep	82.1 ***	STS -	47.2 ***	- -	STS -
Port Innisherrich Benthic	- -	- -	1.2 NS	- -	- -
Port Innisherrich Pelagic	STS -	STS -	STS -	- -	- -
Port Innisherrich Littoral	37.9 ***	STS -	STS -	STS -	39.1 ***
Braevallich	6.3 **	8.1 **	STS -	STS -	14.7 ***

STS=Sample too small, *=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant.

Brown trout were caught in greatest numbers in the late winter/early spring and in the late autumn, and were only caught in small numbers during the summer. Rainbow trout followed a similar pattern, but the seasonal variation was less pronounced.

The catch of 22 benthic charr was restricted to November and December, with the majority being caught in the former. They are thought to spawn in the littoral zone at this time (see maturation section).

The majority of perch were caught in the summer months, with only a few being caught later in the year. This is further evidence of their incomplete winter migration to deeper water that was observed at Tervine, and reported by Craig (1977). One juvenile salmon was caught in March.

3.3.5.3 Hayfield Pelagic

The 35 fish caught at Hayfield Pelagic comprised 21 brown trout, 2 rainbow trout, 9 benthic charr and 3 perch (Figure 3.10). Only the catch of brown trout showed significant seasonal variation ($P<0.01$) (Table 3.7). It peaked in the summer months, coinciding with the period of least abundant at the littoral sites. The other species were not caught in sufficiently large numbers for any seasonal trends to be discerned.

3.3.5.4 Hayfield Benthic

The 121 fish caught at Hayfield Benthic comprised 4 brown trout, 1 rainbow trout, 1 pelagic charr and 114 benthic charr (Figure 3.11). Only benthic charr were caught in numbers large enough to perform statistical analysis. They were caught in small numbers in the first half of 1987, their numbers rose to a maximum of 26 in September and fell to 9 in December, the seasonal variation was highly significant

Figure 3.10 Monthly variation in the catch of each species at Hayfield Pelagic in 1987.

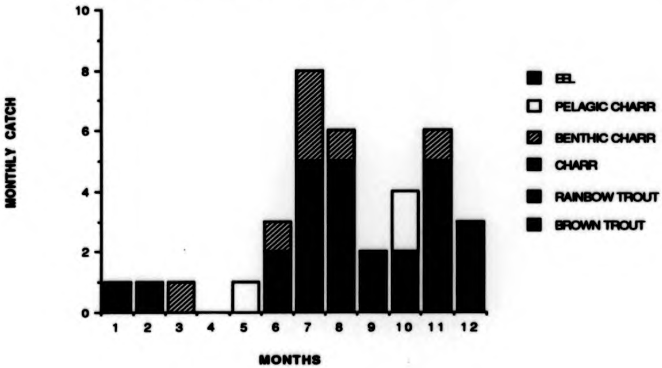


Figure 3.11 Monthly variation in the catch of each species at Hayfield Benthic in 1987.

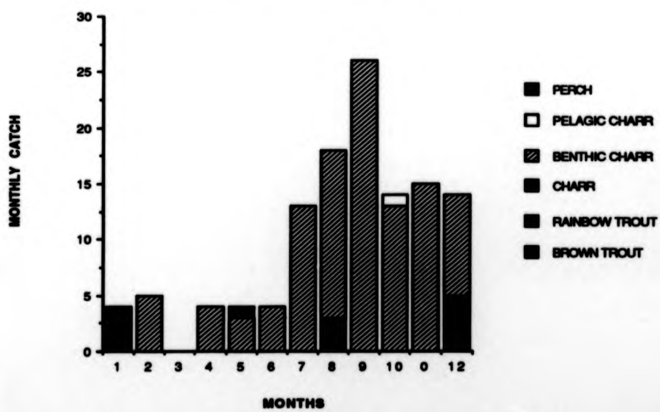


Figure 3.12 Monthly variation in the catch of each species at Coillaig Shallow Littoral in 1987.

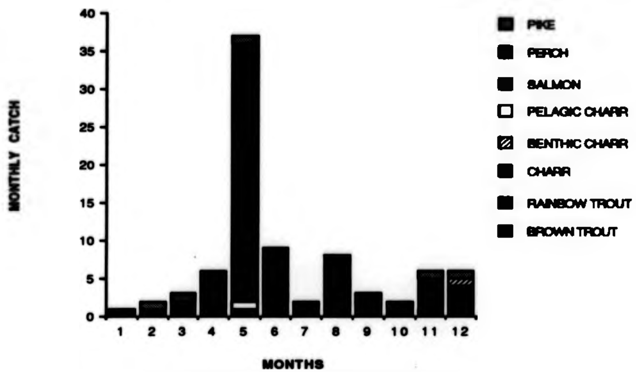
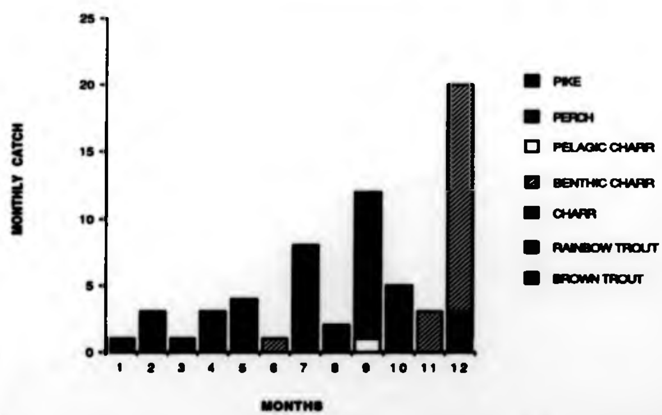


Figure 3.13 Monthly variation in the catch of each species at Coilliaig Deep Littoral in 1987.



(P<0.001) (Table 3.7). The decline in their catch at the end of the year coincided with their spawning migration to the littoral zone.

The other species were not caught in large enough numbers for any seasonal trends to be discerned. It is possible that the brown trout, rainbow trout and perch were caught while the net was being set or lifted, as their presence in the deep benthic zone was unexpected. The highly distended swim bladders found in the benthic charr indicated that they had been brought rapidly to the surface from a great depth, and the eel damage to some of them indicates that they were caught when the net was on the bottom. The other species did not have distended swim bladders, and showed no signs of eel damage.

3.3.5.5 Coillaig Shallow Littoral

The 85 fish caught at Coillaig Shallow Littoral comprised 10 brown trout, 11 rainbow trout, 4 benthic charr, 1 pelagic charr, 1 salmon, 53 perch and 5 pike (Figure 3.12). The perch catch showed highly significant seasonal variation (P<0.001) (Table 3.7). The other species were not present in large enough numbers to perform statistical analysis.

As with the other littoral sites the catch of perch was largely restricted to the summer months, but contrary to the results from the two previous littoral sites, they were not caught after September.

3.3.5.6 Coillaig Deep Littoral

The 65 fish caught at Coillaig Deep Littoral comprised 4 brown trout, 4 rainbow trout, 27 benthic charr, 1 pelagic charr, 21 perch and 6 pike (Figure 3.13). The seasonal variation in the catch of benthic charr (P<0.001) and perch (P<0.01) showed significant seasonal variation, the samples of the other species were too small to perform statistical analysis (Table 3.7).

The abundance of benthic charr peaked in December, but occurred in small numbers throughout the year. The peak in December is in agreement with the findings from the other littoral sites. It is noted that the peak was more pronounced in the deep littoral site than at the previous shallow sites.

The summer increase in perch abundance was of a lower magnitude, and occurred September, later than at the other sites. Comparing the two Coillaig sites it was shown that perch preferred the shallow littoral habitat in the summer and that the winter spawning of benthic charr was largely restricted to the deep littoral zone.

The catch of brown trout at the two Coillaig sites was surprisingly low. The most likely reason for this was the presence of pike. It was only after part of the sampling programme had been completed, that I learned that what I had been calling Coillaig was known locally as "Pike Bay".

3.3.5.7 Ballimeanoch Shallow Littoral

The 171 fish caught at Ballimeanoch Shallow Littoral comprised 66 brown trout, 73 perch, 17 benthic charr, 10 rainbow trout, 3 pelagic charr, 1 stickleback and 1 pike (Figure 3.14). Only brown trout, perch and benthic charr were present in sufficient numbers to perform statistical analysis. The seasonal variation in abundance of brown trout and perch was slightly more significant than benthic charr, ($P<0.001$) as opposed to ($P< 0.05$).

The brown trout catch fell from January through the spring to a minimum in mid-summer, it increased again to the end of the year, but to lower

Figure 3.14 Monthly variation in the catch of each species at Ballimeanoch Shallow Littoral in 1987.

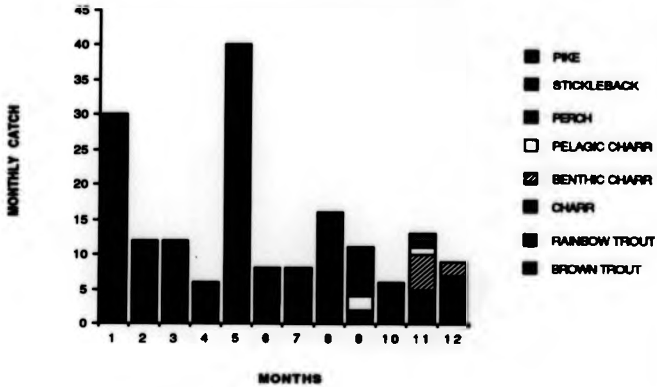
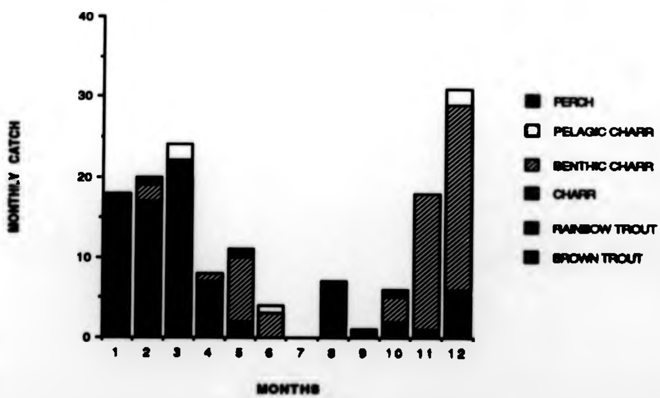


Figure 3.15 Monthly variation in the catch of each species at Ballimeanoch Deep Littoral in 1987.



level than in the previous January.

The main period of perch activity was again largely restricted to the late spring and summer months. Their maximum catch was in May and in common with Tervine and Hayfield Littoral a few were caught in the late autumn and early winter.

In common with the other littoral sites the benthic Arctic charr were caught in November and December, however they were also caught in January. Those caught in January were probably late spawners from the previous year.

3.3.5.9 Ballimeanoch Deep Littoral

The 148 fish caught at Ballimeanoch Deep Littoral comprised 65 brown trout, 67 benthic charr, 7 rainbow trout, 5 pelagic charr and 4 perch (Figure 3.15). Only brown trout and benthic charr showed significant seasonal variation ($P<0.001$). The samples of the other species were too small to perform statistical analysis (Table 3.7).
The catch of brown trout showed the same seasonal variation that had been observed at Ballimeanoch shallow. The benthic charr were caught in small numbers throughout the year, with a sharp rise occurring in November and December. Individual perch were caught throughout the year, and did not show the summer maximum that had been found at the shallow littoral sites. The catch of perch and benthic Arctic charr showed a similar pattern of capture at the deep and littoral sites at Coillaig and Ballimeanoch, benthic charr predominating in the former and perch predominating in the latter.

3.3.5.9 Port Innisherrich Benthic

The 70 fish caught at Port Innisherrich Benthic comprised 64 benthic Arctic charr, 4 pelagic Arctic charr, 1 brown trout and 1 rainbow trout

(Figure 3.16). Only the catch of benthic charr showed significant seasonal variation (P<0.001) (Table 3.7). In common with Hayfield Benthic they were caught throughout the year, with a peak occurring in the autumn prior to their decline in November and December, which coincided with the timing of their spawning migration into the deep littoral zone.

The abundance of the other species was too small for any seasonal pattern to be observed. As at Hayfield Benthic it is possible that the rainbow trout and brown trout were caught as the net was being set or lifted.

3.3.5.10 Port Innisherrich Pelagic

The 21 fish caught at Post Innisherrich Pelagic comprised 7 brown trout, 2 rainbow trout, 9 benthic charr and 3 pelagic charr (Figure 3.17). None of the species were present in large enough numbers to perform statistical analysis (Table 3.7).

3.3.5.11 Port Innisherrich Littoral

The 162 fish caught at Port Innisherrich Littoral comprised 88 brown trout, 50 perch, 12 rainbow trout, 3 pelagic Arctic charr, 3 salmon (1 juvenile and 2 adults), 2 benthic Arctic charr, 1 pike and a minnow (Figure 3.18). Only the catch of brown trout and perch showed significant seasonal variation (P<0.001). The samples of the other species were too small to perform statistical analysis (Table 3.7).

The brown trout catch increased from January to April, fell to its minimum in August, then increased to its highest level in November. In this respect Port Innisherrich Littoral differs from the previous littoral sites where more were caught in the earlier part of the year than at the end. A possible explanation for this anomaly is that Port

Figure 3.16 Monthly variation in the catch of each species at Port Innisherrich Benthic in 1987.

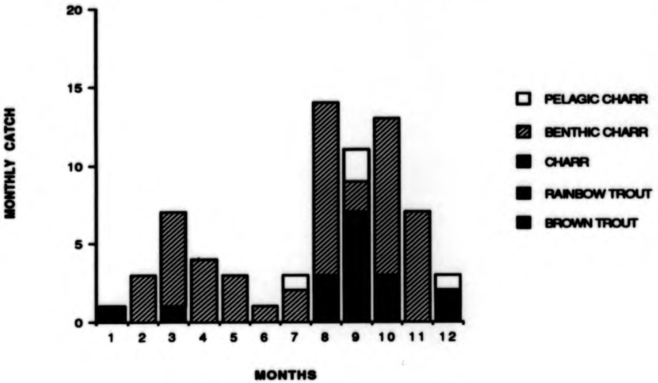


Figure 3.17 Monthly variation in the catch of each species at Port Innisherrich Pelagic in 1987.

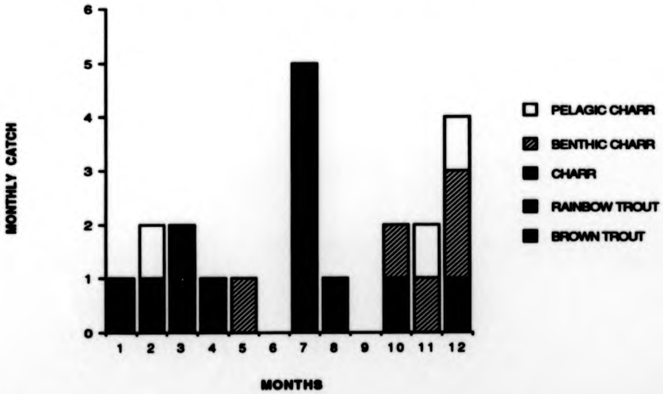


Figure 3.18 Monthly variation in the catch of each species at Port Innisherrich Littoral in 1987.

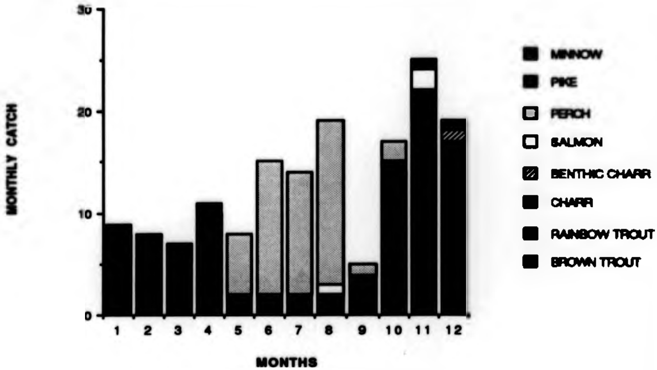
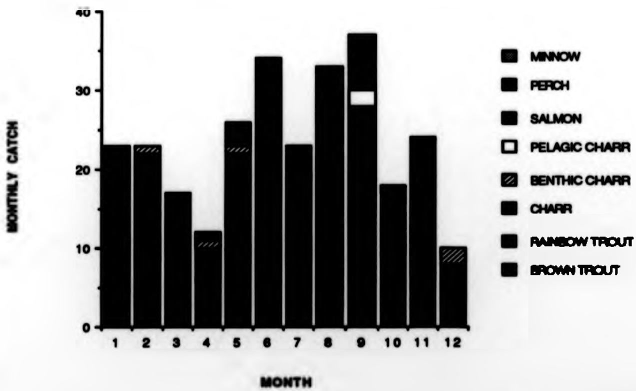


Figure 3.19 Monthly variation in the catch of each species at Braevallich in 1987.



Innisherrich was used as an exploratory gill netting site in November and December 1986, when catches of brown trout comparable with the sites mentioned above were recorded. This may have lowered the population in the area prior to the start of the 1987 survey.

Perch abundance was again restricted to the middle part of the year with their numbers peaking in late summer, rather than early summer as in the other littoral sites.

3.3.5.12 Braevallich

The 290 fish caught at Braevallich comprised 75 brown trout, 147 rainbow trout, 44 perch, 11 juvenile salmon, 10 benthic charr, 2 pelagic charr and 1 minnow (Figure 3.19). Only the samples brown trout, rainbow trout and perch were large enough to perform statistical analysis. They all showed significant seasonal variation, rainbow trout, brown trout ($P<0.01$) and perch ($P<0.001$) (Table 3.7).

The seasonal distribution of brown trout at Braevallich was slightly different from that described at the other shallow littoral sites. Instead of the bimodal distribution pattern peaking at the start and end of the year, their numbers peaked in the spring and autumn.

The seasonal distribution of rainbow trout is markedly different from that at Tervine. Again there was considerable variation between months, but the lowest catches occurred at the start of the year rather than the summer. It is unclear if this seasonal pattern is due to fish losses from the farm or whether it is under natural control. Another explanation is that like Port Innisherrich Littoral, Braevallich was an exploratory gill netting site at the end of 1986, when large catches of rainbow trout were recorded. The perch catch was again restricted to the summer months peaking in mid-summer.

3.3.6 Seasonal distribution of fish in 1988.

The variation in the number of brown trout caught in each month was highly significant (X^2=33.1, $P < 0.001$) (Table 3.8). They were most abundant in March, and their numbers declined until September (Figure 3.20). This is in agreement with the findings at the littoral sites from March to September in 1987. Presumably if netting had continued past September an increase in the brown trout catch would have been recorded.

The monthly catch of rainbow trout was considerably lower than brown trout, more being caught in March and September than in May and July (Figure 3.20), although the difference was not significant (X^2=5.6 $P>0.05$) (Table 3.8).

The monthly variation in the catch of benthic charr was statistically significant (X^2=120.3 $P < 0.001$) (Table 3.8). The motivating force for the large movement into the shallow littoral zone in May cannot be explained (Figure 3.20), as no similar trend was observed in 1987.

The monthly variation in the catch of salmon was statistically significant (X^2=15.4 $P< 0.01$), with most being caught in July and September. As none of those caught showed any signs of smolting it is likely that they migrated into the loch from the nursery streams prior to smolting in the spring of 1989.

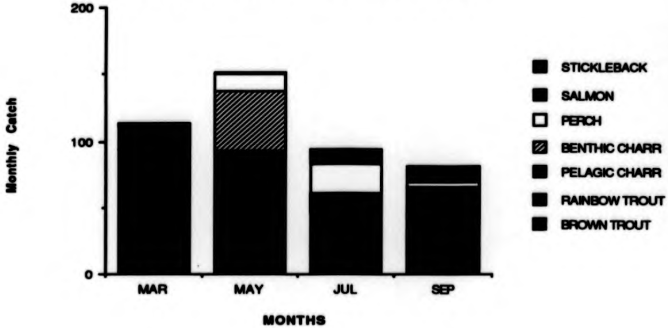
The monthly variation in the catch of perch was significant (X^2=29.4 $P < 0.001$). The increase in their numbers in the littoral zone in late spring was followed by a decline in the autumn, similar to the pattern described in 1987. This migration pattern is as described by Giles & Tippet (1987) in Loch Lomond and Allen (1935) in Windermere.

Table 3.8 The X^2 values and their significance for the seasonal variation in the catch of brown trout, rainbow trout, pelagic Arctic charr, benthic Arctic charr, Atlantic salmon, perch and sticklebacks at all of the sites in 1988.

	X^2	Significance
Brown trout	33.1	***
Rainbow trout	5.6	N.S
Pelagic charr	STS	
Benthic charr	120.3	***
Perch	29.4	***
Salmon	15.4	**
Stickleback	STS	

STS=Sample too small, *=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant.

Figure 3.20 Monthly variation in the catch of each species in the N-series of nets in 1988.



There are insufficient data for any monthly variation in the capture of pelagic Arctic charr and sticklebacks to be ascertained.

3.3.7 Habitat use by juvenile and adult brown trout and rainbow trout .

Age group A included fish in age classes 0+-2+, and age group B included fish in age classes 3+-6+. In 1987 the abundance of brown trout in age groups A and B in the littoral zone declined from winter to summer, and increased from summer to winter (Figure 3.21). The summer decline was more pronounced in the older age group. This variation in the distribution of the two age groups was statistically significant ($P<0.05$ $X^2=20.95$). It is probably due to a combination of the older fish moving offshore, and an influx of juveniles from the loch's afferent streams to the littoral zone during the summer months.

The two age classes of brown trout were caught in small numbers in open water throughout 1987. Both age classes were caught in small numbers in the early part of the year. During the summer there was a small increase in the catch of older fish, which coincided with the period of low abundance in the littoral zone (Figure 3.22). Due to the low catch it was not possible to perform any statistical analysis.

There was no distinct seasonal pattern in the distribution of juvenile or adult rainbow trout at the littoral sites in 1987 (Figure 3.23). However when the catches from the fish farms are removed a slight drop during the summer in the age group A was observed. Due to the small catch of age group B, no statistical analysis was possible.

In the pelagic habitat rainbow trout were only caught in small numbers in the winter of 1987. (Figure 3.24). The sample was too small to perform statistical analysis.

Figure 3.21 Annual distribution of brown trout in age classes A (0+-1+) and B (3+-6+) at the littoral sites in 1987.

Figure 3.22 Annual distribution of brown trout in age classes A (0+-2+) and B (3+-6+) at the pelagic sites in 1987.

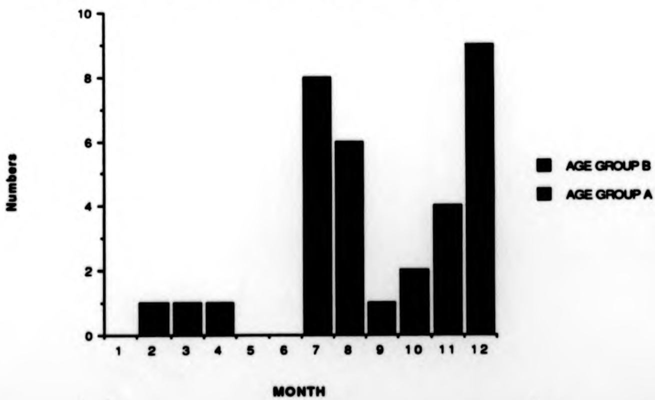


Figure 3.23 Annual distribution of rainbow trout in age classes A (0+-2+) and B (3+-6+) at the littoral sites in 1987.

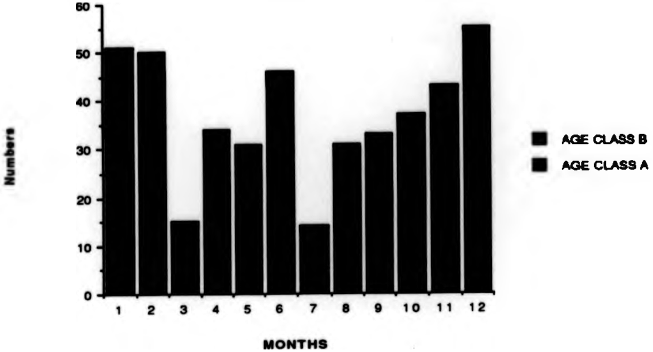
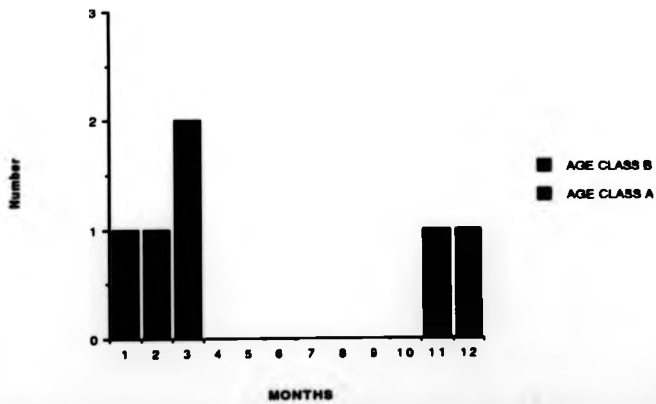


Figure 3.24 Annual distribution of rainbow trout in age classes A (0+-2+) B(3+-6+) at the pelagic sites in 1987.



In 1988 the variation in the distribution of juvenile and adult brown trout at the littoral sites in March, May, July and September was highly significant ($P<0.001$ $X^2= 27.4$). Again there was a summer migration of older fish from the littoral zone, and contrary to the previous year's results the abundance of juvenile fish increased at this time (Figure 3.25). The sites fished in 1988 would have been particularly sensitive to such a migration of juveniles as they were all close to the inflow of a large spawning stream.

No similar pattern was observed for rainbow trout in the littoral zone in 1988. Juveniles dominated the catch in each netting period (Figure 3.26). It is likely that the relative composition of juveniles and adults is dictated by the pattern of loss from the fish farm, due to its close proximity to the netting sites. It was not possible to perform a X^2 test as the sample of the older age class was too small.

3.3.8 Sex ratios of brown trout, rainbow trout, Arctic charr, and perch.

In 1987 there was a greater number of females than males caught in all species except perch. In brown trout and rainbow trout the difference was significant but in benthic charr it was not. In the case of pelagic charr and perch the samples were too small to derive firm conclusions (Table 3.9).

The sex ratio for brown trout is similar to the findings of Haraldstad & Jonsson (1983) working in Lake Myrkdalsvatnet. The very high percentage of female rainbow trout to males is due to the fish farms using all female stock. The technique used to produce all female stock is not completely successful and it is for this reason that a small number of males will always be found. The sex ratio found in the benthic charr is consistent with that found by Le Cren & Kipling

Figure 3.25 Monthly distribution of brown trout caught in age groups A (0+-2+) and B (3+-6+) at the littoral sites in 1988.

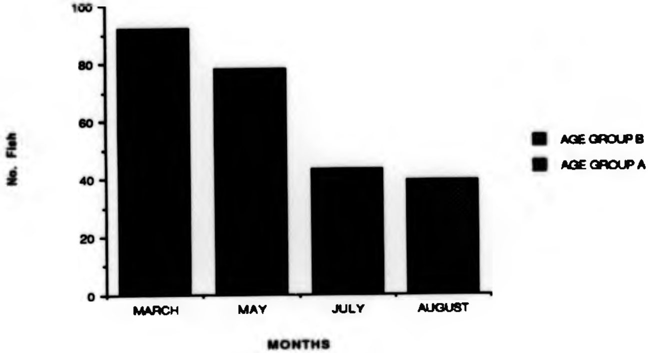


Figure 3.26 Monthly distribution of rainbow trout caught in age groups A (0+-2+) and B (3+-6+) at the littoral sites in 1988.

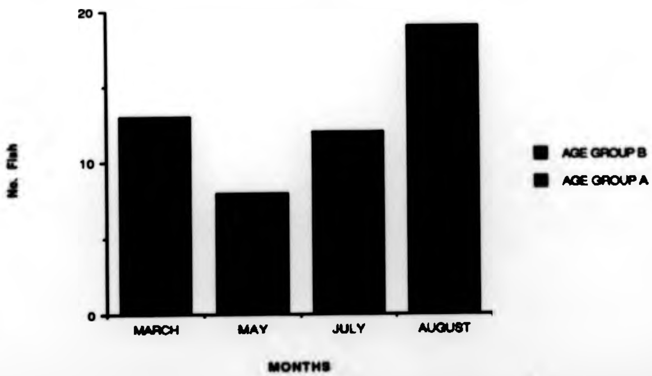


Table 3.9 The sex ratios of brown trout, rainbow trout, Arctic charr and perch in the complete sample of fish caught in 1987, with X^2 tests on deviations from ratios of 1:1.

	Male No.	%	Female No.	%	X^2	Significance
Brown Trout	167	42.0	231	58.0	10.3	**
Rainbow Trout	86	29.7	204	70.3	48.0	***
Pelagic Charr	7	24.1	22	75.9	7.8	**
Benthic Charr	133	46.5	153	53.5	1.4	N.S
Perch	51	68.9	23	31.1	10.6	**

*=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant.

Table 3.10 The sex ratios of brown trout, rainbow trout, Arctic charr and perch in the complete sample of fish caught in 1988, with X^2 tests on deviations from ratios of 1:1.

	Male No.	%	Female No.	%	X^2	Significance
Brown Trout	104	41.6	146	58.4	7.1	**
Rainbow Trout	8	15.7	43	83.4	24.0	***
Pelagic Charr	3	25.0	9	75.0	3.0	N.S
Benthic Charr	13	31.7	28	68.3	5.5	*
Perch	2	20.0	8	80.0	3.6	N.S

*=P<0.05, **=P<0.01, ***=P<0.001, N.S=Not Significant.

(1963) in Windermere.

In 1988 there was a greater number of females than males caught in all species (Table 3.10). The brown trout and rainbow trout sex ratios were similar to that observed in 1987, but the catch of the latter, as with the other species was too small for firm conclusions to be drawn.

In both years it is possible that the data were biased by the position of the netting sites, and further in 1988 by the sampling being restricted to the spring, summer and autumn. This is due to temporal and spatial variation exhibited by the two sexes in each species. This is investigated in the following sections.

3.3.9 Seasonal variation in habitat use by male and female brown trout, rainbow trout, Arctic charr and perch.

The habitats are classified as littoral and open water, the same criteria used when looking at the variation in the distribution of age classes. In 1987 there was a greater proportion of female brown trout caught in the littoral zone than males, in the summer the situation was reversed with a greater proportion of males being caught (Figure 3.27). However the difference was not significant ($P>0.05$ $X^2=9.3$). Throughout 1987 a greater number of female brown trout were caught in open water than males, but the small sample size precluded any statistical analysis.

In 1987 the monthly variation in the distribution of male and female rainbow trout in the littoral habitat was statistically significant ($P<0.05$ $X^2=26.4$). The proportion of females in the catch declined over the summer, but it is unclear if this was due to the pattern losses from the fish farms or whether it was due to a sex based variation in habitat use (Figure 3.29). Due to the low number of rainbow trout

Figure 3.27 The monthly distribution of male and female brown trout caught in the littoral zone in 1987.

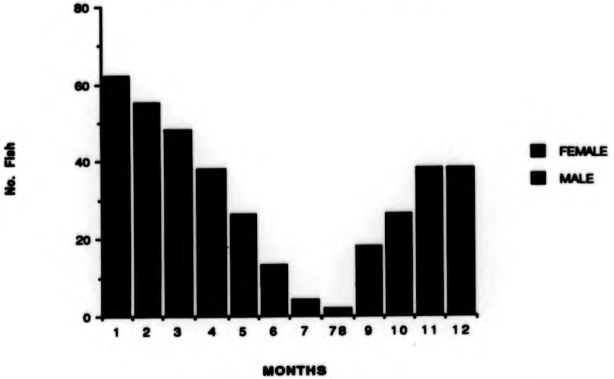


Figure 3.28 The monthly distribution of male and female brown trout caught in the pelagic zone in 1987.

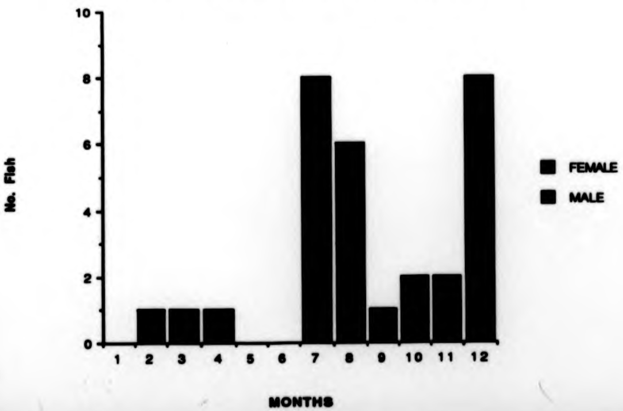


Figure 3.29 The monthly distribution of male and female rainbow trout caught in the littoral zone in 1987.

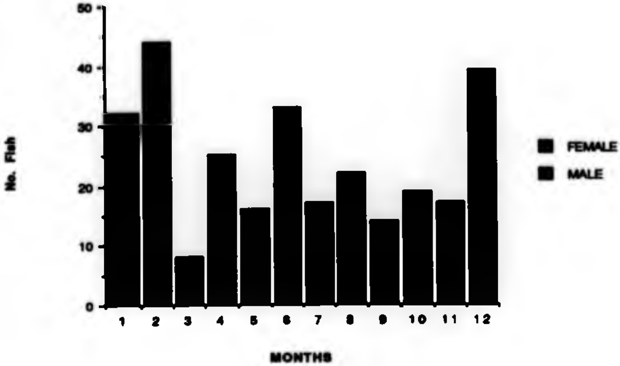
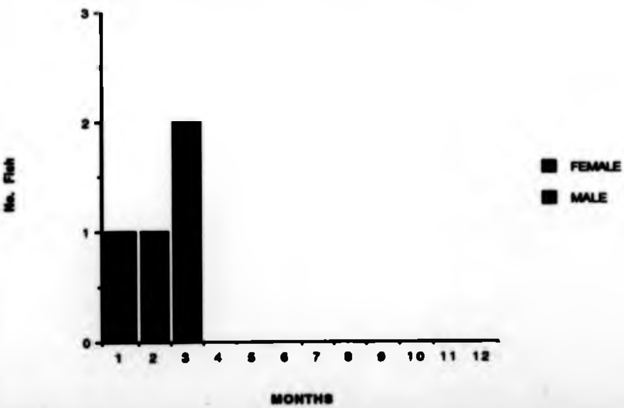


Figure 3.30 The monthly distribution of male and female rainbow trout caught in the pelagic zone in 1987.



caught in pelagic habitat in 1987 no discernable trend was apparent and no statistical analysis was performed (Figure 3.30).

Due to the low catch of male and female benthic charr, pelagic charr, and perch in the littoral and open water habitats in 1987 it was not possible to examine any sex based variation in habitat use (Figures 3.31-3.35).

In 1988 there was a greater catch of male than female brown trout in the littoral zone in May and July, with the opposite being true in March and September (Figure 3.36). The variation in monthly distribution of the two sexes was statistically significant ($P< 0.01$ $X^2=7.1$), similar to that observed in 1987 and is further evidence of a female off-shore summer migration.

In the months sampled in 1988 there was a greater catch of female than male rainbow trout in the littoral zone. In common with brown trout their abundance declined in the summer (Figure 3.37). Due to the low number of males caught in each month no statistical analysis could be performed.

The catch of benthic charr in the littoral zone in 1988 was almost entirely restricted to May, when the sex ratio strongly favoured females (Figure 3.38). Due to the restricted distribution of the catch no statistical analysis was performed.

The low numbers of pelagic Arctic charr and perch caught precluded any meaningful analysis.

Figure 3.31 Monthly distribution of male and female benthic Arctic charr caught in the littoral zone in 1987.

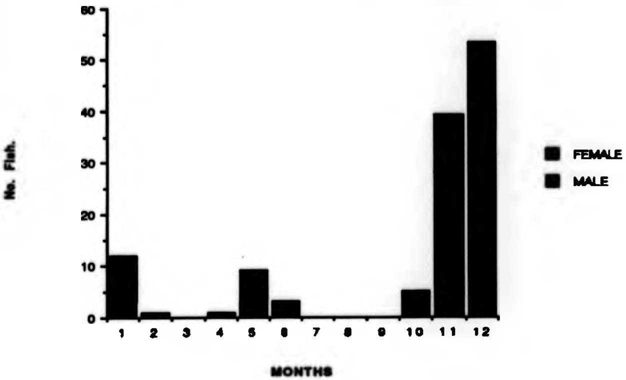


Figure 3.32 The monthly distribution of male and female benthic Arctic charr caught in open water in 1987.

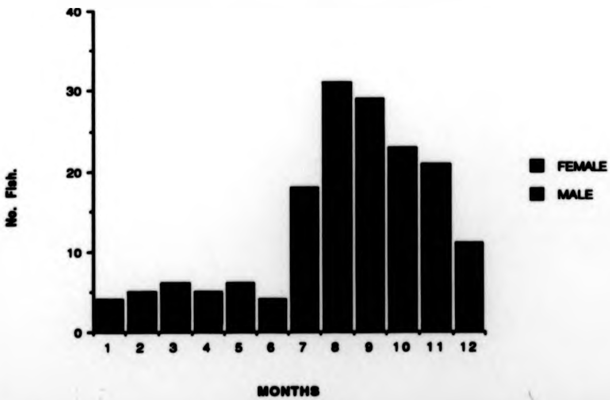


Figure 3.33 The monthly distribution of male and female pelagic Arctic charr in the littoral zone in 1987.

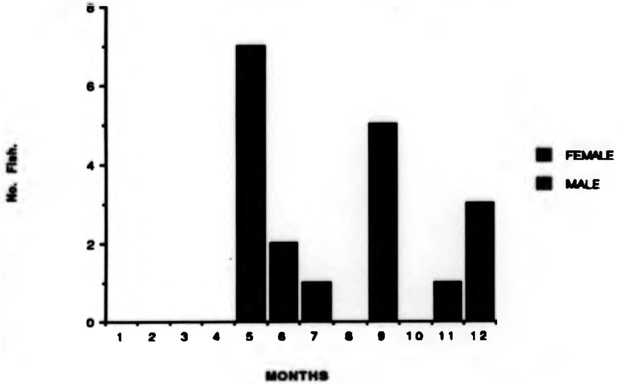


Figure 3.34 The monthly distribution of male and female pelagic Arctic charr caught in open water in 1987.

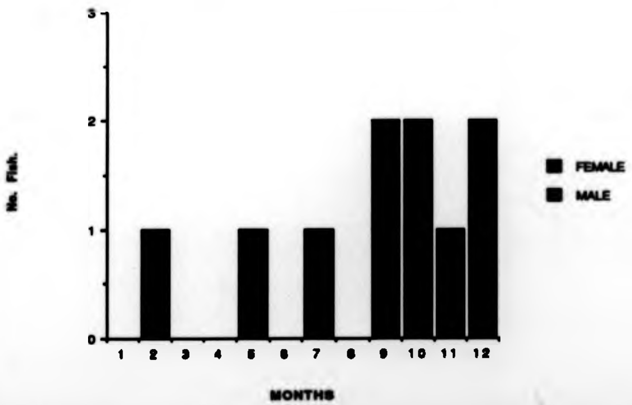


Figure 3.35 The monthly distribution of male and female perch caught in the littoral zone in 1987.

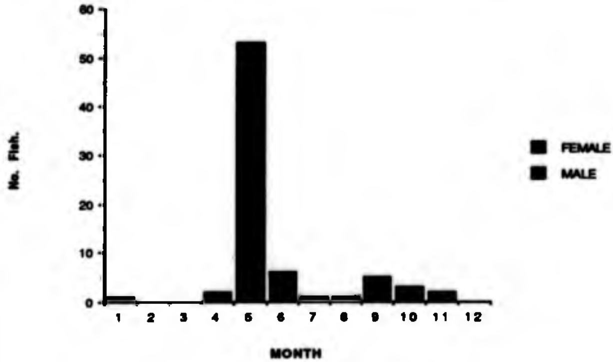


Figure 3.36 The number of male and female brown trout caught in the littoral zone in 1988.

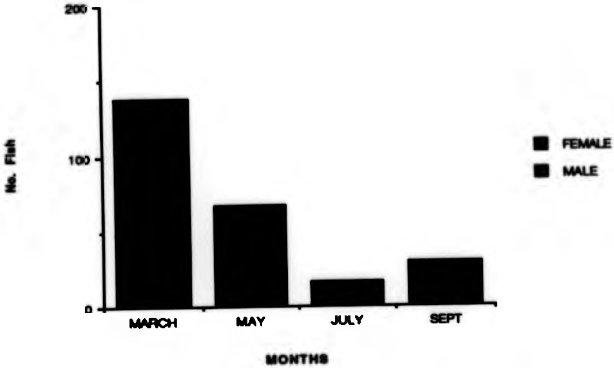


Figure 3.37 The number of male and female rainbow trout caught in the littoral zone in 1988.

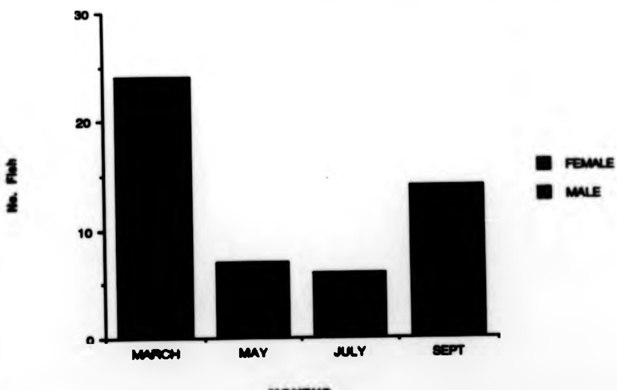
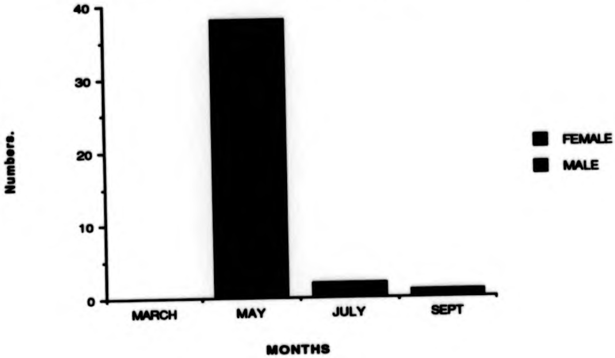


Figure 3.38. The monthly distribution of male and female benthic Arctic charr caught in the littoral zone in 1988.



3.3.10 Sexual maturity.

3.3.10.1 Age of sexual maturity in brown trout and rainbow trout.

In Loch Awe male and female brown trout reach sexual maturity at 2+ and 3+ respectively. In rainbow trout both sexes became sexually mature at 2+. Only 8.4% of the rainbow trout caught during September - December were males, of which only 2.9% were mature. During the same period only 28.8% of the total catch were positively identified as females of which 5.0% were mature. No evidence was found of rainbow trout becoming sexually mature in the spring.

3.3.10.2 Timing of sexually maturity.

In both male and female brown trout visible gonad development started at the end of July (Figure 3.39). The mean gonad weight expressed as a percentage body weight in males increased until August, then fell until November, and increased again in December. In females it increased until October falling in November before increasing in December. The decline after October could be due to the most gravid fish moving into the loch's tributaries to spawn first, leaving the ones with the lower gonad weight in the loch to spawn later.

The quality of the rainbow trout data is affected by the small sample size. However it was still possible to measure an increase in their gonad weight expressed as a percentage of body weight in both sexes in age classes 2+ and 3+ from September - December. As no sexually mature fish were found in the spring, it would suggest that the rainbow trout in Loch Awe are the autumn spawning race (Figure 3.40).

In male and female benthic Arctic charr it increased from mid summer to its maximum in December. In common with the other species the female gonads were heavier than the male (Figure 3.41). Contrary to the findings for brown trout the mean gonad weight of benthic charr did not

Figure 3.39 The mean (+SD) of male and female brown trout gonad weight (g) (GW) expressed as a percentage of body weight (g) (BW) caught by gill net in 1987.

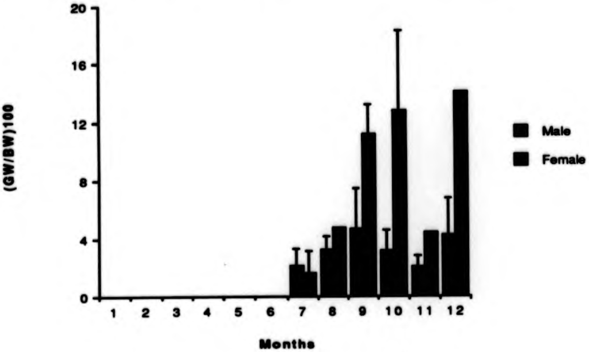


Figure 3.40 The mean (+SD) of male and female rainbow trout gonad weight (g) (GW) expressed as a percentage of body weight (g) (BW) caught by gill net in 1987.

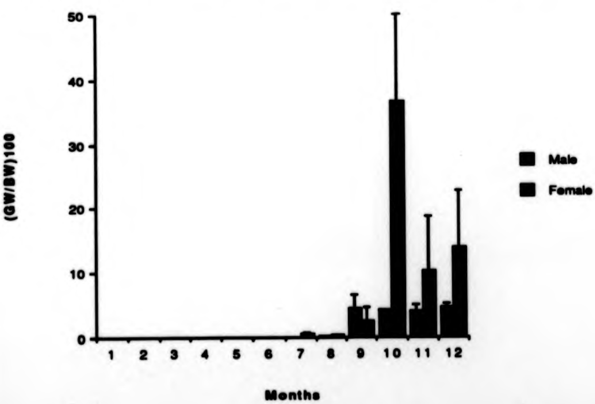


Figure 3.41 The mean (+SD) of male and female benthic Arctic charr gonad weight (g) (GW) expressed as a percentage of body weight (g) (BW) caught by gill net in 1987.

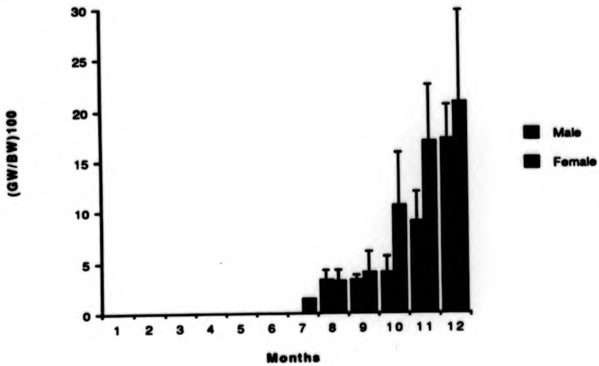
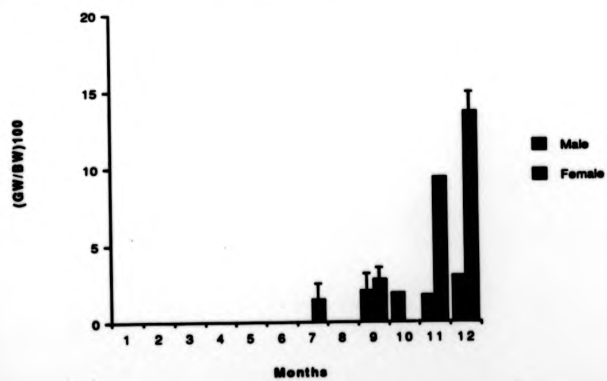


Figure 3.42 The mean (+SD) of male and female pelagic Arctic charr gonad weight (g) (GW) expressed as a percentage of body weight (g) (BW) caught by gill net in 1987.



decline in October or November. The most likely reason for this is that the charr remain in the loch to spawn. The mean gonad weight of male and female pelagic charr increased from July until December (Figure 3.42), it is likely that the data for this morph is again adversely affected by the small sample size. The December spawning behaviour of the two morphs in Loch Awe is different to that reported in charr populations elsewhere in Britain where autumn spawning is the norm (Maitland et al., 1984), except Windermere where a spring spawning population has been reported (Frost, 1965). Arctic charr show marked variation in the timing of their spawning throughout their distribution (Johnson, 1980).

3.3.11 Growth.

3.3.11.1 Annual instantaneous growth rate.

Each year class of brown trout caught in 1987 and 1988 showed the same pattern in the decline of their annual instantaneous growth rate (Figures 3.43 and 3.44). In their first year it was between 95-110 (% $annum^{-1}$), falling to between 50-60 (% $annum^{-1}$) in their second. The small increase or check in the decline that occurred during the third year represents the improved growing conditions that young trout encounter when they enter the loch. After their third year it declined steadily through the remainder of their life. In both 1987 and 1988 the 1+ fish caught in the loch had a higher growth rate than the other year classes. This early migration of the faster growing individuals in the population has also been recorded by Jonsson (1985) and Jonsson & Gravem (1985).

It is shown in Figure 3.45 that the growth of brown trout in Loch Awe compares favourably with those in other Scottish lochs. The range selected is representative of the growth conditions that are available for trout in Scotland.

Figure 3.43 The mean annual instantaneous growth rate (+S.D) of brown trout caught in Loch Awe in 1987 in YC's 1981-86.

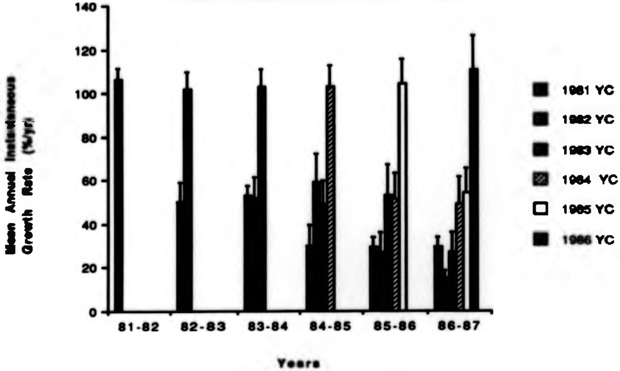


Figure 3.44 The mean annual instantaneous growth rate (+S.D) of brown trout caught in Loch Awe in 1988, YC's 1983-87.

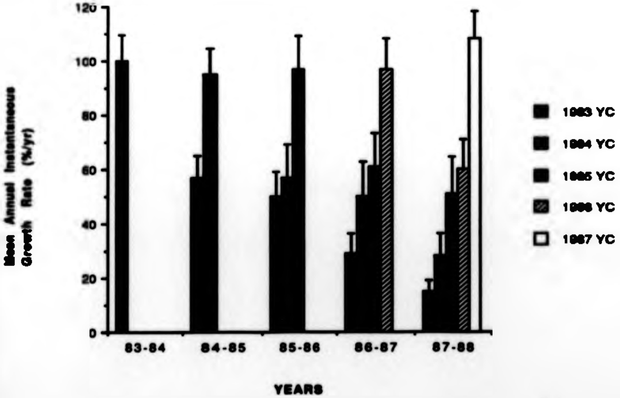
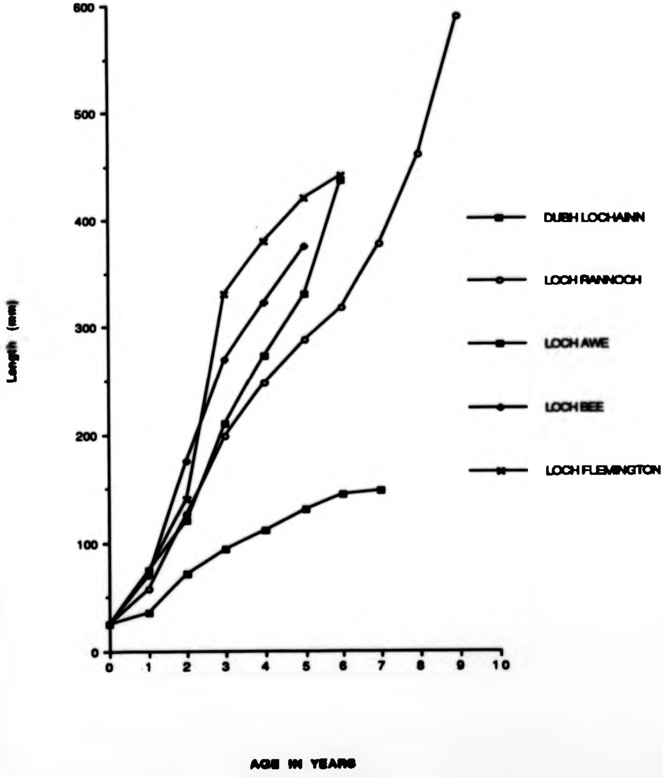


Figure 3.46 A comparison of the back calculated lengths of brown trout from Loch Awe and a selection of other Scottish lochs (Campbell, 1971).



The growth rate of rainbow trout caught in 1987 and 1988 showed a similar pattern to that of brown trout, however the rainbow trout's was considerably higher (Figures 3.46 and 3.47). There are two reasons for this, rainbow trout have spent at least part of their life in a fish farm being fed a high energy diet, and they have a higher innate growth rate than brown trout. This is one of the reasons why they are preferred by the aquaculture industry.

Although rainbow trout have a high growth rate in Loch Awe, it is interesting to note that higher rates have been recorded in the wild in north America. However in the northern part of their range, Lake Babine, their growth is considerably slower (Figure 3.38). Their growth in Loch Awe is very similar that of escapee rainbow trout in Loch Tay.

3.3.11.2 Comparing the growth of brown trout and rainbow trout in the fish farm and littoral habitats.

There was no consistent sex based size difference in brown trout caught in 1987 or 1988 (Tables 3.11 & 3.12). In the 37 comparisons possible males were larger on 19 occasions, two of which were significant ($P<0.05$), females were larger on 17 occasions, and in the other they were the same length.

There was no consistent sex based size advantage in rainbow trout caught in 1987 or 1988. In the 16 comparisons made each sex was larger on eight occasions, and in one instance which favoured the females the difference was significant ($P<0.05$) (Tables 3.13 & 3.14). As there was no consistent sex based size advantage held by either species, the data for male and female trout in each habitat was pooled.

There was no consistent pattern in brown trout growth between the littoral sites at Hayfield, Ballimeanoch and Port Innisherrich

Figure 3.46 The mean annual instantaneous growth rate (+S.D) of rainbow trout caught in Loch Awe in 1987, in YC's 1983-86.

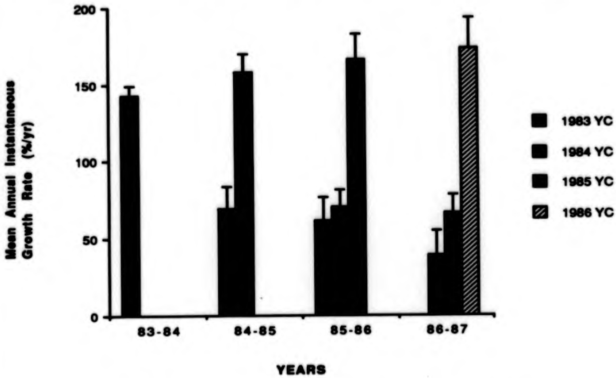


Figure 3.47 The mean annual instantaneous growth rate (+S.D) of rainbow trout caught in Loch Awe in 1988, in YC's 1985-87.

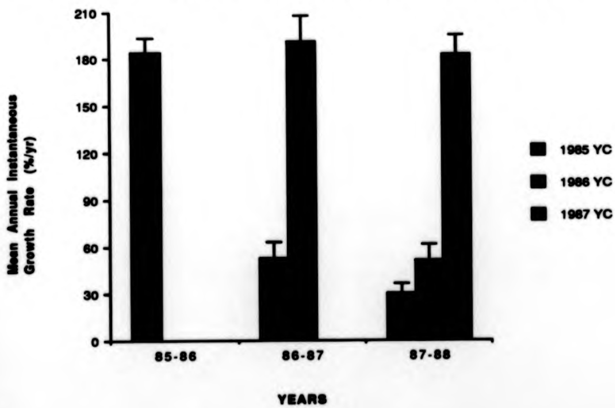


Figure 3.48 A comparison of the back calculated lengths of rainbow trout from Loch Awe (1984 YC), Lake Babine (Beacham & McDonald, 1982), Manistee River, Muskegon River, (Greeley, 1933) and Dee Lagoon (Davies & Sloane, 1986).

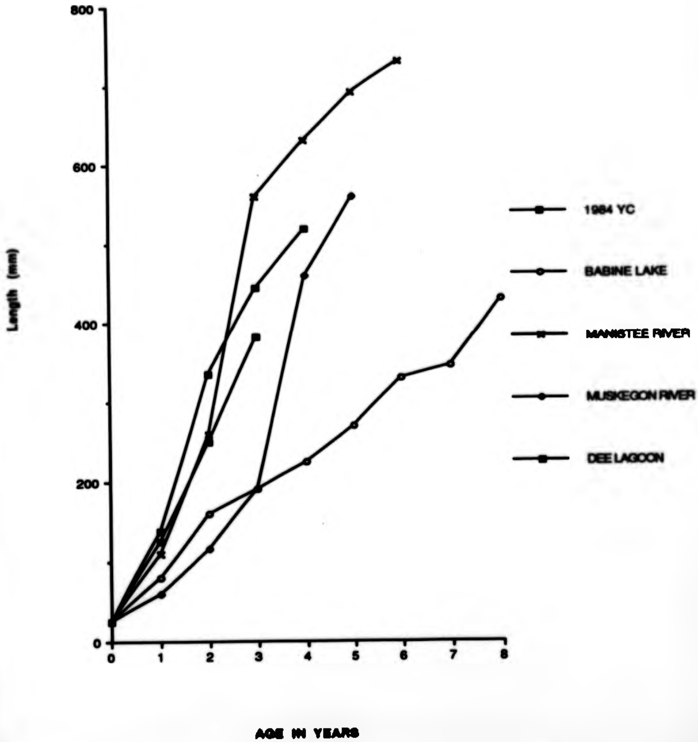


Table 3.11 A comparison of the mean length (mm) of male and female brown trout ages 1+-6+ by the Mann-Whitney test at the time of capture in 1987.

Age	Sex	J/F	M/A	M/J	J/A	S/O	N/D
1+	M	**154**	96	109	107	-	-
	F	147	-	-	-	155	153
	S	N.S					
2+	M	**196**	**196**	**163**	165	171	**213**
	F	173	158	139	**188**	**179**	188
	S	*	*	N.S	N.S	N.S	N.S
3+	M	249	227	**235**	**232**	249	254
	F	249	**228**	222	221	**258**	**255**
	S	N.S	N.S	N.S	N.S	N.S	N.S
4+	M	292	**282**	**305**	**327**	**299**	288
	F	**295**	279	283	255	286	**295**
	S	N.S	N.S	N.S	N.S	N.S	N.S
5+	M	**331**	308	407	315	-	348
	F	312	**328**	**433**	**364**	312	-
	S	N.S	N.S	N.S	N.S		
6+	M	-	-	-	-	-	-
	F	-	483	387	-	505	-

S=Significance, N.S=Not significant, *=P<0.05, M=Male, F=Female

Table 3.12 A comparison of the mean length (mm) of male and female brown trout ages 1+-6+ by the Mann-Whitney test at the time of capture in 1988.

Age	Sex	March	May	July	September
1+	M	-	105	**136**	-
	F	-	**113**	131	150
	S		N.S	N.S	
2+	M	**178**	163	160	**161**
	F	158	**167**	**165**	140
	S	N.S	N.S	N.S	N.S
3+	M	222	221	**227**	224
	F	**226**	**227**	213	**269**
	S	N.S	N.S	N.S	N.S
4+	M	247	257	-	**308**
	F	**264**	**274**	261	295
	S	N.S	N.S		N.S
5+	M	**297**	-	-	325
	F	284	354	-	**365**
	S	N.S			N.S

S=Significance, N.S=Not significant, *=P<0.05, M=Male, F=Female

Table 3.13 A comparison of the mean length (mm) of male and female rainbow trout ages 1+-3+ by the Mann-Whitney test at the time of capture in 1987.

Age	Sex	J/F	M/A	M/J	J/A	S/O	N/D
0+	M	171	-	-	-	-	**181**
	F	**194**	-	181	-	-	170
	S	N.S					N.S
1+	M	260	232	**250**	-	**255**	**336**
	F	**268**	**243**	226	256	238	273
	S	N.S	N.S	N.S		N.S	N.S
2+	M	310	314	281	**335**	328	**367**
	F	**333**	**319**	**296**	317	**386**	362
	S	N.S	N.S	N.S	N.S	*	N.S
3+	M	**574**	-	324	-	-	-
	F	520	421	**425**	-	531	493
	S	N.S		N.S			

S=Significance, N.S=Not significant, *=P<0.05, M=Male, F=Female

Table 3.14 A comparison of the mean length (mm) of male and female rainbow trout ages 1+-3+ by the Mann-Whitney test at the time of capture in 1988.

Age	Sex	March	May	July	September
0+	M	-	-	-	-
	F	157	-	-	-
	S				
1+	M	-	-	-	-
	F	286	236	243	230
	S				
2+	M	-	-	-	313
	F	363	334	291	348
	S				N.S
3+	M	-	-	-	-
	F	435	-	-	412
	S				

S=Significance, N.S=Not significant, *=P<0.05, M=Male, F=Female

(Table 3.15). In the 22 comparisons possible, best growth was achieved on 12 occasions at Ballimeanoch and at Port Innisherrich and Hayfield on 5 occasions each, none of the differences being statistically significant. This test assumes that fish remain in the same area of the loch throughout their life. If trout ranged throughout the whole loch their growth would not be representative of the area in which they were caught, and the need for this analysis would be negated. The findings are inconsistent with the water quality data presented in the previous chapter, which show that the loch's nutrient status increased in a north south direction. This is due to a combination of large differences in the rate of water exchange between the north and south ends, and the slow weathering nutrient poor rocks found in the loch's northern catchment.

The above results allowed data from the littoral sites to be pooled. Due to the small number of rainbow trout caught away from the fish farms the data had to be pooled without testing.

In the limited number of brown trout comparisons possible in 1987 between the two farm sites, best growth was recorded at Tervine in five out of the six comparisons and in the other better growth was achieved at Braevallich. None of the differences were statistically significant (Table 3.16).

In the 17 rainbow trout comparisons possible in 1987 between the two farm sites, best growth was recorded at Braevallich on 14 occasions, 3 of which were significant, 2 at ($P<0.05$) and 1 at ($P<0.01$), and at Tervine on 3 occasions (Table 3.17). It is unlikely that these differences reflect differences in productivity between the two ends of the loch, but are due instead to the sizes at which the fish escaped from the cages.

Table 3.15 **A comparison of the mean length (mm) of brown trout in age classes 1+-5+ caught at Hayfield littoral, Ballimeanoch deep and shallow littoral and Port Innisherrich littoral by the Mann-Whitney test in 1987.**

Age	Site	J/F	M/A	M/J	J/A	S/O	N/D
1+	H	146	90	102	**112**	90	-
	B	**149**	**102**	-	-	-	-
	P	113	-	**116**	73	**98**	-
	S	N.S	N.S	N.S	N.S	N.S	
2+	H	**198**	168	**171**	-	164	210
	B	180	**174**	141	-	**209**	**215**
	P	163	166	-	-	181	187
	S	N.S	N.S	N.S		N.S	N.S
3+	H	245	217	**255**	210	264	254
	B	**249**	**236**	222	-	**266**	252
	P	240	218	211	**234**	263	**269**
	S	N.S	N.S	N.S	N.S	N.S	N.S
4+	H	290	274	265	-	286	288
	B	286	**285**	**271**	-	292	**296**
	P	**298**	278	-	-	**294**	290
	S	N.S	N.S	N.S		N.S	N.S
5+	H	-	**332**	-	-	-	-
	B	-	308	-	-	-	-
	P	-	-	-	-	-	-
	S		N.S				

H=Hayfield, B=Ballimeanoch, P=Port Innisherrich, N.S=Not Significant.

Table 3.16 A comparison of the mean length (mm) of brown trout caught at Braevallich and Tervine in 1987 by the Mann-Whitney test.

Age		J/F	M/A	M/J	J/A	S/O	N/D
1+	T	143	-	117	-	-	-
	B	-	-	-	134	155	174
2+	T	-	-	161	-	-	-
	B	148	182	156	159	156	189
	S			N.S			
3+	T	-	-	234	-	-	-
	B	272	221	229	235	245	232
	S			N.S			
4+	T	312	262	312	-	-	-
	B	293	285	292	-	299	290
	S	N.S	N.S	N.S			
5+	T	-	-	420	-	-	-
	B	311	323	365	-	312	-
	S			N.S			

T=Tervine, B=Braevallich, N.S=Not Significant.

Table 3.17 A comparison of the mean length (mm) of rainbow trout caught at Braevallich and Tervine in 1987 by the Mann-Whitney test.

Age		J/F	M/A	M/J	J/A	S/O	N/D
0+	T	187	-	144	154	126	148
	B	-	157	-	-	143	187
	S					N.S	**
1+	T	245	227	222	263	209	248
	B	268	229	230	228	236	237
	S	*	N.S	N.S	N.S	N.S	N.S
2+	T	304	298	276	298	339	343
	B	360	333	300	329	373	348
	S	N.S	N.S	*	N.S	N.S	N.S
3+	T	521	-	320	-	533	-
	B	547	472	533	430	489	461
	S	N.S		N.S		N.S	

T=Tervine, B=Braevallich, *=P<0.05, **=P<0.01.

As neither species held a growth advantage at Braevallich or Tervine, or in the littoral sites away from the fish farms the data within each was pooled. The growth of the two species at the littoral and fish farm site in 1987 and 1988 was then tested.

In the 23 brown trout comparisons made in 1987 between the fish farm and littoral habitats those caught in the littoral zone were larger on 12 occasions, 2 of which were statistically significant, ($P<0.05$) and ($P<0.01$), and at the fish farms they were larger on 10 occasions, one of which was significant ($P<0.05$). In the remaining one the fish in the two habitats had the same mean length (Tables 3.18). In the 10 comparisons made in 1988 those caught at the fish farms were larger on 6 occasions, one of which was significant ($P<0.01$), at the fish farms they were larger on 4 occasions none of which were significant (Table 3.19).

In the 10 rainbow trout comparisons made in 1987 between the littoral and farm habitats those caught in the littoral habitat were larger on 6 occasions one of which was significant ($P<0.05$), and in the remaining 4 there was better growth at the fish farm habitat, none of which were significant (Tables 3.20 & 3.21). In the 8 comparisons made in 1988, best growth was achieved in each habitat on 4 occasions, none of which were significant.

In conclusion, there was no consistent significant size difference in either species caught in either habitat.

Table 3.18 **A comparison of brown trout mean length (mm) in age classes 1+-6+ caught in the fish farm and littoral habitats in 1987 by the Mann Whitney test.**

Age	Site	J/F	M/A	M/J	J/A	S/O	N/D
1+	FF	143	-	**117**	**136**	**155**	**174**
	L	**145**	96	102	88	95	139
	S	N.S		N.S	N.S	N.S	N.S
2+	FF	148	**196**	154	-	158	194
	L	**182**	172	**164**	206	**185**	**203**
	S	**	N.S	N.S		*	N.S
3+	FF	**272**	221	224	-	245	239
	L	247	**227**	**231**	218	**261**	**260**
	S	*	N.S	N.S		N.S	N.S
4+	FF	**306**	279	**303**	-	**303**	289
	L	290	279	280	328	291	**291**
	S	N.S	N.S	N.S		N.S	N.S
5+	FF	311	**323**	420	-	312	-
	L	**322**	320	-	364	**392**	348
	S	N.S	N.S			N.S	
6+	FF	-	-	-	-	-	-
	L	-	-	387	-	505	-

FF=Fish farms, L= Littoral, N.S=Not Significant, *=P<0.05, **=P<0.01

Table 3.19 **A comparison brown trout mean length (mm) in age classes 1+-5+ caught in the fish farm and littoral habitats in 1988 by the Mann Whitney test.**

Age	Site	March	May	July	September
1+	FF	-	-	**132**	-
	L	100	104	131	147
	S			N.S	
2+	FF	154	160	**159**	147
	L	**161**	**163**	157	**154**
	S	N.S	N.S	N.S	N.S
3+	FF	-	**239**	**235**	-
	L	222	217	213	255
	S		N.S	N.S	
4+	FF	**283**	**296**	-	292
	L	257	253	261	**301**
	S	N.S	**		N.S
5+	FF	-	365	-	-
	L	290	-	-	355

FF=Fish farms, L= Littoral, N.S=Not Significant, *=P<0.05, **=P<0.01

Table 3.20 A comparison of the mean length (mm) of rainbow trout in age classes 0+-3+ caught in the fish farm and littoral habitats in 1987 by the Mann whitney test.

Age	Site	J/F	M/A	M/J	J/A	S/O	N/D
0+	FF	187	-	144	154	128	155
	L	-	-	-	-	-	-
1+	FF	255	**229**	224	250	220	248
	L	**272**	207	-	**273**	-	**305**
	S	N.S	N.S		N.S		*
2+	FF	**323**	307	286	**328**	356	357
	L	320	**316**	-	321	**405**	**384**
	S	N.S	N.S		N.S	N.S	N.S
3+	FF	534	**477**	391	430	504	493
	L	-	312	-	-	-	-
	S		N.S				

FF=Fish Farm, L=Littoral, N.S=Not Significant, *=P<0.05

Table 3.21 A comparison of the mean length (mm) of rainbow trout in age classes 0+-3+ caught in the fish farm and littoral habitats in 1988 by the Mann whitney test.

Age	Site	March	May	July	September
0+	FF	157	-	-	-
	L	-	-	-	-
1+	FF	**222**	209	**199**	230
	L	194	**227**	150	-
	S	N.S	N.S	N.S	
2+	FF	**368**	327	292	354
	L	340	**364**	**327**	**357**
	S	N.S	N.S	N.S	N.S
3+	FF	464	-	-	-
	L	-			

FF=Fish Farm, L=Littoral, N.S=Not Significant

3.4 Discussion.

3.4.1 Distribution.

3.4.1.1 Brown trout.

The seasonal variation in habitat use shown by brown trout in Loch Awe, at and away from the fish farms was similar to that reported in other large nutrient poor lakes of glacial origin where rainbow trout are not found (Dahl, 1917; Allen, 1938; Ball & Jones, 1961; Svardson, 1976; Haraldstad & Jonsson, 1984; Jonsson & Gravem, 1985; Jonsson, 1989; Hegge et al., 1989). The brown trout overwinter in the littoral zone and in the late spring start to move offshore assuming a pelagic existence during the summer. There is a surplus of older female fish involved in this migration. In Loch Awe this was demonstrated by examining the pattern of summer catches in the pelagic zone and noting the surplus of male and younger fish in the littoral zone at this time. During the summer juvenile brown trout move from the nursery streams into the loch and in the autumn the pelagic migrants move back onshore in preparation for their spawning migration into the loch's tributaries in November and December. Also at this time there was a small increase in the catch of adult and juvenile brown trout at the pelagic sites, but the reasons for this are unclear.

It is likely that the winter and summer gill net catches of brown trout in the littoral zone were respectively under and overestimated. This is due to seasonal variations in water temperature and its effect on fish activity. In the winter when it is low fish activity is low and in the summer when it increases fish activity increases (Swift, 1962). As gill nets sample fish populations passively the likelihood of fish capture increases with fish activity, therefore as water temperature increases the probability of capture will increase.

Intraspecific segregation of food and habitat by size/age occurs to minimise competition (Keast, 1977; Werner, 1977; Mittlebach, 1981) and occurs when resources become limiting (Nilsson, 1967; Pyke et al., 1977; and Werner et al., 1981). The intraspecific segregation by age/size found in Loch Awe was also reported in brown trout by Haraldstad & Jonsson (1984), Gravem & Jonsson (1985) and Jonsson (1989). Similar findings have been described in bluegill sunfish by Mittlebach (1981) and Werner et al. (1983).

Small juvenile fish find more cover and visual isolation in the heterogeneous environment found in the littoral zone (Stuart, 1953). Larger fish with fewer predators are free to move offshore exploiting the zooplankton, pelagic pupae and terrestrial insects that are trapped on the water surface. Jonsson & Haraldstad (1984) and Gravem & Jonsson (1985) explained sexual segregation in terms of foraging profitability. Reproductive success in female brown trout increases exponentially with size. As small opportunist male parr have been shown to successfully fertilise female eggs even in the presence of a large dominant male there is no size selective pressure on them. Therefore it is females that have to maximise their foraging net energy gain by moving to the areas of greatest foraging profitability, like the open water in the summer (Hindar & Jonsson, 1982; Haraldstad & Jonsson, 1983 and Jonsson & Gravem, 1985). Although sexual maturity occurred earlier in male brown trout, and habitat segregation by sex occurred in Loch Awe, no difference in male and female growth was observed. Jonsson (1989) demonstrated there could also be a genetic component controlling the migration of brown trout in lakes.

3.4.1.2 Rainbow trout.

In Loch Awe rainbow trout were caught in greatest numbers around the fish farms, and were only present in small numbers away from them. At the farm sites the catch of rainbow trout declined over the summer in a similar manner to that described in brown trout, however it was not possible to determine the influence of seasonal variation in habitat use, and stock losses from the farms in this observation. There low catch in the littoral habitat away from the fish farms precluded any analysis. Allopatric populations of rainbow trout elsewhere show a preference for pelagic feeding during the summer (Rowe, 1984). May (1973) demonstrated that their distribution in the pelagic habitat was limited by the 21°C isotherm and as it is unlikely that such temperatures would occur in Britain it is clear that rainbow trout could feed freely in the surface waters of Loch Awe. Evidence of this is seen in the rainbow trout's quicker use of surface prey when it becomes available in the late spring. (See Chapter 4 for a full discussion of the rainbow trout's dietary habits).

As with brown trout it is likely that the winter and summer catches of rainbow trout in the littoral zone would have been under and overestimated respectively.

No attempt was made to assess the genetic fitness of rainbow trout in Loch Awe. However it is highly likely that in common with domesticated rainbow trout elsewhere that the inbreeding associated with hatchery programmes has reduced their genetic base (Donaldson & Olson, 1957; Kincaid, 1976 & 1983; Klupp et al., 1973). It is also likely that as with salmonids elsewhere such breeding programmes have diminished their success in the wild (Brauhn & Kincaid, 1982; Dwyer & Piper, 1984; Flick & Webster, 1964 & 1976) and possibly even reduced their ability to breed.

3.4.1.3 Arctic Charr.

The two distinct ecological morphs of Arctic charr described by Walker et al. (1988) and Gardner et al. (1988) in Loch Rannoch were also found in Loch Awe. Electrophoretic analysis demonstrated that the benthic morph in Loch Awe were genetically similar to those found in Loch Rannoch, but that the pelagic morph were quite different (S. Hartley pers. comm.). Only a small number of the pelagic morph were caught, and it was not possible to discern any seasonal pattern in their movements. The benthic morph as its name suggests was caught most consistently in the benthic sites, although they were also caught at the littoral sites particularly in November and December; this coincided with the period of their highest mean gonad weight. Exploratory gill netting in December 1986 revealed a very high number of benthic charr in spawning condition on the bottom in 10-20 m of water. A similar pattern of behaviour was described by Walker et al. (1988). However, contrary to their findings, this gathering did not occur adjacent to running water and occurred slightly later in the year. Further evidence for this preference for the deeper littoral zone at this time is seen in the higher numbers of benthic charr caught at the deep compared to shallow littoral sites. The only exception to this occurred at the shallow littoral site at Hayfield where 17 were caught in November. The predominance of males in the littoral sample at this time, and of females in the benthic sample agrees with the findings of Johnson (1980), who suggested that this could be due to the males staying longer in the vicinity of the redds.

As with brown trout it is likely that the winter and summer catches of Arctic charr at the littoral and pelagic sites would have been under and overestimated respectively. It is unlikely that such an effect would have occurred at the benthic sites as the temperature does not show the same level of seasonal variation in the deeper water (Table 2.2).

3.4.1.4 Perch.

The seasonal distribution of perch in Loch Awe is similar to that described by Allen (1935) and Craig (1977) in Windermere and by Giles & Tippet (1987) in Loch Lomond, where perch moved from their deep water winter habitat into the shallow littoral zone in the late spring. Giles & Tippet (1987) demonstrated that their migration into shallow water coincided with the period of maximum day length, and suggested that it was under photoperiod control. Perch are also sexually mature at this time, spawning on vegetation in the shallow littoral zone. The small number of perch caught at the deep littoral sites is evidence that their vertical distribution at this time is very restricted. The incomplete migration away from the littoral zone in the autumn, presumably to deeper water described by Craig (1977), was also found in the present study with a few individuals being caught at the littoral sites between the autumn and December. As with brown trout it is likely that the winter and summer catches of perch in the littoral zone would have been under and overestimated respectively.

3.4.2 Interaction between rainbow trout and the native fish species.

3.4.2.1 Brown trout.

The present study suggests that rainbow trout only have an adverse effect on the distribution of brown trout when the rainbow trout :brown trout ratio is very high. At the two fish farms in 1987 the mean monthly catch of rainbow trout was significantly higher than the catch of brown trout, with more being caught at Tervine than at Braevallich. There was no significant difference in the mean monthly catch of brown trout between Braevallich and the other littoral sites, however at Tervine significantly fewer brown trout were caught than at the other littoral sites. There are two possible explanations: it could be due to the rainbow trout actively excluding the brown trout from around Tervine, or it could be due to there only having been small numbers of brown trout around Tervine prior to the fish farm being established. Evidence collected in April 1989 supports the former hypothesis. In the gill netting survey performed to assess the impact of the large escape of rainbow trout in February 1989 a mean catch of 7.33 brown trout was obtained at three sites within 600m to the east of Tervine. As this was only slightly lower than the mean catch at the littoral sites in April 1987 of 10.67, it is concluded that the rainbow trout excluded brown trout from the immediate vicinity of fish farms when the rainbow trout :brown trout ratio is high.

In the 1988 survey the mean monthly catch of brown trout at Braevallich exceeded that of rainbow trout, although the difference was not significant. More brown trout were caught in the littoral zone than at Braevallich, but the difference was not significant. The reduction in the catch of rainbow trout between 1987 and 1988 at Braevallich coincided with the site being run more efficiently. Farm records indicated that feed conversion rates improved over this period, which would result in less uneaten pellets passing through the cages. This in turn could make the fish farm a less attractive feeding station for the escaped rainbow trout and result in them feeding elsewhere.

At the littoral sites away from the fish farms rainbow trout were only caught in small numbers. The difference was statistically significant in both 1987 and 1988. The highly localised nature of their distribution was most apparent in 1988, when all of the littoral sites were within 600m of the fish farm.

Phillips (1982) demonstrated that up to 90% of the rainbow trout stocked into a loch were attracted at times to within 11m of a feeding station. This attraction of fish to cages was also noted by Collins (1971), Loycano & Smith (1976), Kilambi et al. (1978) Hays (1980), and

Phillips et al. (1985). Contrary to their findings this attraction did not extend to Loch Awe's native species. A partial explanation of this is their low utilisation of the uneaten fish farm pellets that pass through the cages (see Chapter 4 for a full discussion of this subject).

Therefore in Loch Awe it would appear that moderately large losses of rainbow trout from the fish farms can be absorbed without adversely affecting the distribution of brown trout. It is only when the rainbow trout :brown trout ratio rises above a high but undefined threshold that it is affected.

3.4.2.2 Arctic Charr.

No evidence was found to suggest that the distribution of the two charr morphs was being adversely affected by the presence of rainbow trout in Loch Awe. However, if the number of rainbow trout increased significantly during a large escape it is likely that the pelagic form would suffer more than the benthic one as they would share the pelagic habitat with the rainbow trout in the summer. It is unlikely that the benthic form would be affected due to the niche segregation that exists between them and rainbow trout.

3.4.2.3 Perch.

It is unlikely that the rainbow trout at their present level are having an adverse effect on the distribution of perch in Loch Awe. This is due to them utilising different habitats throughout the year.

3.4.3 Sexual maturity.

Loch Awe's indigenous salmonids are all autumn spawners, although the introduced rainbow trout can spawn in the autumn or the spring. The gill netting survey revealed that rainbow trout matured in the autumn (a condition thought to have been developed through hatchery breeding programmes) but found no evidence of successful spawning. This is most likely explained by the very small numbers of sexually mature male and female rainbow trout found by the survey. The low survival of their sperm in acid waters has also been implicated by Seamans & McMartin (1962) in their lack of success in establishing self-sustaining populations outside their home range. So long as the fish farmers on Loch Awe continue to use all female or triploid stock, the chances of a self-sustaining rainbow trout population being established will remain at its current low level. However if rainbow trout were to start spawning and their progeny survived it is possible that with their faster growth rate they could adversely affect Loch Awe's indigenous species.

3.4.4 Growth.

The growth of brown trout in Loch Awe is comparable with that from other Scottish freshwater lochs of a similar nutrient status as reported by Campbell (1971). Typically their mean annual instantaneous growth rate is high during the first year, and declines throughout the remainder of their life. When the young fish enter the loch there is a check in the decline of their mean annual instantaneous growth rate (Figures 3.43 & 3.44). There was no discernable reduction in the growth rate of rainbow trout after they had escaped from the cages, in agreement with the findings of Phillips (1982). After escaping many rainbow trout remain near the cages and feed heavily on uneaten pellets that pass through them. Beveridge (1984) estimated that 5-30% of the pellets fed to fish can pass through the cages uneaten. When the growth of feral rainbow trout in Loch Awe is compared with their growth in north America it is seen to be similar to the high levels recorded in some waters. There are two principal reasons for this. The stock used in fish farms are selected for a fast growth rate, and they have been fed a high protein diet to satiation throughout their lives. It is also evident that the domesticated stock die at an earlier age than those in wild populations. In the present study no rainbow trout older than 3+ were found, whereas elsewhere fish aged 7+ and older are caught. The shorter life expectancy in Loch Awe's rainbow trout maybe due to the selective breeding programmes in the aquaculture industry.

Fish farming has the potential to increase the nutrient status of a water body (Phillips et al., 1985). The nutrient loading comes in the form of excreta, egesta, mucus, scales, mortalities and uneaten pellets (Beveridge, 1984). Kilambi et al. (1978), Forbes (1981) and Phillips et al. (1985) have all reported that increased nutrient loading from fish farming has resulted in increased fish growth. While Munro (1961), Mills (1985) and Hyatt & Stockner (1985) recorded a similar response in brown trout, coregonid and Pacific salmon growth simply by adding fertilisers to lakes as a fishery management tool to boost productivity. In the case of fish farming growth of native fish can also be improved by direct feeding on the uneaten pellets. Evidence of this behaviour has been recorded in brown trout by Phillips (1982) and De Rocha & Mills (1984), and to a limited extent in the present study, but in this case without any effect on growth; and in rainbow trout by Forbes (1981), Phillips (1982), and Flores-Nava (1983); and again in the present study.

It is not possible to compare the present water quality and fish growth in the loch, with that prior to the start of fish farming in 1968. However it is possible to determine if there is any difference in fish growth at and away from the fish cages. Neither brown trout nor rainbow trout showed a consistent growth advantage or disadvantage at or away from the cages. Suggesting that the differences in water quality were insufficient to improve fish growth. The lack of a consistent difference in either species growth in the two habitats also confirms that the high rainbow trout :brown trout ratio at the cages has no adverse effect on brown trout growth; and that the low rainbow trout :brown trout ratio in the littoral zone has no adverse effect on rainbow trout growth.

Further evidence of this is seen when the growth rate of brown trout is compared between Tervine and Braevallich. If rainbow trout were having a serious effect on the brown trout's growth one would expect it to be most apparent at Tervine where the rainbow trout :brown trout ratio is considerably higher than it is elsewhere in the loch. However the results show that in 5 of the 6 comparisons possible better growth was recorded at Tervine, although none of the differences were significant. This is further evidence that fish growth is not affected by the spatial variation in water quality. The loch's nutrient status increases in a NE-SW direction, but no consistent difference was seen in brown trout growth between Hayfield, Ballimeanoch and Port Innisherrich. There are two possible explanations for this anomaly. Either the spatial differences in nutrient status are insufficient to stimulate fish growth; or contrary to the findings of Tytler & Holliday (1984) brown trout do not maintain a station and remain in that area, but instead move throughout the whole loch. They would therefore be unlikely to reflect the spatial variations in nutrient loading in their growth. As the study did not include any tagging studies it is not possible to comment further on the latter possibility. The significant difference recorded in brown trout growth in Loch Charn (Phillips et al., 1985) was due to a 15 fold increase in the dissolved reactive phosphorus concentration (the limiting factor in production in most Scottish freshwater lochs) after the start of fish farming. In Loch Awe, the difference in the dissolved reactive phosphorus concentration between the north and south ends was only 1-3 mg\l. It is therefore unlikely that this would produce a detectable difference in fish growth.

3.4.5 Roach.

One roach was caught during a preliminary netting survey in September 1986 in a bay just to the south of Hayfield at NGR NN 073 230, and there was also some anecdotal evidence that they had been caught by anglers in small numbers in 1987 and 1988. This is a concern as it has demonstrated in Ireland by Fitzmaurice (1981) that they can expand their range rapidly, due to their very high rate of fecundity (Mann, 1973). Roach generally feed on detritus, but they have also been shown to have prey in common with brown trout. In some Irish lochs they are caught on a regular basis by fly fishermen, and as such are considered a great nuisance (Fahy, 1989). At present they are only a potential threat to the brown trout fishery on Loch Awe, but if they were to realise their full breeding potential, it is possible that they could pose a real threat to trout fishing on the loch. It is generally accepted that such introductions of coarse fish arise from pike anglers disposing of live bait at the end of their day's fishing.

To summarise, the distribution of rainbow trout in Loch Awe was highly localised with large numbers only being caught around the fish farms. It was only around the farm at Tervine that their density exceeded the high but unquantified threshold, that caused the distribution of the brown trout to be affected. There was no evidence of the other species distribution being affected, and on a few of occasions there was evidence that the cages may even act as an attractant for benthic Arctic charr and perch, but no mechanism could be found to explain this behaviour. Roach were recorded in the loch for the first time.

Sexually mature rainbow trout were only found in the autumn, with only

2.9% of the males and 5.0% of females caught in 1987 being in this condition.

The growth of brown trout was comparable with that from other large Scottish freshwater lochs; and the growth of rainbow trout was similar to that recorded in some north American waters, and higher than the brown trout in the loch. Neither species had a consistent growth advantage at or away from the fish farms. Rainbow trout in Loch Awe had a shorter life expectancy than is normally found in wild populations.

CHAPTER 4

DIETARY ANALYSIS OF THE FISH SPECIES IN LOCH AWE

4.1 Introduction

An organism requires the use of a set of resources in order to survive. In an established community the species show a degree of niche divergence, this variation in resource utilisation facilitates their co-existence. The relationship that exists between species is dynamic, changing throughout their life cycle. It has been shown mathematically and demonstrated in nature (Brian, 1956) that two organisms cannot continue to utilise an essential common resources that is in limited supply. This situation results in either one of the species being excluded from the habitat, or one of them utilising another resource, an idea fully discussed by Nilsson (1967) who outlined such a relationship between Arctic charr and brown trout (Nilsson, 1955; 1960; 1963; 1965).

This phenomenon is most readily observed in fish in their feeding relationships with other species. Such feeding niche divergence has been widely reported between fish species e.g. cutthroat trout *Oncorhynchus clarkii* (Richardson) and bull trout *Salvelinus malma* (Walbaum) by Andrusak & Northcote (1971), Schutz & Northcote (1972), and Hindar *et al*. (1988); rainbow trout and cutthroat trout by Nilsson & Northcote (1981); blue gill sunfish, pumpkinseed sunfish *Lepomis gibbosus* (L.) and green sunfish *Lepomis cyanellus* Rafinesque by Werner & Hall (1976).

If an exotic species is released into a habitat the effect on the established feeding relationships can be profound. In the present study the feeding behaviour of the major fish species in Loch Awe after the introduction of rainbow trout is examined, with particular attention being placed on its impact on brown trout.

4.2 Methods

4.2.1 Fish used in the study.

Fish collected in the 1987 and 1988 gill netting surveys, and from the 1987 angling competitions were used in the study. The 1987 gill netting data was pooled into consecutive two monthly periods, and the 1987 angling competition data and the 1988 gill netting data was assessed on a monthly basis. The habitat descriptions, and the number of fish caught in each one are given in Tables 4.1-4.5.

4.2.2 Fish processing.

The alimentary tract from the oesophagus to the constriction just before the pyloric caecae was used in the analysis. It was removed shortly after the catch was landed and stored in 10% formalin. The stomach contents were dissected from the stomachs and analysed in the laboratory using a dissection and compound microscope, with identification of the prey being made to species where possible. For each stomach the presence or absence of food, the stomach fullness index (Ball, 1961; see Table 4.6) and the volume of food was recorded.

Distended stomachs containing no food were also recorded. According to Treasurer (1988) this state is characteristic of the stomach after regurgitation. Although his work was based on perch and pike the same phenomenon was observed in salmonids in the present study, and was therefore used to measure the occurrence of regurgitation.

4.2.3 Variation in diet composition.

In 1987 the stomachs of all fish caught were examined, and in 1988 a maximum of ten brown trout and rainbow trout were examined from each site.

The diet composition of each species in each sampling period in each

Table 4.1 The fish farm, littoral, pelagic, and benthic sites sampled in the 1987 gill netting survey.

Habitat	Description	Sites
Fish Farm	Littoral areas at the fish farms.	Tervine, Braevallich
Littoral	Littoral areas away from fish farms.	Hayfield littoral, Coillaig shallow and deep littoral, Ballimeanoch shallow and deep littoral, Port Innisherrich littoral.
Pelagic	Surface water away from the littoral zone.	Hayfield pelagic, Port Innisherrich pelagic.
Benthic	Benthic areas in >40m of water.	Hayfield benthic, Port Innisherrich benthic.

Table 4.2 The total number, the number of empty, and the number of stomachs containing food sampled in 1987, split into species, habitat and the consecutive two month periods in which they were caught.

Habitat	Species	No	Two Month Period J/F	M/A	M/J	J/A	S/O	N/D
FF	RT	T	89	37	75	41	72	103
		E	38	6	25	12	18	26
		F	51	31	50	29	54	77
	BT	T	19	19	27	-	13	6
		E	8	6	6	-	7	2
		F	11	13	21	-	6	4
	PE	T	-	-	16	28	5	-
		E	-	-	0	7	2	-
		F	-	-	16	21	3	-
	BC	T	5	-	-	-	-	2
		E	2	-	-	-	-	1
		F	3	-	-	-	-	1
	PC	T	-	-	-	1	2	-
		E	-	-	-	0	1	-
		F	-	-	-	1	1	-
	S	T	-	-	-	7	5	4
		E	-	-	-	3	1	2
		F	-	-	-	4	4	2
L	RT	T	17	16	-	5	5	11
		E	4	4	-	0	1	4
		F	13	12	-	5	4	7
	BT	T	108	78	16	9	35	64
		E	35	11	2	0	1	4
		F	73	67	14	9	25	28
	PE	T	-	-	19	50	31	-
		E	-	-	3	7	2	-
		F	-	-	16	43	29	-
	BC	T	11	-	2	-	4	74
		E	2	-	2	-	3	71
		F	8	-	0	-	1	3

Table 4.2 continued.

Habitat	Species	No.	J/F	M/A	M/J	J/A	S/O	N/D
	PC	T	-	-	3	-	1	-
		E	-	-	0	-	0	-
		F	-	-	3	-	1	-
	S	T	-	-	-	-	-	4
		E	-	-	-	-	-	2
		F	-	-	-	-	-	2
P	RT	T	2	1	-	-	1	-
		E	2	0	-	-	1	-
		F	0	1	-	-	0	-
	BT	T	1	-	-	14	3	8
		E	1	-	-	3	1	6
		F	0	-	-	11	2	2
	BC	T	-	-	2	8	2	3
		E	-	-	0	4	1	2
		F	-	-	2	4	1	1
	PC	T	1	-	1	-	2	2
		E	1	-	0	-	1	2
		F	0	-	1	-	1	0
B	BC	T	12	14	8	44	50	29
		E	2	1	1	9	18	22
		F	10	13	9	35	32	7

(Column heading: Two Month Period)

FF=Fish farm, L=Littoral, P=Pelagic, B=Benthic, RT=Rainbow trout, BT=Brown trout, P=Perch, BC=Benthic charr, PC=Pelagic charr, S=Salmon, T=Total, E=Empty, F=Contains food

Table 4.3 The total number, the number of empty, and the number of stomachs containing food in the sample of rod caught brown and rainbow trout in the angling competitions in April, May and June 1987.

		April	May	June
Brown trout	T	23	67	6
	E	0	2	0
	F	23	65	6
Rainbow trout	T	8	19	9
	E	0	3	0
	F	8	16	9

Table 4.4 The fish farm and littoral sites sampled in 1988.

Habitat	Description	Sites
Fish farm	Littoral area at Braevallich.	Braevallich
Littoral	Littoral area away from Braevallich	N2, N3, N4, N5 and N6

Table 4.5 The total number, the number of empty, and the number of stomachs containing food sampled in 1988, split into species, habitat and their month of capture.

Habitat	Species	No	March	May	July	September
FF	RT	T	6	5	9	10
		E	1	1	1	3
		F	5	4	8	7
	BT	T	3	10	8	2
		E	0	1	1	1
		F	3	9	7	1
L	RT	T	9	3	4	7
		E	0	0	2	0
		F	9	3	2	7
	BT	T	62	45	28	32
		E	6	10	0	16
		F	56	35	28	16

FF=Fish farm, L=Littoral, RT=Rainbow trout,
BT=Brown trout, T=Total, E=Empty, F=Contains food

Table 4.6 The Fullness Index used in the diet analysis. Ball(1961).

State of Stomach	Points
Empty	0
1/4 Full	1
1/2 Full	2
3/4 Full	3
Full	4
Distended	5

habitat was expressed as percentage occurrence, percentage number and percentage volume. It was necessary to use all three to avoid the conceptual inadequacies that each on their own suffers which can bias the results (Hyslop, 1980). The occurrence of each prey item was expressed as a percentage of the stomachs examined and the volume and numbers as a percentage of their respective totals.

Volumes were measured by the displacement of water in a series of measuring cylinders (5ml - 1 litre). Smaller prey items were measured in 1 and 2ml syringes. The volumes used in the analysis are those measured from the stomachs and do not represent any reconstructions from partially digested prey. Before being measured each item (where possible) was dried on a tissue paper to remove surface moisture. The data is described to the species level, and in the following broader prey categories: Mollusca, Peracarida, aquatic insects, pelagic pupae, zooplankton, fish, aerial insects, fish farm pellets, ground bait and miscellaneous. The ground bait category included maggots, sweet corn and large earth worms, obviously of terrestrial origin, which are thrown into the water by anglers to attract fish. The miscellaneous category included vegetation, stones, cigarette filters and fish eggs.

Overlap in the diets of brown trout and rainbow trout caught at the fish farm and littoral habitats in each of the data sets was assessed by calculating Schoener's (1970) overlap index. The calculation was based on percent volume of the broader prey categories described above.

$$\alpha = 1 - 0.5 (n \sum |pxi - pyi|)$$

where,

pxi = proportion of species i in the diet of species x,

pyi = proportion of species i in the diet of species y,

and n = number of food categories.

Schoener's index was used in preference to others available, as reviews by Wallace (1981) and Linton et al. (1981) demonstrated that it suffers from less inadequacies than others that are available. In particular Linton et al. (1981) demonstrated that Schoener's Index estimated overlap most adequately over the majority of the potential range.

In the diet analysis the excessive contribution of some large prey items would have been reduced had the average volume percentage been calculated, however familiarity with the data set as it was calculated prevented the bias that such items introduced being misinterpreted.

4.2.4 Food availability.

In 1987 it had been intended to assess food availability in the loch, however pilot studies on the littoral benthos and zooplankton demonstrated that too many samples would have to be collected in order to provide representative samples. The sampling intensity required for each species was assessed using the formula described by (Elliott, 1977):

where,

$$n = \frac{s^2}{D^2 . x^2}$$

n = required number of samples,

s^2 = variance,

D = ratio of standard error to the mean,

and, x = mean.

In the above D=0.2 (20%)

The results for littoral invertebrates and zooplankton are given in Tables 4.7 & 4.8 respectively.

Samples were collected as it was thought that they would provide useful

Table 4.7 The number of samples required to be collected at Ballimeanoch and Port Innisherrich in February 1987 in order to obtain a representative sample of the species listed below, assuming an allowable error of 20%.

Species	Ballimeanoch	Port Innisherrich
Asellus aquaticus	57	-
Physa fontinalis	33	33
Gammarus lacustris	41	-
Lymnaea peregra	100	17
Ancylus fluviatilis	82	5
Ecdyonurus dispar	-	11
Lepidostoma hirtum	-	33

Table 4.8 The number of zooplankton samples required at Hayfield Littoral and Port Innisherrich Littoral in March 1987 to obtain a representative sample of the species listed below, assuming an allowable error of 20%.

	Hayfield	Port Innisherrich
Diaptomus gracilis	12	7
Bosmina coregoni	7	2
Cylops abyssorum	34	10
Daphnia hyalina	18	40

information on general trends in prey abundance. The results are not presented but they are available from the author on request. Littoral invertebrates were collected by lifting stones from a 0.25m^2 quadrat for 2 minutes and removing any invertebrates on them. A shortage of manpower meant that more representative samples collected by a Freshwater Biological Association air lift sampler could not be attempted. Zooplankton were sampled using a zooplankton net, diameter 300mm, mesh size 125 um. The sampling schedules for littoral invertebrates and zooplankton are given in Tables 4.9 & 4.10 respectively.

4.2.5 Analysis of the amount of food consumed.

4.2.5.1 A comparison of the number of brown trout and rainbow trout with empty stomachs in 1987.

Variation in the percentage of brown trout and rainbow trout with empty stomachs caught in each sampling period in the littoral and fish farm habitats and the angling competitions in 1987 was compared by the non parametric Kruskal-Wallis test.

4.2.5.2 Analysis of the quantity of food consumed.

The mean fullness index (MFI) was calculated for each species caught in the gill netting survey and for brown trout and rainbow trout caught in angling competitions in 1987. This was plotted to show seasonal variation in food consumption. In 1988 the MFI was only calculated for brown trout and rainbow trout.

The mean volume per stomach (MVS) was calculated for rainbow trout and brown trout caught at the fish farm and littoral sites in 4 length classes: 0-199mm, 200-299mm, 300-399mm and 400mm+. This approach removed any bias due to samples containing fish of different sizes. Length classes were preferred to age classes as brown and rainbow trout

Table 4.9 The number of macroinvertebrate samples collected at each site in 1987.

Month	Ter	Hay	Coil	Bal	Port	Brae
January	-	-	-	-	-	-
February	4	4	4	4	4	4
March	-	-	-	-	-	-
April	-	-	-	-	-	-
May	4	4	4	4	4	4
June	4	4	4	4	4	4
July	3	4	3	4	4	4
August	4	4	4	4	4	4
September	4	4	4	4	4	4
October	4	4	4	-	-	-
November	4	4	4	4	4	4
December	4	4	4	-	-	-

Ter=Tervine, Hay=Hayfield Littoral, Coil=Coillaig Littoral, Bal=Ballimeanoch littoral, Port=Port Innisherrich Littoral, Brae=Braevallich

Table 4.10 **The number of zooplankton samples collected at each site in 1987.**

	TE	HL	HP	HB	HPB	CO	BA	PL	PP	PB	PBP	BR
January	-	-	-	-	-	1	-	-	-	-	-	-
February	1	1	1	2	-	2	-	1	1	2	-	2
March	-	4	4	8	-	4	4	4	4	8	-	4
April	4	4	4	8	-	4	4	4	4	8	-	4
May	4	4	-	-	4	4	4	4	-	-	4	4
June	4	4	-	-	4	4	4	4	-	-	4	3
July	4	4	-	-	4	4	4	4	-	-	3	3
August	3	4	-	-	4	4	4	4	-	-	3	4
September	4	4	-	-	4	4	4	4	-	-	3	4
October	4	4	-	-	4	-	4	4	-	-	4	4
November	3	4	-	-	4	4	4	4	-	-	4	4
December	4	4	-	-	4	4	4	4	-	-	4	3

TE=Tervine, HL=Hayfield littoral, HP=Hayfield pelagic, HB=Hayfield benthic, HPB=Hayfield benthic and pelagic combined, CO=Coillaig, BA=Ballimeanoch, PL=Port Innisherrich littoral, PP=Port Innisherrich pelagic, PB=Port Innisherrich benthic, PBP=Port Innisherrich benthic and pelagic combined, BR=Braevallich have different growth rates (See Chapter 3), and it is size rather than age that determines food intake. Comparisons were made between species and within habitats; and within species between habitats by one way analysis of variance (ANOVA). When the data failed to meet the pre-requisites of the test a log (100.x) transformation was performed (Sokal & Rholf, 1981) to normalise the data, and when it failed to do so, the non parametric Mann Whitney test was used instead.

The same comparison was made between brown trout and rainbow trout caught in angling competitions, with a further test being made to determine if there was any difference in the volume of food consumed by fish caught in gill nets and by angling.

4.3 Results

4.3.1 Diet analysis.

4.3.1.1 Seasonal variation in the diet of fish caught in the 1987 gill netting survey.

A detailed description of the diet of all fish species in each habitat is given in Appendix 1 by percent occurrence, number and volume; a breakdown by broader prey groups as percent volume is presented in Figures 4.1-4.12.

Brown trout littoral.

The diet of brown trout in the littoral zone comprised a wide variety of conventional trout prey, insect nymphs, Peracarida (large Crustacea), Mollusca, zooplankton, aerial insects and pelagic pupae, with a small amount of non-conventional items such as stones and vegetation also being consumed. Their feeding behaviour can be divided into two distinct periods. In winter/spring the diet is almost exclusively based on bottom-living prey whereas in the summer/autumn prey found in the surface/pelagic zone predominates. However a small amount of bottom-dwelling prey was retained in the diet throughout the summer (Figure 4.1).

In January/February the brown trout diet was almost exclusively based on bottom-living invertebrates. The most important group were the Peracarida, of which Gammarus lacustris Sars occurred in 21.8% of stomachs (% occ) and contributed 9.9% to the total volume (% vol), and Asellus aquaticus (L.) which occurred in 47.3% (% occ.) of the stomachs and made up 47.3% of the volume (% vol.) (Appendix 1). Insect nymphs/larvae were the next most important group with Plecoptera, Ephemeroptera, Coleoptera, Trichoptera and Diptera all being consumed. No single order of insects made a greater contribution to the diet than any other. A limited range of Mollusca were consumed in small

Figure 4.1 Seasonal variation in the diet of brown trout caught in the littoral zone in 1987, expressed as percentage volume.

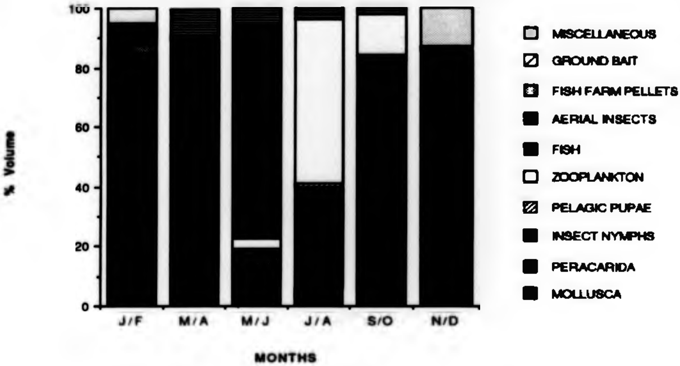
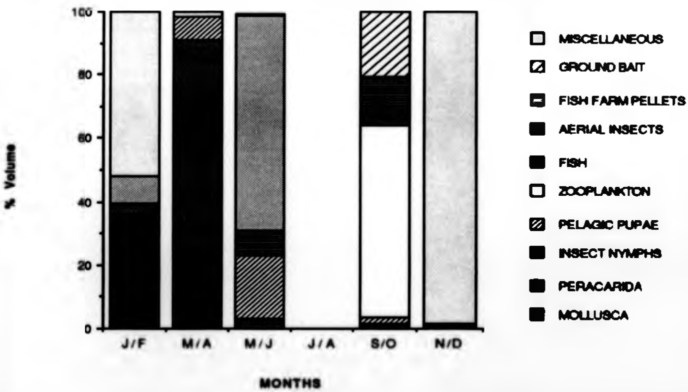


Figure 4.2 Seasonal variation in the diet of brown trout caught at the fish farms in 1987, expressed as percentage volume.



quantities, the most important being Lymnaea peregra (Muller) and Physa fontinalis (L.).

In March/April the majority of the brown trout diet still comprised bottom-dwelling prey, however a small amount of surface/pelagic prey was also eaten, (Figure 4.1 & Appendix 1). The three main groups Mollusca, Peracarida and the insect nymphs/larvae retained their order of importance, but the amount of insects consumed increased at the expense of the Peracarida. This increase could be related to the increased levels of activity found in insect nymphs and larvae at this time (Lillehammer, 1973), associated with their preparations prior to emergence (Ball, 1961). The broadening of the diet to include surface/pelagic prey coincided with the start of the main flying period for adult insects. An unidentified Daphniidae (most likely Daphnia hyalina Leydig) was the species of zooplankton eaten, the decomposed state of the individuals prevented a more precise identification. The pelagic pupae included unidentified Chironomidae, Tanypodinae and Orthocladius sp. and the aerial insects included Diptera, Psocoptera and Hymenoptera. Aerial insects get trapped on the water surface and become concentrated along foam lines that develop on the water surface parallel to the shore in strong winds (Norlin, 1967). This concentration provides a ready supply of food for trout that are surface feeding.

In May/June the diet of brown trout was in transition from winter to summer feeding mode with bottom-dwelling and surface/pelagic prey both contributing to their diet (Figure 4.1 and Appendix 1). In terms of volume the importance of fish is probably overstated and by implication the importance of the other categories is understated. In the bottom-dwelling component L. peregra was the only Mollusca eaten (% occ 26.6 and % vol 9.8). In the Peracarida A. aquaticus were consumed in greatest quantities (% occ 13.3, % vol 3.1), with G. lacustris being less important. The Trichoptera larvae Sericostoma personatum (Spence) was the most important insect larvae in their diet (% occ 13.3 and % vol 3.0). Of the surface/pelagic prey consumed aerial insects were the most important. Diptera (% occ 26.7, % vol 2.3) and Hymenoptera (% occ 20.0, % vol 3.6) were consumed in the largest quantities with small amounts of Ephemeroptera, Hemiptera and Coleoptera also being eaten (Appendix 1). D.hyalina and Bythotrephes longimanus Leydig were the principal species of zooplankton eaten, with small amounts of Orthocladius sp. and Macropelopia sp. pupae also being consumed. The change in feeding behaviour is driven by the change in food availability at this time of the year.

In July/August their diet was split between surface/pelagic and bottom-dwelling prey, with the former being the most important. The surface/pelagic component comprised zooplankton, aerial insects and pelagic pupae, in that order of importance (Figure 4.1). B. longimanus made the largest contribution of any species (% occ 44 and % vol 50.4), but Eurycercus lamellatus Muller and D.hyalina were also present in smaller quantities (Appendix 1). The contribution of zooplankton to the diet was greatest when it had passed its period of maximum abundance in the late spring. The volume of aerial insects in the diet was low at 3.6%, due possibly to the poor weather conditions prior to netting which depressed the activity of flying insects. The pelagic pupae represented by an unidentified Trichoptera only made a small contribution to the diet (Figure 4.1). The bottom-dwelling prey largely comprised Peracarida with smaller amounts of Mollusca and insect nymphs also being eaten. The higher than expected contribution of the Peracarida was mostly of A. aquaticus (% occ 55.6, % vol 24.7). The appearance of Ephemerella ignita (Poda) in the diet coincided with the period just prior to its emergence. The remainder of the insect component comprised larval and adult stages of Coleoptera and Trichoptera larvae. Mollusca were represented in small numbers by L. peregra. Potamopyrgus jenkinsi (Smith) and Ancylus fluviatilis Muller (Appendix 1).

In September/October the brown trout diet appeared to be dominated by Mollusca, however the results were strongly biased by the stomach contents of one fish. This stomach contained considerably more food than any of the other brown trout examined in the study, it was highly distended and contained only L. peregra and P. fontinalis (Appendix 1). If the stomach contents of this unrepresentative fish are excluded from the calculations, it is clear that the overall diet was still dominated by surface/pelagic prey. Unlike the previous two month period no pelagic pupae were present in this sample (Figure 4.1). In all other respects the diet was similar, B. longimanus being the most important species (% occ 23.5, % vol 6.6%), and the aerial insects being comprised of Diptera, Hymenoptera and Ephemeroptera. The importance and diversity of the insect nymph and larvae component increased at this time. No preference was shown among the macro-invertebrates consumed. Mollusca consumed included L. peregra. P. fontinalis and Planorbis contortus (L.). The Peracarida were less important than in previous periods, however Gammarus pulex (L.) was eaten as well as the two more common species G. lacustris and A. aquaticus (Figure 4.1).

By November/December the diet of brown trout was dominated by littoral macroinvertebrates, as occurred in January/February, although small amounts of zooplankton and aerial insects were also consumed. In the miscellaneous category, fish eggs and vegetation were eaten (Figure 4.1). In the littoral invertebrate component the insect nymphs and larvae, and the Peracarida were of equal importance with the Mollusca being less important. Trichoptera made the largest contribution to their diet in the insect category, Lepidostoma hirtum (Fabricius) (% occ 14.7, % vol 10.7%), and L. peregra were the Mollusca consumed in greatest quantities, with smaller amounts of P. fontinalis, Planorbis laevis Alder, Valvata cristata Muller, P. jenkinsi and Pisidium obtusale (Lamarck) also being eaten (Appendix 1).

Brown trout-fish farms.

The diet of brown trout at the fish farms largely comprised conventional trout prey, and the seasonal variation described in the littoral zone was again apparent. However in a few of the sampling periods the results were strongly biased by a few individual brown trout feeding heavily on unconventional prey items (Appendix 1 & Figure 4.2).

In January/February the conventional component was dominated by Mollusca, P. fontinalis (% occ 17.7, % vol 20.3) and L. peregra (% occ 29.4, % vol 7.7), with smaller amounts of other species also eaten (Appendix 1). Peracarida were only represented by G. lacustris (% occ 17.4, % vol), no A. aquaticus being consumed by brown trout caught in any of the sampling periods at the fish farms. This was surprising as A.aquaticus are often associated with light organic enrichment (Moss, 1980), which can be found around fish farms. The remainder of the conventional component included the nymphs and larvae of aquatic insects, (% vol 2.7) (Appendix 1). By volume, non-conventional prey appear to be the most important source of food for brown trout feeding close to the cages. However, the occurrence shows that they are only found in a few stomachs, and are therefore less important on a population basis (Appendix 1). In this category, fish eggs, vegetation, and fish farm pellets were all consumed. The most likely source of eggs was from sexually mature rainbow trout in the cages. The cages are also the most likely source of the fish farm pellets.

In March/April their diet was still dominated by littoral invertebrates (Figure 4.2). There was a rise in the importance of insect nymphs and a decline in the importance of Mollusca and Peracarida. In particular Anabolia nervosa Curtis (% occ 22.2, % vol 35.9) made a significant contribution to their diet (Appendix 1). The unidentified Chironomidae pupae eaten by one fish was the first sign of their summer/autumn feeding behaviour.

By May/June the shift in feeding behaviour from winter to summer was almost complete. The majority of conventional prey was obtained from the surface/pelagic zone but a small proportion of bottom-dwelling prey was retained in their diet. In common with earlier samples there was a large volume of fish farm pellets in the diet, but they were only eaten by a few individuals, so once again they are less important in terms of the whole population than they first appear (Appendix 1 and Figure 4.2). Pelagic pupae and aerial insects were consumed in the surface/pelagic zone, with the former being the most important. Unidentified pupae of Chironomidae and Trichoptera, and adult Diptera, Psocoptera, Hymenoptera and Trichoptera were all eaten. The bottom-dwelling component comprised insect larvae and Mollusca, with the former only being half as important as they had been in the previous sampling period. Ground bait occurred in the stomach of one fish. This item is more commonly found in the stomachs of fish caught around the cages than those in the littoral zone. A small amount of vegetation was also eaten. No brown trout were caught at the fish farms in July/August.

In September/October brown trout were only caught at Braevallich. They had been feeding almost exclusively on prey associated with the surface/pelagic zone, however small amounts of bottom-dwelling invertebrates and ground bait were also eaten (Figure 4.2).

Zooplankton, aerial insects and pelagic pupae were all consumed, with the former being the most important. The zooplankton was largely made up of an unidentified Daphniidae (probably D. hyalina). The aerial component (% vol 15.2) comprised unidentified Diptera, and a caterpillar, which presumably fell from overhanging vegetation. Of less importance were the unidentified Trichoptera and Chironomidae pupae (% vol 2.1). All of the bottom-dwelling categories were present, but only in trace amounts. The importance of ground bait in terms of volume was overstated as it only occurred in one stomach and consisted of four large terrestrial earthworms (Appendix 1).

In November/December the sample was very small (n=4) and was again restricted to Braevallich. Their diet had narrowed to the winter/spring feeding mode, with Mollusca, insect nymphs and fish eggs all being eaten. In terms of volume and number the diet was dominated by fish eggs, however in terms of occurrence they are no more important than other prey items. The source of eggs is unclear, but could have come from sexually mature rainbow trout in the cages or from brown trout or charr spawning in the loch or in one of its tributaries (Figure 4.2 and Appendix 1).

Brown trout-pelagic zone.

The stomach samples that contained food were restricted to July/August, September/October and November/December. The diet was almost entirely based on zooplankton except in July/August when a few other surface/pelagic prey were also consumed (Appendix 1 & Figure 4.3).

In July/August B.longimanus and D. hyalina were consumed in the greatest quantities, with a small amount of Leptodora kindti (Focke) also being eaten. Unidentified Diptera adults and Chironomidae larvae were also consumed in small amounts. In September/October and

Figure 4.3 Seasonal variation in the diet of brown trout caught in the pelagic zone in 1987, expressed as percentage volume.

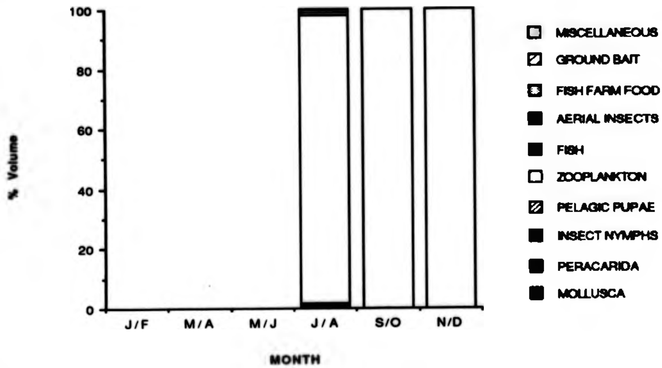
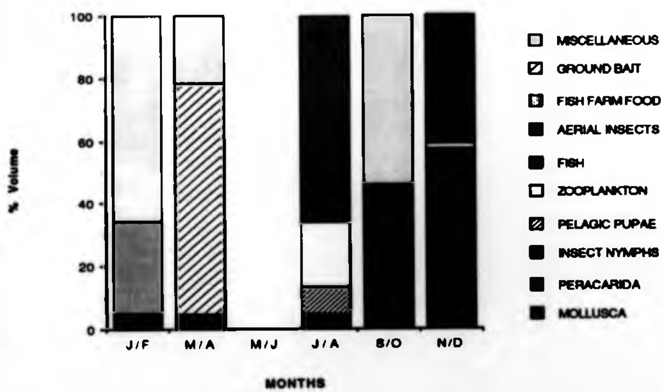


Figure 4.4 Seasonal variation in the diet of rainbow trout caught in the littoral zone in 1987, expressed as percentage volume.



November/December their diet was restricted to B. longimanus and L. kindti (Appendix 1).

Rainbow trout littoral zone.

Rainbow trout consumed a higher proportion of non-conventional prey than brown trout. Most of these items were of limited nutritional value. The conventional portion of their diet followed a similar pattern to brown trout but was consumed in smaller quantities (Appendix 1 & Figure 4.4)

January/February was very typical of the non-conventional diet. It included vegetation, stones, a cigarette filter and fish farm pellets, with vegetation being most important (% occ 33.3, % vol 37.7) (Appendix 1). The similarity of the cigarette filter's shape to a fish farm pellet may explain its inclusion in the diet. The fish with pellets in its stomach was caught at Port Innisherrich which was the furthest distance away from the cages that such a fish was caught. The distance between Braevallich (the closest farm) and Port Innisherrich is well within the daily swimming capability of salmonids (Holliday et al., 1974; Phillips, 1982). It is therefore possible that the fish could have fed on pellets at Braevallich and have been caught at Port Innisherrich. Rainbow trout consumed far lower quantities of conventional prey than brown trout in the same habitat at this time, but in common with them, Peracarida, insect nymphs and Mollusca were eaten. A. aquaticus was consumed in the largest quantities (% occ 16.7, % vol 1.4) (Appendix 1).

In March/April their diet was dominated by ground bait and miscellaneous prey items with small amounts of Peracarida and insect nymphs/larvae also being eaten (Figure 4.4). Although ground bait dominated the diet in terms of volume (73.4%) it was only found in two stomachs, whereas the miscellaneous category (stones and vegetation) was found in six stomachs, but only contributed 21.8% in terms of volume. It is clear that fish feeding on the maggots and sweet corn had found it in super abundance and gorged themselves on it, accounting for its high volume to occurrence ratio (Appendix 1). Rainbow trout may be attracted to maggots because of their similarity to fish farm pellets as they pass through the water column, this being one of the few food search images that they have learned in the cages prior to their escape. The bright yellow colour of sweet corn may make it particularly conspicuous. No rainbow trout were caught in the littoral zone in May/June.

In July/August there was a marked shift in the rainbow trout's feeding behaviour from non-conventional to conventional prey. Within the surface/pelagic category they fed most heavily on aerial insects (% vol 65.2), with Diptera, Coleoptera, Hemiptera, Plecoptera, Hymenoptera and Trichoptera all being consumed. Only two species of zooplankton were eaten B. longimanus and D. hyalina (% vol 20.6). The pelagic pupae were represented by an unidentified Chironomidae, and the bottom-dwelling invertebrates by insect nymphs which included E. ignita (Appendix 1). Their appearance in the rainbow trout diet coincided with the period when they were found in the brown trout's diet.

In September/October the scope for meaningful analysis was limited by the small number of stomachs containing food (n=4). Their diet largely comprised non-conventional prey, with the conventional component having changed from summer back to winter mode (Figure 4.4). The miscellaneous group consisted of vegetation (% occ 60.0, % vol 51.3) and stones (% occ 20 %, vol 3.4). Fish appear to dominate the conventional component of the diet, but when their occurrence is considered they are seen to be no more important than the other items. A small amount of adult

Diptera was also consumed (Appendix 1). Mollusca, Peracarida and insect nymphs were all consumed during bottom feeding.

In November/December their diet was almost entirely based on conventional prey, the most important being the Mollusca; L.Peregra (% occ 20.0, % vol 57.5), with smaller amount of insects also eaten. Fish, zooplankton and a small amount of vegetation were also included in their diet (Appendix 1).

Rainbow trout-fish farm.

The diet of rainbow trout caught around the fish farms was dominated by uneaten pellets that pass through the cages. Ground bait, vegetation and stones were also eaten, but in smaller quantities. Only a small amount of conventional prey was consumed and it followed the seasonal pattern described previously (Appendix 1 & Figure 4.5)

In January/February their diet was based almost entirely on non-conventional prey items ie; fish farm food, vegetation, stones and fish eggs. Only trace amounts of conventional prey were consumed (Figure 4.5). Fish farm pellets were consumed in the largest quantity (% occ 51.2, % vol 83.1), occurring in 87.5% of the stomachs that contained food. The miscellaneous category comprised fish eggs, stones and vegetation, the most important being the eggs (% occ 4.9, % vol 13.4). The high volume:occurrence ratio for eggs indicates that only a small number of fish had been feeding heavily on them (Appendix 1). It is highly likely that the eggs in their diet came from maturing rainbow trout in the cages. A small amount of ground bait and conventional prey was also eaten.

In March/April their diet was again dominated by fish farm pellets, and the very small conventional component showed the first signs of

Figure 4.5 Seasonal variation in the diet of rainbow trout caught at the fish farms in 1987, expressed as percentage volume.

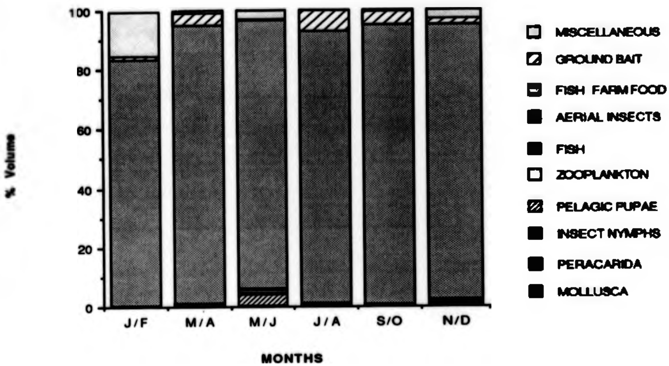
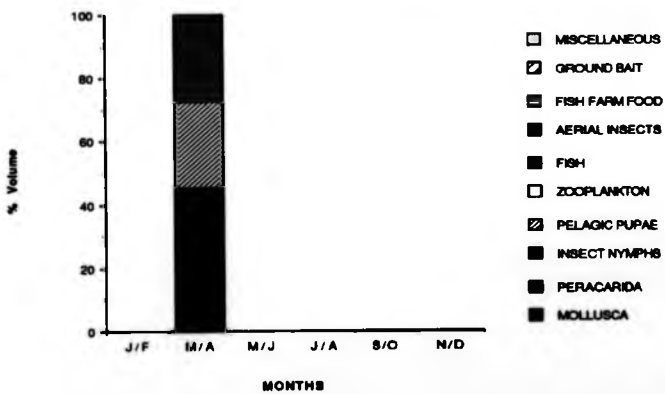


Figure 4.6 Seasonal variation in the diet of rainbow trout caught in the pelagic zone in 1987, expressed as percentage volume.



transition from winter to summer feeding mode. The pellets made up 93.9% of the total volume of food consumed and occurred in 75% of the stomachs examined (Appendix 1) (90% of those containing food). This high reliance on a single food source was not observed in any other species in any habitat. The slight increase in consumption of ground bait coincided with the start of the angling season. In the miscellaneous category a small amount of vegetation was consumed. It is unclear if rainbow trout feed on plant material when it is attached and living on the bottom, or whether they consume fragments that are floating on the surface. In common with rainbow trout in the littoral zone they do not increase their utilisation of insect nymphs at this time, this being contrary to the behaviour of brown trout in the two habitats. This result suggests that they spend less time than brown trout foraging on the bottom. Alternatively it could be explained by rainbow trout at the cages securing enough food from fish farm pellets. In keeping with the "up looking" feeding behaviour required to consume pellets a small amount of pelagic pupae were eaten (Figure 4.5).

In May/June their diet was again dominated by fish farm pellets, but compared to the previous sampling period it was found in fewer stomachs. The conventional component largely comprised prey found in the surface/pelagic zone (Figure 4.5). Fish farm pellets contributed 90.1% to the volume of food consumed, however there was a marked decline in its occurrence 28.6% (Appendix 1) (42.6% of those containing food). Although no water quality measurements were taken it is generally accepted that it declines in the immediate vicinity of the cages at this time of year, this may have acted as a deterrent to fish feeding around the cages. Alternatively it is possible that the increased feeding activity of rainbow trout in the cages reduces the number of pellets that pass through the cages uneaten. Small amounts of ground bait, vegetation and stones were also eaten. The conventional component mostly comprised prey found in the surface/pelagic zone, with Chironomidae pupae being consumed in the largest quantities (% occ 31.4, % vol 3.7). This was the largest component of conventional prey in their diet in any of the sampling periods at the fish farms. A wide variety of aerial insects including; Diptera, Coleoptera, Ephemeroptera and Trichoptera were consumed along with the zooplankton species D.hyalina and L.kindti. Each of the bottom-living groups were consumed, but only in very small amounts (Appendix 1).

In July/August the pattern of food consumption was similar to the previous period. Their diet being dominated by non-conventional food, principally fish farm pellets, but again its occurrence was considerably lower than previously. The conventional component mainly consisted of surface/pelagic prey (Figure 4.5). Fish farm food contributed 91.5% to the total volume of food eaten, however it only occurred in 37.8% of the stomachs examined (53.1% of those containing food). The possible reasons for the lower summer levels were discussed previously. Aerial insects were the most important conventional prey in their diet, and both zooplankton and pelagic pupae declined in importance (Appendix 1).

In September/October their diet was almost entirely composed of non-conventional prey (% vol 99.4). The small amount of conventional prey eaten largely consisted of surface/pelagic prey (Figure 4.5). The occurrence of fish farm pellets increased from the low summer levels to 56.8% of the fish in the sample (Appendix 1) (73.7% of those containing food). The low consumption of conventional prey items coincided with their period of lowest availability. The insect eggs laid in the loch are just starting to hatch, the number of pupae in the surface/pelagic zone has greatly declined, and the main insect flying period has ended.

In November/December their feeding pattern had returned to that found at the start of the year with non-conventional prey dominating their diet and the conventional component consisting of bottom-dwelling invertebrates (Figure 4.5). Fish farm pellets made up 95.4% of the food eaten, occurring in 58% of the stomachs in the sample (76.3% of these containing food). This result shows that more fish are feeding under the cages than in the summer (Appendix 1). The conventional component had again reverted to the winter/spring feeding mode, reflecting the seasonal changes in food availability. Small amounts of vegetation, stones and ground bait were also eaten, the latter indicating that anglers were still fishing in the close season.

Rainbow trout-pelagic.

Only one rainbow trout was caught in the pelagic zone with food in it's stomach. This occurred in March/April, it had been feeding on Capnia sp. nymphs, and the larvae, pupae and adults of Chironomidae suggesting that it had been feeding on bottom-dwelling prey in the littoral zone as well as feeding at the surface (Appendix 1 & Figure 4.6).

Benthic Arctic charr-littoral.

The diet of benthic Arctic charr was similar to that of other wild salmonids in the littoral zone, following the changes in seasonal variation of the major salmonid prey items. (Appendix 1 & Figure 4.7).

In January/February their diet consisted of bottom-dwelling prey, some of which were associated with stony substrates, others with soft sediments. Chironomidae larvae were consumed in the largest quantity (% occ 63.6, % vol 37.4), with an unidentified Trichoptera larvae being the only other insect eaten. The Peracarida were represented by A.aquaticus and G.lacustris. The bivalve P. obtusale and the benthic zooplankton Cyclops viridis (Jurine) were the species associated with

Figure 4.7 Seasonal variation in the diet of benthic Arctic charr caught in the littoral zone in 1987, expressed as percentage volume.

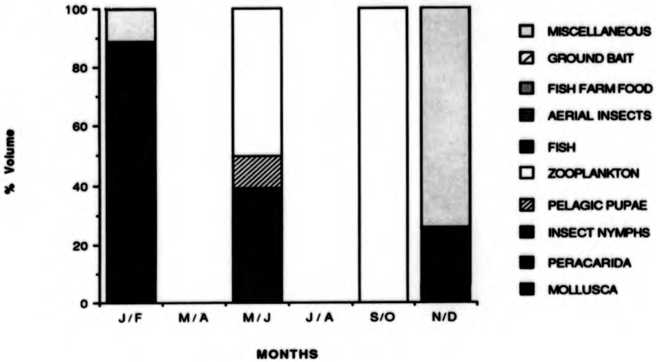
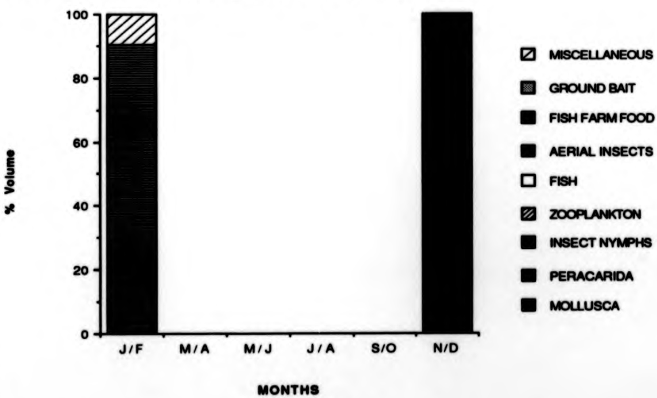


Figure 4.8 Seasonal variation in the diet of benthic Arctic charr caught at the fish farms in 1987, expressed as percentage volume.



soft sediments found consumed (Appendix 1). These species were not found in the diet of brown trout, and only in the stomach of one rainbow trout. The fish eggs found in their stomachs were a similar size to those found in sexually mature charr, suggesting that they feed on eggs from their redds that are being constructed at that time.

No benthic Arctic charr were caught in the littoral zone in March/April. In May/June the analysis was based on a small number of stomachs. Even with the limited data set it was clear that their feeding behaviour had changed from winter to summer mode. The surface/pelagic component consisted of D. hyalina and Chironomidae pupae. In common with the two trout species at that time a small amount of bottom-dwelling prey was retained in their diet, with A.aquaticus, Sialis lutaria (L.) and C.viridis being consumed (Appendix 1).

No benthic Arctic charr were caught in the littoral zone in July/August. In September/October only one stomach contained food, which consisted of Eurycercus lamellatus Muller, a Crustacea species associated with loch and pond margins.

By November/December their diet had reverted back to the high dependence on bottom-living invertebrates. In terms of volume their diet was dominated by fish eggs, although when occurrence is considered, it is seen that their importance was overstated. The littoral invertebrates included Mollusca, Ephemeroptera and Chironomidae, and there was evidence of feeding in soft sediments (Appendix 1 and Figure 4.7).

Benthic Arctic charr-fish farms.

The analysis was based on four stomachs caught in January/February and November/December, when they had been feeding on Mollusca Peracarida, insect larvae, fish farm pellets and fish eggs. There was no evidence of any variation between the two sampling dates (Appendix 1 & Figure 4.8).

Benthic Arctic charr-pelagic.

Their diet followed the seasonal pattern described previously. In winter they fed on bottom-living invertebrates e.g. C. viridis, P. obtusale and Cyrnus flavidus. In the summer they fed on zooplankton D. hyalina, B. longimanus and a Chironomidae larvae. (Appendix 1 & Figure 4.9).

Benthic Arctic charr-benthic.

A feature of the benthic morph's diet in the benthic habitat was their high dependence throughout the year on invertebrates associated with soft sediments in water at least 50m deep. Superimposed onto this was the consumption of prey found in shallow water depending upon their seasonal abundance (Appendix 1 & Figure 4.10).

In January/February their diet was almost entirely based on invertebrates associated with soft sediments. They included P. obtusale, an unidentified Chironomidae larvae and C. viridis. The fine sediments in the stomachs of charr are further evidence of the prey's association with it. A small amount of pelagic zooplankton was also consumed, but it could only be identified to Daphniidae. It is highly likely that it was D. hyalina (Appendix 1).

In March/April their diet largely consisted of invertebrates associated with soft sediments. Although A. aquaticus, Capnia sp., and E. lamellatus which are associated with the littoral zone were also eaten. This indicates that benthic charr make regular forays into this habitat from the deep water where they were caught (Appendix 1).

Figure 4.9 Seasonal variation in the diet of benthic Arctic charr caught in the pelagic zone in 1987, expressed as percentage volume.

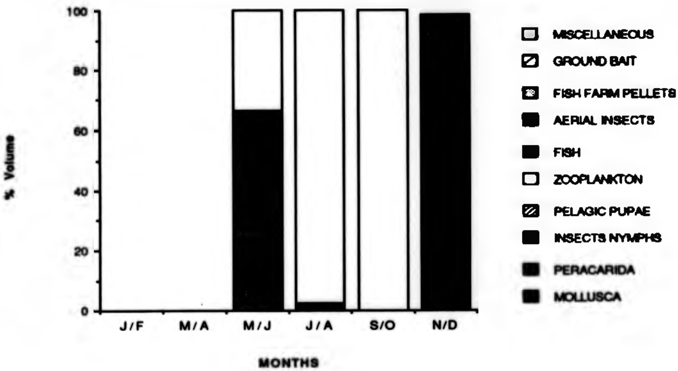
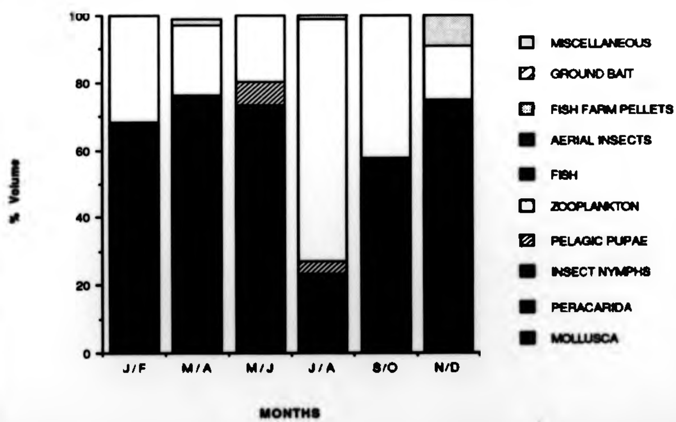


Figure 4.10 Seasonal variation in the diet of benthic Arctic charr caught in the benthic zone in 1987, expressed as percentage volume.



In May/June their diet was similar to that observed in March/April, and in common with the two trout species their diet also included the Chironomidae pupae _Macropelopia_ sp. and _Psectrotanypus_ sp.. The Trichoptera larvae eaten by charr were all caseless whereas those eaten by the two trout species were almost all cased. The underlying reason for this selectivity is unclear and would require further investigation.

In July/August their high dependence on _P. obtusale_, _C. viridis_ and Chironomidae larvae continued. They also consumed bottom-dwelling invertebrates associated with the shallow littoral areas, and in common with the two trout species zooplankton and pelagic pupae were also at this time. The absence of aerial insects in their diet is noted. The zooplankton consumed were _D. hyalina_, _B. longimanus_ and _L. kindti_, and the Chironomidae pupae included _Procladius_ sp., _Aspectrotanypus_ sp. and _Arctopelopia_ sp. (Appendix 1).

In September/October they again had a high dependence on prey associated with soft sediments. No Chironomidae pupae were eaten and there was a reduction in the number and diversity of shallow littoral invertebrates and pelagic zooplankton in their diet (Appendix 1). These findings are in agreement with the seasonal decline in their abundance.

By November/December their diet had reverted to the narrow range of prey items consumed at the start of the year. Prey normally associated with loch margins were present in the stomachs of fish caught in the benthic zone indicating that they still undertook migrations from deep to shallow water.

Pelagic Arctic charr.

Only a small number of this morph were caught in the survey. They were caught between January/February and September/October in the littoral, fish farm and pelagic habitats. Throughout the period their diet was restricted to pelagic zooplankton. Appendix 1 gives a detailed breakdown of the diet by species.

Perch-littoral.

Throughout the period of their summer migration into shallow water their diet comprised fish, bottom-living invertebrates, pelagic pupae, zooplankton and aerial insects, with the relative importance of each group being subject to seasonal availability. The complete absence of Mollusca in their diet is noted (Appendix 1 & Figure 4.11).

In May/June their diet was dominated by fish in terms of volume, but if occurrence is considered it is clear that the littoral invertebrates are of greater importance at a population level. The high incidence of E. ignita in the diet is consistent with the period prior to its flight period, Caenis horaria (L.) and an unidentified species of Coleoptera larvae was also consumed but were less important. The limited seasonal appearance of E. ignita in the diet of fish in Loch Awe is due to the timing of its life cycle. The zooplankton species D. hyalina, B. longimanus, and to a lesser extent E. lamellatus and Polyphemus pediculus L. all occurred in a high percentage of stomachs but only contributed a small amount to the total volume eaten. The absence of Cyclopoidea is again noted (Appendix 1). In July/August fish, mainly sticklebacks were the most important food source for perch. In the remainder of their diet the emphasis changed from littoral invertebrates to zooplankton, the most important of which were B. longimanus, D. hyalina, with a small amount of Bosmina coregoni Baird also being consumed (Figure 4.11). The decline in the importance of the littoral invertebrates was typified by the reduction in the importance of E. ignita. There was also a marked decline in the consumption of

Figure 4.11 Seasonal variation in the diet of perch caught in the littoral zone in 1987, expressed as percentage volume.

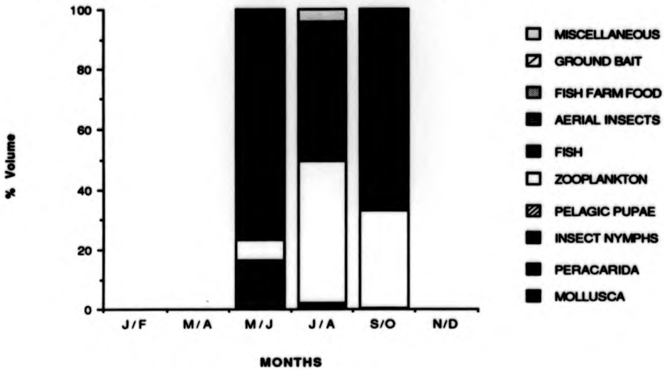
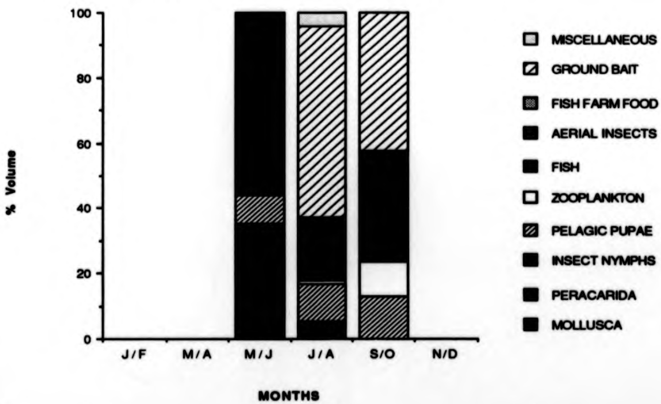


Figure 4.12 Seasonal variation in the diet of perch caught at the fish farms in 1987, expressed as percentage volume.



Chironomidae pupae.

In September/October the trends which had started to appear in July/August became more apparent. Littoral invertebrates were dropped from their diet and the contribution of fish rose (% vol 65.5). The volume of zooplankton dropped slightly to 32.7%, and the consumption of pelagic pupae remained at a low level (Figure 4.11).

Perch-fish farms.

Their feeding pattern at the fish farms followed a very similar pattern to that described for perch in the littoral habitat. Fish dominated their diet and the other conventional prey were eaten in accordance with their seasonal availability. In May/June and September/October the scope for analysis was limited by the small sample sizes (Appendix 1 & Figure 4.12).

In May/June fish were consumed by 37.5% of the perch in the sample and they contributed 75.4% to the total volume eaten. The remainder of the conventional component consisted of littoral invertebrates and surface/pelagic prey. In terms of volume the importance of ground bait was over stated as it was only eaten by one fish. If it is excluded from the analysis it is seen that fish were the most important conventional prey consumed (% vol 18.9). The diversity of littoral invertebrates consumed increased but their volumetric contribution per fish remained at a similar level. The surface/pelagic category comprised pelagic pupae, zooplankton and aerial insects (Appendix 1). In the non-conventional component vegetation and ground bait were consumed. In September/October their diet comprised pelagic pupae, fish, zooplankton and ground bait.

Atlantic salmon-littoral.

The analysis was based on two stomachs containing food in

November/December. Both fish had been feeding on cased Trichoptera larvae (Appendix 1).

Atlantic Salmon-fish farms.

The analysis was based on a small number of stomachs collected in July/August, September/October, and November/December (Appendix 1 & Figure 4.13). In July/August their diet was dominated by prey found in the surface/pelagic zone, the most important of which was zooplankton, although there was also some evidence of feeding on bottom-dwelling prey. In September/October their diet was again restricted to prey from the surface/pelagic zone. The zooplankton species D. hyalina being the most important. In November/December they had been feeding on bottom-dwelling invertebrates e.g. P. jenkinsi and larvae of Colymbetes sp., a water beetle.

4.3.1.2 Diet comparisons of brown trout and rainbow trout in the fish farm and littoral habitats in 1987.

Overlap indices (Schoener, 1970) were calculated to determine the overlap in the diets of brown trout and rainbow trout at and away from the fish farms. A score of 0 indicates completely different diets, and a score of 1 indicates complete overlap.

Brown trout littoral vs rainbow trout littoral.

The main difference in this instance was the high proportion of non-conventional prey items found in the rainbow trout's diet, whereas the majority of the brown trout diet included conventional prey.

In January/February the overlap index was 0.24 (Table 4.11) indicating little similarity in their diets. The diet of rainbow trout largely comprised vegetation and stones whereas, the diet of brown trout almost entirely comprised littoral invertebrates (Figure 4.1 and 4.4). Only

Figure 4.13 Seasonal variation in the diet of Atlantic salmon caught at the fish farms in 1987, expressed as percentage volume.

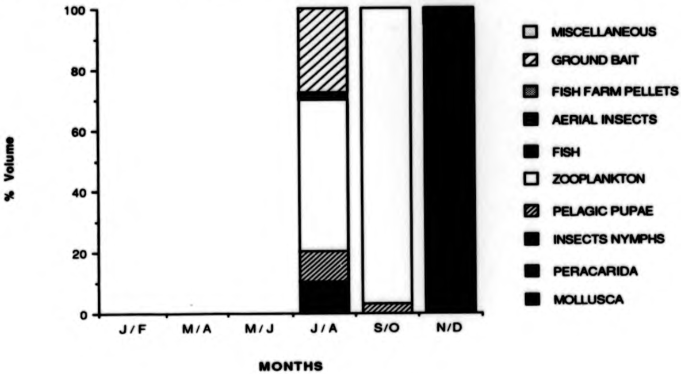


Table 4.11 **Overlap index values for the diets of brown and rainbow trout caught in the gill netting survey in 1987 at and away from the fish farms.**

	J/F	M/A	M/J	J/A	S/O	N/D
BT vs RT, FF	0.24	0.02	0.14	-	0.05	0.04
BT vs RT, LI	0.24	0.05	-	0.31	0.14	0.23
LI vs FF, BT	0.25	0.55	0.09	-	0.17	0.15
LI vs FF, RT	0.45	0.05	-	0.02	0.01	0.03

BT=Brown Trout, Rt=Rainbow Trout, LI=Littoral, FF=Fish Farm

Table 4.12 **Overlap index values of brown and rainbow trout caught in the 1987 angling competitions**

	April	May	June
Brown trout vs Rainbow trout	0.45	0.28	0.17

a small number of rainbow trout consumed littoral invertebrates.

In March/April the overlap index was 0.05 (Table 4.11) indicating even less similarity in their diets than there had been in the previous period. Rainbow trout ate vegetation, stones and a small amount of Peracarida and insect nymphs, whereas the brown trout's diet almost entirely comprised conventional prey, the majority of which were littoral invertebrates (Figures 4.1 and 4.4).

No rainbow trout were caught in May/June therefore no comparison was made. In July/August the overlap index was 0.31 (Table 4.11), this was the highest index value achieved in this group. However, it may be an artefact of the small sample of fish involved in the comparison. The diet of the two species largely comprised conventional prey. Rainbow trout consumed surface/pelagic prey, whereas the brown trout although securing some of their diet from the surface also retained a proportion of bottom-dwelling invertebrates in their diet (Figures 4.1 and 4.4). This small degree of niche divergence is unlikely to be a result of interspecific segregation. Rainbow trout are present in very small numbers in the littoral zone and are therefore unlikely to exert any real pressure on brown trout.

In September/October the overlap index was 0.14 (Table 4.11) indicating very little similarity in their diets. The quality of the data may have been adversely affected by the small sample of rainbow trout. The brown trout diet only contained conventional prey, whereas more than half of the food eaten by the rainbow trout included vegetation and stones (Figures 4.1 and 4.4). The overlap that existed in the conventional component is unlikely to result in competition, as it was only found in small quantities in a few of the rainbow trout stomachs examined.

In November/December there was little overlap in the two species diets, the overlap index being 0.23 (Table 4.11). Although the two species diets were almost exclusively based on conventional prey, they fed on different groups. This could be considered as evidence of competition for limited resources, but as stated previously it is unlikely that the low number of rainbow trout found in the littoral zone could exert any real pressure on the brown trout population.

The rainbow trout's lack of experience in foraging wild prey could explain the difference found in the relative utilisation of conventional and non-conventional prey by the two species, rather than the rainbow trout being marginalised by brown trout. It is possible that when rainbow trout escape from cages that they only have a limited repertoire of prey search images and this results in them consuming objects that are reminiscent of fish farm pellets.

Brown trout cages vs rainbow trout cages.
The differences in the relative importance of conventional and non-conventional prey in the two species diets at the fish farm sites is more apparent than at the littoral sites. This is largely due to the rainbow trout's continued high reliance on fish farm pellets after escaping. The results of the overlap index for each sampling periods are shown in Table 4.11.

In terms of volume the lowest contribution of fish farm pellets to the rainbow trout diet was 83.1%. The remainder of their diet comprised ground bait, stones, vegetation and conventional prey. The small amount of conventional prey was consumed according to the seasonal variation in its abundance. In contrast the diet of brown trout was based almost exclusively on conventional prey. When large volumes of novel prey were consumed it was usually due to one individual gorging on it. This is verified by the high stomach fullness index, and the lack of other prey found in the stomachs of such fish.

As only a small number of brown trout altered their feeding behaviour at the cages compared to those at the littoral sites, it is clear that their feeding behaviour is unaffected by the large number of rainbow trout found around the cages. This point is investigated further in the next section.

Brown trout cages vs brown trout littoral.

In January/February their diets would have been very similar had it not been for the consumption of fish farm pellets and fish eggs by three fish caught at the cages. Therefore, the differences between their diets can be accounted for by variations in food availability between the sites, the eggs and pellets only being available at the fish farms. The fact that the brown trout were able to feed under the cages (the preferred rainbow trout feeding area) suggests that their opportunistic feeding behaviour is unaltered.

In March/April the highest overlap index, 0.54 for any of the comparisons was achieved (Table 4.11). In the two habitats brown trout diet consumed largely conventional prey. The differences between the sites being due to the greater importance of Peracarida at the littoral sites. Both groups also showed the first signs of transition from winter to summer feeding. The similarity i.e. the high utilisation of bottom-dwelling invertebrates, indicates that brown trout at fish farms do not suffer from interspecific competition.

In May/June the comparison of diets between the sites was skewed (in terms of volume) by the consumption of pellets at the fish farm, and of fish in the littoral zone. If these data are excluded from the analysis there is a greater similarity between the sites. In each habitat conventional prey from the loch bottom and the surface/pelagic zone was eaten, with those caught in the littoral habitat consuming more of former and those caught at the fish farms consuming more of the latter. The design of the survey does not allow the mechanism behind such subtle differences to be explained. As rainbow trout at the cages were also feeding on surface/pelagic prey, it is likely that the differences are due to variations in food availability rather than competition. In July/August no brown trout were caught at the fish farms, therefore no comparison was made.

In September/October the overlap index (Table 4.11) was strongly biased by the contents of the largest brown trout stomach examined in the survey, which was full of Mollusca. If this is excluded from the analysis the only other large difference between the feeding in the two habitats was the inclusion of ground bait in the diet of those caught at the fish farms. As variation in their diets can be explained by differences in food availability, it is again concluded there is little difference in the diet of brown trout at the fish farms and littoral sites.

In November/December the data quality was affected by the low number of fish with food in their stomachs. In both habitats they had reverted to feeding on littoral invertebrates, however fish eggs were also consumed. This was particularly apparent at the fish farms where their importance was exaggerated by the small sample size.

Once the biases found in the data sets have been considered it is clear that there was considerable similarity in the types of food consumed by the brown trout in each habitat, with most of the variation being accounted for by differences in food availability. The high number of rainbow trout found around the fish farms do not cause brown trout in the same habitat to alter their feeding behaviour.

Rainbow trout cages vs rainbow trout littoral.

The results of the diet comparison of rainbow trout in the two habitats are shown in Table 4.11. In both habitats their was a high dependency on non-conventional prey e.g. fish farm pellets, stones, vegetation and ground bait, the small amount of conventional prey eaten was determined by the seasonal variation in its availability. Within the non-conventional component there was a large difference in the relative utilisation of prey categories between the two habitats, this being due to differences in food availability. The scope for meaningful analysis is limited by the low numbers of rainbow trout caught in the littoral habitat, particularly from July onwards. The main difference in the diets between the two habitats was the very high utilisation of fish farm pellets at the cages. Vegetation, stones and ground bait made the largest contribution in terms of volume to their diet at the littoral sites. The importance of the conventional component increased as the diet changed from winter to summer feeding mode. This could be due to the conventional food that is available in the surface/pelagic zone at that time requiring the same "upward looking" foraging technique that is used in the cages. It appears that the diet of rainbow trout in the two habitats was determined by their lack of expertise in foraging wild prey and that the differences between them were due to the differences in food availability in the two habitats, rather than the rainbow trout in the littoral habitat being marginalised through interspecific competition by brown trout.

4.3.1.3 Variation in the diet of brown trout & rainbow trout caught by anglers in 1987.

Brown trout caught by anglers displayed similar feeding behaviour as those caught in the gill nets over the same period. Their diet consisted of littoral invertebrates, surface/pelagic prey and a small amount of miscellaneous prey. This is typical of feeding behaviour switching from winter to summer feeding mode (Appendix 2 & Figure 4.14).

In April insect nymphs and larvae were the most important group of littoral invertebrates in their diet (%vol 39.6), with cased Trichoptera being particularly important. The Peracarida and Mollusca made up 16.7% and 12.5% vol. respectively, with the largest contribution made by one species being A. aquaticus (% occ 39.1, % vol 15.5) (Appendix 2). The surface/pelagic prey accounted for 27.0% of the volume in their diet. Pelagic pupae made the largest contribution (% vol. 16.9) many of which were unidentified Chironomidae, however those that could be identified further included Tanytarsus sp. and Tanypodinae. Trichoptera pupae and Ephemeroptera nymphs just prior to emergence were also eaten. The ground bait consisted of earthworms and maggots (Appendix 2).

In May a greater proportion of littoral invertebrates were consumed (% vol 74.3), this was largely at the expense of surface/pelagic prey whose share of the diet fell to % vol 21.3, and the miscellaneous component remained at a similar level (% vol 4.3) (Figure 4.14). Within the littoral component the emphasis changed from insect nymphs to Mollusca, this change almost entirely being due to the elevated importance of L. peregra. (% occ 64.6, % vol 33.9). In the insect nymph component a larger range of Plecoptera and Ephemeroptera were consumed, this was probably due to the larger sample size. Cased Trichoptera larvae were again important with A. nervosa, S. personatum and Lepidostoma hirtum (Fabricius) all making significant contributions.

Figure 4.14 Monthly variation in the diet of brown trout caught by anglers in 1987, expressed as percentage volume.

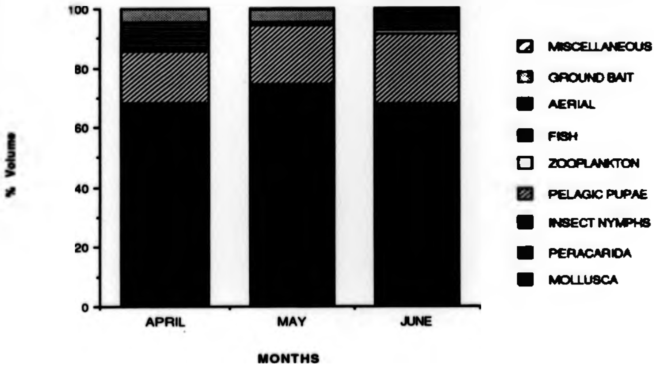
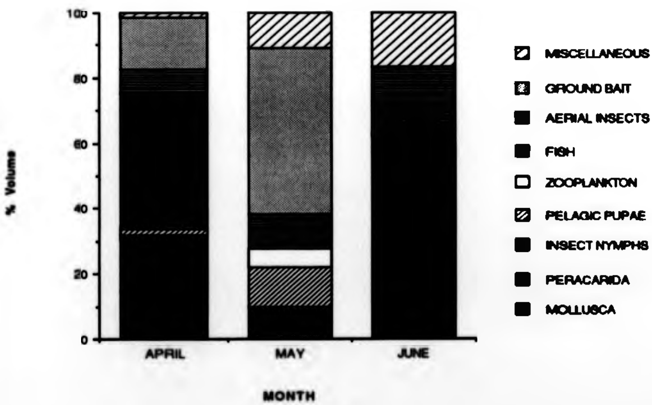


Figure 4.15 Monthly variation in the diet of rainbow trout caught by anglers in 1987, expressed as percentage volume.



In the surface/pelagic component the amount of pelagic pupae consumed increased, and the proportion of aerial insects decreased. Most of the Chironomidae pupae could not be identified, however those that could included Arctopelopia sp., Orthocladius sp., Cricotopus sp. and Paratrichocladius sp.. The most important orders in the aerial component were the Diptera and Ephemeroptera. The small amount of zooplankton eaten consisted of D. hyalina and B. longimanus (Appendix 2).

In June only six fish were caught, therefore the scope for analysis was limited. There was a small decline in the importance of littoral prey % vol 69.7, and an increase in the importance of the surface/pelagic component % vol 31.2 (Figure 4.14). Of the littoral invertebrates consumed Peracarida were the most important followed by Mollusca and insect nymphs. The elevated status of Peracarida was due to the increased consumption of A. aquaticus (%vol 50.0, % occ 37.5), the largest contribution made by a single species, a small amount of G. pulex was also eaten. Mollusca were only represented by L. peregra and P. fontinalis, and in the insect nymph category each species was consumed in similar quantities (Appendix 1). In the surface/pelagic component pelagic pupae were consumed in greatest quantities. The remainder of their diet was made up of aerial insects and zooplankton.

The major difference between the diets of brown trout caught by gill netting and angling was the lower utilisation of surface/pelagic prey by those caught by the anglers. This was unexpected as most of these fish would have been caught in the surface/pelagic zone on lures designed to mimic the prey found in that habitat.

In April 50.9% (volume) of the rainbow trout diet consisted of surface/pelagic prey, 31.7% (volume) of littoral prey, and 17.5% (%

volume) of non-conventional prey. The importance of the unidentified fish in the surface/pelagic component was overstated, as it was only eaten by 2 rainbow trout. In the littoral invertebrate component Peracarida and Mollusca were of similar importance, (% vol 15.5) and (% vol 14.8) respectively. The insect nymphs were less important, (% vol 1.4). The non-conventional component largely comprised ground bait, however some vegetation was also consumed (Appendix 2 & Figure 4.15).

In May their diet was dominated by non-conventional prey (% vol 61.8), with smaller amounts of surface/pelagic prey (% vol 28.5) and littoral invertebrates (% vol 9.8) also being eaten. The ground bait component was dominated by one large earth worm, (% vol 23.9) (Appendix 2). The surface/pelagic component consisted of pelagic pupae, aerial insect and zooplankton in decreasing importance. In the pelagic pupae, Chironomidae were consumed in the largest volume, with Chironomus sp. being particularly important. Also included were Ephemeroptera exuviae which are of little nutritional value. The Diptera made the largest contribution (% occ 21.0, % vol 5.6) of the aerial insects, with Hemiptera, Trichoptera and Plecoptera also being consumed. Zooplankton only contributed a small volume to the diet, although D. hyalina was found in 36.8% of the stomachs examined. All of the littoral invertebrates groups were consumed in similar quantities.

By contrast in June littoral invertebrates were the most important group in their diet (volume 62.1%), the remainder consisting of surface/pelagic prey (% vol 21.4) and non-conventional prey (% vol 16.5%). Insect nymphs were the most important group of littoral invertebrates consumed with Ephemera danica Muller (% occ 100, % vol 61.3) being the most important species, trace amounts of Plecoptera, Coleoptera and Trichoptera were also eaten (Appendix 2). Aerial insects were the most important group in the surface/pelagic component with

Diptera and Ephemeroptera being consumed in the largest quantities. The pelagic pupae were only represented by Chironomidae, of which *Chironomus* sp. was the most important. Only vegetation was consumed in the non-conventional component (% occ 22.2, % vol 16.4).

In each month except June rainbow trout caught by angling had been feeding most heavily in the surface/pelagic zone. Although the amount of non-conventional prey consumed was lower than those caught by gill netting it was still considerably higher than the amount consumed by brown trout.

4.3.1.4 Comparison of brown trout and rainbow trout diets caught by angling in 1987.

The similarity in the diets of brown trout and rainbow trout was measured by Schoener's Overlap Index (Schoener, 1970). This demonstrated very little similarity in the months examined (Table 4.12). In general terms brown trout obtained the majority of their prey by feeding on the bottom, and rainbow trout from the surface/pelagic zone, the only exception to this occurred in June when rainbow trout consumed a large quantity of *E. danica*. They were all final instars and their exuviae had been eaten by rainbow trout in the previous month. It is therefore highly likely that they were close to emerging and behaving in a manner that made them more obvious to the feeding trout. In common with the results of the gill netting survey rainbow trout consumed a greater proportion of non-conventional prey than brown trout. This is again attributable to their limited range of prey search images.

These results show that rainbow trout have a preference for surface/pelagic prey when both this and bottom-dwelling prey are available. Brown trout show a marked preference for bottom-dwelling prey. Further experimentation would be required to ascertain if this is an example of niche divergence shaped by inter-specific competition, or whether the difference is due to the feeding behaviour learned by rainbow trout in the cages.

4.3.1.5 Seasonal variation in the diet of rainbow trout and brown trout caught in the 1988 gill netting survey.

Brown trout-littoral.

The diet of brown trout in March was based entirely on bottom-dwelling invertebrates; Mollusca, Peracarida and insect nymphs/larvae all being consumed. The most important of these were the insect nymphs which included Plecoptera, Trichoptera and Diptera. P. jenkinsi were the most important Mollusca in the diet (%occ 33.0, % vol 15.3), and G. lacustris were the most important Peracarida (% occ 13.0, % vol 9.7). A small amount of vegetation, stones and anglers maggots was also consumed (Appendix 3 & Figure 4.16).

In May their diet was in transition from winter to summer feeding mode, with both surface/pelagic and benthic organisms being consumed (Figure 4.16). P. jenkinsi and G. lacustris were again consumed but were less important than they had been in March. The diversity of insect nymphs and larvae in their diet was slightly lower than it had been the previous month, Athripsodes aterrimus (Stephens) occurred in 27.7% of the stomachs but due to its small size made up 7.1% of the diet by volume. The pelagic pupae were entirely represented by Chironomus sp. and were the most important component in the diet. A small amount of zooplankton, D. hyalina was eaten, and in the non-conventional category stones and maggots were consumed (Appendix 3).

In July, the brown trout's diet was based almost exclusively on organisms found in the pelagic zone, however in common with 1987 a

Figure 4.16 Monthly variation in the diet of brown trout caught in the littoral zone in 1988, expressed as percentage volume.

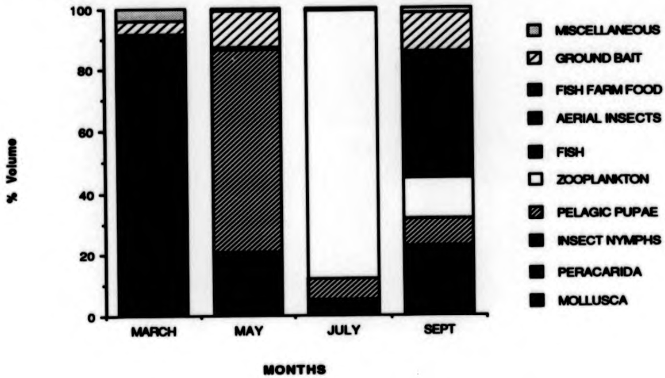
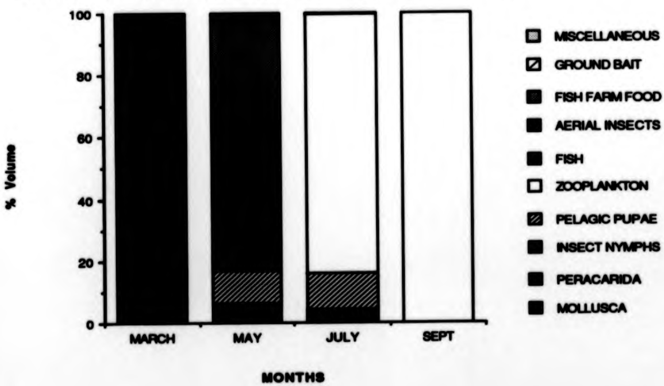


Figure 4.17 Monthly variation in the diet of brown trout caught at the fish farms in 1988, expressed as percentage volume.



small proportion of bottom-dwelling invertebrates were retained (Figure 4.16). Zooplankton was the most important single group in their diet with the following species-D. hyalina (% occ 82.1, % vol 38.9); P. pediculus (% occ 71%, % vol 8.2); and B. longimanus (% occ 75.0, % vol 37.9)-being the most important. The pelagic pupae were of less significance than they were in May with Macropelopia sp. and an unidentified Trichoptera species replacing Chironomus sp. Insect nymphs whose adult stages have flight periods in the late summer and the Mollusca and Peracarida, P. jenkinsi and G. lacustris, made up the bottom-dwelling component (Appendix 3).

In September the brown trout diet was in transition from summer to winter feeding, with an equal preference being shown for bottom and surface/pelagic components. The only category not consumed was fish farm food (Figure 4.16). The small range of bottom-dwelling invertebrates in the diet at this time is a reflection of their low availability. In the surface/pelagic component zooplankton, pelagic pupae, aerial insects and fish were all consumed. The importance of fish in the diet in terms of volume is overstated as only one was consumed. Ground bait was also eaten.

Brown trout-Braevallich.

Their diet in March was entirely composed of bottom-dwelling invertebrates; Mollusca and insect nymphs/larvae (Figure 4.17). The Mollusca were represented by L. peregra (% occ 66.7, % vol 35.0) and P. jenkinsi (% occ 100.0, % vol 14.0), the most important insect larvae in the diet was the Trichoptera A. nervosa (% occ 33.3, % vol 31.1) (Appendix 3). The quality of data in March was adversely affected by the small sample size.

The transitional month of May was again marked by an increase in the consumption of surface/pelagic prey and a decrease in bottom-dwelling prey (Figure 4.17). L. peregra and P. jenkinsi were again important, and in common with brown trout feeding in the littoral zone A. aterrimus was also consumed. Prey from the surface/pelagic zone were dominated by pelagic pupae, the most important of which was Chironomus sp. (% occ 80.0, % vol 10.5), a small amount of unidentified Chironomidae pupae and one unidentified adult Diptera were also eaten. Fish farm pellets contributed the largest volume to the diet (% vol 83.2), but occurred in only 20.0% of the stomachs, therefore in terms of the populations feeding behaviour their importance is overstated (Appendix 3).

In July the diet was dominated by organisms found in the pelagic zone, but in common with the brown trout diets discussed previously a small proportion of bottom-dwelling prey was retained. The pelagic part of the diet largely comprised zooplankton, aerial insects and pupae (Figure 4.17). The benthic component consisted of the stone fly Nemoura avicularis Morton and the leach Erpobdella octoculata (L.) and an unidentified Chironomidae larvae. In September only one stomach was examined and it contained zooplankton.

Rainbow trout-littoral.

In March the diet was dominated by non-conventional prey with fish farm food occurring in 50.0% stomachs and contributing 54.4% to the total volume, smaller amounts of ground bait and miscellaneous prey items were also consumed. The littoral invertebrate component consisted of P. jenkinsi, G. lacustris, L. hirtum and an unidentified Chironomidae larvae (Figure 4.18 and Appendix 3).

In May the change from summer to winter feeding in the small number of rainbow trout caught was more abrupt than was observed in brown trout

Figure 4.18 Monthly variation in the diet of rainbow trout caught in the littoral zone in 1988, expressed as percentage volume.

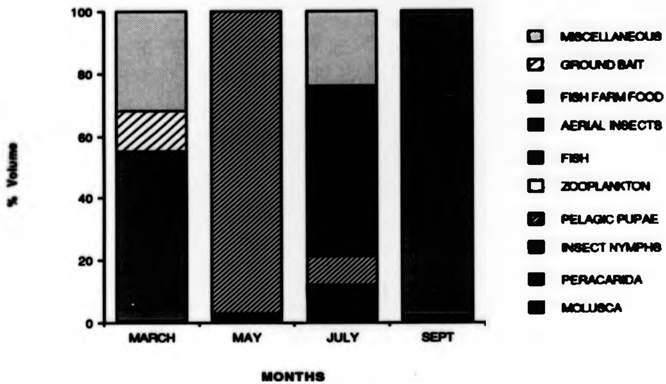
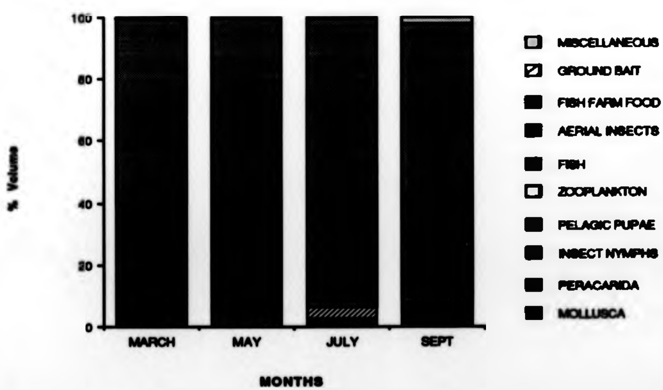


Figure 4.19 Monthly variation in the diet of rainbow trout caught at the fish farm in 1988, expressed as percentage volume.



at that time (Figure 4.18). They had only consumed conventional prey with pelagic pupae dominating their diet. Chironomus sp. occurred in two of the three stomachs sampled and contributed 95.0% of the volume. The benthic component consisted of Mollusca, Trichoptera larvae and large Crustacea (Appendix 3). The quality of the data was adversely affected by the small sample size.

In July the majority of their diet was again obtained by foraging at the surface, the emphasis changing from pelagic pupae to aerial insects (Figure 4.18). In common with brown trout caught in July the Chironomus sp. were replaced by Trichoptera pupae. Vegetation and a small amount of benthic organisms were also consumed. The data quality data was adversely affected by the small sample size.

In September their diet was dominated by fish farm food (% occ 42.9, % vol 97.2) (Appendix 3). The remainder of the diet comprised aerial insects and miscellaneous prey.

Rainbow trout-Braevallich.

In each of the months sampled fish farm food dominated the diet by volume. However its percentage occurrence was lower than in the corresponding period in 1987. The consumption of conventional prey followed the seasonal pattern outlined previously (Appendix 3 & Figure 4.19).

In March their diet was dominated by fish farm food (% occ 33.3, % vol 59.6). Sticklebacks were consumed but their importance was overstated as they were only consumed by one fish. The conventional component of the diet comprised bottom-living invertebrates.

In May the diet was almost exclusively based on fish farm food (% occ

60.0, % vol 99.0). The only conventional food consumed was the pupae of Chironomus sp, from the surface/pelagic zone (Appendix 3).
In July the diet was dominated by fish farm food (% occ 44.4, % vol 93.1). The conventional component was again predominantly pelagic pupae, with Chironomus sp. being replaced by Trichoptera pupae. A small amount of bottom-dwelling invertebrates was also consumed, including E. ignita, Chironomus sp. larvae and E. octoculata (Appendix 3). Hirudinea were rarely eaten by brown trout or rainbow trout in Loch Awe, however Hunt & Jones (1972) reported that they were of major dietary significance for brown trout in Llyn Alaw.

In September fish farm food dominated the diet in terms of volume but only occurred in one stomach. The other fish had been feeding on prey from the surface/pelagic zone and the littoral zone. Mollusca, Peracarida and insect nymphs were all consumed from the littoral zone. Pelagic pupae, aerial insects and zooplankton were all consumed from the surface/pelagic zone. In the zooplankton component C. viridis and C. abyssorum were present. This is interesting as the former had previously only been found in the stomachs of Arctic charr (S. alpinus), and the latter had been consumed by fish on only a few occasions despite being the most abundant zooplankton species found in Loch Awe. A small amount of ground bait and miscellaneous prey were also consumed.

4.3.1.6 Diet overlap in brown trout and rainbow trout caught at Braevallich and the littoral sites in 1988.

Brown trout vs rainbow trout-littoral.

The overlap index of the 2 species diets in March was very low (0.09) (Table 4.13). The difference lies in the relative importance of conventional and non-conventional food, brown trout having a greater dependence on the former and rainbow trout a greater dependence on the

Table 4.13 **Overlap index values for the diets of brown trout and rainbow trout feeding at Braevallich and the littoral sites in 1988.**

	March	May	July	September
BT vs RT, B	0.01	0.84	0.06	0.01
BT vs RT, L	0.09	0.69	0.11	0.03
B vs L, BT	0.68	0.13	0.95	0.13
B vs L, RT	0.55	0.01	0.07	0.91

BT=Brown Trout, R=Rainbow Trout, L=Littoral, B=Braevallich latter. The low utilisation of conventional prey by rainbow trout means that it is highly unlikely that they will have a deleterious effect on the brown trout. The consumption of fish farm food shows that there is movement by rainbow trout away from the immediate vicinity of the fish farm. Their high utilisation of ground bait and miscellaneous prey categories compared to brown trout is further evidence of their lack of experience in foraging wild prey.

The overlap index in the two species' diets in May was comparatively high 0.69 (Table 4.13), indicating a degree of similarity in their diets, although it has to be remembered that there were only three stomachs in the rainbow trout sample. Both species fed most heavily on *Chironomus* sp. pupae, with rainbow trout having the greater dependence on them. The main difference in their diets was the brown trouts' greater dependence on bottom-dwelling invertebrates. The more complete utilisation of surface/pelagic prey by rainbow trout when it became available is noted. It is unlikely that the two species would have been competing for the Chironomidae pupae as competition only occurs when a resource is limited, and it would appear from the level of consumption that pupae were in superabundance, probably just prior to a large hatch. The small number of rainbow trout found in the littoral zone will also reduce the potential conflict between the two species.

As only 2 rainbow trout were caught in the littoral habitat in July the scope for meaningful comparisons between the two species' diets is limited. The value of the overlap index was low, 0.11 (Table 4.11), indicating little similarity. The diet of brown trout was dominated by zooplankton, whereas aerial insects were the most important component in the rainbow trout diet. Subtle differences of this type can be indicative of interspecific competition, but it is unclear if it could be implicated in this situation. Again it is highly unlikely that the low number of rainbow trout would adversely effect the brown trout population at this time.

In September the value of the overlap index was again low, 0.03 (Table 4.13). The conventional component of the brown trout diet was in transition from summer to winter feeding mode, but small amounts of miscellaneous prey items and ground bait were also consumed. By comparison the rainbow trout diet was dominated by non-conventional prey; fish farm food and miscellaneous prey. They also consumed a small amount of adult Diptera. These differences reflect the brown trout's greater reliance on bottom prey, even when there is still prey available in the surface/pelagic zone; and the rainbow trout's greater reliance on non-conventional prey and conventional prey from the surface/pelagic zone.

Brown trout vs rainbow trout-Braevallich.

The overlap index for the two species in March at Braevallich was very low 0.01 (Table 4.13). The brown trout diet was based entirely on Mollusca and insect nymphs, compared to the rainbow trout's which was composed of fish farm food, fish and bottom-dwelling invertebrates. The two species fed on the same bottom-dwelling invertebrates but they were of greater significance in the brown trout diet. The rainbow trout's high dependence on fish farm food and low utilisation of conventional prey means that it is unlikely that interspecific competition will occur.

In May the scope for meaningful analysis was limited by the small sample sizes. The comparatively high overlap index value 0.84 (Table 4.13) masks the real variation in the diet of the two species. The fish farm food eaten by the two species dominated the results in terms of volume, however in terms of occurrence it is clear that it is of greater importance to the rainbow trout (%occ 60), than to the brown trout (%occ 20.0) (Appendix 3). The diet of brown trout was in transition from winter to summer feeding, whereas the conventional component of the rainbow trout diet changed abruptly from winter to summer with only pelagic pupae being eaten.

In July there was little similarity in the two species' diets. Fish farm food was the largest single component in the rainbow trout's diet, with smaller amounts of pelagic pupae, vegetation and insect nymphs also being eaten. The brown trout diet was largely made up of prey from the surface/pelagic zone, but insect nymphs were also consumed. Pelagic pupae, and insect nymphs were consumed by the two species. Because conventional prey contribute such a small part to the rainbow trouts' diet it is unlikely that the overlap between the two species diets would be sufficient to create interspecific competition.

In September only one brown trout was caught therefore no comparisons can be made between the two species.

Brown trout Braevallich vs littoral.

The 4 overlap indices were March 0.68, May 0.13, July 0.95 and September 0.13 (Table 4.13). The low values obtained in May and September were due to a small number of brown trout consuming non-conventional prey. The diversity of conventional prey in the brown trout diet at the cages was considerably lower than it was in the littoral habitat. A possible explanation for this was the small sample caught at the fish farm site. Their diet in both habitats followed the winter and summer feeding modes discussed previously. Therefore it is clear that the brown trout diet is not adversely affected by the presence of rainbow trout at the cages.

Rainbow trout Braevallich vs littoral.

The overlap index values in March, May, July and September are 0.55, 0.01, 0.07 and 0.91 respectively (Table 4.13). In March, fish farm food was the largest component of the rainbow trout's diet in both habitats, indicating that there had been movement between Braevallich and littoral sites. Bottom-dwelling invertebrates were also eaten in the two habitats. In May there was a sharp contrast in their diets between the two sites, those at the cages fed almost entirely on fish farm food, whilst those in the littoral zone fed almost exclusively on pelagic pupae. The marked change from winter to summer feeding is noted in the rainbow trout caught in the littoral zone. Again in July there was a marked difference in the diet of rainbow trout at the two sites. Those at the cages fed most heavily on fish farm food, whilst those caught in the littoral zone fed most heavily on bottom-dwelling invertebrates, surface/pelagic prey, and vegetation. These results are indicative of the differences in food availability between the sites, although the rainbow trout sample from the littoral sites was small and may be unrepresentative. In September the broad similarity in their diets was due to the high proportion of fish farm food consumed at both sites, this again being indicative of fish movement away from the fish farm. At the littoral sites small amounts of aerial insects and miscellaneous prey items were also consumed, whilst at the cages their diet included bottom-dwelling prey.

4.3.2 Analysis of the amount of food consumed.

4.3.2.1 Comparison of the number of brown trout and rainbow trout with empty stomachs.

The number of empty stomachs expressed as a percentage of all the brown trout and rainbow trout stomachs examined at the fish farm and littoral sites in the gill netting survey are shown in Table 4.14.

Table 4.14 **The number of brown trout and rainbow trout in the fish farm and littoral habitats with empty stomachs expressed as a percentage of the number of stomachs examined in each sampling period.**

	J/F	M/A	M/J	J/A	S/O	N/D
Brown trout Cages	42.1	31.5	22.2	-	30.4	33.3
Rainbow trout Cages	42.7	16.2	33.3	29.3	18.0	25.2
Brown trout Littoral	32.4	14.1	12.5	0	28.6	56.3
Rainbow trout Littoral	23.5	25.0	-	0	20.0	36.4

Table 4.15 **The number of brown trout and rainbow trout caught by anglers in 1987 with empty stomachs expressed as a percentage of the number of stomachs examined in April, May and June.**

	April	May	June
Brown Trout	0	3.0	0
Rainbow trout	0	15.8	0

Both species in the littoral zone and the brown trout caught at the cages all had a lower proportion of empty stomachs in the summer than the winter. This is in agreement with the seasonal variation in feeding activity described by Swift (1961) in brown trout. The rainbow trout caught at the fish farms had a greater than expected proportion of empty stomachs during the summer. This coincided with the period when rainbow trout were least successful in securing fish farm pellets. It implies that rainbow trout find it difficult to feed on other prey when they are not feeding on the pellets that pass through the cages. In both species a greater proportion of empty stomachs was recorded at the fish farms than at the littoral sites, although the difference was not significant ($P>0.05$).

In each month examined both species caught by angling had a low percentage of empty stomachs (Table 4.15), this being attributable to the fact that they were actively feeding at the time of capture. This implication can be drawn as the lures used by anglers are designed to imitate the invertebrates that they feed on. In May, the only month when empty stomachs were recorded rainbow trout had a greater proportion than brown trout.

4.3.2.2 Seasonal variation in food consumption by fish caught in the 1987 gill netting survey.

The seasonal variation in the feeding activity of brown trout, rainbow trout, Arctic charr, Atlantic salmon and perch was examined by plotting their mean fullness index (MFI) in the two monthly sampling periods. The fullness index was preferred to volume as it compensates for any bias that may be incorporated into the data set by the samples being comprised of different sized fish. The feeding of brown trout and rainbow trout was considered further by examining the mean volume per stomach (MVS) in length classes 0-199, 200-299, 300-399 and 400+mm.

Brown trout littoral Mean Fullness Index (MFI).

The MFI rises from January/February to its maximum in May/June, after which it declined steadily throughout the year to its lowest level in November/December (Figure 4.20). The timing of the peak coincided with the longest day; similar findings were reported by Swift (1961), Ball (1961) and Hunt & Jones (1972), the latter also reported a peak in January. Although no peak was observed in the Loch Awe data set, the trend at that time was upwards. The increase in feeding at this time was probably due to the fish regaining condition after spawning.

Brown trout littoral Mean Volume Per Stomach (MVS).

When the MVS of individual length classes was examined, length classes 0-199mm (except for a small decline in July/August) and 200-299mm followed a similar pattern to the MFl (Figure 4.21), there was considerable variation in the amount of food consumed by the 200-299mm length class in May/June. A very erratic picture emerged in the 300-399 length class (Figure 4.22). It had two high peaks in May/June and September/October with a large drop occurring between them in July/August. As the data points in May/June and September/October were only based single observations it is highly unlikely that they accurately represent feeding behaviour in the population.

Brown trout fish farms Mean Fullness Index (MFI).

The MFl was at its highest level in January/February and May/June (Figure 4.20). This was similar to the pattern outlined by Hunt & Jones (1972). The first peak as stated previously was probably related to fish improving their condition after spawning and the second one to their seasonal feeding pattern which is controlled by temperature and day length. No data was available for July/August, and the increase that occurred between September/October and November/December was contrary to the findings in the littoral habitat. The sample in

Figure 4.20 The mean fullness index (MFI) (+S.D) of brown trout caught in the littoral, pelagic, and fish farm habitats in 1987.

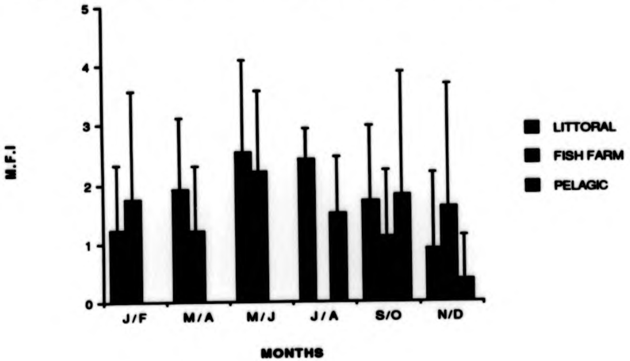


Figure 4.21 Seasonal variation in the mean volume (+S.D) of food consumed by brown trout in length classes 0-199mm and 200-299mm in the littoral zone in 1987.

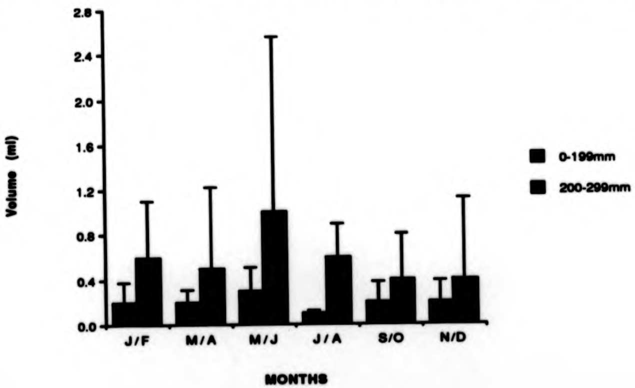


Figure 4.22 Seasonal variation in the mean volume/stomach (+S.D) of brown trout in length class 300-399mm at the littoral sites in 1987.

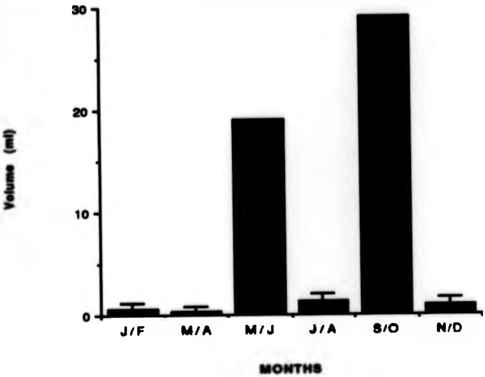
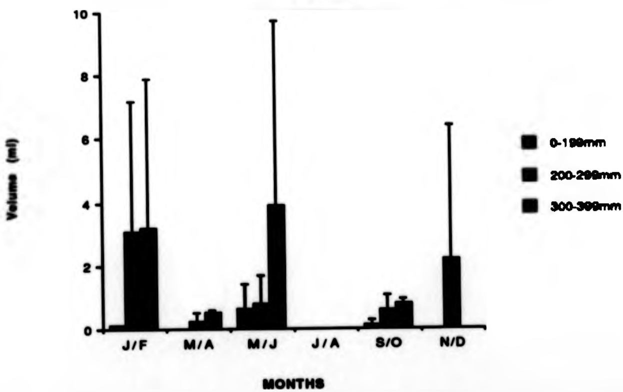


Figure 4.23 Seasonal variation in the mean volume (+S.D) of food consumed by brown trout feeding around the fish farms in 1987.



November/December was small and likely to have been unrepresentative. The higher standard deviations associated with the fish farm MFI's compared to the littoral ones is explained by the smaller samples in the former.

Brown trout, fish farm, Mean Volume Per Stomach (MVS).

The MVS for individual length classes did not follow any distinct pattern. It is likely that the MVS's and their standard deviations were affected by a small number of fish in the samples consuming fish farm pellets or ground bait, which have a higher unit volume than conventional prey (Figure 4.23).

Brown trout pelagic, Mean Fullness Index (MFI).

Data was only available between July/August and November/December. There was a slight increase from July/August to September/October followed by a large decline in November/December (Figure 4.20). These findings are in agreement with seasonal food availability in the surface/pelagic zone, and with the diminution of appetite found in salmonids as the water temperature falls.

Rainbow trout littoral, Mean Fullness Index (MFI).

The rainbow trout MFI followed a similar seasonal pattern to brown trout feeding in the littoral habitat, it increased from winter to spring and declined from summer to winter (Figure 4.24). Unfortunately no data was available for M/J.

Rainbow trout littoral, Mean Volume Per Stomach (MVS).

When the MVS was examined by individual length class it was difficult to ascertain any meaningful trends due to the small sample size in some sampling periods (Figure 4.25). This was also reflected in the high standard deviations associated with some of the means.

Figure 4.24 The mean fullness index (+S.D) of rainbow trout caught in the littoral, fish farm and pelagic habitats in 1987.

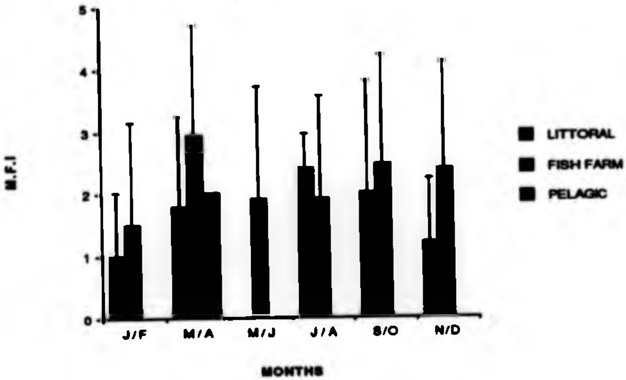
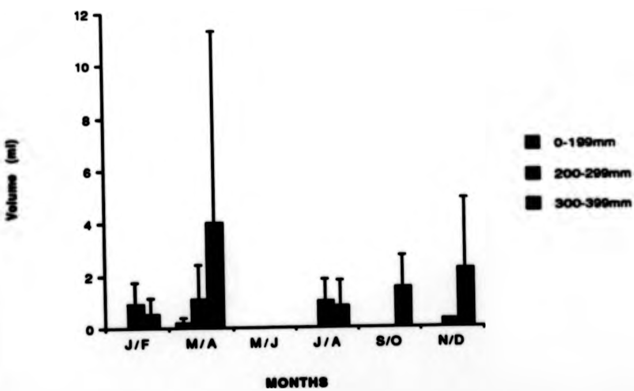


Figure 4.25 Seasonal variation in the mean volume/stomach (+S.D) of rainbow trout caught in the littoral zone in 1987.



Rainbow trout fish farm, Mean Fullness Index (MFI).

In contrast to the clearly defined MFI summer peaks described previously, rainbow trout caught at the fish farms fed less successfully at this time than in the spring and autumn (Figure 4.24).

Rainbow trout fish farm, Mean Volume Per Stomach (MVS).

The MVS of length classes 0-199mm, 200-299mm and 300-399mm followed a similar seasonal pattern to their MFI, each showing a reduction in summer feeding activity (Figure 4.26). The data set for the 400+mm length class behaved in quite an erratic manner, the most likely reason for this being the small bimonthly samples that it was derived from (Figure 4.27). Contrary to the feeding pattern observed in brown trout and in agreement with rainbow trout caught in the littoral zone each length class fed heavily in November/December. The high standard deviations associated with many of the MVS's in this group indicates a large amount of variation within the samples.

The summer trough in their MVS and MFI corresponded with the period when rainbow trout caught at the fish farms had a high proportion of empty stomachs. This suggests that not only do fewer rainbow trout feed in the summer, but those that do are less successful. Implying that there is a shortage of their preferred food at that time and that they have difficulty switching to other food types.

Rainbow trout pelagic.

Insufficient rainbow trout consumed food in the pelagic zone for any meaningful analysis to be performed (Figure 4.24).

Perch littoral, Mean Fullness Index (MFI).

Their MFI increased from May/June to July/August and remained at that level until they migrated back to deeper water at the end of October.

Figure 4.26 Seasonal variation in the mean volume/stomach (+S.D) of rainbow trout in length classes 0-199mm to 300-399mm caught around the fish farms in 1987.

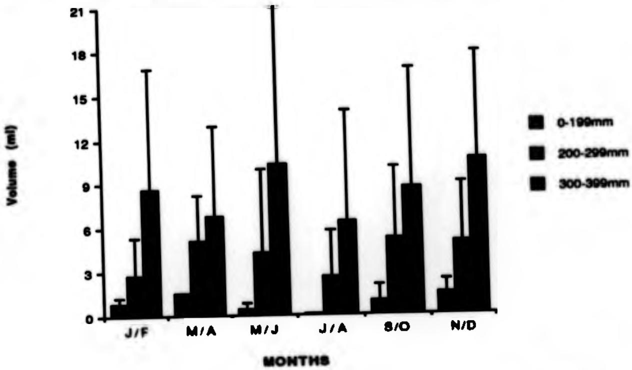
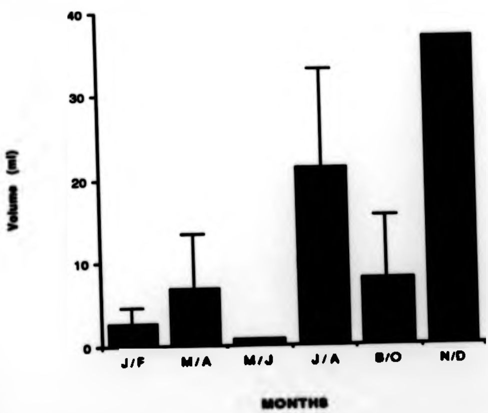


Figure 4.27 Seasonal variation in the mean volume/stomach (+S.D) of rainbow trout in length class +400mm caught at the fish farms in 1987.



In September/October their MFI was 2.5 which was higher than any other species at that time of the year in Loch Awe (Figure 4.28).

Perch fish farm, Mean Fullness Index (MFI).

The data was again restricted to the summer months when perch inhabit the shallow littoral zone. In contrast to perch in the littoral zone their feeding was at its highest level in May/June, after which it declined and then stabilised prior to their migration back to their winter habitat (Figure 4.28).

Arctic charr.

Each category except benthic charr caught in the benthic zone suffers from a paucity of data, this being reflected in the high standard deviations associated with some of the means, this limits the scope for analysis. No analysis is made on the pelagic charr data.

Benthic Arctic charr-benthic, littoral, fish farm and pelagic habitats, Mean Fullness Index (MFI).

In each habitat their feeding behaviour followed a similar pattern. Their MFI was at its highest level in the summer and fell to its lowest level at the end of the year (Figure 4.29). This reduction corresponds with an increase in their mean gonad weight. Similar to the relationship observed in brown trout.

Atlantic salmon littoral Mean Fullness Index (MFI).

No analysis performed, due to the small sample size.

Atlantic salmon fish farm, Mean Fullness Index (MFI).

Stomach samples were only available between July/August and November/December. Contrary to the findings for other indigenous species there was no decline in their MFl in early winter, however

Figure 4.28 The mean fullness index (MFI) (+S.D) of perch caught in the littoral and fish farm habitats in 1987.

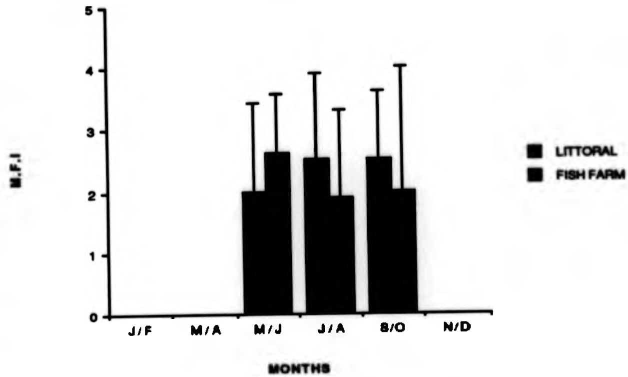
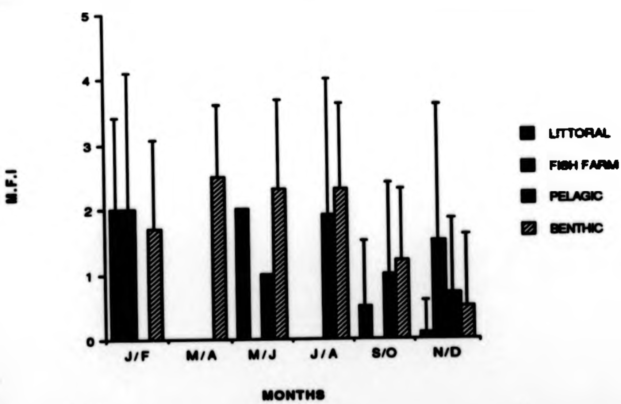


Figure 4.29 The mean fullness index (MFI) (+S.D) of benthic Arctic charr caught in the littoral, fish farm, pelagic and benthic habitats in 1987.



their MFI in November/December also had the highest standard deviation (Figure 4.30). Metcalfe et al. (1986) demonstrated that juvenile salmon can maintain their summer levels of food intake over the winter prior to smolting.

4.3.2.3 A comparison of the volume of food consumed by brown trout and rainbow trout caught in the fish farm and littoral habitats in 1987.

Brown trout vs rainbow trout, littoral.

Ten comparisons were performed, brown trout had a higher MVS in four of them and rainbow trout a higher MVS in six of them. None of the differences were statistically significant (Table 4.16). The comparison in the 300-399mm length class in September/October was heavily biased by a large fish which had been feeding heavily on Mollusca. Therefore in terms of volume neither species had a feeding advantage in the littoral habitat.

Brown trout vs rainbow trout, fish farms.

In the twelve comparisons performed, rainbow trout and brown trout had a higher MVS on 10 and 2 occasions respectively. Three of the comparisons in which rainbow trout had a higher MVS were statistically significant, two at ($P<0.05$) and one at ($P<0.001$) (Table 4.17). The high MVS recorded in rainbow trout is a reflection of their high dependence on fish farm pellets which have a higher unit volume than conventional prey items consumed by brown trout. Therefore although rainbow trout consumed a greater volume of food they were feeding on different prey types.

Fish farm vs littoral, brown trout.

There was no consistent trend in the amount of food consumed by brown trout in either habitat. In the twelve comparisons performed each had

Figure 4.30 The mean fullness index (MFI) (+S.D) of Atlantic salmon caught at the fish farms in 1987.

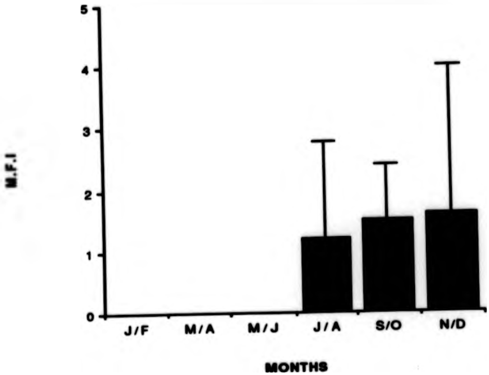


Table 4.16 A comparison between the mean volume (ml) of food consumed by the rainbow trout and brown trout caught in the littoral habitat in each length class in 1987.

LC (mm)		J/F	M/A	M/J	J/A	S/O	N/D
0-199	RT	-	0.17	-	-	-	-
	BT	0.19	0.15	0.34	0.10	0.20	0.24
	S	-	NS	-	-	-	-
200-299	RT	0.83	1.10	-	1.08	-	0.20
	BT	0.56	0.52	1.02	0.59	0.44	0.39
	S	NS	NS	-	NS	-	NS
300-399	RT	0.49	4.02	-	0.79	1.49	2.21
	BT	0.55	0.31	19.00	1.23	30.00	0.86
	S	NS	NS	-	NS	NS	NS
400+	RT	-	-	-	-	-	0.06
	BT	-	-	-	-	-	-
	S	-	-	-	-	-	-

LC=Length class, RT=Rainbow trout, BT=Brown trout, S=Significance

Table 4.17 A comparison between the mean volume (ml) of food consumed by the rainbow trout and brown trout caught in the fish farm habitats and in each length class in 1987.

LC (mm)		J/F	M/A	M/J	J/A	S/O	N/D
0-199	RT	0.78	1.50	0.39	0.10	0.97	1.26
	BT	0.08	-	0.63	-	0.13	-
	S	NS	-	NS	-	NS	-
200-299	RT	2.73	5.10	4.29	2.62	5.24	4.85
	BT	3.06	0.22	0.77	-	0.56	2.21
	S	NS	***	NS	-	*	*
300-399	RT	8.59	6.76	10.33	6.36	8.53	10.45
	BT	3.17	0.45	3.87	-	0.8	-
	S	NS	NS	NS	-	NS	-
400+	RT	2.61	6.93	0.80	21.33	7.91	36.67
	BT	-	-	18.80	-	-	-
	S	-	-	-	-	-	-

LC=Length class, RT=Rainbow trout, BT=Brown trout, S=Significance

J/F 0-199, t-test

a greater MVS on six occasions, only one of which was statistically significant (P<0.05), in favour of those feeding at the cages (Table 4.18). The results show that the large number of rainbow trout around the cages do not adversely affect brown trout feeding success in that area.

Fish farm vs littoral, rainbow trout.
In each of the eleven comparisons performed rainbow trout caught at the cages had a higher MVS than those in the littoral zone, four of which were statistically significant, one at (P<0.05) and three at (P<0.01) (Table 4.19). The results give a clear indication of the high food availability, and utilisation of it by those around the fish farms. The high feeding success that they have around the cages compared to the littoral sites, is reflected in their highly localised distribution around the fish farms.

4.3.2.4 Volume of food consumed by brown trout and rainbow trout caught in angling competitions in 1987.

Brown trout, Mean Fullness Index (MFI).
Their MFI declined from April to May before increasing by a small amount in June (Figure 4.31). This is contrary to the findings of the gill netting survey in which their MFI increased over this period.

Brown trout, Mean Volume Per Stomach (MVS).
Contrary to the results of the MFI where an overall decline was observed, an overall increase in the MVS of each length class was recorded (Figure 4.32). A possible explanation for this discrepancy is that the fish in June within each length class were larger, this would result in a disproportionate increase their MVS over their MFI.

Table 4.18 **A comparison between the mean volume (ml) of food consumed by the brown trout caught in the littoral and fish farm habitats in each length class in 1987.**

LC (mm)		J/F	M/A	M/J	J/A	S/O	N/D
0-199	FF	0.08	-	**0.63**	-	0.13	-
	LT	**0.19**	0.15	0.34	0.1	**0.20**	0.24
	S	NS	-	NS	-	NS	-
200-299	FF	**3.06**	0.22	0.77	-	**0.56**	**2.21**
	LT	0.56	**0.52**	**1.02**	0.59	0.44	0.39
	S	*	NS	NS	-	NS	NS
300-399	FF	**3.17**	**0.45**	3.87	-	0.8	-
	LT	0.55	0.31	**19.00**	1.23	**30.00**	0.86
	S	NS	NS	NS	-	***	-
400+	FF	-	-	18.80	-	-	-
	LT	-	-	-	-	-	-
	S	-	-	-	-	-	-

LC=Length class, FF=Fish farm, LT=Littoral, S=Significance

J/F 0-199 & M/J 300-399, t-test.
J/F 300-399 & N/D 200-299, Mann Whitney test

Table 4.19 **A comparison between the mean volume (ml) of food consumed by the rainbow trout caught in the littoral and fish farm habitats in each length class in 1987.**

LC (mm)		J/F	M/A	M/J	J/A	S/O	N/D
0-199	FF	0.78	**1.5**	0.39	0.10	0.97	1.26
	LT	-	0.17	-	-	-	-
	S	-	NS	-	-	-	-
200-299	FF	**2.73**	**5.10**	4.29	**2.62**	5.24	**4.85**
	LT	0.83	1.1	-	1.08	-	0.2
	S	*	**	-	NS	-	NS
300-399	FF	**8.59**	**6.76**	10.33	**6.36**	**8.53**	**10.45**
	LT	0.49	4.02	-	0.79	1.49	2.21
	S	**	NS	-	NS	NS	**
400+	FF	2.61	6.93	0.80	21.33	7.91	**36.67**
	LT	-	-	-	-	-	0.06
	S	-	-	-	-	-	NS

LC=Length class, FF=Fish farm, LT=Littoral, S=Significance

M/A 0-199 & N/D 200-299 t-test.

Figure 4.31 The monthly mean fullness index (MFI) (+S.D) of brown trout and rainbow trout caught by anglers in 1987.

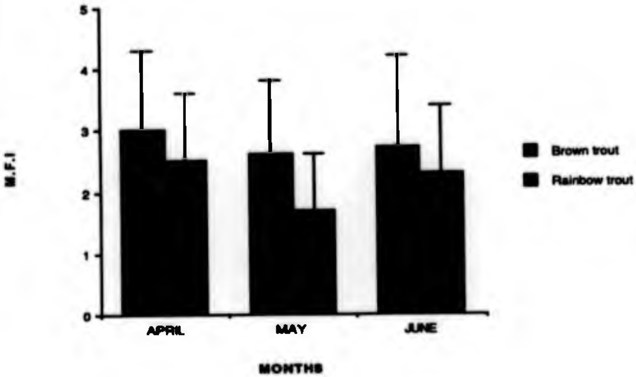
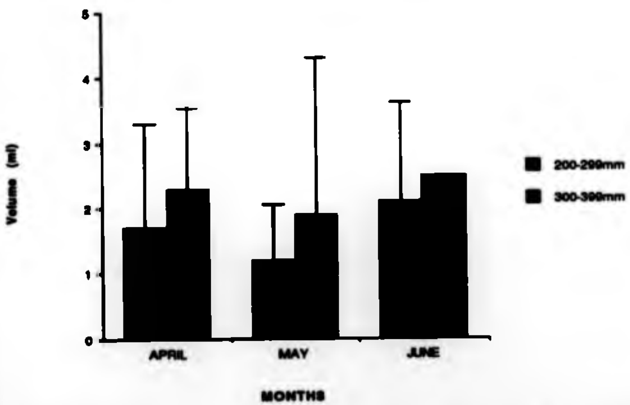


Figure 4.32 The mean volume/stomach (+S.D) of brown trout caught by anglers in 1987.



Rainbow trout, Mean Fullness Index (MFI).

In common with brown trout, the rainbow trout MFI also showed slight decline between April and June, with the lowest level being recorded in May (Figure 4.31).

Rainbow trout, Mean Volume Per Stomach (MVS).

When the MVS was divided into length classes it was shown that the 200-299mm group declined from April to May before increasing to its highest level in June (Figure 4.33). In the 300-399mm length class it decreased from April to June (Figure 4.33). The low level in June is probably due to the sample only being comprised of one fish.

A comparison of the volume of food consumed by brown trout and rainbow trout caught by angling in 1987.

Comparisons were made by one way ANOVA, with log (100.x) transformations being performed when the data failed to meet the tests requirements. In the six comparisons made brown trout had a higher MVS than rainbow trout on five occasions, one of which was statistically significant ($P<0.01$) (Table 4.20). This shows that rod caught brown trout had been feeding with greater success than rainbow trout, although the lack of significance in the majority of comparisons is noted. This is in contrast to the 1987 gill netting survey results which showed that neither species had a distinct feeding advantage in the littoral zone.

A comparison of the volume of food consumed by rainbow trout and brown trout caught by angling and gill netting in 1987.

Comparisons between the MVS of brown trout caught by angling and gill netting showed that in four of the six comparisons those caught by angling had a higher MVS, one of which was statistically significant ($P<0.001$) (Table 4.21). This is in agreement with expectations as the

Table 4.20 **A comparison of the volume (ml) of food consumed by the brown trout and rainbow trout caught by angling in 1987.**

LC (mm)		April	May	June
0-199	BT	-	-	-
	RT	-	-	-
	S	-	-	-
200-299	BT	1.73	1.15	2.07
	RT	0.95	0.61	1.26
	S	NS	*	NS
300-399	BT	2.29	1.92	2.50
	RT	3.30	1.85	1.20
	S	NS	NS	NS
400+	BT	-	-	-
	RT	-	0.12	-
	S	-	-	-

LC=Length class, RT=Rainbow trout, BT=Brown trout, S=Significance, NS=Not Significant, *=P<0.05.

Figure 4.33 The mean volume/stomach (+S.D) of rainbow trout caught by anglers in 1987.

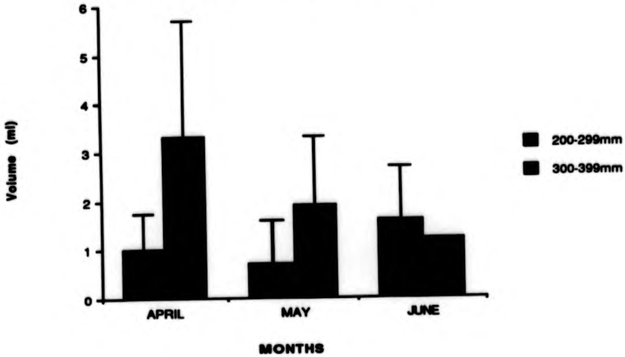


Table 4.21 **A comparison of the volume (ml) of food consumed by the brown trout caught by gill netting and angling in 1987.**

LC (mm)		April	May	June
0-199	A	-	-	-
	G	0.13	0.57	0.27
	S	-	-	-
200-299	A	**1.73**	**1.15**	**2.07**
	G	0.35	0.50	1.77
	S	***	NS	NS
300-399	A	**2.29**	1.92	2.50
	G	0.04	**19.00**	**8.25**
	S	NS	NS	NS

LC=Length class, A=Angling, G=Gill netting, NS=Not significant
***=P<0.001.

Table 4.22 **A comparison of the volume (ml) of food consumed by the rainbow trout caught by gill netting and angling in 1987.**

LC (mm)		April	May	June
0-199	A	-	-	-
	G	0.03	-	-
	S	-	-	-
200-299	A	**0.95**	0.61	1.26
	G	0.33	-	-
	S	NS	-	-
300-399	A	3.30	1.85	1.20
	G	**5.18**	-	-
	S	NS	-	-
400+	A	-	0.12	-
	G	-	-	-
	S	-	-	-

LC=Length class, A=Angling, G=Gill netting, NS=Not significant fish caught by angling are actively feeding whereas those caught in the gill nets do not have this selection criteria. It could also be argued that this was evidence of regurgitation or digestion while the fish were in the gill nets unfortunately there is no way of separating these effects in the present survey. In the two instances where those caught in the gill nets had a higher MVS, one included the large fish that had been feeding very heavily on Mollusca at Coillaig, and the other was based on a comparison between one individual from each sampling technique.

The opportunity to make comparisons between the volume of food consumed by rainbow trout caught by the two techniques was limited due to no rainbow trout being caught at the littoral sites in May and June in the gill netting survey. In the two comparisons made no trends were apparent (Table 4.22). Neither were statistically significant, and were based on only a small number of fish.

4.3.2.5 Monthly variation in the volume of food consumed by rainbow trout and brown trout caught in the fish farm and littoral habitats in 1988.

The summer peak in feeding activity of brown trout caught in the littoral zone was similar to the pattern observed in 1987 (Figure 4.34). However there were two slight differences, the maximum MFI was higher, and it occurred slightly later than in the previous year. The later peak could simply be an artefact of the sampling schedule, as no samples were collected in June the month in which the highest MFI occurred in 1987.

The feeding activity of brown trout at the fish farm was at its highest level in March and July. The reason for the decline in May is unclear, but the decline in September is in line with seasonal expectations

Figure 4.34 The mean fullness index (MFI) (+S.D) of brown trout caught in the littoral and fish farm habitats in 1988.

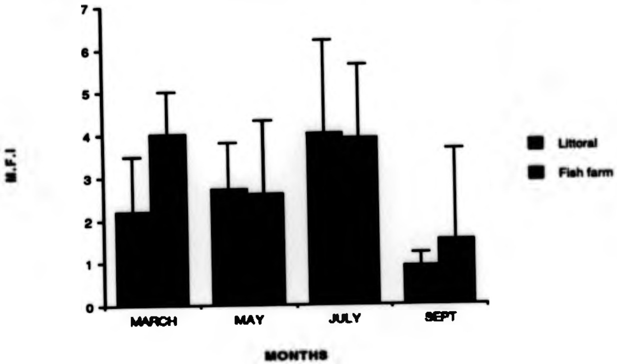
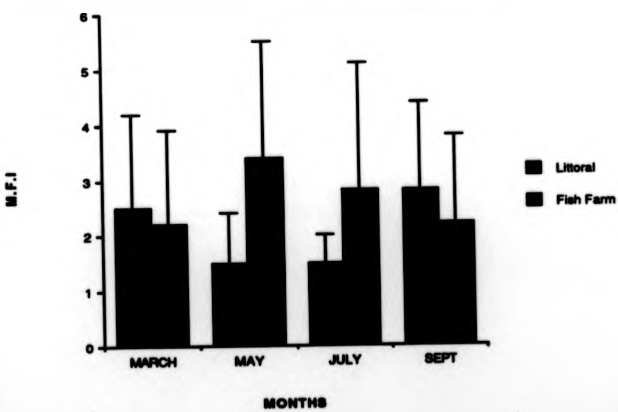


Figure 4.35 The mean fullness index (MFI) (+S.D) of rainbow trout caught in the littoral and fish farm habitats in 1988.



(Figure 4.34).

There was an apparent decline in the summer feeding activity of rainbow trout in the littoral zone (Figure 4.35). However the variation can be explained by the different food types consumed in the different months. In March and September fish in the sample had been feeding on uneaten pellets that pass through the cages, whereas in the other months they had consumed conventional trout prey. As most of the pellets sizes used on the farm have a greater unit volume than the conventional prey their inclusion in the diet will result in a greater fullness index than if the same number of conventional items had been consumed. Also in May and July the sample sizes were small and may not have been representative of the whole population.

The feeding activity of the rainbow trout at the cages peaked in May and declined in July. This is similar to the pattern observed in 1987 (Figure 4.35).

4.3.2.6 A comparison of the volume of food consumed by rainbow trout and brown trout caught in the littoral and fish farm habitats in 1988.

Although there were fewer comparisons than in 1987, and the littoral and fish farm sites were very close to each other, some of the trends observed in 1987 were again apparent.

In the littoral zone rainbow trout had a higher MVS than brown trout in four of the six comparisons, three of which were significant (Table 4.23). At the fish farms rainbow trout and brown trout each had a higher MVS on three occasions (Table 4.24).

As expected rainbow trout consumed more food in the fish farm habitat

Table 4.23 **A comparison of the volume (ml) of food consumed by brown trout and rainbow trout caught in the littoral zone in 1988.**

LC (mm)		March	May	July	September
0-199	RT	7.00	0.20	0.18	-
	BT	0.28	0.46	0.54	0.13
	S	***	NS	NS	-
200-299	RT	-	3.04	-	-
	BT	0.33	1.03	1.58	0.11
	S	-	*	-	-
300-399	RT	7.00	0.19	-	10.80
	BT	0.14	-	-	0.41
	S	**	-	-	NS
400+	RT	8.80	-	-	11.98
	BT	-	-	-	-
	S	-	-	-	-

LC=Length class, RT=Rainbow trout, BT=Brown trout, S=Significance, *=P<0.05, **=P<0.01, ***P<0.001.

Table 4.24 **A comparison of the volume (ml) of food consumed by brown trout and rainbow trout caught at the fish farms in 1988.**

LC (mm)		March	May	July	September
0-199	RT	0.11	-	0.20	-
	BT	0.20	0.18	0.85	0.1
	S	NS	-	NS	-
200-299	RT	3.75	1.25	6.41	1.71
	BT	1.91	6.80	3.00	-
	S	NS	NS	NS	-
300-399	RT	10.35	57.35	0.80	40.41
	BT	-	11.82	-	-
	S	-	NS	-	-

LC=Length class, RT=Rainbow trout, BT=Brown trout, S=Significance, *=P<0.05, **=P<0.01, ***P<0.001.

than they did in the littoral zone (Table 4.25). Whereas brown trout did not exhibit a greater degree of success in either habitat (Table 4.26). These results again demonstrate that brown trout feeding is not suppressed in the immediate vicinity of the fish farms, and that rainbow trout feed more successfully at the fish farms than they do in the littoral zone.

4.3.3 Evidence for stomach content regurgitation in fish caught in the gill nets in 1987 and 1988.

Gill nets have often been criticised for their use in feeding studies as the fish caught in them reportedly regurgitate the food that they have eaten. Such a phenomenon would obviously bias any results used in such studies. In the present study the number of fish that showed evidence of partial or complete regurgitation was measured using the method outlined by Treasurer (1988). This author described stomachs that food had been regurgitated from as being thin walled, distended, having little internal ridging, and being empty or partially empty, and found that regurgitation in perch occurred in less than 9.0% of the stomachs he examined. On the basis of this analysis Treasurer (1988) concluded that gill netting was a legitimate means of sampling perch in feeding studies. In the present study the highest level of regurgitation was 6.3% in pelagic Arctic charr (S. alpinus), and it occurred to a much lesser extent in the other species (Table 4.27). As this is lower than the level recorded by Treasurer for perch (P. fluviatilis), it is concluded that gill netting was a satisfactory technique for collecting fish for the feeding studies in the present study. It is also likely that the stomach contents of fish caught by gill netting would have undergone a degree of digestion if they had been in the nets for the full 24 hours, particularly during the summer.

Table 4.25 **A comparison of the volume (ml) of food consumed by rainbow trout caught in the fish farm and littoral habitats in 1988.**

LC (mm)		March	May	July	September
0-199	CA	0.11	-	0.20	-
	LT	7.00	0.20	0.18	-
	S	*	-	NS	-
200-299	CA	3.75	1.25	6.41	1.71
	LT	-	3.04	-	-
	S	-	NS	-	-
300-399	CA	10.35	57.33	0.80	40.41
	LT	7.00	0.19	-	10.80
	S	NS	NS	-	NS
400+	CA	-	-	-	-
	LT	8.80	-	-	11.89
	S	-	-	-	-

LC=Length class, CA=Cages, LT=Littoral, S=Significance
*=P<0.05, **=P<0.01, ***P<0.001.

Table 4.26 **A comparison of the volume (ml) of food consumed by brown trout caught in the fish farm and littoral habitats in 1988.**

LC (mm)		March	May	July	September
0-199	CA	0.20	0.18	0.85	0.1
	LT	0.28	0.46	0.54	0.13
	S	NS	NS	NS	NS
200-299	CA	1.91	6.80	3.00	-
	LT	0.33	1.03	1.58	0.11
	S	***	NS	NS	-
300-399	CA	-	11.82	-	-
	LT	0.14	-	-	0.41
	S	-	-	-	-

LC=Length class, CA=Cages, LT=Littoral, S=Significance, *=P<0.05, **=P<0.01, ***P<0.001.

Table 4.27 **The level of regurgitation of stomach contentsin each of the species caught in the 1987 and 1988 gill netting surveys. The figures are a mean percentage of the level recorded in each habitat.**

	1987	1988
Brown trout	1.87	3.09
Rainbow trout	2.19	6.11
Atlantic salmon	0	-
Perch	0	-
Benthic Arctic charr	3.30	-
Pelagic Arctic charr	6.3	-

4.4 Discussion.

4.4.1 Diet of each species.

The feeding behaviour of brown trout in allopatry, or at least in the absence of closely related species in large oligotrophic lakes in their home range is characterised by two distinct feeding periods. In winter/spring they feed predominantly on zoobenthos in the littoral zone, and in summer when older members of the population migrate offshore their diet shifts to aerial insects, pelagic pupae and zooplankton. The smaller fish that remain in the littoral zone feed on similar prey, but also retain a small amount of zoobenthos in their diet (Haraldstadt & Jonsson, 1983; Dauod et al., 1986; Jonsson, 1989).

The seasonal variation in their habitat use has been shown here to be driven by the seasonal variation in food supply. In the early spring there is a high abundance of invertebrates in the littoral zone, while the biomass of zooplankton and availability of aerial insects is low (Hindar & Jonsson, 1982). Also at this time semi-aquatic insects are close to emerging and show high levels of activity thereby making themselves more conspicuous to predatory fish (Lillehammer, 1973). During the summer, food availability in the rocky littoral zone decreases and in the surface/pelagic zone it increases with the appearance of pelagic pupae and a rise in zooplankton productivity. Aerial insects are also most active at this time.

In the autumn when surface/pelagic prey abundance declines and the littoral zoobenthos abundance starts to increase the larger fish move back to the shallows prior to spawning (Hindar & Jonsson, 1982). After spawning fish regain condition by feeding in the littoral zone before undertaking the same migration into the pelagic zone in the spring.

In standing water bodies with a higher nutrient status a change in feeding behaviour between winter and summer is also found. In winter they still feed on littoral invertebrates, but in the summer they feed predominantly on mid water prey, with aerial insects being largely absent from their diet, apart from isolated incidents associated with large hatches. This situation has been described in Llyn Alaw, Wales by Hunt & Jones (1972) and in Lough Derg, Ireland (Southern, 1935).

In Loch Leven (Thorpe, 1974) showed that brown trout wintered in open water and moved to the littoral zone in the summer to feed on fully aquatic invertebrates which are present at that time, particularly A. aquaticus. He demonstrated that bottom feeding was the preferred mode for brown trout, as those netted from there were in better condition than fish caught at the same time in the surface waters by anglers. He suggested that trout feeding on benthos held the preferred territory and those that were displaced moved to the surface.

Therefore it is clear that brown trout can prey on a wide variety of prey organisms, and show a degree of plasticity in their feeding behaviour depending upon the type of water that they inhabit.

The diet of brown trout in Loch Awe was similar to their diet in allopatric situations in other large oligotrophic lakes. In winter and spring they fed primarily on bottom-dwelling invertebrates, and as spring changed to summer so their diet gradually shifted to pelagic and surface living organisms. It is at this time the larger fish move offshore, unfortunately the scope for analysing this group's diet is limited by the small number of stomachs examined. The younger fish that remain in the littoral zone retain some bottom-dwelling organisms in their diet. As autumn passes to winter so their diet reverts to a bottom-feeding mode as the larger fish move back onshore.

Rainbow trout feeding behaviour has been described as opportunistic, versatile and being capable of exploiting a variety of food sources, with their diet at a particular time being dictated by their size and food availability (Bernard & Holstrom, 1978). In the Rotorua lakes, New Zealand, Rowe (1984) demonstrated that rainbow trout fed on fish, insects, Mollusca, fish larvae and Crustacea, with the preference at different ages being dictated by a number of complex inter-related factors including turbidity and temperature. In large North American lakes where no forage fish are present McAffee (1966) showed that rainbow trout fed mainly on insects and planktonic Crustacea. Where forage fish were present Mottlely (1947) and Larkin et al. (1957) showed that when rainbow trout reached 350mm and 300mm fork length respectively they adopted a piscivorous habit. This is very similar to changes described by Campbell (1979) in brown trout feeding behaviour when they reach a similar length in the presence of Arctic charr.

In extensive aquaculture systems similar behaviour has been recorded. In Lake Kuakkingarvi, Russia, Arendarenko & Zabolotskiy (1977) demonstrated that their diet ranged from zooplankton at O+, to large benthos and small roach at age 3+. In the winterkill lakes in Western Manitoba, Canada, Bernard & Holstrom (1978) demonstrated a similar progression with age, they also noted a greater degree of piscivorous behaviour in hatchery stock.

The diet variation described above is due to the variations in food availability in the different habitats that have been considered, the fish in each one consuming prey that requires the least expenditure of energy. In this respect the diets of rainbow trout and brown trout are very similar. There is also a broad similarity in the diet of the two species in running water.

There is a marked difference between the diet of rainbow trout in Loch Awe and those found in other systems, the main difference being their high utilisation of non-conventional prey. At the littoral sites away from the cages vegetation, stones and ground bait contributed a large percentage to their diet. At the fish farms they had an even greater dependence on non-conventional prey, with their diet largely consisting of fish farm pellets. Rainbow trout do not have the enzymes and micro-flora required to break down cellulose in the plant cell walls therefore they are not able to derive any nutritional value from the vegetation that they consume (Lindsay & Harris, 1981). The small amount of conventional food in the diet of rainbow trout is similar to that of brown trout. This type of diet is common in fish reared under artificial conditions when they have been released into the wild (Sosiak et al., 1979; O'Grady, 1983). Such fish have been shown to have a lower survival rate than the indigenous stock once they have been released (O'Grady, 1983; Ersbak & Hasse, 1983; Bachman, 1984; Johnsen & Ugedal, 1986). As all of the rainbow trout caught in the course of this study spent at least part of their life in a fish farm, similar behaviour is anticipated in Loch Awe.

A number of researchers have attempted to elucidate the mechanism responsible for this greater mortality rate. The one that has received most attention has been the ability of stocked fish to forage wild prey after they have been released. The studies have provided a wide range of results. Some have shown that stocked fish start feeding on wild prey immediately after release, whereas others have shown that there is a difference in the diet of stocked and wild fish even after one year. A quick shift to wild prey has been reported by Kennedy et al. (1984) and Stradmeyer & Thorpe (1987) in Atlantic salmon, Paszkowski & Olla (1985) in coho salmon Oncorhynchus kisutch Walbaum; and by Kelly-Quinn & Braken (1989) in brown trout. A short transition period, where stocked fish fed on invertebrate exuviae prior to feeding on living prey was reported by Johnsen & Ugedal (1986, 1989) in brown trout. Ersbak & Hasse (1983), O'Grady (1983) and Bachman (1984), all demonstrated that stocked brown trout were less effective at foraging wild prey even after a number of months had elapsed. Ersbak & Hasse (1983) showed that stocked fish had a preference for wild prey that resembled pelleted hatchery food. Sosiak et al. (1979) and O'Grady (1983) showed that stocked fish had a preference for surface prey. The latter author suggested that the greater vulnerability of stocked fish over wild ones to anglers is due to the "upward looking" feeding behaviour that they develop in hatcheries. He also showed that they consumed stones and organic detritus. A possible explanation for the consumption of non-food items could be the limited repertoire of food search images which domesticated fish have, compared with wild ones. A possible explanation for the preference shown for surface prey could be the ratio of visual pigments in the eyes of hatchery stock. Allen et al. (1973) demonstrated that the ratio of porphyropsin and rhodopsin can vary with the season and environmental conditions. Therefore fish that have been surface feeding in hatcheries will have both rhodopsin and porphyropsin in their retinas. This in turn would make them more predisposed to surface feeding after they were liberated.

The liberated rainbow trout in Loch Awe clearly find difficulty in foraging wild prey items, the large percentage of non-conventional prey items in their diet being evidence of this. It is likely that rainbow trout will therefore suffer from the high mortality rates that have been described in stocked fish.

In Loch Awe Atlantic salmon preyed upon littoral invertebrates, zooplankton and pelagic pupae. This is similar to the findings of Pedley & Jones (1978) who demonstrated that juvenile Atlantic salmon in Llyn Dwythwch preyed upon Chironomidae larvae and pupae, aerial insects and Trichoptera larvae, with the littoral Crustacea E. lamellatus and Ephemeroptera nymphs also being commonly consumed. This is similar to the diet of river-dwelling salmon (Carpenter, 1940; Mills, 1964; Robins, 1967; Woodland, 1972).

In Loch Awe benthic Arctic charr derived a large proportion of their diet from the soft sediments over which they were most commonly caught. However, those caught in the littoral zone also consumed invertebrates associated with that habitat, the variation in seasonal availability determining what was consumed. This is similar to the findings of Walker et al. (1988) in Loch Rannoch. The inclusion of E. lamellatus in the diet of Loch Awe's benthic charr a Crustacea normally associated with loch margins, in the same stomachs as P. obtusale and C. viridis which are normally associated with deeper water suggests that the benthic charr regularly undertake migrations between the two habitats. Jonsson and Gravem (1985) suggested that the feeding of benthic charr in deep water, in large oligotrophic lakes is due to their greater feeding efficiency at lower light conditions.

The diet of pelagic charr in Loch Awe was exclusively based on pelagic zooplankton. In loch Rannoch they also had a high dependency upon pelagic zooplankton, but also consumed items that would have been encountered whilst foraging in the surface/pelagic zone (Walker, et al. 1988). It is clear that pelagic Arctic charr are fulfilling the role of planktivores in these habitats.

The summer diet of perch in the littoral zone in Loch Awe consisted of littoral invertebrates, a wide range of zooplankton species, fish, particularly the three spined stickleback, and pelagic pupae. This was very similar to their summer feeding behaviour in Windermere described by McCormick (1970) and Craig (1978), and in Loch Lomond by Giles & Tippett (1987). The main difference between the results of the present survey and that on Loch Lomond was the consumption of D.gracilis by perch there. Although it was present in very high densities in Loch Awe's zooplankton it was not consumed by a single perch the reason for this difference was unclear.

4.4.2 The feeding relationships between the native fish species and rainbow trout in Loch Awe.

When rainbow trout and brown trout are found in sympatry in lotic and lentic habitats a degree of segregation has been observed by a number of workers. In Lake Benmore, New Zealand, McCarter (1986) demonstrated that brown trout were more effective at exploiting bottom-living Mollusca than rainbow trout, rainbow trout being unable to differentiate between empty and full shells in the sediments whereas brown trout could. Further evidence of this lack of discrimination in rainbow trout bottom feeding was the inclusion of stones and sediments in their diet, which was also seen in the present study (but perhaps for different reasons). Although neither species are native to New Zealand it is interesting that some of the differences found in their feeding behaviour in Britain are also found in New Zealand.

Mylechreest (1978) concluded that brown trout partially excluded rainbow trout by interactive segregation from the littoral zone in Lake Waikaremoana forcing them into open water where there were fewer but larger prey.

De Filby (1976) and McAuley (1984) demonstrated a preference for bottom-dwelling prey by brown trout when they were in sympatry with rainbow trout that had escaped from a commercial fish farm. Increased piscivorous behaviour in brown trout has also been noted when the two species are in sympatry (Idyll 1942; & Phillips 1984). Further evidence of the brown trout's preference for prey in deeper water when they are in sympatry with rainbow trout was shown by Brown et al. (1980). They demonstrated in a eutrophic reservoir that the Chironomidae (both larvae and pupae) component of the brown trout's diet largely comprised those found in deep water, whereas the rainbow trout's diet was mostly made up of those preferring shallow water. Their findings were supported by anecdotal evidence from anglers who reported that they had to fish deeper to catch brown trout.

Interspecific segregation has also been recorded in running water. McLennan and McMillan (1984) found segregation occurring in the pool position held by the two species. In the absence of brown trout, rainbow trout held territories throughout the pools, whereas in their presence they were restricted to positions at the top of them. Jenkins (1969) demonstrated that this was the position held by low-ranking fish that were unable to hold territories elsewhere. Armstrong (1979) found that rainbow trout predominated in the turbulent head waters of rivers and that brown trout were found in the turbid slower-flowing downstream sections.

The above clearly demonstrates that when brown trout are in sympatry with rainbow trout the former show a preference for deeper water and poorer light conditions than rainbow trout. This is demonstrated both by brown trout exploiting prey found in deeper water than rainbow trout and by brown trout showing a greater degree of selectivity when feeding at the same depth in turbid waters as rainbow trout. Further evidence of the rainbow trout's preference for surface waters is their greater susceptibility to avian predation (Matkowski, 1989).

Allen et al. (1973) demonstrated a difference in the proportion of visual pigments in the retina of surface and bottom-dwelling freshwater fish. Surface dwelling fish have both porphyropsin and rhodopsin whereas those that are bottom-living have a greater proportion of porphyropsin. Porphyropsin absorbs light of a longer wavelength than rhodopsin and long wavelength light is known to penetrate deep water (Muntz & Wainwright, 1978). Therefore the proportion of porphyropsin in the retina of trout found in deeper water should be higher than those feeding in shallow water. Allen et al. (1973) demonstrated that when brown trout, brook trout *Salvelinus fontinalis* (Mitchill) and rainbow trout were kept under identical photic conditions, brown trout had a higher percentage of porphyropsin in their retinas. These results provide an optical basis for the habitat segregation that has been described when rainbow trout and brown trout are in sympatry.

As well as the proportions of porphyropsin and rhodopsin varying genetically between species, Allen et al. (1973) also demonstrated an environmental control. This could predispose fish reared on a farm to have a preference for surface feeding due to the "upward looking" feeding behaviour encouraging the production of rhodopsin rather than porphyropsin. O'Grady (1983) reported this type of behaviour in recently stocked brown trout in a number of Irish lakes.

Evidence of this niche segregation between brown trout and rainbow trout in Loch Awe was seen in the greater consumption of bottom-dwelling invertebrates by brown trout, and by the greater consumption of food items from the surface/pelagic zone when they were available by the rainbow trout caught in each part of the study. However, it is unclear how important the rainbow trout's innate preference for surface feeding and their hatchery background are in determining their feeding behaviour in Loch Awe.

If rainbow trout were to establish a self-sustaining population in Loch Awe, they would learn to feed on conventional prey from emergence, and thereby pose a greater threat to the loch's native species. This is discussed more fully in Chapter 6.

No previous studies could be found on the feeding relationships between juvenile Atlantic salmon and rainbow trout. However it is clear from the results of this survey that there would be a degree of competition for zooplankton and invertebrates at certain times of the year if demand exceeded supply. As a quantitative assessment of this type was beyond the scope of the project, it cannot be determined if competition occurred. Prior to this study being initiated it was claimed that rainbow trout predated heavily on juvenile Atlantic salmon. From the findings of this study it is clear that the claims were groundless, it may occur to a limited extent, but no evidence was found in this survey.

As with brown trout the threat of interspecific feeding competition from rainbow trout would increase if a self-sustaining population became established in the loch. The scope for such competition in the case of young salmon is reduced by their limited presence in the loch during their migration from their natal streams to the sea.

As with Atlantic salmon no previous studies on the interspecific feeding relationships between perch and rainbow trout were found. In Loch Awe both species consumed zooplankton, pelagic pupae and smaller amounts of littoral invertebrates. This only indicates that there is the potential for competition. As there was a little evidence which showed that the rainbow trout moved offshore when the perch made their migration into the littoral zone the scope for feeding competition is reduced.

There is very little similarity in the diet of benthic Arctic charr and rainbow trout. The charr feed predominantly on invertebrates associated with soft sediments and deep water, due to their ability to feed in low light intensities (Jonsson & Gravem 1985), whereas rainbow trout feed nearer the surface. During the summer charr consumed pelagic zooplankton as well as those associated with the sediments and found in their diet throughout the year. As pelagic plankton undergo diel vertical migrations in the water column, it is possible that the two species could interact at the limits of their depth distribution. Again the consumption of the same species of zooplankton by the two fish species would only result in competition if the prey were in short supply. The inclusion of E.lamellatus a Crustacea typical of littoral areas, in the diet of benthic charr suggests that there could also be the potential for conflict in the littoral zone.

Pelagic Arctic charr and rainbow trout both feed on zooplankton in the surface/pelagic zone during the summer. This combined with the low catches of charr suggests that they would be in the greatest danger if feral rainbow trout were to become naturalised. However due to the small sample size of charr it is difficult to be sure if this is truly representative of their diet. The overlap in this component would only be a problem if prey were in short supply.

4.4.3 Qualitative feeding relationships between rainbow trout and brown trout.

The seasonal feeding activity of the two species is in broad agreement with that described by Swift (1961), Ball (1961), and Hunt & Jones (1972). It peaked in mid May and was at its lowest in early winter prior to spawning. The exception to this occurred in rainbow trout feeding at the fish farm in 1987, where less successful summer feeding was recorded. Other deviations from this pattern were due to small samples collected during the summer.

When the volume of food consumed by brown and rainbow trout at and away from the fish farms is considered it is clear that rainbow trout consume more food than brown trout at the fish farms, but that neither species holds a distinct advantage in the littoral zone. Intraspecific comparisons between the two habitats demonstrated that brown trout feeding around the fish farms was unaffected by the large number of rainbow trout. However this was contrary to the results of the comparison between the number of stomachs that contained food and those that were empty. It showed that brown trout caught at the fish farms had a higher proportion of empty stomachs. It is unclear if this was due to rainbow trout creating a shortfall in the availability of conventional food by eating it themselves, or whether the brown trout's feeding activity was curtailed by the presence of rainbow trout around the farms. In 1988 the mean fullness index of brown trout was higher than it was in 1987 suggesting that their feeding at the fish farm improved when rainbow trout were less abundant.

The rainbow trout intraspecific comparison between the habitats showed that those caught at the fish farms consumed more food than those caught in the littoral zone, principally due to the large amount of pellets consumed by those caught at the fish farms. However what was more interesting was that the proportion of rainbow trout at the fish farms with empty stomachs increased over the summer, and those that had been feeding consumed less food. This coincided with the period when the fish in the cages would be increasing their feeding rate. It is possible that this would result in less food passing through the cages and being available to the rainbow trout that live under them. If this was the case it would mean that a proportion of the rainbow trout around the farms find it very difficult to switch to another food source when their preferred option is in short supply. This hypothesis relies on there being a reduction in the amount of uneaten pellets passing through the cages when the feeding rate of the captive rainbow trout increases over the summer. Unfortunately there are no published results on this matter.

The apparent feeding advantage that the rainbow trout have over brown trout may be less important than previously thought as there is very little overlap in the prey items consumed by the two species. However, this situation could change if rainbow trout were to become naturalised.

In summary, the diet of rainbow trout largely comprised non-conventional prey, with small amounts of conventional items being consumed according to their availability. At the fish farms they had a high dependence on the uneaten pellets that passed through the cages, at the littoral sites this was replaced by stones, twigs and other miscellaneous prey items. Rainbow trout caught by anglers had consumed a greater quantity of conventional prey than those caught in the gill netting survey. This difference was not surprising as the angler sample was biased towards rainbow trout that had made a successful transition to conventional prey, as the lures used by anglers are designed to mimic such items. The diet of native species was based on conventional prey items with macroinvertebrates, aerial insects and zooplankton all being consumed according to their seasonal availability.

Evidence was presented which indicated that rainbow trout showed a preference for surface foraging, and brown trout a preference for bottom foraging. An optical mechanism was provided to explain the difference between the two species. However it was not clear if the difference was due to an expression of the rainbow trout's domestic background, or due to an innate difference.

Rainbow trout were shown to be less successful at feeding around the fish farms than in the littoral zone in the summer. This may be evidence of them having difficulty in switching to an alternative prey type, when the abundance of the pellets declines, as the feeding of the fish in the cages increases at that time. Brown trout also had a greater proportion of empty stomachs around the fish farms, but it is unlikely that this could have been caused by direct competition for food as there was very little overlap in their diet. If rainbow trout were to establish a self-sustaining population in the loch they would be exposed to a full repertoire of prey search images from emergence, and would thereby become a greater threat to the native fish species in the loch, but at present there is very little likelihood of this occurring.

CHAPTER 5

AN EXAMINATION OF THE FEEDING BEHAVIOUR, GROWTH AND SURVIVAL OF ADULT BROWN TROUT AND RAINBOW TROUT AT HIGH DENSITIES.

5.1 Introduction

Angling groups and conservation bodies have recently voiced concern about the impact of non-native rainbow trout on Britain's native salmonids. It is generally accepted that the impact will be greater as the ratio of rainbow trout:native species in a water body increases. By comparing the holding capacity of a commonly used Kames cage containing 10,000 250gm rainbow trout at harvesting against the 85,640 >3+ brown trout population in Loch Leven (Thorpe, 1974), Phillips (1984) demonstrated that the loss of one rainbow trout cage in a loch of that size had the potential for a significant effect on the brown trout population.

In the present study, gill netting surveys in 1986, 1987 and 1988 failed to reveal any part of Loch Awe where large numbers of brown and rainbow trout co-existed away from the fish farms. It was decided to artificially create such conditions, to establish the likely effect on the native brown trout population in Loch Awe if the rainbow trout population increased significantly above their current level.

This chapter describes experiments designed to examine the effect of interspecific competition and previous feeding experience on the growth, survival and feeding behaviour of brown trout and farmed rainbow trout. By stocking two ponds at a high density (approximately twice the normal level), far greater than their normal carrying capacity one with brown trout and the other with brown trout and rainbow trout it was hoped that any changes in the behaviour of the brown trout in the presence of rainbow trout would become intensified and therefore more apparent. This would be achieved by each species making greater use of their potential niches.

5.2 Methods

5.2.1 Source of fish.

At the end of April 1990, 90 wild brown trout were seine netted from the littoral zone around Braevallich, and put into the experimental ponds. However between then and the proposed start of the experiment, they were removed by anglers. A further unsuccessful attempt to net fish from the loch was made in June. It was then decided to buy 90 2+ brown trout from the Castle Fish Farm Inveraray. As the fish had been reared in earth ponds they would have experience in foraging wild prey (Wahab, 1986). In this respect the competitive advantage of brown trout over rainbow trout reared in the cages was retained. The 30 rainbow trout used in the experiment were obtained from the nearby Caledonian Trout Company.

The public interference continued during the experiment, on two occasions anglers were caught fishing in the ponds. As it was not possible to determine if they had caught any fish, it was decided not to add any further fish to the ponds. In an attempt to minimise the interference a careful watch was made of the ponds but this could not be maintained at all times. As a consequence the findings of the experiment may not be wholly accurate. Although the results have been interpreted at face value, it would be necessary to repeat the experiment to verify the findings.

5.2.2 Pond description.

Each pond had a surface area of 255m^2, and was 1.75m deep. Their water supply was drawn from the Braevallich burn via a culvert. It flowed into pond A then into pond B, with the overflow emptying into Loch Awe via a small stream. The ponds were isolated by a series of screens at their inflows and outflows.

The fish were released into the ponds on 8 July 1988, and on the 10 July 1988 a large flood dislodged the screen covering the inlet pipe to pond A. Three tagged brown trout were subsequently caught by anglers in the Braevallich burn and Loch Awe indicating that some fish had escaped. In the early stages of the experiment a small number of fish moved between the ponds, principally from B to A. It was suspected that the cascade of water between the ponds was acting as a stimulus for the downstream fish. By increasing the depth of water in pond B on the 27 August 1988 the waterfall was removed and the movement of fish between the ponds ended.

5.2.3 Experimental protocol.

At the start of the experiment the fish were tagged with individually numbered floy tags and had their length and weight recorded. Each pond was then stocked with 60 fish, pond A with 60 brown trout and pond B with 30 rainbow trout and 30 brown trout. The brown trout stocked on their own were used as a control. Ideally there should have been a control for the rainbow trout but only two ponds were available. During the first netting session a small number of native brown trout were found in the pond A, it was decided to include them in the experiment as they would provide a bench mark against which the feeding of the stocked brown trout in pond A could be compared.

The fish in pond A were examined after one week, however the low volume of food in their stomachs suggested that they had not fully adjusted to their new environment. They were left for a further two weeks and then sampled on 1/8/88 and then every second week until the 27/9/88. The final sampling session was on the 25/10/88. The experiment was then terminated due to the small number of fish remaining in pond B.

In each sampling session the ponds were seine netted three times and the fish held in a large tank prior to processing. This involved anaesthetising them in benzocaine, recording their length and weight, and then removing their stomach contents using a stomach pump, similar in design to that described by Strange & Kennedy (1981). After processing they were returned to the ponds to recover.

The efficiency of the pump was examined on the last sampling day by sacrificing the fish after their stomachs had been pumped, and measuring the volume of food remaining. The efficiency ranged from 94.2% to 100% removal, comparable to the range achieved by Strange & Kennedy (1981).

5.2.4 Invertebrate abundance.

The abundance of bottom-dwelling invertebrates in the two ponds was assessed by taking samples using an Ekman grab. The samples were then sifted in a 1000 u m sieve, and the invertebrates counted. A pilot study was established to determine the sampling intensity required to assess this. It involved taking ten samples from each pond, counting the invertebrates in each one and applying the formula described by (Elliott, 1977) and used previously in section 4.2.4. This demonstrated that it would have been necessary to collect more samples than could have been analysed, and that the required level of sampling would also severely deplete the biomass of bottom-dwelling invertebrates in the ponds (Table 5.1). As a result it was decided not to proceed with this part of the study.

5.2.5 Analysis of stomach contents.

The prey items collected by stomach pumping were preserved in formalin, and returned to the lab for identification using a dissection and compound microscope. The diet was identified to species where possible and the results presented as percent occurrence, percent volume and

Table 5.1 The number of samples required to be collected in pond A in order to obtain a representative sample of the species listed below assuming an allowable error of 10%.

	n	x prey/m^2	No. Samples Required For 10% Accuracy.
Pisidium	10	1.1	210
Formicidae	10	0.1	1000
Haliplidae	10	0.1	1000
Chironomidae(l)	10	10.7	43
Chironomidae(p)	10	0.1	1000
Ephemera danica	10	0.1	1000
Ceratopogonidae	10	0.1	1000
Sialis lutaria	10	0.5	376
Lampetra planeri	10	0.4	300
Limnius volkmari	10	1.1	339

percent number. It was necessary to use all three indices as each one on its own has certain conceptual inadequacies (Hyslop, 1980). The diet overlap in the experimental groups was determined using Schoener's Overlap Index (Schoener, 1970). This index suffers from fewer limitations than are associated with others that are available (Wallace, 19881; Linton, _et al._, 1981). See section 4.2.3.2 for details.

The amount of food consumed by the experimental groups of fish was compared by one way ANOVA with the data being transformed where necessary. If they failed to meet the test criteria after transformation the non-parametric Mann-Whitney U test was used.

5.2.6 Growth rate.

The mean instantaneous growth rate in each sampling period was calculated by recording the weight of individual fish caught on consecutive periods. This removed any bias resulting from the samples being of different sized individuals. The instantaneous growth rate of each group was then compared using a t-test.

No attempt was made to assess fish production in the ponds due to the unknown angler impact in the experiment.

5.2.7 Water temperature.

The water temperature was measured daily at 08:00 hrs, 13:00 hrs, 17:00hrs and 21:00 hrs, and occasionally at 02:00hrs. Each pond was measured at its inflow and outflow.

5.3 Results

5.3.1 Feeding relationships.

The number of stomachs examined in each sampling period is shown in Table 5.2. The diets of brown trout and rainbow trout in ponds A and B on each sampling day were described to species, and are expressed as percent occurrence, percent number and percent volume (Appendix 4). For a summary of their diets expressed as percent volume see Figures 5.1-5.4.

5.3.1.1 Diet descriptions.

Stocked brown trout in pond A fed on a wide variety of bottom-dwelling invertebrates, pelagic pupae, and aerial insects, with smaller amounts of fish, vegetation and invertebrates of terrestrial origin also being consumed (Figure 5.1). This was similar to the range of prey items consumed by brown trout feeding in Loch Awe at this time. The only slight difference was the greater importance of bottom-dwelling invertebrates in the diet of those in the ponds. The change in diet that occurs in response to the seasonal variation in food availability described for brown trout in Loch Awe (Figure 4.1) was also observed in brown trout stocked in pond A. The dietary importance of pelagic pupae and aerial insects declined towards the end of the experiment (autumn), when there was a concomitant rise in the importance of the bottom-dwelling invertebrates. The low consumption of non-food items was also noted.

The diet of indigenous brown trout in Pond A is described in Figure 5.2 and was very similar to that described for the stocked brown trout. The similarity is particularly surprising as there was a large difference in the size of the fish in the two samples. Their diet included bottom dwelling-invertebrates, pelagic pupae and aerial insects. The seasonal change in their diet and their low utilisation of non food-items is

Table 5.2 The number of trout stomachs sampled from the two ponds in each sampling period.

	BT S Pond A	BT I Pond A	BT S Pond B	RT S Pond B
16/7	10	4	-	-
1/8	11	5	6	10
12/8	13	0	7	9
26/8	17	3	10	9
16/9	17	3	8	9
26/9	17	3	9	1
25/10	19	5	4	4

BT=Brown trout, RT=Rainbow Trout, S=Stocked, I=Indigenous.

Table 5.3 Diet overlap indices for the brown trout and rainbow trout in ponds A and B.

	Pond A BT,S vs BT,I	Pond B BT vs RT	Brown Trout Pond A vs B
16/7	0.61	-	-
1/8	0.43	0.42	0.87
12/8	-	0.52	0.69
26/8	0.85	0.07	0.70
16/9	0.48	0.04	0.87
26/9	0.84	0.00	0.87
25/10	0.82	0.01	0.79
Mean	0.67	0.18	0.72

BT=Brown trout, RT=Rainbow Trout, S=Stocked, I=Indigenous.

Figure 5.1 The diet of brown trout stocked into pond A, expressed in percent volume.

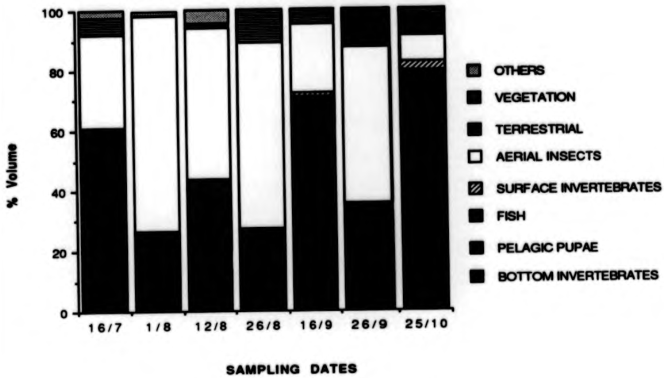
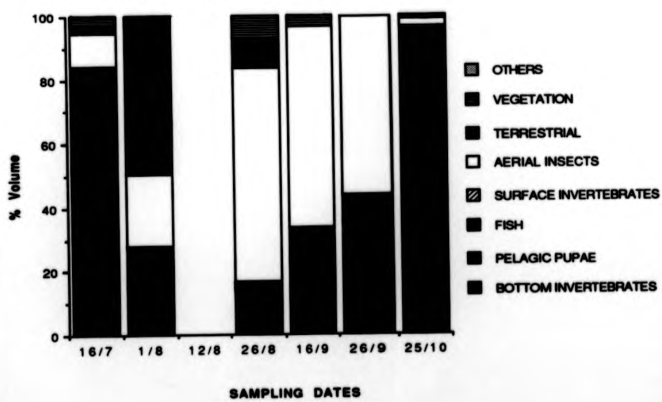


Figure 5.2 The diet of indigenous brown trout in pond A, expressed in percent volume.



again noted.

The diet of rainbow trout stocked in pond B largely comprised non-food items that were available at the pond surface (Figure 5.3). In each sampling period vegetation made the largest contribution to their diet, with stones and feathers also being consumed. The conventional food items consumed included bottom-dwelling invertebrates, pelagic pupae and insects, with the importance of each group changing in each sampling period. This lack of consistency in the results between sampling periods meant that the seasonal utilisation of food described for brown trout was not apparent.

The diet of brown trout stocked into pond B was almost exclusively based on conventional trout prey. In each sampling period the majority of their diet comprised bottom-dwelling invertebrates or aerial insects (Figure 5.4). The other prey categories only contributed a small amount to their diet. As a result their feeding activity was polarised between the surface and bottom of the pond with very few mid-water prey being consumed. The change in their seasonal feeding pattern is in accordance with the seasonal variation in food availability.

5.3.1.2 Diet overlap.

The large overlap in the diets of stocked brown trout in the two ponds was not unexpected as they had been reared in the same pond at Castle Fish Farm (Table 5.3). The high overlap index is also indicative of similar prey being available in the two ponds. Bottom-dwelling invertebrates and aerial insects were the most important prey categories for the two groups. The variation that existed was due to differences in the consumption of pelagic pupae and vegetation, with those in pond A consuming more of both. The high utilisation of vegetation by rainbow trout in pond B may reduce its availability and

Figure 5.3 Diet of rainbow trout stocked into pond B, expressed in percent volume.

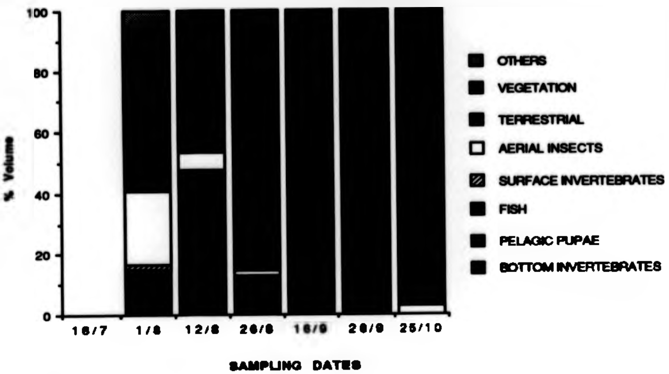
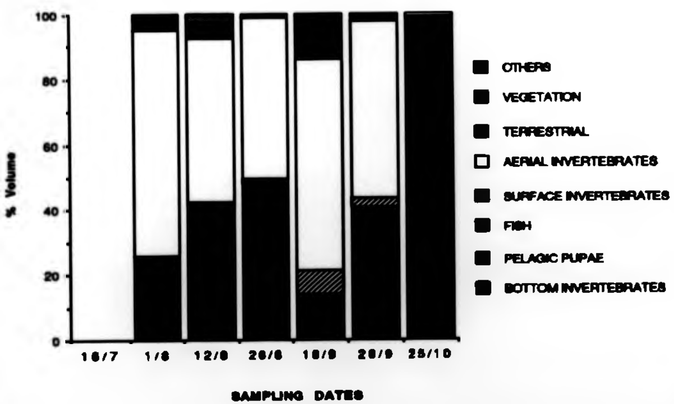


Figure 5.4 The diet of brown trout stocked into pond B, expressed in percent volume.



be responsible for this difference. The reason for their lower consumption of pelagic pupae is unclear, as their high utilisation of aerial insects indicates that they are not being excluded from the surface/pelagic zone by rainbow trout. Therefore it is concluded that brown trout feeding behaviour was unaffected when they were in sympatry with rainbow trout as their diet in pond B was similar to the allopatric population in pond A, and consistent with brown trout feeding in Loch Awe at that time.

The large overlap in the diet of stocked and wild fish in pond A indicates that they also feed in a similar manner (Table 5.3). Their diets largely being based on bottom-dwelling invertebrates and aerial insects. The variation was due to the differing consumption of fish, surface invertebrates and vegetation by the two groups. The variation in fish utilisation is size based, the smaller wild fish (mean length x = 153mm) being less likely to consume large items than the larger stocked fish (x = 250mm). The larger amount of vegetation in the diet of stocked fish may be a limited expression of their fish farm background.

There is very little similarity in the diets of brown and rainbow trout in pond B (Table 5.3). There are two possible explanations for this:

1. the rainbow trout diet has been shaped by niche divergence resulting from interspecific competition with brown trout; or
2. it has been determined by the feeding behaviour that they learned in the cages, which has resulted in them having a low repertoire of prey searching images.

The most likely explanation is the latter because in the cages they are only fed pellets. Had their diet comprised conventional prey with a higher nutritional value from the pond surface niche divergence could have been implicated. The difference was still apparent, at the end of the experiment, 13 weeks after stocking. This shows that rainbow trout find it very difficult to adapt to feeding on wild prey after they have been reared on an artificial diet.

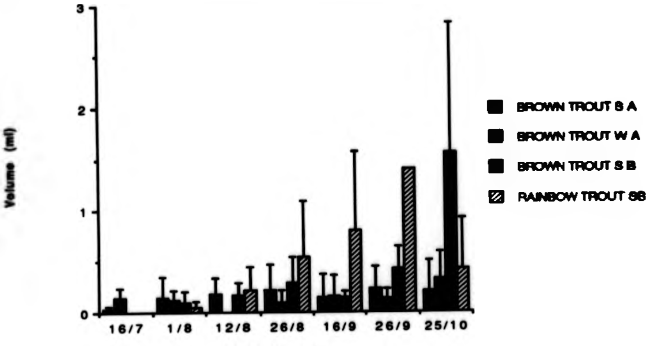
These observations also demonstrate the greater readiness of fish reared in earth ponds, compared to those reared in cages or concrete raceways, to feed successfully once they have been stocked. In ponds fish gain experience in foraging wild prey whereas the potential for this is very limited when they are reared on an artificial substrate.

5.3.1.3 Comparison of feeding success in the two ponds.

Eight days after the start of the experiment the stomach contents of brown trout in Pond A were sampled. This revealed that their food consumption was very low, suggesting that they were still adjusting to their new environment (Figure 5.5). At this time their mean volume per stomach (MVS) was significantly ($P <0.01$) lower than the wild brown trout in pond A. The difference in feeding success between the two groups was even greater than this comparison suggests, as the wild fish were considerably smaller than the stocked ones resulting in them having a smaller stomach volume. As a result, it was decided to extend the adjustment period by two weeks.

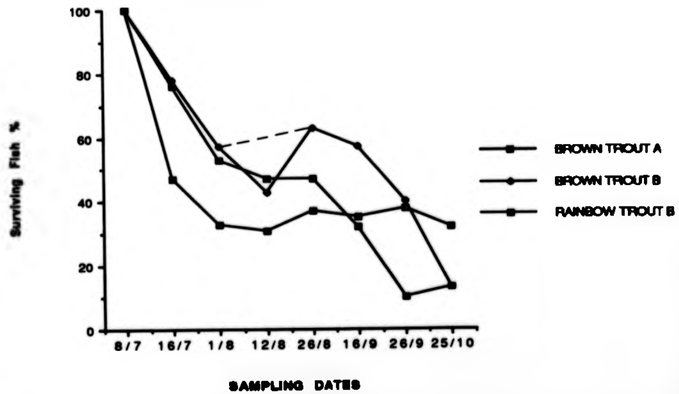
When sampling resumed it became apparent that stocked brown trout in the two ponds followed a similar feeding pattern through most of the experiment. Their food consumption increased from the start of the experiment until the 26/8/88 and declined on the 16/9/88. After this their feeding rates started to change, on the 26/9/88 it was clear that brown trout in pond B were feeding more successfully than those in pond A. This trend continued until the experiment ended when the differences between their MVS's were statistically significant ($P<0.01$) (Figure 5.5

Figure 5.5 The mean volume (ml) (+SD) of food consumed by the experimental groups of fish in the pond experiment.



S=Stocked, W=Wild, A=Pond A, B=Pond B.

Figure 5.6 The survival of the experimental groups in ponds A and B, expressed as a percentage.



and Table 5.4). A combination of low survival and low utilisation of conventional prey by rainbow trout in pond B are likely to result in greater food availability for brown trout and explain their greater feeding success in pond B.

The feeding rate of rainbow trout increased from the start of the experiment until the 26/9/88, after which it fell. However the data quality on that date is questionable as it was only based on one observation. On all but the first and last sampling dates rainbow trout had the highest MVS (Figure 5.5 and Table 5.4). This may be due to them attempting to maintain the high feeding rate that they had in the cages (Ersbak & Hasse, 1983). Due to there being very little overlap in the two species diets the variation in food consumption is less important than if their diets had been similar.

The MVS of wild brown trout throughout the experiment in pond A ranged from 0.1ml to 0.32ml. Only on the first sampling day was it significantly different from the stocked brown trout in the same pond (Figure 5.5 and Table 5.4).

5.3.2 Survival.

The number of stocked brown trout in pond A fell quickly from the start of the experiment until 1/8/88, after which it stabilised at 30% of the original population, remaining at that level until the experiment ended (Figure 5.6). Part of the decline in this period was due to the escape of fish that occurred when the inlet pipe screen to pond A was dislodged during a flood. The three tagged brown trout caught by anglers in Loch Awe and the Braevallich burn confirmed that fish were lost. The catch on 16/7/88 should be regarded as a minimum as it is possible that fish had dropped back into pond B which was not netted on that day. The population decline between 16/7/88/ and 1/8/88

Table 5.4 The mean volume of food (MVS) consumed by the experimental groups in ponds A and B. The group with highest MVS in each comparison is indicated by its first letter under the level of significance.

Date		Pond A BT, S vs BT, W		Pond B BT vs RT		Brown Trout Pond A vs B
16/7		**		-		-
		W				
	S	0.04				
	W	0.14				
1/8		NS		NS		NS
		S		BT		A
	S	0.15	BT	0.1	A	0.15
	W	0.12	RT	0.05	B	0.10
12/8		-		NS		NS
				RT		A
			BT	0.17	A	0.28
			RT	0.22	B	0.17
26/8		NS		NS		NS
		S		RT		B
	S	0.21	BT	0.28	A	0.21
	W	0.10	RT	0.53	B	0.28
16/9		NS		NSa		NS
		W		RT		A
	S	0.25	BT	0.14	A	0.25
	W	0.16	RT	0.79	B	0.14
26/9		NS		**b		NS
		S		RT		B
	S	0.23	BT	0.41	A	0.23
	W	0.13	RT	1.40	B	0.41
25/10		NS		NS		**
		W		BT		B
	S	0.22	BT	1.13	A	0.22
	W	0.32	RT	0.41	B	1.13

A=Pond A, B=Pond B, Bt=Brown Trout, RT=Rainbow Trout, S=Stocked, W=Wild, NS=Not Significant, **=P< 0.01, a=Mann-Whitney Test, b=t-test.

indicates that post-stocking mortality also contributed to the decrease in numbers at the start of the experiment. However, as stated in the methods it is not clear if this was due to fishing or natural mortality. The survival rate in pond A over the whole experiment was 32%.

The number of stocked brown trout and rainbow trout in pond B declined from the start of the experiment until 12 August 1988. Rainbow trout abundance then remained stable for two weeks, after which it declined again on 26/8/88 until the end of the experiment. By contrast the brown trout population increased on 26/8/88. This implies that netting efficiency on the previous sampling day had been low; a similar pattern occurred in pond A, but was less pronounced. If an adjustment is made for this anomaly (see dotted line on Figure 5.6) it is apparent that brown trout numbers also stabilised in mid experiment but at a higher level than rainbow trout. From 26/8/88 the brown trout population also declined until the experiment ended. At the end of the experiment the survival of both species was 13%. Again the relative importance of natural and fishing mortality is unclear.

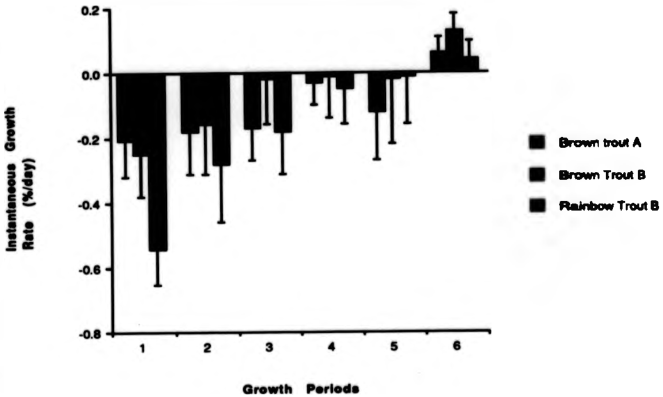
For most of the experiment the survival of the sympatric populations in pond B was better than the allopatric brown trout population in pond A. However by the end of the experiment the situation was reversed with the better survival being recorded in pond A (Figure 5.6).

5.3.3 Growth.

5.3.3.1 Growth rate description.

For most of the experiment brown trout in pond A lost weight, with the greatest loss occurring between the start of the experiment and the first sampling period (Figure 5.7). It is likely that the large weight loss over this period was due to a combination of the very high initial

Figure 5.7 The mean instantaneous (+S.D) growth rate of brown trout and rainbow trout in ponds A and B.



Growth Periods.

1=8/7/88-1/8/88, 2=1/8/88-12/8/88, 3=12/8/88-26/8/88, 4=26/8/88-16/9/88, 5=16/9/88-26/9/88, 6=26/9/88-25/10/88.

stocking density, to recovery from their journey in the fish transporter and becoming acclimatised to their new environment. As the experiment progressed their rate of weight loss declined, and by the last sampling period their mean weight was slightly higher than it had been at the start of the experiment.

The brown trout in pond B showed a similar pattern of weight loss to those in pond A. It was greatest at the start of the experiment and declined as it progressed with a net gain being recorded between the last two sampling days. However contrary to the pattern recorded in pond A their rate of weight loss stabilised in the middle of the experiment for a short period (Figure 5.7).

The rainbow trout in pond B also lost a large amount of weight between the start of the experiment and the first sampling period. But as with the brown trout populations the rate of loss declined after the initial loss. However their rate of loss between the first and second; and the second and third sampling periods was considerably greater than was recorded for the two brown trout populations. It is likely that this was due to their inexperience in foraging wild prey in this semi-natural environment. In the second half of the experiment their growth rate was comparable with the brown trout in the two ponds (Figure 5.7).

5.3.3.2 Comparison of growth rates.

Throughout most of the experiment brown trout in pond B had a slightly greater mean instantaneous growth rate than those in pond A. i.e. when they were losing weight they lost less, and when they were gaining weight they gained more. However none of the differences were statistically significant (P>0.05) (Table 5.5).

Table 5.5 The results of t-tests comparing the growth rates of brown trout caught in ponds A and B. The experimental group with the best growth rate in each comparison is indicated by its initial.

	Brown Trout Pond A vs B	Pond B BT vs RT
8/7-1/8	NS A	*** BT
1/8-12/8	NS B	* BT
12/8-26/8	NS B	NS BT
26/8-16/9	NS B	NS BT
16/9-26/9	NS B	NS RT
26/9-25/10	NS B	NS BT

A=Pond A, B=Pond B, Bt=Brown Trout, RT=Rainbow Trout, NS=Not Significant, *=P<0.05, **=P< 0.01, ***=P<0.001.

In pond B brown trout had a higher growth rate than rainbow trout for most of the experiment, only between 16/9/88 and 26/9/88 was the rainbow trout's higher, and, it was only by a very small margin. In the first two comparisons the differences were statistically significant, $P<0.001$ and $P<0.05$ respectively. During the rest of the experiment the differences were not significant (Table 5.5).

5.3.4 Temperature.

The water temperature ranged between 10°C and 17.4°C throughout the experiment. The warmest temperature being recorded on the 8/8/88 and the coolest on the 25/10/88. Throughout the experiment a temperature gradient of 0.5-1 °C existed between the ponds. The coldest water being found at the inlet to pond A and the warmest at the outlet of pond B. The difference was due to water warming up as it passed through the ponds. It is clear from the feeding and growth analysis (see Figures 5.5 & 5.7) that the water temperature did not fall to the levels that limit growth during the experiment.

5.4 Discussion.

The production of salmonids in a population includes a numerical component determined by reproduction, immigration, mortality and emigration, and a weight component primarily determined by growth (Allen, 1969). All of the processes are inter-related and respond in different ways to competition.

In the present experiment the effect of interspecific competition and previous feeding experience on growth, survival and feeding behaviour of rainbow and brown trout in a semi-natural habitat was investigated. The potential for conflict between the two species is high, because they have evolved in geographic isolation. In these circumstances it is unlikely that they will have evolved the behavioural mechanisms required to minimise competition. The two ponds were stocked well above their normal carrying capacity in order to intensify behavioural interactions thereby making any differences between the two species more apparent.

5.4.1 Feeding behaviour.

Brown trout feeding behaviour in the two ponds throughout the experiment was typical of those in Loch Awe and in other systems at that time of the year (Haraldstadt & Jonsson, 1983; Dauod et al., 1986; Jonsson, 1989). Their diet largely comprised aerial insects and macro-invertebrates. There was very little variation in the feeding behaviour of the allopatric and sympatric brown trout populations, suggesting that rainbow trout presence did not alter their feeding behaviour. The lower consumption of pelagic pupae by brown trout in pond B cannot be explained by the presence of rainbow trout, as they consumed aerial insects which requires the same feeding behaviour.

By contrast, rainbow trout consumed large amounts of vegetation throughout the experiment which is of no nutritional value to them. It is likely that this contributed to their poor growth and survival throughout the experiment. This behaviour is contrary to their feeding behaviour in their home range, where they feed on invertebrates, aerial insects, zooplankton and fish (Larkin et al., 1957; Bernard & Holstrom, 1978). It is however very similar to the feeding behaviour of those caught in Loch Awe away from the fish farms, and further demonstrates the low success of domesticated fish switching to a wild diet. This has also been described by Ball (1961), Sosiak et al. (1979), O'Grady (1983), Johnsen & Ugedal (1986). The consumption of plant material is due to highly domesticated fish having a low repertoire of wild prey search images. Through conditioning farmed fish only recognise pellet-like items as prey. A piece of plant material floating on the surface can have the same visual outline as a pellet.

No evidence of the niche divergence described between the two species by De Filby (1976), Brown et al. (1979), McAuley (1984), McCarter (1986), and alluded to by Matkowski (1989) was found. Some evidence of this was found of in the previous chapter suggesting that rainbow trout have a preference for surface waters, and brown trout a preference for deeper water. Possibly due to a difference in the production of the retinal pigment porphyropsin (Allen et al., 1973) in the two species. It is likely that the small size of the of the ponds was responsible for the absence of niche divergence.

5.4.2 Survival and Growth.

The results showed the response of brown trout in allopatry and sympatry in terms of survival to be quite different. However it was not possible to determine the extent to which interspecific competition on its own was responsible for the differences as conditions in the two ponds were not uniform. Pond A suffered a loss of fish just after the experiment started, and had slightly cooler water. The first would have a positive effect on the growth and survival of remaining fish, and the latter a negative effect.

Brown trout in pond A had a better survival rate than the two species in pond B, which had the same survival rate. Beyond saying that the initial decline in abundance in each of the populations was due to fish escaping when the screen was dislodged it is very difficult to interpret the survival and growth data meaningfully. This is largely due to the unknown impact of bird and angler predation in the two ponds, which may have resulted in mortality that was not due to competition. This combined with the fact that the above unquantifiable effects may have operated in the two ponds to different levels means that it is not possible to analyse the data. The lack of corpses in the two ponds suggest mortality from the above sources may have occurred.

It is generally accepted that stress in fish in depletes energy reserves and upsets osmoregulatory and metabolic functions which ultimately affect growth (Wedemyer, 1972; Selye, 1973; Mazeaud et al., 1973; Strange et al., 1977). Pickering et al. (1982) demonstrated that brown trout took at least a week to recover from an acute stress. It is likely that the stomach pumped fish in this experiment would have had a similar recovery period.

The experimental design could have been improved with replication of the treatments, but a lack of facilities prevented this. If the experiment was to be repeated this would be incorporated into the design.

5.4.3 Implications for Loch Awe.

The implication of these results for brown trout in Loch Awe can be divided into two categories i) feeding and ii) survival although both are inextricably linked.

It is clear that rainbow trout have great difficulty in switching to conventional fish prey once they escape from fish farms. The results of this experiment support the findings of the previous chapter which showed that rainbow trout caught away from the cages had great difficulty in learning to feed on wild prey. Similar poor feeding has been reported in other species when they are released into lakes and rivers aged 1+ and older (Ersbak & Hasse, 1983; O'Grady, 1983). When rainbow trout are close to the farms they rely on uneaten pellets that pass through the cages. This will clearly result in them having a high mortality rate if they move away from them. The low number of rainbow trout caught in the gill nets away from the farms supports this. A study by Cragg-Hine (1975) also demonstrated that they have a poor over-winter survival in Irish lakes.

However Stradmeyer & Thorpe (1987) demonstrated that hatchery reared salmon parr switched very quickly to conventional prey. This suggests that younger salmonids adapt more readily to new environments. This finding was observed in the juvenile behaviour experiment described in the following chapter and has also been reported by Kelly-Quinn & Bracken (1989) and Johnsen & Ugedal (1989). Therefore it is clear that the impact of escapees will be dependant upon their size on release. If they are small they may initially suffer a high mortality rate through predation by native trout, but it is likely that the survivors will eventually learn to successfully feed on wild prey. If this happened it is likely that they would constitute a threat to the native fish species by impinging on their food resources.

The size of the loch in which the loss occurs will also determine the impact on native stocks. Phillips et al. (1985) described how the loss of one Kames type cage (10,000 250g trout) in a loch the size of Loch Leven would have a dramatic effect on the native stock. In Loch Awe, however, when at least 6 Kames cages were lost in a severe storm in 1989, the background number of rainbow trout throughout the loch 4 months later was no higher than it had been before the escape. Admittedly, some fish from the escape would have survived, but by the time they had spread through the loch they would only have been present in very small numbers and it is unlikely that the increase could have been detected using standard population estimates. The remaining escapees probably died, for one of three reasons 1. predation (if they were small enough to be eaten by the resident trout population), 2. starvation, and 3. caught by anglers. Artificially reared salmonids have a greater catchability than wild ones (Jacques, 1974; Taylor, 1978; Coles, 1981; Bryan, 1982; Pawson, 1986).

In summary, the diet of rainbow trout in sympatry with brown trout in pond B was largely based on non-conventional prey items. Whilst that of brown trout in the same pond was similar to the allopatric population of brown trout, which was largely based upon conventional prey items. The two species in pond B had the same survival rate which was lower than the allopatric population of brown trout in pond A. Interpretation of the survival and growth data was not possible as conditions in the two ponds were not uniform at the start of the experiment, and it is suspected that there may have been some mortality due to angling or bird predation.

For rainbow trout to have a significant impact on the brown trout population in Loch Awe they would have to be present in considerably greater numbers than they were after the large escape in 1989.

CHAPTER 6

EARLY LIFE HISTORY INTERACTIONS BETWEEN BROWN TROUT AND RAINBOW TROUT

6.1 Introduction.

In Loch Awe rainbow trout compete poorly with the indigenous fish species. The main reason for this is their low success in securing wild prey items, which is in turn due to the low repertoire of prey searching images that they have when they escape from the cages. If they were to spawn, and their progeny survived and fed on wild prey from emergence, they may be able to compete more effectively with the native species.

Dodge (1983) predicted the wide scale establishment of self-sustaining rainbow trout populations arising from deliberate stocking programmes and accidental stock losses from fish farms. The outcome of interactions between native and exotic species is difficult to predict as it is complicated by a number of biotic and abiotic variables. One of the main factors in determining the outcome of such interactions is the development stage at which they occur, and this is largely determined by the timing of spawning and subsequent emergence of the species involved. The spawning of most native British salmonids is restricted to late autumn and early winter, whereas the spawning behaviour of rainbow trout is characterised by peaks in activity in the autumn and spring. However it has been reported that they move into spawning streams in every month of the year (Dodge, 1983). Before breeding and stock enhancement programmes started there were two strains of rainbow trout, the shasta, which were autumn spawners, and irideus which were spring spawners. The distinction between them has been lost through breeding programmes associated with stock enhancement, and the aquaculture industry. Therefore at best one can say that rainbow trout spawning behaviour is characterised by an annual continuum with peaks of activity in the autumn and spring. This obviously makes it very difficult to confidently predict the outcome of interactions between rainbow trout and other salmonids.

At one extreme Hayes (1984) demonstrated complete domination of brown trout by rainbow trout in a tributary of Lake Alexandrina, New Zealand. This was due to spring spawning rainbow trout over-cutting the redds of autumn spawning brown trout and rainbow trout in a stream with limited spawning area. As a result of the high mortality in the autumn spawned fish very few were recruited into the adult population.

The other extreme is represented by the situation in Lake Eucumbene, Australia where brown trout completely dominate rainbow trout. In this situation there is unlimited spawning available, brown trout are autumn spawning, and rainbow trout spawn in the spring. By virtue of their earlier emergence, greater size and prior residence brown trout cause rainbow trout to emigrate from the streams immediately after emergence. They were subsequently preyed on heavily by large brown trout in Lake Eucumbene which gathered around stream outlets at that time (Tilzey, 1972).

Dodge (1983) reported an intermediate situation where the two species were able to co-exist, but the productivity of each was lower than it would have been had they been in allopatry. Therefore it is clear that a continuum of outcomes are possible when the two species are brought into unnatural sympatry, with the outcome largely being determined by local environmental and genetic factors.

In order to predict the likelihood of rainbow trout establishing a self-sustaining population in Loch Awe, and the outcome resulting from interactions between the two species in the early stages of their lives if spawning was successful, a series of experiments was performed.

As rainbow trout have been reported spawning in a number of Scottish streams (Lever, 1977; Phillips et al., 1984), a trapping programme was initiated on the Kames burn to determine if rainbow trout migrated into Loch Awe's spawning burns.

In order for a self-sustaining population of rainbow trout to become established not only must they migrate into the spawning burns and find a sexually mature mate, but it is also necessary that their eggs are viable and survive to hatching. The survival of brown and rainbow trout from the egg to alevin stage was compared by planting their eggs in boxes in two of Loch Awe's tributaries.

An electrofishing survey was performed to determine if there was any evidence of successful spawning by rainbow trout, and to assess the current status of brown trout and Atlantic salmon stocks in Loch Awe's catchment.

The behavioural interactions between the progeny of autumn-spawned brown trout and spring-spawned rainbow trout, was examined in three simulated streams.

6.2 Methods.

6.2.1 Trapping experiment.

A fish trap was installed in the Kames burn, a recognised salmonid spawning burn, on the 28 October 1986 at NGR NM 981 105. A partial screen line was set across the river to guide the upstream migrating fish into the trap. It was fished twice daily, in the morning and late afternoon.

6.2.2 Egg survival experiment.

Egg survival from fertilisation to hatching in rainbow trout and brown trout was compared at two sites in the Allt Doire nan Sobhrachan NGR (NM 955 074) at Braevallich, and in the Allt na Cuile Riabhaiche NGR (NN 065 212) at Ardbrecknish, two recognised spawning tributaries for brown trout and Atlantic salmon.

In each stream the two sites were separated by 100m, with each species being tested at each site. The position of the artificial redd sites were selected using the criteria described by Stuart (1953) as being optimal for the in-stream incubation of brown trout eggs.

Rainbow trout eggs and milt were obtained from Bibury trout farm Gloucestershire from fish aged 3+. Brown trout eggs and milt were obtained from fish aged 4+, caught by electrofishing the burns that the experiments were performed in, and from Howietoun Fish Farm. It was necessary to get eggs from the fish farm as not enough were obtained from female fish in the streams. It had been intended to start all the replicates on the same date, but due to logistical problems in obtaining the rainbow trout eggs, and to the shortage of female brown trout this was not possible. All rainbow trout replicates were fertilised on the 9/11/88; and the brown trout replicates at the two Braevallich sites and the Ardbrecknish downstream site on the 16/11/88, the Ardbrecknish upstream site eggs were fertilised on the 25/11/88.

At each site two trays (one for each species) containing eight egg boxes were buried 25cm below the stream bottom. The boxes were 600 ml plastic beakers with the sides cut out and replaced with a fine plastic mesh, that allowed water transfer but prevented the intrusion of egg eating invertebrates and the escape of alevins after hatching. Each beaker was sealed with a tight fitting wooden lid which swelled in the water. The eggs were fertilised on the river bank using water from the burns to mix milt around the eggs. Fifty eggs were then put into each box with gravel from the river bed. The survival in each replicate was compared by one way ANOVA after a $\log_{10} + 1$ transformation.

6.2.3 Electrofishing survey.

Quantitative sampling was performed in ten streams on four occasions in the spring and autumn between September 1986 and April 1988. Streams were selected from all around the catchment and included those that entered the loch at the three fish farms. Table 6.1 gives the name and NGR of the sites and the date of each survey.

Each section was isolated from the river by stop nets. This was to prevent the movement of fish from and into the study section, a requirement of the depletion technique that was used to estimate the size of the populations. Cowx (1984) gives a detailed discussion of the conditions which must be met for such population estimates.

On each visit the sites were fished three times with a Killybegs Safari backpack electrofisher. The catch was processed after each run, which involved anaesthetising them (Laird & Oswald, 1975) recording their species, length to the nearest millimetre (fork length in the case of salmonids, minnows and sticklebacks) and taking a sample of scales from

Table 6.1 The electrofishing sites, their NGR's and the dates that they were surveyed.

	Autumn 1986	Spring 1987	Autumn 1987	Spring 1988
Braevallich NM 953 076	22/9/86	31/3/87	23/8/87	25/3/88
Finchairn NM 903 042	24/9/86	25/4/87	27/9/87	22/4/88
Clachan NM 879 997	25/9/86	3/5/87	27/9/87	23/3/88
Allt Mor NM 976 119	23/9/86	1/4/87	29/9/87	22/4/88
Coillaig NN 017 205	23/9/86	1/4/87	29/9/87	23/4/88
Tervine NN 079 262	25/9/86	5/5/87	28/9/87	23/4/88
Duilletter NN 156 309	26/9/86			25/4/88
Teetle NN 131 252	24/9/86		30/9/87	24/4/88
Ballimeanoch NN 013 167		23/4/87	23/8/87	29/3/88
Kames NN 012 167	22/9/86	24/4/87	30/9/87	26/3/88

salmonids greater than 60mm for age determination, those less than 60mm were assumed to be O+. Between runs the survey sections were rested for a minimum of half an hour, which allowed those fish remaining in the stream to recover from the previous electric shock (Bohlin & Harris, 1989). During this time the catches were processed. At the end of each survey all fish, excluding rainbow trout were returned to the stream after total recovery from the anaesthetic.

Population estimates were made by the Zippin maximum likelihood method (Zippin, 1956 & 1958), using the BASIC computer programme described by Higgins (1985). This technique requires a reduction in successive catches. Where this was not achieved the catch and minimum density are presented. Population and density estimates with 95% confidence limits were made for brown trout and Atlantic salmon, and each of their year classes that were caught. All surveys were performed when the water temperature was above 4°C, the temperature described as being critical for salmonid activity (Zalewski & Cowx, 1990).

6.2.4 Juvenile interaction experiment.

Description of the experimental facility.

Three troughs were used in the experiment, trough 1 (T1) contained an allopatric population of rainbow trout; trough 2 (T2) an allopatric population of brown trout, and trough 3 (T3) a sympatric population of brown trout and rainbow trout. The experiment was performed at Braevallich in a clear polythene horticultural tunnel. This ensured that the fish were subjected to a natural light regime. Each trough measured 1.8 x 0.4 x 0.25m and was divided equally into a pool and riffle section by arranging the bottom substrate to different depths. Ten of each species were held in T1 and T2 at a density of $13.9m^{-2}$, and five of each species were held in T3 at density of $6.9m^{-2}$ per species. all fish used in the experiment were 0+. Brown trout were obtained from the Allt nan Sobhrachan, and rainbow trout from the Cloan hatchery at Auchterarder.

The water supply was also drawn from the Allt nan Sobrachan at NGR (NM 955 074) down a pipe system that had been constructed for a hatchery which had previously been on the same site. The inflow to each trough was via a horizontal pipe with a longitudinal cut in it to ensure that the water flow was spread across the entire width, and the outflows were protected by a screen to prevent emigration from them. The discharge into troughs 1-3 was 1.94l/sec, 1.4l/sec and 1.87l/sec respectively. Each trough was covered with a net that allowed invertebrates in the water supply to enter the troughs but prevented fish from jumping out of them. Observations were made from behind a black polythene curtain through perspex windows cut into the trough sides.

Experimental protocol.

The experiment commenced on the 20/6/88 but due to initial problems including the inlet pipe blocking, and fish moving down the pipe from the stream into the troughs, only data from the 20/7/88 to 25/8/88 were used in the behavioural observations, and from 26/7/88 to 29/8/88 in the growth study. The observations were made during four time periods, early morning 06.00-09.00, (this was changed to 06.30-09.30 on the 17/8/88 when poor light conditions reduced visibility in the mornings); mornings, 10.00-13.00; afternoons 14.00-17.00; and evenings 18.00-21.00. Fish were observed twice a day either in the early morning and afternoon, or in the morning and evening. Viewings were generally made on Tuesdays, Wednesdays and Thursdays, with Fridays being reserved for any sessions that were missed on the previous 3 days.

In each trough visible fish were observed for 5 minutes with the

following variables being recorded: feeding rate, agonistic interactions, habitat preference, position in the water column.
Their food consumption was measured by counting the number of food items consumed from the drift, surface and bottom. The frequency of agonistic interactions was based on the criteria outlined by Keenleyside & Yamamoto (1962). For the purposes of analysis the agonistic interactions were grouped into three categories, aggressive which included charge, nip and chase, or any combination of these. Ritualised interactions which included frontal and lateral displays and the third category included all submissive or defensive acts that were made in response to either of the first two categories. In trough 3 a further distinction was made between intra- and inter-specific interactions. Habitat preference was divided into 3 categories: pool, riffle and pool/riffle. The last category was used when a fish held station at the pool riffle interphase or held a territory that included both. Position in the water column was divided into two categories, resting on the bottom, or swimming in the current.

Food availability in each trough was assessed on an hourly basis on Mondays by placing a very fine meshed net below the inflow for one hour periods from 02:00, 08:00, 14:00 and 20:00 hours. The invertebrates were then counted and identified. It was assumed that drift invertebrates were the only food entering the troughs as the nets placed over them and the polythene tunnel prevented any flying insects falling into them.

The temperature in each trough was measured four times daily at 09.00, 13.00, 17.00 and 21.00, and at 02.00 on Mondays when food availability was being measured.

The mean instantaneous growth rate in each trough was calculated by the following formula:

$$Go = \frac{100 \ln (W2-W1)}{t}$$

where,

Go=Mean Instantaneous Growth Rate,

W1=Mean weight at the start of the experiment,

W2=Mean weight at the end of the experiment,

and t=The duration of the experiment, in days.

Using the survival and growth rates production in each trough was calculated by the following formula:

$$P=G.B$$

where,

P=Production (g),

G=Instantaneous rate of increase in weight,

and B=Mean biomass.

Statistical analysis.

The diurnal variation in food supply within each trough, and the variation between troughs was made by one way ANOVA, after a Log 10 transformation to normalise the data. The variation in food consumption from the drift, surface and bottom between the 4 viewing periods was compared by one way ANOVA after a log 10 (x + 1) transformation. The same test was used to compare the feeding rate of fish between the three troughs. The variation in rate and type of agonistic interactions that occurred in the 4 viewing periods in each trough was compared by one way ANOVA after a log 10 (x + 1) transformation of the data. The total number of agonistic interactions between each group was compared in the same manner. The data was further broken down into aggressive, ritualised and defensive interactions. In trough 3 a further distinction was made between intraspecific and interspecific interactions. The variation in habitat use by each group of fish in each trough in each observation period was examined by x^2 test, with the same analysis being used when data were pooled and the comparison was made between different fish groups. The position in the water column in each viewing period in each group was compared by x^2 test, with the same test being used when the data were pooled and comparisons made between different fish groups.

6.3 Results.

6.3.1 Trapping.

After two nights of continuous rain in which no fish were caught, the trap and screen line were severely undercut due to a build up of leaves on their upstream side. This resulted in them being swept out of the river. It was then decided to terminate the trapping programme.

6.3.2 Egg survival.

When the egg boxes at Ardbrecknish were examined after 164, 158 and 148 days for rainbow trout and brown trout at the upstream and downstream sites respectively on 23.3.89 it was discovered that the eggs had been badly affected by a fungus. This resulted in none of the rainbow trout surviving at the two sites, and only a small number of brown trout hatching at the upstream site, as a result it was decided not to include them in the analysis (Table 6.2).

There were no such problems with fungus at Braevallich. There was no significant difference ($P>0.05$) in the mean survival of brown trout in the upstream and down stream replicates, so their results were pooled (Table 6.2). The difference between the two rainbow trout replicates was significant ($P<0.05$), so they were compared separately against the pooled brown trout results. There was no obvious reason for the different survival rates between rainbow trout at the two sites. The difference in mean survival between the pooled brown trout results and those from the two rainbow trout replicates were both highly significant ($P<0.001$), with the survival of brown trout being higher than rainbow trout (Table 6.2). This shows that rainbow trout eggs can survive to the alevin stage in Loch Awe's tributaries, but that their survival is considerably lower than that of brown trout.

Table 6.2 The number of live alevins found in each egg basket at the upstream and downstream sites at Ardbrecknish and Braevallich.

Ardbrecknish

	Rainbow Trout		Brown Trout	
	U/S	D/S	U/S	D/S
	0	0	3	0
	0	0	13	0
	0	0	2	0
	0	0	8	0
	0	0	7	0
	0	0	0	0
	0	0	0	0
	0	0	0	0
Mean	0	0	4.1	0

Braevallich

	Rainbow Trout		Brown Trout	
	U/S	D/S	U/S	D/S
	1	3	11	3
	0	1	11	5
	0	1	22	15
	0	1	14	4
	0	3	0	20
	0	2	7	3
	0	0	22	24
	0	0	7	23
Mean	0.13	1.40	11.8	12.1

U/S=Upstream, D/S=Downstream.

Water quality

The water pH in the Allt Doire nan Sobhrachan and the Allt na Cuile Riabhaiche was 5.9 and 6.0 respectively. Grande et al. (1978) stated that in some natural waters the lower tolerance limit for rainbow trout may be as high as pH 5.5-6.0. The pH of the water in the streams examined in the electrofishing survey ranged from 5.5-6.2. As the pH in some of Loch Awe's tributaries is close to this lower limit it may act as a limiting factor to rainbow trout establishing a self-sustaining population in the catchment.

6.3.3 Electrofishing survey.

The densities of brown trout and Atlantic salmon at each of the sites surveyed are presented in Tables 6.3-6.12. Seven species were caught, they were sea trout/brown trout, Atlantic salmon, rainbow trout, brook lamprey, eels, minnows and sticklebacks. This species list, excluding rainbow trout, is typical of Scottish upland streams and rivers. The two rainbow trout caught in the Clachan Dubh burn and the Kames burn were both adults, no juveniles being found at any of the sites surveyed.

Braevallich.

Only brown trout and Atlantic salmon were caught in the Braevallich burn. Their highest combined density was recorded in the autumn of 1987, which at 2.89 m^{-2}, was the highest density recorded during the project (Table 6.3). It was caused by a large increase in the recruitment of both Atlantic salmon and brown trout over the previous year. In each survey brown trout were present in larger numbers than Atlantic salmon. The greatest over-winter mortality occurred after the year in which the highest autumn density was recorded.

Table 6.3 The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Braevallich burn (figures in parenthesis are 95% confidence limits).

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	1.17	0.39	2.89	0.74
Brown Trout	1.17 (0.17)	0.34 (0.15)	2.03 (0.31)	0.56 (0.31)
0+	1.17 (0.17)	-	2.02 (0.32)	-
1+	-	0.34 (0.15)	-	0.56 (0.31)
2+	-	-	0.02 *	-
3+	-	-	-	-
Atlantic Salmon	-	0.05 *	0.86 (0.09)	0.18 (0.05)
0+	-	-	0.82 (0.10)	-
1+	-	0.05 *	0.05 *	0.18 (0.05)
2+	-	-	-	-

*=minimum density

Table 6.4 The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Finchairn burn (figures in parenthesis are 95% confidence limits).

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	1.65	0.44	1.21	0.5
Brown Trout	0.19 (0.03)	0.11 (0.05)	0.08 (0.02)	0.12 (0.20)
0+	0.19 (0.03)	-	0.06 (0.03)	-
1+	-	0.10 (0.04)	0.02 (0.01)	0.10 (0.16)
2+	-	0.01 *	-	0.01 *
3+	-	-	-	-
Atlantic Salmon	1.46 (0.81)	0.33 (0.23)	1.13 (0.56)	0.38 (0.11)
0+	1.43 (0.50)	-	1.1 (0.81)	-
1+	0.06 (0.02)	0.27 (0.13)	0.16 (0.07)	0.35 (0.04)
2+	0.01 *	0.02 *	0.01 *	0.04 (0.01)

*=minimum density

Finchairn.

The Finchairn burn contained brown trout, Atlantic salmon, eels, minnows, brook lampreys and sticklebacks. Atlantic salmon were most abundant, and only a few non salmonids were caught in each survey. The highest combined salmonid density, 1.65 m^{-2}, was recorded in autumn 1986, in the following autumn it was only 1.21 m^{-2} (Table 6.4). Between these two periods there was a greater decline in percentage terms in the brown trout population, but in absolute terms the decline in the Atlantic salmon population was greater (Table 6.4). Again the highest winter mortality occurred after the highest autumn density was recorded.

Clachan Dubh.

In the Clachan Dubh burn brown trout, Atlantic salmon, rainbow trout, eels and minnows were caught, with Atlantic salmon being caught in greater numbers than brown trout. One sexually mature rainbow trout was caught in autumn 1987. The highest combined salmonid density, 0.22m^{-2}, was recorded in the autumn of 1988, this was low compared with the densities recorded in other streams (Table 6.5). It is likely that the low density is partly responsible for the low mortality rate in the 1987 year class in the 1987-88 winter. Compared to other streams in the catchment the stream residence time of Atlantic salmon and brown trout was low, no brown trout remained by the end of their second growth season, and no Atlantic salmon remained by the start of their 3rd growth season (Table 6.5). In view of the low density this was surprising.

The site on the Clachan Dubh burn was furthest away from Loch Awe, and it was above a small set of falls that may have been impassable for some smaller brown trout. It is possible that these two factors contributed to the low salmonid density in the stream. The salmonid

Table 6.5 The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Clachan Dubh burn (figures in parenthesis are 95% confidence limits).

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	0.18	0.12	0.22	0.18
Brown Trout	0.05 (0.03)	0.02 *	0.02 (0.01)	-
0+	0.03 *	-	-	-
1+	0.02 (0.01)	0.01 *	0.02 (0.01)	-
2+	-	0.01 *	-	-
3+	-	-	-	-
Atlantic Salmon	0.13 (0.04)	0.06 (0.003)	0.20 (0.07)	0.18 (0.10)
0+	0.10 (0.03)	-	0.18 (0.04)	-
1+	0.02 (0.006)	0.06 (0.003)	0.01 *	0.18 (0.10)
2+	-	-	-	-

*=minimum density

Table 6.6 The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Allt Mor (figures in parenthesis are 95% confidence limits).

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	0.5	0.38	0.87	0.6
Brown Trout	0.31 (0.48)	0.18 (0.06)	0.08 (0.19)	0.16 (0.06)
0+	0.29 (0.45)	-	0.04 (0.02)	-
1+	0.08 (0.20)	0.18 (0.06)	0.01 *	0.16 (0.08)
2+	-	-	-	0.01 *
3+	-	-	-	-
Atlantic Salmon	0.19 (0.03)	0.20 (0.06)	0.79 (0.13)	0.44 (0.19)
0+	0.11 (0.02)	-	0.59 (0.06)	-
1+	0.06 (0.04)	0.16 (0.08)	0.16 (0.15)	0.44 (0.21)
2+	0.02 *	0.05 (0.01)	-	0.01 *

*=minimum density

shortfall was made up by minnows which were particularly abundant in the autumn and spring surveys of 1986 and 1987.

Allt Mor.

Brown trout, Atlantic salmon and brook lampreys were caught in the Allt Mor. The highest combined salmonid density was recorded in the autumn of 1987 $0.87m^{-2}$ (Table 6.6). The densities recorded in autumn 1986 should be regarded as minimum values as the electrofishing operator was severely hampered by a large hatch of voracious adult Ceratopogonidae. This reduced the catching efficiency which is reflected in the high confident limits attached to some of the densities (Table 6.6). In autumn 1986 a greater number of brown trout than Atlantic salmon was caught, with the situation being reversed the following year. This change was due to a combination of very low recruitment to the brown trout population, and high recruitment to the Atlantic salmon population. The reason for the poor recruitment of brown trout to the 1987 year class is unclear. Again the greatest over-winter mortality occurred after the autumn in which the highest density was recorded. The relationship in the Allt Mor is less clear than it was at other sites, as the situation is complicated by the low estimates in autumn 1986. All brown trout had migrated from the burn by the end of their second growing season, and all Atlantic salmon had migrated by the start of their 3rd growth season.

Coillaig.

Brown trout, Atlantic salmon, minnows, brook lampreys and eels were caught in the Coillaig burn. The highest salmonid density was recorded in the autumn of 1986, $0.71m^{-2}$, with densities in the remaining surveys being considerably lower (Table 6.7). In the three remaining surveys more minnows than salmonids were caught. The increase in the minnow population is probably due to the decline in the salmonid population.

Table 6.7 The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Coillaig burn (figures in parenthesis are 95% confidence limits).

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	0.71	0.31	0.35	0.34
Brown Trout	0.56 (0.54)	0.16 (0.08)	0.12 (0.002)	0.10 (0.01)
0+	0.38 (0.36)	-	0.04 (0.01)	-
1+	0.09 (0.03)	0.13 (0.06)	0.08 (0.02)	0.01 (0.008)
2+	-	0.03 (0.01	0.02 *	0.008*
3+	-	-	-	-
Atlantic Salmon	0.15 (0.01)	0.15 (0.03)	0.23 (0.18)	0.24 (0.1)
0+	0.01 *	-	0.11 (0.10)	-
1+	0.14 (0.01)	0.10 (0.04)	0.12 (0.19)	0.24 (0.13)
2+	0.01 *	0.05 (0.01)	-	0.08 *

*=minimum density

Table 6.8 The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Tervine burn (figures in parenthesis are 95% confidence limits).

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	0.98	0.69	1.10	0.73
Brown Trout	0.98 (0.13)	0.69 (0.21)	1.10 (0.18)	0.73 (0.10)
0+	0.55 (0.07)	-	0.74 (0.32)	-
1+	0.19 (0.02)	0.57 (0.25)	0.36 (0.05)	0.57 (0.13)
2+	0.02 *	0.13 (0.05)	0.06 *	0.17 (0.01)
3+	0.01 *	-	-	-
Atlantic Salmon				
0+				
1+				
2+				

*=minimum density

similar to that observed in the Clachan Dubh burn. In the 1986 year class brown trout were more abundant than Atlantic salmon, with the opposite being true in the following year class (Table 6.7). This change occurred as a result of very poor brown trout recruitment, however it was compensated by high survival over the following winter. In contrast, recruitment to the 1987 Atlantic salmon year class was higher than it had been in the previous year. The density of the 1986 Atlantic salmon year class increased from autumn 1986 to autumn 1987, and the 1987 year class increased over the 1987-88 winter. It is possible that the increases were due to displaced fish from upstream taking up residence in the section. The low density of fish at this site would facilitate such a process. In common with the previous sites the highest winter mortality occurred after the highest autumn density was recorded. All brown trout and Atlantic salmon had migrated from the stream by the start of their third growth season.

Tervine.

Only brown trout were caught in the Tervine burn, with the highest density being recorded in the autumn of 1987, 1.1m^{-2} (Table 6.8). The difference in the total density recorded in the autumn of 1986 and 1987 was small, however the over-winter mortality was still greatest following the autumn with the highest density. The estimated density of the 1986 year class increased slightly from autumn 1986 to spring 1987. This unexpected finding could have been caused by two factors. The spring estimate may be slightly inaccurate, this being reflected in its high confidence limits, or displaced fish from upstream may have taken up residence in the section examined. The high density of fish in the Tervine burn makes this second scenario less likely than it was in the Coillaig burn, which had a low density of fish.

Duilletter.

Brown trout, Atlantic salmon and eels were caught in the stream at Duilletter, with the largest combined salmonid density being recorded in the autumn of 1986, 0.52m^{-2} (Table 6.9). Only data from the surveys in 1986 and 1988 are included in the analysis due to equipment malfunctions in 1987. Brown trout were more abundant than Atlantic salmon, but the density of both species was low compared to the sites in other parts of the catchment. There are two possible explanations for this. It is highly likely that the streams in Loch Awe's northern catchment will be low in nutrients, and that this will limit their carrying capacity. They flow down steep hills which are composed of slow weathering granite covered by thin soils. This will result in rain water entering the streams quickly, picking up few nutrients in the process. As the stream's catchment has no forestry there will be no additional nutrients from fertiliser run-off, small amounts of which can have a beneficial effect on salmonid growth (Munro, 1961). By contrast the streams that enter the main body of the loch flow over rocks which have pockets of calcium bearing minerals, which are beneficial to trout growth. From observations made whilst performing the surveys it was also clear that the diameter of the bed material at this site was slightly larger than at the others. As larger fish tend to select redd sites over larger bed material than small fish, this would make it a less attractive spawning substrate for smaller fish. This could ultimately reduce the egg deposition rate in the section, and result in it being under populated.

Teetle Water.

Atlantic salmon were the only salmonids caught at the two sites fished in the Teetle water, with small numbers of eels and minnows also being caught. The site fished in autumn 1986 was later judged to be inappropriate for the purposes of the survey, as its population

Table 6.9 **The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Duilletter burn (figures in parenthesis are 95% confidence limits).**

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	0.52	-	-	0.24
Brown Trout	0.34 (0.09)	-	-	0.16 (0.08)
0+	0.12 (0.05)	-	-	-
1+	0.28 (0.16)	-	-	0.16 (0.08)
2+	0.02 *	-	-	0.02 *
3+	-	-	-	-
Atlantic Salmon	0.18 (0.06)	-	-	0.08 (0.02)
0+	0.15 (0.34)	-	-	-
1+	0.05 (0.001)	-	-	0.06 (0.04)
2+	0.01 *	-	-	0.02 (0.003)

*=minimum density

Table 6.10 **The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Teetle Water burn (figures in parenthesis are 95% confidence limits).**

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	0.47	-	0.62	0.22
Brown Trout				
0+				
1+				
2+				
3+				
Atlantic Salmon	0.47 (1.47)	-	0.62 (0.29)	0.22 (0.03)
0+	0.32 (0.84)	-	0.54 (0.48)	-
1+	0.02 *	-	0.12 (0.03)	0.17 (0.02)
2+	0.01 *	-	0.02 *	0.06 (0.07)

*=minimum density

estimates had large confidence limits (Table 6.10). Due to this a new site further upstream was selected, This was only fished in autumn 1987 and spring 1988, as high water prevented sampling in the spring of 1987. The highest density was recorded in the autumn of 1987, 0.62m^{-2}, by the following spring it had fallen to 0.22m^{-2} (Table 6.10). These densities are similar to others recorded in the Loch Awe catchment. A small number of 2+ Atlantic salmon were caught in the autumn survey in 1987, which suggests that the Teetle water produces a small number of 3+ smolts.

Ballimeanoch.

Brown trout, Atlantic salmon, eels and brook lampreys were caught in the Ballimeanoch burn. The combined salmonid density in the stream was above the average at the other sites, with the highest 1.6m^{-2}, being recorded in the autumn of 1987 (Table 6.11). Due to the large confidence limits attached to some of the estimates, their accuracy must be questioned. This is particularly true of the 1986 Atlantic salmon year class which increased over the summer of 1987. It could also have been caused by displaced fish from upstream securing territories in the survey area. However the streams high density makes this scenario unlikely. At the end of the 1987 growing season 0+ brown trout and Atlantic salmon from the 1987 year class were present in similar numbers, but over the winter the survival of Atlantic salmon was lower than brown trout. This resulted in a higher density of trout than salmon the following spring (Table 6.11). Brown trout migration from the stream was complete by the start of their third growth season and the Atlantic salmon migration was complete by the end of their second growth season.

Kames Burn.

Brown trout, Atlantic salmon, eels and minnows and one rainbow trout

Table 6.11 **The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Ballimeanoch burn (figures in parenthesis are 95% confidence limits).**

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	-	0.89	1.60	0.58
Brown Trout	-	0.62 (0.69)	0.74 (0.12)	0.41 (1.84)
0+	-	-	0.64 (0.22)	-
1+	-	0.74 (1.55)	0.14 (0.03)	0.41 (1.84)
2+	-	0.04 (0.01)	0.03 *	-
3+	-	-	-	-
Atlantic Salmon	-	0.27 (0.22)	0.86 (0.60)	0.17 (0.07)
0+	-	-	0.56 (0.48)	-
1+	-	0.27 (0.49)	0.32 (0.42)	0.14 (0.06)
2+	-	0.04 (0.01)	-	0.03 (0.02)

*=minimum density

Table 6.12 **The density (no. m^{-2}) of brown trout and Atlantic salmon in the autumn and spring from 1986-88 in the Kames burn (figures in parenthesis are 95% confidence limits).**

	Autumn '86	Spring '87	Autumn '87	Spring '88
Total	1.24	0.36	1.15	0.35
Brown Trout	0.74 (0.36)	0.21 (0.05)	0.25 (0.12)	0.11 (0.02)
0+	0.41 (0.20)	-	0.22 (0.16)	-
1+	0.02 (0.01)	0.20 (0.05)	0.16 (0.04)	0.09 (0.01)
2+	0.008*	0.01 *	-	0.01 *
3+	-	-	-	-
Atlantic Salmon	0.50 (0.17)	0.15 (0.08)	0.90 (0.29)	0.24 (0.07)
0+	0.62 (3.81)	-	0.88 (0.68)	-
1+	0.17 (0.02)	0.15 (0.08)	0.17 (0.02)	0.13 (0.08)
2+	0.01 *	-	-	0.01 *

*=minimum density

were caught in the Kames burn. The immature rainbow trout was caught in the spring of 1987 and was in poor condition. It had one eye missing, was rather thin, and its fins were eroded, suggesting that it had escaped from one of the fish farms. The Kames burn is recognised locally as a good spawning burn and the densities of salmonids recorded in it agree with this, the highest being recorded in the autumn of 1986, $1.24m^{-2}$ (Table 6.12). At this time more 0+ brown trout than Atlantic salmon were caught, whereas in the following year more salmon than trout were caught. The reversal was due to a combination of low brown trout recruitment and increased salmon recruitment. The reason for the low number of trout in the 1987 year class is not clear. In common with previous sites the highest over-winter mortality occurred after the autumn recording the highest density. The spring densities in 1987 and 1988 were remarkably similar even though the catches were dominated by different species in each year. Both Atlantic salmon and brown trout had migrated from the Kames burn by the start of their third growth season.

6.3.4 Juvenile interaction experiment.

6.3.4.1 Temperature.

There was no variation in the water temperature between the troughs, and so the mean daily temperature was calculated from the data collected in the four time periods, from trough 3. During the course of the experiment the temperature fell from 14.9°C on the 28th June to 9.8°C on the 22th August. There was a large amount of variation in the mean daily temperature, but the overall trend throughout the experiment was downwards, from the high levels recorded in mid-summer at the start of the experiment.

6.3.4.2 Food availability.

There was no significant difference in the mean number of prey items entering the 3 troughs during the experiment ($P>0.05$ $FS=0.76$ $2,69$). Trough 3 had the highest input 24.54 prey items (PI) hr^{-1}, and trough 2 the lowest 18.92 PI hr^{-1}, with an intermediate amount 21.71 PI hr^{-1} entering trough 1. The lower input of food to T2 was probably due to the lower volume of water that entered it, this relationship did not hold for troughs 1 and 3.

There was a highly significant difference ($P<0.001$ $FS = 13.99$ $3,58$) in the amount of food that entered the three troughs in the four time periods sampled. The highest value of 37.5 PI hr^{-1} was collected between 02:00-03:00hrs, with the number falling through the day with only 11.0 PI hr^{-1} being collected during the 20-21:00 hours session. This marked diurnal pattern is a recognised phenomenon (Waters, 1969; Brithain & Eikeland, 1988).

6.3.4.3 Growth.

The growth rate (% body weight/day) of rainbow trout in allopatry and sympatry was 2.299 and 2.712 respectively. This was considerably higher than the rates achieved by brown trout in the same situations, which were 0.555 and 0.692 respectively. Over the duration of the experiment brown trout growth in the troughs was similar to their growth in the stream from which they had been removed, which was 0.661.

6.3.4.4 Survival.

In the sympatric and allopatric brown trout populations survival was 100%, and in the rainbow trout populations it was 40% and 80% respectively (Table 6.13). The two rainbow trout found dead on the screen in T3 had badly damaged caudal regions. This is evidence of nonreciprocal attacks from the rear (Abbot & Dill, 1985).

Combining the last two measures gives production. The highest level was

Table 6.13 The percentage survival in the allopatric and sympatric populations of brown trout and rainbow trout.

		Initial No.s	Final No.s	% Survival
T1	RT	10	8	80
T2	BT	10	10	100
T3	RT	5	2	40
	BT	5	5	100

recorded in the allopatric rainbow trout population 13.55g which was considerably higher than the 6.91g recorded in the allopatric brown trout population. In sympatry rainbow trout production again exceeded that of brown trout, with 8.27g and 5.74g being recorded respectively.

6.3.4.5 Feeding.

There was no significant variation in the feeding rate between the 4 time periods in which observations were made, this allowed the results to be pooled. In the interspecific comparisons rainbow trout had a significantly higher feeding rate than brown trout in both sympatry and allopatry, ($P < 0.001$ Fs 30.798 1,94) and ($P < 0.001$ Fs 48.617 1, 221) respectively (Table 6.14). In intraspecific comparisons both species had a higher feeding rate in allopatry than in sympatry; in rainbow trout the difference was not significant, however in brown trout it was ($P<0.05$ Fs 4.105 1,160).

Each population showed a preference for drift prey items, with the least favoured component being prey from the surface, the difference in each population was highly significant ($P<0.001$). The low surface component contribution is probably due to a combination of the nets being placed over the troughs, and the experiment being performed in a polythene tunnel. The preference of drift prey in the diet of brown trout has been described previously by Bachman (1984), and in other juvenile salmonids by Hunt (1965), Sagar & Glova (1987).

6.3.4.6 Total number of behavioural interactions.

There was no significant variation in the number of interactions in the 4 time periods that observations were made, this allowed the results to be pooled. In interspecific comparisons rainbow trout were involved in a greater number of interactions than brown trout in both allopatric and sympatric situations; however only in the former was the difference

Table 6.14 The mean feeding rates $\log_{10}(x+1)$ (items consumed/5 minutes) of the sympatric and allopatric populations of brown trout and rainbow trout.

		Total	Drift	Surface	Bottom
T1	RT	1.036	0.871	0.176	0.497
T2	BT	0.839	0.671	0.135	0.380
T3	RT	1.023	0.927	0.092	0.391
	BT	0.760	0.557	0.118	0.408

significant (P <0.001 Fs 21.156 1,221) (Table 6.15). In intraspecific comparisons brown trout were involved in more interactions in sympatry than in allopatry, with opposite being the case for rainbow trout. However none of the differences were significant. The agonistic interactions are examined further by dividing them into aggressive, fronto/lateral and defensive acts.

Aggressive.

In interspecific comparisons rainbow trout have a significantly higher attack rate than brown trout in allopatry (P<0.001 Fs 11.606 1,221); whereas in sympatry the opposite was true (P<0.001 Fs 11.565 1,94) (Table 6.15). This higher rate of aggression in sympatric brown trout is probably due to the lower stability resulting from the greater size variation in T3. In intraspecific comparisons brown trout have a significantly higher (P<0.05 Fs 6.648 1,160) attack rate in sympatry than in allopatry; whereas in rainbow trout the opposite is true (P <0.001 Fs 20.975 1,155) (Table 6.15).

Fronto/lateral.

In the more ritualised and less aggressive fronto-lateral displays the same pattern exists as above, but only the comparison between the allopatric populations was significant (P <0.05 Fs = 4.029 1,221) (Table 6.15). It was surprising that brown trout were involved in more fronto-lateral displays in sympatry than they were in allopatry, one would have expected the more ritualised interactions to have been prevalent in the more stable allopatric brown trout population.

Therefore it is clear that in sympatry brown trout are involved in more aggressive interactions than rainbow trout, whereas in allopatry rainbow trout are involved in more aggressive interactions than brown trout.

Table 6.15 The mean number (log_{10} x+1 No./5mins) of behavioural interactions in which the allopatric and sympatric populations of brown trout and rainbow trout were involved in each viewing period.

		Total	Aggressive	Fronto/ Lateral	Defensive
T1	RT	0.471	0.288	0.119	0.204
T2	BT	0.280	0.155	0.072	0.095
T3	RT	0.365	0.056	0.063	0.309
	BT	0.339	0.264	0.124	0.042

Table 6.16 The mean number (log_{10} x+1 No./5mins) of behavioural interactions interactions in trough 3 compared on an interspecifc and intraspecific basis.

	Rainbow Trout	Brown Trout
Intraspecific		
Aggressive	0.050	0.052
Fronto/lateral	0.013	0.045
Defensive	0.054	0.042
Interspecific		
Aggressive	0.007	0.215
Fronto/lateral	0.050	0.086
Defensive	0.258	0.000

Defensive acts.

In interspecific comparisons rainbow trout were involved in significantly more defensive actions than brown trout in both allopatric and sympatric situations; (P<0.001 Fs 14.04 1,221) and (P<0.001 Fs 39.237 1,94) (Table 6.15). This is in agreement with the findings from the analysis of the aggressive interaction data because in both situations rainbow trout were subject to more attacks than brown trout. In intraspecific comparisons brown trout were involved in more defensive actions in allopatry than in sympatry, but the difference was not significant. By contrast rainbow trout were involved in more defensive actions in sympatry than in allopatry, and in this instance the difference was significant, (P<0.05 FS=5.26 1,155) (Table 6.15). The behavioural differences between the two species in sympatry are even more apparent when the interactions in T3 are examined on an interspecific and intraspecific basis.

Interspecific.

Brown trout initiated a significantly greater number of attacks on rainbow trout, than rainbow trout initiated with brown trout (P<0.001 FS 28.30 1,94) (Table 6.16). Rainbow trout fled more often from brown trout, than brown trout fled from rainbow trout in attacks initiated by the latter in each case, (P<0.001) Fs = 40.032 1,94) (Table 6.16). The less aggressive fronto-lateral displays followed the same pattern as the direct attacks, but the difference was not significant.

Intraspecific.

Brown trout were involved in more aggressive interactions (attacks and fronto-lateral encounters) with their conspecifics than rainbow trout (Table 6.16). Rainbow trout fled more often from their conspecifics than brown trout did (Table 6.16). None of the differences between intraspecific comparisons were significant. The number of intraspecific interactions was lower than those recorded between species.

Thus it is clear that when the progeny of spring-spawning rainbow trout share a habitat with the progeny of autumn-spawning brown trout the former are socially dominated by the latter. The most likely reason for this is the size advantage held by brown trout.

6.3.4.7 Distribution.

There was no significant variation in the distribution of either species in any of the populations in the 4 time periods in which observations were made, so the results were pooled. In interspecific comparisons both species in allopatry made use of the pool and riffle, however rainbow trout were observed more often in the pool than brown trout ($P<0.05$ $x^2 = 7.31$ df2). In sympatry the rainbow trout's preference for the pool habitat was even more apparent. On all but three occasions they were observed in the pool, and on each of them they held station at the pool/riffle interphase. Brown trout in sympatry made use of both pool and riffle, but used the latter to a lesser extent than they did in allopatry, and made greater use of pool/riffle interphase. The difference in the two species distributions in sympatry was highly significant ($P<0.001$ $x^2=24.66$ df2). In the intraspecific comparisons there was no significant variation in habitat use by brown trout in the allopatric and sympatric situations ($P>0.05$ $X^2=5.94$ df 2). By contrast rainbow trout in the two situations did show highly significant variation in their use of the two habitats ($P<0.001$, $x^2 = 19.61$ df=2). This implies that rainbow trout distribution was restricted by the presence of brown trout, and that the presence of rainbow trout had no significant effect on the distribution of brown trout.

6.3.4.8 Relation to stream substrate.

There was no significant variation in the position of the two species in the water column in each population in the four time periods, so the data was pooled. In interspecific comparisons rainbow trout showed a preference for holding their position in the water column, whereas brown trout showed a preference for the stream bottom. In both allopatry and sympatry the difference between the species was significant ($P<0.001$ X^2 69.19 df1) and ($P<0.01$ X^2 9.71; df1) respectively. In the intraspecific comparisons there was no significant difference in the number of rainbow trout that held station off the bottom in allopatry and sympatry ($P>0.05$ X^2=0.78; df1), whereas the brown trout in sympatry were recorded off the bottom more often than those in allopatry ($P<0.01$ X^2=7.33; df1).

6.4 Discussion.

6.4.1 Trapping experiment.

Although no information was gained from the trapping programme about the movement of rainbow trout into Loch Awe's spawning tributaries, small amounts were gained from other parts of the project.

On the 1.11.86 the partially eaten corpse of a heavily gravid female rainbow trout length 457mm was found on a riffle in the Allt nan Sobrachan, above the fish farm at Braevallich. The fresh state of the fish suggested that it had been intercepted and killed by a mink or otter whilst on its upstream migration. On the 23.11.86 a ripe male rainbow trout length 485mm, was netted from the mouth of the small burn that enters Loch Awe at the Braevallich fish farm.

During the electrofishing surveys, two adult rainbow trout were caught, one on the 24.4.87 in the Kames burn, and the other in the Clachan Dubh burn on the 27.9.87. The fish in the Clachan Dubh burn was sexually mature. Electrofishing the burns on three occasions in November 1988 for brown trout eggs, for the egg experiment failed to find any rainbow trout.

Therefore the lack of evidence of a large upstream migration of sexually mature rainbow trout, the low percentage of rainbow trout that became sexually mature, and the protracted period over which they can become mature will reduce the probability of ripe male and female rainbow trout making contact with one another in Loch Awe's large number of tributaries.

If spring-spawning rainbow trout were to enter these tributaries to spawn the high availability of spawning area in the catchment would minimise the potential of them over cutting the earlier-cut redds of brown trout and Atlantic salmon. Hayes (1984) demonstrated the damaging effect of this phenomenon on the brown trout population in a tributary of Lake Alexandrina, New Zealand. It would not be necessary for the rainbow trout's eggs or milt to be viable, simply the physical process of redd cutting would dislodge the young trout and salmon and lead to their death. However, the lack of evidence for rainbow trout spawning in the Loch Awe catchment, makes this scenario at present unrealistic.

It is the continued use of all female, and triploid rainbow trout stock on the fish farms that is the major reason for their lack of success in establishing a self-sustaining population in Loch Awe. These findings have been confirmed by field surveys performed by other investigators (Munro et al., 1976; A. Walker pers. com.).

6.4.2 Egg viability.

There has been a very low success rate in the establishment of self-sustaining rainbow trout populations in Europe (Vivier, 1955; Nilsson, 1967; Frost, 1974; and Phillips et al., 1985), with poor egg survival being implicated as the reason in a number of cases. MacCrimmon (1971) in his review of their world distribution examined some of the environmental factors that limit their success. The water temperatures, dissolved oxygen levels, and precipitation patterns found in Scottish streams are well within the critical limits described by him. The factor that has been isolated on a number of occasions (Seamans & McMartin, 1962; Frost, 1974; & Grande et al., 1978) as being responsible for the rainbow trout's lack of success in areas where they might have been expected to thrive is the low pH of the water. Seamans & McMartin (1962) demonstrated that the life span of rainbow trout sperm is reduced by up to 50% in acid waters, and Grande et al. (1978) reported that their lower pH tolerance was between 5.5 and 6.0. The water pH in a large number of Loch Awe's tributaries lies within this critical range, so this may be the reason for their lack of success in establishing a self-sustaining population in this situation. However some rainbow trout eggs did hatch, so there is theoretically the potential for rainbow trout to establish a self-sustaining population in Loch Awe. It is clear from the rudimentary approach in this experiment that further investigations that included analysis of all of the factors that affect salmonid egg survival would be necessary before any firm conclusions could be made.

6.4.3 Electrofishing.

In the 38 electrofishing surveys performed in 10 of Loch Awe's tributaries no juvenile rainbow trout were caught. On its own this does not prove that they are unable to spawn in catchment, but when it is considered with evidence from other parts of the project, it seems likely that this is the case.

By consulting Table 6.17 it is clear that the density of juvenile salmonids in some of the streams in the Loch Awe catchment is low, but not at critical levels. The high densities recorded by Egglishaw & Shackley (1977) are recognised as being exceptional in Scottish terms, and the high spring levels recorded in Glencorse (Duncan, 1984) and Gladhouse (Conner, 1981) are partly maintained by stocking. The autumn densities of juvenile Atlantic salmon recorded in this survey are similar to the results of an independent survey (A. Walker pers. com.) in a number of streams in the Awe's catchment in August 1984. They noted mean densities of $0.54m^{-2}$ 0+ Atlantic salmon, whereas means of $0.44\ m^{-2}$ and $0.70m^{-2}$ were recorded in the autumns of 1986 and 1987 respectively. They made no estimate of brown trout density.

The production of fish in a stream is determined by a number of biotic and abiotic variables. These determine a stream's carrying capacity by

Table 6.17 **The density (no/m²) of brown trout and Atlantic salmon in Loch Awe's catchment compared to other streams in Scotland and England.**

	Density (No./m^2)	
Loch Awe (combined salmonid)		
Autumn 1986	0.82	
Spring 1987	0.46	
Autumn 1987	1.11	
Spring 1988	0.45	
Loch Awe (Atlantic salmon)		
Autumn 1986	0.44	
Spring 1987	0.19	
Autumn 1987	0.70	
Spring 1988	0.24	
Streams In Loch Awe Area (Atlantic salmon)		
Linne nan Beathach	0.16	(Servant pers comm.)
Orchy	1.92	
Etive	0.05	
Kinglass	0.47	
Noe	0.01	
Nant	0.63	
Shelligan Burn (combined salmonid) Autumn mean 1966-75	3.65	(Egglishaw &Shackley 1977)
Black Brows Beck-Brown Trout Autumn mean 1966-77	2.10	(Le Cren, 1972)
English Stream-Brown Trout Mid Summer	0.1-2.7	(Le Cren, 1972)
Cornish & Devon Streams Mid summer mean from 12 streams Brown Trout	0.31	(Huish pers comm.)
Lothian Reservoir Tributaries Brown Trout		
Glencorse Spring 1984	0.72	(Duncan, 1984)
Gladhouse Spring 198	0.74	
Harperrig Spring 198	0.32	
Galloway Streams-Brown trout		(Harriman, 1984)
Not Acidified		
Castramount Autumn 1984	0.73	
Barlay Autumn 1984	0.40	
Drumcleugh 1984	0.27	
Black Laggan 1984	0.88	
Acidified		
Mid Autumn 1984	0.08	
Carrouch 1984	0.13	
Craiglowrie, 1984	<0.05	

acting on recruitment, mortality and migration. From the results of other investigations it is clear that juvenile salmonids can tolerate higher densities than are found in Loch Awe's tributaries. The lower level in Loch Awe could be due to a number of factors that affect salmonid production e.g. a low number of spawning adults, poor water quality, low food availability, the presence of disease, predation, or lack of access to cover.

It is highly unlikely that the juvenile population short-fall is caused by a lack of adults entering the spawning burns. It has been demonstrated in both brown trout and Atlantic salmon that recruitment is only adversely affected by this when the number of spawning adults falls below a very low critical level, above this level low spawning is compensated for by high survival in the resulting progeny (Elliott, 1989; Buck & Hay, 1984). A simple experiment that would involve stocking the areas surveyed in the present project with unfed brown trout fry in the spring, and measuring their density in the autumn, would allow us to determine if the shortfall was due to a shortage of spawning adults. If this was the case, one would expect the stocked fish to secure territories and for the density of fish in the autumn to be higher than had been recorded previously. If there was no increase in the density after stocking one would have to conclude that the streams were at their carrying capacities and were being limited by some other factor. It would then be necessary to investigate water quality and food availability in the streams to examine this further.

Forestry is often criticised for its adverse impact on juvenile salmonid populations, although in this instance there was no difference in the density of fish in forested and non-afforested catchments. By its very nature it is likely that forestry activities would have had some negative effect on the juvenile salmonid stocks in Loch Awe. Over the next twenty years a large amount of felling is planned in the loch's catchment, and there is already a small amount of evidence that suspended solid loads have increased on a number of occasions due to extraction activities.

The spawning area for salmonids in a large number of Loch Awe's tributaries is restricted by impassable falls which are situated only a short distance from the loch. Although spawning populations do exist above them, it is highly likely that recruitment to the loch would be improved if the falls were breached. However before such a scheme was started it would first be necessary to identify the streams that would benefit from such action. Streams considered would have to have a large spawning area above the falls, and have a lower stock above than below them, with the reason for this being the physical obstruction to spawning that the falls caused. Although the current spawning area was not assessed, the breaching of such impassable falls would increase the area and subsequently increase the recruitment of Atlantic salmon and brown trout.

Unfortunately it was not possible to assess the level of recruitment of brown trout from the River Orchy. The site at Duilletter shows that trout do spawn in its tributaries, but it is not known if the juveniles caught were the progeny of brown trout or sea trout. It is also unclear whether they would be recruited to a resident population of brown trout in River Orchy, to the population in Loch Awe, or if they would become sea trout.

It could be argued that the small number and size of the stream sections sampled, were not truly representative of the Loch Awe catchment. Newman & Waters (1989) demonstrated that the variation in fish density within individual streams can be highly significant

(P<0.001). It is likely that similar variation exists within Loch Awe's streams but by comparing other systems with the mean density of the streams examined, and by selecting representative sections within the streams it is hoped that any bias within the data set would have been removed. There is concern that repeated electrofishing adversely affects the growth of the fish. However, Shackley & Egglishaw (1977) and Gatz et al. (1986) demonstrated no adverse effect on the resident salmonid communities with a greater frequency of electrofishing.

6.4.4 Juvenile behavioural interactions.

Despite the large amount that has been written about biological competition, its role in determining species composition is still poorly understood. This is particularly true in the relationship between brown trout and rainbow trout. In this experiment the role of feeding, agonistic interactions and habitat use in social organisation at an early stage in the life history of the two species in sympatry was examined. Gatz et al. (1987) gave three conditions that would have to be met before interspecific competition could be implicated in a relationship: 1) a reduction in population; 2) a reduction in growth/production; and 3) a reduction in a species realised niche when in sympatry. Their fulfilment in the present experiment will now be considered.

In both allopatry and sympatry rainbow trout had a lower survival rate than brown trout, with the lowest rate being recorded in the latter. This meets condition one. There are two possible reasons for the lower survival rate in the two rainbow trout populations. The first applies to both populations and is due to differences in the developmental stages of the two species. In the first month after they emerge from the gravel salmonids suffer heavy mortalities (Buck & Hay, 1984; Elliott, 1989). As rainbow trout hatched two months after brown trout, it is clear that they would be more vulnerable to this mortality, brown trout had passed this critical phase in early May and would not have been affected by it. The second only applies to the sympatric population and is due to the size advantage held by brown trout over rainbow trout. As the survival rate in the sympatric population was lower, it is clear that condition 1 has been met.

The growth rate of rainbow trout was higher than brown trout in both allopatry and sympatry, and again it is likely that the difference is due to the variation in the two specie's developmental stage. Hayes (1988) demonstrated a marked decline in the two species growth rates in the first few months after emergence. As brown trout emerged before rainbow trout it is not surprising that their growth and feeding rates are now lower. Another possible explanation for the rainbow trout's superior growth rate is that their innate rate is higher than brown trout, this being one of the reasons that they are preferred to our native trout by the aquaculture industry. Unfortunately the experimental design did not allow the relative importance of these two effects to be determined. It was surprising that the two species growth rates were higher in sympatry. This may have been caused by the lower density in T3 resulting in a greater availability of food, but the lower feeding rate by both species dismisses this option. A more plausible explanation for the higher growth rate in the rainbow trout is that their growth rate was calculated on those that survived to the end of the experiment, which would have been calculated from the ones with the best growth rate. It is likely that the earlier developmental stage, and the growth rate being based on the fittest survivors also explains the greater production recorded by rainbow trout in both allopatry and sympatry. Therefore the fulfilment of condition 2 is inconclusive.

The lower feeding rate by the two species in sympatry in T3 may be due to the greater number of aggressive and defensive interactions that brown trout and rainbow trout were respectively involved in compared to their allopatric populations. This would result in brown trout having less time to feed, and in rainbow trout being less likely to move to intercept passing food as it would bring them to the attention of the dominant brown trout.

In sympatry the distribution of rainbow trout was restricted to the pool habitat whereas in allopatry they used the pool and riffle. There was no significant variation in the distribution of brown trout in allopatry and sympatry. Therefore condition 3 has been met.

Following the above criteria in this experiment there is very strong evidence that rainbow trout suffer interspecific competition from the dominant brown trout.

The mechanisms by which this was achieved will now be investigated. The results from the two species in allopatry suggest that rainbow trout are more aggressive than brown trout, although this can again be explained by the different developmental stages of the two species. When juvenile stream-dwelling salmonids start to feed after they emerge from the gravel their behaviour is characterised by a high level of unsophisticated aggressive interactions. The aggressive behaviour acts to disperse the newly-emerged individuals as they establish their territories. The competition for space acts as a substitute for competition for food acquiring sites (Chapman, 1966). As fish get older the number of agonistic interactions that they become involved in declines and their nature becomes more ritualised (Chapman, 1962; Mason & Chapman, 1965; Ellis, 1977; Chizar et al., 1975; Cole & Noakes, 1980; Noakes, 1980; Gibson, 1981). This explains the lower number of interactions in the allopatric brown trout population.

Also the brown trout's lower position in the water column will provide them with a greater amount of visual isolation from one another which will further reduce the potential for conflict. Dill (1977) reported that rainbow trout adopt a mid-water position after they emergence, with the same conclusion being reached by Hearn & Kynard (1986) when examining the behavioural relationship between rainbow trout and Atlantic salmon. However it is unclear if their mid-water habit in this experiment was due to the short period that they were reared in a hatchery, or whether it was due to an innate difference between the two species. Hatchery-reared Atlantic salmon have been shown to assume a mid-water position once released into streams (Dickson & MacCrimmon, 1982). This strategy is wasteful of energy and results in a greater mortality rate. The greater number of occasions on which brown trout were observed off the bottom in the sympatric population is in agreement with the greater number of agonistic interactions that they were involved in that situation.

When the two species were brought into sympatry there was an increase and decrease in the number of interactions in which brown trout and rainbow trout were respectively involved. Although rainbow trout were still involved in slightly more interactions than brown trout, the majority of them were defensive, whereas brown trout increased their attack level. It is likely that the change in brown trout behaviour was due to the instability introduced to the population when they shared the trough with smaller rainbow trout. As stream-dwelling salmonids get older they try to increase the size of their territories by engaging their neighbours in aggressive interactions, when a large difference exists between the size of competitors the likelihood of success for the larger species is increased. It is this incentive that causes the brown trout to attack the smaller rainbow trout more often than they do their own species which are of a similar size to themselves.

The advantage of size is a well recognised phenomenon in salmonid behaviour. In particular the behavioural advantage based on size between brown trout and other salmonids has been well documented (Kalleberg, 1958; Nilsson, 1963; Vincent & Miller, 1969; Nyman, 1970; Gard & Seegrist, 1972; Fausch & White, 1981; Waters, 1983; and Gatz et al., 1987). Hence brown trout should dominate any potentially competitive situation with species in their own family (Newman, 1956). Findings by Fausch & White (1981), who reported that brown trout excluded brook trout from their preferred resting areas, and by Shirvell & Dungey (1983) who found that brown trout occupied the same microhabitats whether or not rainbow trout were present, support this.

However in a similar experiment Hayes (1989) demonstrated that the size difference between brown trout and rainbow trout was sufficient to reduce the social conflict between them. This existed until the fingerling stage, by which time brown trout socially dominated rainbow trout.

In the relationship between the progeny of autumn-spawned brook trout and spring-spawned rainbow trout Rose (1986) demonstrated that size was unimportant in determining the outcome of competition between the two species. Rainbow trout were able to reduce the growth rate of larger brook trout when rainbow trout emerged from the gravel. This resulted in brook trout having a greater winter mortality rate than rainbow trout. This was achieved by the brook trout diet being restricted to the upper end of the range that is available to them and this is responsible for the change in dominance changing brook trout to rainbow trout in a number of east coast American rivers.

The dominance demonstrated in brown trout over rainbow trout would result in the latter changing their distribution when they are in sympatry with brown trout. In allopatry both species have been shown to use pool and riffle habitats. However in sympatry their habitat preference is less clear and depends upon the species with which they co-habit. Gatz et al. (1987) and Hayes (1984) demonstrated that when the two species were in sympatry, brown trout preferred the pools, and rainbow trout preferred the riffle. The same habitat preference was shown by rainbow trout when they were in sympatry with coho salmon and brook trout (Hartman, 1965; Fausch, 1988). However when they co-habit with Atlantic salmon, rainbow trout are found in deeper water and salmon utilise the shallower and faster flowing riffles and runs (Hearn & Kynard, 1986). They concluded that the rainbow trout's high position in the water column was better suited to pools and other habitats with low current velocity, they also demonstrated that their higher level of aggression gave them a competition advantage over Atlantic salmon.

When brown trout are found in the same streams as Atlantic salmon, the trout inhabit pools and the salmon riffles (Egglishaw & Shackley, 1982). Fausch & White (1981) demonstrated that when brown trout are found in a stream with brook trout the niche width of the latter is restricted.

Therefore, it is clear that the findings of the present study contradict those of Hayes (1984) and Gatz et al. (1987) who showed that in sympatry brown trout used the pools and rainbow trout used the riffles. In this study the greater pool use by rainbow trout in sympatry is probably related to the higher position that they hold in the water column. In this habitat they will require less energy to maintain their position. This energy conserving mode is all the more important in sympatry owing to the greater number of defensive actions that they are involved in, as such actions have a high energy requirement. By holding station in the pool habitat rainbow trout will maximise their net energy gain. This is the criterion by which salmonids select their territories (Fausch, 1984). The same conclusion was reached by (Hearn & Kynard, 1986) in their study of the inter-relationships between rainbow trout and Atlantic salmon.

In the present study the slightly greater use of the pool by brown trout when they are in sympatry could be related to their higher level of agonistic activity, which requires that energy savings have to be made in other activities, or it could be due to them chasing rainbow trout back to the pool.

Unfortunately a lack of time precluded the investigation of interactions between the progeny of autumn-spawned brown trout and rainbow trout. In such a situation brown trout would not hold the size advantage that they hold by virtue of their earlier emergence, this would clearly increase the scope for competition between the two species. Co-existence, but with each species having lower biomass than had they in allopatry would be the likely outcome of such a scenario. Dodge (1983) has already observed this outcome in spawning tributaries in Ontario.

Although Gatz et al. (1987) provided an uncomplicated group of factors that must be met before interspecific competition can be implicated between fish species, in reality it can be very difficult to provide evidence to satisfy the requirements. This is due to difficulties in the standardisation of field and laboratory experiments caused by variation in resource availability between replicates and in the methods used to quantify them. In essence the problem lies in scientists trying to perceive the resource requirements of animals.

What we regard as being crucial for the survival of a species, may in fact be less important.

6.4.5 Implications for Loch Awe.

The work described here has demonstrated that sexually mature rainbow trout do move into Loch Awe's tributaries. However, no evidence was found to show that they were able to find a mate in a similar condition and spawn. That accepted, it was shown that if such an event was to occur the eggs could survive at least to the alevin stage. The trough experiment provided evidence that if the rainbow trout were the progeny of spring spawners they would find it difficult to compete against the larger brown trout which would by that time have secured their territories. What the experiment did not show was how rainbow trout would interact with Atlantic salmon, and what the response of brown trout would be to the progeny of autumn-spawning rainbow trout.

Perhaps the most important factor that would help the progeny of rainbow trout establish themselves in the loch is that they were shown to feed and grow successfully in a stream environment if they are introduced to wild food at a young enough age. It is this lack of experience which limits the success of rainbow trout that escape from the cages into the loch when they are older.

Under the current circumstances it is unlikely that the rainbow trout would be able to form a self-sustaining population in Loch Awe.

CHAPTER 7

ANGLER CENSUS

7.1 Introduction.

In recent years anglers on Loch Awe have complained about the dwindling catches of brown trout. The aim of this chapter is to investigate the validity of these claims by comparing the present day catches with those from historic data sets. The complaint is not one that is unique to Loch Awe as similar sentiments have been voiced about other brown trout fisheries by anglers and fishery managers throughout the country. A nationwide survey by the Game Conservancy Council has revealed widespread concern about the declining stocks of wild brown trout in Britain (Giles, 1989), and a conference was held by the Freshwater Biological Association in 1988 to address this specific issue. Investigations on individual fisheries by Burns et al. (1984), Swales & Fish (1986) and Turnpenny et al. (1987, 1988) have implicated acidification and the combination of acidification and forestry as reasons for the decline of brown trout fisheries.

On Loch Awe the popular belief is that the introduction of rainbow trout has been responsible for the decline in brown trout catches. In other waters where the two species co-exist a variety of responses from brown trout populations to the introduction of rainbow trout have been recorded.

Frost (1974) reported that the introduction of rainbow trout to waters which previously held only brown trout, had no adverse impact on brown trout catches by anglers. However, in the same report she also cited evidence from a fishery where the catch of brown trout declined when rainbow trout stocking started and increased once it had ended. Brown et al. (1979) reported that anglers had to fish deeper for brown trout when they were in sympatry with rainbow trout. As trout anglers generally fish the surface waters, they are more likely to encounter rainbow trout and this segregation gives the impression that rainbow trout are more abundant than brown trout although this may not be the case. This niche segregation was also alluded to by Coles (1981). The rainbow trout's greater susceptibility to bird predation further supports this hypothesis of niche segregation (Matkowski, 1989).

Giles (1989) found in the Game Conservancy Council survey that where brown trout occurred alone, a significantly higher number of returns recorded a perceived decline in stocks compared with those fisheries in which brown trout and rainbow trout co-existed.

In fisheries sustained by stocking it is a broadly held belief that rainbow trout have a greater catchability than brown trout (Jacques, 1974; Fleming-Jones & Stent, 1975; Crisp & Mann, 1977; Taylor, 1978; Coles, 1981; Bryan, 1982; Pawson, 1986; Pawson & Purdom, 1987). This can give anglers the false impression that brown trout are less abundant than they are reality.

The aim of this chapter is to put the current angler catch of brown trout from Loch Awe into a historical perspective and to examine the performance of the fishery in relation to changes in land use, angler pressure and the introduction of rainbow trout.

7.2 Methods

7.2.1 Historical

Fishing registers were available from three hotels, the Loch Awe Hotel 1887-1929, the Ford Hotel 1926-1965 and the Port Sonachan Hotel 1931-1978. From the registers, the annual catch, the annual number of successful rod days (this had to be calculated as there was no record of the unsuccessful days in the fishing registers), the catch per successful rod day (C.P.S.R), and the average weight of fish were calculated. In order to perform the analysis it was assumed that a person had been fishing for the entire day when an entry was made in the register. No regression analysis was performed on the historic data set as the variables were not sufficiently robust.

7.2.2 Angler census.

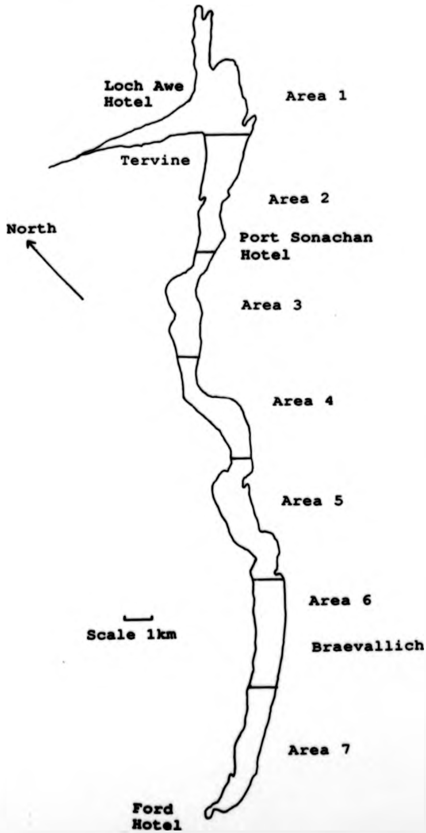
During 1987 and 1988 anglers fishing on the loch were issued with return cards and asked to record the following details:
Name, Date, Hours Fished, Number of Rods, the Species and Weight of each Fish Caught, and to mark on a map the area of the loch which had been fished. See Appendix 5. The need to return cards even when no fish were caught was strongly emphasised.

Publicity for the census was gained through the national, local and angling press, by contacting angling clubs, and by mounting a poster campaign around the loch. Cards were available from and could be returned to, local shops, hotels and holiday cottages. They were also sent to angling clubs who were holding competitions on the loch, and distributed personally to anglers fishing the shores.

From the returns, the annual catch, average weight, annual catch per unit of effort (CPUE) in rod hours and rod days were calculated for brown trout and rainbow trout in the two years. The catch per successful rod day was also calculated so that limited comparisons could be made with the historic data sets (see discussion).

The data were then sub-divided on a monthly and loch section basis to compare temporal and spatial variation in the catch of brown trout and rainbow trout. To achieve the latter the loch was divided into seven sections of approximately equal size (Figure 7.1). Variation in the catch of brown trout and rainbow trout between each month and site was tested by X^2.

Figure 7.1 **The loch areas used in the 1987 and 1988 angler census.**



7.2.3 Estimation of total catch in 1987 and 1988.

To estimate the total number of fish caught and thereby the catch and yield per area it was necessary to obtain an estimate of the total annual effort on the fishery. This was achieved by driving around the loch and counting anglers on randomly selected days throughout the season. As there is considerably greater angler pressure on the loch at weekends compared to weekdays, the sampling was stratified in order to compensate this potential bias.

In each month of the angling season one weekday and one weekend day were randomly selected for the angler count to be made. From this the average number of anglers fishing Loch Awe on each weekday and weekend day of the angling season was calculated. The estimates should be regarded as minima as it is likely that some anglers were not counted. In addition no allowance was made for night and winter angling, a practice which has started since rainbow trout (a species for which there is no closed season) appeared in the loch.

7.3 Results.

7.3.1 Historic data analysis.

7.3.1.1 Loch Awe Hotel-total catch.

There was considerable variation around the mean of 826 in the annual catch of brown trout at the Loch Awe Hotel which is situated in the northern part of the loch (Figures 7.1 and 7.2). The data set was dominated by three peaks from 1888-1896, 1902-1912 and 1920 -1927. The highest annual catch, 2016, was recorded in 1922, and the lowest catch, 0, was recorded in 1917. It is highly likely that the absence of data in 1917 was due to the population's involvement in the First World War

Figure 7.2 The annual catch of brown trout at the Loch Awe Hotel, 1887-1927.

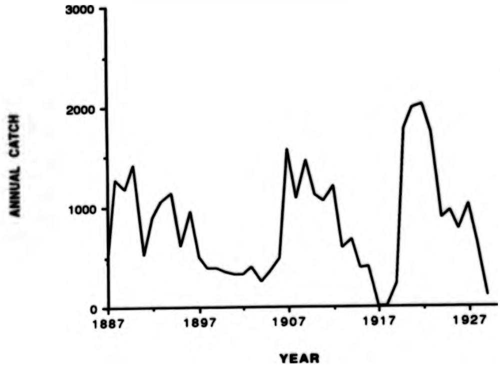
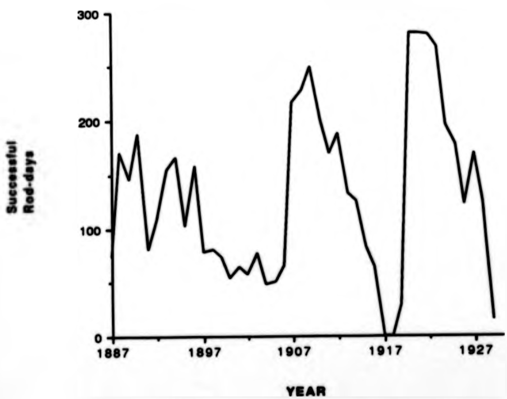


Figure 7.3 The annual number of successful rod-days at the Loch Awe Hotel, 1887-1927.



and the high catch in 1922 to the resumption of leisure pursuits when it ended. The low level of angling effort during the war would also have allowed stocks to build up in the loch, ensuring good catches when angling resumed. The lowest catch in years when landings were recorded was 96 and occurred in 1929. It is unclear how representative this was of the catch that year, as declining catches were a feature of the end of each period in which records were available from each of the hotels. It is strongly suspected that it is a measure of apathy on the part of the hoteliers, rather than a true reflection of the fishery's performance.

Successful rod days.

There was a large variation in the number of days that anglers caught fish (Coefficient of variation (C.V) 54.7%) (Figure 7.3), and the data closely mirrored the trends seen in total catch (Figure 7.2). The mean was 136 successful rod days/year, the highest, 281, was recorded in 1920, with the lowest, 0, being recorded in 1917 and 1918, again due to the First World War. The lowest number of successful rod days in a year when anglers visited the loch was recorded in 1929 at the end of the data set. The possible reasons for this were discussed above.

Catch per successful rod-day (C.P.S.R).

There was less variation (C.V. 16.6%) in the CPSR data than in the two variables from which it was calculated. In the lead up to the war when the catch and effort data declined, the CPSR remained comparatively flat suggesting that catchability, angler skill and techniques did not change throughout the period (Figure 7.4).

The highest CPSR, 8.26, was recorded in 1892, with the lowest, 0, being recorded in 1917 and 1918 when no records were kept. Contrary to the catch and effort findings the lowest CPSR, 4.39, was recorded in 1913

Figure 7.4 The annual catch per successful rod-day (CPSR) at the Loch Awe Hotel, 1887-1927.

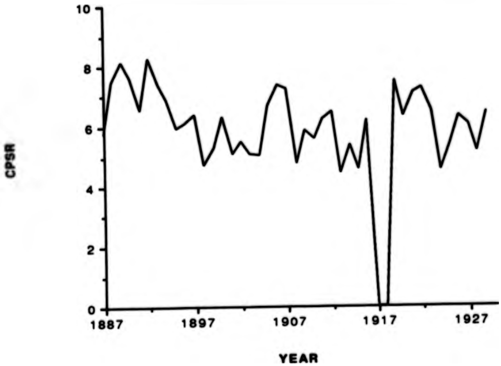
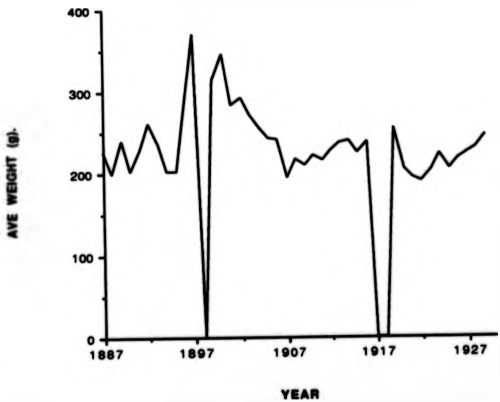


Figure 7.5 The annual average weight (g) of brown trout caught at the Loch Awe Hotel, 1887-1927.



and not 1929, again it is unlikely that the data in the last few years were truly representative of the fisheries performance (Figure 7.4). The mean CPSR was 6.15, as expected a high level was recorded in the immediate post war period after the trout population had been allowed to increase.

Weight.

The highest annual mean weights were recorded between 1896-1903 (Figure 7.5). Throughout the rest of the data set the mean annual weight was lower and was characterised by less variation, the mean and C.V. were 238 g and 18.67% respectively. The highest annual average was recorded in 1897 and the lowest, 189g, recorded in 1922. It is interesting to note that the year in which the highest mean weight was recorded corresponds with a period of low catch, effort and CPSR, and that the lowest mean weight corresponds with a period of high catches, effort and CPSR.

7.3.1.2 Ford Hotel-annual catch.

There was a large amount of variation in the number of brown trout caught at the Ford Hotel at the loch's southern end (Figure 7.1) between 1926-65 (C.V. 60.39%) (Figure 7.6). The greatest number of fish, 1674, were caught in 1939, and the lowest number, 15, in 1964. The average annual catch was 783 fish. The catch figures were dominated by two peaks, one before and one after the Second World War. The decline during the war was due to the lower level of effort on the fishery. After the second peak the annual catch fell steadily until records ended in 1964. It is probable that the decline in this instance was due not only to poor record keeping by the hotel, but also by changes in angler behaviour. As the road system improved and car ownership increased, anglers tended to visit Loch Awe as day visitors rather than staying in hotels. Therefore fewer of the fish caught on

Figure 7.6 The annual catch of brown trout at the Ford Hotel, 1926-64.

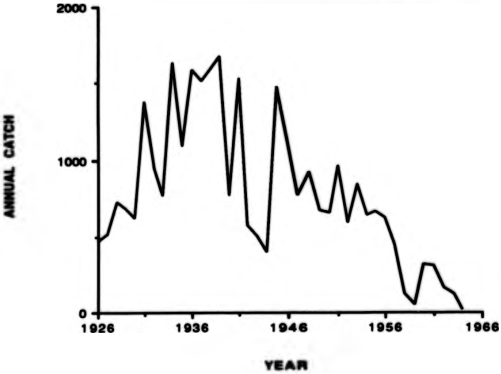


Figure 7.7 The annual number of successful rod-days at the Ford Hotel, 1926-64.

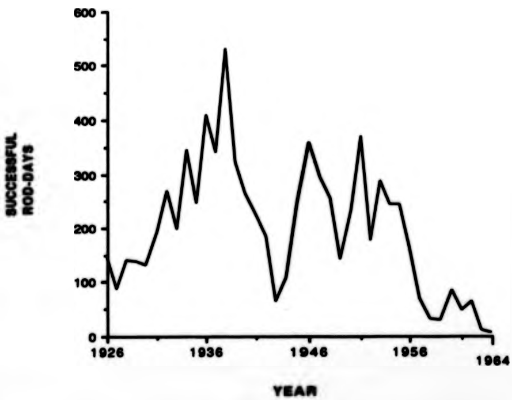


Figure 7.8 The annual catch per successful rod-day (CPSR) at the Ford Hotel, 1926-64.

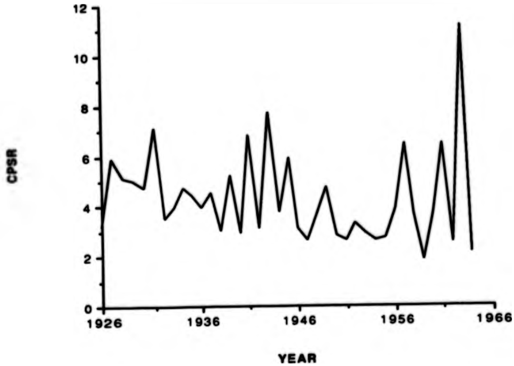
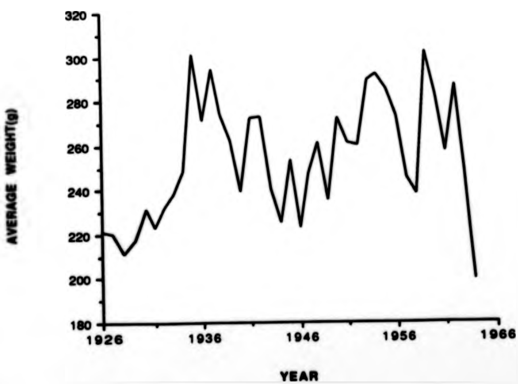


Figure 7.9 The annual average weight (g) of brown trout caught at the Ford Hotel, 1926-64.



the loch were recorded by the hotels.

Successful rod days.

Again there was a large amount of annual variation in the number of successful rod days on the fishery. The C.V. was 61.35%, with a mean being 198 successful rod days/year (Figure 7.7). The distribution of effort followed a similar pattern to that observed in the annual catch, with the pre and post war peaks, and the decline towards the end of the data set all being apparent. The highest number of successful rod days, 531, was recorded in 1937, and the lowest, 7, in 1964, but as stated previously this was probably not representative of angling behaviour on Loch Awe at that time (Figure 7.7).

Catch per successful rod-day (C.P.S.R)

There was a large amount of variation in the annual CPSR (C.V. 43.33%), the highest, 11.1, and lowest, 1.8, were recorded in 1963 and 1959 respectively. There was a small but discernable decline in the CPSR from 1926-55. It is likely that the figures after 1955 are not representative of the fishery as they were only based on a small number of observations. When the level of effort declined during the war the CPSR increased.

Mean weight.

The mean weight of fish caught was dominated by two peaks, one before and one after the Second World War. The C.V. was 10.32%, with the highest mean weight, 302g, being recorded in 1959 and the lowest, 199g, being recorded in 1964, but as discussed previously the quality of the data at the end of the record was questionable (Figure 7.9). The annual mean weight for the complete data set was 255 g, which is higher than that recorded at the Loch Awe Hotel. The decline in the mean weight in the mid 1940's corresponds with the period of low effort and high CPSR's. It is possible that the low cropping level allowed the numbers of brown trout in the loch to increase, which caused the CPSR to rise, and the mean weight of each fish to decline. However as stated previously, without access to data on other variables which also affect growth it is not possible to comment further.

7.3.1.3 Port Sonachan Hotel-total annual catch.

The total annual catch at the Port Sonachan Hotel followed a similar pattern to that observed at the Ford Hotel. It was dominated by two peaks, one before and one after the Second World War, however they differ with respect to their timing (Figure 7.10). At the Port Sonachan hotel the pre-war peak was recorded earlier than at Ford (1935 as opposed to 1939) and the post war peak occurred later (1957 as opposed to 1947). The reason for the sharp decline in the immediate post war period is unclear, as no similar trend was recorded at the Ford Hotel. In common with the two previous data sets the catch fell towards the end of the period for which records are available. The average annual catch of 1562, was almost double that recorded at the other two hotels, but the variation in the data set was only slightly lower (C.V. 48.45%). The highest annual catch of 3856 was recorded in 1957, and the lowest, 256, in 1947 (Figure 7.10).

Successful rod days.

The distribution of successful rod days followed a similar pattern to that described for the annual catch, with a peak occurring either side of the Second World War and a decline occurring after it (Figure 7.11). The mean annual number of successful rod days was 396, which in common with the average annual catch from the hotel was slightly more than twice that recorded from the other hotels. There was less variation in the number of rod days at the Port Sonachan than there had been in the two previous data sets (C.V. 40.2% as opposed to 54.7% and 61.7%).

Figure 7.10 The annual catch of brown trout caught at the Port Sonachan Hotel, 1931-78.

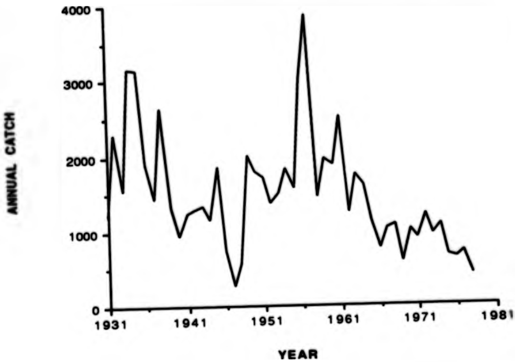
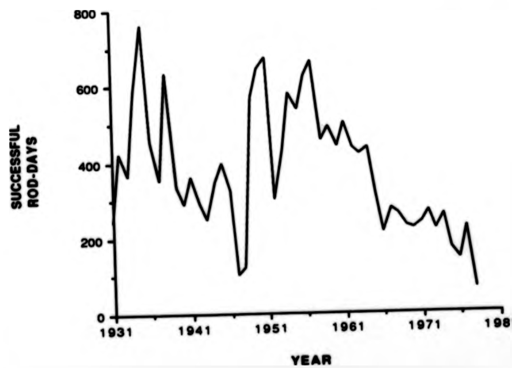


Figure 7.11 The annual number of successful rod-days at the Port Sonachan Hotel, 1931-78.



The highest level of effort, 761 successful rod days, was recorded in 1935, and the lowest, 62, in 1978.

Catch per successful rod-day (C.P.S.R)

The variation in the data set (C.V. 21.9%) was lower than that from the Ford Hotel but higher than that from the Loch Awe Hotel. The highest CPSR, 6.4, was recorded in 1978 and the lowest, 2.3, in 1946 (Figure 7.12). Although the total annual catch of fish at the Port Sonachan Hotel was almost twice that of the other hotels, it was caught by slightly more than twice the amount of effort, resulting in the mean CPSR of 3.93 being lower than at the two previous hotels.

Mean weight.

Although there was only a small amount of variation in the annual mean weight (C.V. 9.4%), two trends were apparent. From 1931-69, there was a steady decline, and from 1969-78, it increased from its lowest level, 194 g, to its highest, 276g, in 1976 (Figure 7.13). Following the argument outlined previously, the trends in mean weight imply that until 1969 the population had been increasing, causing the growth of individual fish to decline, and in the second period the population declined, resulting in an increase in average weight. However as stated previously it is difficult be confident about such inferences.

The annual mean weight of fish, 234 g, was lower than that from the two previous hotels. As the data from the Ford and Port Sonachan Hotels were collected over approximately the same time period, it suggests that the higher nutrient status at the southern end of the loch in this instance may be expressed in improved fish growth. This is contrary to the findings of the gill netting survey. However, as above, more information would be required before cause and effect could be concluded.

Figure 7.12 The annual catch per successful rod-day (CPSR) at the Port Sonachan Hotel 1931-78.

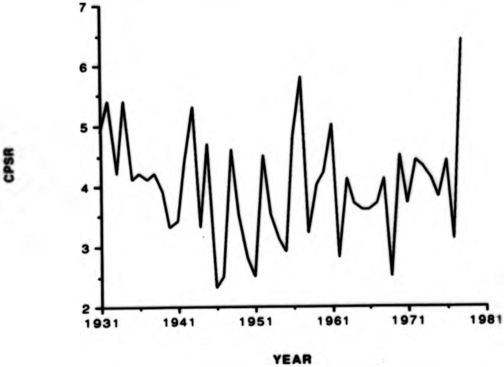
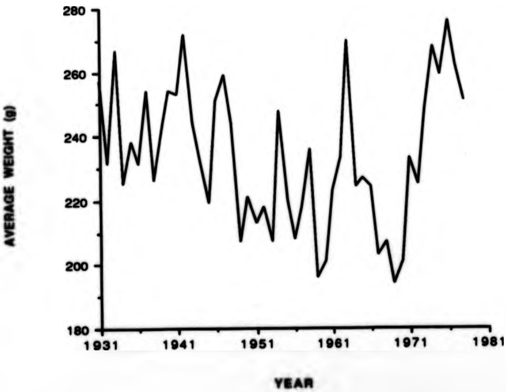


Figure 7.13. The average annual weight (g) of brown trout caught at the Port Sonachan Hotel 1931-78.



The catch of rainbow trout in the historic records.

Rainbow trout were recorded in small numbers in the Port Sonachan data set from 1973-78, but were considerably less abundant than at present (see next section). The most likely reason for this is that the first farms operating in the catchment were land based, and were less prone to the losses of fish that cage systems suffer. It is likely that the numbers of rainbow trout in the loch only started to increase as the form of production changed from ponds and tanks on the land to cages in the loch and as the size of the farms increased towards the end of the 1970's.

7.3.2 Angler census.

7.3.2.1 1987.

In 1987, the estimated catches (estimated angler visits X CPUE) of brown trout and rainbow trout on Loch Awe were 7,060 and 13,211 respectively, this gave catch rates of 1.84 and 3.43 fish/ha/year (Table 7.1). The average weights of brown trout and rainbow trout were 268 g and 526 g respectively, which gave annual yields of 0.49 kg/ha and 1.81 kg/ha (Table 7.1). In the case of rainbow trout it is not strictly accurate to describe their catch in terms of yield as it implies that their growth has been derived from the loch's productivity, whereas it is more closely related to their growth in the farms and the number that escape. A more accurate measure of their catch would have been to express it in terms of the number of fish that had been lost from the farms, but this information was not available.

Analysis of catch by month-monthly catch.

In 1987 there were significantly more ($P < 0.001$) rainbow trout than brown trout caught each month (Figure 7.14). The catch of rainbow trout had two clearly defined peaks in May and September. The monthly catch of brown trout had a similar bimodal distribution but the autumn

Table 7.1 Angler catch details for brown trout and rainbow trout in 1987 and 1988.

	1987			1988		
	BT	RT	Total	BT	RT	Total
Angling Days	6972	6972	6972	6105	6105	6105
CPUE/Day	0.70	1.31	2.01	1.39	0.35	1.74
Catch	4880	9133	14013	8486	2137	10623
Area(ha)	3846	3846	3846	3846	3846	3846
Catch/Area	1.27	2.37	3.64	2.21	0.56	2.77
Ave Wt(kg)	0.27	0.53		0.31	0.40	
Total Wt(kg)	1308	4804		2614	853	
kg/ha	0.34	1.25		0.68	0.22	

BT=Brown trout, RT=Rainbow trout.

peak was less distinct and occurred a month before that of the rainbow trout. Monthly variation in the catch of the two species was also highly significant ($P<0.001$).

Mean weight.

The mean weight of brown trout fell from March to July, with a small increase occurring in June. After July it rose to a level similar to that recorded at the start of the season (Figure 7.15). The mid-summer decline is probably due to the larger fish having moved offshore and the catch including a greater proportion of younger fish that remain in the littoral zone at that time. The mean weight of rainbow trout showed a more pronounced seasonal pattern, however it is unlikely that this is due to natural growth or migration patterns. Most rainbow trout were caught around the fish farms so it is probable that their mean weight was determined by the size of the fish that escaped from the cages in different months, and therefore would have had growth rates typical of cultured fish.

Catch per unit of effort (C.P.U.E).

The combined CPUE for brown trout and rainbow trout had a midsummer plateau, although this may not be a true reflection of the stock abundance (Figure 7.16). In May the value was derived from a large sample and is therefore reliable, whereas the small samples in June and July do not allow meaningful conclusions to be made.

The monthly rainbow trout CPUE followed a similar pattern to the combined data set, whereas the brown trout's CPUE peaked in May and fell gradually to the end of the season (Figure 7.16). Angling activity peaked in May and September (Figure 7.17).

Figure 7.14. The monthly catch of brown trout and rainbow trout by anglers in 1987.

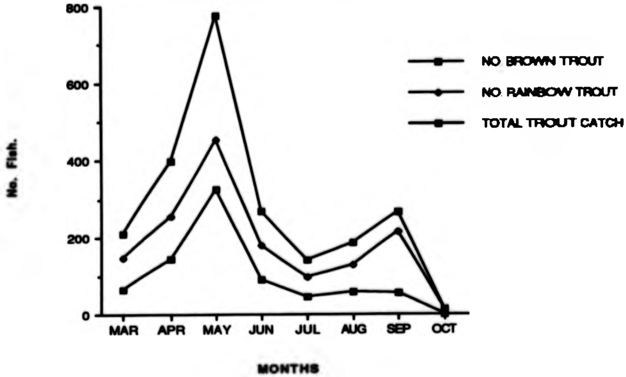


Figure 7.15 The monthly mean weight (g) of brown trout and rainbow trout caught by anglers in 1987.

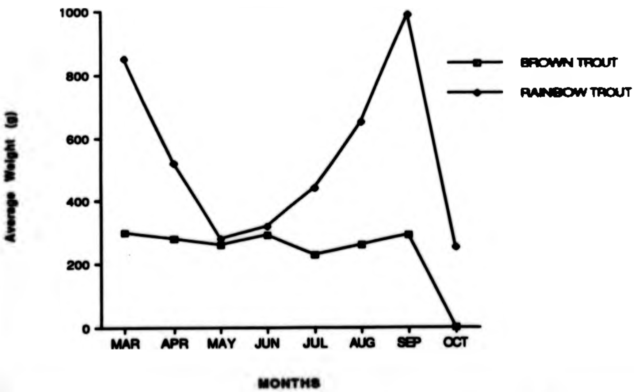


Figure 7.16. The monthly CPUE (catch per rod hour) for brown trout and rainbow trout in 1987.

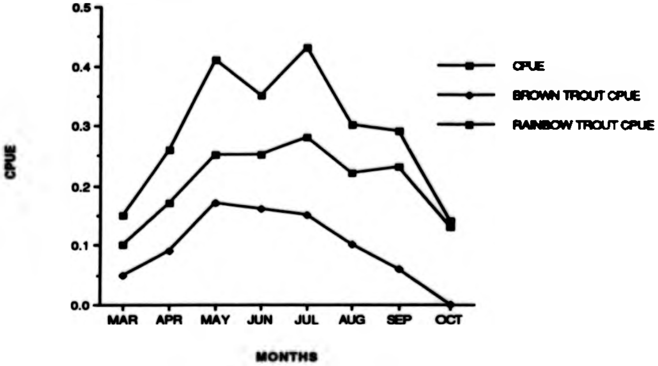
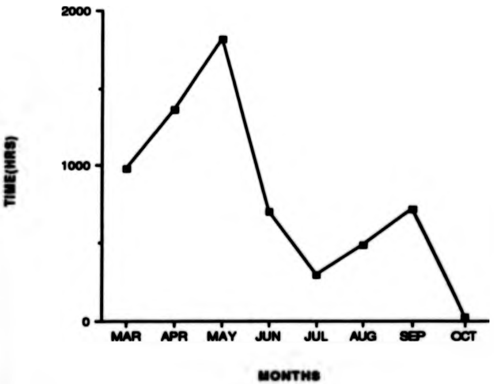


Figure 7.17. The monthly distribution of angling effort in 1987.



Analysis of catch by site-total catch.

In the sites that contained the fish farms, more rainbow trout than brown trout were caught, with this being most pronounced in area 1. In the other areas the two species were caught in similar numbers (Figure 7.18). There were more rainbow trout caught in area 1 than in the other areas combined. The catch fell from area 1 to area 4, where it levelled off and there was a small increase in areas 6 and 7, where Loch Awe's other fish farms are situated (Figure 7.1). The highest catch of brown trout was recorded in area 2 and fell towards area 7, the exception to this occurred in area 6 where a small increase was observed.

The between-site variation in the catch of each species was highly significant ($P<0.01$), and the variation in the catch of the two species at each site was only significant at sites 1 and 6, those which contained the two large fish farms on the loch.

Average weight.

There was considerable variation in the mean weight of brown trout throughout the loch, with no obvious pattern being apparent (Figure 7.19). This is in agreement with the results of the gill netting survey and further evidence that the NE/SW nutrient gradient was not translated into fish growth. The highest mean weight of rainbow trout was recorded in the areas containing the fish farms or those adjacent to them. This is due to the larger rainbow trout remaining in the immediate vicinity of the cages when they escape (Phillips, 1982).

Catch per unit of effort (C.P.U.E).

The combined CPUE for rainbow trout and brown trout was at its highest level in areas 1 and 6, this was due to the large number of rainbow trout caught in the immediate vicinity of the fish farms (Figure 7.20). The lowest combined CPUE's were recorded in areas 2 and 3. The brown

Figure 7.18. The catch of brown trout and rainbow trout by anglers in each area of Loch Awe in 1987.

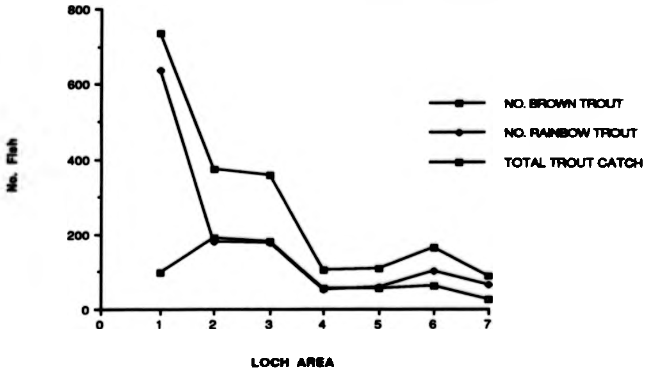


Figure 7.19 The mean weight (g) of brown trout and rainbow trout caught by anglers in each area of Loch Awe in 1987.

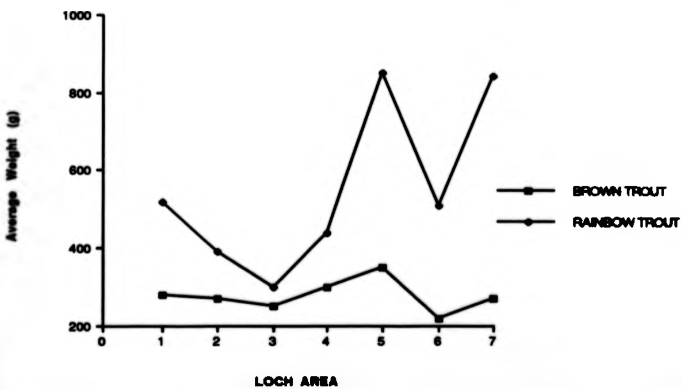


Figure 7.20. The CPUE (catch per rod hour) by loch area for rainbow trout and brown trout in 1987.

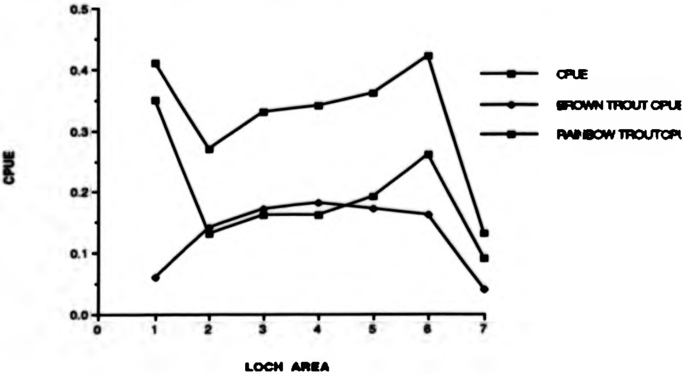
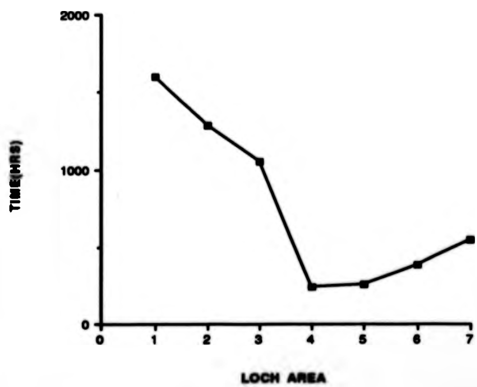


Figure 7.21. The distribution of angling effort by loch area in 1987.



trout CPUE plateaued between areas 2 and 6, and the rainbow trout CPUE peaked in areas 1 and 6. The higher angler CPUE for rainbow trout at the farm in area 1 compared to area 6 is in agreement with the findings of the gill netting survey in 1987. The angling effort was highest in area 1, it declined until area 4, after which it increased towards the loch's south end (Figure 7.21).

7.3.2.2 Angler census 1988.

In 1988, the estimated catches of brown trout and rainbow trout on Loch Awe were 14,039 and 3,535 respectively, this gave annual catch rates of 3.65/ha and 0.92 fish/ha (Table 7.1). The average weights of brown trout and rainbow trout were 308 g and 399 g respectively, which gave yields of 1.12 kg/ha and 0.37 kg/ha. There was a large increase and decrease in the catch of brown trout and rainbow trout respectively between 1987 and 1988.

Analysis of the catch by month-monthly total catch.

The monthly angler catch of brown trout and rainbow trout in 1988 peaked in the late spring and early autumn (Figure 7.22). This was similar to the pattern described in 1987, but in contrast to the previous year brown trout dominated the catch, the only exception to this occurred in March, when only a few fish were caught. Between April and September the difference in the monthly catch of each species was statistically significant ($P<0.001$). In March there was no significant variation, and in October the samples were too small to perform the analysis. Monthly variation in the catch of the two species was also highly significant ($P<0.001$).

Average weight.

There was considerable variation in the average weight of brown trout between months, however no overall seasonal trend was apparent (Figure

Figure 7.22 The monthly catch of brown trout and rainbow trout by anglers in 1988.

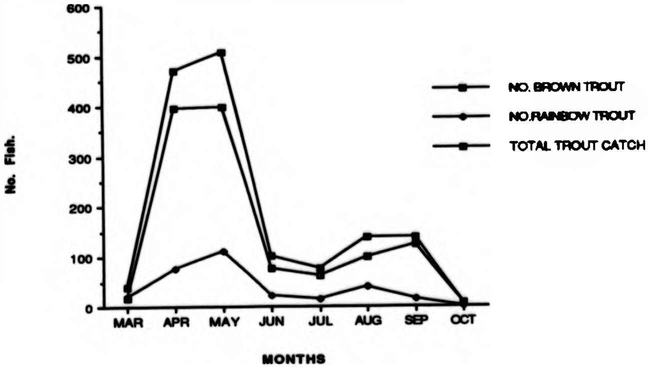
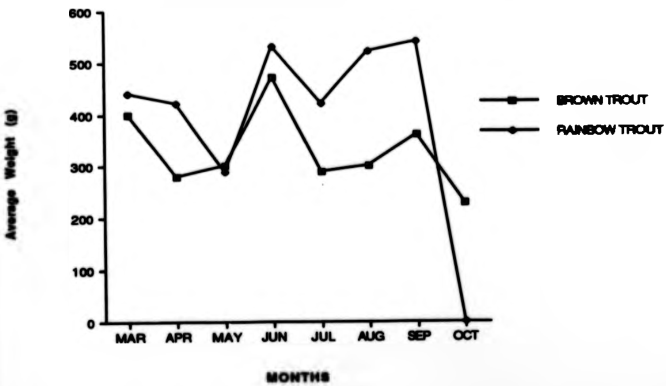


Figure 7.23 The monthly mean weight (g) of brown trout and rainbow trout caught by anglers in 1988.



7.23). The mean weight of rainbow trout also showed a large amount of variation (Figure 7.23).

Catch per unit of effort (C.P.U.E).

There was considerable variation in the combined rainbow trout and brown trout CPUE (Figure 7.24). The pattern was largely determined by the CPUE of brown trout which dominated catches in most months. If it had not been for the high value recorded in July, the CPUE would have followed a similar trend as the results of the gill netting survey. It is possible that the small sample in that month adversely affected the quality of the data. The rainbow trout CPUE was very low and showed little variation between months, from July until the end of the fishing season it fell gradually to zero. The monthly distribution of effort was bimodal peaking in May and August (Figure 7.25). This was similar to the pattern described in 1987.

Analysis of catch by site-total catch.

Only in area 1 did the catch of rainbow trout exceed the brown trout catch (Figure 7.26). The highest combined catches of the two species were caught in areas 2, 3 and 4. As with 1987 the number of fish fell towards area 7 at the south end of the loch. Compared to the previous year fewer rainbow trout were caught in each area, and as with brown trout their numbers fell towards site 7, where the lowest number were caught. Contrary to the previous year there was no increase in the catch of either species in area 6.

The variation in catch of the two species between loch areas was highly significant ($P<0.001$), and the variation between the catch of the two species in each area was statistically significant ($P<0.05$ in area 1 and $P<0.001$ in the others).

Figure 7.24. The monthly CPUE (catch per rod hour) for brown trout and rainbow trout caught by anglers in 1988.

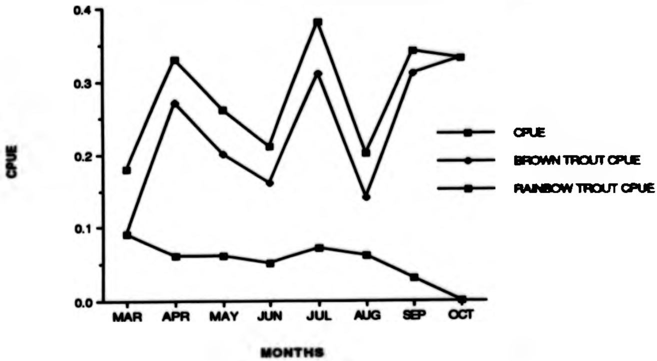


Figure 7.25. The monthly distribution of angling effort in 1988.

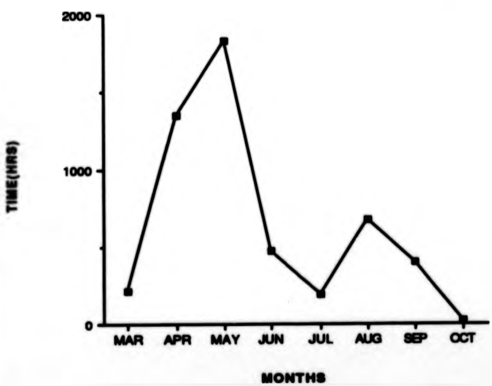


Figure 7.26. The catch of brown trout and rainbow trout by anglers in each area of Loch Awe in 1988.

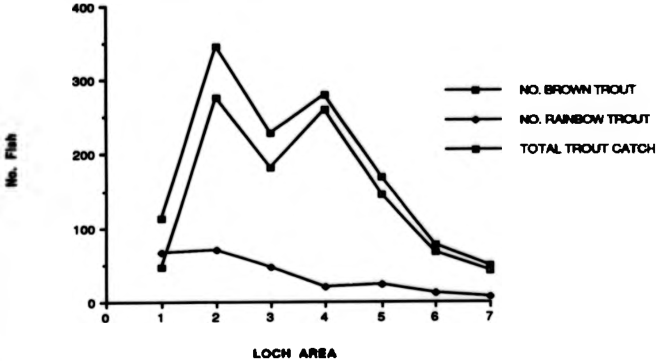
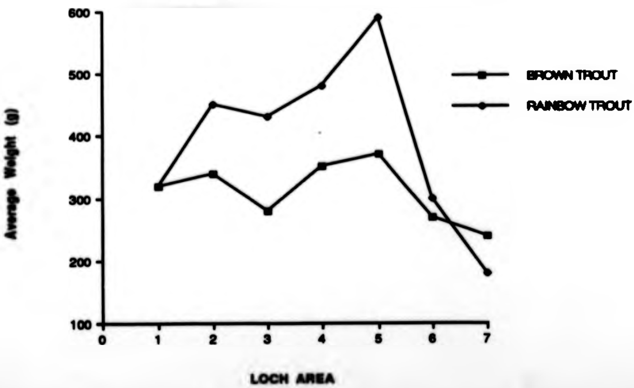


Figure 7.27 The mean weight (g) of brown trout and rainbow trout caught by anglers in each area of Loch Awe in 1988.



Mean weight.

There was no trend between mean weight and the area of capture for brown trout in the loch (Figure 7.27). It was similar to that observed in 1987, which is further evidence that the higher nutrient status at the southern end of the loch is not translated into fish growth. There was considerable variation in the mean weight of rainbow trout caught in the different areas, with the overall trend increasing towards area 7. However it is unlikely that this was due to the changing nutrient status as rainbow trout do the majority of their growing in the fish farms, and have been shown to have low success when feeding on natural prey. The high mean weights recorded in the southern part of the loch are probably due to an artefact created by the small sample sizes at these sites, with large fish positively skewing the mean.

Catch per unit of effort (C.P.U.E).

The combined brown trout and rainbow trout CPUE was highest in area 4, largely due to the brown trout CPUE (Figure 7.28). The comparatively low brown trout CPUE in areas 2 and 3 were largely due to the high levels of effort in them, which was in turn due to their proximity to the main road (Figure 7.29). Conversely the high CPUE's in areas 4 and 5 are principally due to the low effort.

The highest rainbow trout CPUE was recorded in area 1, this was due to the high availability of rainbow trout around the fish farm. It fell to 0.05 fish per rod hour in area 2, and varied little in the other areas. It is clear that the availability of rainbow trout was lower in each area than it had been in 1987.

Angler response.

In the present survey daily response rates ranged from 0-19%, which is in close agreement with the number of completed return cards expressed

Figure 7.28 The CPUE (catch per rod hour) by loch area for rainbow trout and brown trout in 1988.

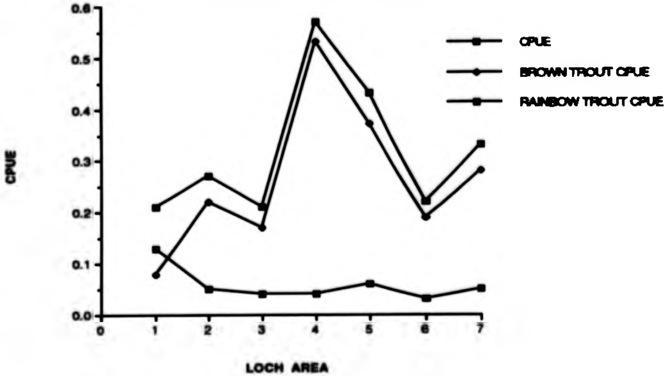
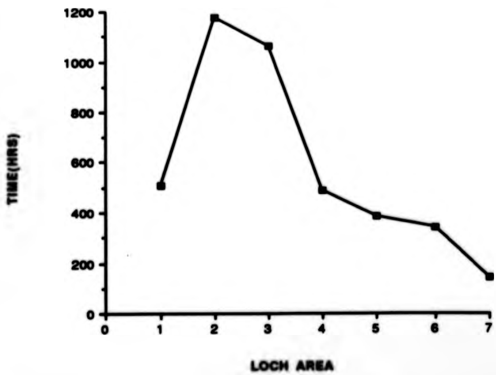


Figure 7.29. The distribution of angling effort by loch area in 1989.



as a percentage of the number of estimated rod days in 1987 and 1988, which were 16.9% and 13.9% respectively. O'Grady (1979) could only achieve a 70% return rate on a closely monitored single exit fishery.

7.4 Discussion.

In fisheries science there are conflicting reports on the reliability of catch statistics as the sole indicator of a fisheries status. Some authors believe that they are a good indicator (Moore, 1982; Swales & Fish, 1986; Giles, 1989), whereas others have strongly questioned their reliability, (Shuter et al., 1987). With such polarised views it is prudent to discuss their shortcomings and merits before we consider the results of the Loch Awe census.

The use of catch and effort statistics hinges on the critical assumption that catch and effort figures recorded in a survey are consistent indicators of the annual total catch and the annual fishing mortality rate, and that they are obtained in a consistent manner (Shuter et al., 1987).

In a long time-series data set the greatest problem is ensuring that the catching power of a unit of effort remains constant. If it changes it will subsequently alter any population estimates made using the CPUE. Factors that can affect it are variations in the skill level, changes in angler behaviour, e.g. changing bait, or changing the type of boats used e.g. changing from rowing boats to powered engines. In Loch Awe these types of changes have occurred.

Originally the majority of fishing was from rowing boats but they have been replaced by boats with engines which are able to cover larger areas and subsequently have greater catching power. With regards to skill it has been clearly demonstrated (Alabaster & Reid, 1988) that the catch of brown trout increases with experience, and Crisp & Robson (1982) demonstrated that a small proportion of skilled anglers were responsible for catching a high proportion of the annual catch in Cow Green Reservoir. Pawson (1986) also recognised the bias that this would introduce to a data set. Unfortunately skill is a very difficult factor to quantify and as a result there is no measure of its variation through the years.

Over the last 30 years there has been a growing trend for anglers to use more than one rod when fishing on Loch Awe and the evidence from the angler census suggested that this was not always acknowledged on the return cards. This is probably due to fishing with a set line being illegal as it is considered a fixed engine in fishing law. Also over this period there has been a move away from artificial flies as bait to a greater use of worms and maggots. O'Grady & Hughes (1980) demonstrated that worms were more effective at catching trout than artificial lures. Waters (1960) implicated hook shyness and the mortality associated with hooking as the reason for the CPUE declining at a faster rate than the population density, and similarly Beukema (1970) demonstrated a decline in the CPUE of carp held at constant densities as the carp gained experience.

Therefore it is clear that there is considerable scope for variation in the relationship between catch and effort in a fishery, and that some of the factors described have occurred in Loch Awe. Shuter et al. (1987) and Small (1987) recommended periodic independent population assessment, by methods such as cohort analysis or mark recapture, to make adjustments between the catch and effort relationship. Unfortunately the scale of this project and the size of Loch Awe precluded such an independent assessment. The analysis of long time series data sets is further complicated by changes that may occur in the productivity of the water.

Comparing the historic and modern data sets on Loch Awe.

It is not possible to make direct comparisons between the CPSR in the historic data set and the CPUE in the current survey. This is due to the historic data measuring the catch on successful rod-days only and the present survey calculating the catch rate on the total number of recorded rod-days. A more accurate comparison would be between the CPSR in the two data sets, this would be achieved by re-calculating the current survey results without the blank days. As expected this results in a rise in the catch rate (Table 7.2). Figure 7.30 shows the relationship between the modern and historic CPSR's. Even this comparison is unsatisfactory as it still does not include any information on the number of blank days in the two surveys.

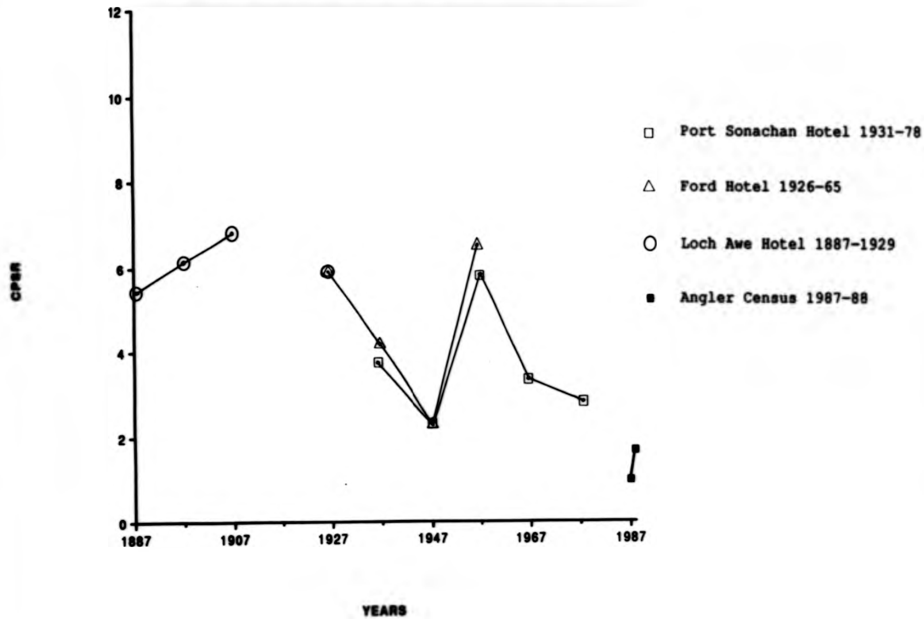
Given these shortcomings, a limited comparison between the historic and modern surveys clearly demonstrates that there has been a very large increase in the effort on Loch Awe in recent times. It is difficult to refute that this must at least be partially responsible for the decline in the catch rate on the loch. The increase in effort has coincided with a change in angler behaviour. Previously the majority of angling was organised through the hotels whereas it is now more common for anglers to visit the loch on day trips or to spend one or two nights camping on the loch side. It is likely that they will be fishing for a large part of their visit and commonly with more than one rod.

Loch Awe has a catch rate and yield for brown trout similar to that recorded in other unstocked upland reservoirs and this is further evidence that it is not under-performing. The present survey recorded catch rates of 1.3 and 2.2 brown trout ha^{-1} yr^{-1} and yields of 0.3 and 0.9 kg ha^{-1} yr^{-1} in 1987 and 1988 respectively while Crisp & Mann (1977b) recorded catch rates of 2.1-6.2 fish ha^{-1} yr^{-1} and yields of 0.5-1.2 kg ha^{-1} yr^{-1} from unstocked upland brown trout reservoirs which had been impounded at least ten years previously. It is likely that the decline in individual catch rates is due to the total catch being

Table 7.2 The catch per rod-day (C.P.U.E) and the catch per successful rod-day (C.P.S.R) of rainbow trout and brown trout recorded in the 1987 and 1988 angler census.

	1987		1988	
	Brown Trout	Rainbow Trout	Brown Trout	Rainbow Trout
CPUE	0.70	1.32	1.39	0.35
CPSR	0.98	1.82	1.68	0.42

Figure 7.30 The CPSR (catch per successful rod day) from the Loch Awe, Ford and Port Sonachan Hotels, and the 1987-88 angler census.



spread over a greater number of anglers.

An alternative to using catch rates as index of fish abundance in long time-series data sets is the mean weight. Campbell (1971) demonstrated that when all other factors are equal the mean weight of trout in lochs with large populations was low and conversely when the population was small that the mean weight increased. This latter effect is seen most clearly in the response of trout populations to acidification. As recruitment declines the amount of food available to each fish increases, and so the mean weight of the remaining fish in the population increases. The relationship between population size and mean weight ideally requires all other variables in the ecosystem to remain constant, which in a long time series data set is unlikely.

In Loch Awe four events may have altered its ecology and possibly had a bearing on brown trout growth. These are the introduction of rainbow trout, the construction of the Loch Awe barrage, the greater use of fertilizers in agriculture and the increased afforestation in the catchment.

When an exotic species is introduced to a habitat, there will be an adjustment in the behaviour of the native species. The amount of adjustment required will be determined by the availability of resources that are shared by the exotic and native species. If they are in short supply a large amount of adjustment will be required, and if there is no shortage the new species should be accommodated with less upheaval. Diet analysis demonstrated that rainbow trout consumed some of the prey items preferred by the loch's native species which may have affected their growth, although the impact in this instance would be minimised by the rainbow trout's low success in switching from an artificial to a wild diet.

Just prior to the start of fish farming on Loch Awe the North of Scotland Hydro Electric Board built a barrage over the River Awe which had the effect of reducing the annual variation in Loch Awe's water level. This has been shown by Hunt & Jones (1972) to improve the production of littoral invertebrates and as this group constitute a high proportion of the brown trout's diet this will benefit trout growth.

Since the early 1900's there has been a gradual increase in the amount of commercial forestry in the catchment (Figure 2.1). Forestry can have both detrimental and beneficial effects on fisheries. On the negative side the quality of spawning burns can be reduced, which will ultimately reduce recruitment (Mills,1971). On the positive side modern forestry practice requires fertilisers to be applied to plantations, with large amounts eventually making their way into water courses, where the increased level of phosphorus will boost primary productivity, which will ultimately boost fish production. Swift (1987) demonstrated that 5% of the phosphorus applied to a plantation in Glen Orchy was lost in runoff in the first few months after application. Modern farming practices also have a greater reliance on fertilisers, it is therefore likely that they would contribute to the productivity of the loch through runoff. Similarly fish farming itself can increase the nutrient status of a water body. Beveridge et al. (1990) reported that between 5-20% of the pellet dry weight fed to fish in cages is not consumed which will contribute to the productivity of the loch.

As the above influences have had an unquantifiable impact on the loch's productivity it would be erroneous to use the mean weight of rod caught brown trout as an accurate indicator of population size.

Monthly and area variation in 1987 and 1988.

The current monthly distribution of the angling catch and effort on Loch Awe is similar to that observed in the historic data sets. The peaks in activity occur in late spring and autumn following the seasonal variation in the catch of brown trout in the gill nets at the littoral sites. It has been demonstrated that this is due to a migration pattern controlled by food availability.

In 1987 the highest catches of brown trout were recorded in areas 2 and 3 (those with the main boat hiring businesses). Although less fish were caught in sections 4-7 their CPUE suggests that fish were as abundant in these areas as they were in the northern parts of the loch. In 1988 the highest catches were again recorded in area 2 with good catches also being recorded in area 4 confirming the results of the previous years CPUE. In 1987 more rainbow trout were caught in area 1 than at the other sites combined. This was due to the majority of angling occurring in the immediate vicinity of the fish farms, and to the high availability of rainbow trout in that habitat which is reflected in their high CPUE. In 1988 considerably fewer rainbow trout were caught, suggesting that they were less abundant than they had been the previous year. This is reflected in the distribution of effort, with more anglers preferring to fish in area 2 than 1, although this may be due to the sample being comprised of a greater proportion of boat than shore anglers in 1988. As mentioned above the main boat hiring establishments are in areas 2 and 3, whereas the ease of access for shore anglers from the A85 which runs around the north end of the loch makes area 1 a more popular destination with shore anglers. The decline in the rainbow trout's CPUE between the two years at each site in the loch further suggests that there had been a large decline in their abundance. As no evidence was found of rainbow trout breeding in the catchment, it has to be assumed that less rainbow trout had escaped from the farms. This combined with their poor over-winter survival (Cragg-Hine, 1975) would jointly conspire to reduce the catch. The small samples from the southern sections of the loch makes the data from them less reliable than from the northern end where the majority of angling occurs.

As stocked fish have a greater catchability than wild fish (Crisp & Mann, 1977; O'Grady, 1983), and rainbow trout have greater catchability than brown trout (Jacques, 1974; Taylor, 1978; Coles, 1981; Bryan, 1982; Pawson, 1986), it is clear that the escapee rainbow trout in Loch Awe will have a greater catchability than the native brown trout. This explains the discrepancy between the gill netting, which showed that away from the fish farms rainbow trout were only caught in very small numbers and the angler surveys, which showed the difference in their abundance to be less distinct. The differing vulnerability of the escapee and wild fish is principally due to the former's lack of experience in foraging wild prey and to their lack of discrimination when feeding.

In summary, it was not possible to make direct comparisons between the results of the historic data sets and the present day angler census. This was principally due to differences between the data collection systems in the two surveys, although other external factors had an effect. These include changes in angler behaviour, and variations in the loch's productivity. There has been a large decline in the CPUE in the loch in recent years, with the most likely reasons for this being the large increase in effort that has occurred. It is unlikely that the increase in effort has reduced the stock of fish in the loch, as the annual angling yield from it is comparable with that from other upland fisheries. Between 1987 and 1988 there was a marked decline in the catch of rainbow trout in the loch, these results are supported by the findings of the gill netting survey and suggest that there was a marked decline in their population over that period.

CHAPTER 6

SUMMARY

Rainbow trout were first introduced to Loch Awe in 1968 when fish farming started. Since then their population has been maintained by escapes of domesticated fish from the fish farms. This is contrary to some unsubstantiated reports that they were breeding in the loch's tributaries. The present investigation found no proof to support this. Evidence of their domesticated nature was revealed in most parts of this study. It is highly likely that selective breeding programmes have reduced their genetic base and adversely affected many aspects of their life history which ultimately has reduced their survival and breeding success in Loch Awe.

The gill netting survey demonstrated that rainbow trout were only found in large numbers in the immediate vicinity of the two large fish farms on the loch. The results from the angler census appeared to disagree with this, suggesting that as well being present in large numbers at the fish farms they were also present in moderate numbers away from them. This discrepancy is explained by the rainbow trout's greater probability of capture by anglers. As gill netting does not suffer from this bias its results must be considered as being more accurate in this situation. The growth rate of rainbow trout was comparable to what it is in their home range, and higher than brown trout in Loch Awe. This was due to the high energy diet that they are fed in the cages prior to their escape. There was no difference in their growth rate at or away from the fish farms.

It was only around the fish farm at Tervine that the distribution of the native species was restricted. At this site rainbow trout were present in greater numbers than they were at Braevallich, the other large farm on the loch. Therefore it would appear that the distribution of the native species is only adversely affected when the rainbow trout to native species ratio exceeds a certain unspecified level. On a limited number of occasions benthic Arctic charr and perch were caught in moderate numbers around the fish farms suggesting that they were being attracted to the sites.

Brown trout over-wintered in the littoral zone, and as the winter passed to spring and early summer they migrated offshore to the pelagic habitat. A greater proportion of older female fish were involved in this movement. In the autumn they moved back to the littoral zone prior to spawning in the loch's tributaries. The growth of brown trout was comparable with that from some other Scottish freshwater lochs, and did not vary at or away from the fish farm sites.

All of the Atlantic salmon that migrate from the catchment must pass through the loch, although it is not clear how long they spend in it. Some will simply pass through, whereas others will remain for up to a year or longer. They were caught in greatest numbers in mid-summer at the littoral sites that were situated close to where tributaries entered the loch, but showed no evidence of smoltification at that time. It is possible that they were destined to become part of an autumn smolt migration, it is more likely however that they would remain in the loch until the following spring, the main period for smolt migration.

The benthic morphs of Arctic charr were caught in each habitat throughout the year, but were present in greatest numbers at the benthic sites. In November and December they moved from the deep water into the deep littoral zone to spawn. There was also a small amount of evidence from the feeding survey that they under-took a diel migration into the littoral zone, but there was no strong evidence from the distribution study to support this. The pelagic morph of Arctic charr were caught in small numbers in the littoral and pelagic habitats throughout the year.

Perch were caught in greatest numbers in the littoral zone in the late spring, and their numbers declined through the summer as they moved back into deeper water where they overwintered.

The presence of roach in Loch Awe was recorded for the first time, it is likely that they were introduced by pike anglers who had used them as live bait.

Although no eels were caught in the gill nets, the mucous deposits and the mutilated fish that were left in them indicated that they were present in each habitat that was sampled.

The reasons for these distribution patterns became clear when the feeding behaviours of the rainbow trout and the native species were investigated. At the fish farms rainbow trout have a very high dependence on the uneaten pellets that pass through the cages. During the summer when the feeding rate of the trout in the cages is higher, a greater proportion of rainbow trout caught at the cages had empty stomachs and those that were feeding consumed less. This could be caused by the availability of uneaten pellets declining due to the fish in the cages feeding more heavily. It is known that fish are fed more during the summer and that their conversion efficiency is also higher, but it is not known if their is any seasonal variation in the amount of uneaten pellets that pass through the cages. If their availability did decline it would be strong evidence that rainbow trout have great difficulty in switching to alternative food types when the abundance of their preferred food type declines. Further evidence of this was seen when rainbow trout are denied access to pellets. This situation arose on two occasions during the study; 1. in the loch feeding survey when rainbow trout were caught away from the cages; and 2. in the pond experiment when rainbow trout from Braevallich fish farm were released into a pond with brown trout. On both occasions rainbow trout consumed large quantities of material that was of no nutritional value, including vegetation, stones and polystyrene. Some conventional prey was consumed but only in small amounts.

The diet analysis of the rainbow trout caught by anglers disagreed with this showing that they were successful in securing wild prey. This is not surprising as the lures used by anglers are designed to mimic wild prey, so the sample will be biased towards fish that have learned to feed on conventional prey items. Of the conventional food that they consumed they showed a slight preference for those items obtained through surface feeding.

All the native species consumed a conventional diet both at and away from the fish farms, this included littoral invertebrates, zooplankton, pelagic pupae and aerial insects. A small number of native fish did consume pellets at the fish farms but in terms of occurrence it was only a very small proportion of the fish that were caught. In terms of volume it appeared to be more important, but this was due to each pellet having a greater volume than conventional prey items. Therefore it is clear that rainbow trout need to remain around the cages to secure their preferred food items, whereas the native species were able to feed well both at and away from the fish farms.

The diet of brown trout comprised bottom-dwelling invertebrates in the winter, this changed to zooplankton, pelagic pupae and aerial insects in the summer. A small amount of bottom-dwelling invertebrates were retained throughout the summer. Those caught at the fish farms had a greater proportion of empty stomachs than those caught at the littoral sites, it is unlikely that this was caused by direct competition for food with rainbow trout as there was very little overlap in the diet of the two species in that habitat.

Benthic Arctic charr preyed on invertebrates that were associated with the soft sediments over which they were caught, they included P. obtusale, C. viridis and Chironomidae larvae. Small amounts of littoral invertebrates were also consumed, which suggests that they undertook regular migrations into shallow water. The diet of pelagic Arctic charr was restricted to zooplankton.

When perch were in the littoral zone during the summer their diet largely comprised zooplankton and sticklebacks, with smaller amounts of aerial and littoral invertebrates also being consumed. The diet of juvenile Atlantic salmon comprised littoral invertebrates and zooplankton.

At present the scope for competition between the loch's native species and rainbow trout is limited by their lack of success in switching from an artificial diet to a conventional one when they escape from the fish cages. The two species that would be at greatest risk if they were to start feeding successfully on the wild prey would be pelagic Arctic charr and brown trout. The effect on brown trout would be limited by the niche divergence that the two species show when they are brought into sympatry, brown trout adopt a bottom feeding mode and rainbow trout adopt a surface feeding mode, this being facilitated by the different proportions of the visual pigments that the two species have in their retinas. Although this would increase total fish production in the loch, the production of brown trout would be lower than if the rainbow trout were not present. As anglers tend to fish the surface waters such divergence would result in the rainbow trout having a greater catchability than brown trout, and thereby appearing to be more abundant. The threat to pelagic Arctic charr is through the rainbow trout's preference for surface feeding although it would be reduced by the large availability of the open water habitat in which the two species would compete for aerial insects and zooplankton.

It is likely that rainbow trout would be more successful if they were able to feed on wild prey from an earlier age. There are two scenarios in which this might occur: 1. if the fish were to escape from the cages shortly after they were introduced to the loch, and 2. if rainbow trout started breeding in the catchment. In both instances the young fish would be exposed to a greater repertoire of prey search images than those reared in the cages, and it is likely that this would result in them being able to feed on wild prey items. The ability of the young rainbow trout from a hatchery to feed on wild prey items just after their yolk sack had been absorbed was observed in the trough experiment.

The outcome of interspecific interactions is largely determined by the developmental stage that they occur. At present there is no evidence of interactions between the loch's native species and rainbow trout in the tributaries. Sexually mature and immature adult rainbow trout were occasionally recorded in the tributaries, but they did not adhere to any pattern, and there was no evidence of them moving into the spawning burns in large numbers at a time when they become sexually mature. It was demonstrated in an experiment that rainbow trout eggs could hatch and survive at least to the alevin stage in the loch's feeder streams. However the electrofishing survey did not find any evidence of this occurring naturally. It did show that the tributaries of the loch were reasonably well stocked with juvenile brown trout and Atlantic salmon.

An experiment designed to examine the interactions between the progeny of spring-spawned rainbow trout, and autumn-spawned brown trout demonstrated the latter's behaviourial superiority. This was achieved by brown trout increasing their attack rate when they were in sympatry, which resulted in a reduction in the distribution and survival of rainbow trout. Unfortunately a lack of time precluded the analysis of the interactions between brown trout and autumn- spawned rainbow trout, or the inclusion of juvenile Atlantic salmon to the system.

The impetus for this study was the claim by anglers that the loch's brown trout fishery was in decline, and that this was due to the introduction of rainbow trout. Attempts were made to determine if this was the case, by comparing present day catches with those from the past. However, this was complicated by a number of factors.
The most useful statistic for making comparisons between the two data sets was the CPSR, however even its use was limited as it did not include a measure of blank days, which are likely to have varied between years. Accepting the above shortcoming a comparison between the present census and the historic CPSR showed that it is considerably lower than it was previously, resulting in each angler that visits the loch catching fewer fish. It is likely that some of the variation is due to differences between the two collection systems. However, another contributing factor to the CPSR reduction is the large and unregulated increase in fishing pressure that has occurred over the past two decades. This suggests that the fishery is not in decline and that the annual catch of brown trout is similar to what it was in the past, it is now being spread around a greater number of anglers giving the impression of a declining fishery. This is further supported by the similarity in brown trout yield from Loch Awe and other British upland fisheries.

An attempt was also made to assess the fisheries status by using the annual mean weight of fish caught by anglers but this was frustrated by unquantifiable variations in the productivity of the loch throughout the period that records are available.

Overall, the impact of rainbow trout on the native fish species in Loch Awe, is limited by their lack of success in switching from a pelleted diet, to a natural one. The strongest evidence of this was the high dependence of rainbow trout on pellets when they escape from the cages and their restricted distribution around the fish farms. No evidence was found of rainbow trout spawning in the loch's tributaries, although it was shown that they could survive at least to the alevin stage should they be successful in spawning. Survival past this stage would ensure that they would learn to feed on a wild diet, which would allow them to become a greater threat to the loch's native species. At present there is little likelihood of this occurring as only 5.0% of the females and 2.9% of the males caught in 1987 were sexually mature, the continued use of all female or triploid stock on the fish farms should further ensure that a self-sustaining population does not become established.

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APPENDICES

Appendix 1. **The diet of the fish caught in the 1987 gill netting survey expressed as percentage volume, number and occurrence.**

Brown Trout Littoral 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	3.3	10.3	9.8	3.0	41.4	16.6
Physa fontinalis	4.2	0.9			30.3	2.9
Planorbus laevis	0.5	0.3				
Planorbus contortus	1.0	0.4		0.5	10.9	
Valvata piscinalis		1.2				
V. cristata						*
Potamopyrgus jenkinsi	0.4	0.2		2.3		0.9
Ancylus fluviatilis	0.1	0.4		0.3		
Pisidium obtusale	0.2	0.1				*
Gammarus pulex	*	0.3			*	
G. lacustris	9.9	5.9	0.2		*	4.4
Asellus aquaticus	44.9	33.9	3.1	24.7	*	29.7
Plecoptera		0.6				
Nemoura sp.		*				
N. avicularis		0.4				
N. cinerea	1.4					
Leuctra sp.		0.1			*	
Capnia sp.		*				
C. atra		1.8				
Perlodidae	0.4	0.1				
Isoperla grammatica						
Diura bicaudata	1.5	1.0				
Dinocras cephalotes						0.2
Ephemeroptera		1.1		1.8		
Ephemera danica			0.4			
Caenis horaria						
Ephemerella ignita		*		1.2		
Ecdyonurus sp.		0.2				
E. venosus	0.1					
Rhithrogena semicolorata			0.1			0.2
Baetis sp.						0.3
Coleoptera (A)		0.2				
Dytiscinae (A)		*	0.1			
Platambus maculatus (A)	0.4	0.1				
Limnius volkmari (A)		*				
Curculionidae (A)		0.1	0.2			
Coleoptera	0.5	*				

	J/F	M/A	M/J	J/A	S/O	N/D
Dytiscinae	0.4	0.2				
Colymbetes	*	0.2	*	0.3	*	0.2
Haliplidae				0.5	0.1	
Elmis aenea		*				
Trichoptera	8.2	3.0		1.3		
Leptoceridae		1.6	*		*	0.2
Athripsodes sp.		0.2	0.2			
A. aterrimus			0.5			1.2
A. cinereus		0.5	0.5			
A. bilineatus		2.2			0.1	1.6
A. nigronervosus						1.7
Myastacides sp.		*	0.5			
M. azurea				0.3		2.4
Ocestris testacea		0.2				0.5
Apatania wallengreni					0.3	2.6
Limnephilus sp.	2.1	3.7		0.5		
L. borealis		0.4				
L. subcentralis			0.5			
L. vittatus	1.0					
L. lunatus	0.9	0.9				
Anabolia nervosa		1.5				
Potamophyllax latipennis						
Stenophyllax sp.	9.6	2.9				
R. dorsalis		0.4				
Agapetus fuscipes						*
Plectronemia conspersa		0.1				
Polycentropus sp.				0.7		
P. kingi				1.3		
P. flavomaculatus						0.4
Sericostoma personatum	0.5	4.3	3.0		0.1	7.7
Lepidostoma hirtum	0.4	6.0			0.6	10.7
Beraeodes minutus				0.5		
Phryganea sp.		*				
P. grandis						0.6
Hydroptila tineoides					0.1	
Sialis lutaria		1.4		0.7		
Ceratopogonidae		*	*		*	
Empididae		0.2				
Chironomidae		0.3	*		*	*
Tipulidae	0.5					
Simuliidae			*			
Daphniidae		0.9	0.4		6.5	
Daphnia hyalina			3.1	4.3	0.7	0.5
Bosmina coregoni					*	

	J/F	M/A	M/J	J/A	S/O	N/D
Eurycercus lamellatus				0.3		
Bythotrephes longimanus			0.1	50.4	6.6	*
Cyclops strenuus abyssorum	*					
Chironomidae (P)		0.3				
Tanypodinae (P)		0.4				
Macropelopia sp. (P)			*			
Orthocladius sp.(P)		0.2	*	0.3		
Chironomus sp. (P)				0.3		
Trichoptera (P)				0.7		
Fish			70.7			
Diptera (Ar)		2.3	2.3	0.5	1.8	0.6
Psocoptera (Ar)			0.5			
Coleoptera (Ar)			0.7	0.2		
Hemiptera (Ar)			0.2			
Lepidoptera (Ar)	*					
Ephemeroptera (Ar)			0.2		0.1	
Hymenoptera (Ar)		4.8	3.6	2.7	*	
Trichoptera (Ar)				0.7		
Vegetation	5.3	0.3				0.6
Fish eggs						12.0

P=pupae Ar=Aerial food source *=< 0.1% FP=Food Present

Brown Trout Littoral 1987.
Number

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	2.7	4.3	2.3	*	2.9	8.8
Physa fontinalis	8.0	1.7			7.0	2.8
Planorbus laevis	1.5	0.6				
Planorbus contortus	0.1	1.4		0.1	7.6	2.2
Valvata piscinalis		0.5				
V. cristata						0.2
Potamopyrgus jenkinsi	0.8	*		0.2		2.7
Ancylus fluviatilis	0.1	0.4		*		
Pisidium obtusale	0.4	0.2				0.2
Gammarus pulex	*	0.5			*	
G. lacustris	13.3	5.7	*		*	1.3
Asellus aquaticus	55.5	33.6	1.3	1.2	*	20.5
Plecoptera		2.6				
Nemoura sp.		*				
N. avicularis		0.6				
N. cinerea	1.5					

	J/F	M/A	M/J	J/A	S/O	N/D
Leuctra sp.		*			*	
Capnia sp.		0.1				
C. atra		2.9				
Perlodidae	0.4	*				
Diura bicaudata	1.4	0.2				
Dinocras cephalotes						0.2
Ephemeroptera		1.1		0.2		
Ephemera danica			*			
Ephemerella ignita		*		*		
Ecdyonurus sp.		0.2				
E. venosus	*					
Rhithrogena semicolorata			0.1			0.2
Baetis sp.						0.5
Coleoptera (A)		0.2				
Dytiscinae (A)		*	*			
Platambus maculatus (A)	0.2	0.1				
Limnius volkmari (A)		*				
Curculionidae (A)		0.1	0.2			
Coleoptera	0.6	*				
Dytiscinae	0.7	0.1				
Colymbetes	*	0.1	*	*	*	0.2
Haliplidae				*	*	
Elmis aenea		*				
Trichoptera	4.0	2.1		*		
Leptoceridae		0.6	*		*	0.5
Athripsodes sp.		0.1	*			
A. aterrimus			0.2			3.0
A. cinereus		0.3	*			
A. bilineatus		1.1			*	3.1
A. nigronervosus						1.3
Mystacides sp.		*	0.2			
M. azurea				*		5.4
Oecetris testacea		0.1				0.3
Apatania wallengreni						2.4
Limnephilus sp.	1.2	1.0		*		
L. borealis		0.1				
L. subcentralis			0.1			
L. vittatus	0.6					
L. lunatus	0.7	0.5				
Anabolia nervosa		1.0				
Stenophylax sp.	3.5	0.2				
R. dorsalis		0.1				
Agapetus fuscipes						0.2
Plectronemia consperesa		*				

	J/F	M/A	M/J	J/A	S/O	N/D
Polycentropus sp.				*		
P. kingi				*		
P. flavomaculatus						0.3
Sericostoma personatum	0.4	1.4	0.4		*	3.3
Lepidostoma hirtum	1.8	3.5			*	7.8
Beraeodes minutus				*		
Phryganea sp.		*				
P. grandis						0.3
Hydroptila tineoides					*	
Sialis lutaria		0.6		*		
Ceratopogonidae		*	*		*	
Empididae		0.1				
Chironomidae		0.7	*		*	0.2
Tipulidae	0.2					
Simuliidae			*			
Daphniidae		13.9	8.3		38.8	
Daphnia hyalina			82.7	15.5	9.2	29.9
Bosmina coregoni					0.4	
Eurycercus lamellatus				*		
Bythotrephes longimanus			0.8	82.0	33.1	1.6
Cyclops strenuus abyssorum	*					
Chironomidae (P)		0.4				
Tanypodinae (P)		1.0				
Macropelopia sp. (P)			*			
Orthocladius sp. (P)			2.5	*	*	
Cricotopus sp. (P)						
Chironomus sp. (P)				*		
Trichoptera (P)				*		
Fish			*			
Diptera (Ar)		3.0	1.5	*	0.5	0.2
Psocoptera (Ar)			1.0			
Coleoptera (Ar)			0.2	*		
Hemiptera (Ar)			*			
Lepidoptera (Ar)	*					
Ephemeroptera (Ar)			*		*	
Hymenoptera (Ar)		6.7	1.1	*	*	
Trichoptera (Ar)				*		
Vegetation	FP	*				0.3
Fish eggs						1.9

P=pupae Ar=Aerial food source *=< 0.1% FP=Food Present

Brown Trout Littoral 1987.
Occurrence

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	12.7	17.1	26.6	11.1	5.9	14.7
Physa fontinalis	10.0	7.9			8.8	4.4
Planorbus laevis	7.3	1.3				
Planorbus contortus	1.8	6.6		11.1	2.9	7.4
Valvata piscinalis		1.3				
V. cristata						1.5
Potamopyrgus jenkinsi	3.6	2.6		22.2		3.0
Ancylus fluviatilis	1.8	2.6		11.1		
Pisidium obtusale	3.6	4.0				1.5
Gammarus pulex	0.9	1.3			2.9	
G. lacustris	21.8	19.7	6.7		2.9	3.0
Asellus aquaticus	47.3	31.6	13.3	55.6	2.9	5.9
Plecoptera		2.6				
Nemoura sp.		1.3				
N. avicularis		5.3				
N. cinerea	3.6					
Leuctra sp.		1.3			2.9	
Capnia sp.		1.3				
C. atra		9.2				
Perlodidae	1.8	1.3				
Diura bicaudata	10	2.6				
Dinocras cephalotes						1.5
Ephemeroptera		9.2		22.2		
Ephemera danica			13.3			
Ephemerella ignita		1.3		33.3		
Ecdyonurus sp.		1.3				
E. venosus	0.9					
Rhithrogena semicolorata			1.3			1.5
Baetis sp.						1.5
Coleoptera (A)		2.6				
Dytiscinae (A)		1.3				
Platambus maculatus (A)	0.9	2.6				
Limnius volkmari (A)		1.3				
Curculionidae (A)		2.6	13.3			
Coleoptera	3.6	1.3				
Dytiscinae	5.5	2.6				
Colymbetes	0.9	2.6	6.7	11.1	2.9	1.5
Haliplidae				11.1	2.9	
Elmis aenea		1.3				
Trichoptera	18.2	15.8		11.1		
Leptoceridae		5.3	6.7		2.9	1.5

	J/F	M/A	M/J	J/A	S/O	N/D
Athripsodes sp.		1.3	6.7			
A. aterrimus			20.0			1.5
A. cinereus		2.6	13.3			
A. bilineatus		6.6			5.9	1.5
A. nigronervosus						5.9
Mystacides sp.		1.3	6.7			
M. azurea				11.1		1.5
Oecetis testacea		1.3				3.0
Apatania wallengreni					2.9	10.3
Limnephilus sp.	10.0	6.6		11.1		
L. borealis		2.6				
L. subcentralis			6.7			
L. vittatus	4.6					
L. lunatus	3.6	4.0				
Anabolia nervosa		6.6				
Stenophyllax sp.	11.8	2.6				
R. dorsalis		2.6				
Agapetus fuscipes						1.5
Plectronemia conspersa		1.3				
Polycentropus sp.				11.1		
P. kingi				11.1		
P. flavomaculatus						3.0
Sericostoma personatum	2.7	6.6	13.3		2.9	11.8
Lepidostoma hirtum	15.5	26.3			14.7	14.7
Beraeodes minutus				11.1		
Phryganea sp.		1.3				
P. grandis						2.9
Hydroptila tineoides					2.9	
Sialis lutaria		7.9		11.1		
Ceratopogonidae		1.3	6.7		2.9	
Empididae		1.3				
Chironomidae		9.2	6.7		2.9	
Tipulidae	0.9					
Simuliidae			1.3			
Daphniidae		1.3	6.7		17.6	
Daphnia hyalina			13.3	22.2	14.7	1.5
Bosmina coregoni					2.9	
Eurycercus lamellatus				11.1		
Bythotrephes longimanus			13.3	44.4	23.5	3.0
Cyclops strenuus abyssorum	0.9					
Chironomidae (P)		6.6				
Tanypodinae (P)		1.3				
Macropelopia sp. (P)			6.7			
Orthocladius sp. (P)			1.3	6.7	11.1	

	J/F	M/A	M/J	J/A	S/O	N/D
Chironomus sp. (P)				11.1		
Trichoptera (P)				11.1		
Fish			6.7			
Diptera (Ar)		4.0	26.7	22.2	14.7	1.5
Psocoptera (Ar)			1.3			
Coleoptera (Ar)			26.7	11.1		
Hemiptera (Ar)			13.3			
Lepidoptera (Ar)	0.9					
Ephemeroptera (Ar)			6.7		5.9	
Hymenoptera (Ar)		4.0	0.2	22.2	2.9	
Trichoptera (Ar)				11.1		
Vegetation	0.9	1.3				1.5
Fish eggs						1.5

Brown Trout at Fish Farms 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	7.7	9.3	0.5			
Physa fontinalis	20.3	8.3	0.2			
Planorbus laevis			0.3			
Planorbus contortus				*		
V. cristata		0.3				
Potamopyrgus jenkinsi	0.3	2.4	*		0.2	1.2
Ancylus fluviatilis	*	0.3	*			
Pisidium obtusale		0.3	*			
G. lacustris	7.4	4.1			0.4	
Plecoptera	0.3					
C. atra		0.3				
Ephemeroptera		4.8				
Ephemerella ignita		0.7				
Colymbetinae (A)		0.7	*			
Coleoptera			*			
Trichoptera	0.7	11.0	0.9			
M. azurea	0.9					
Limnephilus sp.		1.7	0.8			
L. lunatus	0.9					
Anabolia nervosa		35.9				
Polycentropus sp.			0.2			
Lepidostoma hirtum						0.5
Phryganea sp.		1.0				
Sialis lutaria		4.1				
Ceratopogonidae			*			

	J/F	M/A	M/J	J/A	S/O	N/D
Chironomidae			1.8		0.8	
<u>Erpobdella octoculata</u>	0.6	2.4				
Daphniidae					43.3	
<u>Bythotrephes longimanus</u>					17.1	
Chironomidae (P)		7.2	19.3		1.9	
Trichoptera (P)			0.3		0.2	
Diptera (Ar)			7.5		14.1	
Psocoptera (Ar)				*		
Lepidoptera (Ar)	0.3					
Hymenoptera (Ar)			0.2			
Trichoptera (Ar)			*			
Caterpillar					1.1	
Fish farm food	8.7		67.2			
Vegetation		4.8	0.6			
Fish eggs	51.1					98.4
Earthworms					20.9	
Maggots			0.2			

P=pupae Ar=Aerial food source *=< 0.1%

<u>Brown Trout at Fish Farms 1987.</u>
<u>Number.</u>

	J/F	M/A	M/J	J/A	S/O	N/D
<u>Lymnaea peregra</u>	5.3	5.6	0.5			
<u>Physa fontinalis</u>	36.7	9.0	0.2			
<u>Planorbus laevis</u>			0.7			
<u>Planorbus contortus</u>			0.2			
<u>V. cristata</u>		1.1				
<u>Potamopyrgus jenkinsi</u>	1.3	2.3	0.1		*	7.0
<u>Ancylus fluviatilis</u>	0.1	1.1	0.1			
<u>Pisidium obtusale</u>		1.1	0.2			
<u>G. lacustris</u>	14.2	6.7			*	
Plecoptera	0.7					
<u>C. atra</u>		1.1				
Ephemeroptera		7.9				
<u>Ephemerella ignita</u>		2.3				
Colymbetinae (A)		1.1	0.2			
Coleoptera			0.2			
Trichoptera	0.7	9.0	1.0			
<u>M. azurea</u>	0.9					
<u>Limnephilus</u> sp.		1.1	1.0			
<u>L. lunatus</u>	0.9					

	J/F	M/A	M/J	J/A	S/O	N/D
Anabolia nervosa		20.2				
Polycentropus sp.			0.1			
Lepidostoma hirtum						1.4
Phryganea sp.		1.1				
Sialis lutaria		3.4				
Ceratopogonidae			0.7			
Chironomidae			9.3		*	
Erpobdella octoculata	0.2	1.1				
Daphniidae					76.7	
Bythotrephes longimanus					21.6	
Chironomidae (P)		23.6	50.0		0.2	
Trichoptera (P)			0.4		*	
Diptera (Ar)			28.9		1.3	
Psocoptera (Ar)				0.2		
Lepidoptera (Ar)	0.1					
Hymenoptera (Ar)			0.3			
Trichoptera (Ar)			0.1			
Caterpillar					*	
Fish farm food	0.6		6.5			
Vegetation		1.1	0.1			
Fish eggs	37.7					91.5
Earthworms					*	
Maggots			0.1			

P=pupae Ar=Aerial food source *=< 0.1%

Brown Trout at Fish Farms 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	29.4	11.1	11.5			
Physa fontinalis	17.7	5.6	3.9			
Planorbus laevis	23.5					
Planorbus contortus			7.7			
V. cristata		5.6				
Potamopyrgus jenkinsi	17.7	11.1	3.9		5.3	20
Ancylus fluviatilis	5.9	5.6	3.9			
Pisidium obtusale		5.6	7.7			
G. lacustris	17.7	11.1			5.3	
Plecoptera	5.9					
C. atra		11.1				
Ephemeroptera		11.1				
Ephemerella ignita		11.1				

	J/F	M/A	M/J	J/A	S/O	N/D
Colymbetinae (A)		11.1	3.9			
Coleoptera			7.7			
Trichoptera	11.8	11.1	26.9			
M. azurea	5.9					
Limnephilus sp.		5.6	7.7			
L. lunatus	5.9					
Anabolia nervosa		22.2				
Polycentropus sp.			3.9			
Lepidostoma hirtum						20
Phryganea sp.		5.6				
Sialis lutaria		5.6				
Ceratopogonidae			3.9			
Chironomidae			19.2		10.5	
Erpobdella octoculata	5.9	5.6				
Daphniidae					42.1	
Bythotrephes longimanus					5.3	
Chironomidae (P)		5.6	57.7		5.3	
Trichoptera (P)			3.9		5.3	
Diptera (Ar)			15.4		10.5	
Psocoptera (Ar)				3.9		
Lepidoptera (Ar)	5.9					
Hymenoptera (Ar)			3.9			
Trichoptera (Ar)			3.9			
Caterpillar					5.3	
Fish farm food	5.9		7.7			
Vegetation		5.6	3.9			
Fish eggs	11.8					20
Earthworms					5.3	
Maggots			3.9			

P=pupae Ar=Aerial food source *=< 0.1%

Brown Trout Pelagic 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Chironomidae				1.2		
Daphniidae				7.5		
Daphnia hyalina				37.7	74.0	80.0
Bythotrephes longimanus				51.1	26.0	20.0
Leptodora kindti				0.2		
Chironomidae (P)				0.3		
Diptera (Ar)				2.0		

P=pupae Ar=Aerial food source *=< 0.1%

Brown Trout Pelagic 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Chironomidae				*		
Daphniidae				6.7		
Daphnia hyalina				46.9	89.1	98.2
Bythotrephes longimanus				46.2	10.9	1.8
Leptodora kindti				*		
Chironomidae (P)				*		
Diptera (Ar)				0.2		

P=pupae Ar=Aerial food source *=< 0.1%

Brown Trout Pelagic 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Chironomidae				14.3		
Daphniidae				14.3		
Daphnia hyalina				64.3	33.3	28.6
Bythotrephes longimanus				57.1	64.7	14.3
Leptodora kindti				7.1		
Chironomidae (P)				7.1		
Diptera (Ar)				7.1		

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout Littoral 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	0.5				10.9	57.5
Physa fontinalis	0.4				0.7	
Valvata piscinalis					1.7	
G. lacustris	*					
Asellus aquaticus	1.4	2.9			1.5	
Plecoptera		0.1				
C. atra		0.2				
Ephemeroptera		0.5				
Ephemera danica					0.2	
Ephemerella ignita				0.3		

	J/F	M/A	M/J	J/A	S/O	N/D
Baetis sp.						*
Dytiscinae (A)		0.1				
Potamonectes depressus (A)				0.3		
Dytiscinae	0.2					
Colymbetes		0.1			0.2	
Trichoptera	0.8					
Leptoceridae		0.1				
Limnephilus sp.	0.7	0.5				
Sericostoma personatum					1.4	
Lepidostoma hirtum		0.2				
Ceratopogonidae				0.3		
Simuliidae			*			
Daphniidae						1.2
Daphnia hyalina				7.3		*
Bythotrephes longimanus				13.5		
Chironomidae (P)				2.3		
Trichoptera (P)	0.8			5.2		
Fish					28.0	40.6
Diptera (Ar)				4.4	1.0	
Coleoptera (Ar)				10.7		
Hemiptera (Ar)				17.7		
Plecoptera (Ar)				0.5		
Hymenoptera (Ar)				34.6		
Trichoptera (Ar)				2.1		
Fish farm food	29.3					
Vegetation	37.7	14.3		0.8	51.3	0.3
Stones	24.1	7.2			3.4	
Silver foil		0.4				
Cigarette	3.9					
Sweet corn		71.1				
Maggots		2.4				

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout Littoral 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	3.0				15.2	8.3
Physa fontinalis	3.0				4.0	
Valvata piscinalis					5.1	
G. lacustris	6.1					
Asellus aquaticus	21.2	22.5			9.1	
Plecoptera		1.3				
C. atra		2.7				
Ephemeroptera		3.3				
Ephemera danica					1.0	
Ephemerella ignita				*		
Baetis sp.						0.2
Dytiscinae (A)		0.7				
Potamonectes depressus (A)				*		
Dytiscinae	3.0					
Colymbetes		0.7			1.0	
Trichoptera	3.0					
Leptoceridae		5.9				
Limnephilus sp.	3.0	2.0				
Sericostoma personatum					1.0	
Lepidostoma hirtum		0.7				
Ceratopogonidae				*		
Simuliidae			0.7			
Daphniidae						81.3
Daphnia hyalina				54.1		4.1
Bythotrephes longimanus				36.3		
Chironomidae (P)				0.8		
Trichoptera (P)	3.0			1.1		
Fish					2.0	3.5
Diptera (Ar)				0.3	4.0	
Coleoptera (Ar)				1.0		
Hemiptera (Ar)				4.5		
Plecoptera (Ar)				*		
Hymenoptera (Ar)				1.5		
Trichoptera (Ar)				0.2		
Fish farm food	21.2					
Vegetation	3.0	9.3		0.1	54.6	FP
Stones	27.3	0.7			3.0	
Silver foil		0.7				
Cigarette	3.0					
Sweet corn		49.7				
Maggots		4.6				

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout Littoral 1987.

Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	5.6				40.0	20.0
Physa fontinalis	5.6				20.0	
Valvata piscinalis					40.0	
G. lacustris	5.6					
Asellus aquaticus	16.7	23.5			40.0	
Plecoptera		11.8				
C. atra		5.9				
Ephemeroptera		5.9				
Ephemera danica					20.0	
Ephemerella ignita				20.0		
Baetis sp.						10.0
Dytiscinae (A)		5.9				
Potamonectes depressus (A)				20.0		
Dytiscinae	5.6					
Colymbetes		5.9			20.0	
Trichoptera	5.6					
Leptoceridae		5.9				
Limnephilus sp.	5.6	11.8				
Sericostoma personatum					20.0	
Lepidostoma hirtum		5.9				
Ceratopogonidae				20.0		
Simuliidae			5.9			
Daphniidae						10.0
Daphnia hyalina				20.0		10.0
Bythotrephes longimanus				40.0		
Cyclops virdis				60.0		
Trichoptera (P)	5.6			20.0		
Fish					20.0	20.0
Diptera (Ar)				40.0	20.0	
Coleoptera (Ar)				80.0		
Hemiptera (Ar)				40.0		
Plecoptera (Ar)				20.0		
Hymenoptera (Ar)				40.0		
Trichoptera (Ar)				20.0		
Fish farm food	5.6					
Vegetation	33.3	29.4		20.0	60.0	10.0
Stones	16.7	5.9			20.0	
Silver foil		5.9				
Cigarette	5.6					
Sweet corn		5.9				
Maggots		5.9				

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout at Fish Farms 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	*					1.1
Physa fontinalis			*	*		*
Planorbus contortus						*
Valvata piscinalis			*	*		
Potamopyrgus jenkinsi	*	*	*	*	*	0.3
Pisidium obtusale			*	*		
G. lacustris	0.1	*	*			*
L. hippopus				*		
C. atra		*				
Dinocras cephalotes				*		
Ephemerella ignita		*			*	
Coleoptera (A)			*			
Curculionidae (A)			*			
Dryopidae (A)		*				
Coleoptera					*	
Colymbetes						*
Dryopidae						
Haliplidae			*			*
Trichoptera	*	*				
Leptoceridae						*
A. aterrimus						*
Ocestris testacea						*
Limnephilus sp.			*			
Anabolia nervosa				*		
Lepidostoma hirtum	*				*	*
Sialis lutaria				*		
Ceratopogonidae			*	*		
Empididae		*				
Chironomidae	*			0.1	*	*
Tipulidae					*	
Simuliidae				*		
Daphniidae			0.3	0.2	0.4	
Daphnia hyalina			0.1			
Bythotrephes longimanus				*	*	
Leptodora kindti			*			
Chironomidae (P)		0.6	3.7	*	*	
Nanocladius sp. (P)		*				
Chironomus sp. (P)				*	*	
Phaenospectra sp. (P)		*				
Trichoptera (P)		*		*		
Fish				0.1		0.9
Stickleback	*					*

	J/F	M/A	M/J	J/A	S/O	N/D
Diptera (Ar)		*	1.7	0.4	*	
Psocoptera (Ar)				*	*	
Coleoptera (Ar)			*	*		
Lepidoptera (Ar)			*			
Ephemeroptera (Ar)			*			
Plecoptera (Ar)				*		
Hymenoptera (Ar)		*	*	*		
Trichoptera (Ar)			*	*	*	
Fish farm food	84.1	93.8	90.1	88.6	94.4	95.4
Vegetation	0.9	1.2	0.9	2.1		1.2
Fish eggs	13.4				0.6	*
Stones	0.2		1.9			
Cigarette			*	*		0.3
Sweet corn	1.2	4.0	0.4	6.5	1.4	0.1
Maggots		0.1	0.2	0.2	3.1	0.5

P=pupae   Ar=Aerial food source *=< 0.1%

Rainbow Trout at Fish Farms 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	0.2					3.4
Physa fontinalis			*	0.1		0.3
Planorbus contortus						0.5
Valvata piscinalis			0.1	0.1		
Potamopyrgus jenkinsi	0.3	0.9	0.2	0.2	0.1	12.1
Pisidium obtusale			0.2	0.1		
G. lacustris	1.1	0.4	0.1			0.1
L. hippopus				0.2		
C. atra		0.2				
Dinocras cephalotes				0.1		
Ephemerella ignita		0.2			*	
Coleoptera (A)			*			
Curculionidae (A)			0.1	*		
Dryopidae (A)		0.2				
Coleoptera					0.1	
Colymbetes						0.2
Haliplidae			*			0.1
Trichoptera	0.1	0.2				
Leptoceridae						0.1
A. aterrimus						0.2
Oecetris testacea						0.4

	J/F	M/A	M/J	J/A	S/O	N/D
Limnephilus sp.			0.1			
Anabolia nervosa				0.2		
Lepidostoma hirtum	0.3				0.1	0.3
Sialis lutaria				0.1		
Ceratopogonidae			0.1	0.2		
Empididae		0.2				
Chironomidae	0.5			4.1	0.2	0.1
Tipulidae					*	
Simuliidae				0.8		
Daphniidae			7.9	10.3	63.2	
Daphnia hyalina			19.3			
Bythotrephes longimanus				11.8	2.4	
Leptodora kindti			0.4			
Chironomidae (P)		24.6	33.4	1.2	0.6	
Nanocladius sp. (P)		0.7				
Chironomus sp. (P)				0.7	0.2	
Phaenospectra sp.(P)		0.7				
Trichoptera (P)		0.4		0.8		
Fish				0.5		0.1
Stickleback	0.1					0.2
Diptera (Ar)		0.4	10.8	17.6	1.8	
Psocoptera (Ar)				*	0.2	
Coleoptera (Ar)			0.1	0.1		
Lepidoptera (Ar)			0.1			
Ephemeroptera (Ar)			0.1			
Plecoptera (Ar)				0.1		
Hymenoptera (Ar)		0.2	0.1	0.1		
Trichoptera (Ar)			0.2	0.3	0.1	
Fish farm food	35.7	64.4	23.7	43.3	25.7	79.5
Vegetation	0.1	FP	0.1	FP		0.3
Fish eggs	60.7				0.7	0.1
Stones	0.1		0.1			
Cigarette			*	0.1		0.1
Sweet corn	0.8	6.0	1.2	6.9	1.5	0.2
Maggots		0.5	0.3	0.5	3.1	1.9

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout at Fish Farms 1987.

Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra	2.4					4.9
Physa fontinalis			1.4	2.2		2.9
Planorbus contortus						3.9
Valvata piscinalis			2.9	2.2		
Potamopyrgus jenkinsi	1.2	1.28	4.3	4.4	2.7	4.9
Pisidium obtusale			4.3	2.2		
G. lacustris	2.4	5.6	2.9			0.1
L. hippopus				2.2		
C. atra		2.8				
Dinocras cephalotes				2.2		
Ephemerella ignita		2.8			1.4	
Coleoptera (A)			1.4			
Curculionidae (A)			1.4			
Dryopidae (A)		2.8				
Coleoptera					1.4	
Colymbetes						0.2
Haliplidae			1.4			
Trichoptera	1.2	2.8				
Leptoceridae						0.9
A. aterrimus						0.9
Ocestris testacea						0.9
Limnephilus sp.			2.9			
Anabolia nervosa				2.2		
Lepidostoma hirtum	1.2				1.4	2.9
Sialis lutaria				2.2		
Ceratopogonidae			2.9	4.4		
Empididae		2.8				
Chironomidae	2.4			6.7	2.7	0.9
Tipulidae					1.4	
Simuliidae				1.4		
Daphniidae			2.9	2.2	4.1	
Daphnia hyalina			1.4			
Bythotrephes longimanus				6.7	1.4	
Leptodora kindti			1.4			
Chironomidae (P)		22.2	31.4	6.7	2.8	
Nanocladius sp. (P)		2.8				
Chironomus sp. (P)				8.9	1.4	
Phaenospectra sp.(P)		2.8				
Trichoptera (P)		2.8		4.4		
Fish				6.7		0.9
Stickleback	1.2					0.9
Diptera (Ar)		2.8	10	8.9	8.1	

	J/F	M/A	M/J	J/A	S/O	N/D
Psocoptera (Ar)				1.4	2.2	
Coleoptera (Ar)			2.9	2.2		
Lepidoptera (Ar)			2.9			
Ephemeroptera (Ar)			2.9			
Plecoptera (Ar)				2.2		
Hymenoptera (Ar)		2.8	1.4	2.2		
Trichoptera (Ar)			1.4	4.4	1.4	
Fish farm food	51.2	75.0	28.6	37.8	56.8	56.3
Vegetation	3.7	2.8	5.7	8.9		2.9
Fish eggs	4.9				1.4	0.9
Stones	1.2		1.4			
Cigarette			1.4	2.2		2.0
Sweet corn	1.2	5.6	2.9	6.7	5.4	0.9
Maggots		5.6	5.7	4.4	8.1	2.9

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout Pelagic 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Capnia sp.		27.3				
Chironomidae (L)		18.2				
Chironomidae (P)		27.3				
Diptera (Ar)		27.3				

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout Pelagic 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Capnia sp.		30.0				
Chironomidae		20.0				
Chironomidae (P)		20.0				
Diptera (Ar)		30.0				

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout Pelagic 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Capnia sp.		100				
Chironomidae		100				
Chironomidae (P)		100				
Diptera (Ar)		100				

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Charr Littoral 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Planorbus contortus						3.2
Pisidium obtusale	7.6					3.2
G. lacustris	2.2					
Asellus aquaticus	12.5		16.7			
Ephemeroptera						3.2
Trichoptera	9.8					3.2
Leptoceridae	19.0					3.2
Psychomiidae sp.						6.5
Sialis lutaria			22.2			
Chironomidae	37.4					3.2
Daphnia hyalina			50.0			
Eurycercus lamellatus					100	
Cyclops viridis	0.2		*			
Chironomidae (P)			11.1			
Vegetation	8.1					12.9
Fish eggs	4.3					64.5

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Charr Littoral 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Planorbus contortus						6.3
Pisidium obtusale	12.8					12.5
G. lacustris	1.0					
Asellus aquaticus	9.2	2.2				
Ephemeroptera						6.3
Trichoptera	7.2					6.3
Leptoceridae	11.8					6.3
Psychomiidae						12.5
Sialis lutaria			1.2			
Chironomidae	52.8					12.5
Daphnia hyalina			92.2			
Eurycercus lamellatus					100	
Cyclops viridis	3.1		2.3			
Chironomidae (P)			2.3			
Vegetation	0.5					6.3
Fish eggs	0.5					37.5

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Charr Littoral 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Planorbus contortus						1.4
Pisidium obtusale	36.4					1.4
G. lacustris	18.2					
Asellus aquaticus	27.3		50.0			
Ephemeroptera						1.4
Trichoptera	27.3					1.4
Leptoceridae	9.1					1.4
Psychomiidae						1.4
Sialis lutaria			50.0			
Chironomidae	63.6					1.4
Daphnia hyalina			100			
Eurycercus lamellatus					25.0	
Cyclops virdis	27.3		50.0			
Chironomidae (P)			50.0			
Vegetation	9.1					1.4
Fish eggs	9.1					1.4

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Arctic Charr at Fish Farms 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Planorbus contortus						47.6
Potamopyrgus jenkinsi	1.1					52.3
G. lacustris	0.5					
Dytiscinae	0.5					
Chironomidae	1.9					
Fish farm food	86.3					
Fish eggs	9.7					

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Arctic Charr at Fish Farms 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Planorbus contortus						40.0
Potamopyrgus jenkinsi	5.7					60.0
G. lacustris	1.9					
Dytiscinae	1.9					
Chironomidae	46.2					
Fish farm food	13.5					
Fish eggs	30.6					

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Charr at Fish Farms 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Planorbus contortus						50.0
Potamopyrgus jenkinsi	20.0					50.0
G. lacustris	20.0					
Dytiscinae	20.0					
Chironomidae	20.0					
Fish farm food	20.0					
Fish eggs	40.0					

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Arctic Charr Pelagic 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Pisidium obtusale						16.4
Holocentropus dubius						81.9
Chironomidae			66.7	2.4		
Daphniidae			33.3			
Daphnia hyalina				36.3	20.0	
Bythotrephes longimanus				61.3	80.0	
Cyclops viridis						*

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Arctic Charr Pelagic 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Pisidium obtusale						33.3
Holocentropus dubius						16.7
Chironomidae			9.1	0.2		
Daphniidae			90.9			
Daphnia hyalina				45.2	36.8	
Bythotrephes longimanus				54.7	63.2	
Cyclops viridis						50.0

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Arctic Charr Pelagic 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Pisidium obtusale						33.3
Holocentropus dubius						33.3
Chironomidae			100	12.5		
Daphniidae			100			
Daphnia hyalina				37.5	50.0	
Bythotrephes longimanus				50.0	50.0	
Cyclops viridis						33.3

P=pupae Ar=Aerial food source *=< 0.1%

Benthic Arctic Charr Benthic 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Potamopyrgus jenkinsi					1.1	
Pisidium obtusale	28.7	21.6	10.7	7.4	25.9	19.9
G. lacustris			3.4			
Asellus aquaticus		2.1	1.7			
L. inermis				0.7		
L. fusca					2.6	
Capnia sp.		1.0				
Coleoptera				0.3		
Trichoptera			1.7	0.3		
Polycentropus sp.		5.2			1.5	
P. kingi				0.4		
Holocentropus dubius			20.6			
Ceratopogonidae				0.1		
Chironomidae	39.4	46.3	35.2	14.0	26.3	21.4
Polycelis sp.						9.2
Erpobdella octoculata				2.2		
Daphniidae	0.5			1.4		
Daphnia hyalina				12.8		
Eurycercus lamellatus		3.1	2.6	7.0	24.3	10.7
Bythotrephes longimanus				33.9	*	
Leptodora kindti				0.7		
Cyclops viridis	31.4	17.6	17.2	16.1	17.9	5.3
Chironomidae (P)			2.6	1.1	0.4	
Macropelopia sp. (P)			2.6			
Procladius sp. (P)				0.4		
Aspectrotanypus sp. (P)				0.3		
Psectrotanypus sp. (P)				0.1		
Pentaneurini (P)			1.7			
Arctopelopia sp. (P)				1.5		
Rheopelopia sp. (P)				0.4		
Arachnidae (Ar)		1.0				
Vegetation		1.0				

Benthic Arctic Charr Benthic 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Potamopyrgus jenkinsi						0.4
Pisidium obtusale	24.5	16.7	11.2	1.3	11.4	20.8
G. lacustris			0.9			
Asellus aquaticus		0.4	0.3			
L. inermis				*		

	J/F	M/A	M/J	J/A	S/O	N/D
<u>L. fusca</u>					0.3	
<u>Capnia</u> sp.		0.4				
Coleoptera				*		
Trichoptera			0.3	*		
<u>Polycentropus</u> sp.		0.8		0.2		
<u>P. kingi</u>				*		
<u>Holocentropus dubius</u>			7.3			
Ceratopogonidae				*		
Chironomidae	30.7	41.4	32.0	2.1	8.5	17.6
<u>Polycelis</u> sp.						2.4
<u>Erpobdella octoculata</u>				*		
Daphniidae	2.8		2.6			
<u>Daphnia hyalina</u>				24.8		
<u>Eurycercus lamellatus</u>		6.5	4.5	3.0	30.3	26.4
<u>Bythotrephes longimanus</u>				45.8		
<u>Leptodora kindti</u>				0.2		
<u>Cyclops viridis</u>	42.0	46.4	40.5	19.5	48.8	31.2
Chironomidae (P)			1.5	0.1	0.1	
<u>Macropelopia</u> sp. (P)			0.9			
<u>Procladius</u> sp. (P)				*		
<u>Aspectrotanypus</u> sp. (P)				*		
<u>Psectrotanypus</u> sp. (P)				*		
Pentaneurini (P)			0.6			
<u>Arctopelopia</u> sp. (P)				0.2		
<u>Rheopelopia</u> sp. (P)				*		
Arachnidae (Ar)		0.4				
Vegetation		0.4				

P=pupae   Ar=Aerial food source   *=< 0.1%

<u>Benthic Arctic Charr Benthic 1987.</u>
<u>Occurrence.</u>

	J/F	M/A	M/J	J/A	S/O	N/D
<u>Potamopyrgus jenkinsi</u>					2.0	
<u>Pisidium obtusale</u>	58.3	64.3	35.3	42.3	34.0	20.7
<u>G. lacustris</u>			5.9			
<u>Asellus aquaticus</u>		7.1	5.9			
<u>L. inermis</u>				4.6		
<u>L. fusca</u>					4.0	
<u>Capnia</u> sp.		7.1				
Coleoptera				2.3		
Trichoptera			5.9	2.3		

	J/F	M/A	M/J	J/A	S/O	N.D
Polycentropus sp.		7.1		4.0		
P. kingi				2.3		
Holocentropus dubius			5.9			3.5
Ceratopogonidae				4.6		
Chironomidae	66.7	78.6	41.2	50.0	38.0	20.7
Polycelis sp.						3.5
Erpobdella octoculata				2.3		
Daphniidae	8.3			2.3		
Daphnia hyalina				27.3		
Eurycercus lamellatus		21.4	5.9	52.5	36.0	6.9
Bythotrephes longimanus				22.7	2.0	
Leptodora kindti				6.8		
Cyclops viridis	75.0	85.7	35.3	59.1	56.0	10.3
Chironomidae (P)			5.9	9.1	2.0	
Macropelopia sp. (P)			11.8			
Procladius sp. (P)				2.3		
Psectrotanypus sp. (P)				2.3		
Pentaneurini (P)			5.9			
Arctopelopia sp. (P)				15.9		
Rheopelopia sp. (P)				2.3		
Arachnidae (Ar)		7.1				
Vegetation		7.1				

P=pupae   Ar=Aerial food source   *=< 0.1%

Pelagic Arctic Charr at Littoral Sites 1987. Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			96.8		48.5	
Bosmina coregoni					4.0	
Bythotrephes longimanus			3.2		47.5	

P=pupae   Ar=Aerial food source   *=< 0.1%

Pelagic Arctic Charr at Littoral Sites 1987 . Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			98.9		68.6	
Bosmina coregoni					7.9	
Bythotrephes longimanus			1.1		23.5	

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr at Littoral Sites 1987. Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			100		100	
Bosmina coregoni					100	
Bythotrephes longimanus			66.7		100	

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr at Fish Farms 1987. Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina				75.0		
Bythotrephes longimanus				25.0	100	100

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr at Fish Farms 1987. Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina				73.2		
Bythotrephes longimanus				26.8	100	

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr at Fish Farms 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina				100		
Bythotrephes longimanus				100	50	

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr Pelagic.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			99.1		98.3	
Bythotrephes longimanus			*		1.7	

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr Pelagic 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			99.1		99.9	
Bythotrephes longimanus			0.9		0.1	

P=pupae Ar=Aerial food source *=< 0.1%

Pelagic Arctic Charr Pelagic 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			100		50.0	
Bythotrephes longimanus			100		50.0	

P=pupae Ar=Aerial food source *=< 0.1%

Perch Littoral 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
G. lacustris			1.2	0.7		
Asellus aquaticus				0.3		
Plecoptera			0.2			
Capnia sp.			0.2			
Ephemeroptera			0.4	*		
Caenis horaria			*			
Ephemerella ignita			13.2	0.2		
Coleoptera			0.4			
Dytiscinae				*		
Polycentropus sp.				*		
Chironomidae				0.2		
Daphniidae			*	0.5	3.7	
Daphnia hyalina			3.5	7.8	14.0	
Bosmina coregoni				0.1	1.6	
Eurycercus lamellatus			0.7			
Polyphemus pediculus			0.2			
Bythotrephes longimanus			1.9	39.1	13.6	
Cyclops strenuus abyssorum					*	
Chironomidae (P)			0.3			
Tanypodinae (P)			*			
Arctopelopia sp. (P)			*			
Chironomus sp. (P)				*		
Trichoptera (P)				0.3	0.5	
Fish			78.1	17.8	65.9	
Stickleback				28.7		
Diptera (Ar)					0.3	
Trichoptera (Ar)					0.3	
Vegetation				*		
Stones				4.0		

P=pupae   Ar=Aerial food source   *=< 0.1%

Perch Littoral 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
G. lacustris			0.2	*		
Asellus aquaticus				*		
Plecoptera			*			
Capnia sp.			*			
Ephemeroptera			*	*		

	J/F	M/A	M/J	J/A	S/O	N/D
Caenis horaria			*			
Ephemerella ignita			5.6	*		
Coleoptera			*			
Dytiscinae				*		
Polycentropus sp.				*		
Chironomidae				*		
Daphniidae			1.1	1.0	9.4	
Daphnia hyalina			78.7	57.1	55.0	
Bosmina coregoni				0.9	9.9	
Eurycercus lamellatus			1.6			
Polyphemus pediculus			0.1			
Bythotrephes longimanus			12.0	77.8	25.4	
Cyclops strenuus abyssorum					0.2	
Chironomidae (P)			0.1			
Tanypodinae (P)			*			
Arctopelopia sp. (P)			*			
Chironomus sp. (P)					*	
Trichoptera (P)					*	
Fish			0.2	*	0.1	
Stickleback				*		
Diptera (Ar)					*	
Trichoptera (Ar)					*	
Vegetation				*		
Stones				*		

P=pupae   Ar=Aerial food source   *=< 0.1%

Perch Littoral 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
G. lacustris			25.0	4.0		
Asellus aquaticus				2.0		
Plecoptera			6.3			
Capnia sp.			6.3			
Ephemeroptera			12.5	2.0		
Caenis horaria			6.3			
Ephemerella ignita			31.3	2.0		
Coleoptera			6.3			
Dytiscinae				2.0		
Polycentropus sp.				2.0		
Chironomidae				2.0		
Daphniidae			6.3	4.0	6.5	

	J/F	M/A	M/J	J/A	S/O	N/D
Daphnia hyalina			56.3	42.0	45.2	
Bosmina coregoni				2.0	16.1	
Eurycercus lamellatus			12.5			
Polyphemus pediculus			6.3			
Bythotrephes longimanus			37.5	52.0	48.4	
Cyclops strenuus abyssorum					3.2	
Chironomidae (P)			12.5			
Tanypodinae (P)			6.3			
Arctopelopia sp. (P)			6.3			
Chironomus sp. (P)				2.0		
Trichoptera (P)				4.0		
Fish			12.5	14.0	29.0	
Stickleback				16.0		
Diptera (Ar)					3.2	
Trichoptera (Ar)					3.2	
Vegetation				2.0		
Stones				2.0		

P=pupae Ar=Aerial food source *=< 0.1%

Perch at Fish Farms 1987.
Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra				0.2		
Potamopyrgus jenkinsi			0.5	0.4		
G. lacustris			3.3	0.4		
Plecoptera			0.2			
L. hippopus				*		
Ephemera danica				*		
Caenis horaria						
Ephemerella ignita				0.3		
Esolus parallelepipedus (A)				*		
Hygrobiidae			1.8			
Dytiscinae				0.7		
Colymbetes						
Trichoptera			0.8	0.6		
Rhyacophilla sp.				0.2		
Polycentropus sp.				0.2		
Chironomidae			0.7	1.5		
Erpobdella octoculata				0.7		
Daphniidae				0.9	10.6	
Daphnia hyalina				0.5		

	J/F	M/A	M/J	J/A	S/O	N/D
Bosmina coregoni			0.2			
Eurycercus lamellatus				*		
Chironomidae (P)			5.3	4.0	12.8	
Tanypodinae (P)				0.4		
Macropelopia sp. (P)				7.2		
Ephemeroptera (P)			1.8			
Fish			75.4	12.5	34.0	
Stickleback				6.5		
Lepidoptera (Ar)				0.2		
Trichoptera (Ar)				0.4		
Vegetation			9.5	3.8		
Sweet corn				5.9		
Earthworms					42.6	

P=pupae Ar=Aerial food source *=< 0.1%

Perch at Fish Farms 1987.
Numbers.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra				0.1		
Potamopyrgus jenkinsi			1.4	0.6		
G. lacustris			9.7	0.3		
Plecoptera			0.7			
L. hippopus				0.4		
Ephemera danica				0.1		
Ephemerella ignita				0.5		
Esolus parallelepipedus (A)				0.1		
Hygrobiidae			3.5			
Dytiscinae				1.3		
Trichoptera			1.4	0.3		
Rhyacophilla sp.				0.1		
Polycentropus sp.				0.1		
Chironomidae			4.2	6.1		
Erpobdella octoculata				0.1		
Daphniidae				47.6	97.0	
Daphnia hyalina				27.9		
Bosmina coregoni			9.1			
Eurycercus lamellatus				0.3		
Chironomidae (P)			30.8	6.8	2.7	
Tanypodinae (P)				1.4		
Macropelopia sp. (P)				30.2		
Ephemeroptera (P)			2.1			

	J/F	M/A	M/J	J/A	S/O	N/D
Fish			7.8	0.8	0.3	
Stickleback				1.9		
Lepidoptera (Ar)				0.1		
Trichoptera (Ar)				0.5		
Vegetation			FP	0.3		
Sweet corn				0.4		
Earthworms					1.1	

P=pupae Ar=Aerial food source *=< 0.1% FP=Food Present

Perch at Fish Farms 1987.
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Lymnaea peregra				3.6		
Potamopyrgus jenkinsi			12.5	10.7		
G. lacustris			37.5	7.1		
Plecoptera			6.3			
L. hippopus				3.6		
Ephemera danica				3.6		
Ephemerella ignita				7.1		
Esolus parallelepipedus (A)				3.6		
Hygrobiidae			6.3			
Dytiscinae				14.3		
Trichoptera			12.5	7.1		
Rhyacophilla sp.				3.6		
Polycentropus sp.				3.6		
Chironomidae			12.5	25.0		
Erpobdella octoculata				3.6		
Daphniidae				7.1		
Daphnia hyalina				6.3		
Bosmina coregoni			6.3			
Eurycercus lamellatus				3.6		
Chironomidae (P)			50.0	21.4	20.0	
Tanypodinae (P)				3.6		
Macropelopia sp. (P)				3.6		
Ephemeroptera (P)			6.3			
Fish			37.5	17.9	20.0	
Stickleback				10.7		
Lepidoptera (Ar)				3.6		
Trichoptera (Ar)				3.6		
Vegetation			12.5	7.1		
Sweet corn				10.7		
Earthworms					20.0	

P=pupae Ar=Aerial food source *=< 0.1%

Juvenile Atlantic Salmon at Littoral Sites 1987.

	J/F	M/A	M/J	J/A	S/O	N/D
A. aterrimus						80.0
Lepidostoma hirtum						20.0

P=pupae Ar=Aerial food source *=< 0.1%

Juvenile Atlantic Salmon at Littoral Sites 1987 Number.

	J/F	M/A	M/J	J/A	S/O	N/D
A. aterrimus						88.9
Lepidostoma hirtum						11.1

P=pupae Ar=Aerial food source *=< 0.1%

Juvenile Atlantic Salmon at Littoral Sites 1987 Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
A. aterrimus						50.0
Lepidostoma hirtum						25.0

P=pupae Ar=Aerial food source *=< 0.1%

Juvenile Atlantic Salmon at Fish Farms 1987. Volume.

	J/F	M/A	M/J	J/A	S/O	N/D
Potamopyrgus jenkinsi						94.7
Colymbetes						5.3
Limnephilus sp.				10.3		
Daphniidae					79.3	
Daphnia hyalina				19.5	8.6	
Bythotrephes longimanus				29.9	8.6	
Chironomidae (P)				10.3	3.4	
Hemiptera (Ar)				2.3		
Maggots				27.5		

P=pupae Ar=Aerial food source *=< 0.1%

Juvenile Atlantic Salmon at Fish Farms 1987.
Number.

	J/F	M/A	M/J	J/A	S/O	N/D
Potamopyrgus jenkinsi						97.7
Colymbetes						2.3
Limnephilus sp.				0.1		
Daphniidae					79.1	
Daphnia hyalina				36.3	15.3	
Bythotrephes longimanus				60.8	5.4	
Chironomidae (P)				1.7	0.2	
Hemiptera (Ar)				0.1		
Lepidoptera (Ar)						
Maggots				0.9		

P=pupae Ar=Aerial food source *=< 0.1%

Juvenile Salmon at Fish Farms 1987 .
Occurrence.

	J/F	M/A	M/J	J/A	S/O	N/D
Potamopyrgus jenkinsi						25.0
Colymbetes						25.0
Limnephilus sp.				14.3		
Daphniidae					60.0	
Daphnia hyalina				14.3	20.0	
Bythotrephes longimanus				42.9	20.0	
Chironomidae (P)				14.3	20.0	
Hemiptera (Ar)				14.3		
Maggots				14.3		

P=pupae Ar=Aerial food source *=< 0.1%

Appendix 2. Percentage composition of the monthly food intake of each food item by volume, number and occurrence brown trout and rainbow trout caught in angling competitions in 1987.

Volume.

	B/A	B/M	B/J	R/A	R/M	R/J
Lymnaea peregra	7.9	30.9	17.9	10.2		
Physa fontinalis		3.0	2.3			
P. contortus	*	0.2				
Valvata piscinalis	1.7	0.2		4.7		
Potamopyrgus jenkinsi	0.7	0.3				
Ancylus fluviatilis	1.9	1.8				
Pisidium obtusale	0.1	0.2				
Gammarus pulex		1.0	1.7			0.2
G. lacustris	1.1	1.8				
Asellus aquaticus	15.5	6.7	37.5	15.4	0.2	
Plecoptera	*	0.5		*	0.2	
Nemoura sp.		*	0.3			
N. cambrica		0.2				
N. avicularis	0.5	*				
Leuctra sp.	0.2					*
L. fusca		*			0.1	
C. atra	1.3	0.9				
Isoperla grammatica		*				
Diura bicaudata		0.4				
Chloroperla tripunctata		0.4			0.2	
Ephemeroptera	0.2	0.5	0.1		1.6	
Ephemera danica	0.3	*	3.3			61.3
Ephemerella ignita		*	0.2			
Ecdyonurus sp.	0.1	0.3				
E. dispar		0.6				
Rhithrogena semicolorata			0.1	1.0		
Baetis sp.	*	0.3	0.3			
Potamonectes depressus (A)		0.2				
P. grisseostriatus (A)	*					
H. fulvus (A)				0.1		
Esolus parallelepipedus (A)		*				
Curculionidae (A)				*		
Dryopidae (A)	*					
Coleoptera	0.1	0.1				
Hygrobiidae	*					
Dytiscinae	*					*
Colymbetes	3.2	0.4		0.2		

	B/A	B/M	B/J	R/A	R/M	R/J
Elmis aenea				*		
Limnius volkmari	0.2			*		
Trichoptera	1.7	0.6		*		0.2
Leptoceridae	*	*				
A. aterrimus		*				
A. cinereus	*	0.3				
A. bilineatus		1.1	1.2			
Ceraclea dissimilis		*				
M. azurea		*				
Limnephilus sp.	1.7	1.7				
L. borealis	6.2	0.5				
L. lunatus	0.8	*			1.3	
L. rhombicus					0.1	
Anabolia nervosa	0.3	12.5			1.6	
Potamophyllax latipennis			0.2			
Polycentropus sp.		*				
P. kingi		*	0.6		0.2	
Sericostoma personatum	2.9	2.5	1.2			
Lepidostoma hirtum	0.5	3.4				
Beraeodes minutus	0.1					
P. varia	1.8					
Sialis lutaria	11.9	0.7				
Ceratopogonidae					0.1	0.2
Empididae					0.9	
Chironomidae	3.0	0.6	0.1	0.7	0.3	
Simuliidae			*			0.2
Corixa sp. (A)					1.7	
Corixidae	*					
Hydracarina						*
Daphnia hyalina		0.2	0.7	0.4	0.56	0.1
Bosmina coregoni					*	
Bythotrephes longimanus		*	0.4		0.1	
Cyclops abyssorum					*	
Chironomidae (P)	14.5	6.7		1.6	0.3	*
Tanypodinae (P)	*			*	0.1	*
Procladius sp. (P)		0.3			0.1	*
Pentaneurini (P)					0.7	
Arctopelopia sp. (P)		1.6				
Diamesinae sp. (P)		*				
Orthocladius sp. (P)		5.5		0.2	0.9	0.2
Cricotopus sp. (P)		2.2				
Isocladius sylvesteris (P)		0.2				
Paratrichocladius sp. (P)		1.3				
Chironomus sp. (P)		0.2			3.0	0.5

	B/A	B/M	B/J	R/A	R/M	R/J
Microtendipes sp. (P)		0.1			1.2	
Phaenospectra sp.(P)		*				
Sergentia sp. (P)		0.2				
Paratanytarsus sp. (P)		*				
Tanytarsus sp. (P)	0.2	*		*		
Trichoptera (P)	1.8	0.7	0.3	0.1	0.3	
Ephemeroptera (P)	0.3	1.1	23.1		2.8	
Exuviae					2.7	
Fish	1.7			41.1		
Diptera (Ar)	2.8	0.8		2.2	5.6	4.5
Psocoptera (Ar)	0.4					*
Coleoptera (Ar)	1.6	*	2.2	0.9		0.9
Hemiptera (Ar)	0.3				0.1	2.0
Ephemeroptera (Ar)	0.1	0.1	1.5			7.4
Plecoptera (Ar)	0.7	*			2.8	
Hymenoptera (Ar)	2.4		2.0	4.1		3.4
Trichoptera (Ar)	0.1	*	1.8		2.0	1.9
Arachnidae (Ar)	0.3	*		*		
Vegetation		0.4		1.7	10.0	16.4
Stones					1.1	
Earthworms	3.8	1.8		2.9	23.9	
Maggots	0.7	2.2		13.0	26.6	

P=pupae   Ar=Aerial food source   *=< 0.1%   B=Brown Trout
R=Rainbow Trout   A=April   M=May   J=June

Number.

	B/A	B/M	B/J	R/A	R/M	R/J
Lymnaea peregra	2.3	7.3	8.1	5.3		
Physa fontinalis		0.9	1.7			
P. contortus	*	0.2				
Valvata piscinalis	0.8	0.1		4.3		
Potamopyrgus jenkinsi	1.1	0.4				
Ancylus fluviatilis	1.4	2.5				
Pisidium obtusale	0.4	0.6				
Gammarus pulex		0.6	1.3			0.3
G. lacustris	0.8	1.2				
Asellus aquaticus	10.2	5.3	21.7	23.6	*	
Plecoptera	0.1	7.0		0.2	*	
Nemoura sp.		*	0.4			
N. cambrica		0.2				
N. avicularis	0.6	*				

	B/A	B/M	B/J	R/A	R/M	R/J
Leuctra sp.	0.3					0.3
L. fusca		*			*	
C. atra	2.0	7.7				
Isoperla grammatica		*				
Diura bicaudata		*				
Chloroperla tripunctata		0.2			*	
Ephemeroptera	0.5	0.3			0.4	
Ephemera danica	0.2	*	0.9			47.8
Ephemerella ignita		*	0.4			
Ecdyonurus sp.	0.1	0.2				
E. dispar		0.2				
Rhithrogena semicolorata			0.2	0.6		
Baetis sp.	0.1	0.2	0.2			
Potamonectes depressus (A)		*				
P. grisseostriatus (A)	*					
H. fulvus (A)				0.2		
Esolus parallelepipedus (A)		*				
Curculionidae (A)				0.4		
Dryopidae (A)	*					
Coleoptera	0.2	*				
Hygrobiidae	*					
Dytiscinae	*					0.3
Colymbetes	1.7	0.3		0.2		
Elmis aenea				0.3		
Limnius volkmari	0.4			0.2		
Trichoptera	0.9	0.2		0.2		0.5
Leptoceridae	*	0.1				
A. aterrimus		*				
A. cinereus	*	0.1				
A. bilineatus		1.0	0.4			
Ceraclea dissimilis		*				
M. azurea		*				
Limnephilus sp.	0.4	0.2				
L. borealis	2.8	0.3				
L. lunatus	0.6	*			0.1	
L. rhombicus					*	
Anabolia nervosa	0.4	4.0			0.1	
Potamophyllax latipennis			*			
Polycentropus sp.		*				
P. kingi		*	0.4		0.1	
Sericostoma personatum	0.8	0.6	0.2			
Lepidostoma hirtum	0.14	4.3				
P. varia	0.6					
Sialis lutaria	2.7	0.2				

	B/A	B/M	B/J	R/A	R/M	R/J
Ceratopogonidae					*	0.5
Empididae					*	
Chironomidae	5.8	2.8	0.2	4.7	0.2	
Simuliidae			*			0.1
<u>Corixa</u> sp. (A)					0.7	
Corixidae	*					
Hydracarina						0.5
<u>Daphnia hyalina</u>		9.9	40.3	36.4	82.2	12.5
<u>Bosmina coregoni</u>					0.5	
<u>Bythotrephes longimanus</u>		0.8	11.1		0.9	
<u>Cyclops abyssorum</u>					0.5	
Chironomidae (P)	33.1	16.9		4.9	0.2	0.3
Tanypodinae (P)	*			0.2	*	0.3
<u>Procladius</u> sp. (P)		0.9			*	0.3
Pentaneurini (P)					0.4	
<u>Arctopelopia</u> sp. (P)		2.6				
<u>Diamesinae</u> sp.(P)		*				
<u>Orthocladius</u> sp. (P)		16.4		0.8	0.7	0.8
<u>Cricotopus</u> sp. (P)		8.3				
<u>Isocladius sylvesteris</u> (P)			0.6			
<u>Paratrichocladius</u> sp. (P)		3.1				
<u>Chironomus</u> sp. (P)		0.4			1.7	1.5
<u>Microtendipes</u> sp. (P)		0.3			1.1	
<u>Phaenospectra</u> sp.(P)		0.1				
<u>Sergentia</u> sp. (P)		0.5				
<u>Paratanytarsus</u> sp. (P)		*				
<u>Tanytarsus</u> sp. (P)	0.8	0.1		0.6		
Trichoptera (P)	7.0	0.6	0.4	0.2	*	
Ephemeroptera (P)	0.5	0.3	7.5		0.9	
Exuviae					2.0	
Fish	0.1			1.2		
Diptera (Ar)	6.9	2.0		0.3	3.9	6.6
Pscoptera (Ar)	2.3					0.3
Coleoptera (Ar)	2.0	*	0.6	0.8		0.3
Hemiptera (Ar)	0.5				*	4.3
Ephemeroptera (Ar)	0.2	*	0.6			6.1
Plecoptera (Ar)	0.6	*			1.0	
Hymenoptera (Ar)	6.1		0.2	0.4		1.8
Trichoptera (Ar)	*	*	1.7		0.3	1.3
Arachnidae (Ar)	0.7	*		0.2		
Vegetation		0.2		*	0.4	13.7
Stones					*	
Earthworms	0.2	*		0.2	*	
Maggots	0.2	0.2		5.3	0.9	

P=pupae   Ar=Aerial food source   *=< 0.1%

Occurrence.

	B/A	B/M	B/J	R/A	R/M	R/J
Lymnaea peregra	34.8	64.6	33.3	50.0		
Physa fontinalis		7.7	33.3			
P. contortus	4.3	7.7				
Valvata piscinalis	4.3	4.6		12.5		
Potamopyrgus jenkinsi	17.4	12.3				
Ancylus fluviatilis	4.3	6.2				
Pisidium obtusale	4.3	6.2				
Gammarus pulex		7.7	33.3			11.1
G. lacustris	17.4	23.1				
Asellus aquaticus	39.1	33.9	50.0	37.5	5.3	
Plecoptera	8.7	12.3		12.5	5.3	
Nemoura sp.		1.5	16.7			
N. cambrica		3.1				
N. avicularis	8.7	1.5				
Leuctra sp.	8.7					11.1
L. fusca		1.5			5.3	
C. atra	17.4	7.7				
Isoperla grammatica		1.5				
Diura bicaudata		4.6				
Chloroperla tripunctata		3.1			10.5	
Ephemeroptera	8.7	13.9	16.7		5.3	
Ephemera danica	4.3	4.6	16.7			100
Ephemerella ignita		1.5	16.7			
Ecdyonurus sp.	8.7	12.3				
E. dispar		6.2				
Rhithrogena semicolorata			1.5	16.7		
Baetis sp.	4.3	1.5	16.7			
Potamonectes depressus (A)		3.1				
P. grisseostriatus (A)	4.3					
H. fulvus (A)				12.5		
Esolus parallelepipedus (A)		3.1				
Curculionidae (A)				12.5		
Dryopidae (A)	4.3					
Coleoptera	4.3	1.5				
Hygrobiidae	4.3					
Dytiscinae	4.3					11.1
Colymbetes	52.2	10.7		12.5		
Elmis aenea				12.5		
Limnius volkmari	8.7			12.5		

	B/A	B/M	B/J	R/A	R/M	R/J
Trichoptera	13.0	6.2		12.5		11.1
Leptoceridae	4.3	6.2				
A. aterrimus		1.5				
A. cinereus	4.3	1.5				
A. bilineatus		15.4	33.3			
Ceraclea dissimilis		1.5				
M. azurea		1.5				
Limnephilus sp.	17.4	4.6				
L. borealis	13.0	6.2				
L. lunatus	17.4	1.5			5.3	
L. rhombicus					5.3	
Anabolia nervosa	13.0	30.8			5.3	
Potamophylax latipennis			3.1			
Polycentropus sp.		3.1				
P. kingi		3.1	16.7		5.3	
Sericostoma personatum	13.0	16.9	16.7			
Lepidostoma hirtum	30.4	29.6				
Beraeodes minutus	4.3					
P. varia	8.7					
Sialis lutaria	17.4	12.3				
Ceratopogonidae					5.3	22.2
Empididae					5.3	
Chironomidae	21.7	23.1	16.7	12.5	10.5	
Simuliidae			1.5			5.3
Corixa sp. (A)					5.3	
Corixidae	4.3					
Hydracarina						11.1
Daphnia hyalina		3.1	16.7	12.5	36.8	22.2
Bosmina coregoni					5.3	
Bythotrephes longimanus		3.1	16.7		10.5	
Cyclops abyssorum					5.3	
Cyclops viridis						
Chironomidae (P)	30.4	35.4		25.0	5.3	11.1
Tanypodinae (P)	4.3			12.5	5.3	11.1
Procladius sp. (P)		15.4			5.3	11.1
Pentaneurini (P)					5.3	
Arctopelopia sp. (P)		16.9				
Diamesinae sp. (P)		1.5				
Orthocladius sp. (P)		13.9		12.5	10.5	22.2
Cricotopus sp. (P)		9.2				
Isocladius sylvestaria (P)			16.7			
Paratrichocladius sp. (P)		12.3				
Chironomus sp. (P)		7.7			42.1	33.3
Microtendipes sp. (P)		4.6			10.5	

	B/A	B/M	B/J	R/A	R/M	R/J
<u>Phaenospectra</u> sp. (P)		1.5				
<u>Sergentia</u> sp. (P)		4.6				
<u>Paratanytarsus</u> sp. (P)		1.5				
<u>Tanytarsus</u> sp. (P)	8.7	3.1		12.5		
Trichoptera (P)	34.8	9.2	16.7	12.5	5.3	
Ephemeroptera (P)	4.3	1.5	33.3		10.5	
Exuviae					31.6	
Fish	4.3			25.0		
Diptera (Ar)	56.5	18.5		37.5	21.0	44.4
Pscoptera (Ar)	17.4					11.1
Coleoptera (Ar)	65.2	1.5	16.7	37.5		11.1
Hemiptera (Ar)	17.4				5.3	55.6
Ephemeroptera (Ar)	4.3	1.5	50.0			44.4
Plecoptera (Ar)	21.7	1.5			15.8	
Hymenoptera (Ar)	69.6		33.3	25.0		33.3
Trichoptera (Ar)	4.3	3.1	33.3		15.8	44.4
Arachnidae (Ar)	8.7	1.5		12.5		
Vegetation		6.2		25.0	15.8	22.2
Stones					5.3	
Earthworms	8.7	1.5		12.5	5.3	
Maggots	8.7	1.5		25.0	15.8	

P=pupae Ar=Aerial food source *=< 0.1%
B=Brown Trout, R=Rainbow trout, A=April, M=May, J=June.

Appendix 3. The diet of brown trout and rainbow trout caught in the 1988 gill netting survey, expressed as percentage volume, number and occurrence.

Brown Trout at Littoral Sites 1988.
Volume.

	Mar	May	Jul	Sep
Lymnaea peregra	1.2			
Physa fontinalis	0.5			
Planorbus sp.	0.4		0.1	
P. contortus		*		
Potamopyrgus jenkinsi	15.3	1.5	0.5	9.7
Ancylus fluviatilis	0.1			
Pisidium obtusale	0.2	*		
G. lacustris	9.7	1.5	0.3	1.2
Plecoptera	1.5	0.4		
Taeniopterygidae	0.3			
Brachyptera risi	8.6			
Protonemura	0.3			
Nemoura sp.	1.0	0.1		
N. cambrica	0.1			
N. avicularis	0.1			
Leuctra sp.			0.2	2.7
L. fusca	0.1	0.1	0.2	
L. hippopus	0.1			
Diura bicaudata		0.5		
Ephemeroptera	1.6			
Ecdyonurus sp.	0.2			
Rhithrogena semicolorata		0.7		
Baetis sp.	4.5			
B. rhodani	3.9	0.1	1.0	
Coleoptera (A)	0.1			
Colymbetes sp.	0.8	0.1	0.1	1.5
Trichoptera	3.9			
Leptoceridae	0.8			
A. aterrimus	0.2	7.8		
A. cinereus			0.2	
A. bilineatus	0.1			
Mystacides azurea		0.5		
Oecetis testacea	0.3			
Limnephilus sp.	5.1	7.3	1.4	
L. politus	0.5			
Anabolia nervosa	7.1	1.1		
Plectronemia conspersa				1.2

	Mar	May	Jul	Sep
Polycentropus sp.	1.0			
P. kingi	0.7	0.1		
Sericostoma personatum	4.1	0.6		
Lepidostoma hirtum	2.4	1.9		4.2
Hydroptila tineoides	0.1			
Sialis lutaria	0.7			
Empididae	4.3			
Chironomidae	4.3	2.3		
Chironomus sp.			1.1	2.3
Simuliidae		5.1		0.2
Hydracarina	*			
Daphniidae		0.2	2.4	9.3
Daphnia hyalina		0.3	38.9	
Polyphemus pediculus			8.2	
Bythotrephes longimanus			37.9	3.9
Cyclops viridis	*			
Chironomidae (P)		8.1		
Macropelopia sp. (P)			4.0	
Chironomus sp. (P)	53.4			
Trichoptera (P)			3.0	7.7
Fish				38.6
Diptera (Ar)				2.7
Coleoptera (Ar)			0.2	
Hemiptera (Ar)				0.4
Vegetation	3.2		0.4	1.5
Stones	0.7	0.8		
Maggots	4.6	11.3		13.1

P=pupae   Ar=Aerial food source *=< 0.1%

Brown Trout at Littoral Sites 1988.
Number.

	Mar	May	Jul	Sep
Lymnaea peregra	1.4			
Physa fontinalis	0.6			
Planorbus sp.	0.8		*	
P. contortus		*		
Potamopyrgus jenkinsi	36.8	1.6	*	2.8
Ancylus fluviatilis	0.1			
Pisidium obtusale	0.5	*		
G. lacustris	4.4	0.5	*	0.2
Plecoptera	1.6	0.3		
Taeniopterygidae	0.3			

	Mar	May	Jul	Sep
Brachyptera risi	6.5			
Protonemura	0.3			
Nemoura sp.	1.3	*		
N. cambrica	0.1			
N. avicularis	0.1			
Leuctra sp.			*	0.7
L. fusca	0.3	*	*	
L. hippopus	0.1			
Diura bicaudata		*		
Ephemeroptera	1.5			
Ecdyonurus sp.	0.1			
Rhithrogena semicolorata		0.6		
Baetis sp.	4.3			
B. rhodani	6.9	*	*	
Coleoptera (A)	0.1			
Colymbetes sp.	0.5	*	*	0.4
Trichoptera	3.6			
Leptoceridae	1.9			
A. aterrimus	0.1	4.0		
A. cinereus			*	
A. bilineatus	0.1			
Mystacides azurea		0.6		
Ocestris testacea	0.3			
Limnephilus sp.	1.5	0.1	*	
L. politus	0.1			
Anabolia nervosa	5.9	0.3		
Plectronemia conspersa				0.1
Polycentropus sp.	0.8			
P. kingi	0.3	*		
Sericostoma personatum	1.1	0.2		
Lepidostoma hirtum	1.6	1.4		1.0
Hydroptila tineoides	0.1			
Sialis lutaria	0.3			
Empididae	0.9			
Chironomidae	3.0	1.9		
Chironomus sp.			*	1.0
Simuliidae		2.3		*
Hydracarina	0.1			
Daphniidae		4.6	2.1	59.5
Daphnia hyalina		12.4	46.8	
Polyphemus pediculus			17.7	
Bythotrephes longimanus			33.2	31.1
Cyclops viridis	*			
Chironomidae (P)		10.3		

	Mar	May	Jul	Sep
Macropelopia sp. (P)			0.1	
Chironomus sp. (P)		58.5		
Trichoptera (P)			*	0.4
Fish				0.1
Diptera (Ar)				0.8
Coleoptera (Ar)			*	
Hemiptera (Ar)				0.1
Vegetation	4.5		*	1.0
Stones	0.9	0.1		
Maggots	1.6	1.7	0.8	

P=pupae   Ar=Aerial food source *=< 0.1%

Brown Trout at Littoral Sites 1988.
Occurrence.

	Mar	May	Jul	Sep
Lymnaea peregra	5.6			
Physa fontinalis	5.6			
Planorbus sp.	7.4		3.6	
P. contortus		2.1		
Potamopyrgus jenkinsi	33.3	10.6	14.3	17.7
Ancylus fluviatilis	1.9			
Pisidium obtusale	7.4	2.1		
G. lacustris	13.0	6.4	3.6	5.9
Plecoptera	14.8	6.4		
Taeniopterygidae	1.9			
Brachyptera risi	14.8			
Protonemura	1.9			
Nemoura sp.	11.1	2.1		
N. cambrica	1.9			
N. avicularis	1.9			
Leuctra sp.			3.6	5.9
L. fusca	3.7	2.1	3.6	
L. hippopus	1.9			
Diura bicaudata		2.1		
Ephemeroptera	5.6			
Ecdyonurus sp.	1.9			
Rhithrogena semicolorata		1.9		
Baetis sp.	1.9			
B. rhodani	16.7	2.1	7.1	
Coleoptera (A)	1.9			
Colymbetes sp.	7.4	2.1	3.6	5.9
Trichoptera	16.7			

	Mar	May	Jul	Sep
Leptoceridae	9.3			
A. aterrimus	1.9	27.7		
A. cinereus			7.1	
A. bilineatus	1.9			
Mystacides azurea		6.4		
Ocestris testacea	3.7			
Limnephilus sp.	13.0	4.3	10.7	
L. politus	1.9			
Anabolia nervosa	18.5	4.3		
Plectronemia conspersa				2.9
Polycentropus sp.	7.4			
P. kingi	3.7	2.1		
Sericostoma personatum	11.1	2.1		
Lepidostoma hirtum	9.3	4.3		11.8
Hydroptila tineoides	1.9			
Sialis lutaria	1.9			
Empididae	5.6			
Chironomidae	18.5	2.8		
Chironomus sp.			3.6	2.9
Simuliidae		11.1		7.1
Hydracarina	1.9			
Daphniidae		2.1	7.1	8.8
Daphnia hyalina		2.1	82.1	
Polyphemus pediculus			7.1	
Bythotrephes longimanus			75.0	2.9
Cyclops viridis	1.9			
Chironomidae (P)		10.6		
Macropelopia sp. (P)			7.1	
Chironomus sp. (P)		25.5		
Trichoptera (P)			17.9	5.9
Fish				2.9
Diptera (Ar)				5.9
Coleoptera (Ar)			3.6	
Hemiptera (Ar)				2.9
Vegetation	16.7		3.6	2.9
Stones	5.6	2.1		
Maggots	3.7	4.3		20.6

P=pupae Ar=Aerial food source *=< 0.1%

Brown Trout Fish Farms 1988.
Volume.

	Mar	May	Jul	Sep
Lymnaea peregra	35.8	3.5		
P. contortus		0.5		
Valvata piscinalis		0.5		
Potamopyrgus jenkinsi	14.0	0.6		
Pisidium obtusale	0.3	*		
N. avicularis	6.2		1.4	
B. rhodani	0.5			
Colymbetes sp.	4.4			
A. aterrimus	1.6	0.6		
Limnephilus sp.	6.2			
Anabolia nervosa	31.1			
Lepidostoma hirtum		0.1		
Chironomidae		0.4	1.4	
Erpobdella octoculata			1.7	
Daphnia hyalina			63.3	
Polyphemus pediculus			12.5	
Bythotrephes longimanus			7.1	100
Cyclops strenuus abyssorum			0.5	
Chironomus sp. (P)		10.5	1.0	
Trichoptera (P)			10.6	
Diptera (Ar)		0.4	0.5	
Fish farm food		83.2		

P=pupae   Ar=Aerial food source *=< 0.1%

Brown Trout Fish Farms 1988.
Number.

	Mar	May	Jul	Sep
Lymnaea peregra	8.9	3.6		
P. contortus		3.3		
Valvata piscinalis		1.5		
Potamopyrgus jenkinsi	59.7	7.8		
Pisidium obtusale	0.8	0.6		
N. avicularis	7.3		*	
B. rhodani	0.8			
Colymbetes sp.	2.4			
A. aterrimus	2.4	1.5		
Limnephilus sp.	5.6			
Anabolia nervosa	12.1			
Lepidostoma hirtum		0.3		

	Mar	May	Jul	Sep
Chironomidae		5.4	*	
Erpobdella octoculata			*	
Daphnia hyalina			82.0	
Polyphemus pediculus			12.4	
Bythotrephes longimanus			4.5	100
Cyclops strenuus abyssorum			0.5	
Chironomus sp. (P)		46.2	*	
Trichoptera (P)			0.3	
Diptera (Ar)		0.3	*	
Fish farm food		29.4		

P=pupae Ar=Aerial food source *=< 0.1%

Brown Trout Fish Farms 1988.
Occurrence

	Mar	May	Jul	Sep
Lymnaea peregra	66.7	20.0		
P. contortus		20.0		
Valvata piscinalis		20.0		
Potamopyrgus jenkinsi	100	40.0		
Pisidium obtusale	33.3	10.0		
N. avicularia	66.7		37.5	
B. rhodani	33.3			
Colymbetes sp.	66.7			
A. aterrimus	33.3	10.0		
Limnephilus sp.	66.7			
Anabolia nervosa	33.3			
Lepidostoma hirtum		10.0		
Chironomidae		10.0	12.5	
Erpobdella octoculata			12.5	
Daphnia hyalina			75.0	
Polyphemus pediculus			37.5	
Bythotrephes longimanus			62.5	100
Cyclops strenuus abyssorum			12.5	
Chironomus sp. (P)		80.0	12.5	
Trichoptera (P)			50.0	
Diptera (Ar)		10.0	12.5	
Fish farm food		20.0		

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout at Littoral Sites 1988.
Volume.

	Mar	May	Jul	Sep
Potamopyrgus jenkinsi	0.1	1.8		
Ancylus fluviatilis			8.6	
G. lacustris	0.1	0.6		
Baetis sp.			8.6	
A. aterrimus		0.9		
Lepidostoma hirtum	1.3			
Chironomidae	0.1			
Chironomidae (P)		1.8		
Chironomus sp. (P)		95.0		
Trichoptera (P)			8.6	
Diptera (Ar)			34.3	1.4
Coleoptera (Ar)			8.6	
Hymenoptera (Ar)				0.9
Caterpillar			8.6	
Fish farm food	53.4			97.2
Vegetation	24.3		22.9	0.5
Stones	5.9			
Cigarette	2.3			
Maggots	12.5			

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout at Littoral Sites 1988.
Number.

	Mar	May	Jul	Sep
Potamopyrgus jenkinsi	3.3	4.0		
Ancylus fluviatilis			8.0	
G. lacustris	0.5	1.0		
Baetis sp.			8.0	
A. aterrimus		1.0		
Lepidostoma hirtum	2.7			
Chironomidae	4.3			
Chironomidae (P)		0.5		
Chironomus sp. (P)		88.9		
Trichoptera (P)			12.0	
Diptera (Ar)			48.0	45.3
Coleoptera (Ar)			8.0	
Hymenoptera (Ar)				17.9
Caterpillar			4.0	
Fish farm food	34.8		35.6	

	Mar	May	Jul	Sep
Vegetation	9.8		12.0	1.2
Stones	9.2			
Cigarette	0.5			
Maggots	34.8			

P=pupae   Ar=Aerial food source   *=< 0.1%

Rainbow Trout at Littoral Sites 1988.
Occurrence.

	Mar	May	Jul	Sep
Potamopyrgus jenkinsi	20.0	33.3		
Ancylus fluviatillis			25.0	
G. lacustris	10.0	33.3		
Baetis sp.			25.0	
Athripsodes sp.		33.3		
Lepidostoma hirtum	10.0			
Chironomidae	10.0			
Chironomidae (P)		33.3		
Chironomus sp. (P)		66.7		
Trichoptera (P)			25.0	
Diptera (Ar)			25.0	42.9
Coleoptera (Ar)			25.0	
Hymenoptera (Ar)				14.3
Caterpillar			25.0	
Fish farm food	50.0		42.9	
Vegetation	40.0	25.0	14.3	
Stones	30.0			
Cigarette	10.0			
Maggots	10.0			

P=pupae   Ar=Aerial food source   *=< 0.1%

Rainbow Trout at Fish Farms 1988.
Volume.

	Mar	May	Jul	Sep
Lymnaea peregra				1.1
P. contortus				*
Valvata piscinalis				0.1
Potamopyrgus jenkinsi	0.7			3.9
Pisidium obtusale				*
G. lacustris	0.2			*

	Mar	May	Jul	Sep
Ephemerella ignita			0.4	
Baetis sp.			0.2	
A. aterrimus	0.1			
Limnephilus sp.				1.5
Chironomidae			0.1	
Chironomus sp.			1.5	
Erpobdella octoculata			0.4	
Daphnia hyalina				0.1
Bythotrephes longimanus				0.2
Cyclops strenuus abyssorum				*
Cyclops viridis				*
Chironomus sp. (P)		1.0		
Polypedilum sp. (P)			0.4	
Trichoptera (P)			3.3	*
Stickleback	39.3			
Diptera (Ar)				0.6
Hymenoptera (Ar)				0.3
Fish farm food	59.6	99.0	93.1	90.2
Vegetation			0.3	2.0
Maggots				0.3

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout at Fish Farms 1988.
Number.

	Mar	May	Jul	Sep
Lymnaea peregra				1.8
P. contortus				0.4
Valvata piscinalis				0.5
Potamopyrgus jenkinsi	25.0			18.1
Pisidium obtusale				*
G. lacustris	3.1			*
Ephemerella ignita			3.9	
Baetis sp.			1.2	
A. aterrimus	3.1			
Limnephilus sp.				1.6
Chironomidae			27.1	
Erpobdella octoculata			0.4	
Daphnia hyalina				15.2
Bythotrephes longimanus				20.9
Cyclops strenuus abyssorum				20.9

	Mar	May	Jul	Sep
Cyclops viridis				1.5
Chironomus sp. (P)		26.2		
Polypedilum sp. (P)			5.8	
Trichoptera (P)			30.6	*
Stickleback	15.6			
Diptera (Ar)				5.2
Hymenoptera (Ar)				1.6
Fish farm food	53.1	73.8	27.1	9.4
Vegetation			1.9	1.6
Maggots				0.5

P=pupae Ar=Aerial food source *=< 0.1%

Rainbow Trout at Fish Farms 1988.
Occurrence.

	Mar	May	Jul	Sep
Lymnaea peregra				30.0
P. contortus				20.0
Valvata piscinalis				10.0
Potamopyrgus jenkinsi	33.3			50,0
Pisidium obtusale				10.0
G. lacustris	16.7			10.0
Ephemerella ignita			22.2	
Baetis sp.			11.1	
A. aterrimus	16.7			
Limnephilus sp.				20.0
Chironomidae			11.1	
Chironomus sp.			11.1	
Erpobdella octoculata			11.1	
Daphnia hyalina				10.0
Bythotrephes longimanus				10.0
Cyclops strenuus abyssorum				10.0
Cyclops viridis				10.0
Chironomus sp. (P)		40.0		
Polypedilum sp. (P)			11.1	
Trichoptera (P)			55.6	10.0
Stickleback	16.7			
Diptera (Ar)				30.0
Hymenoptera (Ar)				30.0
Fish farm food	33.3	60.0	44.4	10.0
Vegetation			11.1	30.0
Maggots				10.0

P=pupae Ar=Aerial food source *=< 0.1%

Appendix 4 **Detailed diet description of brown trout and rainbow trout in the pond experiment expressed as percent volume, number and occurrence.**

Stocked Brown Trout Pond A
Volume.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra				0.7		4.0	0.2
Pisidium sp.		2.5	0.9	0.4		1.0	0.2
Gammarus sp.					0.7		0.4
Gammarus lacustris							0.2
Nemoura avicularis					0.7	0.3	6.4
Leuctra inermis	4.3			0.4	0.4	0.3	0.2
Ephemoptera		1.2					
Ephemera danica		1.2					
Ephemerella ignita	11.5	1.2					
Paraleptophlebia submarginata					0.4	0.3	0.2
Procloeon sp.			0.3				
Baetis sp.	0.7		1.7				
Baetis rhodani			1.3	6.4	2.2	1.0	0.4
Haliplus ruficollis					0.4		
Hydroporus sp.			0.4				
Curculionidae				0.4			
Haliplus sp.						0.3	
Colymbetes sp.				0.4	0.7	0.8	0.6
Trichoptera					3.6		0.2
Limnephilus sp.				1.1	2.2		11.8
L. lunatus	4.3						
L. coenosus	4.3						
L. extricatus						18.8	34.2
L. rhombicus					7.3	0.5	

	1	2	3	4	5	6	7
Apatania wallengreni					34.1		0.4
Glyphotaelius pellucidus						0.8	0.6
Potamophylax sp.					2.5		
P. latipennis							1.9
Anabolia nervosa		2.5					0.6
Hydatophylax infumatus					1.5	2.3	6.0
Chaetopteryx villosa	2.9						
Polycentropus sp.	0.7					0.3	
Sericostoma personatum			2.2				6.6
Lepidostoma hirtum				1.1			
Chironomidae (L)	5.6	3.7	1.3	5.0	2.2	1.3	1.5
Ceratopogonidae (L)	0.7	0.6		0.4	0.7		*
Empididae (L)		1.2					
Tipulidae (L)						0.3	
Hydracarina		3.7	2.2	0.4	*	0.3	0.4
Corixidae (N)				0.4			
Corixidae (A)	0.7						
Sialis lutaria	6.5		3.5	2.1	1.1		2.1
Chironomidae (P)		0.6					
Tanypodinae (P)	*						
Aspectrotanypus (P)	0.7	1.2		0.7			
Macropelopia sp.(P)	1.4			0.4			
Macropelopia nebulosa (P)		0.6	1.3	0.7			
Pentaneurini (P)					0.4		
Conchapelopia sp(P)	1.4						
Prodiamesa sp. (P)	2.9		1.7	2.5	4.7	0.3	
Chironominae (P)	2.2						
Endochironomus sp (P)					0.4		
Endotendipes sp.(P)	5.8	0.6	0.4				
Paratendipes sp.(P)		*					
Paraspectra sp. (P)	2.2				0.7	0.5	
Paratanytarsus (P)			1.3	1.1	2.2		
Stempellina sp.(P)		1.9	1.3	1.4	1.5	0.5	
Microspectra sp(P)		1.2					
Trichoptera (P)	2.2				0.7		

	1	2	3	4	5	6	7
Stickleback		2.5	23.8	1.1		0.8	1.5
Gerridae					1.5	1.0	
<u>Velia caprai</u>							7.7
Diptera (A)	13.7	64.0	46.3	53.7	15.9	34.8	7.7
Trichoptera (A)	3.6			2.8	0.7	5.3	
Coleoptera (A)	2.2		0.9		0.4	0.8	
Elateridae (A)	0.7						
Staphylinidae (A)				0.4	0.7	0.5	
Hemiptera (A)		0.6	0.4	0.4			
Reduviidae (A)			0.9				
Saldidae (A)			0.4	1.8	1.8	0.8	
Cercopidae (A)		1.9	0.9	1.1	0.4		
Homoptera (A)	4.3						
Lepidoptera (A)	3.6						
Trichoptera (A)		1.2		0.7			
Cynipidae (A)						*	
Gasterupidae (A)					0.7		
Ichnuemonidae (A)					0.4	2.3	0.6
Formicidae (A)		3.7	0.4	0.4	1.1	4.8	0.4
Sphecidae (A)					0.4	2.5	
Apoidea (A)	2.9						
Collembella			0.4				*
Slug					12.5		6.4
Arachnid					0.4		0.2
Vegetation	5.7	0.6	1.3	11.3	5.1	0.8	2.1
Stones	2.2	1.2	3.9				

L=Larvae, N=Nymph, P=Pupae, A=Adult

1=16/7/88, 2=1/8/88, 3=12/8/88, 4=26/8/88, 5=16/9/88, 6=26/9/88
7=25/10/88

Stocked Brown Trout Pond A.
Number.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra				0.2		0.5	0.4
Pisidium sp.		1.6	1.2	0.2		1.0	0.4
Gammarus sp.					0.4		0.4
Gammarus lacustris							0.4
Nemoura avicularis							9.3
Leuctra inermis	5.4			0.2	0.4	0.3	0.4
Ephemoptera		0.4					
Ephemera danica		0.4					
Ephemerella ignita	8.1	0.4					
Paraleptophlebia submarginata					0.4	0.3	0.4
Procloeon sp.				0.4			
Baetis sp.	0.9		2.0				
Baetis rhodani			1.6	5.9	3.9	1.0	0.8
Haliplus ruficollis					0.4		
Hydroporus sp.			0.4				
Curculionidae				0.2			
Haliplus sp.						0.3	
Colymbetes sp.				0.2	0.8	0.7	1.2
Trichoptera					1.6		0.4
Limnephilus sp.				0.2	0.8		12.0
L. lunatus	1.8						
L. coenosus	1.8						
L. extricatus						9.1	13.6
L. rhombicus					0.4	0.3	
Apatania wallengreni					6.6		0.4
Glyphotaelius pellucidus						0.5	0.4
Potamophylax sp.				0.4			
P. latipennis							0.4

	1	2	3	4	5	6	7
Anabolia nervosa		0.4					0.4
Hydatophylax infumatus					0.8	0.7	1.6
Chaetopteryx villosa	0.9						
Polycentropus sp.	0.9					0.3	
Sericostoma personatum			0.4				2.3
Lepidostoma hirtum				0.2			
Chironomidae (L)	9.0	13.2	3.9	9.5	5.4	2.0	5.4
Ceratopogonidae (L)	1.8	1.2		0.2	1.2		0.4
Empididae (L)		0.4					
Tipulidae (L)						0.3	
Hydracarina		5.6	5.9	1.1	0.8	1.0	2.3
Corixidae (N)				0.2			
Corixidae (A)	0.9						
Sialis lutaria	1.8		0.8	0.5	0.4		0.8
Chironomidae (P)		0.4					
Tanypodinae (P)	0.9						
Aspectrotanypus (P)	0.9	0.8		1.8			
Macropelopia sp.(P)	2.7			0.2			
Macropelopia nebulosa (P)		0.4	1.6	0.5			
Pentaneurini (P)					0.4		
Conchapelopia sp(P)	1.8						
Prodiamesa sp. (P)	5.4		4.3	1.8	11.6	0.2	
Chironominae (P)	2.7						
Endochironomus sp (P)					0.2		
Endotendipes sp.(P)	9.9	0.8	0.4				
Paratendipes sp.(P)		0.4					
Paraspectra sp. (P)	2.7				0.8	0.5	
Paratanytarsus (P)			1.6	2.7	2.3		
Stempellina sp.(P)		5.2	5.9	0.9	6.2	1.7	
Microspectra sp(P)		1.2					
Trichoptera (P)	0.9				0.4		
Stickleback		0.4	0.8	0.2		0.3	
Gerridae					0.8	0.5	
Velia caprai							3.9
Diptera (A)	15.3	61.8	58.0	63.6	35.3	64.2	31.0
Trichoptera (A)	3.6			1.1	0.4	0.3	

	1	2	3	4	5	6	7
Coleoptera (A)	1.8		0.8		0.4	0.3	
Elateridae (A)	0.9						
Staphylinidae (A)				0.2	0.8	0.3	
Hemiptera (A)		0.4	0.8	0.2			
Reduviidae (A)			0.4				
Saldidae (A)			0.4	1.1	1.9	0.7	
Cercopidae (A)		1.6	0.8	0.2	0.4		
Homoptera (A)	3.6						
Lepidoptera (A)	1.8						
Trichoptera (A)		0.4		0.2			
Cynipidae (A)						0.3	
Gasterupidae (A)					0.4		
Ichnuemonidae (A)					0.4		0.4
Formicidae (A)		2.0	0.4	0.9	1.9	6.9	1.2
Sphecidae (A)					0.4	2.5	
Apoidea (A)	0.9						
Collembella			0.4				0.4
Slug						0.5	1.2
Arachnid					0.4	0.4	
Vegetation	6.3	0.4	3.9	4.7	9.7	1.0	3.9
Stones	4.5	0.4	2.7				
Feather			0.4				

L=Larvae, N=Nymph, P=Pupae, A=Adult

Stocked Brown Trout Pond A. Occurrence.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra				5.9		12.5	5.3
Pisidium sp.		7.7	7.7	5.9		6.3	5.3
Gammarus sp.					5.9		5.3
Gammarus lacustris							5.3
Nemoura avicularis					11.8	6.3	31.6
Leuctra inermis	14.8			5.9	5.9	6.3	5.3
Ephemoptera		7.7					

	1	2	3	4	5	6	7
Ephemera danica		7.7					
Ephemerella ignita	22.2	7.7					
Paraleptophlebia submarginata					5.9	6.3	5.3
Procloeon sp.				7.7			
Baetis sp.	3.7		7.7				
Baetis rhodani			15.4	41.2	35.3	25.0	10.5
Haliplus ruficollis					5.9		
Hydroporus sp.			7.7				
Curculionidae				5.9			
Haliplus sp.						6.3	
Colymbetes sp.				5.9	11.8	12.5	15.8
Trichoptera					11.8		5.3
Limnephilus sp.				5.9	11.8		15.8
L. lunatus	7.4						
L. coenosus	3.7						
L. extricatus						18.8	21.1
L. rhombicus					5.9	6.3	
Apatania wallengreni					11.8		5.3
Glyphotaelius pellucidus						12.5	5.3
Potamophylax sp.					5.9		
P. latipennis							5.3
Anabolia nervosa		7.7					5.3
Hydatophylax infumatus					11.8	18.8	10.5
Chaetopteryx villosa	3.7						
Polycentropus sp.	3.7					6.3	
Sericostoma personatum			7.7				10.5
Lepidostoma hirtum				5.9			
Chironomidae (L)	25.9	15.4	23.1	58.8	29.4	43.8	36.8
Ceratopogonidae (L)	7.4	7.7		5.9	11.8		5.3
Empididae (L)		7.7					
Tipulidae (L)						6.3	
Hydracarina		15.4	30.8	5.9	11.8	12.5	10.5

	1	2	3	4	5	6	7
Corixidae (N)				5.9			
Corixidae (A)	3.7						
Sialis lutaria	7.4		7.7	11.8	5.9		10.5
Chironomidae (P)		7.7					
Tanypodinae (P)	3.7						
Aspectrotanypus (P)	3.7	15.4		5.9			
Macropelopia sp.(P)	11.1			5.9			
Macropelopia nebulosa (P)		7.7	15.4	11.8			
Pentaneurini (P)					5.9		
Conchapelopia sp(P)	11.1						
Prodiamesa sp. (P)	18.5		23.1	29.4	23.5	6.3	
Chironominae (P)	7.4						
Endochironomus sp (P)					5.9		
Endotendipes sp.(P)	18.5	15.4	7.7				
Paratendipes sp.(P)		7.7					
Paraspectra sp. (P)	3.7			11.8	12.5		
Paratanytarsus (P)			23.1	17.6	29.4		
Stempellina sp.(P)		23.1	23.1	5.9	23.5	12.5	
Microspectra sp(P)		7.7					
Trichoptera (P)	3.7				5.9		
Stickleback		7.7	15.4	5.9		6.3	5.3
Gerridae					11.8	12.5	
Velia caprai							21.1
Diptera (A)	37.0	76.9	92.3	100	88.2	87.5	63.2
Trichoptera (A)	11.1			23.5	5.9	6.3	
Coleoptera (A)	7.4		7.7		5.9	6.3	
Elateridae (A)	3.7						
Staphylinidae (A)				5.9	11.8	6.3	
Hemiptera (A)		7.7	7.7	5.9			
Reduviidae (A)			7.7				
Saldidae (A)			7.7	17.7	17.7	18.8	
Cercopidae (A)		15.4	15.4	5.9	5.9		
Homoptera (A)	11.1						
Lepidoptera (A)	7.4						
Trichoptera (A)		7.7		5.9			
Cynipidae (A)						6.3	
Gasterupidae (A)					5.9		
Ichnuemonidae (A)					5.9	12.5	5.3
Formicidae (A)		30.8	7.7	11.8	11.8	37.5	15.8
Sphecidae (A)					5.9	25.0	
Apoidea (A)	3.4						

	1	2	3	4	5	6	7
Collembella			7.7				5.3
Slug						6.3	15.8
Arachnid					5.9		5.3
Vegetation	25.9	7.7	15.4	41.2	52.9	18.8	15.8
Stones	7.4	7.7	7.7				
Feather			7.7				

L=Larvae, N=Nymph, P=Pupae, A=Adult

Indigenous Brown Trout Pond A
Volume.

Sampling Period

	1	2	3	4	5	6	7
Lymnaea peregra						1.2	
Pisidium sp.						1.2	
Nemoura avicularis						10.1	
Leuctra inermis			3.3				
Baetis sp.		1.9					
Baetis rhodani			3.3	7.9	2.4		
Hydroporus ferrugineus			3.3				
Haliplus sp.	1.5				2.4		
Colymbetes sp.					2.4	1.8	
Trichoptera(L)	2.9	5.6			19.5		
Oecestis sp.					2.4		
Limnephilus sp.	27.5					34.5	
L. lunatus						1.2	
L. extricatus					7.3	16.7	
Glyphotaelius pellucidus						1.8	
Hydatophylax infumatus						1.2	
Chaetopteryx villosa	5.8						
Sericostoma personatum		5.6				20.8	

	1	2	3	4	5	6	7
Lepidostoma hirtum						0.6	
Chironomidae (L)	4.3	1.9	3.3	3.9	7.3	0.6	
Tipulidae (L)						0.6	
Sialis lutaria	36.2					1.8	
Chironomidae (P)			3.3				
Aspectrotanypus (P)	1.5						
Macropelopia sp. (P)	1.5						
Prodiamesa sp. (P)		3.7		2.0			
Endotendipes sp. (P)		1.9					
Paratanytarsus (P)	1.5						
Stempellina sp. (P)	1.5	7.4		20.0			
Diptera (A)	2.9	11.1	46.7	39.2	34.1	1.8	
Trichoptera (A)		3.7	6.7				
Elateridae (A)			3.3				
Staphylinidae (A)	1.5		3.3	7.8			
Hemiptera (A)						0.6	
Saldidae (A)				5.9			
Cercopidae (A)	5.8	3.7					
Cynipidae (A)					12.2		
Ichnuemonidae (A)				5.9			
Formicidae (A)	*	3.7	6.7	3.9	2.4		
Sphecidae (A)					7.3		
Slug		50.0	10.0				
Arachnid	2.9						
Vegetation	2.9		6.7	3.9		1.2	

L=Larvae, N=Nymph, P=Pupae, A=Adult
1=16/7/88, 2=1/8/88, 3=12/8/88, 4=26/8/88, 5=16/9/88, 6=26/9/88
7=25/10/88

Indigenous Brown trout Pond A.
Number.

Sampling Period

	1	2	3	4	5	6	7
Lymnaea peregra						1.3	
Pisidium sp.						1.3	
Nemoura avicularis						11.5	

	1	2	3	4	5	6	7
Leuctra inermis			2.2				
Baetis sp.		2.3					
Baetis rhodani			4.3	5.8	1.3		
Hydroporus ferrugineus			2.2				
Haliplus sp.	2.2				1.3		
Colymbetes sp.					1.3	5.1	
Trichoptera	2.2	2.3			5.3		
Oecestis sp.					1.3		
Limnephilus sp.	17.8					39.7	
L. lunatus						1.3	
L. extricatus					1.3	9.0	
Glyphotaelius pellucidus						2.6	
Hydatophylax infumatus						1.3	
Chaetopteryx villosa	2.2						
Odontocercum albicorne						1.3	
Sericostoma personatum		2.3					
Lepidostoma hirtum						1.3	
Chironomidae (L)	13.3	4.7	8.7	9.6	13.3	5.1	
Tipulidae (L)						1.3	
Sialis lutaria	20.0					1.3	
Chironomidae (P)			1.0				
Aspectrotanypus (P)	2.2						
Macropelopia sp. (P)	2.2						
Prodiamesa sp. (P)		7.0		1.0			
Endotendipes sp. (P)		2.3					
Paratanytarsus (P)	2.2						
Stempellina sp. (P)	8.9	32.6		44.2			
Diptera (A)	4.4	27.9	54.3	26.9	53.3	6.4	
Trichoptera (A)		2.3	2.2				
Elateridae (A)			2.2				
Staphylinidae (A)	2.2		2.2	1.0			
Hemiptera (A)						1.3	
Saldidae (A)				2.9			
Cercopidae (A)	6.7	4.7					

	1	2	3	4	5	6	7
Cynipidae (A)					16.0		
Ichnuemonidae (A)				1.0			
Formicidae (A)	2.2	9.3	4.3	3.9	1.3		
Sphecidae (A)					4.0		
Slug		2.3	2.2				
Arachnid	4.4						
Vegetation	6.7		6.5	3.9		2.6	

L=Larvae, N=Nymph, P=Pupae, A=Adult

Indigenous Brown Trout Pond A.
Occurrence.

Sampling Period

	1	2	3	4	5	6	7
Lymnaea peregra						20.0	
Pisidium sp.						20.0	
Nemoura avicularis						40.0	
Leuctra inermis			33.3				
Baetis sp.		20.0					
Baetis rhodani			33.3	66.7	33.3		
Hydroporus ferrugineus			33.3				
Haliplus sp.	20.0				33.3		
Colymbetes sp.					33.3		
Trichoptera	20.0	20.0			33.3		
Oecestis sp.					33.3		
Limnephilus sp.	40.0					40.0	
L. lunatus						10.0	
L. extricatus					33.3		
Glyphotaelius pellucidus						20.0	
Hydatophylax infumatus						20.0	
Chaetopteryx villosa	20.0						
Odontocercum albicorne						20.0	

	1	2	3	4	5	6	7
Sericostoma personatum		20.0				60.0	
Lepidostoma hirtum						20.0	
Chironomidae (L)	40.0	20.0	33.3	33.3	66.7	20.0	
Tipulidae (L)						20.0	
Sialis lutaria	40.0					20.0	
Chironomidae (P)			33.3				
Aspectrotanypus (P)	20.0						
Macropelopia sp. (P)	20.0						
Prodiamesa sp. (P)		40.0		33.3			
Endotendipes sp. (P)		20.0					
Paratanytarsus (P)	20.0						
Stempellina sp. (P)	20.0	100		100			
Diptera (A)	40.0	60.0	33.3	66.7	66.7	20.0	
Trichoptera (A)		20.0	33.3				
Elateridae (A)			33.3				
Staphylinidae (A)	20.0		33.3	33.3			
Hemiptera (A)						20.0	
Reduviidae (A)				33.3			
Cercopidae (A)	20.0	40.0					
Cynipidae (A)					33.3		
Ichnuemonidae (A)				33.3			
Formicidae (A)	20.0	40.0	66.7	33.3	33.3		
Sphecidae (A)					33.3		
Slug		20.0	33.3				
Arachnid	20.0						
Vegetation	20.0		33.3	66.7		20.0	

L=Larvae, N=Nymph, P=Pupae, A=Adult

Stocked Rainbow Trout Pond B.
Volume.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra			0.9				
Baetis rhodani			1.4	0.8	1.0		

	1	2	3	4	5	6	7
Haliplus ruficollis				0.3			
Haliplus sp.		1.5					
Colymbetes sp.							
Trichoptera (L)				1.5			
L. decipiens		6.1					
L. griseus					0.3		
Anabolia nervosa		3.0	36.9				
Chironomidae (L)		3.0	1.4		0.3		
Hydracarina					*		
Sialis lutaria			2.7	1.7			
Chironomidae (P)			0.9				
Tanypodinae (P)							
Aspectrotanypus (P)		1.5					
Macropelopia sp. (P)					0.1		
Macropelopia nebulosa (P)			1.4				
Prodiamesa sp. (P)			0.5		0.1		
Endotendipes sp. (P)		*					
Stempellina sp. (P)			*				
Plecoptera Exuviae				6.0	1.4		
Trichoptera (P)			1.4	2.0			
Stickleback				0.8			
Hydrometra stagnorum		1.5					
Diptera (A)		12.1	3.6	0.3			3.0
Elateridae (A)		1.5					
Berytinidae (A)		1.5					
Saldidae (A)			0.5	0.3			
Cercopidae (A)		9.1	0.5				
Trichoptera (A)				0.8			
Gasterupidae (A)			0.5				
Formicidae (A)			0.5				
Slug		21.2					
Arachnid		4.6					
Vegetation		27.3	47.3	85.3	95.4	100	97.0
Stones					1.4		
Feather		6.1		0.5			

L=Larvae, N=Nymph, P=Pupae, A=Adult
1=16/7/88, 2=1/8/88, 3=12/8/88, 4=26/8/88, 5=16/9/88, 6=26/9/88
7=25/10/88

Stocked Rainbow Trout Pond B.
Number.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra			1.6				
Baetis rhodani			4.8	1.3	3.7		
Haliplus ruficollis				0.9			
Haliplus sp.		2.1					
Trichoptera				0.9			
L. decipiens		2.1					
L. griseus					0.6		
Anabolia nervosa		4.1	9.5				
Chironomidae (L)		4.1	4.8		1.8		
Hydracarina					0.4		
Sialis lutaria			4.8	0.4			
Chironomidae (P)			1.6				
Aspectrotanypus (P)		4.1					
Macropelopia sp. (P)					0.6		
Macropelopia nebulosa (P)			4.8				
Prodiamesa sp. (P)			1.6		0.6		
Endotendipes sp. (P)		9.1					
Stempellina sp. (P)			3.2				
Plecoptera Exuviae				26.2	14.0		
Trichoptera (P)			4.8	2.2			
Stickleback				0.4			
Hydrometra stagnorum		2.0					
Diptera (A)		12.2	14.2	0.4			7.1
Elateridae (A)		2.0					
Berytinidae (A)		2.0					
Saldidae (A)			1.6	0.4			
Cercopidae (A)		8.2	1.6				
Trichoptera (A)				0.4			
Gasterupidae (A)			1.6				
Formicidae (A)			1.6				
Slug		2.0					
Arachnid		4.1					
Vegetation		44.9	39.7	64.0	72.6	100	92.9

	1	2	3	4	5	6	7
Stones					6.1		
Polystyrene							
Feather		4.1		1.8			

L=Larvae, N=Nymph, P=Pupae, A=Adult

Stocked Rainbow Trout Pond B.
Occurrence.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra			11.1				
Baetis rhodani			33.3	30.0	50.0		
Haliplus ruficollis				10.0			
Haliplus sp.		9.1					
Trichoptera				20.0			
L. decipiens		9.1					
L. griseus					10.0		
Anabolia nervosa		18.2	22.2				
Chironomidae (L)		18.2	33.3		30.0		
Hydracarina					10.0		
Sialis lutaria			33.3	10.0			
Chironomidae (P)			11.1				
Aspectrotanypus (P)		9.1					
Macropelopia sp. (P)					10.0		
Macropelopia nebulosa (P)			11.1				
Prodiamesa sp. (P)			11.1		10.0		
Endotendipes sp. (P)		9.1					
Stempellina sp. (P)			11.1				
Plecoptera Exuviae				40.0	40.0		
Trichoptera (P)			11.1	30.0			
Stickleback				10.0			
Hydrometra stagnorum		9.1					
Diptera (A)		36.4	33.3	10.0			25.0
Elateridae (A)		9.1					

	1	2	3	4	5	6	7
Berytinidae (A)		9.1					
Saldidae (A)			11.1	10.0			
Cercopidae (A)		18.2	11.1				
Trichoptera (A)				10.0			
Gasterupidae (A)			11.1				
Formicidae (A)			11.1				
Slug		9.1					
Arachnid		18.2					
Vegetation		54.6	66.7	60.0	70.0	50.0	100
Stones					10.0		
Feather		18.2		30.0			

L=Larvae, N=Nymph, P=Pupae, A=Adult

Stocked Brown Trout Pond B.
Volume.

	Sampling Period						
	1	2	3	4	5	6	7
Lymnaea peregra				7.0	8.4	2.2	
Planorbus laevis		1.6				0.3	
Ancylus fluviatilis						0.6	
Pisidium sp.						3.6	
Leuctra inermis				0.9			
Baetis rhodani			1.0	1.3			
Coleoptera		3.2					
Helophorus sp.						0.3	
Haliplus sp.			1.0				
Colymbetes sp.		1.6			0.9	0.3	
Trichoptera					1.9		
Limnephilus sp.							1.1
L. subcentralis							0.7
L. extricatus						20.8	62.3
Glyphotaelius pellucidus							3.1
P. latipennis							1.3

	1	2	3	4	5	6	7
Anabolia nervosa		37.5	38.5				
Sericostoma personatum				3.9		6.8	28.0
Lepidostoma hirtum				1.3			
Chironomidae (L)			*	1.3	0.9	0.3	
Empididae (L)						0.3	1.5
Hirudinea						1.4	
Oligochaeta				17.5			
Sialis lutaria				14.8		4.1	1.0
Chironomidae (P)				0.4			
Macropelopia sp. (P)			1.0				
Prodiamesa sp. (P)					0.9		
Stempellina sp. (P)					*		
Gerridae					5.6		
Gerris lacustris					1.9		
Hydrometridae				0.9			
Velia caprai						2.5	0.3
Diptera (A)		54.8	42.7	32.3	51.4	48.5	0.7
Trichoptera (A)		3.2	4.2	14.4	7.5		
Coleoptera (A)					0.9		
Staphylinidae (A)					0.9		
Berytinidae (A)		1.6					
Saldidae (A)			1.0	1.3		0.8	
Cercopidae (A)		9.7		0.4			
Trichoptera (A)						2.2	
Ichnuemonidae (A)			1.0		0.9		
Formicidae (A)			1.0	0.9	2.8	2.7	0.2
Collembella						0.3	
Slug					14.0	1.9	
Arachnid		4.8		0.4		0.3	
Vegetation			5.2	0.9	0.9		
Stones			3.1				

L=Larvae, N=Nymph, P=Pupae, A=Adult

1=16/7/88, 2=1/8/88, 3=12/8/88, 4=26/8/88, 5=16/9/88, 6=26/9/88
7=25/10/88

Stocked Brown Trout Pond B.
Number.

	Sampling Period						
	1	**2**	**3**	**4**	**5**	**6**	**7**
Lymnaea peregra				2.8	2.4	0.4	
Planorbus laevis		1.4				0.2	
Ancylus fluviatilis						0.2	
Pisidium sp.						2.6	
Leuctra inermis				1.7			
Baetis rhodani			1.3	2.2			
Coleoptera		1.4					
Helophorus sp.						0.2	
Haliplus sp.			1.3				
Colymbetes sp.		1.4			0.8	0.2	
Trichoptera					0.8		
Limnephilus sp.							0.9
L. subcentralis							0.9
L. extricatus						3.1	58.3
Glyphotaelius pellucidus							3.7
P. latipennis							0.9
Anabolia nervosa		5.4	8.9				
Sericostoma personatum				1.7		1.2	20.4
Lepidostoma hirtum				0.6			
Chironomidae (L)			1.3	2.8	0.8	0.2	
Empididae (L)						0.2	4.6
Hirudinea						0.2	
Oligochaeta				0.6			
Sialis lutaria				5.0		0.6	1.9
Chironomidae (P)				2.2			
Macropelopia sp.(P)			1.3				
Prodiamesa sp. (P)					0.8		
Stempellina sp.(P)					1.6		
Gerridae					1.6		

	1	2	3	4	5	6	7
Gerris lacustris					0.8		
Hydrometridae				0.6			
Velia caprai						1.0	0.9
Diptera (A)		78.4	69.6	65.9	81.0	83.5	6.5
Trichoptera (A)		1.4	2.5	6.2	2.4		
Coleoptera (A)					0.8		
Staphylinidae (A)					0.8		
Berytinidae (A)		1.4					
Saldidae (A)			1.3	2.2		0.8	
Cercopidae (A)		6.8		0.6			
Trichoptera (A)						0.4	
Ichnuemonidae (A)			1.3		0.8		
Formicidae (A)			1.3	1.7	3.2	4.3	0.9
Collembella						0.2	
Slug					0.8	0.2	
Arachnid		2.7		0.6		0.2	
Vegetation			7.6	2.2	0.8		
Stones			1.3				

L=Larvae, N=Nymph, P=Pupae, A=Adult
1=16/7/88, 2=1/8/88, 3=12/8/88, 4=26/8/88, 5=16/9/88, 6=26/9/88
7=25/10/88

Stocked Brown Trout Pond B.
Occurrence.

Sampling Period

	1	2	3	4	5	6	7
Lymnaea peregra				20.0	12.5	22.2	
Planorbus laevis		20.0				11.1	
Ancylus fluviatilis						11.1	
Pisidium sp.						22.2	
Leuctra inermis				10.0			
Baetis rhodani			12.5	20.0			
Coleoptera		20.0					
Helophorus sp.						11.1	

	1	2	3	4	5	6	7
Haliplus sp.			12.5				
Colymbetes sp.		20.0			12.5	11.1	
Trichoptera					12.5		
Limnephilus sp.							25.0
L. subcentralis							25.0
L. extricatus						22.2	75.0
Glyphotaelius pellucidus							75.0
P. latipennis							25.0
Anabolia nervosa		40.0	37.5				
Sericostoma personatum				10.0		22.2	75.0
Lepidostoma hirtum				10.0			
Chironomidae (L)			12.5	20.0	12.5	11.1	
Empididae (L)						11.1	50.0
Hirudinea						11.1	
Oligochaeta				10.0			
Sialis lutaria				50.0		33.3	50.0
Chironomidae (P)				10.0			
Macropelopia sp.(P)			12.6				
Prodiamesa sp. (P)					12.5		
Stempellina sp.(P)					12.5		
Gerridae					25.0		
Gerris lacustris					12.5		
Hydrometridae				10.0			
Velia caprai						44.7	
Diptera (A)		100	50.0	60.0	75.0	77.8	25.0
Trichoptera (A)		20.0	25.0	30.0	25.0		
Coleoptera (A)					12.5		
Staphylinidae (A)					12.5		
Berytinidae (A)		20.0					
Saldidae (A)			12.5	10.0		33.3	
Cercopidae (A)		80.0		10.0			
Trichoptera (A)						22.2	
Ichnuemonidae (A)			12.5		12.5		
Formicidae (A)			12.5	10.0	25.0	44.4	25.0
Collembella						11.1	
Slug					12.5	11.1	
Arachnid		40.0		10.0		11.1	

	1	2	3	4	5	6	7
Vegetation			25.0	10.0	12.5		
Stones			12.5				

L=Larvae, N=Nymph, P=Pupae, A=Adult
1=16/7/88, 2=1/8/88, 3=12/8/88, 4=26/8/88, 5=16/9/88, 6=26/9/88
7=25/10/88

Appendix 5. The card used in the 1987 and 1988 angler census.

LOCH AWE FISHERIES PROJECT
INSTITUTE OF AQUACULTURE
UNIVERSITY OF STIRLING

Record the weight of each fish caught

Brown Trout	
Rainbow Trout	
SeaTrout	
Salmon	
Charr	
Other Species	

Mark Area Fished With An X

Name: Fishing Time (hrs):

Number of Rods:

Date: Shore/Boat

INSTRUCTIONS

(1) ONLY use this card when fishing on Loch Awe

(2) Fill in the information asked for overleaf, using a new card each day. if you don't have any scales, estimate the fish weight and annotate the entry with "E". if a fish is returned estimate the weight and annotate with "R". EVEN IF NO FISH ARE CAUGHT RETURN THE COMPLETED CARD WITH THE TIME SPENT FISHING.

(3) For "Other Species" caught annotate the weight with "Pe" for Perch, "P" for Pike and "Ee" for Eel.

(4) Completed cards should be returned to Loch Awe Fisheries Project boxes at any of the hotels etc. that are listed on the posters or to: WILLIAM DUNCAN, INSTITUTE OF AQUACULTURE, STIRLING UNIVERSITY, STIRLING, FK9 4LA

Thanks are expressed to George Ballentine & Son Ltd. the whisky distillers, who have kindly paid for the production of these cards.
THANK YOU FOR YOUR COOPERATION