The post-stocking behaviour of hatchery-reared brown trout (*Salmo trutta* L.)

by

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for my dad

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Declaration

This thesis presents the research work conducted by the candidate at the Institute of Aquaculture, University of Stirling, during the period of October 1997 to August 2000. The thesis has been composed by the candidate and no part of this work has been submitted for any other degree. All work referred to has been duly acknowledged.

Signature of candidate:

James Ian Deverill

Abstract

Stocking, transfer and introductions of hatchery-reared salmonids are commonly used to enhance recreational or commercial fisheries and to preserve or re-establish threatened populations (Cowx, 1994). Whilst a lot of effort has been directed toward understanding the production and stocking methods of hatchery-reared salmonids, relatively little is known about the post-stocking survival and behaviour of these fish (Hickley, 1994). In particular there is little available information concerning the post-stocking dietary habits, dispersion and behaviour of hatchery-reared brown trout; particularly following release into standing waters. Consequently, a study was instigated to examine the relative post-stocking dispersion and temporal changes in the diets of hatchery-reared brown trout released to support a commercial recreational fishery, Carron Valley Reservoir. Further laboratory studies examined if resident brown trout display a prior-resident competitive advantage over stocked conspecifics, if hatchery-reared brown trout display non-cost effective aggressive behaviour and the short-term changes in the feeding efficiency of naïve hatchery-reared brown trout when experiencing novel prey.

1000 commercially produced hatchery-reared brown trout were marked with a subcutaneous alcian blue tattoo and released into Carron Valley Reservoir at the start of the 1999 fishing season. Stomach samples were taken from angler recaptured hatchery-reared fish along with consecutively captured resident brown trout. The diets of the two groups were compared to assess the relative post-stocking temporal changes in the diets of the hatchery-reared brown trout. This study found hatchery-reared brown trout to consume lower weights and numbers of prey, and they appeared to exhibit a preconditioned 'look up' dietary response to surface prey immediately following release than resident conspecifics. It was further observed that although hatchery-reared brown trout did not immediately adapt to natural diets, their relative foraging efficiency increased over the sample period. In laboratory experiments naïve hatchery-reared brown trout further demonstrated the improved feeding efficiency with experience.

1000 commercially produced hatchery-reared brown trout were tagged with a combination of Visible Implant (VI) and 'Floy' style tags prior to release during the 1998, 1999 and 2000 fishing seasons. An angler survey programme was instigated to record the reported recapture positions of these tagged fish in order to assess the post-stocking gross dispersion patterns of hatchery-reared brown trout in Carron Valley Reservoir. A further 3 trout were radiotagged to elucidate the fine scale post-stocking dispersion of these fish. This study found hatchery-reared brown trout to disperse quickly from their respective release sites, although over a relatively restricted area. Individual hatchery-reared brown trout were observed to exhibit high levels of activity immediately following release, during which period they covered relatively large total distances within a relatively restricted area.

In an artificial stream environment, established wild brown trout displayed a prior-resident competitive advantage over later introductions of both hatchery-reared and wild conspecifics. Established wild fish initiated more aggressive acts and maintained home stations closer to a point source of feed than introduced trout. Introduced hatchery-reared brown trout were more aggressive and exhibited a lower mean specific growth rate than simultaneously stocked wild conspecifics, suggesting that excessive expenditure of energy for unnecessary aggression may contribute to the poor post-stocking survival in hatchery-reared brown trout.

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Appendix 4	Deverill, J.I., Adams, C.E. & Bean, C.W. (1999). Prior-residence, aggression and territory acquisition in hatchery-reared and wild brown trout. *Journal of Fish Biology* **55**, 868-875.

Chapter 1

General Introduction

1.1 Phylogeny and distribution of the brown trout and powan

The salmonid family contains three sub-families; Coregonidae, Salmoninae and Thymallinae. The sub-family Salmoninae contains the genus *Salmo*, along with six others (*Brachymystax*, *Salmothymus*, *Acantholinqua*, *Hucho*, *Salvelinus* and *Oncorhynchus*) (Bagliniere & Maisse, 1991). The genus *Salmo* contains only two species, the brown trout, *Salmo trutta* L., and the Atlantic salmon, *Salmo salar* L. (Figure 1.1). Ten separate brown trout species were once recognised in the British Isles, and many were given common names which persist today (including sewin, dollaghan, galway, gillaroo and sea-trout)(Elliott, 1994). However, these species have since been grouped together into one polymorphic species, *Salmo trutta* L. (Elliott, 1994). Of the four species of coregonine whitefish that survive in the British Isles today, three are glacial relict populations isolated in freshwater lakes (Brown & Scott, 1994). These include *Coregonus pollan* Thompson (pollan) found in Loughs Neagh, Erne, Ree and Derg in Ireland, *Coregonus albula* L. (vendace) found in Bassenthwaite and Derwentwater and *Coregonus lavaretus* L. (powan) which occurs in Lochs Lomond and Eck in Scotland (Brown & Scott, 1994).

The brown trout is essentially a native European species (Figure 1.2). Its northern range limits are Iceland, northern Scandinavia and Russia. Western limits are simply defined by the European coastline and the southern limits by the northern coastline of the Mediterranean Sea as well as the islands of Corsica, Sardinia and Sicily, and the Atlas mountains of North Africa. The eastern limits are more difficult to define, but are probably the Ural mountains and Caspian Sea (Elliott, 1994). Whilst the southern range extends as far as the upper reaches of the Orontes river in Lebanon (Elliott, 1994). Anadromous sea trout populations occur in the water courses feeding the White Sea and the gulf of Cheshkaya, the Baltic Sea, North Sea, Irish Sea, the English Channel, the Atlantic Ocean as far as the Bay of Biscay, the

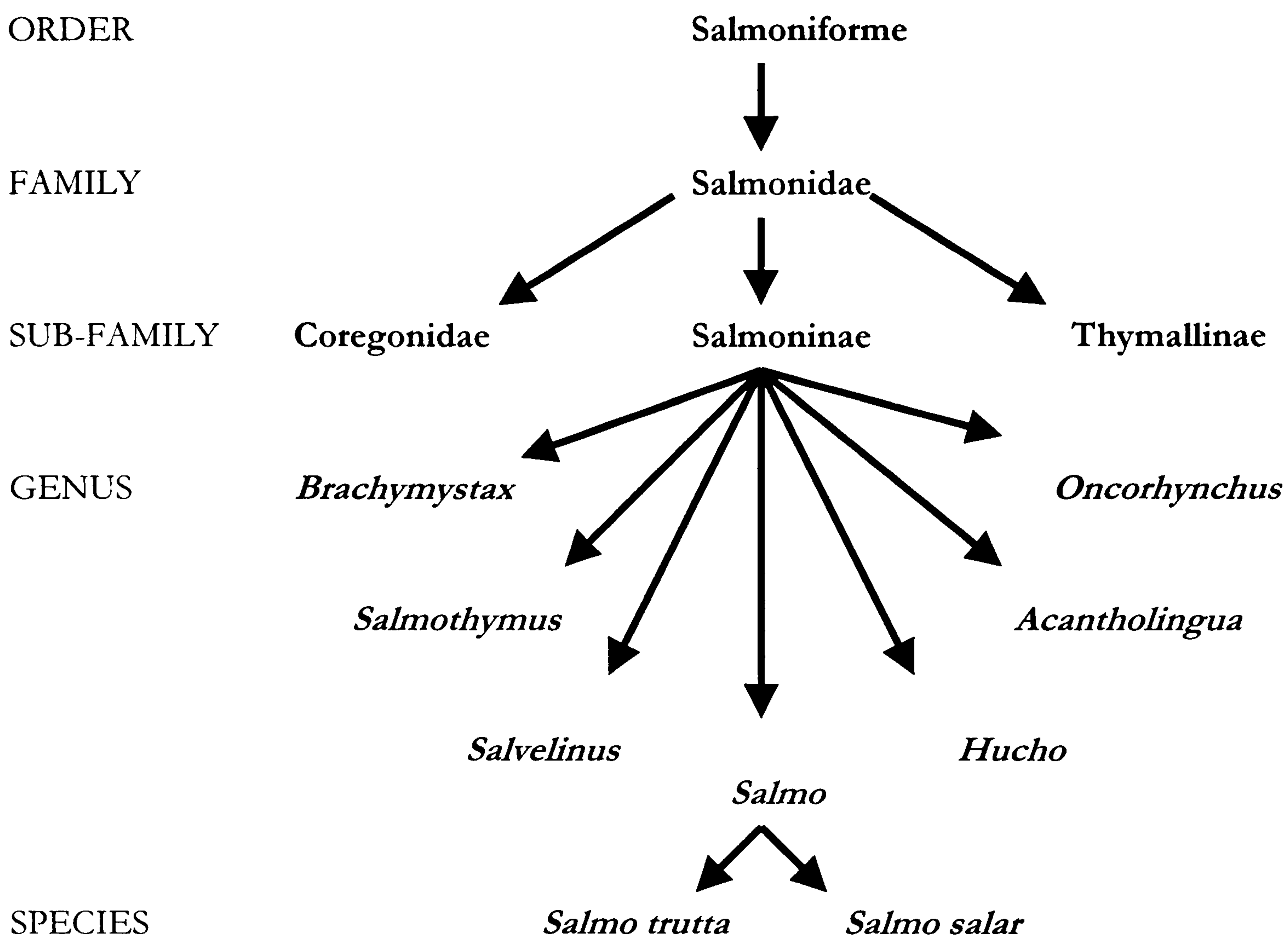


Figure 1.1 – A phylogenetic key to the salmonid family (after Bagliniere and Maisse, 1991).

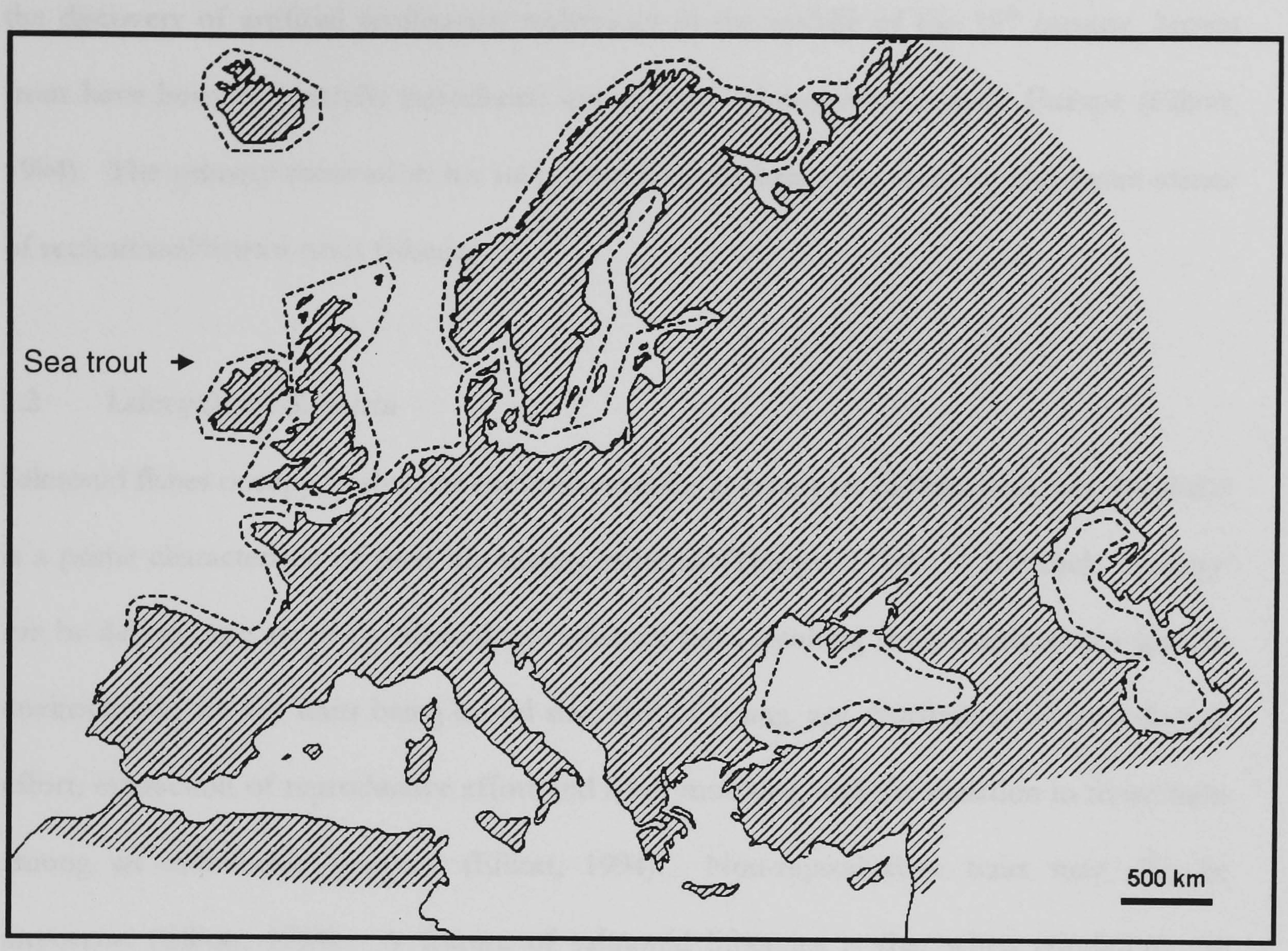


Figure 1.2 – The Native distribution of brown trout; the dashed lines indicate sea trout distributions (after Elliott, 1994).

Black Sea, Caspian Sea and the Aral Sea (Figure 1.2) (Bagliniere & Maisse, 1991). Following the discovery of artificial fertilisation techniques in the middle of the 19th century, brown trout have been successfully introduced into at least 24 countries outside Europe (Elliott, 1994). The primary motivation for such introductions being the creation and maintenance of recreational brown trout fisheries.

1.2 Lifecycle of *S. trutta*

Salmonid fishes occupy freshwater environments for at least part of their lives, and flexibility is a prime characteristic of their life history patterns (Thorpe, 1974). A life cycle 'strategy' can be defined as a set of co-adapted reproductive traits resulting from selection in a specific environment, the key traits being brood size, size of young, age distribution of reproductive effort, interaction of reproductive effort and adult mortality, and the variation in these traits among an individuals' progeny (Elliott, 1994). Non-reproductive traits may also be important (Elliott, 1994). A feature of salmonid lifecycles is that when conditions are favourable, sexual maturity occurs as early as possible and reproduction usually takes priority over growth (Thorpe, 1974).

When living together in nature or under artificial rearing conditions, male and female brown trout grow at the same rate. However, as females mature later than males, their size at maturation is larger. This indicates that there is a genetic difference in age at maturation that is not related to growth. It is also suggested that in natural environments, female fish tend to inhabit more risky habitats which offer potentially better sources of food (Jonsson, 1989), thereby giving them potential for higher growth rates.

Brown trout normally spawn in running water during the late autumn (usually October and November). The spawning area is also the nursery area for the young when they start to feed during the following spring (Jonsson, 1989). The process of spawning requires the female trout to create depressions in the gravel ('redds') by repeated flexures of her body. Eggs are laid in these depressions, where they are immediately fertilised by one of several male trout. (Bagliniere & Maisse, 1991). The female then covers over the fertilised eggs with gravel as she makes the next depression upstream (Elliott, 1994). The fecundity and depth at which the eggs are buried increases with female size; for example, burial depth was approximately 4 cm for a population of small resident trout but 17.5 cm for larger sea trout in a neighbouring stream (Elliott, 1994). The probability of egg wash out during spates decreases with increasing egg burial depth (Elliott, 1994). The eggs develop in the redd over the winter and hatch the following spring (January-March) after approximately 444 degree days. During the early fry stages mortalities are high whilst the young trout establish feeding territories. After a few weeks the trout develop into parr. These fish are characterised by the presence of 9-10 black stripes down the flanks and a red/orange adipose fin. In simple brown trout lifecyles the fish may spend their whole lives in their natal stream, where sexual maturity is usually achieved after 2-3 years dependent on stream productivity (Elliott, 1994). Brown trout may spawn in several successive years and live for many years. A lifecycle extending 5-8 years has been recorded in many populations (Elliott, 1994).

Brown trout of all ages have been shown to be dependent on a largely aquatic macro-invertebrate diet. Dietary choice varies with age. It is generally accepted that the diet of year 0+ trout is dominated by aquatic invertebrates whilst adult terrestrial invertebrate forms become a progressively more important dietary component with increasing fish age, especially at certain times of the year (Kelly-Quinn & Bracken, 1990).

1.3 Habitat use of *S. trutta*

There are ranges of biotic and abiotic factors which are thought to both initiate and modify salmonid movement rates and habitat selection (Elliott, 1986), these include temperature, water velocity, food availability, age and population density. Brown trout often utilise several different habitats during their life spans (Jonsson, 1989). Brown trout usually spawn in running water, the spawning area is also the nursery. As fish grow older, they move down-stream often into lake-habitats. It is accepted that upon emergence, stream-dwelling brown trout frequently establish territories in shallow riffles (Bridcut & Giller, 1993). Characteristically these habitats have small substrate particles (Heggenes *et al.*, 1990) and low water velocities (Heggenes, 1988). The critical water velocity at which brown trout of less than 40 mm total length could no longer maintain their position in a stream has been reported as 14 cms^{-1} (Heggenes, 1988) and 20 cms^{-1} (Heggenes *et al.*, 1990), although this is dependant on several factors including water temperature and substrate type. Substrate choices of fingerling brown trout are varied and include both silt (Hubert *et al.*, 1994) and gravel (Heggenes, 1988). It is has been shown that 0+ brown trout conceal themselves under cover in the form of substrate, vegetation or woody debris (Hubert *et al.*, 1994).

According to Gerking (1953) a territory is defined as any defended area. The area over which an animal normally travels, and within which territories are established, is termed the home range (Bachman, 1984). It has been suggested that both biological and environmental factors are influential in governing trout movements and home range size, including population density, the amount of available forage and substrate type (Bagliniere & Maisse, 1999).

Brown trout partially segregate in habitat by size and age (Jonsson, 1989). This may be partly due to different size fishes having different abilities to capture, handle and eat food organisms of the same size and behaviour (Jonsson, 1989). The youngest and smallest parr, which are most vulnerable to predation, occupy the most sheltered habitats in the stream environment, where predators are most likely to be confused (Jonsson, 1989). It has been suggested that as 0+ brown trout grow they select habitats with higher water velocities, deeper water and larger substrates (Hubert *et al.*, 1994). The effect of partial habitat and diet segregation is to reduce intraspecific competition between small and large fish (Jonsson, 1989); this trait may be especially important when food is limited.

Brown trout populations may exhibit several life history strategies. For example, trout may migrate at the parr stage into another, usually larger, stream, river or lake and only return to their natal stream to spawn (Stuart, 1953). Alternatively, parr may undergo smoltification and emigrate to the estuarine and marine environment to ongrow only returning to the natal stream as sea trout at spawning time (Elliott, 1994).

Habitat variations may occur both diurnally and seasonally. Diurnal shifts in habitat use by 0+ brown trout are known to occur. It is suggested that 0+ brown trout hide in the substrate more during the day than at night, and that 0+ fish may move closer to the stream edge at night (Hubert *et al.*, 1994). Both of these responses are deemed to be adaptations to predation threat. Seasonal variations in habitat use are also likely to be caused by changes in water velocity, reproductive factors and temperature (Bagliniere & Maisse, 1991) The swimming ability of young salmonids is reduced at lower temperatures, and brown trout were found to bury themselves within the substratum at low temperatures (Heggenes, 1988).

Life history strategies for stream dwelling salmonids have been relatively well described (Elliott, 1984; Elliott, 1986; Heggenes, 1988; Heggenes *et al.*, 1990; Hubert *et al.*, 1994), less is known about habitat utilisation in lakes and reservoirs (Garrett & Bennett, 1995). In lakes, brown trout are usually most abundant in the near-surface water and littoral zone (Thorpe, 1974), especially during the summer when their densities decrease with increasing depth (Jonsson, 1989). This is assumed to be largely due to the visual feeding strategy of trout (Haraldstad & Jonsson, 1983). The three main factors thought to govern lake habitat use by brown trout are food supply, intraspecific competition and predator avoidance (Thorpe, 1974). Juvenile fish (1-2yr) are largely constrained to the sheltered littoral environment, whilst larger fish are able to shift habitat dependent on food availability (pelagic during the summer, benthic during the winter) (Haraldstad & Jonsson, 1983). Garrett and Bennett (1995) determined that lake living trout moved out of littoral zone when water temperatures exceeded 18 ^{0}C and into cooler waters, either below the thermocline or near inflowing streams. Lake living trout usually spawn in streams, however if a suitable stream spawning habitat is not available trout will either not spawn or else will deposit eggs in a less suitable area e.g. spawning on gravel patch in Loch Moraig, Perthshire (Mills, 1971).

1.4 Carrying capacity of the environment and *S. trutta*

The carrying capacity of a given environment is the maximum number of individuals of a particular species that can be supported indefinitely by a given pat of that environment

(Lawrence, 1995). Under conditions of suitable water quality and recruitment the capacity of a stream to hold salmonid fish is largely a function of discharge and the physical structure of the stream channel (Milner *et al.*, 1985). The carrying capacity of stream salmonids appears to be governed by habitat quality, food availability and wintering conditions (Naslund, 1992). In most cases of restocking, the carrying capacity of the system (both lentic and lotic) is unknown (Kelly-Quinn & Bracken, 1989). Consequently, there are many examples of overstocking, both numerically and in terms of fish size, which invariably lead to high mortalities (Kelly-Quinn & Bracken, 1989). Naslund (1992), in a study of stocking programs in Swedish Lapland, found that fish introductions did not result in increased densities or standing crop. Instead, population size appears to be controlled by the carrying capacity of the stream (Naslund, 1992).

1.5 Recreational fisheries and the brown trout

Natural flowing and standing freshwater bodies have evolved ecosystems over time without human intervention; however, many freshwater bodies are to a greater or lesser extent impacted by anthropogenic activity and consequently may require some form of interventional management (Nielsen & Lackey, 1980). One of the many potential anthropogenic disturbances to natural aquatic ecosystems is fishing, both commercial and recreational. Recreational fishing is defined as being the pursuit of fish solely for the pleasure associated with the experience (Hickley & Tompkins, 1998). Angling is a major recreational pastime for approximately 2 million people (3.5% of the total population) in the United Kingdom, generating an estimated expenditure of £4 billion per annum (Hickley & Tompkins, 1998). Although angling is of national economic importance, the values ascribed to recreational fishing by the anglers themselves are relatively abstract with the actual capture of fish only constituting a small part of the total experience (Tierney & Richardson, 1992).

The brown trout is a globally important freshwater fish species in relation to sports fisheries (Bagliniere & Maisse, 1991), with brown trout in Scottish waters being the basis of a national pastime and tourist attraction of considerable importance (Campbell, 1979, Stephen & McAndrew, 1990). Increasing exploitation due to a rise in the numbers of anglers and heightened angler expectations mean that it is now necessary to manage many of the most popular and easily accessible recreational brown trout fisheries in Scotland. Fishery management strategies should be developed and implemented as a direct response to the observed problems in each individual aquatic system, consequently many of the techniques used to manage recreational fisheries are equally applicable to managing natural fish populations for conservation (Templeton, 1971). Where applicable it is considered best practice to utilise 'indirect' management techniques, including habitat modification, improving water quality, conserving natural populations, etc (Templeton, 1971). However, commercially managing highly exploited recreational fisheries using indirect management techniques to allow the sustainable harvesting of large numbers of salmonids is essentially impossible (Nielsen & Lackey, 1980). Consequently, in order to maintain accessible stocks of catchable sized trout in recreational fisheries it is often necessary to implement 'direct' fishery management techniques which include supplementing populations by stocking (Templeton, 1971).

1.6 Stocking and fisheries management

Stocking, transfer and introduction of fish are commonly used to mitigate loss of stocks, enhance recreational or commercial catches and restore or create new fisheries (Cowx, 1994; Hickley, 1994). That restocking is necessary in brown trout fisheries with inadequate spawning facilities, high angling pressure and predation and/or to replace the fish taken by anglers is generally accepted (Templeton, 1971). However, few quantitative data have been presented concerning the efficiency of current commercial salmonid restocking practices (Hickley, 1994).

1.6.1 Stocking considerations

Stocking of fish should occur at a time that ensures maximum survival and consequent returns to anglers (Hesthagen & Jonsson, 1989). Several factors may influence the relative efficiency of stocking strategies. These include preconditioning to receiving waters, handling and transportation of stock, productivity of receiving waters, resident stocks of trout or competing fish, mechanism of fish release, stocking density, size at stocking, time of stocking and fishing pressure (Wiley *et al.*, 1993).

There is a growing body of evidence to suggest that trout should be preconditioned to the quality of the water in the receiving water body (Cowx, 1994). The stocking of commercially-reared brown trout into lentic systems (ponds, lakes and lochs) has been shown to yield higher returns over a longer period of time than similar stockings into lotic environments (Ersbak & Haase, 1983). Helfrich and Kendall (1982) suggested that poor performance in stream stocked fish may be influenced by differences in water temperature and stream flow when compared to the rearing environment. It has also been suggested that inadequate stream cover and numbers of holding pools may result in poor post-stocking performance (Cresswell, 1980). Water quality may also affect stocking success, for example Wiley *et al.* (1993) found that planted brown trout from two hatcheries failed to survive in Inyan Kara Creek, Wyoming, due to increased total dissolved solid levels.

Handling and transportation inevitably causes stress and possible damage to fish, which can subsequently affect post-stocking survival (Cowx, 1994). Brown trout are considered a stress sensitive species and even relatively minor amounts of handling may disturb them (Heggenes, 1988). Bridcut and Giller (1993) attributed observed downstream displacement of native brown trout in the Glenfinish River to be a stress induced movement. Ersbak and Haase (1983) suggested that stress probably initiates the tendency for higher mortality in stream stocked salmonids. Stickney (1983) suggested that handling stress could be reduced through the use of mild anaesthesia, by ensuring a good oxygen supply during transportation and by the cessation of feeding 72 hours before transport.

Although it is possible in the short term to release catchable trout into unproductive waters it is generally accepted that streams and lakes must have enough food to support introduced trout (Wiley, *et al.*, 1993). Without sufficient availability of a suitable food source and habitat type, trout will move to a more cost-effective foraging site (Bachman, 1984). Naslund (1992) stated that stocking streams often does not increase the standing crop of fish due to insufficient suitable habitat, food availability and overwintering conditions.

There are three accepted mechanisms for fish release; spot planting where all fish are introduced at the same site at the same time, scatter planting where the fish are introduced in several sites in one single stocking and trickle planting where the fish are introduced over a period of time (Cowx, 1994). Cresswell and Williams (1982) noted higher recapture rates for spot plantings than for scatter plantings on the Afon Taf River, Wales; whereas, L'Abee-Lund and Langeland (1995) found higher recapture rates for scatter planted brown trout than spot planted trout in a Norwegian lake. Higher recapture rates for spot planted trout may be attributed to increased angler exploitation at these stocking points (Cresswell and Williams, 1982). Therefore, for successful fishery management it may be more prudent to practice scatter stocking to avoid rapid exploitation of stocked fish and extend the benefits of stocking to a fishery (Cresswell and Williams, 1982).

There has been much debate over the most appropriate size or age of fish at stocking (Cowx, 1994). The release of smaller fish has the advantages of costing less per fish released and an increase in the feral characteristics of the catchable sized fish (Cresswell, 1980). However, investigations on small trout in the U.S.A. suggest a survival rate to catchable size of only 3%, thus reducing the cost effectiveness of stocking small fish (Cresswell, 1980). Several studies have indicated that larger fish yield better returns. In two year old Norwegian brown trout each 3cm increase in mean size doubled the recapture rate, and in France the best returns (upto 90%) were obtained when hatchery trout of legal size were stocked during the fishing season (Welcomme *et al.*, 1993). Finnish investigators recommend minimum stocking sizes of 18-25cm total length for brown trout (Welcomme *et al.*, 1993).

It is generally agreed that spring stocking of brown trout yields better returns than autumn stocking in both rivers and lakes (Welcomme *et al.*, 1993; O'Grady, 1984). Templeton (1971) determined that there were more recaptures of spring- than autumn-stocked brown trout at

Chelker reservoir, Yorkshire; this was attributed to either poor overwintering performance of autumn stocked individuals or the autumn stocked fish becoming wilder and less catchable. Kennedy *et al.* (1982) reported that spring stocked yearling brown trout gave over seven times better return to the angler than autumn stocked fish. Cowx (1994) recommends that stocking should preferably take place when water temperatures are generally low but when natural productivity of the receiving water body is high, but not during the spawning period.

Commercial, recreational fisheries are typically managed to yield a certain catch rate per angler effort (Miko *et al.*, 1995). Stocking rates are generally based on the experience of fishery managers (Cowx, 1994). One accepted method of managing stocking densities is to build a database of experiences to provide guidelines as to which densities maximise the benefits in terms of improving stock (Hickley, 1994). Within this framework, consideration must also be given to the existing stock biomass, migration/dispersion, predation and predicted survival (Cowx, 1994).

1.6.2 Implications of Stocking

Stocking programs for brown trout represent a major component of coldwater sportfisheries management. For example, each year in the United States more than 70 million trout of a catchable size, produced at a cost of $18 million, are stocked to provide recreational fishing for about 18 million anglers (Louis *et al.*, 1982). The principle objective of such programmes is to maximise the return of stocked trout to the angler. Since stocked trout that move out of authorised fishing waters, or into inaccessible areas, constitute a significant recreational and economic loss, the anticipated dispersion patterns of commercially-reared trout and the factors that influence movement are important management considerations (Louis *et al.*, 1982). The dispersion patterns also need to be known to enable the assessment and mitigation of various human impacts, especially in the area of stream regulation (Heggenes *et al.*, 1990).

The conservation of genetically pristine or 'wild' brown trout stocks has become increasingly important in recent years. Possibly the greatest threat to 'wild' brown trout populations is the growing dependence on stocking in rivers and still-waters for recreational fishing (Rangely-Wilson, 1997). Skaala *et al.* (1994) described a considerable contribution of genetic material from introduced hatchery brown trout in the river Oyreselo, Norway. Moran *et al.* (1989) recommended that attempts to repopulate or stock waters should be carried out exclusively using autochthonous stocks. This concern has lead to the formation of angler-based wild brown trout preservation societies such as 'Trout Unlimited' in the United States and 'The Wild Trout Society' in Britain. Both organisations seek to reduce the reliance on stocking policies with an increased use of habitat management strategies. 'Catch and Release' policies are also being advocated by these societies in order to maintain fisheries for the future (Comins, 1997).

To the angler, the number of fish caught is a test of the fishery's worth (Pawson, 1991). Stocking streams and lakes can increase angler catches by increasing the numbers of available fish and by increasing angler effort (Moring, 1993). Pawson (1991) identified a strong and persistent relationship between increased stocking densities leading to increases in catch per unit effort. This is corroborated by Miko *et al.* (1995) who found larger catch rates per angler effort for the higher stocking densities of 2100 and 1400 trout per hectare than 700 trout per hectare. Pawson (1991) also determined that stocking densities were directly linked to angling ability, with less proficient anglers requiring higher stocking densities to achieve an 'average' catch rate.

1.7 Aims of the study

The outcome of stockings aimed at re-establishing or supplementing trout populations will vary depending on the method of stocking and the environment into which they are stocked (Thorve & Carlstein, 1998). Whilst a lot of effort has been directed toward understanding the production of and stocking methods using hatchery-reared salmonids, relatively little is known about the post-stocking behaviour and survival of these fish (Hickley, 1994). Several authors have reported return rates of stocked brown trout varying from <1% to >50% (Wiley *et al.*, 1993; L'Abee-Lund & Langeland, 1995); consequently this variability in stocking success may have profound ecological and economic consequences.

Most brown trout post-stocking behavioural studies have concentrated on flowing rather than standing water bodies, with the general conclusion being that hatchery-reared brown trout are less successful than wild conspecifics (O'Grady, 1983; Johnsen & Ugedal, 1989; Kelly-Quinn & Bracken, 1989). There is little available information concerning the dietary habits of brown trout stocked in lakes (Johnsen & Ugedal, 1989), the post-stocking movements of hatchery-reared salmonids stocked in lakes or the behavioural interactions between wild and hatchery-reared brown trout. Recent studies indicate that: (1) the change from artificial food to natural feeding is considered critical for the successful stocking and subsequent adaptation of hatchery-reared salmonids (Ersbak & Haase, 1983; Bachman, 1984), and that hatchery-reared salmonids may display preconditioned feeding behaviours including ‘look up’ feeding responses (O’Grady, 1983); (2) hatchery-reared salmonids disperse poorly from the site of stocking (Cresswell, 1980; Vehanen *et al.*, 1998); (3) resident salmonids may display a prior resident competitive advantage over stocked salmonids (Brannas, 1995; Glova & Field-Dodgson, 1995; Huntingford & De Leaniz, 1997); and (4) hatchery-reared trout exhibit non-cost effective behaviour which may influence post-stocking survival (Bachman, 1984).

The aims of this study were to:

(1) Compare the growth and diets of the resident brown trout and a potential competitor, the powan (*Coregonus lavaretus* L.) in a large-scale recreational fishery (Carron Valley Reservoir) in order to assess if the available food resource may limit the success of past and present salmonid stocking.

(2) Examine the relative post-stocking temporal changes in the diets of hatchery-reared brown trout (Howietoun strain) following release, with particular emphasis on evidence of a ‘look up’ feeding response and subsequent adaptation to natural prey types in Carron Valley Reservoir.

(3) Examine the ability of hatchery-reared brown trout (Howietoun strain) to maintain body condition following release into Carron Valley Reservoir.

(4) Examine the post-stocking dispersion patterns of hatchery-reared brown trout (Howietoun strain) at Carron Valley Reservoir and conclude if there is any management advantage from adopting ‘scatter planting’ stocking strategies.

(5) Determine if stream resident wild brown trout display a prior resident competitive advantage over subsequent introduced wild and hatchery-reared conspecifics.

(6) Determine if hatchery-reared brown trout (Howietoun strain) display non-cost effective aggressive behaviour.

(7) Determine how quickly hatchery-reared brown trout learn to forage on a novel prey, and examine the subsequent relative short-term changes in feeding efficiency when compared to experienced wild conspecifics.

Chapter 2

Site Description

2.1 Introduction

Lyle and Smith (1994) estimated that there are approximately 31,460 lochs and lochans in Scotland, with 830 surface water sources of potable water. The Carron Valley Reservoir impoundment is the third largest in Scotland supplying 125 Mlday^{-1} (Maitland *et al.*, 1994), with only Loch Lomond and Loch Katrine providing more potable water. Carron Valley Reservoir (Figure 2.1) is situated in the Campsie Hills (Ordnance Survey Grid Reference NS 693078) and has a catchment area of 38.7 km^2 utilised predominantly for hill farming and commercial forestry. The water surface area covers 405 hectares with a mean depth of 8.3m and a maximum depth of approximately 12m at an altitude of 220m above sea level. The Carron Valley was dammed in 1939 to meet the demands of the petrochemical and manufacturing industries at Grangemouth; and now supplies drinking water to Grangemouth, Falkirk, Kirkintilloch, Cumbernauld, Lennoxtown and Milton of Campsie. Although the primary use of the reservoir is as a public water supply, it has been used for the last 50 years as a brown trout fishery. Fishery management strategies at Carron Valley Reservoir have varied over the years from relying completely on natural recruitment to an annual stocking of 15,000 6-8 inch brown trout (Patterson, 1993). Since 1994 a supplemental stocking policy has been implemented to increase the numbers of larger fish available to the anglers, with approximately 3,000 12-14 inch Howietoun strain brown trout, 'scatter planted' in relatively small numbers throughout the early part of the fishing season.

The efficiency and success of stocking with fish may be significantly affected by an extensive array of limnological factors (Wiley *et al.*, 1993). Consequently, it is essential to perform a limnological study of any habitat into which fish are to be stocked in order to identify the potential factors that may influence success. This chapter is a basic overview of the

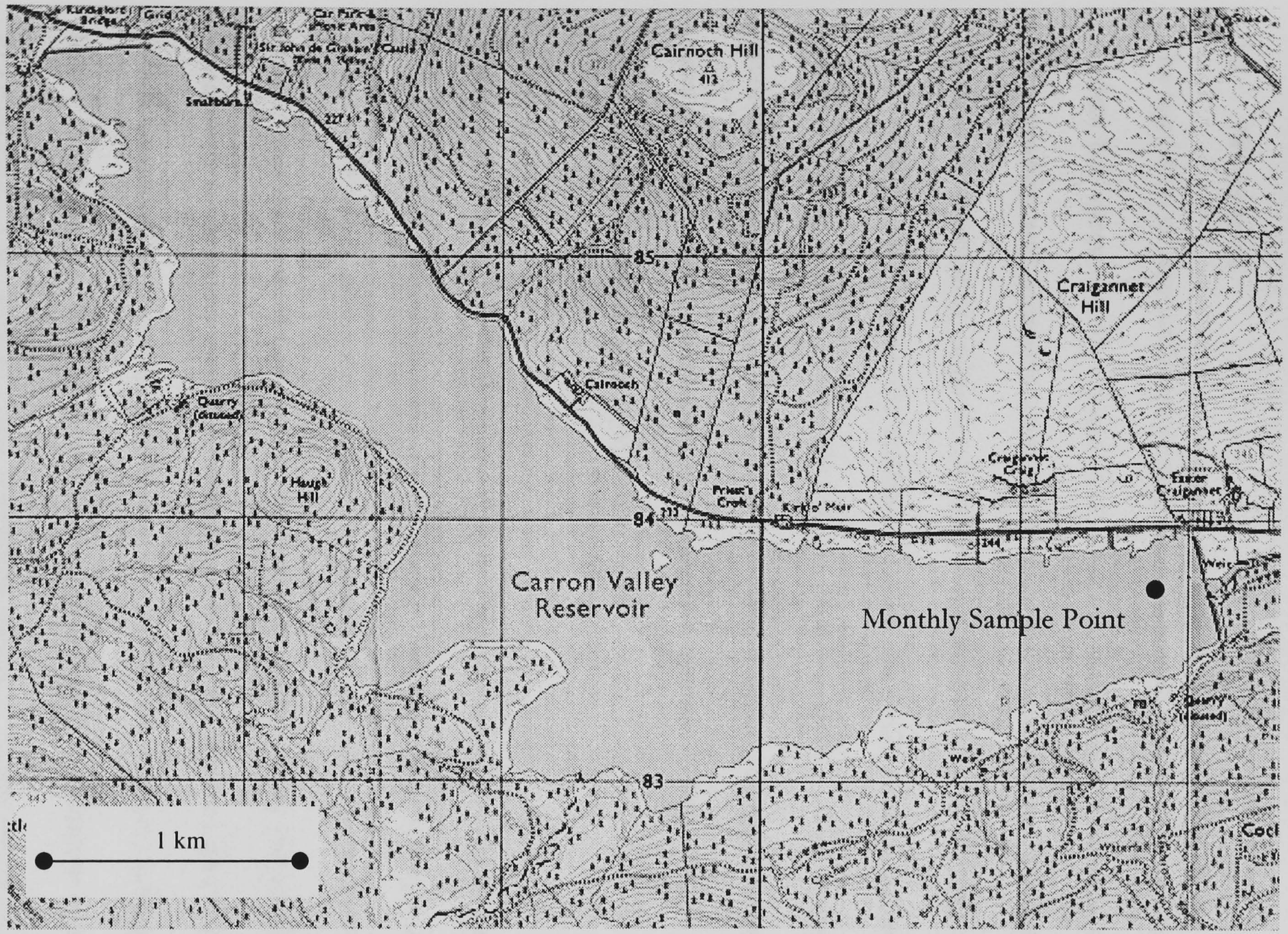


Figure 2.1 - Location of the sample site for water, zooplankton, phytoplankton and profundal macrobenthos sampling at Carron valley Reservoir, 1999

limnological features of Carron Valley Reservoir. The condensed nature of this chapter means that the methods, results and discussions are presented together.

2.2 Water level

The regulation or impoundment of rivers and lakes may result in sub-optimal conditions for resident fish species (L'Abee-Lund *et al.*, 1992) resulting from the restriction of fish access and migration and profound changes in water level and flow conditions (Swales, 1994). Significantly fluctuating water levels reduce the productivity of benthic fauna in littoral zones, which in turn reduces the available food for the resident fish populations, in particular littoral foraging brown trout (Mutenia & Salonen, 1994). This reduction of littoral productivity may cause the trout to switch their foraging strategies to exploit alternative more abundant food items such as other fish species (L'Abee-Lund *et al.*, 1992) or zooplankton (Hesthagen *et al.*, 1995).

Water level data for 1999 were obtained from the East of Scotland Water monitoring station at Carron Valley Reservoir. Figure 2.2 shows the water level changes at Carron Valley Reservoir during 1999. The reservoir remained at/or near maximum capacity between January and mid May. Water levels then steadily declined until the middle of September when water levels in the reservoir reached an annual low of 2.2m below maximum capacity. Levels remained low between mid September and mid November, ranging from 2.2-1.7m below maximum capacity, before steadily increasing back to maximum capacity by the end of December. This trend in water fluctuation change is representative of previous annual water level changes at Carron Valley Reservoir (*pers. comm.*, R. Paton).

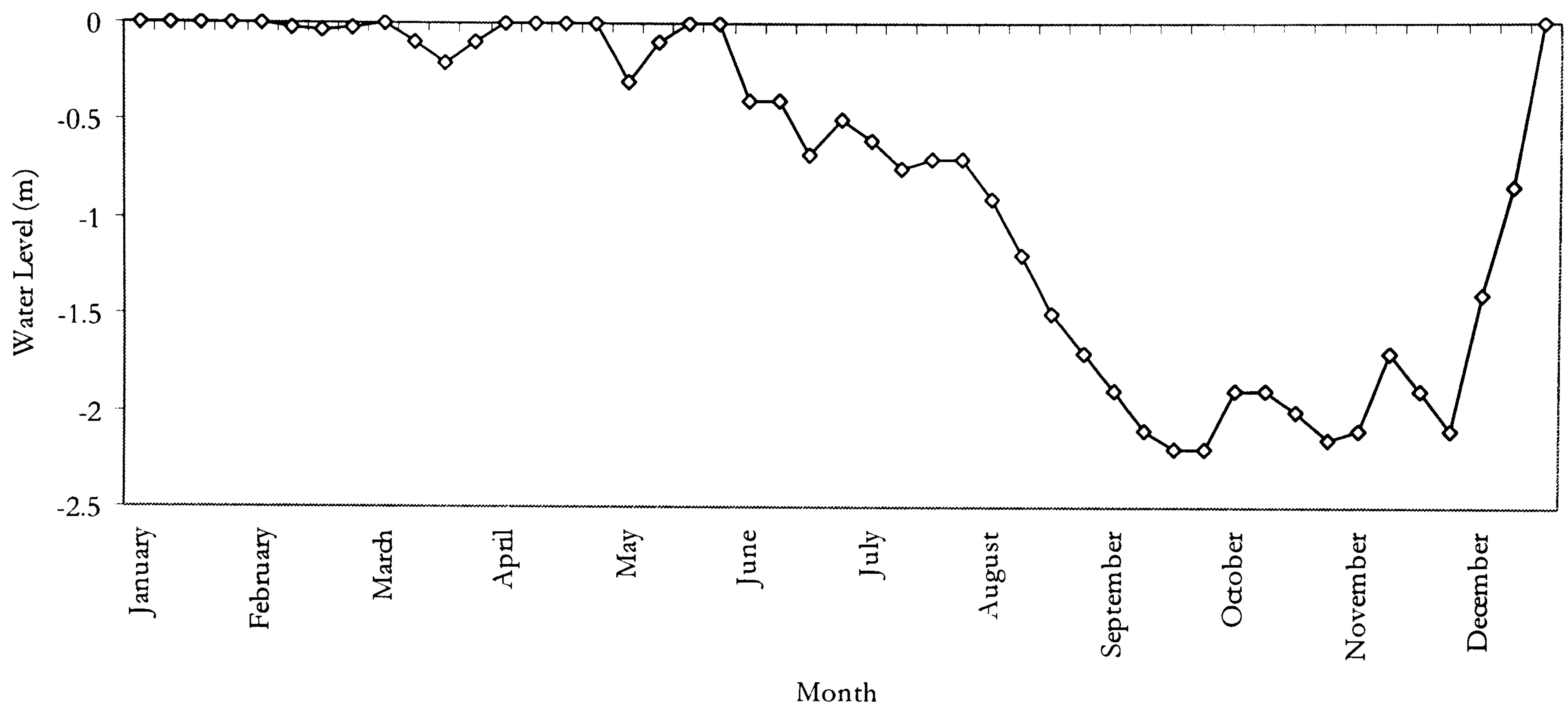


Figure 2.2 - Weekly change in recorded water levels at Carron Valley Reservoir during 1999, expressed as meters below maximum capacity (0m).

Studies examining the impacts of impoundments on ecological systems have shown that benthic macroinvertebrates may be limited by increased siltation, increased nutrient enrichment and fluctuating water levels (Isom, 1971). Hesthagen *et al.* (1999) concluded that the observed limited macroinvertebrate productivity in Vinstervatna Reservoir, Norway was a result of fluctuating water levels and subsequent increased inter and intraspecific competition for the limited food resource by resident fish species. In the same study, Hesthagen *et al.* (1999) observed hatchery-reared brown trout to grow more slowly and exhibit shorter life expectancies than native conspecifics, following release into Vinstervatna Reservoir, Norway. Consequently, the observed annual 'draw down' of Carron Valley Reservoir may significantly affect productivity and the subsequent survival and performance of both native and stocked brown trout.

2.3 Trophic status

The trophic status or productivity of a water body stocked with brown trout has significant implications for both resident and stocked fish communities; affecting primary productivity, habitat diversity, invertebrate prey population dynamics and basic physiological demands such as dissolved oxygen availability (Bean, 1992).

To gauge the baseline water chemistry parameters of the study site, water samples were collected and analysed on a monthly basis during 1999. Water samples were collected from mid-water at the same sample point (Figure 2.1) using a 5l 'Van Dorn' water sampler. All samples were analysed for pH, conductivity, total phosphorous (T.P.), nitrate (NO_3), suspended solids (S.S.) and chlorophyll-a; the methods used were described by Stirling

(1984). Temperature and dissolved oxygen (D.O.) were measured 'in situ' using a portable Clarendon YSI Oxygen/Temperature meter (Model 57).

2.3.1 Water Chemistry

The dissolution and weathering of rocks and soils determines the acid/base status of most Scottish freshwaters, especially those located in upland areas (Harriman & Pugh, 1994). Despite a diverse geological environment, many of the common geological types produce waters of similar quality in Scotland (Harriman & Pugh, 1994). Carron Valley Reservoir is situated in the 'Midland Valley' that is characterised by post-Caledonian igneous geomorphology (Werritty *et al*, 1994). The underlying geology of Carron Valley Reservoir is dominated by Lower Carboniferous Granite (Browne *et al.*, 1993). A Darleith soil association dominates the catchment area that consists mainly of 'Brown Forest', 'Peaty Podzol' and 'Gley' soils (Grieve, 1993). Conductivity, chlorophyll-a, nitrate and total phosphorous are most commonly used as indicators of the trophic status of standing water bodies (Stirling, 1984; Bean, 1992).

Figures 2.3 and 2.4 show the monthly, water chemistry values for 1999. The slightly acidic pH is typical of Scottish standing waters (Harriman & Pugh, 1994), although the large proportion of commercially forested land within the catchment may reduce the pH below its natural level. The reservoir appears to be mildly enriched. With maximum observed gross chemistry values in 1999 of; 21.2 μgl^{-1} of total phosphorous (mean 17.9 μgl^{-1}), 318.8 μgl^{-1} of nitrate (mean 150.1 μgl^{-1}), 8.84 μgl^{-1} of chlorophyll-a (mean 5.42 μgl^{-1}) and a maximum conductivity value of 64.6 μScm^{-1} (mean 61.5 μScm^{-1}). Harriman and Pugh (1994) classified freshwaters in Scotland exhibiting total phosphorous values between 10-30 μgl^{-1} and nitrate

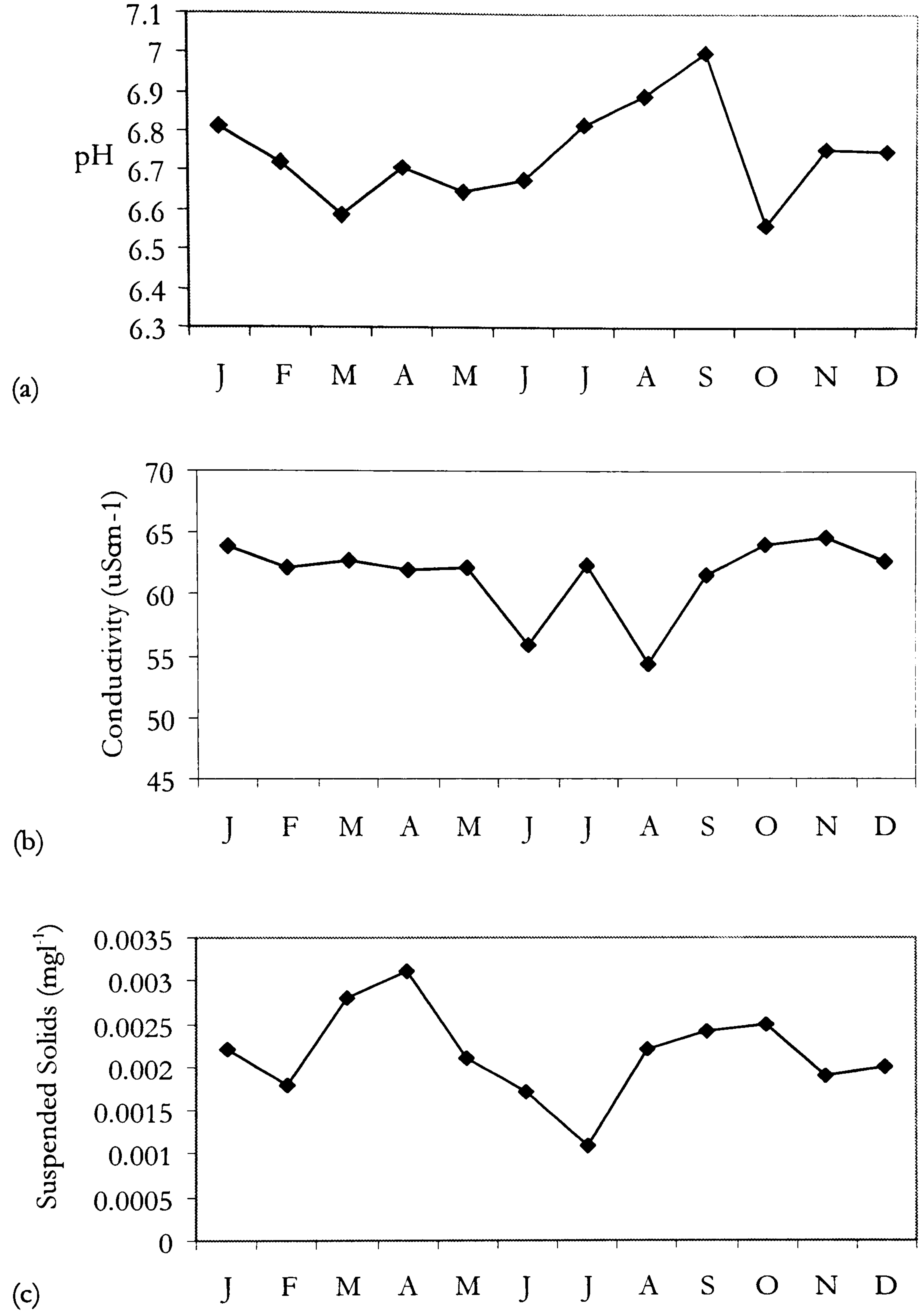


Figure 2.3 - (a) pH, (b) Conductivity and (c) Suspended Solids values for Carron Valley Reservoir for each month of 1999.

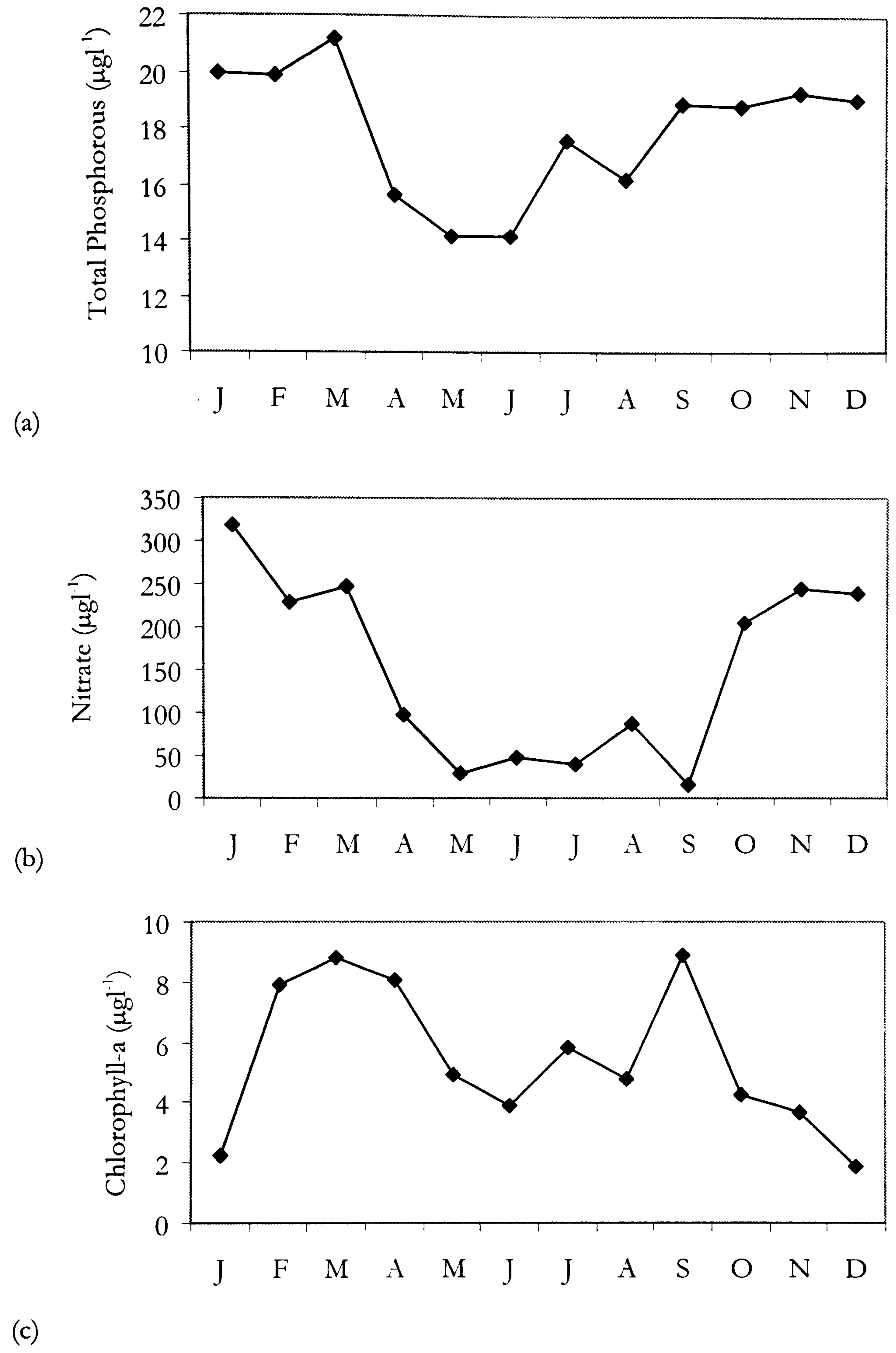


Figure 2.4 - (a) Total Phosphorous, (b) Ammonia and (c) Chlorophyll-a values for Carron Valley Reservoir for each month of 1999.

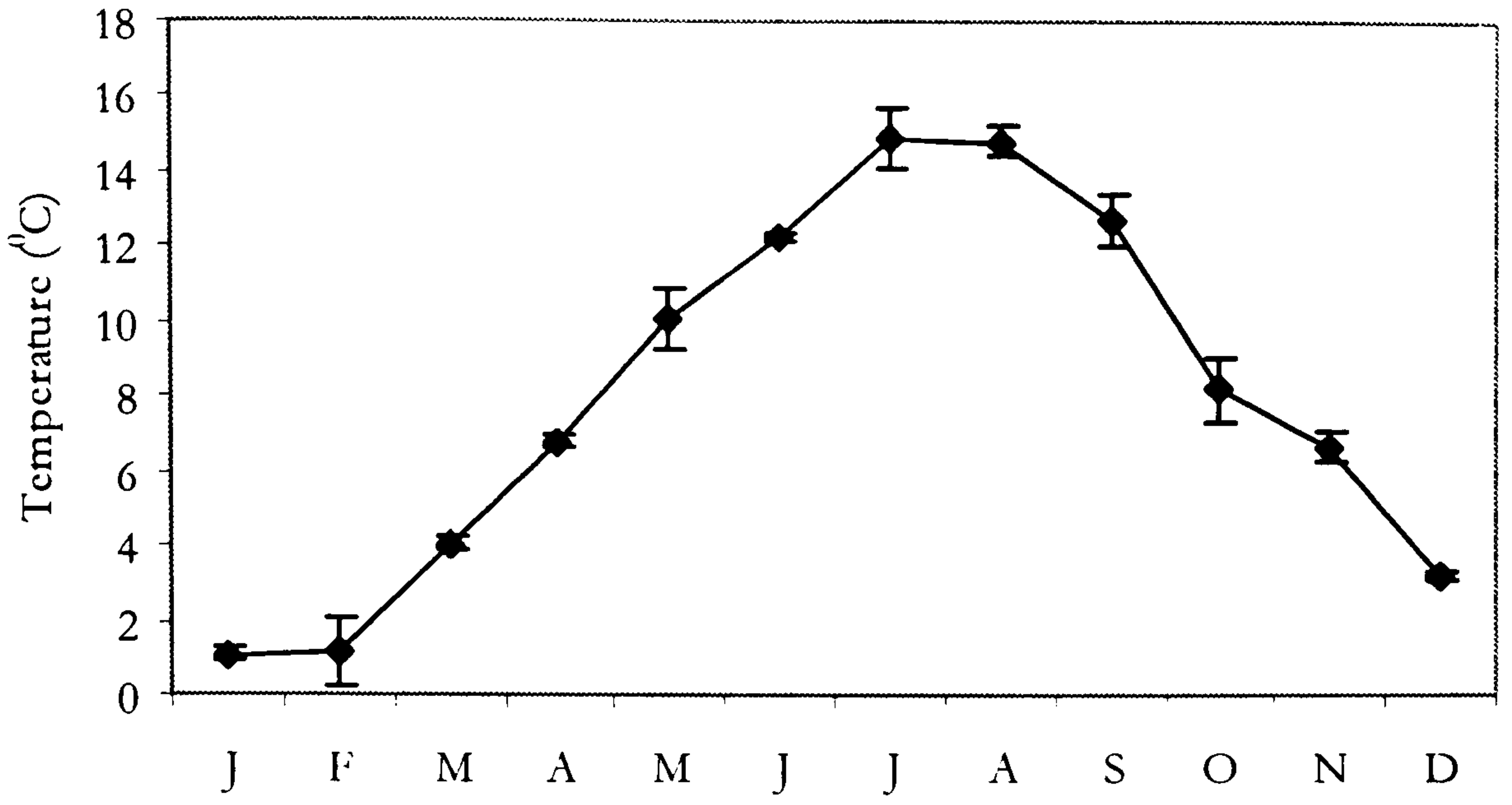
values between 300-650 μgl^{-1} as being meso-eutrophic. The seasonal total phosphorous and nitrate concentrations observed correspond to meso-eutrophic trends observed in other western European freshwaters with the relative P and N concentrations reducing during the summer months. Reynolds (1984) observed nutrient enrichment occurring in standing waters with long hydraulic retention times (such as dammed reservoir systems) in relation to the relative accumulation of autochthonous and allochthonous organic material. It seems likely that the deposition of organic matter from the surrounding forested areas into this dammed catchment system must have some impact on the nutrient availability within the sediments. The periodicity of the suspended solid values (Figure 2.3) suggests that much of the organic deposition and wind induced re-suspension of the upper sediment layers occurs in the autumn and winter periods. The water chemistry at Carron Valley Reservoir may be influenced by the predominance of commercial forestry as the major landuse in the catchment. It has long been established that afforestation decreases pH and increases nitrogen, potassium and phosphorous loading in freshwater systems through pollutant interception and fertiliser leaching, whilst deforestation increases organic and suspended solid inputs into freshwater systems (Best, 1994).

2.3.2 Temperature and Oxygen

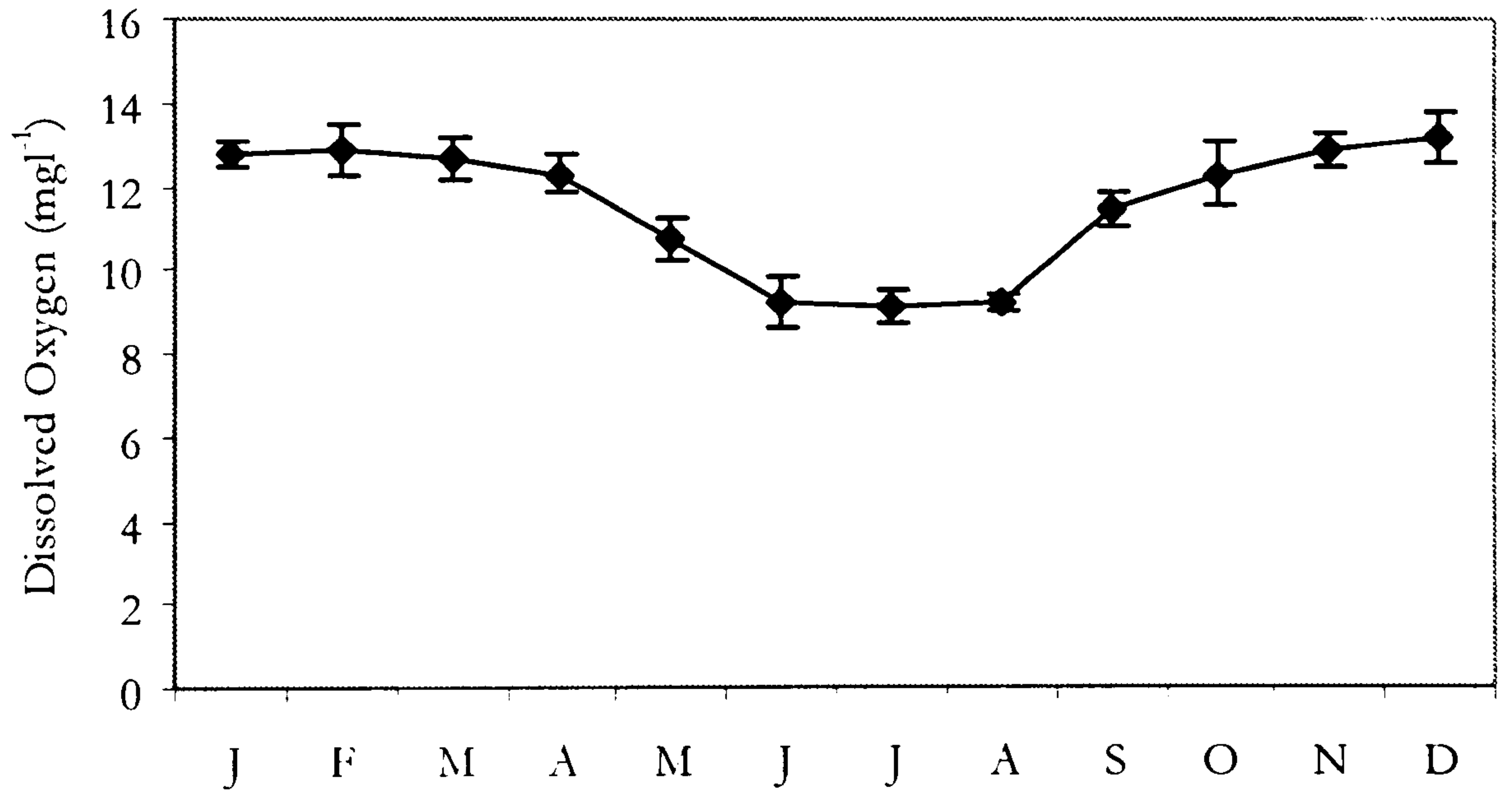
Adequate temperature levels are an essential pre-requisite for primary production, which in turn affects the amount of dissolved oxygen in lentic habitats (Alabaster & Lloyd, 1980). Temperature is an important determinant of geographical range for many biota (Varley, 1967) and as most aquatic animals exhibit poikilothermic physiologies, water temperature has important effects on activity levels, survivorship, growth and recruitment (Weiser, 1991). Variations in the dissolved oxygen concentrations in natural waters arise from a number of both spatial and temporal sources with salmonid fish being particularly sensitive to any change (Elliott, 1994). Brown trout require a temperature range of between 4.0-19.5°C for successful growth, with a lower limit for survival of 0°C and an upper limit of between 25-30°C (Elliott, 1994). Salmonids require higher dissolved oxygen concentrations than most other fish species, with a minimum concentration of $5mgl^{-1}$ for survival (Elliott, 1994).

In 1999 mean surface water temperature in Carron Valley Reservoir ranged from a winter low of 1°C to a summer high of 14°C (Figure 2.5). Carron Valley Reservoir in 1999 was monomictic with relatively little surface freezing due to wind action preventing the formation of large ice sheets. Seasonal temperature profiles (Figure 2.6) revealed that the reservoir was generally isothermic with little or no thermal stratification due to the effects of wind action and convection currents in the relatively shallow waters. These seasonal trends in water temperature changes is representative of previous annual water level changes at Carron Valley Reservoir (*pers. comm.*, R. Paton). Throughout 1999, water temperature remained within the range for brown trout survival and was within the optimal range for growth between April to November.

Mean surface dissolved oxygen concentrations ranged from a summer low of $9.1mgl^{-1}$ to a winter high of $12.9mgl^{-1}$ (Figure 2.5). Despite increased photosynthetic activity during the summer months, dissolved oxygen concentrations were the lowest during this period (Figure 2.7). Increased temperatures and microbial activity are probably the causative agents for oxygen depletion during this period (Bean, 1992). However throughout 1999, dissolved oxygen levels remained well within the range required for the survival and growth of brown trout.



(a)



(b)

Figure 2.5 - The mean (a) annual water temperature (± S.E.) and (b) annual dissolved oxygen concentrations for Carron Valley Reservoir during 1999.

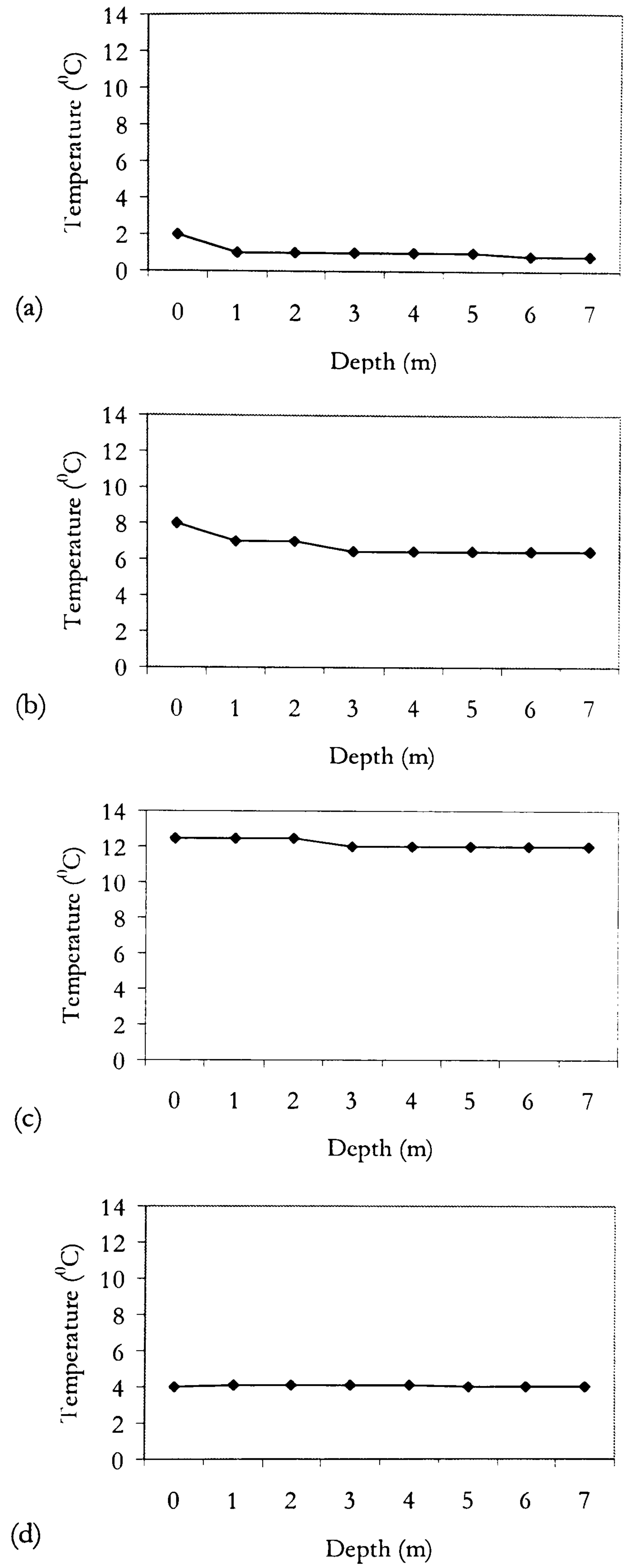


Figure 2.6 - (a) Winter, (b) Spring, (c) Summer and (d) Autumn temperature profiles for Carron Valley Reservoir during 1999.

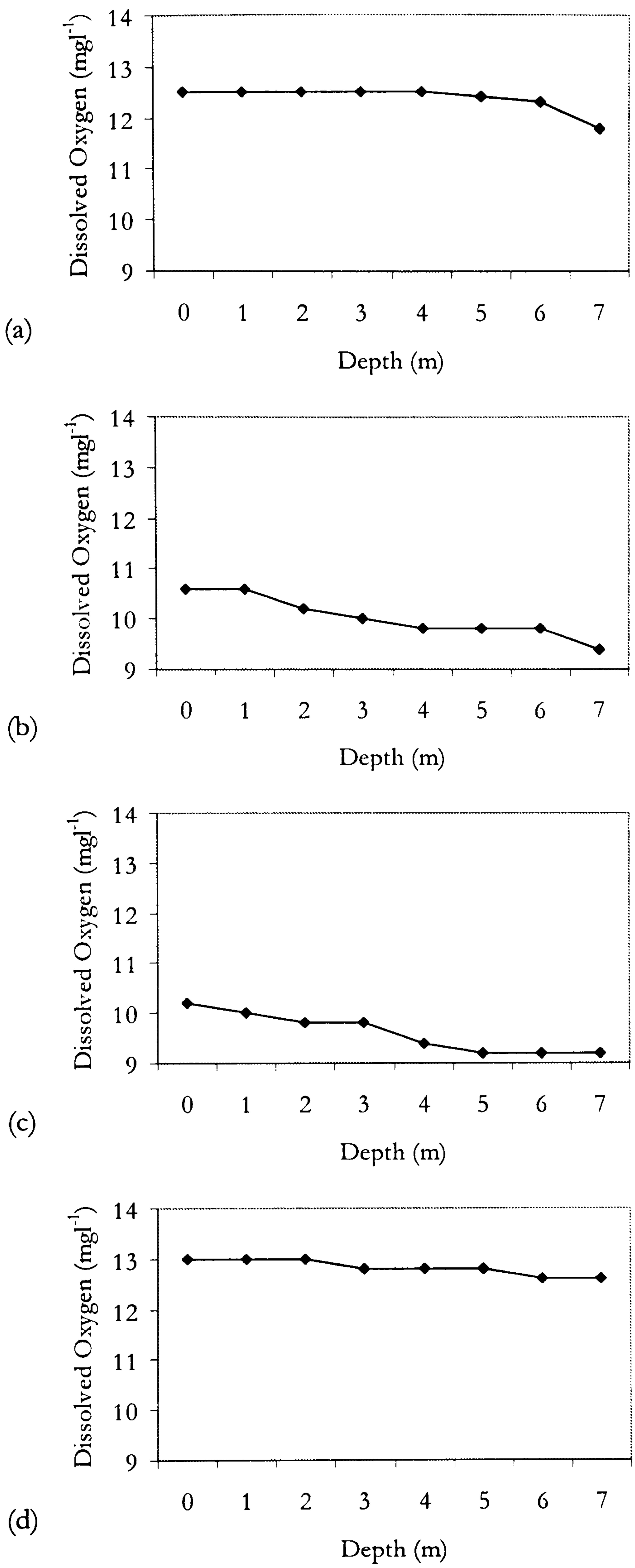


Figure 2.7 - (a) Winter, (b) Spring, (c) Summer and (d) Autumn Dissolved Oxygen profiles for Carron Valley Reservoir during 1999.

2.4 The Biota

2.4.1 Phytoplankton

Primary production is the capacity of an ecosystem to build up primary organic compounds using energy derived from external radiant and chemical sources (Vollenweider, 1972). The accumulated observations on phytoplankton and the relative ease with which phytoplankton communities may be sampled has led to its emphasis as the major primary producer within static freshwater systems (Westlake, 1980). Phytoplankton are particularly important in freshwater ecosystems because of their close relationship with zooplankton, and ultimately fish, biomass (Bean, 1992).

Total phytoplankton content (chlorophyll-a) was measured from 11 water samples using the spectrophotometer technique described by Vollenweider (1972) (Figure 2.3(c)). Surface phytoplankton samples were collected monthly using trawled phytoplankton nets (53µm mesh size). Samples were preserved in 100ml plastic containers with the addition of 'Lugols Iodine' (Bean, 1992). Phytoplankton samples were subsequently examined under a compound microscope (Olympus BH-2 phase-contrast), where species were recorded and the abundance of the dominant species was quantified using a haemocytometer (Neubauer, Germany).

Table 2.1 shows the phytoplankton species present in Carron Valley Reservoir during 1999. Whilst recognising the spatial and temporal patchiness of phytoplankton communities, the phytoplankton community at Carron Valley Reservoir follows the general seasonal trends observed in a wide range of temperate lakes (Reynolds, 1984) (Figure 2.8). The spring population is dominated by Bacillariophyceae (diatoms): *Asterionella formosa, Tabellaria* sp. and

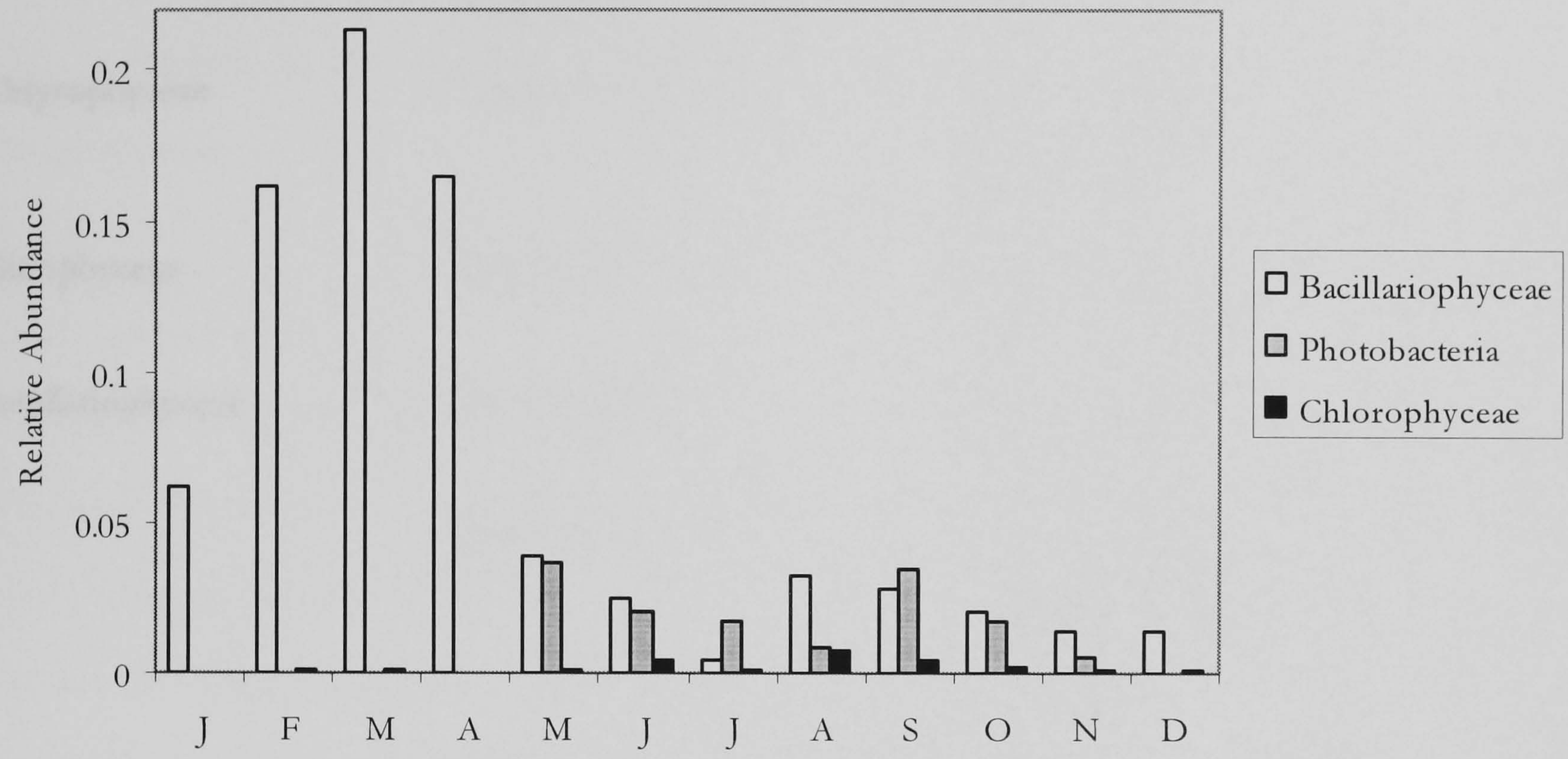


Figure 2.8 - The seasonal relative abundance's of the dominant phytoplankton species in Carron Valley Reservoir during 1999 (after Reynolds, 1984).

Table 2.1 - Phytoplankton species observed in Carron Valley Reservoir during 1999 (after Reynolds, 1984).

Class	Order	Species
Photobacteria	Chroococcales	*Microcystis flos-aquae* *Coelosphaerium kuetzingianum*
	Nostocales	*Oscillatoria redekii*
Chrysophyceae	Ochromonadales	*Dinobryon divergens* *Mallamonas acaroides* *Synura ulvella*
Dinophyceae	Peridinales	*Peridinium* sp. *Ceratium hirundinella*
Bacillariophyceae	Biddulphiales	*Melosira varians* *Stephanodiscus* sp.
	Bacillariales	*Tabellaria fenestrata* *Tabellaria flocculosa* *Asterionella formosa* *Synedra ulna* *Nitzschia* sp.
Chlorophyceae	Chlorococcales	*Pediastrum boryanum* *Ankistrodesmus falcatus* *Kirchneriella obesa* *Scenedesmus denticulatus*
	Zygnematales	*Staurastrum anatinum* *Staurastrum singulum* *Staurastrum punctulatum* *Staurastrum orbiculare* *Staurastrum longispinium* *Cosmatium circulare* *Cosmarium pyramidatum* *Cosmarium praemorsum* *Spondylosium planum*

Melosira varians, probably due the relative ability of diatoms to maintain overwintering populations and consequently provide the largest initial inoculum in the early spring. During the summer months, the relative dominance of diatoms reduced as the relative abundance of Photobacteria (blue/green algae) and Chlorophyceae (green algae) species increased. With *Microcystis flos-aquae* and *Oscillatoria redekii* being the dominant Photobacteria, and *Kirchneriella obesa, Pediastrum boryanum, Cosmarium* sp. and *Staurastrum* sp. being the dominant Chlorophyceae.

2.4.2 Zooplankton

The importance of zooplankton in transferring energy from phytoplankton, bacteria and organic detritus to higher trophic levels has been well documented (Lazzaro *et al.*, 1992)). Due to the size selective feeding of salmonids, zooplankton prey are of particular dietary importance to juvenile fish (Wankowski & Thorpe, 1979), whilst at times of peak zooplankton abundance they may become the dominant prey items of resident adult fish populations in still waters (Pomeroy, 1991). Consequently the intensity of fish predation may determine the composition of the zooplankton community in any given ecosystem (Fozzard *et al.*, 1994). The Scottish zooplankton fauna is characterised by common European species with Arctic and sub-alpine elements, with individual zooplankton communities being composed of relatively few species (Fozzard *et al.*, 1994).

Zooplankton were sampled monthly from mid-water using a 5l 'Van Dorn' water sampler as a modified Patalas trap. The trap has a rapid closing system which may reduce the possibility of zooplankton avoidance reactions and can be easily handled from a boat (Bean, 1992). The 5l zooplankton samples were condensed to a total volume of 90ml by filtering through a phytoplankton net (53µm mesh size) to ensure no Rotifera were lost. Samples were preserved by the addition of 10ml of 100% ethanol. Zooplankton samples were subsequently analysed using a dissecting microscope (Olympus SZ40), identified using current Freshwater Biological Association taxonomic keys and counted.

The zooplankton fauna of Carron Valley Reservoir was found to be relatively simple (Table 2.2). Figures 2.9 and 2.10 show the mean monthly abundances of the major zooplankton groups. Rotifers dominated the samples throughout the year, with *Keratella cochlearis* the most abundant species. Cladocera tended to increase in abundance in tandem with temperature and primary productivity, consequently maximum abundances for *Daphnia hyalina* and *Bosmina longirostris* were observed in the spring and summer months. *Holopedium gibberum* is absent in many of the winter, spring and autumn samples but dominates the cladoceran community during July. The predatory cladoceran *Leptodora kindtii* occurred regularly in relatively small numbers throughout the spring and summer months. Fozzard *et al.* (1994) concluded that zooplankton communities dominated by *Keratella cochlearis* and cladoceran species are indicative of mesotrophic Lochs in Scotland. However, the sporadic dominance of *Cyclops strenuus abyssorum* suggests a shift towards a eutrophic environment (Fozzard *et al.*, 1994).

2.4.3 Macroinvertebrates

In functional terms, macroinvertebrates are secondary producers and an important component of freshwater ecosystems. Macroinvertebrates are an important component of the diets of most species of freshwater fish (Fozzard *et al.*, 1994). Several studies examining

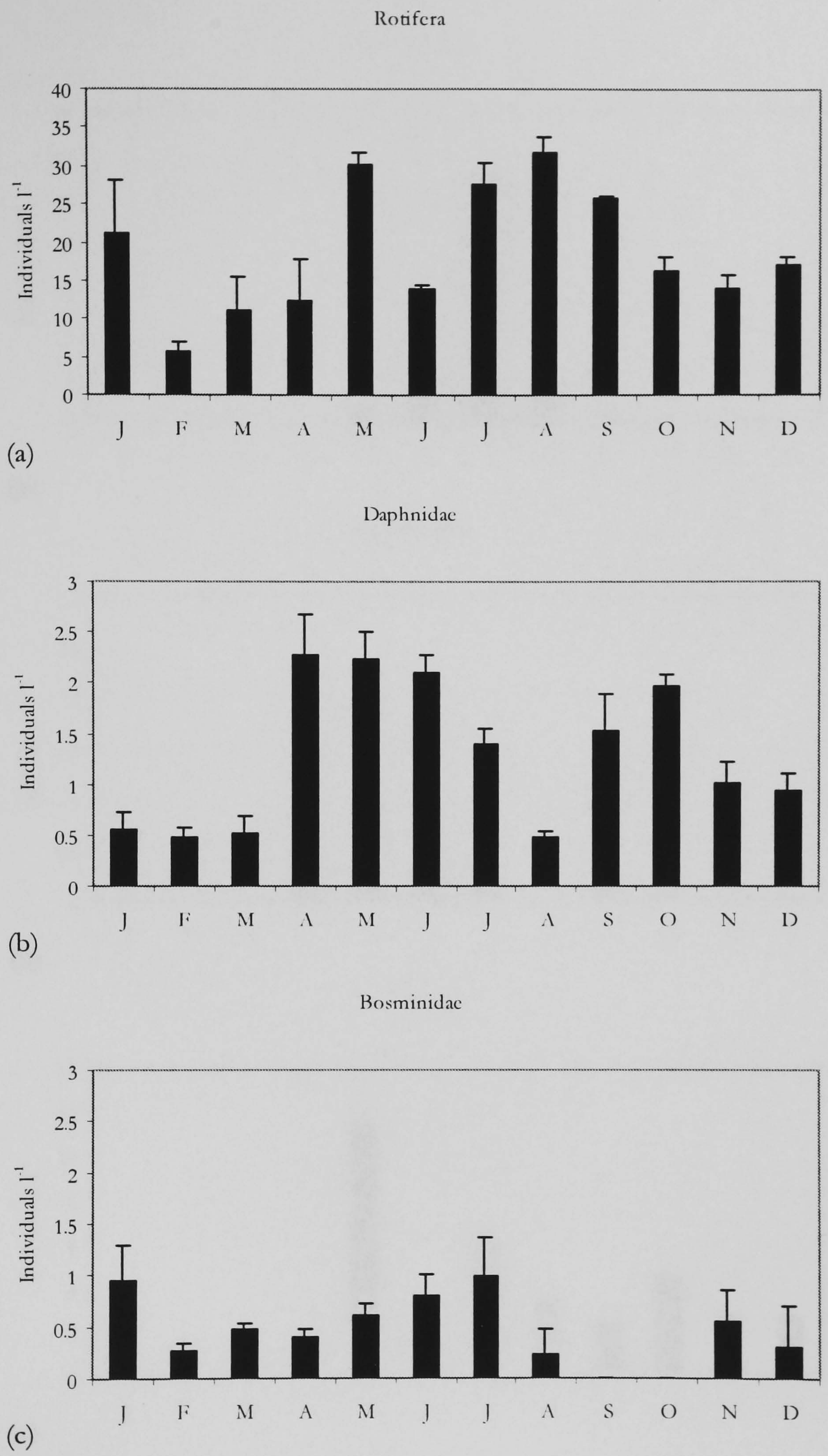


Figure 2.9 - Mean (± S.E.) monthly abundance's of (a) Rotifera, (b) Daphnidae and (c) Bosminidae observed in Carron Valley Reservoir during 1999.

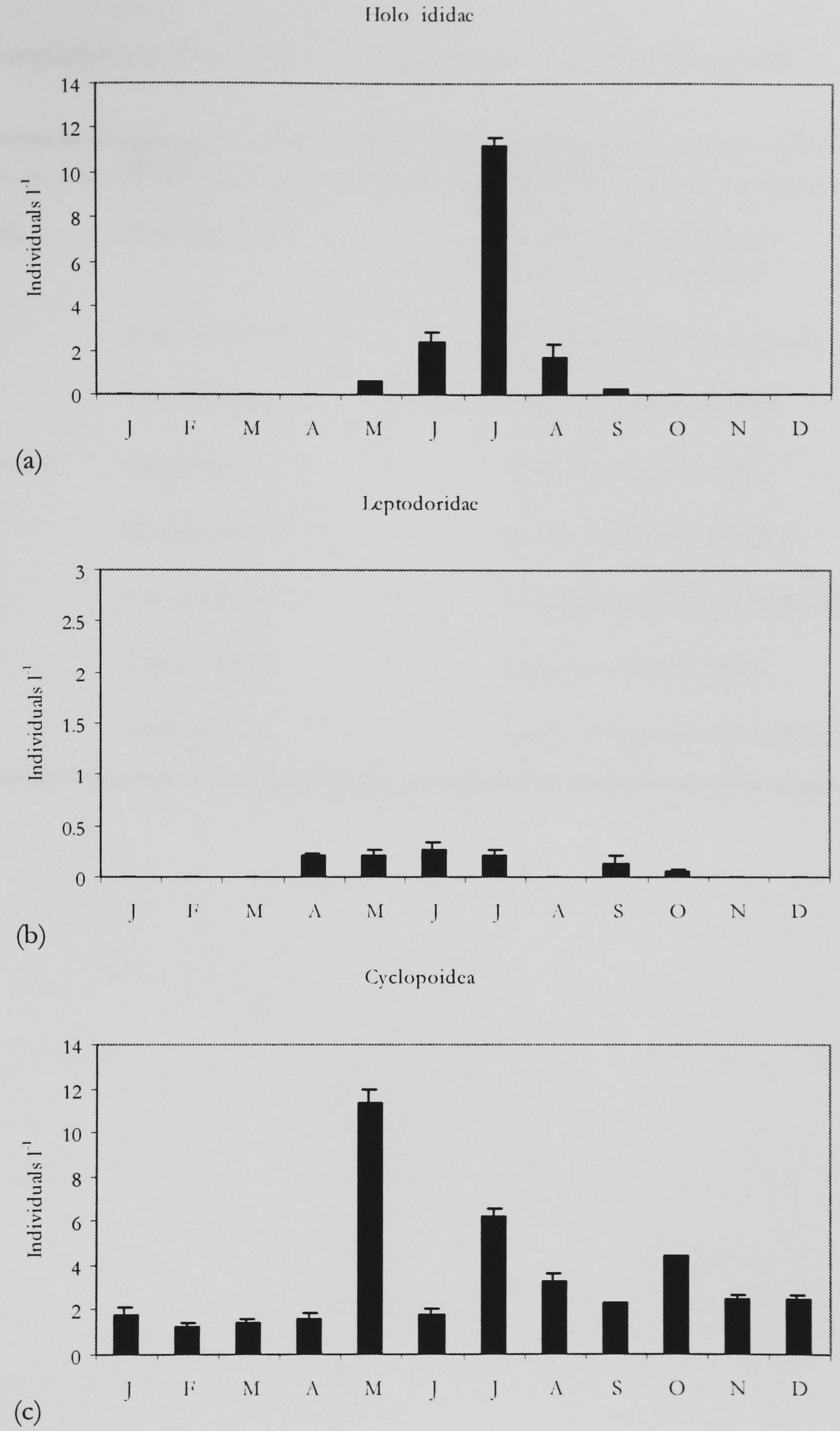


Figure 2.10 - Mean (± S.E.) monthly abundance's of (a) Holopididae, (b) Leptodoridae and (c) Cyclopoidea observed in Carron Valley Reservoir during 1999.

Table 2.2 - Zooplankton species observed in Carron Valley Reservoir during 1999.

	Family	Species
Planktonic Rotifera	Branchionidae	*Keratella cochlearis* (Gosse) *Brachionus rubens* (Ehrb)
	Asplanchnidae	*Asplanchna priodonta* (Gosse)
	Synchaetidae	*Polyarthra vulgaris* (Carlin)
Planktonic Cladocera	Daphnidae	*Daphnia hyalina* (Leydig)
	Bosminidae	*Bosmina longirostris* (Muller)
	Holopedidae	*Holopedium gibberum* (Zaddach)
	Leptodoridae	*Leptodora kindti* (Focke)
Copepoda	Cyclopoidea	*Cyclops strenuus abyssorum* (Sars)

the diets of resident lotic and lentic dwelling salmonids have identified macroinvertebrate prey as one of the most significant food groups (O'Grady, 1983; Kelly-Quinn & Bracken, 1989; Johnsen & Ugedal, 1990; Bridcut & Giller, 1995; Johnson *et al.*, 1996).

Samples were taken at three monthly intervals throughout 1999. During each sample period five profundal benthos samples were obtained using a 0.25m^2 Ekman grab, whilst five littoral samples were collected using a kicknet. It soon became apparent that due to substrate differences and patchiness within the invertebrate communities, the relatively low numbers of samples collected were of little use as a quantifiable technique. Consequently the collected macroinvertebrate data were only used as a qualitative measure. All collected macroinvertebrate samples were stored in 100% ethanol and later identified under a dissection microscope (Olympus SZ40) using current F.B.A taxonomic keys.

The macroinvertebrate species found in Carron Valley Reservoir during 1999 are shown in Table 2.3. The reservoir is relatively species-rich, with 29 species of macroinvertebrates from 26 families spanning 12 groups. Several nutrient tolerant macroinvertebrate forms were observed (e.g. *Sericostoma personatum, Phryganea* sp., *Limnephilus* sp., *Anabolia* sp., *Stenophylax* sp., *Philopotamus* sp., *Polycentropus* sp. and *Nemoura* sp.) suggesting that the water quality in the reservoir is relatively pollution free but with some organic enrichment. In lakes and lochs generally, littoral zones have the highest rates of primary and secondary production with the highest diversity of macroinvertebrates (Bean, 1992). However, little species differentiation was observed between the littoral and profundal environments at Carron Valley Reservoir, probably due to invertebrate abundance patchiness, low sampling frequency and fluctuating water levels. Fozzard *et al.* (1994) stated that in shallow non-

Table 2.3 – Macroinvertebrate species observed in Carron Valley Reservoir during 1999.

Order	Family	Species
Oligochaeta	Tubificidae	*Tubifex* sp.
Rhynchobdellae	Glossiphoniidae	*Helobdella stagnalis*
Pharyngobdellae	Erpobdellidae	*Erpobdella octoculata*
Prosobranchia	Valvatidae	*Valvata piscinalis*
Pulmonata	Lymnaeidae	*Lymnea stagnalis*
	Planorbidae	*Planorbis (Coretus) vorneus*
	Ancylidae	*Acroloxus lacustris*
Cyrenodonta	Sphaeriids	*Pisidium* sp.
Amphipoda	Gammaridae	*Gammarus* sp.
Isopoda	Asellidae	*Asellus aquaticus*
Plecoptera	Nemouridae	*Nemoura* sp
Hemiptera	Corixidae	*Corixa sp.*
Megaloptera	Sialidae	*Sialis* sp.
Trichoptera	Philopotamidae	*Philopotamus* sp.
	Polycentropidae	*Polycentropus* sp.
	Hydropsychidae	*Hydropsyche* sp.
	Glossosomatidae	*Glossoma* sp.
	Phryganeidae	*Phryganea* sp.
	Limnephilidae	*Anabolia* sp. *Stenophylax* sp. *Limnephilus* sp.
	Sericostomatidae	*Sericostoma personatum*

Table 2.3 – continued from previous page

Order	Family	Species
Diptera	Tipulidae	*Tipula* sp.
	Simuliidae	*Simulus* sp.
	Chironomidae	*Chironomus* sp.
Coleoptera	Dytiscidae	*Dytiscus* sp.. *Platambus* sp.
	Hydrophiliidae	*Helochares lividus*
	Helodidae	*Helodes* sp.

stratifying lochs the benthos throughout the whole loch may resemble a sub-littoral fauna (e.g. Gartmorn Dam, Clackmannan).

2.4.4 Fish

The freshwater fish fauna of Scotland is substantially impoverished compared to the communities found further south in Britain and elsewhere in Europe, however 42 of the 55 recorded British species are found in Scotland (Maitland, 1994). The colonisation of Scotlands' fresh waters by fish has occurred since the last ice age by the natural distribution of euryhaline species (e.g. Atlantic salmon, brown trout, powan, etc.), the natural dispersal of freshwater species (e.g. pike, minnow, stone loach, etc.) and by deliberate introduction (e.g. rainbow trout, common carp, ruffe, etc.) (Maitland, 1994).

In comparison with nearby Loch Lomond, the species composition of Carron Valley Reservoir is relatively poor. A complete list of the species present in Carron Valley Reservoir is shown in Table 2.4. The brown trout, minnow, three-spined stickleback and stone loach probably all spread into the Carron Valley catchment naturally prior to the damming of the valley. However, following the construction of the dam considerable numbers of brown trout from a variety of farmed and wild sources were introduced, effectively eliminating the potential for an identifiable genetic population of wild brown trout at Carron Valley Reservoir. Powan were introduced into Carron Valley Reservoir from Loch Lomond in 1988 and 1989 as a conservation measure when the sustainable status of the Loch Lomond Powan was in doubt.

Table 2.4 - Fish species observed in Carron Valley Reservoir in 1999.

'Common' name	**Family**	**Species**
Brown trout	Salmonidae	*Salmo trutta* L.
Powan	Coregonidae	*Coregonus lavaretus* L.
Minnow	Cyprinidae	*Phoxinus phoxinus* L.
Three-spined Stickleback	Gasterosteidae	*Gasterosteus aculeatus* L.
Stone loach	Cobitidae	*Neomachilus barbatulus* L.

Chapter 3

General methods and a review of method choices

3.1 Marking and tagging

Marking is an essential technique for fisheries researchers and managers, and many different styles of marking have been tried. Ideally marks should remain unaltered during the fishes' lifetime. This means that ideally the mark should not affect the fish's behaviour or vulnerability to predators, not tangle in weeds or nets, be inexpensive, fit all fish sizes, be easy to apply, create no health hazard to the fish and be easy to detect in the field (Nielson, 1992). However no single marking system has been found that satisfies all of these requirements (Nielson, 1992). Generally the different marking methods available for use by the research scientist fall into one of several groups; these are external tags, external marks, internal tags, natural marks, biotelemetric tags, genetic identifiers and chemical markers.

3.1.1 External marks and tags

Fin clipping is a method of fish marking that involves either total or partial fin removal (Nielson, 1992). All fins have been used for marking at one time or another, but current preference is for clipping adipose, pelvic or pectoral fins. The advantages that fin clipping present to the researcher are that the procedure is easily carried out, is inexpensive and allows the rapid identification of stocked fish (Nielson, 1992). Partial fin clips are most often useful for short-term purposes. However, clipped fins do not identify individual fish and mistakes may be made in identification of clipped individuals if naturally mutilated fish are captured. Fin clipping can also result in significant mortalities (Nielson, 1992). Mortality and reduced fish performance depends on which fin is clipped and the species of fish that is to be marked (Nielson, 1992). In salmonids it was found that the removal of the adipose fin caused the lowest increase in mortalities of any fin clipping method; however, the mortality rate in adipose fin clipped individuals was still 50% higher than that of the natural population (Nicola & Cordone, 1973).

External tags fall into three categories; (a) transbody tags, protrude through both sides of the fish, (b) dart-style tags, protrude through only one surface of the fish and (c) internal-anchor tags, flat disc anchor system that is inserted through a small incision (Nielson, 1992). Problems of tag loss, mortality and reduced growth have been associated at times with external tags (Bryan & Ney, 1994).

3.1.2 Internal tags

Internal tags have until recently fallen into two main categories; gastric tags, inserted orally and intraperitoneal tags inserted surgically (Nielson, 1992). Recent advances include coded wire tags, which are inserted into the 'nose' of a fish, have a high retention rate and are easily applied (Nielson, 1992). The most recent internal tag to be developed are visible implant (VI) tags. A VI tag consists of an alphanumerically labelled strip of plastic that is injected under transparent skin tissue by syringe (Bryan & Ney, 1994). These tags combine the advantages of an internal tag (no behavioural impacts, does not tangle in nets) with the advantages of an external tag (easy to identify individuals) (Nielson, 1992). These tags are suitable for marking juvenile brown trout over a minimum size of 15 cm (Niva, 1995). Tag retention has been observed at 65% (Bryan & Ney, 1994) and is assumed to increase with increasing fish size and tagging experience of the operator (Niva, 1995).

Both 'Visible Implant' and 'Floy' style tags were used in this study in conjunction with an angler survey programme to examine the gross post-stocking distribution patterns of hatchery-reared brown trout released into Carron Valley Reservoir. The relative reporting rates of both 'Visible Implant' and 'Floy' style tags were compared to assess their relative benefits in angler survey programmes (Chapter 6). A combination of Alcian Blue 'panjet' marks were used to batch mark all of the hatchery-reared brown trout stocked into Carron Valley Reservoir during the 1999 fishing season. Angler returns of the Alcian Blue marked hatchery-reared trout were used to assess time series post-stocking dietary analysis (Chapter 5), and to establish the relative dietary differences between angler and gillnet caught trout (Chapter 5).

3.1.3 Biotelemetry

In addition to conventional tagging methods, fish movements and habitat use patterns can be elucidated using radio or ultrasonic tracking systems. Ultrasonic tags are less convenient than radio tags as signal frequency may drift substantially and the signals must be received underwater; whereas, radio tag signals are detectable in air and the frequency drifts less (Nielson, 1992). Radio tags produce electromagnetic waves between a frequency range of 25-500MHz (Biotrack Ltd, Dorset, UK), that allow individual fish to be located with receiving equipment. The advantages of the use of radio tags are that they allow remote sensing of animals, allow constant monitoring of individual fish, and the signals have a large detection area (Nielson, 1992). The disadvantages of using radio tags are that they are expensive, they may effect growth and behaviour of tagged fish and they cannot be used in saline water (Nielson, 1992). It has also been found that radio tags must not weigh more than 1.5% of the fishes body weight and that the tags may decrease the fishes ability to escape predators (Ross & McCormick, 1981).

Several hatchery-reared brown trout were radiotagged (Figures 3.1 & 3.2) and tracked during the 1999 fishing seasons to provide fine scale movement information on the post-stocking distribution of hatchery-reared brown trout in Carron Valley Reservoir (Chapter 6).

3.2 Methods of fish capture

3.2.1 Gill netting

Gill nets are widely used as a research tool for routinely sampling reservoir fish populations (Borgstrom, 1992). They can be used to sample nearshore and offshore sites, and vertical population distribution when horizontal nets are placed at specific depths or when nets are fished vertically (Hamley, 1975). Vertical gill nets have been found to be more effective for measuring depth distribution of fish than horizontal nets of different depths (Van Den Avyle *et al.*, 1995). Hamley (1975) listed several factors that may effect gillnet selectivity, these included mesh size, elastic and inelastic stretching of the net, strength and visibility of the twine, hanging coefficient of the net and shape of the fish. It is suggested that the probability of catching a fish in a gill net is largely a function of the probability of encounter (Borgstrom, 1992). The probability of encounter is likely to be proportional to the distance travelled, swimming speed and search pattern of the fish (Borgstrom, 1992). Hamley (1975) recognised three ways in which a fish may become stuck in a gill net:

- the fish may become wedged - where it is held by the mesh around the body.
- the fish may become gilled - where the mesh is caught on the gill opercula.
- the fish may become entangled - where the fish is held by body projections such as fins, maxilla and teeth.

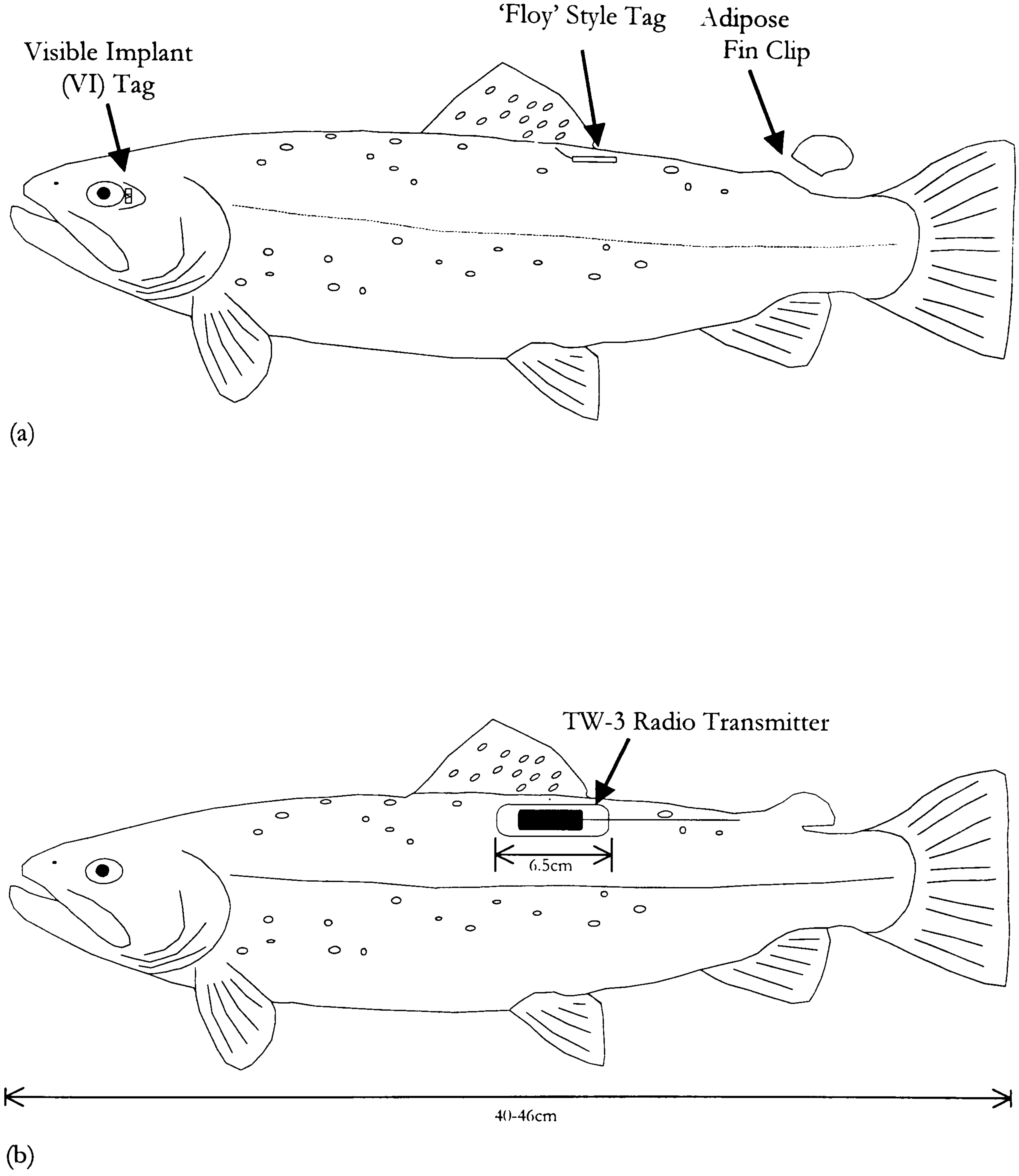


Figure 3.1 - External view of (a) the tag application position for Visible Implant (VI) tags, 'Floy' style tags and adipose fin clips; and (b) the comparative size and position of the sub-dorsally mounted radio transmitters used to monitor the gross and fine scale distribution of hatchery-reared brown trout at Carron Valley Reservoir between April 1998 and June 2000.

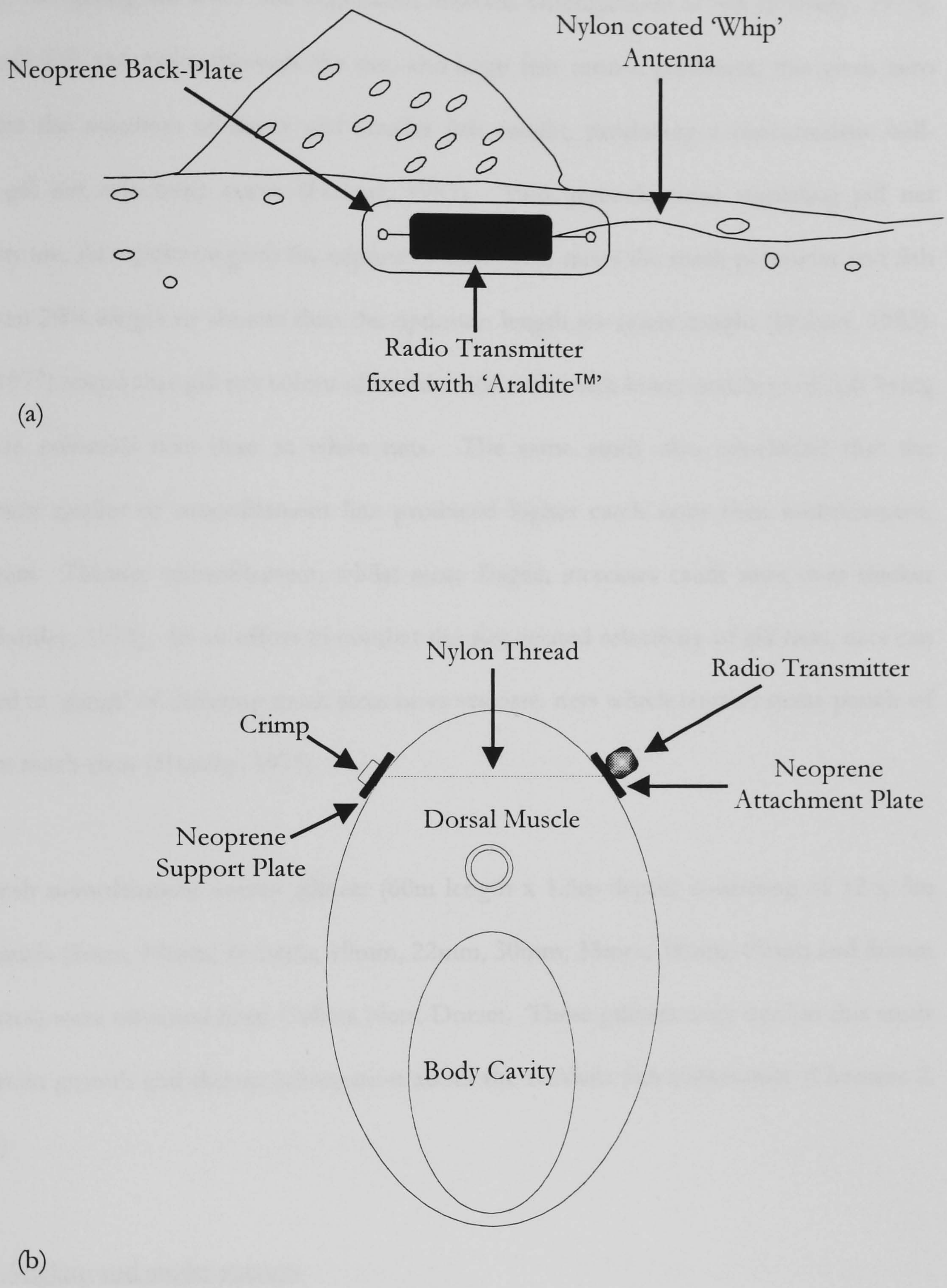


Figure 3.2 - An (a) external view and (b) cross-sectional view of the method of radio transmitter attachment.

Wedging and gilling are both size dependent whereas entanglement is not (Hamley, 1975). Very small fish can swim through the net, and large fish cannot penetrate; this gives zero values for the numbers of larger and smaller fish caught, producing a characteristic bell-shaped gill net selectivity curve (Hubert, 1983). Two generalisations regarding gill net selectivity are, the optimum girth for capture is about 1.25 times the mesh perimeter and fish more than 20% longer or shorter than the optimum length are rarely caught (Hubert, 1983). Jester (1977) stated that gill net colour affected catch rates, with lower numbers of fish being caught in coloured nets than in white nets. The same study also concluded that the transparent quality of monofilament line produced higher catch rates than multifilament, twine nets. Thinner monofilament, whilst more fragile, increases catch rates over thicker lines (Hamley, 1975). In an effort to combat the size related selectivity of gill nets, nets can be fished in 'gangs' of differing mesh sizes or as research nets which contain many panels of different mesh sizes (Hamley, 1975).

Multimesh monofilament survey gillnets (60m length x 1.5m depth) consisting of 12 x 5m mesh panels (8mm, 10mm, 16.5mm, 19mm, 22mm, 30mm, 33mm, 38mm, 45mm and 50mm mesh sizes) were obtained from Collins Nets, Dorset. These gillnets were used in this study to ascertain growth and dietary information about the resident fish community (Chapters 2, 4 and 5).

3.2.2 Angling and angler surveys

In the U.K., information relating to the fish stocks of large rivers and lakes is sparse, primarily because of the difficulties in accurately sampling the fisheries quantitatively (Cowx, 1994). Catch statistics and angler surveys provide an insight into the behaviour of fish and anglers (Pawson, 1991), and can be used to estimate growth rates, mortalities/survival, age structures, food habits, length-weight relationships, returns to anglers and post stocking distribution patterns (Pollock *et al.*, 1991). The two most basic statistics collected by freshwater fishery managers are the number of rods fishing and the number of fish taken from the water (Cane, 1980). Catch per unit effort (CPUE) is the parameter most widely used to evaluate the state of fish populations and returns to anglers (Beaumont *et al.*, 1996). In fish-tagging experiments, the investigator typically conducts the release phase of mark-recapture experiments and relies on anglers and fisheries for data recovery (Orach-Meza, 1991). Pollock *et al.* (1991) stated that tag return experiments can be significantly affected by unreported lost tags and poor angler reporting of tags. Small (1991) reported that the proportion of anglers returning tag data varied from 5% on a remote upland loch to 95% on a well controlled small lake. One method of increasing the likelihood of anglers reporting tags is through the use of a tag return reward or incentive scheme (Pollock *et al.*, 1991). Anderson and Thompson (1991) concluded that the most important factors attributing to the success of an angler survey program are a well designed reporting/monitoring system and a high level of co-operation from fisheries and, most importantly, anglers. However, the use of angler survey programs have limitations, the most important being the unknown validity of the capture data (e.g. angling effort is unlikely to be evenly distributed throughout the study area)(Helfrich & Kendall, 1982).

An angler survey programme was instigated at Carron Valley Reservoir to examine the post-stocking distribution patterns of hatchery-reared brown trout (Chapter 6).

3.3 Sampling protocol

3.3.1 Gill netting

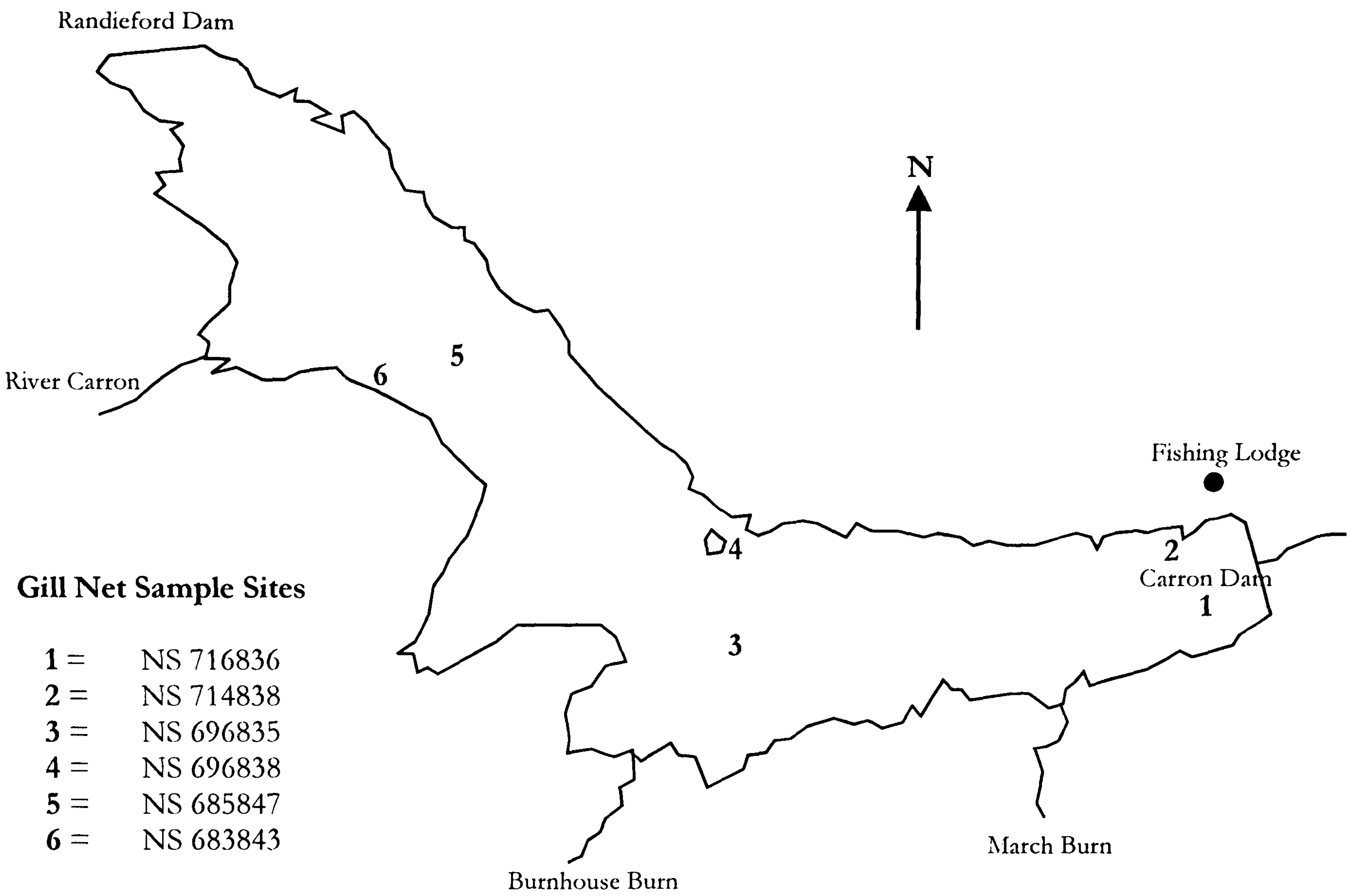
Due to the constraints of working on a commercial brown trout fishery the number of gillnet samples taken was kept to a minimum. One littoral and one offshore gillnet were set at a monthly sample station, with a gang of six gillnets being set seasonally throughout 1999 (Figure 3.1). This provided a seasonal analysis of the relative diets of the resident powan and brown trout populations (Chapter 4) and allowed the examination of differences in the diets an condition of gillnet and angler caught resident brown trout (Chapter 5).

3.3.2 Field treatment of fish for dietary analysis

Following capture in the gillnets or upon presentation of fish samples by the anglers, the fork length (± 1mm) was measured on a lengthing board and wet body weight (± 1g) measurements were taken on a set of portable strain gauge digital scales (EKS Ltd, UK). The alimentary tract from the start of the oesophagus to the constriction just before the pyloric ceacae was removed from the sampled fish and stored in 70% alcohol (Duncan, 1991).

3.3.3 Laboratory analysis of stomach contents

The stomach contents were dissected from the stomachs and analysed using both dissecting and compound microscopes. Since zooplankton, macroinvertebrates and small fish were ingested whole they were readily identifiable. All prey items occurring within the oesophagus and stomach were identified to species level where possible, along with their respective stage of development (larvae, pupae or adult). The number of individual prey



Gill Net Sample Sites

1 =	NS 716836
2 =	NS 714838
3 =	NS 696835
4 =	NS 696838
5 =	NS 685847
6 =	NS 683843

Figure 3.3 - The littoral (positions 2,4 and 6)and offshore (positions 1, 3 and 5)gill net positions used at Carron Valley Reservoir for monthly (positions 1 and 2) and seasonal (positions 1 to 6)assessments of the resident fish community.

items per species was recorded for each sampled stomach. Individual prey items were blotted on tissue paper to remove excess moisture and weighed using a Mettler AJ100 digital balance (± 0.001g) to obtain wet weights of prey items.

3.4 Dietary analysis

In field studies, analysis of stomach contents is often the only available means of assessing the feeding ecology of fish populations (Amundsen *et al.*, 1996). Traditional methods of describing dietary data include; the frequency of occurrence (number of predators containing prey x), numerical abundance (number of prey x expressed as a proportion of the total number of prey items ingested) and volumetric or gravimetric abundance (weight/volume of prey x expressed as a proportion of the total weight/volume of the prey ingested)(Hyslop, 1980). Frequency of occurrence data represent population-wide habits, numerical abundance is informative regarding feeding behaviour and volumetric or gravimetric measures reflect dietary nutritional values (Cortes, 1997). However, Hyslop (1980) concluded that in order to obtain the maximum amount of information from dietary samples, at least one method of measuring the amount of prey and one method of measuring the bulk of prey should be used consecutively. Analysis of fish foraging strategies using percentage abundance and percentage occurrence measurements have been attempted both graphically (Costello, 1990) and with a coefficient of dietary importance (CI)(Ersbak & Haase, 1983). However, by incorporating bulk, amount and occurrence measurements an index of relative importance (IRI) can provide a more representative description of dietary importance (Hyslop, 1980). Cortes (1997) suggested that expressing dietary observations as percent IRI values would standardise methodological approaches to dietary information and facilitate comparisons with other feeding studies. Selectivity indices can provide valuable comparisons of intra and interspecific dietary choice, however they rely heavily on the accurate quantification of all the available forage. Consequently selectivity indices were not used in this study due to time constraints precluding the collection of enough available forage data to remove the potential bias of invertebrate patchiness.

In commercial recreational fisheries the removal of large numbers of fish for research is not always economically viable. However, angler caught fish provide a potentially large source of samples (Easton & Morgan, 1974). Every type of sampling gear used as a research tool is to a greater or lesser degree selective (Hayes, 1983), with regurgitation being the major bias of concern in dietary studies (Bowen, 1983). Angling may be classed as an active sampling technique where the odds of landing a fish are dependent on spatial and temporal distribution, the chance an individual will attack a hook and the probability that an attack will result in a capture (Deriso & Parma, 1987). Deriso and Parma (1987) also concluded that irrespective of the abundance of a population the amount of fish an angler can catch in any given time period is limited. Favro *et al.* (1986) demonstrated that angling and electrofishing sampled different sub-populations within stream trout communities; whilst, Morrison (1997) suggested that angler caught brown trout may display greater numbers of terrestrial prey than gillnet caught conspecifics. Consequently, angler caught diet samples may not be representative of the resident fish community as a whole.

The 'Percent Index of Relative Importance' (%IRI) was used to assess the seasonal differences in the resident powan and brown trout diets (Chapter 4) as well as a time series assessment of the post-stocking changes in hatchery-reared brown trout diets in comparison to concurrently sampled wild conspecifics (Chapter 5).

3.5 Laboratory analysis of post-stocking behaviour in hatchery-reared brown trout

3.5.1 Artificial Streams

Artificial stream environments are increasingly being used to gain insights into natural stream salmonid behaviour (Jenkins, 1971; Mesa, 1991; Grossman & Boule, 1991; Staso & Rahel, 1994; Wang & White, 1994; Kocik & Taylor, 1994; Huntingford & De Leaniz, 1997). Although the general channel configuration is artificial, the biological and physical details closely resemble those of a natural stream (Jenkins, 1971). Jenkins (1971) identified several features an experimental artificial stream should possess in order to be scientifically useful and representative of the natural stream environment. These included a known discharge (constant or variable), a stable stream configuration, the absence of extraneous fish and a supply of natural stream food. Other researchers require the streams to be representative in terms of depth (Grossman & Boule, 1991), substrate type (Mesa, 1991) and habitat availability i.e. pools and riffles (Kocik & Taylor, 1994; Wang & White, 1994). Grossman and Boule (1991) stated that although differences exist between artificial and natural stream channels, these differences do not appear to drastically alter the behaviour, growth and mortality of experimental stream salmonids.

An artificial stream fluvarium situated at the Glasgow University Field Station, Loch Lomond was used to examine prior-residence, aggression and territory acquisition in hatchery-reared and wild brown trout (Chapter 7). Experiments were also carried out to examine how quickly naïve hatchery-reared brown trout learn to forage on natural prey and the subsequent changes in short-term feeding efficiency when compared to experienced wild conspecifics (Chapter 8).

Chapter 4

Growth and food resource use of resident brown trout (*Salmo trutta* L.) and powan (*Coregonus lavaretus* L.)

4.1 Introduction

Stocking, transfer and introductions of hatchery-reared salmonids are commonly used to enhance recreational and commercial fisheries and to preserve or re-establish threatened populations (Cowx, 1994). The powan (*Coregonus lavaretus* L.) naturally occurs in only two waters in Scotland (Lochs Lomond and Eck) and is consequently considered to be in need of conservation action (Maitland & Lyle, 1990). Attempts have been made to establish additional stocks using fry from the Loch Lomond powan population, in Loch Sloy and Carron Valley Reservoir, with the main objective being to increase the number of populations to what is believed to be a safe level (Maitland & Lyle, 1990).

The capacity of an aquatic environment to support a sustainable salmonid population is largely a function of suitable water quality, habitat quality, adequate spawning habitat, overwintering conditions and food availability (Milner *et al.*, 1985; Naslund, 1992). In most cases of restocking the carrying capacity of the system (both lotic and lentic) is unknown (Kelly-Quinn & Bracken, 1989), and often little thought is given to the amount of food available in the receiving water and the population density of existing fish stocks (Millichamp, 1974). Several authors have suggested that stocking fish into a body of water which already supports a large community of native fish, may result in overcrowding and a consequent increase in mortality and a decrease in growth of both the stocked and native fish (Crisp & Mann, 1977; Marrin & Erman, 1982).

In any fish community the total food resource can be subdivided notionally into different parts, which may be exploited by a combination of different species and life history stages (Gerking, 1994). It has been proposed that inter- and intraspecific competition for food may be an important factor in defining food partitioning and may lead to dietary switching (Gerking, 1994). It has been further suggested that competition for finite resources may limit the survival and growth of both stocked and native fish (Mason & Chapman, 1965; Grant & Kramer, 1990). Adams (1994) stated that introductions of competitively superior fish species with niches overlapping with existing native fish populations may exclude native species from resources that are in short supply such as food. Marrin and Erman (1982) suggested that exploitative competition between or within fish species may be a mechanism that contributes to poor salmonid survival and growth in some ecosystems. Weiland and Hayward (1997) further suggested that stocking with trout may create the potential for excessive exploitation of limited foraging resources with a subsequent reduction in the total available food resource resulting in the reduced performance of both resident and stocked fish.

Diet overlap amongst fish species and different life history strategies have been calculated to help explain community structure and to clarify competitive interactions (Wallace, 1981). Gerking (1994) identified diet overlap as a possible indicator of food partitioning and as evidence of the relative adaptability of fish species to changes in the trophic structure in which they live. Fausch (1988) suggested that because stocked fish did not evolve in sympatry with native fish there has been no opportunity for natural selection to produce different resource uses and consequently in species exhibiting similar foraging characteristics, there is likely to be increased overlap regardless of resource availability. It has also been demonstrated that dietary overlap tends to increase when resources become abundant and decrease as resources approach scarcity (Seaburg & Moyle, 1964; Pedley & Jones; 1978). However, a lack of quantifiable data regarding the amounts of different forage items in a given environment may limit the confidence with which competitive interactions are inferred (Wallace & Ramsey, 1983).

Dietary overlap between sympatric species may also be increased within impounded water bodies due to the reduction in available forage associated with fluctuating water levels (L'Abee-Lund *et al.*, 1992). The regulation or impoundment of rivers and lakes may result in severe conditions for resident fish species (L'Abee-Lund *et al.*, 1992). Significantly fluctuating water levels reduces the productivity of benthic fauna in littoral zones, which in turn reduces the available food for the resident fish populations in particular littoral feeding brown trout (Mutenia & Salonen, 1994). This reduction of littoral productivity may cause the trout to switch their foraging strategies to exploit the remaining available food items such as other fish species (L'Abee-Lund *et al.*, 1992) or zooplankton (Hesthagen *et al.*, 1995).

As part of a conservation programme, approximately 12000 powan fry were stocked into Carron valley reservoir between 1989 and 1990, whilst 2000-3000 hatchery-reared brown trout are stocked annually to supplement the recreational fishery. The success of the historical stocking of powan as a conservation measure and the continued stocking of hatchery-reared brown trout to support the commercial fishery may be influenced by the availability of food within Carron Valley Reservoir. The present study reports on the growth and diets of resident brown trout and powan at Carron Valley Reservoir in order to assess if the available food resource may limit the success of past and present salmonid stocking. Particularly, if food resources are limited in Carron Valley Reservoir, (1) then the powan may exploit similar food resources to the resident brown trout, and (2) the growth of both the resident brown trout and powan may be reduced in sympatry.

4.2 Materials and methods

4.2.1 Fish capture

A total of 153 resident brown trout and 118 powan were captured in monthly gill net surveys between December 1998 and November 1999 at Carron Valley Reservoir. Multimesh survey gill nets (60m length x 1.5m depth (Collins nets, Dorset, England)) consisting of 12 x 5m mesh panels (8mm, 10mm, 16.5mm, 19mm, 22mm, 25mm, 30mm, 33mm, 38mm, 45mm and 50mm half mesh) were set at six sampling sites, including 3 littoral (mean depth 2m ± 0.196) and 3 offshore areas (mean depth 9.1m ± 0.686) (Figure 3.1). Because Carron Valley Reservoir is a commercial recreational fishery, the number of fish removed was kept to a minimum by fishing gillnets only between 10a.m. and 1.00pm for a period of 2½ hours. This relatively short sampling period also reduced the loss of easily digestible prey items from gillnet caught fish. As a result of the small numbers of each age class of fish captured all monthly samples were pooled for subsequent analysis.

4.2.2 Field and laboratory treatment of fish

Following capture, the fish were taken back to the laboratory where fork length (±1mm) was measured on a measuring board and wet body weight was determined using a Mettler BB2400 digital balance (±0.1g). The alimentary tract from the start of the oesophagus to the constriction immediately anterior to the pyloric ceacae was removed from each fish within 3 hours of mortality to reduce the loss of easily digestible prey items (Elliott & Persson, 1978), and stored in 70% alcohol (Duncan, 1991). To determine the diet, the stomach and oesophagus contents were removed from the stomachs and examined using both dissecting and compound microscopes. Since zooplankton, macroinvertebrates and small fish were ingested whole they were readily identifiable, and all prey items were identified to family level. For insect prey their stage of development (larvae, pupae, adult) was also recorded. The number of individual prey items was recorded for each taxonomic group in each fish sampled. For each stomach, all prey items from each taxonomic group were blotted on tissue paper to remove excess moisture and group weighed using a Mettler AJ100 digital balance (±0.001g) to obtain a wet weight per taxonomic prey group for each stomach.

Scale samples for fish age determination were obtained from the 'preferred scale' region above the lateral line and below the anterior ray of the dorsal fin (Bagenal, 1974). Approximately ten scales were removed from each fish using forceps and stored in individually labeled scale packets. Before scale reading, the scales were cleansed of residual epithelial tissue via immersion in a solution of 5% hydrogen peroxide (Bean, 1992). The scales were then placed on a microfiche projector (Bell & Howell ABR-20) and viewed at a magnification of x33. Replacement scales were discarded, whilst four scales per fish with easily identifiable annuli were read for age. To back-calculate growth, the radius of the sampled scales was recorded along with the distance from the mid-point of the scale nucleus to each annulus along a common axis (Steinmetz, 1974).

4.2.3 Computational methods

Due to the relatively low numbers of samples in any one month, all monthly samples were amalgamated into seasonal groups for the purposes of data analysis.

Seasonal variation in prey consumption and dietary overlap

The seasonal prey consumption of the resident brown trout and powan was assessed using a Percent Index of Relative Importance (%IRI) (Cortes, 1997) which was based on the 'Index of Relative Importance' (IRI) (Hysolp, 1980). This compound index of dietary importance has been identified as providing a more accurate description of dietary importance than just numerical or gravimetric abundance alone (Hyslop, 1980; Cortes, 1997). The Index of Relative Importance was calculated as:

$$\mathbf{IRI} = (\%N + \%W) \times \%F$$

Where: %N = percentage of prey 'x' in the sampled diets by number; %W = percentage of prey 'x' in the sampled diets by weight; %F = frequency of occurrence of prey 'x' in sampled diets.

The Percent Index of Relative Importance was calculated as:

$$\mathbf{\%IRI}_i = 100 \ \mathrm{IRI}_i \ / \sum_{i=1}^{n} \mathrm{IRI}_i$$

Where: i = family group; n = total number of food categories.

As no single measure of diet can adequately describe dietary overlap, it has been suggested that a compound index of dietary importance may provide a more realistic measure of diet (George & Hadley, 1979). Consequently, the Percent Index of Relative Importance values for each prey category was used to calculate dietary overlap. The degree of diet overlap was calculated according to Schoener's (1968) similarity index (*D*), which has been identified as the most appropriate dietary overlap measure in the absence of resource availability data

(Wallace, 1981). Index D varies between 0 and 1, representing no and complete food overlap respectively; with an interspecific overlap value of greater than 0.60 being considered as indicating biologically significant dietary overlap (Wallace & Ramsey, 1983). Schoener's similarity index was calculated as:

$$D = 1 - 0.5 \left(\sum_{i=1}^{n} \left| P_{xi} - P_{yi} \right| \right)$$

Where: D = overlap index; P_{xi} = proportion of food category i in the diet of species x; P_{yi} = proportion of food category i in the diet of species y; and n = the number of food categories.

The comparative growth of the resident brown trout and powan

Back-calculations of length

Back-calculations are a convenient way of investigating the growth history of various year classes from within a population with periods of good and bad growth evident (Bean, 1992). Due to the relatively low numbers of younger age class fish captured, back-calculations of length were used to compare the relative growth rates of the Carron Valley Reservoir brown trout and powan stocks with other communities. Plots of the scale radii measurements against fork length indicated that the growth of both the resident brown trout and powan were allometric, with a log-log transformation giving a good fit between fork length and scale radius (regression analysis; brown trout, N=35, r^2=0.960, p<0.0001; powan, N=49, r^2=0.946, p<0.001). Consequently a logarithmic relationship between scale radii and age was used to determine the back-calculated lengths for both the resident brown trout and the powan. Back-calculations of size can be achieved using (Bagenal & Tesch, 1978):

$$\mathrm{Log}_{10}\ \text{length} = K + n(\mathrm{Log}_{10}\ \text{scale width})$$

Where: K = intercept on the ordinate (in Log_{10} units); n = slope of the relationship.

Therefore brown trout lengths were back calculated using:

$$\mathrm{Log}_{10}\ \text{fork length (mm)} = 2.2636 + (0.8198 \times \mathrm{Log}_{10}\ \text{scale width(mm)})$$

And powan lengths were back-calculated using:

$$\mathrm{Log}_{10}\ \text{fork length (mm)} = 2.101 + (0.7887 \times \mathrm{Log}_{10}\ \text{scale width(mm)})$$

Length-age relationship

In order to compare the relative growth of the resident brown trout and powan populations at Carron Valley Reservoir with other populations a length-age relationship for each species was constructed using the back-calculated lengths. Plots of back-calculated fork length against age were used to examine actual differences with other Scottish waters whilst the length-age relationship was statistically described using the von Bertalanffy predictive growth equation and Ford-Walford plots (Simply Growth, Pisces Conservation Ltd), where the von Bertalanffy equation is:

$$L_t = L_\infty \{1-\exp[-K(t-t_0)]\}$$

Where: L_t = length at age t; L_∞ = asymptotic length; and K = speed at which asymptotic length is reached.

Ford-Walford plots are a graphical transformation of the von Bertalanffy growth equation which are constructed using mean back-calculated lengths. Lengths at time t+1 were plotted against lengths at time t, and straight lines were fitted using the method of least squares regression (Bagenal, 1974).

4.3 Results

4.3.1 Seasonal variation in prey consumption

Resident brown trout

Trout captured from December 1998 to February 1999 (winter) and September to November 1999 (autumn) consumed significantly fewer prey items (median of 2 per stomach) than trout captured between May to August 1999 (spring and summer)(median of 19 per stomach)(Kruskal-Wallis, H=23.851, d.f.=1, $p<0.001$). From December 1998 to February 1999 the sampled trout diets were dominated by cladoceran, trichopteran and isopodan prey (Table 4.1); with Gasterosteidae, dipteran larvae, pulmonatan and cyrenodontan prey occurring in a smaller percentage of the sampled stomachs (Table 4.1). During this period 25.7% of the sampled stomachs contained no prey items. In the samples collected between March and May 1999 trichopteran prey dominated the resident trout diets both in numerical (%N) and gravimetric abundance (%W) (Table 4.2). Dipteran larvae, isopodan and dipteran pupae occurred in a large proportion of the sampled diets whilst salmonidae and gasterosteidae prey occurred in very few stomachs but contributed heavily to the total weight of the sampled stomach contents (Table 4.2). During this period only 3.8% of the sampled stomachs contained no prey items. Between June and August 1999 4.5% of the sampled trout stomachs contained no prey items with the trout diets dominated by cladoceran, dipteran pupae and to a lesser extent trichopteran prey (Table 4.3). Dipteran larvae and cyrenodontan prey occurred in a relatively large proportion of the stomachs. Gasterosteidae prey occurred in a small percentage of the stomachs but accounted for a large proportion of the total stomach contents weight (Table 4.3). Between September and November 1999 the number of empty stomachs increased to 22.4% of the collected samples. During this period cladoceran prey dominated the trout diets with trichopteran prey ranking second (rank of %IRI) (Table 4.4). Cyprinidae and gasterosteidae prey occurred in a small percentage of the sampled stomachs but contributed highly to the total weight of the stomach contents.

Resident powan

Powan captured during December 1998 to February 1999 (winter) and September to November 1999 (autumn) consumed significantly fewer prey items (median of 11 per stomach) than powan captured between May to August 1999 (spring and summer)(median of 74 per stomach)(Kruskal-Wallis, H=21.362, d.f.=1, p<0.001). From December 1998 and February 1999 the powan diets were dominated by cladoceran prey with dipteran larvae and cyclopoidean prey ranking second and third respectively (rank of %IRI) (Table 4.1). Cyrenodontan, trichopteran and isopodan prey occurred in a small proportion of the stomachs but contributing relatively highly to the total stomach contents weight (Table 4.1). During this period 36.7% of the sampled stomachs contained no prey items. In the samples

Table 4.1 – A comparison of the prey preferences of resident brown trout and resident powan, sampled between December 1998 and February 1999. Where: %N = percentage of diet by number; %W = percentage of diet by weight; %O = percentage frequency of occurrence; IRI = Index of Relative Importance; %IRI = Percent Index of Relative Importance; and '-' denotes food item absent from sampled stomach.

Food Type	Trout (n = 35)						Powan (n = 49)					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	88.78	4.79	22.85	2138	50.34	1	83.29	17.38	46.93	4724	81.15	1
Cyclopoidea	1.79	0.10	5.71	11	0.26	7	5.03	1.09	22.45	137	2.35	3
Amphipoda	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda	1.79	25.10	28.57	768	18.08	3	0.15	11.37	6.12	71	1.22	6
Prosobranchia	-	-	-	-	-	-	-	-	-	-	-	-
Pulmonata	0.19	6.73	2.85	20	0.47	6	-	-	-	-	-	-
Cyrenodonta	0.47	0.53	11.42	11	0.26	7	1.56	8.79	10.20	106	1.82	4
Hemiptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	4.30	42.25	25.71	1197	28.18	2	0.39	14.22	6.12	89	1.53	5
Diptera – Adult	0.28	0.58	5.71	5	0.12	10	-	-	-	-	-	-
- Pupae	0.75	1.04	2.85	5	0.12	10	-	-	-	-	-	-
- Larvae	0.19	1.60	20.00	36	0.85	5	9.57	47.13	12.24	694	11.92	2
Coleoptera	0.19	1.67	5.71	11	0.26	7	-	-	-	-	-	-
Cyprinidae	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	0.08	15.62	2.85	45	1.06	4	-	-	-	-	-	-

Table 4.2 – A comparison of the prey preferences of resident brown trout and resident powan, sampled between March and May 1999. Where: %N = percentage of diet by number; %W = percentage of diet by weight; %O = percentage frequency of occurrence; IRI = Index of Relative Importance; %IRI = Percent Index of Relative Importance; and '-' denotes food item absent from sampled stomach.

Food Type	Trout (n = 26)						Powan (n = 43)					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	10.36	0.05	7.69	80	1.20	6	23.19	0.52	37.21	882	6.73	3
Cyclopoidea	-	-	-	-	-	-	1.61	0.04	13.95	23	0.18	6
Amphipoda	0.45	0.21	7.69	5	0.08	11	-	-	-	-	-	-
Isopoda	3.15	9.81	53.85	698	10.50	3	0.37	2.27	18.60	49	0.37	5
Prosobranchia	-	-	-	-	-	-	-	-	-	-	-	-
Pulmonata	0.45	0.40	7.69	7	0.11	10	-	-	-	-	-	-
Cyrenodonta	4.05	1.91	11.53	69	1.04	7	48.30	81.93	76.74	9994	76.31	1
Hemiptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	45.72	19.01	69.23	4481	67.41	1	1.32	2.43	23.35	88	0.67	4
Diptera – Adult	0.23	0.04	3.85	1	0.02	12	-	-	-	-	-	-
- Pupae	8.11	1.00	30.76	280	4.21	4	0.71	0.39	11.62	13	0.10	7
- Larvae	19.81	2.29	34.62	765	11.51	2	24.26	12.43	55.81	2047	15.63	2
Coleoptera	0.68	0.32	7.69	8	0.12	9	-	-	-	-	-	-
Cyprinidae	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	0.23	60.3	3.85	233	3.51	5	-	-	-	-	-	-
Gasterosteidae	0.23	4.98	3.85	20	0.30	8	-	-	-	-	-	-

collected between March and May 1999 the number of empty stomachs fell to 9.3% of the collected samples. During this period cyrenodontan prey dominated the powan diets in both numerical (%N) and gravimetric abundance (%W); with dipteran larvae and cladoceran prey ranking second and third respectively (rank of %IRI) (Table 4.2). Between June and August 1999 cladoceran and dipteran larvae prey occurred in a relatively large proportion of the sampled stomachs with cyrenodontan and trichopteran prey occurring in fewer stomachs but contributing relatively highly to the total stomach contents weight (Table 4.3). During this period, all of the sampled stomachs (100%) were found to contain prey items. In the samples collected during September to November 1999 cladoceran and cyclopoidean prey dominated the powan diets (Table 4.4). Cyrenodontan and dipteran larvae were the only other prey items found (Table 4.4), with 12.5% of the sampled stomachs containing no prey items.

Dietary overlap

Over the entire sampling period (December 1998 to November 1999) the trout contained a significantly greater number of prey species than the concurrently sampled powan (Kruskal-Wallis, H=7.308, d.f.=1, p=0.007). Schoener's index *D* was relatively low between December 1998 and May 1999 (Table 4.5) indicating little dietary overlap between the resident trout and powan during this period. However, dietary overlap between the resident trout and powan was relatively high ($D>0.60$ (Schoener, 1968) in the samples collected between June and November 1999 (Table 4.5) suggesting overlap in diets.

Table 4.3 – A comparison of the prey preferences of resident brown trout and resident powan, sampled between June and August 1999. Where: %N = percentage of diet by number; %W = percentage of diet by weight; %O = percentage frequency of occurrence; IRI = Index of Relative Importance; %IRI = Percent Index of Relative Importance; and '-' denotes food item absent from sampled stomach.

Food Type	Trout (n = 44)						Powan (n = 12)					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	71.70	3.86	52.27	3950	54.39	1	83.03	19.32	66.67	6824	70.52	1
Cyclopoidea	1.39	0.10	6.82	10	0.13	7	5.16	0.93	58.33	355	3.67	5
Amphipoda	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda	0.05	0.64	2.27	2	0.03	10	-	-	-	-	-	-
Prosobranchia	0.05	0.36	2.27	1	0.01	11	-	-	-	-	-	-
Pulmonata	0.10	0.15	2.27	1	0.01	11	-	-	-	-	-	-
Cyrenodonta	2.68	5.67	18.18	152	2.09	6	6.78	40.11	25.00	1172	12.11	2
Hemiptera	0.28	0.64	4.55	4	0.06	9	-	-	-	-	-	-
Trichoptera	6.51	25.56	34.09	1093	15.05	3	0.74	21.63	16.67	373	3.85	4
Diptera – Adult	0.28	1.02	4.55	5	0.07	8	-	-	-	-	-	-
- Pupae	12.93	15.44	50.00	1419	19.54	2	2.29	9.61	58.33	694	7.17	3
- Larvae	3.74	4.23	29.55	236	3.25	5	1.99	8.37	25.00	259	2.68	6
Coleoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	0.32	42.46	9.09	389	5.36	4	-	-	-	-	-	-

Table 4.4 – A comparison of the prey preferences of resident brown trout and resident powan, sampled between September and November 1999. Where: %N = percentage of diet by number; %W = percentage of diet by weight; %O = percentage frequency of occurrence; IRI = Index of Relative Importance; %IRI = Percent Index of Relative Importance; and '-' denotes food item absent from sampled stomach.

Food Type	Trout (n = 49)						Powan (n = 16)					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	91.57	5.20	26.53	2567	78.50	1	73.55	31.52	75.00	7860	77.28	1
Cyclopoidea	0.34	0.02	2.04	1	0.03	11	21.08	8.89	50.00	1499	14.73	2
Amphipoda	-	-	-	-	-	-	-	-	-	-	-	-
Isopoda	1.12	2.82	6.12	24	0.73	5	-	-	-	-	-	-
Prosobranchia	-	-	-	-	-	-	-	-	-	-	-	-
Pulmonata	0.90	2.11	6.12	18	0.55	6	-	-	-	-	-	-
Cyrenodonta	0.90	0.97	6.12	11	0.34	10	5.02	56.35	12.50	767	7.54	3
Hemiptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	2.58	12.24	26.53	393	12.01	2	-	-	-	-	-	-
Diptera – Adult	1.01	0.51	8.16	12	0.37	9	-	-	-	-	-	-
- Pupae	1.01	1.16	8.16	18	0.55	6	-	-	-	-	-	-
- Larvae	0.79	0.97	10.20	18	0.55	6	0.33	3.23	12.50	45	0.44	4
Coleoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae	0.34	25.46	6.12	158	4.83	3	-	-	-	-	-	-
Salmonidae							-	-	-	-	-	-
Gasterosteidae	0.44	48.54	2.04	100	3.06	4	-	-	-	-	-	-

The comparative growth of the resident brown trout and powan

Back-calculations of length

The back-calculated length values for the resident brown trout (Table 4.6) were found to be significantly smaller than the observed lengths at that age (ANOVA, F=10.921, d.f=1, p=0.003). Similarly, the back-calculated fish lengths for the resident powan (Table 4.7) were also found to be significantly smaller than the observed lengths (ANOVA, F=18.748, d.f.=1, p<0.001). These differences are assumed to be due to 'Lee's phenomenon', where back-calculated lengths tend to be smaller than observed lengths, especially in older fish (Bagenal & Tesch, 1978).

Length-age relationships

Resident brown trout

The relative growth rate of the resident brown trout in Carron Valley Reservoir is intermediate when compared to other Scottish populations (Figure 4.1(a)). The mean fork length attained by one year old resident trout in this study is 85mm (Table 4.6) which is higher than that of the comparative populations illustrated (Figure 4.1(a)). The mean back-calculated fork length of the resident brown trout in year 2 falls below the observed fork lengths of Loch Lussa and Loch Bee, whilst the calculated fork lengths in years 3, 4 and 5 fall below those observed in Loch Awe and Loch Bee (Figure 4.1(a)).

Growth of the resident trout observed in this study followed the von Bertalanffy growth model and is shown graphically in Figure 4.2. The growth parameters obtained for the resident trout in this study are presented alongside comparative values for other Scottish waters in Table 4.8. The asymptotic length (L_∞ = 645mm) calculated for the resident brown

Table 4.5 – Diet Overlap between resident brown trout and powan in Carron Valley Reservoir, December 1998 to November 1999.

	Winter	Spring	Summer	Autumn
Schoener's Index (*D*)	0.486	0.182	0.716	0.780

Table 4.6 – Back-calculated mean fork lengths (mm) of resident brown trout captured between December 1998 and November 1999.

Recruitment year	**Age (years)**					**N**
	1	**2**	**3**	**4**	**5**	
1994	80	137	195	244	309	6
S.E.	1.66	3.67	3.34	6.49	7.09	
1995	84	133	194	242		14
S.E.	2.74	4.32	5.08	4.99		
1996	93	143	201			7
S.E.	8.12	10.19	11.87			
1997	86	139				3
S.E.	2.44	3.81				
Mean Length ± s.e.	85 ± 2.72	138 ± 2.08	196 ± 2.19	243 ± 1.00	309 ± 7.09	

Table 4.7 – Back-calculated mean fork lengths (mm) of resident powan captured between December 1998 and November 1999.

Recruitment year	**Age (years)**							**N**
	1	**2**	**3**	**4**	**5**	**6**	**7**	
1992	98	197	273	333	359	386	403	5
S.E.	2.18	1.22	4.25	3.81	5.94	5.11	5.45	
1993	92	213	259	303	335	357		9
S.E.	1.79	1.99	4.00	3.02	4.66	5.27		
1994	95	210	270	304	331			7
S.E.	1.86	4.87	4.60	5.12	4.14			
1995	105	192	249	264				10
S.E.	2.60	2.92	5.34	5.43				
1997	89	172	238					1
S.E	1.99	3.73	5.26					
1998	96	165						2
S.E	2.17	2.89						
Mean Length ± s.e.	92 ± 2.52	191 ± 7.99	257 ± 6.52	301 ± 14.16	341 ± 8.74	371 ± 14.50	403 ± 8.94	

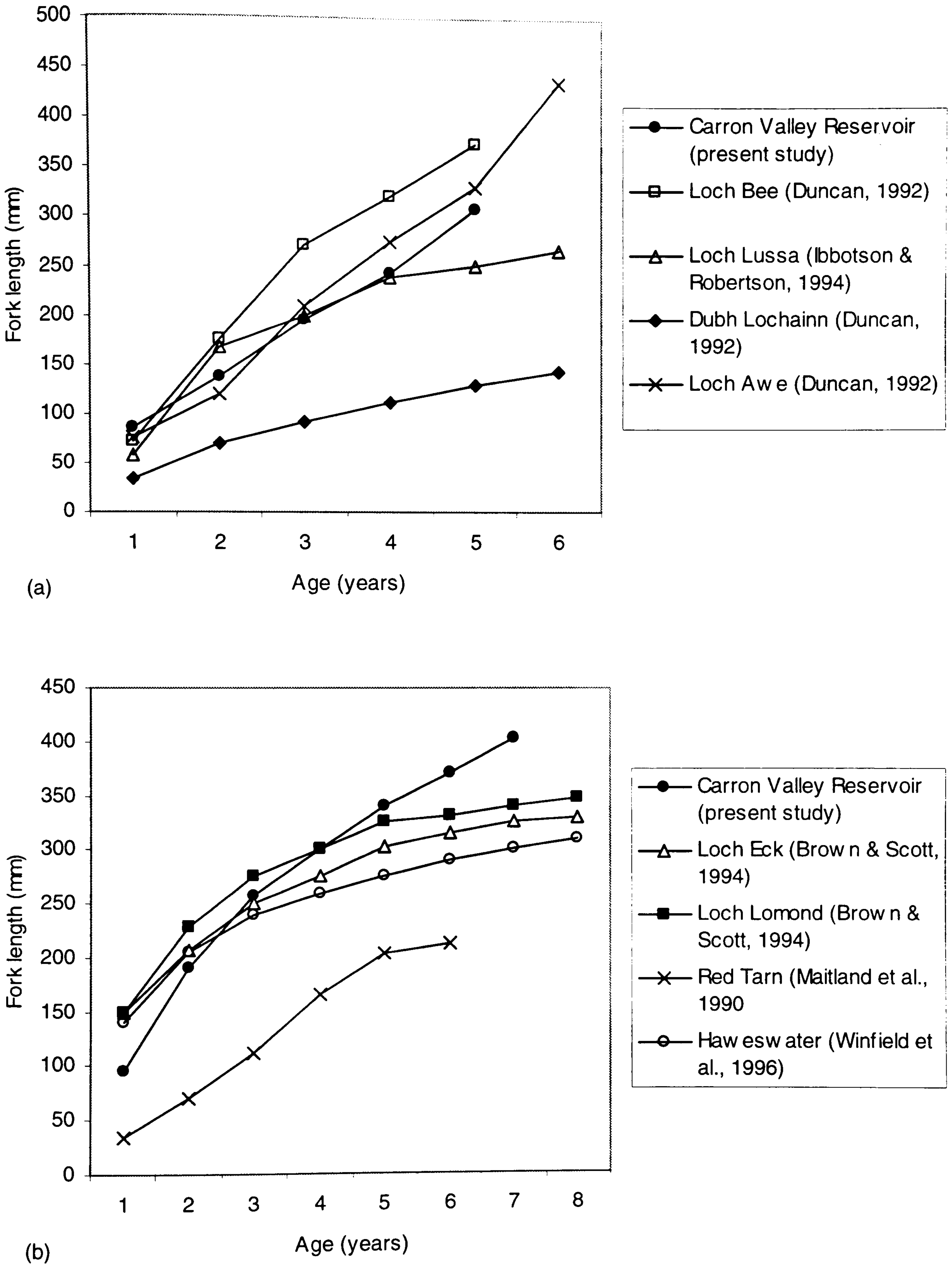


Figure 4.1 - Comparison of the (a) resident trout population, and the (b) resident powan population growth with those found in a selection of UK waters.

trout in Carron Valley Reservoir was higher than those calculated for the comparison sites; whilst the growth rate (k) was lower (Table 4.8).

Resident powan

The relative growth rate of the resident powan at Carron Valley Reservoir when compared is relatively high when compared with other British populations (Figure 4.1(b)). The mean fork lengths attained by the one and two year old powan at Carron Valley Reservoir are lower than those observed in both the two natural Scottish populations and in Haweswater (Figure 4.1(b)). The mean back-calculated fork lengths of the resident powan were only lower than those of the Loch Lomond population in year 3 and were greater than all those of the comparative populations in years 5, 6 and 7 (Figure 4.1(b)).

Growth of the resident powan observed in this study followed the von Bertalanffy growth model and is shown graphically in Figure 4.3. The growth parameters obtained for the resident powan in this study are presented alongside those of comparable British populations in Table 4.9. The asymptotic length (L_∞ = 473mm) calculated for the resident powan in Carron Valley Reservoir was higher than those calculated for the comparison sites, and the growth rate (k) was lower (Table 4.9).

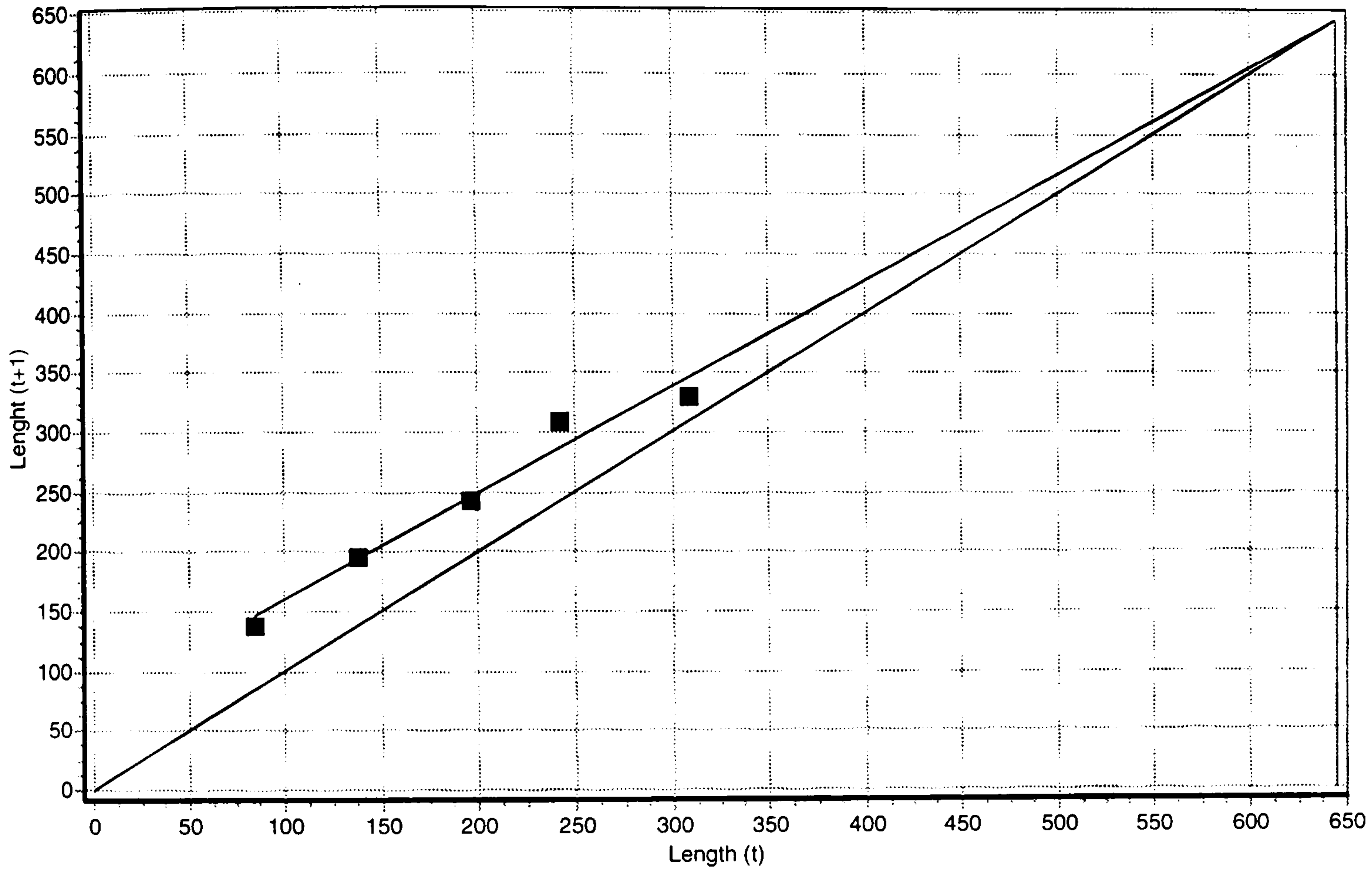


Figure 4.2 - 'Ford-Walford' graphical von Bertalanffy plot used to determine the growth parameters of the resident brown trout population, Carron Valley Reservoir.

Table 4.8 – Comparison of the Carron Valley Reservoir resident brown trout von Bertalanffy growth parameters with those found in other U.K. waters.

Site	Author	Sex	L∞ (mm)	k
Carron Valley Reservoir	Present study	all	645	0.115
Dubh Lochainn	Duncan, 1992	all	176	0.274
Loch Lussa	Ibbotson & Roberts, 1994	all	260	0.696
Loch Bee	Duncan, 1992	all	529	0.269

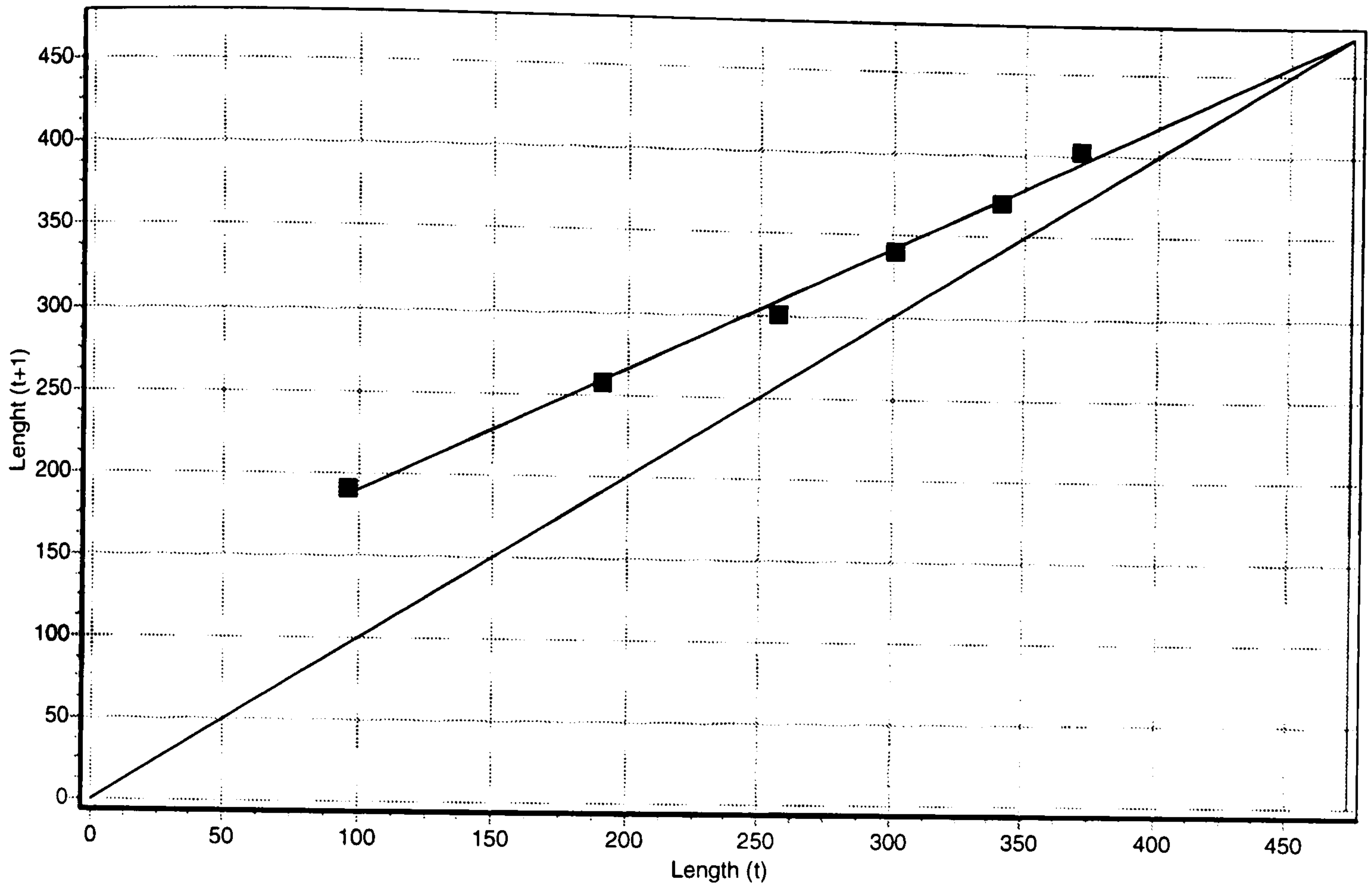


Figure 4.3 - 'Ford-Walford' graphical von Bertalanffy plot used to determine the growth parameters of the resident powan population, Carron Valley Reservoir.

Table 4.9 – Comparison of the Carron Valley Reservoir resident powan von Bertalanffy growth parameters with those found in other U.K. waters.

Site	Author	Sex	L∞ (mm)	k
Carron Valley Reservoir	Present study	all	473	0.273
Loch Lomond	Brown & Scott, 1994	all	353	0.474
Loch Eck	Brown & Scott, 1994	all	346	0.351
Haweswater	Winfield et al., 1998	all	326	0.371

4.4 Discussion

4.4.1 Seasonal variation in prey consumption and dietary overlap

Foraging behaviour involves decisions which include where to feed, when to feed and what to feed on (Hughes, 1997). Several studies have shown that prey distributions and abundance influence the foraging strategies of lotic dwelling salmonids (Haraldstadt & Jonsson, 1983; Olson *et al*, 1988; Lachance & Magnan, 1990; Weiland & Hayward; 1997). Optimal foraging theory and trophic adaptability suggests that fish populations may respond to the seasonal changes in prey abundance by switching prey preferences between the most energetically cost effective forage items in any given environment (Gerking, 1994; Hughes, 1997).

Reduced prey consumption and a subsequent increase in the proportion of empty stomachs during autumn and winter months have been reported in several studies of salmonid diets (Haraldstad & Jonsson, 1983; Naesje *et al.*, 1991; Pomeroy, 1991). This study supports these findings with both resident brown trout and powan consuming fewer prey and with an increase in the proportion of empty stomachs observed in the autumn and winter samples when compared to those collected in the spring and summer. Elliott (1976) suggested that reduced feeding during winter months resulted from low water temperatures which reduce basal metabolic rates and activity in brown trout and consequently reduces the relative foraging requirements during low temperature periods.

The results from this study show the diets of the resident trout and powan were heterogenous, with seasonal variability in the relative contributions of the different prey types evident for both fish species. This supports the findings of several studies which have described the heterogeneity of the diets and foraging strategies of wild salmonid populations (Ersbak & Haase, 1983; Kelly-Quinn & Bracken, 1990; Bridcut & Giller, 1995). In this study benthic macroinvertebrates dominated the resident brown trout diets during the winter and spring with nektonic prey (cladocerans and dipteran pupae) increasing in importance in the summer and autumn samples. This agrees with the findings of Haraldstad & Jonsson (1983) found brown trout to shift from feeding on benthic macroinvertebrates in the spring to foraging on zooplankton in the summer, which they suggested was a result of the changing relative abundances of the different prey items. The relative prey preferences of the powan observed in this study also changed seasonally, with zooplankton prey items being of primary importance in the winter, summer and autumn samples and macroinvertebrate prey dominating the spring samples. Naesje *et al.* (1991) found powan to switch between epibenthic and zooplankton foraging strategies dependent on their comparative seasonal abundances, with macroinvertebrate prey dominating in the spring and autumn and zooplankton prey items dominating in the summer. However, Pomeroy (1991) found the parent powan population in Loch Lomond to feed almost exclusively on zooplankton at all times of the year to the exclusion of almost everything else.

Interspecific diet overlap between the resident brown trout and powan was observed in the summer and autumn samples at Carron Valley Reservoir. The relatively low of dietary overlap in the spring samples may be attributed to a degree of specialisation of the trout and powan as selectively preyed on trichopteran and cyrenodontan prey respectively. In the summer samples both fish species foraged predominantly on cladoceran zooplankton species with dipteran pupae and to a lesser extent trichopteran prey also being important, whilst during the autumn cladoceran zooplankton species almost exclusively dominated both species diets. Olsen *et al.* (1988) suggested that high dietary overlap between brown trout and lake trout (*Salvelinus namaycush*) in Lake Ontario indicated that both species were exploiting similar, highly abundant prey items. Maitland (1965) concluded that dietary overlap often occurs when fish species with relatively heterogenous diets are compared as there may be many abundant food items on which they browse. Naesje *et al.* (1991) found dietary overlap between powan and vendace (*Coregonus albula* L.) when zooplankton abundances peaked in summer months. Conversely, Raitaniemi *et al.* (1999) suggested that relatively high levels of interspecific competition and dietary overlap between powan and roach (*Rutilus rutilus* L.) may result from a reduction in the abundance of zooplankton prey. Weiland & Hayward (1997) also suggested that excessive competition and predation pressure for limited food resources may result in the poor post-stocking performance of rainbow trout (*Oncorhynchus mykis* Walbaum). Alternatively, several authors have suggested that dietary overlap in impounded waters may be a result of fluctuating water levels significantly reducing littoral fauna abundance and consequently increasing inter- and intraspecific competition between the resident fish species as the available forage reduces (Bryan, 1982; Borgstrom *et al.*, 1992; Winfield *et al.*, 1996). The present study supports the findings of Bryan (1982) who found the relative contribution of benthic macroinvertebrates to the diets of sampled trout to decrease and the contribution of chironomidae and zooplankton to increase in response to a summer drop in the water level in an impounded water. Borgstrom *et al.* (1992) theorised that a decline in zoobenthos as a result of fluctuating water levels results in a shift from benthivory to planktivory in brown trout.

4.4.2 The comparative growth of the resident brown trout and powan

Indeterminate growth is a major element of the life history of fish (Gerking, 1994). Asymptotic size appears to be dependent on food quantity and quality, reproductive status, competition, predation and temperature (Bean, 1992). Consequently, high levels of competition and limited foraging resources may limit fish growth. Raitaniemi *et al.* (1999) identified poor growth as a major factor affecting the success and profitability of stocking. It has been suggested that population density may be the principle determinant of growth in powan populations, with higher growth rates at low population densities (Niva & Julkunen, 1996). It has been further suggested that both powan and brown trout populations may suffer from increased inter and intraspecific competition for limited food resources (Lehtonen & Niemela, 1996; Raitaniemi *et al.*, 1999). This hypothesis was supported by Cowx (1983) who identified poor growth in fish assemblages exhibiting high degrees of dietary overlap.

This study found that the resident brown trout displayed relatively intermediate growth characteristics when compared to other Scottish populations. Although, the growth characteristics of the resident brown trout were intermediate a very high asymptotic length (L_∞) was found. Campbell (1978) found that in many Scottish lochs where growth is limited in younger age classes, the fish can ultimately attain a size threshold above which a dietary shift to teleost prey can result in sudden increases in growth. This supports the theory that as fish grow, their food changes in quantity and/or size (Gerking, 1994). Consequently, the presence of Cyprinidae, Salmonidae and Gasterosteidae prey in small numbers of the sampled trout stomachs may indicate a dietary shift by larger resident trout to exploit nutrient dense teleost prey items, and this may explain the relatively high asymptotic size.

Lehtonen & Niemela (1996) attributed poor growth performance in powan in shallow, low altitude lakes to high summer temperatures. Although Carron Valley Reservoir is a relatively shallow, low altitude waterbody the observed growth characteristics of the resident powan were relatively high compared to other Scottish and British populations. Brown & Scott (1994) reported that powan in Loch Lomond displayed a significantly greater mean size after a population crash in 1968 than before. Consequently the relatively high levels of growth and the relatively high asymptotic length (L_∞) observed in the powan population at Carron Valley Reservoir may result from a relatively low population density; although relatively low levels of predation and high levels of food availability may also influence the potential growth of the population.

4.4.3 Summary

A degree of foraging partitioning between the species was evident although they readily consumed the same common prey items but in different concentrations, which may indicate some limitations to the amount of available forage (Seaburg & Moyle, 1964; Pedley & Jones, 1978). However the intermediate growth of the brown trout and the relatively high growth of the powan when compared to other Scottish populations, suggests that resident fish at Carron Valley Reservoir are not constrained by a limited food resource. The relatively high growth of the powan may also be attributed to relatively low population densities. The observed dietary overlap between the two species could be attributed to the lack of distinction between the different size classes of both species observed (i.e. 1+ trout overlaping with 4+ powan). However, the low dietary overlap in the winter and spring months suggests that the lack of size distinction in the analysis does not account for all the overlap. The prey species consumed by both the powan and trout in Carron Valley

Reservoir reflect the trends observed in other impounded waters (Borgstrom *et al.*, 1992). Consequently, the high dietary overlap observed in the Summer and Autumn months may be linked to the reduction in water level during the summer months and the time lag in recolonisation of the littoral zone following reinundation by benthic macroinvertebrates during the autumn. This study suggests that currently the largest constraint to the fish productivity in Carron Valley Reservoir is likely to be the fluctuating water levels as a result of impoundment.

Chapter 5

The post-stocking temporal changes in quantity of prey consumed, prey preference, foraging habitat use and body condition of hatchery-reared brown trout in comparison to resident conspecifics.

5.1 Introduction

Malnutrition has been proposed as a potential source of poor post-stocking performance in hatchery-reared salmonids (Vinyard *et al.*, 1982; Ersbak & Haase, 1983; Bachman, 1984). The change from artificial food to natural feeding is considered to be critical for the successful stocking and subsequent adaptation of hatchery-reared salmonids after release (Ersbak & Haase, 1983; Bachman, 1984; Johnsen & Ugedal, 1989). Hatchery-reared salmonids are confronted by a change from an environment characterized by the homogeneity of feed administration (i.e. temporal, spatial and quality) to the natural environment which is categorised by the spatial and temporal heterogeneity of prey availability (Johnsen & Ugedal, 1989). Salmonids are predominantly visual feeders (Stradmeyer & Thorpe, 1987) with wild salmonids selecting prey based on characteristics including size (Wankowski & Thorpe, 1979), colour (Clarke & Sutterlin, 1985), movement (Irvine & Northcote, 1983) and abundance (O'Grady, 1983). Conversely, hatchery-reared salmonids may become visually conditioned to respond to physically, chemically and nutritionally uniform pelleted feeds (Ersbak & Haase, 1983; Stradmeyer & Thorpe, 1987). Consequently, poor prey recognition (Steward & Bjornn, 1990), inefficient foraging (Bachman, 1984), excessive activity and agnostic behaviour (Fenderson *et al.*, 1968; Symons, 1969) and inappropriate behavioural traits inherited through domestication or learned through culture conditions (Ruzzante, 1994) may all contribute to the ability of hatchery-reared salmonids to adapt to natural foods.

Several authors have suggested that hatchery-reared salmonids have little trouble adapting to natural foods (Stradmeyer & Thorpe, 1987; Johnsen & Ugedal, 1989; L'Abee-Lund *et al.*, 1992). However, hatchery-reared salmonids have been shown to ingest fewer prey than wild conspecifics (Ersbak & Haase, 1983; Bachman, 1984; Kelly-Quinn & Bracken, 1989) and may be unable to maintain their overall condition (Ersbak & Haase, 1983). Bachman (1984) suggested that excessive energy expenditure, inefficient foraging behaviour and an inability to obtain sufficient food among hatchery-reared brown trout released into the wild may contribute to declining condition factors. Due to the energy-dense nature of hatchery diets, hatchery-reared salmonids often exhibit higher body lipid levels than wild conspecifics (Sosiak, 1982) which may suppress appetite in hatchery fish. Pawson and Purdom (1991) concluded that well-fed hatchery-reared rainbow trout (*Oncorhynchus mykiss* Walbaum) are not so impelled to feed as are less well-fed conspecifics. It has also been suggested that there is a maximum size that a salmonid can attain in any given environment and consequently if stocked hatchery-reared trout exceed this size they may be unable to maintain their condition (Bachman, 1984).

An inability to adapt to natural foraging may have profound effects on the post-stocking survival and returns to anglers of hatchery-reared brown trout. The present study aimed to: (1) examine the post-stocking temporal changes in the quantity of prey consumed by hatchery-reared brown trout and compare them with resident conspecifics during the summer in Carron Valley Reservoir, (2) examine the post-stocking temporal changes in the prey preference and foraging habitat use of hatchery-reared brown trout and compare with resident conspecifics during the summer in Carron Valley Reservoir, and (3) examine the post-stocking temporal changes in the body condition of hatchery-reared brown trout and compare with resident conspecifics during the summer in Carron Valley Reservoir.

5.2 Materials and methods

5.2.1 Fish used in this study

1000 hatchery-reared brown trout from a commercially available strain held at the Howietoun fishery were stocked at 3 different locations around Carron Valley Reservoir in 3 batches of 300, 400 and 300 fish on the 27th March, 29th March and the 2nd April 1999 respectively. The first batch of fish was stocked from the pier, the second batch at the 'roadside' site and the final batch at the 'Smallburn' (Figure 5.1). All fish ranged between 30-35cm in fork length and were marked with subcutaneous Alcian blue dye batch mark, to allow anglers to easily identify stocked fish.

5.2.2 Subcutaneous dye marking procedure

Prior to release, each fish was individually anaesthetised and batch marked on the ventral surface between the pectoral fins with a subcutaneous alcian blue dye (Fisher Scientific, Manchester, UK) tattoo using a 'Panjet' inoculator (F.H. Wright Dental Manufacturing Co., Dundee, Scotland). This method produced a small, easily distinguishable mark that enabled both the sampler and anglers to easily identify stocked experimental fish.

5.2.3 Field methods

Fish capture

Fish caught by angling between the 3rd April and the 26th June 1999, and fish captured in April, May and June monthly gill netting surveys were used in the study. Angler-caught fish samples were collected on weekends, when the largest proportion of anglers fished the water. Anglers were asked to participate in the study by making all captured fish available for dietary analysis at the end of their respective fishing sessions, at which point both

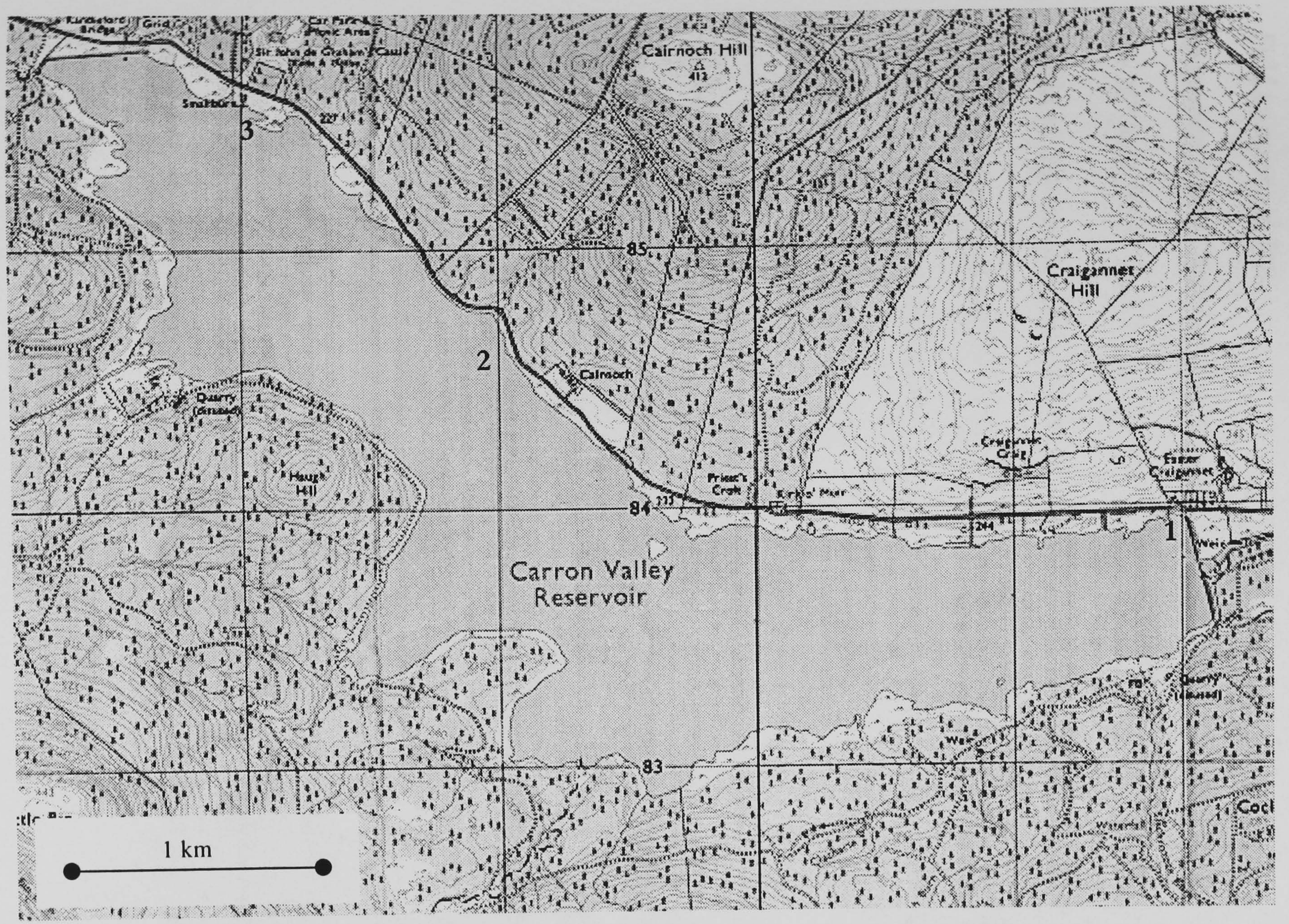


Figure 5.1 – The sites at which the panjet marked hatchery-reared brown trout were stocked. Where: 1 = 300 trout stocked on 27th March 1999; 2 = 400 trout stocked on 29th March 1999; 3 = 300 trout stocked on 2nd April 1999.

resident and hatchery-reared fish were sampled and returned to the anglers. Gill net captured fish were sampled according to the general methods (Chapter 3).

Field treatment of fish

85 resident and 112 hatchery-reared, angler caught trout were collected between 3rd April and the 26th June 1999. Fork length (± 1mm) was measured on a measuring board and wet body weight (± 1g) was determined using a set of portable strain gauge digital scales (EKS Ltd, UK). The alimentary tract from the start of the oesophagus to the constriction immediately anterior to the pyloric ceacae was removed from the each fish and stored in 70% alcohol (Duncan, 1991).

5.2.4 Laboratory analysis

To determine diet, the stomach and oesophagus contents were dissected from the stomachs and examined using both dissecting and compound microscopes. Since zooplankton, macroinvertebrates and small fish were ingested whole they are readily identifiable. All prey items were identified to species level where possible, and for insect prey their stage of development (larvae, pupae or adult). The number of individual prey items was recorded for each taxonomic group in each fish sampled. Prey items were blotted on tissue paper to remove excess moisture and all the prey items in each taxonomic group were batch weighed using a Mettler AJ100 digital balance (± 0.001g) to obtain the wet weights of prey items.

5.2.4 Computational methods

Due to the relatively low numbers of samples in any one week, with the exception of 1 week after stocking with hatchery-reared trout, all weekly samples were grouped into bi-weekly sample groups for the purposes of data analysis.

Quantity of prey consumed

Prey consumption data were tested for normality using a Kolmogorov-Smirnov test using the statistical package SigmaStat (Jandel Corporation, 1995). Prey consumption data expressed as the number of prey items consumed were not normally distributed, whilst prey consumption data expressed as wet weights per taxa was normally distributed.

Consequently, a Kruskal-Wallis analysis of variation by ranks was used to compare the number of prey consumed by resident and hatchery-reared trout. With a Mann-Whitney 'U' test used to test for differences in numbers of prey consumed at bi-weekly intervals post-stocking.

Wet weight of stomach contents for both fish groups were Log_{10} transformed prior to testing for a significant difference between resident and hatchery-reared trout using a one-way ANOVA. To examine differences between the two fish groups at bi-weekly intervals, post-stocking student t-tests on the Log_{10} transformed data, were used.

Prey preference

To assess the relative prey preferences of the angler caught resident and hatchery-reared trout, the prey previously identified as near to taxa level as possible were reclassified to their respective orders, whilst still differentiating between the various developmental stages (larvae, pupae and adult). 17 orders of prey items were identified, which prohibited the use of three-dimensional graphical analysis. Consequently, the dietary analysis results for prey preferences was presented in tabular form, including (as in the graphical analysis of Cortes, 1997) Percent Index of Relative Importance, percent by number, percent by weight and frequency of occurrence data.

Index of relative importance

To assess the dietary importance of both individual prey taxa and foraging habitats a percent 'index of relative importance' (%IRI)(Cortes, 1997) was calculated for trout of wild and hatchery-reared origins for all 2 week periods. The Index of Relative Importance (IRI) (Hyslop, 1980) was calculated as:

$$\mathbf{IRI} = (\%N + \%W) \times \%F$$

Where: %N = percentage of prey 'x' in the sampled diets by number; %W = percentage of prey 'x' in the sampled diets by weight; %F = frequency of occurrence of prey 'x' in sampled diets.

Percent index of relative importance

The percent index of relative importance (%IRI)(Cortes, 1997) was calculated as:

$$\mathbf{\%IRI}_i = 100\ \mathrm{IRI}_i \ / \sum_{i=1}^{n} \mathrm{IRI}_i$$

Where: i = family group; n = total number of food categories.

Foraging habitat use and trend interpretation

To examine the relative changes in foraging habitat use for resident and hatchery-reared trout, each prey species was classified as being found in one of three habitat types. These were:

- Surface-prey items of terrestrial origin + aerial aquatic invertebrates + pleuston
- Nekton of zooplankton prey species + chironomid pupae + teleost species
- Benthic invertebrates.

To increase the ease of foraging habitat use trend interpretation a three-dimensional model suggested by Cortes (1997) (Figure 5.2) was applied to the collected data. Each point on the graph represents the percent occurrence (%O) and abundance (in terms of weight (%W) and numbers (%N)) for a prey category. Any prey point located close to 100% O, W and N is the dominant food type (Figure 5.2 – *a*), whilst any prey point located close to 0% O, W and N is a rare food type (Figure 5.2 – *b*). A prey point located close to 100% O, 1% W and N is indicative of a generalised diet (Figure 5.2 – *c*) whilst a prey point located close to 1% O, 100% W and N is indicative of a specialised diet (Figure 5.2 – *d*). A prey point located close to 100% O and N, 1% W would indicate a light food item consumed by most predators (Figure 5.2 – *e*) whilst a prey point close to 100% O and W, 1%N would indicate few heavy items consumed by most predators (Figure 5.2 – *g*). A prey point located close to 1% O and N, 100% W would indicate a specialised data by a few predators consuming a few heavy prey items (Figure 5.2 – *f*). A prey point located close to 1% O and W, 100% N would indicate a specialised diet by a few predators consuming large numbers of light food items (Figure 5.2 – *h*).

Comparison of fish body condition between wild and hatchery-reared conspecifics

The condition factor was calculated for each individual fish and one-way ANOVA used to test for differences between the resident and hatchery-reared trout. Differences between the two fish groups, at different times after stocking with hatchery-reared trout, was assessed *post hoc*, using student t-tests. Condition factor (k) was calculated as (Nielson & Johnson, 1983):

$$\mathbf{k} = \frac{\text{Total wet body weight of fish (g)}}{(\text{Fork length (cm)})^3} \times 100$$

Total wet body weight values for both fish groups were Log10 transformed prior to testing for a significant difference between resident and hatchery-reared trout using a one-way ANOVA. Differences between the two fish groups at different times after stocking were assessed using student t-tests on the Log10 transformed data.

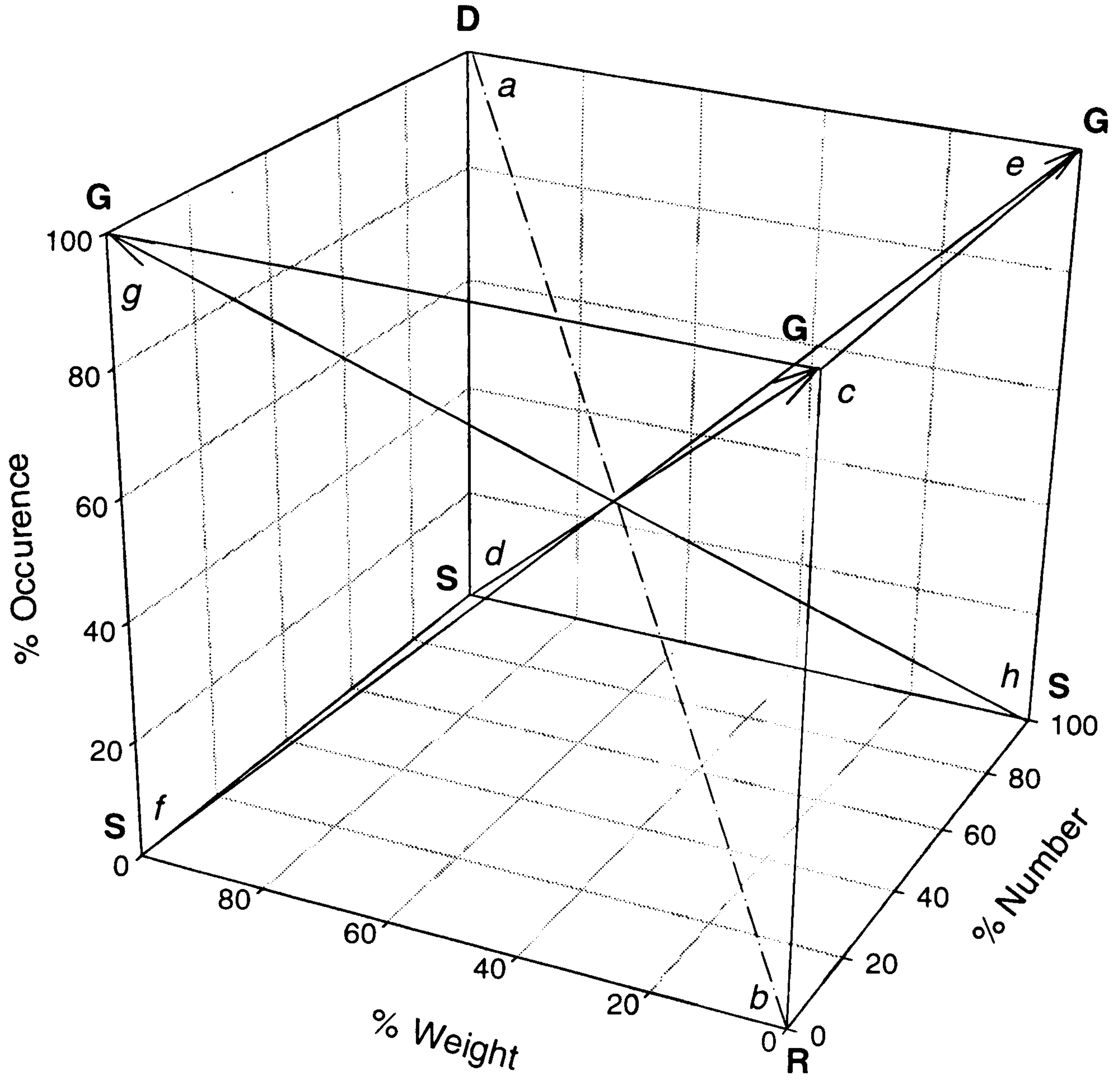


Figure 5.2 - Three-dimensional graphical representation of stomach content data as proposed by Cortes (1997). D= dominant food category; R= rare food category; G= generalised diet; S= specialised diet. See text for definitions of *a,b,c,d,e,f,g* and *h*.

5.3 Results

5.3.1 Post-stocking changes in the quantity of prey consumed by angler caught resident and hatchery-reared brown trout

Number of prey items consumed

Concurrently sampled resident trout consumed a significantly greater total number of prey items than hatchery-reared trout over the entire sampling period (Kruskal-Wallis; H=36.99, d.f.=1, P<0.001), with resident trout consuming a median of 36 and hatchery-reared trout consuming a median of 11 prey items per stomach. In the resident trout, the median number of prey items per stomach ranged from 21 to 47 organisms, and remained relatively constant throughout the sampling period (Pearsons' Product Moment Correlation, correlation coefficient=0.160, p=0.155) (Table 5.1). In the hatchery-reared trout the median number of prey items per stomach ranged from 7 to 28 organisms; and increased significantly over the entire sample period (Pearsons' Product Moment Correlation, correlation coefficient=0.239, P=0.011) (Table 5.1). The resident trout ingested significantly more prey items than the hatchery-reared trout in the samples taken between 1 and 7 weeks after stocking with hatchery-reared trout. In the stomachs sampled during weeks 9, 11 and 13 after stocking with the hatchery-reared trout, there was no significant difference in the median number of prey items ingested by concurrently sampled resident and hatchery-reared trout (Table 5.1).

Weight of stomach contents

The concurrently sampled resident brown trout population consumed a significantly greater wet weight of prey than the stocked hatchery-reared trout over the entire sampling period (ANOVA; $F_{1,184}=63.1$, P<0.001), with resident trout exhibiting a mean wet weight of

Table 5.1 – The median number of prey items per stomach in angler caught resident and hatchery-reared brown trout caught between the 3rd April and 26th June 1999, at different times after initial stocking.

Time after stocking (weeks)	Fish Type	Sample Size (n)	Median No. of Prey Items per Stomach	U	P
1	Resident	13	46.00	120.00	=0.003*
	Stocked	13	7.00		
3	Resident	12	24.50	307.50	=0.004*
	Stocked	17	4.00		
5	Resident	13	36.50	339.00	=0.001*
	Stocked	26	8.00		
7	Resident	14	43.50	249.50	=0.021*
	Stocked	19	11.00		
9	Resident	11	30.00	154.00	=0.354
	Stocked	13	20.00		
11	Resident	12	21.00	52.50	=0.329
	Stocked	6	16.00		
13	Resident	10	47.00	134.50	=0.081
	Stocked	18	28.00		

* = significant difference

Table 5.2 - The mean wet weight of prey per stomach in angler caught resident and hatchery-reared brown trout caught between the 3rd April and 26th June 1999, at different times after initial stocking.

Time after stocking (weeks)	Fish Type	Sample Size (n)	Mean wet weight of prey (g) per stomach	S.E. on mean	t♦	d.f.	P
1	Resident	13	1.18	0.315	6.06	24	<0.001*
	Stocked	13	0.15	0.075			
3	Resident	12	1.71	0.437	5.67	27	<0.001*
	Stocked	17	0.18	0.040			
5	Resident	13	1.89	0.659	5.98	33	<0.001*
	Stocked	26	0.19	0.041			
7	Resident	14	1.53	0.382	3.98	26	<0.001*
	Stocked	19	0.38	0.076			
9	Resident	11	1.38	0.488	2.31	19	=0.032*
	Stocked	13	0.33	0.051			
11	Resident	12	1.83	0.529	2.24	16	=0.040*
	Stocked	6	0.31	0.038			
13	Resident	10	1.94	0.709	2.24	27	=0.033*
	Stocked	18	0.53	0.120			

* significant difference; S.E.=standard error of the mean wet weight of prey per stomach; ♦ t-test performed on Log_{10} transformed data.

stomach contents of 1.63g (S.E. ±0.189) whilst hatchery-reared trout exhibited a mean of 0.29g (S.E. ±0.029); with the resident trout consuming significantly greater wet weights of prey than hatchery-reared conspecifics in all the sampling periods (Table 5.2). In the resident trout population the mean wet weight of stomach contents ranged from 1.18 to 1.94g, and remained relatively constant over the entire sample period (Pearsons' Product Moment Correlation, correlation coefficient=0.0697, p=0.536) (Table 5.2). In the hatchery-reared trout, the mean wet weight of stomach contents ranged from 0.15 to 0.53g, and increased significantly with time after stocking over the sample period (Pearsons' Product Moment Coefficient, correlation coefficient=0.416, P<0.001) (Table 5.2).

5.3.2 Post-stocking changes in the prey preferences of angler caught resident and hatchery-reared brown trout

Resident trout

Over the entire sample period resident trout exhibited great diversity in their selection of prey with 38 different families of prey being identified and a median number of 4 prey species per stomach. In the samples taken during 3, 5 and 9 weeks after initial stocking, trichopteran larvae dominated the concurrently sampled resident trout diets (Tables 5.4, 5.5 and 5.7). Dipteran pupae dominated the concurrently sampled resident trout diets in weeks 1 and 7 (Tables 5.3 and 5.6), dipteran larvae in week 11 (Table 5.8) and hemipteran species in week 13 (Table 5.9). Benthic prey items including pulmonatan, prosobranchian, isopodan, amphipodan, cyrenodontan and dipteran larvae ranked relatively highly (rank of %IRI) in the concurrently sampled resident trout diets between 1 and 9 weeks after stocking with hatchery-reared trout (Tables 5.3-5.7). With the exception of dipteran larvae and cyrenodontan species, all benthic prey items accounted for a greater percentage of the total

Table 5.3 – A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 1 week after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda	0.49	0.51	7.69	8	0.06	10	-	-	-	-	-	-
Isopoda	10.53	8.04	23.08	429	3.51	5	-	-	-	-	-	-
Prosobranchia	-	-	-	-	-	-	-	-	-	-	-	-
Pulmonata	0.65	16.26	23.08	390	3.20	6	-	-	-	-	-	-
Cyrenodonta	7.13	4.25	38.46	438	3.58	4	-	-	-	-	-	-
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera	0.32	0.13	15.38	7	0.06	10	-	-	-	-	-	-
Megaloptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	20.42	28.95	92.31	2693	37.36	2	-	-	-	-	-	-
Diptera – Adult	0.65	0.47	15.38	17	0.14	9	3.81	26.87	30.76	944	10.25	2
- Pupae	40.59	14.47	84.62	4646	38.20	1	52.08	48.49	76.92	7736	52.08	1
- Larvae	18.64	5.43	61.53	1480	12.14	3	-	-	-	-	-	-
Coleoptera	0.81	0.91	30.80	53	0.43	8	-	-	-	-	-	-
Hymenoptera	-	-	-	-	-	-	44.10	23.63	7.69	521	5.66	3
Cyprinidae – Fish	0.16	20.40	7.69	158	1.30	7	-	-	-	-	-	-
- Eggs	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	-	-	-	-	-	-	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

Table 5.4 - A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 3 weeks after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda	1.96	5.08	16.67	117	0.87	6	0.93	3.46	5.88	26	0.22	5
Isopoda	1.43	4.14	25.00	139	1.04	5	-	-	-	-	-	-
Prosobranchia	-	-	-	-	-	-	-	-	-	-	-	-
Pulmonata	2.14	11.60	50.00	687	5.12	3	-	-	-	-	-	-
Cyrenodonta	0.18	0.79	8.33	8	0.06	10	-	-	-	-	-	-
Plecoptera	0.54	1.59	8.33	18	0.13	8	-	-	-	-	-	-
Hemiptera	0.54	0.11	25.00	16	0.12	9	10.65	10.79	17.65	378	3.22	3
Megaloptera	0.36	0.08	8.33	4	0.03	11	-	-	-	-	-	-
Trichoptera	24.64	72.34	75.00	7274	54.25	1	2.78	30.08	23.53	773	6.58	2
Diptera – Adult	1.07	0.68	8.33	15	0.10	12	-	-	-	-	-	-
- Pupae	51.04	1.64	83.33	4390	32.74	2	84.72	53.73	76.47	10587	89.69	1
- Larvae	14.46	1.22	41.67	76	4.87	4	-	-	-	-	-	-
Coleoptera	1.43	0.73	41.67	90	0.67	7	0.93	1.94	11.76	34	0.29	4
Hymenoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae – Fish	-	-	-	-	-	-	-	-	-	-	-	-
- Eggs	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	-	-	-	-	-	-	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

Table 5.5 - A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 5 weeks after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	30.26	0.50	7.69	237	2.13	4	19.13	0.73	7.69	153	1.68	4
Ostracoda	2.23	0.24	7.69	18	0.16	10	-	-	-	-	-	-
Amphipoda	0.28	0.68	15.38	15	0.13	11	-	-	-	-	-	-
Isopoda	1.53	3.84	38.46	207	1.86	6	-	-	-	-	-	-
Prosobranchia	2.37	0.21	23.08	56	0.53	8	0.91	2.00	7.69	22	0.24	6
Pulmonata	8.10	32.12	30.77	1238	11.19	3	1.14	2.83	3.85	15	0.17	7
Cyrenodonta	3.63	1.28	23.08	113	1.02	7	0.91	0.48	3.85	5	0.06	9
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-	-	-	-	-	-	-
Megaloptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	20.08	46.84	92.31	6177	55.88	1	5.69	47.89	34.62	1855	20.50	2
Diptera – Adult	1.67	0.84	7.69	19	0.17	9	8.43	12.39	11.54	240	2.65	3
- Pupae	23.43	9.18	84.62	2759	24.96	2	60.82	30.83	73.08	6698	74.07	1
- Larvae	7.39	1.66	23.08	209	1.89	5	1.59	0.85	3.85	9	0.09	8
Coleoptera	0.27	0.27	15.38	8	0.07	12	1.36	1.79	15.38	48	0.53	5
Hymenoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae – Fish	-	-	-	-	-	-	-	-	-	-	-	-
- Eggs	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	-	-	-	-	-	-	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

weight of the stomach contents (%W) than of the total number of prey items ingested (%N). Cladoceran species occurred in a small proportion of the concurrently sampled resident trout stomachs but ranked relatively highly (rank of %IRI) in the samples taken 5, 7 and 9 weeks after stocking with hatchery-reared trout (Tables 5.5, 5.6 and 5.7). Both dipteran pupae and cladoceran species accounted for a greater percentage of the total number of prey items ingested (%N) than of the total weight of the stomach contents (%W). Gasterosteidae, salmonidae and cyprinidae species occurred infrequently in the concurrently sampled resident trout diets taken between 1 and 9 weeks after stocking with hatchery-reared trout (Tables 5.3-5.7), but ranked relatively highly (rank of %IRI) in weeks 11 and 13 (Tables 5.8 and 5.9). These teleost prey items occurred in a small proportion of the sampled stomachs, contributing little to the total number of prey items ingested (%N) but greatly to the total weight of the sampled stomach contents (%W). Surface prey items including dipteran adults, hemipteran, hymenopteran and coleopteran species exhibited relatively low %IRI values and occurred infrequently in the concurrently sampled resident trout diets between 1 and 9 weeks after stocking with hatchery-reared trout (Tables 5.3-5.7). In the concurrently sampled resident trout diets taken 11 weeks after stocking with hatchery-reared trout, hemipteran and coleopteran species maintained relatively low %IRI values whilst dipteran adults increased their relative dietary importance (rank of %IRI) to rank third (Table 5.8). Although dipteran adults were absent from the concurrently sampled resident trout diets taken 13 weeks after stocking with hatchery-reared trout, coleopteran and hymenopteran species increased their relative dietary contributions whilst hemipteran species dominated (Table 5.9).

Table 5.6 - A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 7 weeks after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	16.33	0.25	7.14	118	1.33	7	24.45	0.87	5.26	133	1.25	4
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda	0.40	1.26	21.43	36	0.39	10	0.22	0.76	5.26	5	0.05	8
Isopoda	0.80	6.20	21.43	150	1.69	5	0.22	1.46	5.26	9	0.06	7
Prosobranchia	2.29	2.02	14.28	62	0.68	8	-	-	-	-	-	-
Pulmonata	7.42	13.07	21.43	439	4.95	3	-	-	-	-	-	-
Cyrenodonta	1.48	5.52	7.14	50	0.55	9	1.53	0.74	5.26	12	0.11	6
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-	-	-	-	-	-	-
Megaloptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	11.06	35.76	64.29	3010	33.97	2	7.64	46.38	63.16	3412	32.23	2
Diptera – Adult	1.08	0.87	7.14	14	0.15	12	2.84	14.51	21.05	365	3.45	3
- Pupae	53.04	16.57	64.29	4475	50.50	1	56.77	33.00	73.68	6614	62.48	1
- Larvae	7.83	1.91	14.28	139	1.57	6	4.59	2.28	5.26	36	0.34	5
Coleoptera	0.40	1.03	21.43	31	0.34	11	-	-	-	-	-	-
Hymenoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae – Fish	-	-	-	-	-	-	-	-	-	-	-	-
- Eggs	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	0.67	15.30	21.43	342	3.86	4	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

Table 5.7 - A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 9 weeks after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	51.46	0.54	9.09	473	6.32	4	-	-	-	-	-	-
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda	0.32	0.20	18.18	9	0.12	10	0.60	1.69	7.69	18	0.15	6
Isopoda	3.08	0.66	27.27	102	1.36	6	-	-	-	-	-	-
Prosobranchia	4.05	11.26	45.45	696	9.31	3	-	-	-	-	-	-
Pulmonata	4.10	22.34	36.36	961	12.86	2	0.90	2.19	15.38	48	0.42	5
Cyrenodonta	1.95	1.37	18.18	60	0.80	8	0.30	0.19	7.69	4	0.04	7
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera	0.16	0.11	9.09	2	0.03	12	-	-	-	-	-	-
Megaloptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	30.03	46.24	63.64	4854	64.95	1	6.02	37.98	46.15	2031	18.03	2
Diptera – Adult	-	-	-	-	-	-	-	-	-	-	-	-
- Pupae	0.16	0.34	9.09	5	0.07	11	75.30	54.04	69.23	8954	79.57	1
- Larvae	1.29	1.00	18.18	42	2.98	5	3.01	1.94	15.38	76	0.67	4
Coleoptera	0.97	0.02	18.18	18	0.24	9	-	-	-	-	-	-
Hymenoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae – Fish	-	-	-	-	-	-	-	-	-	-	-	-
- Eggs	2.27	5.68	9.09	72	0.96	7	14.46	1.97	7.69	126	1.12	3
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	-	-	-	-	-	-	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

Stocked, hatchery-reared brown trout

Hatchery-reared trout ingested significantly fewer prey species over the entire sample period than the concurrently sampled resident trout (Kruskal-Wallis, H=61.681, d.f.=1, P<0.001) with a median number of 2 prey species per stomach. 1 week after stocking, only 3 different prey species were present in the hatchery-reared trout stomach samples (Table 5.3). However, diversity of prey selection in hatchery-reared trout significantly increased with increasing time from stocking (Pearsons Product Moment Coefficient, correlation coefficient=0.425, P<0.001). Dipteran pupae dominated the hatchery-trout diets over the entire sampling period, occurring in a large proportion of the sampled stomachs and accounting for a greater percentage of the total number of prey items ingested (%N) than of the total weight of the stomach contents (%W). In the samples taken 1 week after stocking, along with dipteran pupae, dipteran adults and hymenopteran species comprised the whole of the hatchery-reared trout stomach contents (Table 5.3). Surface prey items including hemipteran, coleopteran, hymenopteran and dipteran adults ranked relatively highly (rank of %IRI) in the hatchery-reared trout stomachs sampled between 1 and 7 weeks after stocking (Tables 3-6) and in the samples taken in week 13 (Table 5.9). With the exception of coleopteran species, all surface prey items accounted for a greater percentage of the total number of prey items ingested (%N) than of the total weight of the stomach contents (%W). In the hatchery-reared trout samples taken between 5 and 7 weeks after stocking cladoceran species ranked relatively highly (rank of %IRI), but only occurred in a small proportion of the sampled stomachs (Tables 5.5 and 5.6). All cladoceran species accounted for a greater percentage of the total number of prey items ingested (%N) than of the total weight of the stomach contents (%W). Trichopteran species ranked second in dietary importance in the samples taken between 3 and 13 weeks after stocking (Tables 5.4-5.9), occurring in a

Table 5.8 - A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 11 weeks after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	36.25	0.71	8.33	308	8.06	7	-	-	-	-	-	-
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda	0.36	0.71	16.67	12	0.47	13	-	-	-	-	-	-
Isopoda	-	-	-	-	-	-	-	-	-	-	-	-
Prosobranchia	1.45	0.83	8.33	19	0.49	12	0.94	4.67	16.60	93	0.71	6
Pulmonata	1.82	12.26	25.00	352	9.21	6	11.32	7.79	16.60	317	2.24	5
Cyrenodonta	13.84	1.86	16.67	262	6.86	8	1.89	1.36	16.60	54	0.41	7
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera	0.18	0.28	8.33	4	0.10	14	-	-	-	-	-	-
Megaloptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	3.28	9.69	50.00	649	16.20	2	12.26	45.52	83.33	4815	36.77	2
Diptera – Adult	10.02	5.84	25.00	397	10.37	3	6.60	13.33	16.60	331	2.53	4
- Pupae	6.92	2.21	41.67	380	9.95	4	55.67	28.37	83.33	7003	53.48	1
- Larvae	22.59	1.41	33.33	800	20.94	1	6.60	3.02	50.00	997	3.67	3
Coleoptera	1.28	2.11	25.00	85	2.23	10	-	-	-	-	-	-
Hymenoptera	-	-	-	-	-	-	-	-	-	-	-	-
Cyprinidae – Fish	-	-	-	-	-	-	-	-	-	-	-	-
- Eggs	2.00	0.04	16.67	34	0.89	11	-	-	-	-	-	-
Salmonidae	0.18	43.02	8.33	360	9.42	5	-	-	-	-	-	-
Gasterosteidae	0.36	21.57	8.33	183	4.79	9	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

Table 5.9 - A comparison of the prey preferences of angler caught resident and hatchery-reared brow trout, sampled 13 weeks after stocking with hatchery-reared trout.

Food Type	Resident trout						Stocked trout					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda	-	-	-	-	-	-	-	-	-	-	-	-
Amphipoda	3.20	1.01	10.00	42	1.00	8	1.44	9.44	5.56	60	0.73	7
Isopoda	0.69	1.18	10.00	19	0.45	10	0.72	0.90	11.11	18	0.22	9
Prosobranchia	-	-	-	-		11	-	-	-	-	-	-
Pulmonata	0.92	0.71	10.00	16	0.38	-	-	-	-	-	-	-
Cyrenodonta	-	-	-	-	-	-	-	-	-	-	-	-
Plecoptera	-	-	-	-	-	-	-	-	-	-	-	-
Hemiptera	16.48	9.43	60.00	1555	36.99	1	1.63	1.98	16.67	60	0.73	7
Megaloptera	-	-	-	-	-	-	-	-	-	-	-	-
Trichoptera	2.52	23.33	40.00	1034	24.60	3	5.58	23.62	50.00	1460	17.67	2
Diptera – Adult	-	-	-	-	-	-	6.31	9.59	16.67	265	3.21	4
- Pupae	55.15	3.82	20.00	1179	28.04	2	48.65	31.65	72.22	5799	70.20	1
- Larvae	11.90	0.48	10.00	124	2.95	7	4.68	2.54	16.67	120	1.45	6
Coleoptera	0.92	1.17	20.00	42	1.00	8	0.36	0.29	11.11	7	0.08	10
Hymenoptera	5.95	1.31	20.00	145	3.45	6	27.75	1.87	11.11	329	3.98	3
Cyprinidae – Fish	1.14	39.11	20.00	805	19.15	4	2.71	10.14	11.11	143	1.73	5
- Eggs	-	-	-	-	-	-	-	-	-	-	-	-
Salmonidae	-	-	-	-	-	-	-	-	-	-	-	-
Gasterosteidae	0.69	19.45	10.00	201	4.78	5	-	-	-	-	-	-

- Note: %N = percentage of diet by number, %W = percentage of diet by weight, %O = Percentage frequency of occurrence, IRI = Index of Relative Importance, %IRI = percent Index of Relative Importance, '-' denotes food item absent from sampled stomachs.

progressively greater percentage of the sampled stomachs with increasing time after stocking. Other benthic prey items including amphipodan, isopodan, prosobranchian, pulmonatan, cyrenodontan and dipteran larvae occurred in a relatively small proportion of the sampled stomachs and contributed relatively little to the total number of prey items ingested (%N) and the total weight of the stomach contents (%W). With the exception of dipteran larvae and cyrenodontan species, all benthic prey items accounted for a greater percentage of the total weight of the stomach contents (%W) than of the total number of prey items ingested (%N). Cyprinidae eggs occurred in a small number of the hatchery-reared stomach samples taken 9 weeks after stocking (Table 5.7), whilst cyprinidae adults occurred in a small number of the stomach samples taken in week 13 (Table 5.9). Salmonidae and Gasterosteidae prey were absent from the sampled hatchery-reared stomachs over the entire sampling period.

5.3.3 Post-stocking changes in foraging habitat use of angler caught resident and hatchery-reared brown trout

Resident brown trout

The resident trout exhibited a relatively heterogenous, generalised diet over the entire sampling period. Between 1 and 9 weeks after stocking with hatchery-reared trout, the concurrently sampled diets of the resident trout were dominated by benthic prey items, with nektonic prey items ranking second in dietary importance and surface prey items contributing the least to the sampled diets (Figure 5.3(a)-(e)). In the samples taken 11 and 13 weeks after stocking with hatchery-reared trout, nektonic prey items dominated the diets of the concurrently sampled resident trout, whilst the relative contribution of benthic prey items progressively fell and the relative contribution of surface prey items progressively increased (Figures 5.3(f) and (g)).

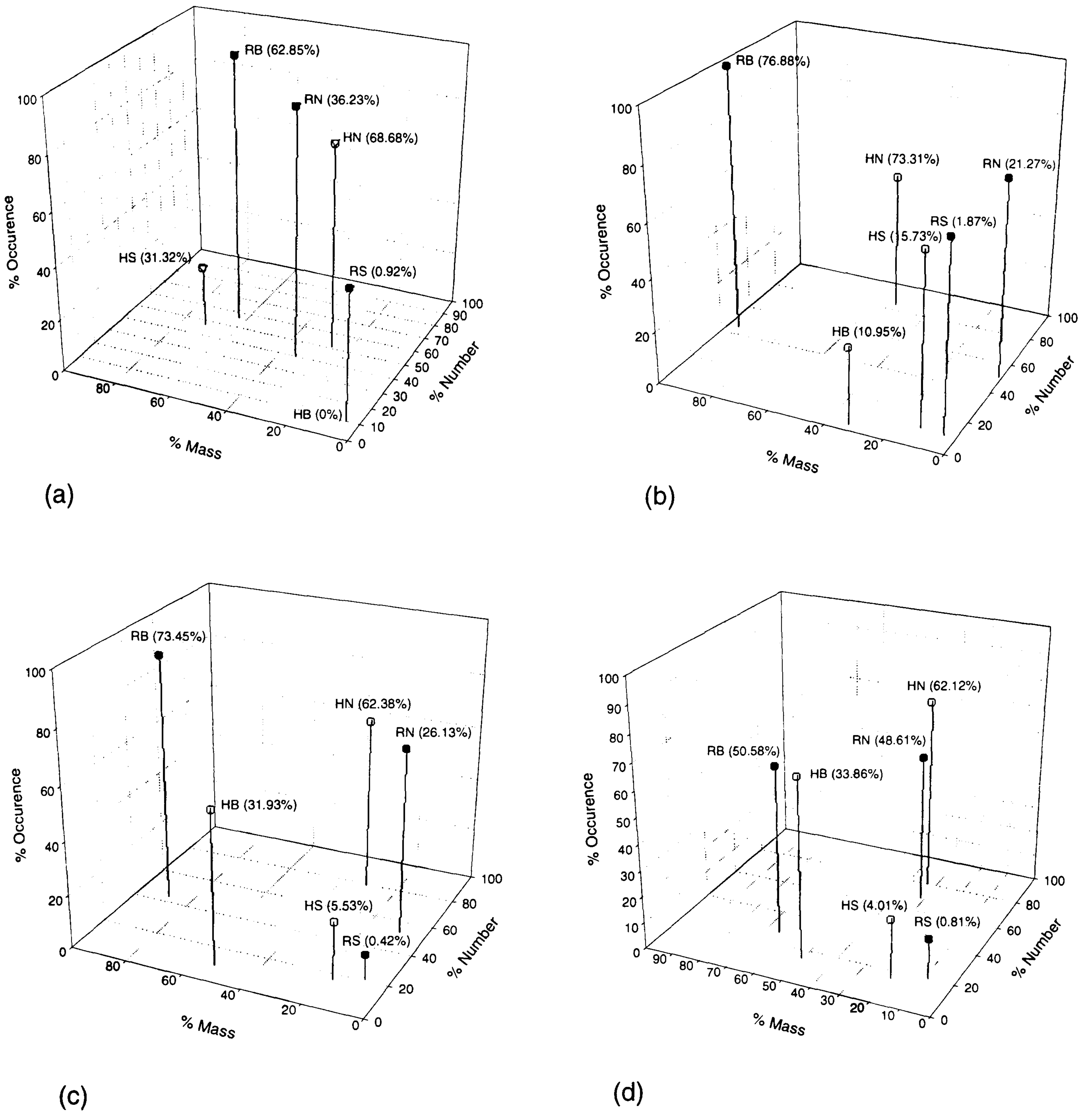
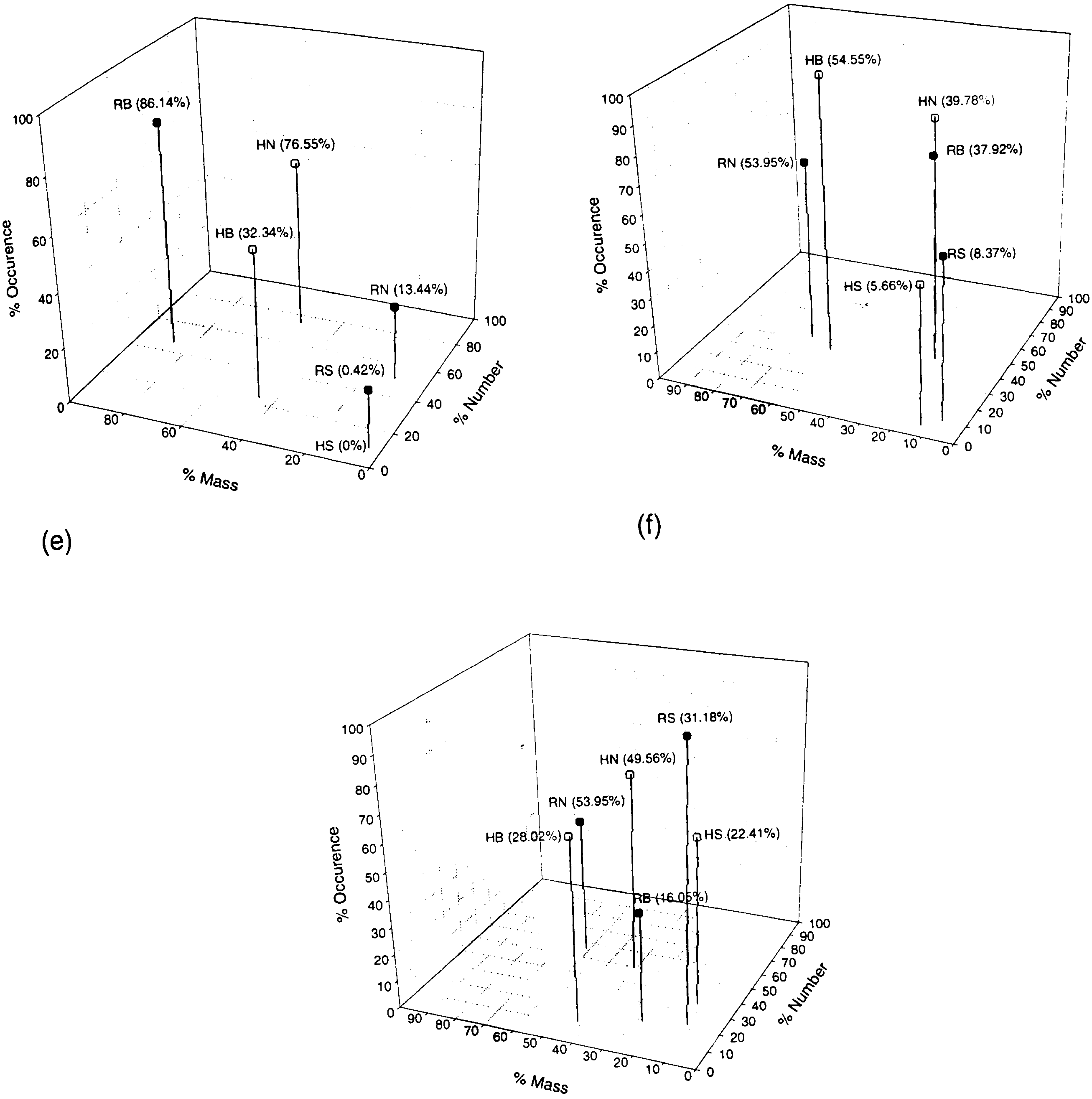


Figure 5.3 – Variation in foraging strategy between angler caught resident and hatchery-reared brown trout captured (a) 1 week, (b) 3 weeks, (c) 5 weeks, (d) 7 weeks, (e) 9 weeks, (f) 11 weeks and (g) 13 weeks after initial stocking with hatchery-reared fish(continued over page). Where: RB= resident trout benthic dietary component, RN= resident trout nektonic dietary component, RS= resident trout surface dietary component, HB= hatchery-reared trout benthic dietary component, HN= hatchery-reared trout nektonic dietary component, HS= Hatchery-reared trout surface dietary component and (x%)= Percentage Index of Relative Importance.



(e)

(f)

(g)

Figure 5.3 – continued from previous page

Stocked, hatchery-reared brown trout

Between 1 and 3 weeks after stocking (Figure 5.3(a) and (b)), hatchery-reared trout exhibited relatively specialist feeding behaviour which gradually became more generalised in the samples taken between 5 and 13 weeks after stocking (Figure 5.3(c)-(f)). In all the sampled stomachs, except those taken 11 weeks after stocking, nektonic prey items dominated the diets of hatchery-reared trout, displaying the highest %IRI values (Figure 5.3(a)-(e) and (g)). Surface prey items ranked second in terms of %IRI in the samples taken 1 and 3 weeks after stocking (Figure 5.3(a) and (b)). Benthic prey items were absent from the hatchery-reared stomachs sampled 1 week after stocking (Figure 5.3(a)), but occurred in 29.41% of the sampled stomachs taken 3 weeks after stocking accounting for 33.54% of the total weight of the sampled stomach contents (Figure 5.3(b)). In the samples taken 3 weeks after stocking nektonic prey only occurred in 52.94% of the stomachs but accounted for 84.72% of the total number of prey items ingested at that time (Figure 5.3(b)). Between 1 and 9 weeks after stocking the relative contribution of surface prey items to the hatchery-reared trout diets progressively fell (Figure 5.3(a)-(e)) but increased in the samples taken in weeks 11 and 13 (Figure 5.3(f) and (g)). The relative contribution of benthic prey items to the diets of hatchery-reared trout progressively increased in the samples taken between 3 and 9 weeks after stocking and dominated the diets of hatchery-reared trout in the samples taken in week 11, and only fell in the samples taken in week 13.

5.3.4 Post-stocking changes in the condition factor and body weight of angler caught resident and hatchery-reared brown trout

Condition factor

Concurrently sampled resident brown trout displayed a significantly lower mean condition factor (k) than the hatchery-reared trout over the entire sampling period (ANOVA; $F_{1,156}$=27.59, P<0.001), with a mean condition factor of 1.04 (S.E. ±0.089) observed in the resident trout and 1.15 (S.E. ±0.149) observed in the hatchery-reared trout. Following stocking, hatchery-reared trout exhibited a significantly higher condition factor than concurrently sampled resident trout (Table 5.10). The condition factor of the hatchery-reared trout declined significantly over the remainder of the sampling period (Pearsons Product Moment Correlation, correlation coefficient=-0.541, p<0.001) reaching comparable levels to the resident trout by 9 weeks after stocking (Table 5.10). The condition factor of the concurrently sampled resident trout increased significantly with increasing time over the entire sampling period (Pearsons Product Moment Correlation, correlation coefficent=0.248, P=0.048).

Body Weight of angler caught fish

Concurrently sampled resident brown trout had a significantly lower mean wet body weight than hatchery-reared trout over the whole sampling period (ANOVA; $F_{1,194}$=65.4, P<0.001), with a mean wet body weight of 307.3g (S.E. ± 9.1) observed in the resident trout and 536.2g (S.E. ±23.3) observed in the hatchery-reared trout. Resident trout had lower mean wet body weights than hatchery-reared conspecifics in all sample periods (Table 5.11). The mean wet body weight of the resident fish ranged from 296.1 to 317.6g and remained relatively constant over the whole sampling period (Table 5.11). The mean wet body weight of the

Table 5.10 – Changes in the condition factor of angler caught resident and stocked brown trout sampled between the 3rd April and 26th June 1999.

Time after stocking (weeks)	Fish Type	Sample Size (n)	Mean Condition Factor (k)	S.E. on mean	t	d.f.	P
1	Resident	13	0.98	0.0204	9.187	24	<0.001*
	Stocked	13	1.27	0.0243			
3	Resident	12	1.06	0.0145	5.138	27	<0.001*
	Stocked	17	1.20	0.0212			
5	Resident	13	1.10	0.0284	3.072	33	=0.005*
	Stocked	26	1.19	0.016			
7	Resident	14	1.01	0.0298	5.137	26	<0.001*
	Stocked	19	1.17	0.0145			
9	Resident	11	1.08	0.0293	0.921	19	=0.370
	Stocked	13	1.11	0.0169			
11	Resident	12	1.05	0.0353	2.415	16	=0.042*
	Stocked	6	1.16	0.0261			
13	Resident	10	1.07	0.0279	0.945	27	=0.356
	Stocked	18	0.97	0.0686			

* significant difference; S.E.=standard error of the mean condition factor.

Table 5.11 - The mean wet body weight per fish in angler caught resident and hatchery-reared brown trout caught between the 3rd April and 26th June 1999, at different times after initial stocking.

Time after stocking (weeks)	Fish Type	Sample Size (n)	Mean total wet body weight per fish (g)	S.E. On mean	t♦	d.f.	P
1	Resident	13	311.5	25.0	5.01	24	<0.001*
	Stocked	13	599.0	69.2			
3	Resident	12	314.9	17.1	5.13	27	<0.001*
	Stocked	17	667.5	82.2			
5	Resident	13	304.8	18.6	5.64	33	<0.001*
	Stocked	26	512.7	31.2			
7	Resident	14	299.3	30.0	4.37	26	<0.001*
	Stocked	19	512.7	54.5			
9	Resident	11	317.6	22.8	2.72	19	=0.012*
	Stocked	13	515.5	97.8			
11	Resident	12	296.1	24.8	2.99	16	=0.009*
	Stocked	6	465.1	64.5			
13	Resident	10	307.3	30.8	4.21	27	<0.001*
	Stocked	18	457.2	24.7			

* significant difference; S.E.=standard error of mean total wet body weight per fish; ♦ t-test performed on Log$_{10}$ transformed data.

hatchery-reared fish ranged from 457.2 to 667.5g and decreased significantly with increasing time after stocking (Pearsons'Product Moment Coefficient, correlation coefficient=-0.226, P=0.017)(Table 5.11).

5.3.5 Comparison of the quantity of prey consumed by gillnet and angler caught resident brown trout

Number of prey items contained

Angler caught trout consumed a significantly greater number of prey items than conspecific gillnet captured trout over the same time period (Kruskal-Wallis, H=4.975, d.f.=1, P=0.026), with an observed median number of prey per stomach of 36 in the angler caught and 11 in the gillnet caught trout.

Weight of the stomach contents

No significant difference was found in the mean wet weight of prey per stomach between the conspecific gillnet and angler caught trout (ANOVA, $F_{1,94}$=0.171, P=0.680), with an observed mean wet weight of prey per stomach of 1.63g (S.E. ±0.189) in angler caught trout and 1.89g (S.E. ±1.09) in gillnet caught trout.

5.3.6 Comparison of the prey preferences of gillnet and angler caught resident brown trout

Angler caught trout consumed a significantly greater number of prey species per sampled stomach than conspecific gillnet captured trout over the same time period (Kruskal-Wallis, H=4.590, d.f.=1, P=0.032). Trichopteran larvae dominated the diets of both trout groups, with dipteran pupae ranking second (rank of %IRI) in angler caught trout diets and dipteran larvae ranking second (rank of %IRI) in gillnet captured trout diets (Table 5.12). In the

Table 5.12 - A comparison of the prey preferences of gillnet and angler caught resident brown trout captured between April and June 1999.

Food Type	Gillnet Caught						Angler Caught					
	%N	%W	%O	IRI	%IRI	Rank of %IRI	%N	%W	%O	IRI	%IRI	Rank of %IRI
Cladocera	23.43	0.17	6.67	157	2.85	6	24.04	0.28	4.76	116	1.57	7
Ostracoda	-	-	-	-	-	-	0.45	0.03	1.19	1	0.01	18
Amphipoda	0.24	0.13	6.67	2	0.04	12	0.65	1.25	14.29	27	0.37	13
Isopoda	1.69	0.91	33.33	87	1.58	7	3.46	3.76	21.43	155	2.10	5
Prosobranchia	0.24	0.09	6.67	2	0.04	12	1.97	2.41	14.29	66	0.89	9
Pulmonata	0.48	3.52	13.33	53	0.96	8	4.65	15.52	27.38	552	7.47	3
Cyrenodonta	1.93	1.58	6.67	23	0.42	9	4.89	2.12	17.86	125	1.69	6
Plecoptera	-	-	-	-	-	-	0.08	0.28	1.19	0.4	0.01	18
Hemiptera	0.72	0.17	6.67	6	0.11	11	2.22	1.12	14.29	48	0.65	11
Megaloptera	-	-	-	-	-	-	0.07	0.01	1.19	0.1	0.01	18
Trichoptera	27.78	10.81	66.66	2572	46.62	1	19.82	39.56	70.24	4171	56.45	1
Diptera – Adult	1.45	0.09	13.33	21	0.38	10	2.31	3.09	17.86	96	1.30	8
- Pupae	13.04	1.65	40.00	588	10.66	3	20.95	7.17	54.76	1540	20.84	2
- Larvae	27.54	2.57	40.00	1204	21.82	2	11.54	1.72	27.38	363	4.91	4
Coleoptera	-	-	-	-	-	-	0.99	0.61	25.00	40	0.54	12
Hymenoptera	-	-	-	-	-	-	0.73	0.15	2.38	2	0.03	17
Cyprinidae – Fish	-	-	-	-	-	-	0.17	6.95	3.57	25	0.34	14
- Eggs	-	-	-	-	-	-	0.70	0.05	3.57	3	0.04	16
Salmonidae	0.24	57.59	6.67	386	7.00	5	0.03	5.38	1.19	5	0.05	15
Gasterosteidae	1.21	19.61	20.00	416	7.54	4	0.28	8.68	5.95	53	0.72	10

- '-' denotes food item absent from sampled stomachs gillnet captured stomach samples trichopteran larvae accounted for a greater percentage of the total number of prey items ingested (%N) than of the total stomach contents weight (%W)(Table 5.12). Conversely in the angler caught stomach samples trichopteran larvae accounted for a greater percentage of the total stomach contents weight (%W) than of the total number of prey items ingested (%N)(Table 5.12). Pulmonatan, dipteran larvae, isopodan and cyrenodontan benthic prey species occupied the 3rd to 6th ranks of dietary importance (rank of %IRI) respectively in the angler caught trout diets (Table 5.12). Whilst dipteran pupae, gasterosteidae, salmonidae and cladoceran nektonic prey species occupied the 3rd to 6th ranks of dietary importance (rank of %IRI) respectively in gillnet caught trout diets (Table 5.12). Gasterosteidae and Salmonidae prey species occurred in a greater percentage of gillnet captured stomachs than in angler caught stomachs, accounting for a much higher percentage of the total stomach contents weight (%W) in gillnet captured trout than in angler caught trout (Table 5.12). Dipteran adults, hemipteran and coleopteran surface prey species occurred in a greater percentage of angler caught diets than in gillnet captured diets, accounting for a higher percentage of the total stomach contents weight (%W) in angler caught trout than in gillnet captured trout (Table 5.12). Dipteran adults, isopodan, pulmonatan, cyrenodontan, amphipodan, prosobranchian and hemipteran species exhibited relatively low dietary importance (%IRI) in gillnet captured trout (Table 5.12). Cladoceran, prosobranchian, amphipodan, cyprinid eggs, plecopteran, megalopteran and ostracodan species exhibited relatively low dietary importance (%IRI) in angler caught trout (Table 5.12).

5.3.7 Comparison of the foraging habitat use of gillnet and angler caught resident brown trout

Benthic prey items dominated the diets of the angler caught trout, with nektonic prey items of secondary importance (Figure 5.4). Conversely, nektonic prey items dominated the diets of gillnet captured trout with benthic prey items of secondary importance (Figure 5.4). For both trout groups surface prey items contributed the least to the sampled diets; however, surface prey items exhibited a higher %IRI in the angler caught trout diets than in gillnet captured trout diets (Figure 5.4).

5.3.8 Comparison of the condition factor and body weight of gillnet and angler caught resident brown trout

Condition factor

No significant difference was found between the condition factors (k) of the gillnet and angler caught trout (ANOVA, $F_{1,77}$=0.321, P=0.572), with an observed mean condition factor of 1.04 (S.E. ±0.089) in the angler caught trout and 1.06 (S.E. ±0.27) in the gillnet caught trout..

Wet body weight per fish

No significant difference was found in the mean wet body weight per fish between the conspecific gillnet and angler caught trout (ANOVA, $F_{1,96}$=1.13, P=0.290), with an observed mean wet body weight per fish of 307.3g (S.E. ±9.07) in angler caught trout and 282.2g (S.E. ± 24.1) in gillnet caught trout.

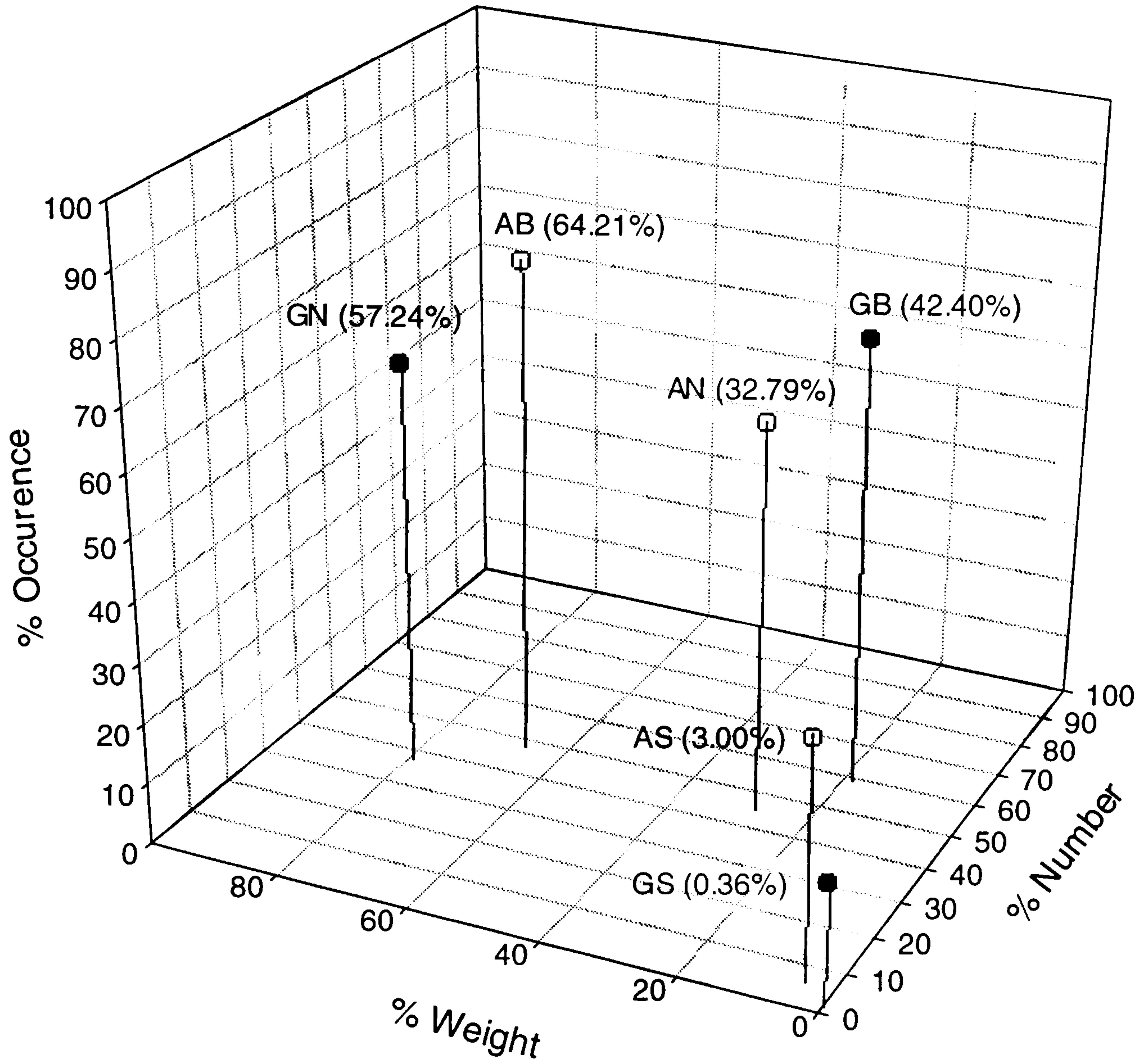


Figure 5.4 – Variation in foraging strategy between gillnet caught and angler caught resident brown trout captured between April and June 1999. Where: RB= resident trout benthic dietary component, RN= resident trout nektonic dietary component, RS= resident trout surface dietary component, HB= hatchery-reared trout benthic dietary component, HN= hatchery-reared trout nektonic dietary component, HS= Hatchery-reared trout surface dietary component and (x%)= Percentage Index of Relative Importance.

5.4 Discussion:

5.4.1 Comparison of the diets of angler caught resident and hatchery-reared trout

Quantity of prey consumed and foraging efficiency

The ability of hatchery-reared salmonids to adapt to a new environment following stocking determines how successful they will be (Ersbak & Haase, 1983). The domestication of hatchery-reared salmonids has resulted in the development of behavioural patterns and foraging strategies appropriate to culture situations, but which are significantly different from those exhibited by natural salmonid populations (Swain & Riddell, 1990). Several authors have suggested that following release into natural environments hatchery-reared trout display unnaturally high levels of movement and aggression, which resulted in an excessive expenditure of energy and a reduction in the time spent feeding (Fenderson *et al.*, 1968; Bachman, 1984). It has also been suggested that hatchery-reared trout may lack appropriate 'search images' to enable them to recognise natural prey (Sosiak *et al.*, 1979) and must consequently learn to recognise natural prey and forage efficiently (Steward & Bjornn, 1990; Wiley *et al.*, 1993). Sosiak *et al.* (1979) further suggested that although hatchery-reared salmonids may learn appropriate 'search images' which enable them to recognise natural prey, wild salmonids may posses a greater variety of prey 'search images' resulting in a competitive advantage and a more varied diet. It has also been suggested that even though most hatchery-reared trout will learn to feed on natural food, a proportion of the stocked fish may never learn (Bachman, 1984); and consequently a behaviourally non-adaptable minority may contribute to the poor survival and feeding performance of hatchery-reared salmonids (Paszkowski & Olla, 1985).

In this study the hatchery-reared trout consumed significantly lower numbers and weights of prey than the concurrently sampled resident trout. This supports the findings of Sosiak *et al.* (1979) and Johnsen *et al.* (1996) who found hatchery-reared Atlantic salmon to consume fewer prey items than wild conspecifics. The significantly larger size of the hatchery-reared fish examined in this study results in a greater potential stomach capacity than the relatively smaller resident conspecifics. Indeed in traditional dietary analysis the weight of the sampled stomach contents would be expressed as a percentage of body weight to remove any size related bias (Hyslop, 1980). However in this study, although the hatchery-reared trout had a greater potential stomach capacity, they exhibited significantly lower stomach content weights over the entire sample period than the concurrently sampled resident trout. Therefore, even without removing any potential size bias, the hatchery-reared fish are consuming significantly less than their resident conspecifics. However, this study also showed that the median number of prey items ingested by the hatchery-reared fish increased significantly over the sampling period; and after 9 weeks post-stocking there was no significant difference in the median number of prey per stomach between the two groups. This significant increase in the number of prey items ingested supports the idea that the foraging efficiency of hatchery-reared fish improves with experience (Ibrahim & Huntingford, 1992). Godin (1978) demonstrated that prey recapture rates in pink salmon (*Oncorhynchus gorbuscha* Walbaum) increase with increasing experience of a prey item; and Winfield *et al.* (1983) reported an increase in successful prey capture with increasing experience in bream (*Abramis brama* L.). These results support the findings of several studies in which hatchery-reared brown trout were observed to undergo a learning process in choosing food items, and that food intake is low in newly released trout (O'Grady, 1983; Johnsen & Ugedal, 1989; Lábee-Lund & Langeland, 1995). However, Ersbak & Haase

(1983) suggested that an apparent ability to adapt to natural prey after release into natural environments may not necessarily ensure survival. Energy inefficient foraging (Fenderson *et al.*, 1968; Bachman, 1984), the selection of sub-optimal diets (Sosiak *et al.*, 1979), inter- and intraspecific competition (Bachman, 1984) or an increased susceptibility to predation may all contribute to poor post-stocking survival. Although in these observations the number of prey items ingested by the hatchery-reared trout following release increased; the significantly lower stomach content weights of the hatchery-reared fish in all samples supports the idea that even with experience, these fish may be less efficient at foraging than the resident trout and thus may not be able to maintain high condition factors acquired in the hatchery-environment.

Prey preference and foraging habitat use

It has been suggested that foraging behaviour involves decisions which include where to feed, when to feed and what to feed on (Hughes, 1997). Several studies have described the relative heterogeneity of the diets and foraging strategies of wild salmonid populations (Ersbak & Haase, 1983; Kelly-Quinn & Bracken, 1990; Bridcut & Giller, 1995). Prey selection in wild salmonids has been shown to be influenced by colour (Clarke & Sutterlin, 1985), contrast (Wankowski & Thorpe, 1977), movement (Irvine & Northcote, 1983), size (Wankowski & Thorpe, 1977) and vulnerability of prey items (Ware, 1972). In contrast, salmonid culture is typified by regular feeding with uniform feeds (Ruzzante, 1994) which promote 'scramble feeding' strategies in response to overhead stimuli (Wiley *et al.*, 1993). Consequently, as well as the potential maladaptive behavioural traits which may be associated with domestication, hatchery-reared trout may be conditioned to elicit a 'look up' feeding response following stocking (O'Grady, 1983). Ersbak & Haase (1983) suggested that any behaviour that leads to inflexibility in the foraging pattern of hatchery-reared trout following stocking may limit post-stocking performance, and 'look up' feeding response may result in a reduction in the efficient utilisation of all the available forage by the hatchery-reared fish following stocking.

Although it has been demonstrated that the Howietoun hatchery-reared brown trout do experience a variety of benthic prey items during their ongrowing in earth ponds (Wahab *et al.*, 1989), in this study the hatchery-reared trout were found to consume only nektonic and surface prey items 1 week after stocking. This supports the findings of Sosiak *et al.* (1979) and O'Grady (1983) who found that hatchery-reared salmonids initially favour food items which were on or near the surface. Both studies suggested that this may be evidence of a 'look up' behavioural response in recently stocked hatchery-reared salmonids. Thorpe (1974) also observed relatively large abundances of surface prey items in the diets of hatchery-reared trout after stocking, but offered an alternative theory, that the hatchery-reared trout may be competitively displaced from benthic foraging zones by wild conspecifics. However, several authors have demonstrated that hatchery-reared trout may exhibit higher levels of aggressive behaviour than wild conspecifics (Fenderson *et al.*, 1968; Swain & Riddell, 1990) and may displace wild trout from occupied foraging zones (Bachman, 1984). In this study, the progressive increase in the relative contribution of benthic prey items to the diets of the hatchery-reared trout over the sample period lends support to the theory that the lack of benthic prey items in the diets 1 week after sampling may be due to a conditioned 'look up' feeding response rather than interspecific competition. This is further supported by the significant increase in the number of prey species consumed by the hatchery-reared trout in this study with increasing time after stocking, which may indicate an increase in the prey recognition.

Fish are expected to feed in the most profitable habitats and on the most profitable prey, and consequently to shift habitat or prey choice if the relative profitability of one prey type drops below that of another (Jonsson, 1989). The seasonal abundance of different aquatic invertebrates requires trout to readily switch between prey types (Morrison, 1997). Ersbak & Haase (1983) suggested that hatchery-reared trout may have difficulty in detecting and exploiting the changing densities of forage items, possibly due to a lack of prey recognition or some prey fixation and consequently may take a longer period of time to switch to new food items. Ersbak & Haase (1983) further suggested that due to conditioning hatchery reared trout may select organisms which are similar in size, shape and colour to pelleted diets.

In this study the resident trout exploited a wide variety of different prey items at different times, indicating a flexibility in their dietary choices and a relatively broad foraging niche. However, the diets of the hatchery-reared trout were dominated by dipteran pupae (almost exclusively chironomidae) in all the samples, with the relative importance (%IRI) of this food type never dropping below 50%. Dipteran pupae contributed more (higher %IRI) to the overall diets of the hatchery-reared trout than similar ranking prey items contributed to the resident trout diets. This suggests that the hatchery-reared trout became relatively fixated on dipteran pupae, potentially with energetic consequences if resident trout diets are to be used as indicators of efficient foraging. This is further supported by the samples taken 13 weeks after stocking with hatchery-reared trout, where hemipteran prey become of primary importance in the diets of the resident trout. However, no corresponding increase in the relative importance of hemipteran prey is seen in the diets of the hatchery-reared trout, which may be further evidence of prey fixation on dipteran pupae or of an inability to detect and exploit a change in the relative densities of the available forage. Stradmeyer & Thorpe (1987) suggested that prey recognition and adaptation to novel prey may not be as significant to the post-stocking survival of hatchery-reared salmonids as their ability to successfully locate and capture such prey. Therefore, relative importance of dipteran pupae in the diets of the hatchery-reared trout in this study may be as a response to their ease of location in comparison to more cryptic and evasive benthic invertebrates. This suppports the conclusions of Johnsen & Ugedal (1989) who suggested that surface prey items were more vulnerable to predation than other aquatic forage items as they lack protection and possibilities for escape. The increasing importance of trichopteran larvae in the hatchery-reared trout diets over the entire sampling period would suggest an increase in foraging efficiency with experience. It has been suggested that trichopteran larvae may resemble artificial pelleted diets in size, shape and colour; and consequently through classical conditioning hatchery-reared trout may be predisposed to elicit a feeding response when encountering such prey (Ersbak & Haase, 1983). However, the increase in the overall diversity of the prey items and the forage zones utilised by the hatchery-reared trout over the observation period suggests an increase in general foraging efficiency rather than a predisposition to forage on trichopteran larvae alone. Indeed the samples taken 13 weeks after stocking closely resembled the foraging strategies of the concurrently sampled resident trout. This supports the findings of several studies which all found hatchery-reared salmonids to adapt to natural foraging after release into the natural environment (Johnsen & Ugedal, 1989; Kelly-Quinn & Bracken, 1989; L'Abee-Lund & Langeland, 1995).

Condition factor and body weight

Some evolutionary ecologists would view growth and relative condition as possible surrogate measures of fitness (Hughes, 1997). The physical components of a trout's habitat and its available supply of food determine and limit basal metabolism, reproductive success and growth (Ersbak & Haase, 1983). Hatchery-reared trout are subject to fewer physical and energetic constraints during rearing than wild conspecifics; critically in terms of the available food supply (Wiley *et al.*, 1993). Several authors have demonstrated that hatchery-reared trout exhibit higher body lipid levels than wild conspecifics, and that condition factor decreases with lower body lipid content (Pinder & Eales, 1969; Sosiak, 1982). Accordingly, hatchery-reared trout may be expected to exhibit higher condition factors at the time of stocking than wild conspecifics (Bachman, 1984). In this study, the hatchery-reared brown trout displayed a significantly higher mean condition factor 1 week after stocking than the concurrently sampled resident trout. This supports the findings of Ersbak & Haase (1983) who found hatchery-reared brook trout (*Salvelinus fontinalis* L.) to exhibit a higher mean coefficient of condition than concurrently sampled wild brown trout immediately after stocking.

Although a higher condition factor indicates a possible energy advantage for hatchery-reared trout following release into natural environments, it has been suggested that these fish exhibit higher basal metabolic rates than wild conspecifics and may have difficulty finding an ecological niche that will satisfy their bioenergetic demands (Ersbak & Haase, 1983). It has also been suggested that post-stocking body condition loss in hatchery-reared salmonids may be due to a lack of prey recognition (Steward & Bjornn, 1990) and foraging skills (Ersbak & Haase, 1983; Bachman, 1984). Bachman (1984) further postulated that in any given environment there may be a maximum sustainable size which may be attained by the resident trout stocks. Consequently, hatchery-reared trout which exceed a given environment's maximum size at the time of stocking may be too big to maintain condition. In this study the hatchery-reared trout exhibited significantly larger mean wet body weights than resident conspecifics at each sampling interval; and progressively lost condition until reaching comparable levels with resident trout 9 weeks after stocking, suggesting the hatchery-reared trout may exceed the maximum sustainable size in Carron Valley Reservoir. These findings agree with the studies of Riemers (1963), Hunt & Jones (1972) and Ersbak & Haase (1983) who all reported a decline in the condition of stream stocked hatchery-reared trout after release. Riemers (1963) suggested that a rapid and severe post-stocking loss of body weight in hatchery-reared trout may result in mortality through physiological attrition.

5.4.2 Comparison of the diets of gillnet and angler caught resident trout

Collecting unbiased data from fisheries is difficult (Nielson & Jonson, 1983). The susceptibility of trout to capture by angling is very poorly documented (Pawson & Purdom, 1991). However, O'Grady (1983) found that stocked trout were more susceptible to angling than wild trout. Size restrictions prevent the anglers from keeping fish below 25cm at Carron Valley Reservoir; which when combined with the variability in individual anglers' skill and the restriction of fishing method to artificial lures and flies make angling a biased sampling method. Consequently angler caught samples are not necessarily representative of the resident population as a whole. No difference was found between the mean condition factors or the mean wet body weights of the gillnet and angler caught resident trout. However, gillnet captured resident trout consumed a greater mean weight of prey, whilst angler caught resident trout consumed a greater number of prey respectively. This observed difference was due to the gilllnet captured trout consuming larger amounts of teleost prey than the angler caught trout. Although trichopteran larvae were the dominant prey type for both fish groups, other benthic species and dipteran pupae were of more importance in the angler caught diets than in the gillnet caught diets. Surface prey items occurred in a greater percentage of the angler caught diets than in the gillnet captured fish diets suggesting that the angler caught fish may be foraging more in the surface layers than gillnet captured fish. These observations suggest that the angler caught resident trout diets may under represent the importance of fish prey species and over represent the relative importance of benthic and surface prey species. Teleost prey are the most energy dense aquatic forage available for larger teleosts to consume; with maximum energy gain for minimum energy expenditure. The prevalence of teleost prey within gillnet caught samples lends weight to the argument that maximum attainable size within Carron Valley Reservoir may be smaller than the initial stocking size of the hatchery-reared trout.

5.4.3 Summary

Several field studies have suggested that hatchery-reared salmonids may experience difficulty in adapting to natural foraging; maladaptive behaviour acquired through domestication, poor prey recognition and an inability to locate evasive prey may all contribute to the poor post-stocking foraging efficiency of hatchery-reared salmonids. This study examined the post-stocking temporal changes in; (1) the quantity and type of prey consumed, (2) the foraging habitat use, and (3) the body condition of hatchery-reared brown trout in Carron Valley Reservoir over a 13 week period during the spring/summer fishing season in 1999. This study also compared these findings with those of resident brown trout consecutively sampled using the same methods. This study has shown that hatchery-reared trout consumed significantly lower numbers and weights of prey than concurrently sampled resident conspecifics; however the median number of prey items ingested by the hatchery-reared trout increased significantly over the sample period, suggesting that the foraging efficiency of hatchery-reared brown trout increases with experience. In this study the dominance of dipteran pupae in the hatchery-reared trout diets suggests that stocked fish may be unable to locate and exploit cryptic and evasive prey species as efficiently as resident fish. Whilst the high proportion of prey that was located on or near the water surface in the diets of the hatchery-reared trout suggests a preconditioned 'look up' dietary response. However, a reduction in the importance of dipteran prey and a decrease in the proportion of surface or near-surface prey in the post-stocking diets of the hatchery-reared trout with time is further evidence suggesting that foraging efficiency of stocked brown trout increases with experience. The loss of post-stocking body condition observed in the hatchery-reared fish in this study may be due to maladaptive behavioural traits, poor prey recognition and poor prey location. The post-stocking loss of condition in the hatchery-reared trout may also indicate that the size at stocking exceeded the maximum sustainable body size for resident trout in Carron Valley Reservoir.

Chapter 6

The post-stocking dispersion of hatchery-reared brown trout

6.1 Introduction

The brown trout (*Salmo trutta* L.) is an important recreational species in the lochs, lakes, reservoirs and rivers of Europe (Jonsson *et al.*, 1995). Stocking, transfer and introductions of hatchery-reared salmonids are commonly used to enhance recreational or commercial fisheries and to preserve or re-establish threatened populations; often without any definite objectives or evaluation of the potential success of the exercise (Cowx, 1994). It is generally accepted that stocking is necessary in trout fisheries with inadequate spawning facilities, high levels of predation and high levels of angling pressure (Templeton, 1971); with the success of stocking with hatchery-reared trout being the subject of a variety of investigations for the past half century (Cresswell, 1980). The objectives of such releases vary from supporting heavily exploited recreational fisheries into which catchable trout are released, to rehabilitating or re-establishing impoverished natural populations into which a variety of life history stages may be stocked (Naslund, 1998).

To an angler, the number of fish caught is often a test of the fishery's worth (Pawson, 1991). Stocking recreational fisheries with hatchery-reared fish can increase angler catches by increasing the numbers of available fish and by increasing angler effort (Moring, 1993). Many recreational trout fisheries in Britain have adopted a policy of introducing a large portion of each year's stock prior to the opening of the fishing season at a small number of stocking sites ('spot' planting), with supplementary stockings at intervals during the remainder of the season (Pawson, 1982). The post-stocking distribution of hatchery-reared salmonids is considered important to maximising the efficiency of stocking strategies (Jokikokko, 1999) as it has been assumed that hatchery-reared salmonids are unable to disperse quickly and evenly into all the available habitats (Helfrich & Kendall, 1982;

Jokikokko, 1999). Consequently, stocking strategies that include the release of large numbers of fish at very few sites may have several potential economic and ecological drawbacks (Pawson, 1982). These may include high catch rates during the first few days of the fishing season (Pawson, 1982), high catch rates in the vicinity of the stocking site (Vehanen *et al.*, 1998), increased localised competition for limited resources (e.g. food and habitat)(Ersbak & Haase, 1983; Bachman, 1984) and an increased susceptibility to predation (McKinnell & Lundqvist, 2000). It has been suggested that a prudent fishery management practice may be to combine 'trickle' (stocking spread over time) and 'scatter' (stocking spread spatially) stocking strategies in an attempt to minimise economic losses and maximise the potential survival of hatchery-reared trout (Cresswell & Williams, 1982). However, both 'trickle' and 'scatter' stocking strategies reduce the economic profitability of recreational fisheries due to increased labour and transportation costs (Cresswell & Williams, 1982).

The dispersion patterns of hatchery-reared salmonids following release into lotic environments have been the subject of several studies (Mills & Ryan, 1973; Scullion & Edwards, 1979; Cresswell, 1980; Cresswell & Williams, 1982; Helfrich & Kendall, 1982), with most research suggesting that a large proportion of stocked salmonids remain within the vicinity of the release site. Though many of the findings are conflicting, it is possible that there are several factors that may affect post-stocking movements of hatchery-reared salmonids. These may include the method of fish introduction (i.e. spot or scatter planting)(Cresswell & Williams, 1982), the time of stocking (i.e. spring or winter)(Trembley, 1943), the size of the receiving water body (Ratledge & Cornell, 1953; Cresswell & Williams, 1979; Cresswell, 1980) and water temperature (Cooper, 1952). However, little is known about the post-stocking dispersion patterns of brown trout stocked into lentic water bodies (L'Abee-Lund & Langeland, 1995; Vehanen *et al.*, 1998).

Various methods have been used to monitor the dispersion of salmonids in both lotic and lentic environments, including tag-recapture (Shetter, 1967; Vehanen *et al.*, 1998) and radio and acoustic tracking (Tytler *et al.*, 1978; Gowans *et al.*, 1999). Tag with gill net recapture methods have been used to assess the post-stocking dispersion of 'scatter' and 'spot' planted native brown trout (L'Abee-Lund & Langeland, 1995), non-native brown trout (L'Abee-Lund & Langeland, 1995; Vehanen *et al.*, 1998) and landlocked Atlantic salmon (*Salmo salar* L.)(Vehanen *et al.*, 1998) in lentic water bodies. Tagging techniques have been combined with angler surveys to assess the post-stocking survival of hatchery-reared rainbow trout (*Oncorhynchus mykiss* Walbaum)(Cragg-Hine, 1976) and the post-stocking movements of hatchery-reared brown trout in Afon Taf river, south Wales (Cresswell & Williams, 1982) and the river Tweed (Mills & Ryan, 1973). Acoustic transmitters have been used to monitor the movements of many species. For example adult Atlantic salmon through Loch Faskally (Gowans *et al.*, 1999), released hatchery-reared rainbow trout in Loch Fad (Phillips *et al.*, 1985) and native rainbow trout in Lake Coleridge, New Zealand (James & Kelso, 1995). Radio transmitters have been widely used to monitor fish movements, for example adult Atlantic salmon through a fish pass (Gowans *et al*, 1999) and the post-stocking movements of hatchery-reared brown trout released into a stream (Deverill, 1997).

Despite extensive stocking, the dispersal of catchable sized, hatchery-reared brown trout in lentic water bodies has not been extensively studied in Scotland. The present study aimed to examine aspects of the post-stocking dispersal and fine scale movement patterns of hatchery-reared brown trout at Carron Valley Reservoir. Particularly, (1) to assess how quickly, if at all, 'spot' planted hatchery-reared brown trout dispersed from the site of release, (2) to estimate how accurate anglers were at reporting tagged fish recapture positions, and (3) to observe the post-stocking dispersion of hatchery-reared brown trout using biotelemetry techniques.

6.2 Materials and methods

6.2.1 Dispersal

Tag selection

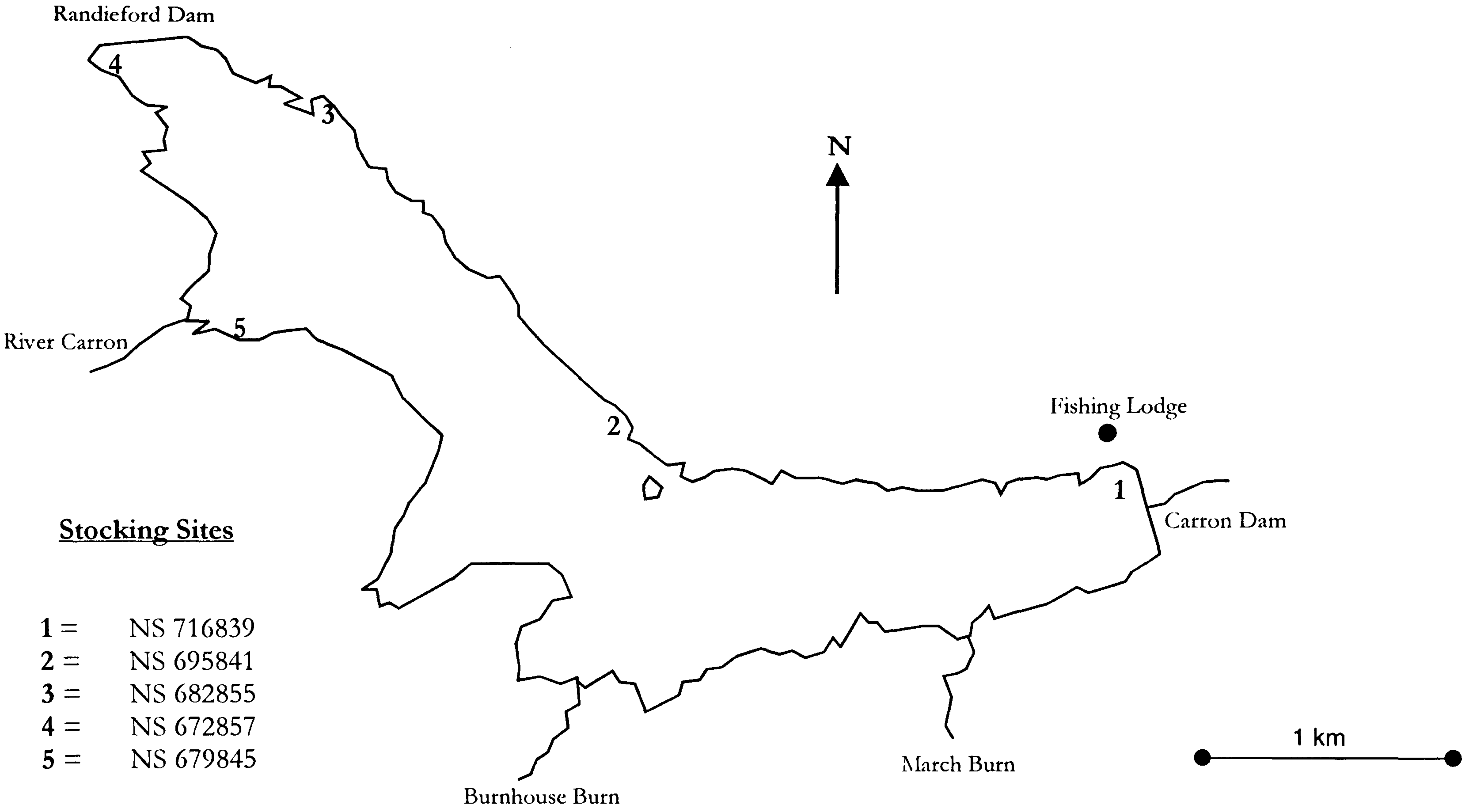
The relative advantages and disadvantages of the different tag types available for both individually and batch marking fish have already been discussed in chapter 3. Initially in 1998, Visible implant (VI) tags were used in conjunction with adipose fin clipping to identify individual stocked hatchery-reared Howietoun brown trout. However, relatively low return rates and '*in situ*' interviews with the local anglers identified that even with the addition of an adipose fin clip and a comprehensive angler survey programme (Appendices 1-3) the VI tagged fish were not being recognised by the anglers. Consequently, during the 1999 and 2000 angling seasons, 'Floy' style tags were chosen for the gross stocking distribution study in an attempt to increase the recognition of experimental fish by the anglers. Due to the relative expense of purchasing branded alphanumeric 'Floy' tags for use in a batch mark experiment, commercially available coloured clothing tags ('Ezi-Tag') were sourced and purchased (Avery-Dennison, USA). These tags, whilst not being alphanumerically numbered, use the same technology as branded 'Floy' tags for anchoring within the muscle mass, and are applied using the same techniques resulting in a highly visible colour coded batch mark.

Tagging methods

A total of 1000 catchable sized hatchery-reared brown trout from the Howietoun fishery, destined for commercial stocking into Carron Valley Reservoir were randomly selected and tagged prior to or during the 1998, 1999 and 2000 angling seasons (April-September).

In 1998, 500 hatchery-reared brown trout (length range 300-351mm) were split into two groups of 250 individuals and tagged with sequentially numbered unique alphanumeric Visible Implant (VI) tags (1.3mm wide x 4.0mm long x 0.18mm thick). Fish were individually anaesthetised with Benzocaine (Ethyl p-Amino-Benzoate, Sigma Chemicals, St. Louis, USA), measured for fork length (±1mm) and weighed (±5g). A single VI tag was inserted into the post-ocular adipose tissue posterior to the left eye of each fish using a hand-held syringe-style applicator (Northwest Marine Technology, Washington, USA). The adipose fin was excised from each VI tagged individual to increase the ease of identification of VI tagged experimental fish to anglers and to allow the identification of fish with lost tags. Each group of fish was held according to commercial practice at the Howietoun fishery for 24hrs in 6m diameter circular tanks supplied by flow-through water to ensure initial tag retention and survival of all the experimental fish. Each group of fish was then transported to the fishery in oxygenated transportation tanks according to commercial practices and stocked into separate previously identified locations (Figure 6.1) on the 7th April 1998.

In the 1999 angling season a further 100 hatchery-reared trout (length range 300-402mm) were batch marked with colour coded 'Floy' style anchor tags, with a further 400 hatchery-reared trout (length range 300-376mm) being marked in the same way during the 2000 angling season. Fish were individually anaesthetised and measured for length as described above. Colour coded 'Floy' style anchor tags were inserted into the muscle mass at the base of the dorsal fin of each anaesthetised fish using a commercially available hand held applicator gun (Swiftach System Mark III Tool, Avery-Dennison Ltd, USA) producing colour coded highly visible batch marks. Care was taken to gently pull each tag after



Stocking Sites

1 =	NS 716839
2 =	NS 695841
3 =	NS 682855
4 =	NS 672857
5 =	NS 679845

Figure 6.1 - The stocking positions used at Carron Valley Reservoir into which Visible Implant (VI), 'Floy' style and radio transmitter tagged hatchery-reared brown trout were stocked between April 1998 and June 2000.

application to ensure that it was locked in place within the muscle mass (Mourning *et al.*, 1994). Each group of fish was held according to commercial practice at Howietoun fishery for 24hrs, transported and stocked in Carron Valley Reservoir at previously identified locations as described above (Figure 6.1).

Angler survey and tag collection

During the 1998, 1999 and 2000 angling seasons at Carron Valley Reservoir, the gross distribution of the hatchery-reared brown trout was monitored using tag returns from anglers. Initially, during the 1998 angling season a relatively complex angler survey was instigated. Each angler was required to complete a catch return card (Appendix 1(a)) which allowed the maximum amount of catch return information to be gathered. To increase the likelihood of anglers recognising the experimental fish, photographic identification posters were placed around the fishery and within each of the boats (Appendix 2). As an incentive to complete the survey cards a prize draw was widely advertised for all participants (Appendix 3). Despite the completion of survey cards being mandatory on all East of Scotland Water recreational fisheries many anglers did not take the time to complete the survey cards, or completed them incorrectly which resulted in lower than expected tag returns. Consequently, during the 1999 and 2000 angling seasons the aim of the angler survey was redefined in an attempt to minimise angler confusion and maximise survey card returns. The 1999 and 2000 angler surveys aimed only to identify the positions at which colour coded, batch marked hatchery-reared trout were recaptured. This was attempted by simplifying the survey card design to a plan map of Carron Valley Reservoir onto which the position of any recaptured, tagged fish should be marked (Appendix 1(b)). The plan map was attached to an A5 envelope into which the respective returned 'Floy' style tags should be placed. An angler incentive scheme was again operated in an attempt to increase reporting rates.

Data analysis

Due to the relatively low number of tag returns for each tag group in any one week, with the exception of 1 week after stocking with hatchery-reared trout, all weekly samples were grouped into biweekly sample groups for the purpose of data analysis. The gross distribution patterns of hatchery-reared brown trout following stocking were examined by estimating the distance between the point of release and recapture directly from the maps on the returned survey cards. A one-way ANOVA was used to test for significant differences between the estimated distance between release and recapture for the individual tag groups at 1, 3, 5, 7 and 11 weeks after release.

Accuracy of the angler reported recapture positions

Anglers are often overlooked as a large potential source of fisheries information (Easton & Morgan, 1974); however the accuracy of angler survey information often depends on the type of angler, the type of fishery and the time and effort expended to collect the data (Small & Downham, 1985). The accuracy of the estimated gross distribution patterns of the hatchery-reared trout used in this study depend entirely on the accuracy of the anglers when marking the recapture positions of the tagged fish on the provided survey cards. In an attempt to quantify the tag position reporting accuracy of anglers at Carron Valley Reservoir an accuracy estimation study was performed. During the 1999 angling season, 100 anglers were approached whilst fishing and asked to mark position of their boat on a plan of the fishery. A hand held GPS (Garmin 12XL, Garmin Ltd, USA) system was then used to record the boats actual position. The difference between the 2 positions was then estimated from plotted points on a 1:25,000 Ordnance Survey map of Carron Valley Reservoir (Pathfinder 392, Ordnance Survey, UK). On the assumption that the GPS (± 100m) reported position was correct, the difference between the angler reported position and the GPS reported position was tested using a Kruskal-Wallis analysis of variance by ranks.

6.2.2 Fine scale movements

Although radio transmitters are relatively expensive pieces of equipment, in this study it was intended that at least 6 hatchery-reared brown trout would be released and tracked in Carron Valley Reservoir in order to elucidate the post-stocking fine scale movements. However, due to supervisory staff departure the home office project licence under which this procedure was governed was voided, thus preventing further fish from being tagged and tracked. Consequently, only the initial 3 experimental fish were successfully tagged and tracked.

The radio-transmitters

Fish location radio transmitters generally fall into four categories: continuous wave, simple pingers, synchronous pingers and transponders (Bean, 1992). Two types of commercially available single-stage radio transmitters were obtained from Biotrack Ltd. (Wareham, Dorset). A single TW-4 button cell tag powered by an Ag392 cell (19mm long x 9mm wide x 7mm high) and two TW-3 tags powered by single AAA alkaline batteries (45mm long x 12mm wide x 12mm high). The radio circuitry and batteries were sealed inside a Plastidip™ coating with a 10cm whip antenna protruding from one end. The single TW-4 tag weighed 1.6g in air whilst the two TW-3 tags individually weighed 6.5g in air. The TW-4 transmitter had an expected life of 6-9 weeks and a line of site detectable range in air of 1-5km. The TW-3 transmitters had an expected life of 10-12 weeks and a line of site detectable range in air of 1-10km.

Transmitter attachment

The two TW-3 and single TW-4 transmitters were attached to three hatchery-reared brown trout that were obtained from the Howietoun Fishery. A summary of the individual morphological and radio transmitter details of each fish is presented in Table 6.1. Each transmitter was mounted on a small neoprene patch using Araldite™ adhesive. The radio transmitter and neoprene patch were then attached to an anaesthetised trout using a non-invasive 'sub-dorsal fin mount procedure' (Solomon & Storeton-West, 1983) (Figure 3.1 & 3.2). All three transmitters plus saddles did not exceed the recommended 1.25% of the fish's body weight out of water (Beaumont *et al.*, 1996) (Table 6.1). After tag attachment each fish was placed in a 6m diameter holding tank at the Howietoun fishery for 24hrs to allow each fish to recover and make buoyancy adjustments to counteract the newly acquired weight of the transmitter and harness. All three fish were then transported to the fishery in oxygenated transportation tanks according to commercial practices and stocked into Carron Valley Reservoir at site 1 (Figure 6.1) at 8.00am on the 16th August 1999.

Tracking procedure

Radio signals were detected using a 3 element 'Yagi' antenna and were decoded and amplified on a 'Mariner 57' low powered radio receiver (Mariner Radar Ltd, Lowestoft, England). The relatively large size of Carron Valley Reservoir meant that all tracking work was carried out from one of the available boats already present on the water.

Table 6.1 - Summary of the individual morphological and radio transmitter details for each of the hatchery-reared brown trout released into Carron Valley Reservoir for the purpose of fine scale distribution pattern assessment.

Fish Code	Length (mm)	Weight (g)	Condition Factor (k)	Transmitter Type	Weight of Radio Transmitter & Saddle (in air)(g)	Weight of Radio Transmitter & Saddle (in air)(as % body weight)	Date of Release	Date of End of Tracking	Total Number of Days Tracked
Fish 1	401	709	1.10	TW-3	8.76	1.24	16th August 1999	6th September 1999	22
Fish 2	460	979	1.01	TW-3	8.91	0.91	16th August 1999	2nd September 1999	17
Fish 3	330	355	0.99	TW-4	2.04	0.57	16th August 1999	21st August 1999	5

On commencement of tracking, the antenna was initially raised to a vertical position. Theoretically, for every doubling in antenna height above the water surface, the gain (or signal strength) should increase by 6 dB (Bean, 1992) and increase the working range twofold (Kenward, 1987). After confirming a signal and taking an initial bearing, the signal was followed along the line of interception until the signal was no longer directional (Bean, 1992). In order to more precisely fix each fish's individual position it was found that a continued adjustment of the gain of the receiver allowed a more accurate locational fix. However, the relatively deep water and continual movement of the individual fish reduced accurate position fixing to ± 2m. After locating each individual, the position of the fish was recorded by using both a handheld GPS (Garmin 12XL, Garmin Ltd, USA) and by taking back bearings from two or more visual features and plotting both positions on a 1:25,000 Ordnance Survey map of Carron Valley Reservoir.

During the first 24hrs following release the position of each individual fish was recorded every hour. After this initial 24hr tracking period the position of each individual was recorded at approximately 9.00am every morning until the respective signal was lost. The lower powered TW-4 transmitter was successfully tracked during the initial 24hrs but was lost relatively quickly due to the relatively low detection range of the tag, especially when the fish entered deeper waters. The two TW-3 transmitters were successfully located for several weeks before the signal was lost; it was noted that tag location became significantly more difficult after approximately 10 days as the relative strength of the individual signals appeared to reduce daily until lost.

The patterns of movement of the three fish have been described using track diagrams which are the most effective method of illustrating migratory behaviour in fish (Stasko *et al.*, 1973). Plots of the migration distance from the release point against time and the distance moved between daily location points were used to assess trends in individual migratory behaviour. A one way ANOVA was used to test for significant differences in the diel activity patterns of the stocked hatchery-reared trout.

6.3 Results

6.3.1 Dispersal

In total, 188 (18.8%) of the 1000 Visible Implant (VI) and 'Floy' style tagged hatchery-reared brown trout were reported recaptured by anglers at Carron Valley Reservoir between April 1998 and June 2000 (Table 6.2). Relatively low reporting rates were observed for the Visible Implant (VI) tagged hatchery-reared trout released during the 1998 angling season, in comparison to the relatively high reporting rates for 'Floy' style tagged trout stocked during the 1999 and 2000 angling seasons (Table 6.2). The Visible Implant (VI) and 'Floy' style tagged trout stocked during 1998 and 1999 displayed a higher median time from stocking to recapture than the 'Floy' style tagged fish stocked in 2000 (Table 6.2)

There were no significant differences in the estimated migration distances between the 7 independent stocking events (both VI and 'Floy' style tags) in any of the bi-weekly samples (Table 6.3). Consequently, the 7 independent stocking events were pooled to provide a single data set of estimated distances between release and recapture sites at each time period.

Figure 6.2 illustrates the mean migration distance moved before recapture at bi-weekly intervals by the tagged hatchery-reared trout stocked into Carron Valley Reservoir between April 1998 and June 2000. Although the mean migration distance is lower in the fish recaptured 11 weeks after initial stocking, there was no significant difference between migration distance and time before the fish were recaptured (ANOVA, $F_{5,182}=0.390$, $p=0.852$). Consequently, Figure 6.3 demonstrates the migration distance frequency for all 188 reported tagged trout combined. Over half (53%) of the reported tagged trout were

Table 6.2 - Summary of the hatchery-reared brown trout tag groups stocked into and recaptured from Carron Valley Reservoir between April 1998 and June 2000. The position of the stocking sites is illustrated in Figure 6.1.

Tag Type	Stocking Site	Date Stocked	No. Fish Stocked	Length Range (mm)	No. Fish Reported	Reporting Rate (%)	Mean Migration Distance (m)(SE)	Median Time from Stocking to Capture (weeks)
VI	1	7th April 1998	250	300-351	23	9.2	828 (±142.4)	5
	5	7th April 1998	250	300-351	24	9.6	835 (±135.2)	5
Floy - Yellow	1	9th August 1999	100	300-402	32	32.0	994 (±185.1)	5
Floy - Red	1	10th April 2000	100	300-376	29	29.0	990 (±127.6)	3
- White	2	10th April 2000	100	300-376	36	36.0	1196 (±119.8)	3
- Blue	3	10th April 2000	100	300-376	23	23.0	1248 (±174.3)	3
- Yellow	4	10th April 2000	100	300-376	21	21.0	1463 (±277.3)	3

Table 6.3 - Mean migration distance moved by Visible Implant (VI) and Floy tagged hatchery-reared brown trout before recapture at Carron Valley Reservoir between April 1998 and June 2000 and ANOVA test of difference in mean migration distance between stocking events within bi-weekly pots-stocking recovery periods. Position of the release sites is illustrated in Figure 6.1.

Time (weeks post-stocking)	Tag type	Release site	Sample size (n)	Mean migration distance (m)	S.E.	F	d.f.	p
1	VI 1998	1	5	949	342.5	1.58	6	0.173
	VI 1998	5	6	710	300.4			
	Yellow Floy 1999	1	4	866	450.5			
	Red Floy 2000	1	9	728	142.5			
	White Floy 2000	2	15	1207	182.8			
	Blue Floy 2000	3	8	915	232.1			
	Yellow Floy 2000	4	9	1849	562.9			
3	VI 1998	1	7	765	270.1	0.36	6	0.901
	VI 1998	5	4	961	288.9			
	Yellow Floy 1999	1	7	798	512.3			
	Red Floy 2000	1	8	1117	235.4			
	White Floy 2000	2	10	1189	248.0			
	Blue Floy 2000	3	7	1215	290.7			
	Yellow Floy 2000	4	6	1181	1180.8			
5	VI 1998	1	4	1030	368.7	0.47	6	0.828
	VI 1998	5	5	734	179.3			
	Yellow Floy 1999	1	6	1258	331.4			
	Red Floy 2000	1	6	854	526.8			
	White Floy 2000	2	6	1264	232.8			
	Blue Floy 2000	3	5	1494	262.2			
	Yellow Floy 2000	4	4	1174	489.1			

Table 6.3 (continued)

Time (weeks post-stocking)	Tag type	Release site	Sample size (n)	Mean migration distance (m)	S.E.	F	d.f.	p
7	VI 1998	1	4	1143	951.5	0.01	6	0.996
	VI 1998	5	4	1172	615.1			
	Yellow Floy 1999	1	4	1408	528.3			
	Red Floy 2000	1	2	809	466.4			
	White Floy 2000	2	3	1065	385.0			
	Blue Floy 2000	3	1	1502	-			
	Yellow Floy 2000	4	2	1156	641.1			
9	VI 1998	1	2	802	555.0	1.10	5	0.409
	VI 1998	5	3	708	158.3			
	Yellow Floy 1999	1	5	726	502.7			
	Red Floy 2000	1	4	1620	199.2			
	White Floy 2000	2	2	1135	592.5			
	Blue Floy 2000	3	2	1953	673.3			
	Yellow Floy 2000	4	0	-	-			
11	VI 1998	1	3	582	143.4	0.67	2	0.547
	VI 1998	5	2	322	78.0			
	Yellow Floy 1999	1	4	992	487.6			
	Red Floy 2000	1	0	-	-			
	White Floy 2000	2	0	-	-			
	Blue Floy 2000	3	0	-	-			
	Yellow Floy 2000	4	0					

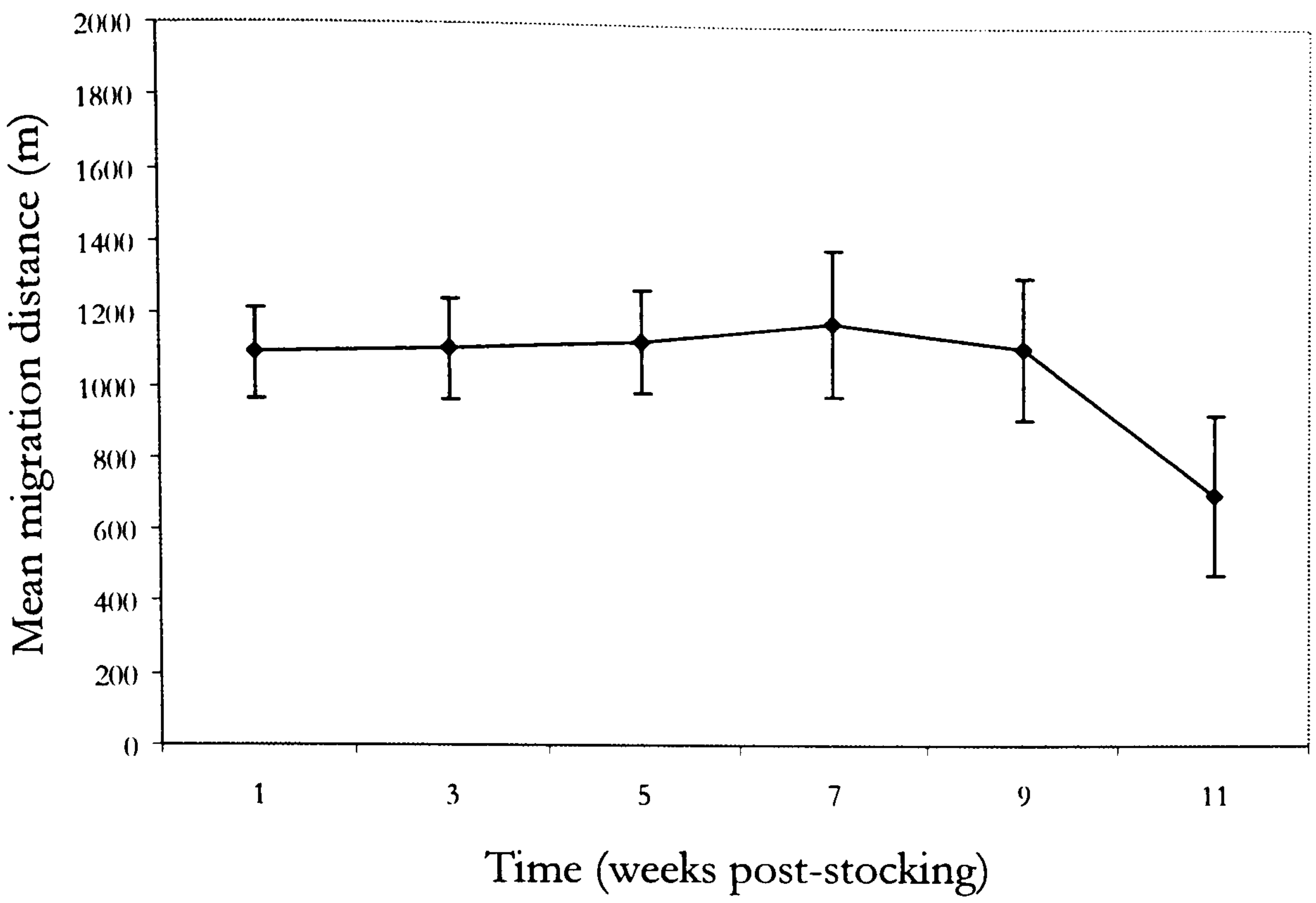


Figure 6.2 - Mean (±S.E) migration distance moved by Visible Implant (VI) and Floy tagged hatchery-reared brown trout before recapture at Carron Valley Reservoir between April 1998 and June 2000.

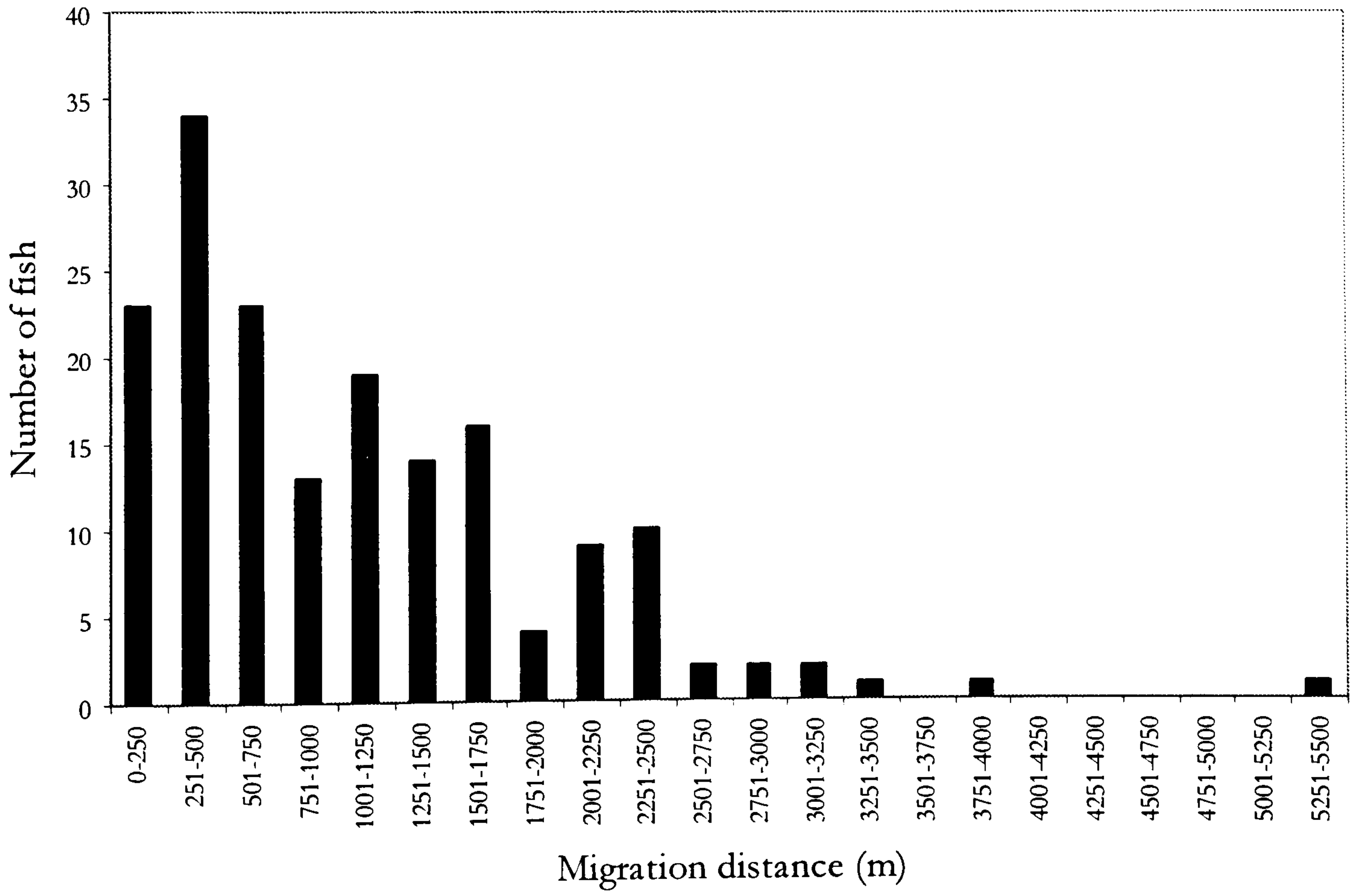


Figure 6.3 - Migration distance distribution of recaptured Visible Implant (VI) and Floy tagged hatchery-reared brown trout in relation to the release points (0m) in Carron Valley Reservoir between April 1998 and June 2000.

recaptured within 1000m of their respective release sites, with 72% recaptured within 1500m and 95% within 2500m of their respective release sites.

6.3.2 Accuracy of the angler reported recapture positions

There was a significant difference between the GPS and angler reported positions recorded during August 1999 at Carron Valley Reservoir (Kruskal-Wallis, $H=84.95$, d.f.=1, $p<0.001$), with a median distance of 356.5m between the two points. Figure 6.4 shows the frequency of distance differences between the GPS and angler reported positions. Only 15% of the angler reported positions were within 200m of their respective GPS reported positions, whilst 66% of the angler reported positions were between 201 and 600m from their respective GPS reported positions. Overall 95% of the anglers reported their position to within 1000m of their respective GPS reported positions.

6.3.3 Radiotracking

24hr Sampling

During the first 24hrs following release, the hatchery-reared brown trout were relatively active (Figures 6.5, 6.6 and 6.7) with estimated mean hourly migration rates ranging between 96.0 and 185.7m and total estimated mean migration rates for the first 24hrs ranging between 2209 and 4438m (Table 6.4). Given that the maximum linear distance obtainable at Carron Valley Reservoir is 4750m, movements of this magnitude constitute a major displacement. No significant differences were found between the diurnal and nocturnal estimated hourly migration distances of Fish 1 (ANOVA, $F_{1,23}=0.058$, $p=0.813$), Fish 2 (ANOVA, $F_{1,23}=0.010$, $p=0.902$) or Fish 3 (ANOVA, $F_{1,23}=0.348$, $p=0.563$). Figure 6.11(a) shows that the movement of Fish 1 and Fish 2 initially constituted a phase of steady

Table 6.4 - Summary of the post-stocking migration distances of three radiotagged hatchery-reared brown trout stocked into Carron Valley Reservoir on the 8th August 1999.

Fish	Mean estimated hourly migration distance in the 1st 24hrs (mhr^{-1})		Total estimated distance moved in the 1st 24hrs (m)	Mean estimated daily migration distance (mday^{-1})			Total estimated distance moved over the sample period (m)
	Mean (±S.E.)	Range		Number of sample days	Mean (±S.E.)	Range	
1	96.0	36-232	2209	20	178.0	39-610	3560
	9.26				*33.4*		
2	185.7	60-627	4438	15	424	81-1256	5371
	29.5				*101.1*		
3	103.4	40-268	2574	4	159.0	110-263	536
	14.3				*35.1*		

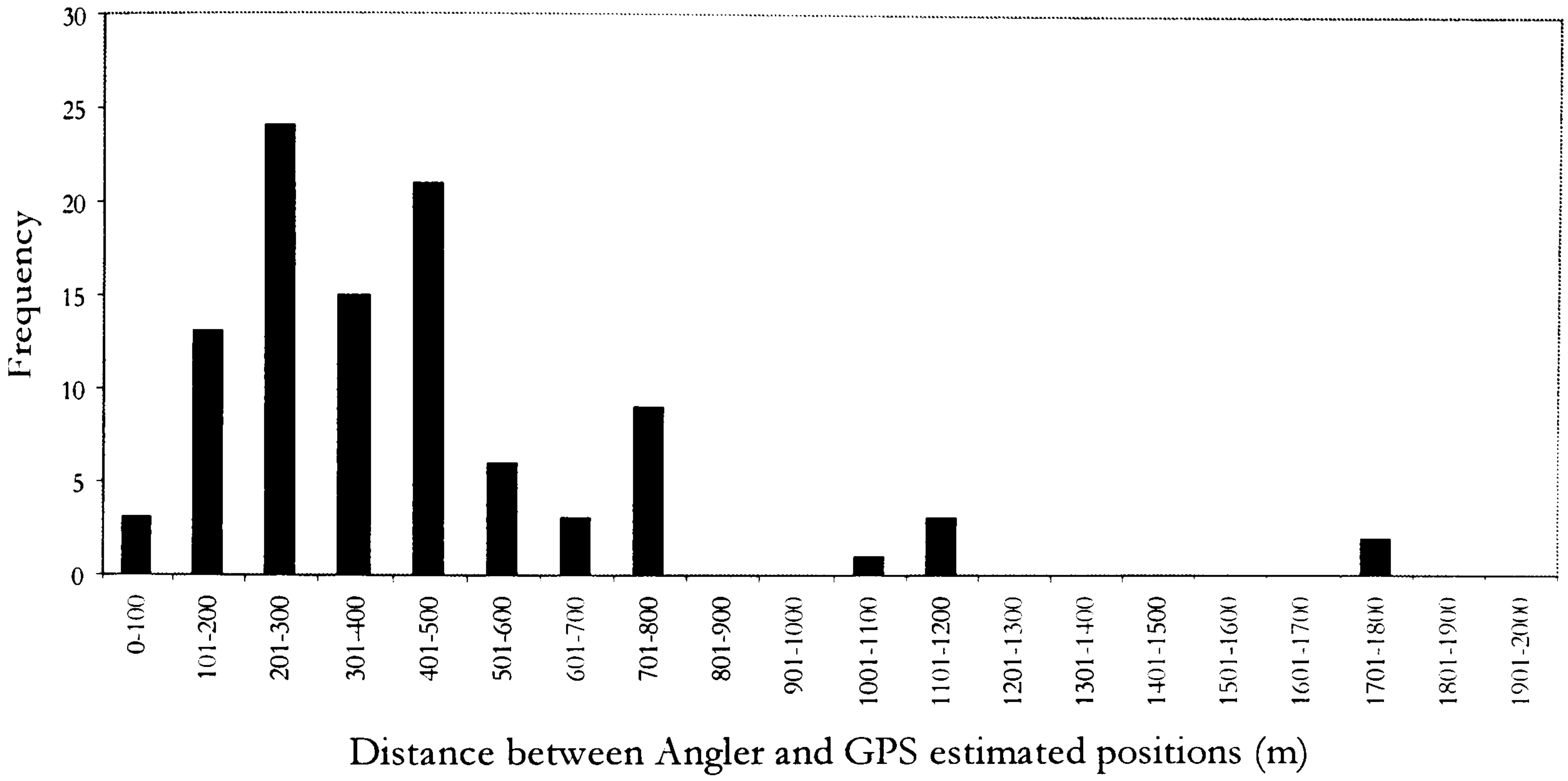


Figure 6.4 - Difference between simultaneously recorded angler reported and GPS positions at Carron Valley Reservoir.

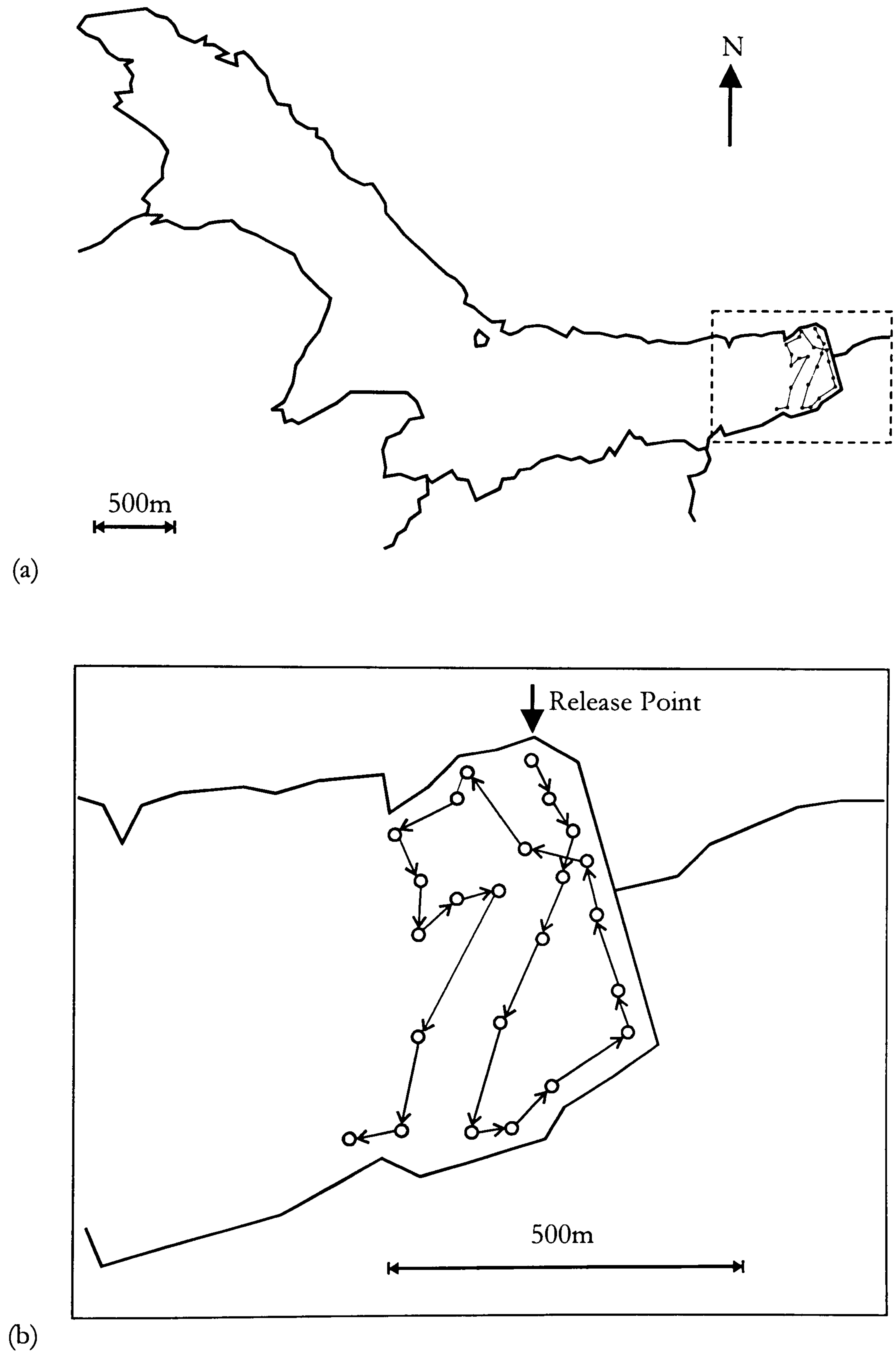


Figure 6.5 – The movement of a single radiotagged hatchery-reared brown trout (Fish 1) during the first 24hrs (8am-8am) following release into Carron Valley Reservoir on the 16th August 1999. (a) movement of Fish 1 in relation to Carron Valley Reservoir. (b) detailed 24hr movement of Fish 1. (o) shows the recorded hourly positions.

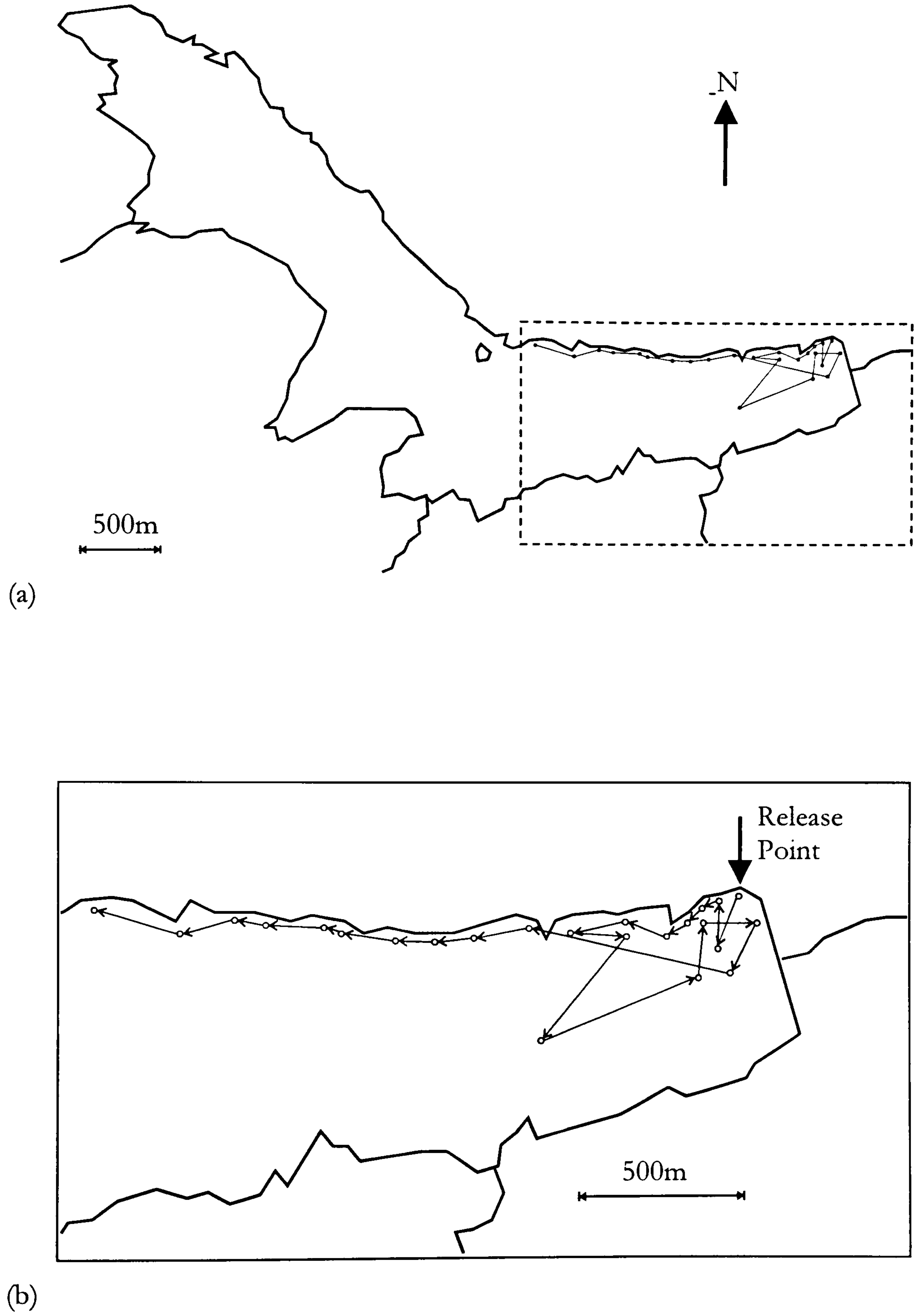


Figure 6.6 – The movement of a single radiotagged hatchery-reared brown trout (Fish 2) during the first 24hrs (8am-8am) following release into Carron Valley Reservoir on the 16th August 1999. (a) movement of Fish 2 in relation to Carron Valley Reservoir. (b) detailed 24hr movement of Fish 2. (o) shows the recorded hourly positions.

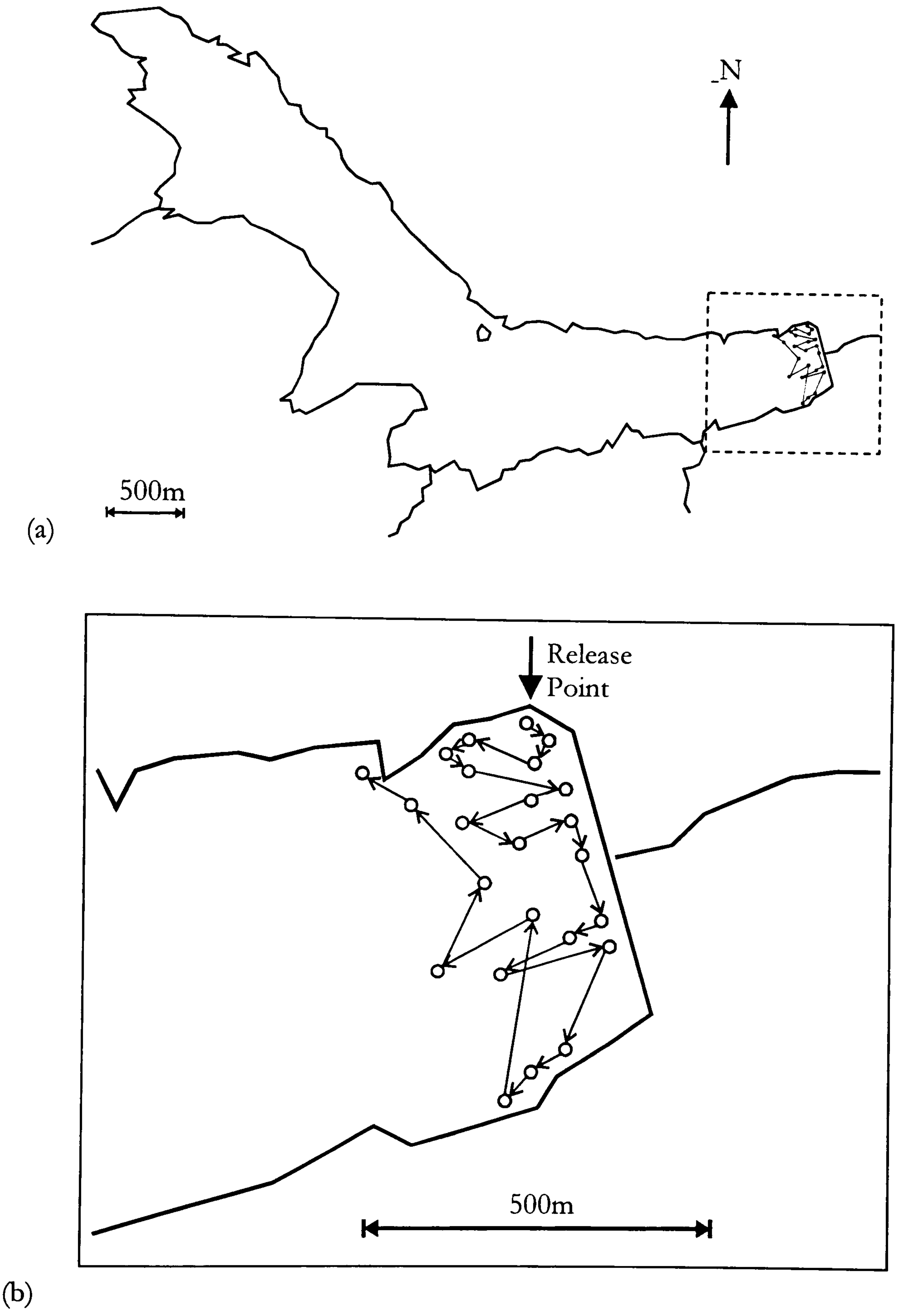


Figure 6.7 – The movement of a single radiotagged hatchery-reared brown trout (Fish 3) during the first 24hrs (8am-8am) following release into Carron Valley Reservoir on the 16th August 1999. (a) movement of Fish 3 in relation to Carron Valley Reservoir. (b) detailed 24hr movement of Fish 3. (o) shows the recorded hourly positions.

migration away from the release site followed by a phase where the individual fish migrated back towards the release site, with a third phase where the fish again migrated away from the release site. Fish 3 exhibited a slightly different pattern, but still initially moved relatively slowly away from the release site, followed by a phase where the fish moved back towards the release site.

Daily observations

The type of radio transmitter dramatically affected the ease with which the tagged fish could be located. The 2 more powerful TW-3 radio transmitters mounted on Fish 1 and Fish 2 allowed the successful location of these fish for a total of 22 and 17 days respectively following release (Figures 6.8 & 6.9). However, the less powerful TW-4 transmitter signal was lost relatively quickly when the fish migrated into the deeper areas of the reservoir only 5 days after release (Figure 6.10).

During the daily observations all the tagged trout remained relatively active with mean estimated daily migration rates ranging from 159.0 to 424.0m and total estimated migration distance of between 3560m for Fish 1, 5371m for Fish 2 and 536m for Fish 3 (Table 6.4). Figure 6.12 suggests that during the 10day period following release both Fish 1 and Fish 2 migrated relatively large distances between daily locations. However, after this initial phase of relatively high migration activity, both Fish 1 and Fish 2 reduced their apparent daily migration distances (Figure 6.12) and were located within relatively confined areas of the reservoir (Figures 6.8 & 6.9). During the initial 10 day phase of relatively high migration activity, Fish 2 moved away from the release point before occupying a relatively confined area between 3833-4167m linearly distant (Figure 6.11(b)); whilst Fish 1 moved in a circular

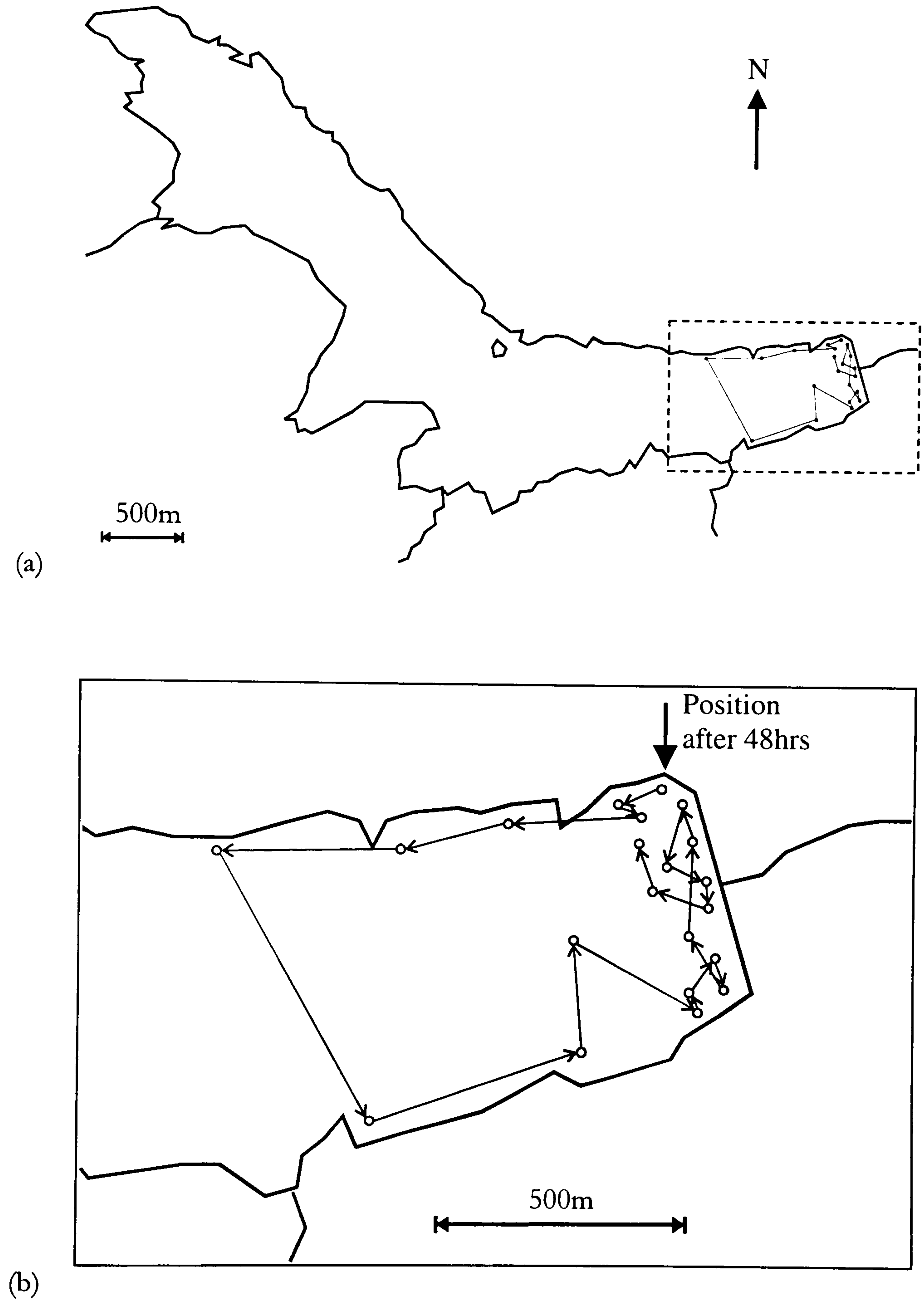


Figure 6.8 – The movement of a single radiotagged hatchery-reared brown trout (Fish 1) over a 20 day period in Carron Valley Reservoir between 18th August and 6th September 1999. (a) movement of Fish 1 in relation to Carron Valley Reservoir. (b) detailed daily movement of Fish 1. (○) shows the recorded daily positions.

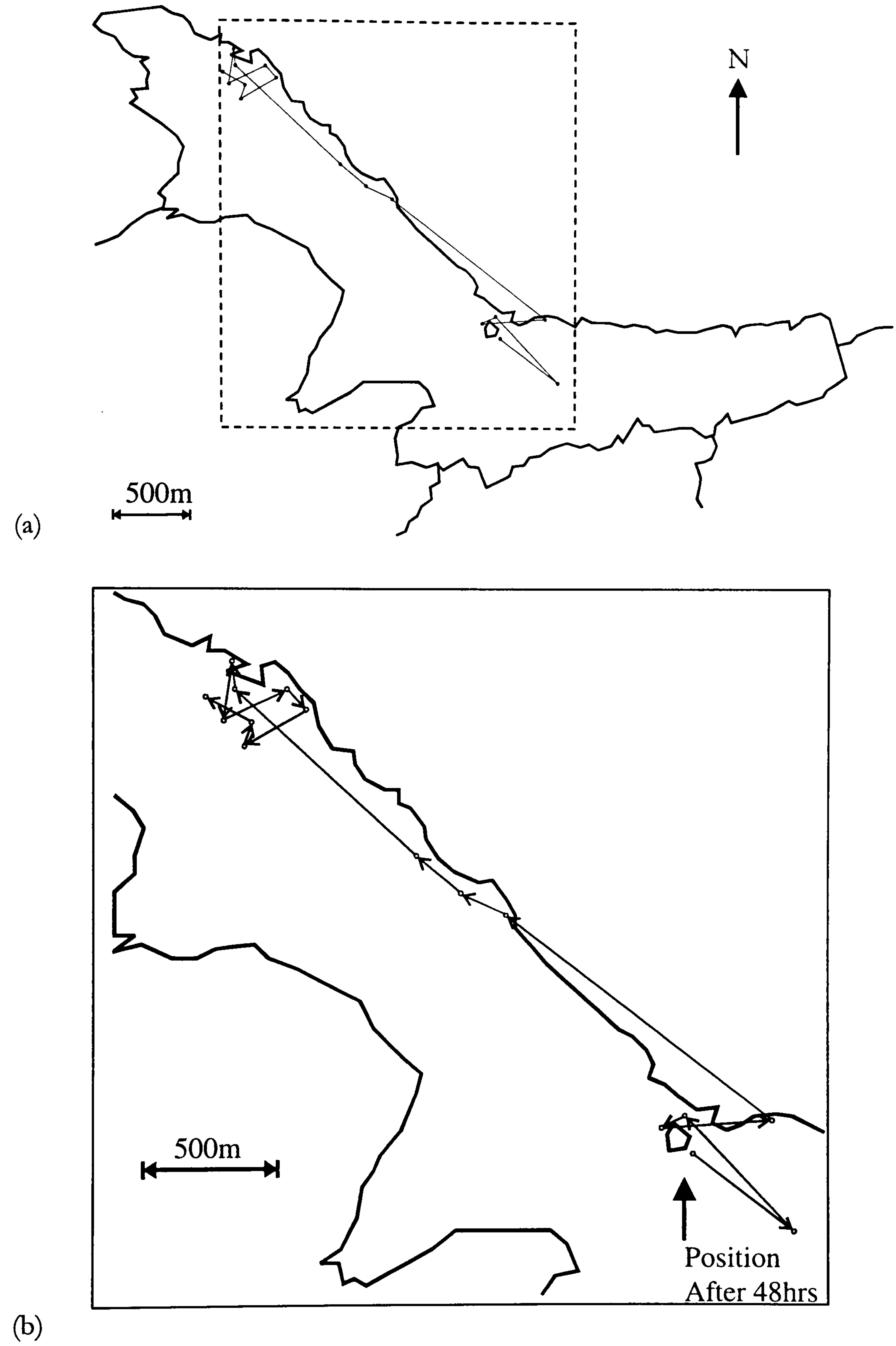


Figure 6.9 – The movement of a single radiotagged hatchery-reared brown trout (Fish 2) over a 15 day period in Carron Valley Reservoir between 18th August and 2nd September 1999. (a) movement of Fish 2 in relation to Carron Valley Reservoir. (b) detailed daily movement of Fish 2. (o) shows the recorded daily positions.

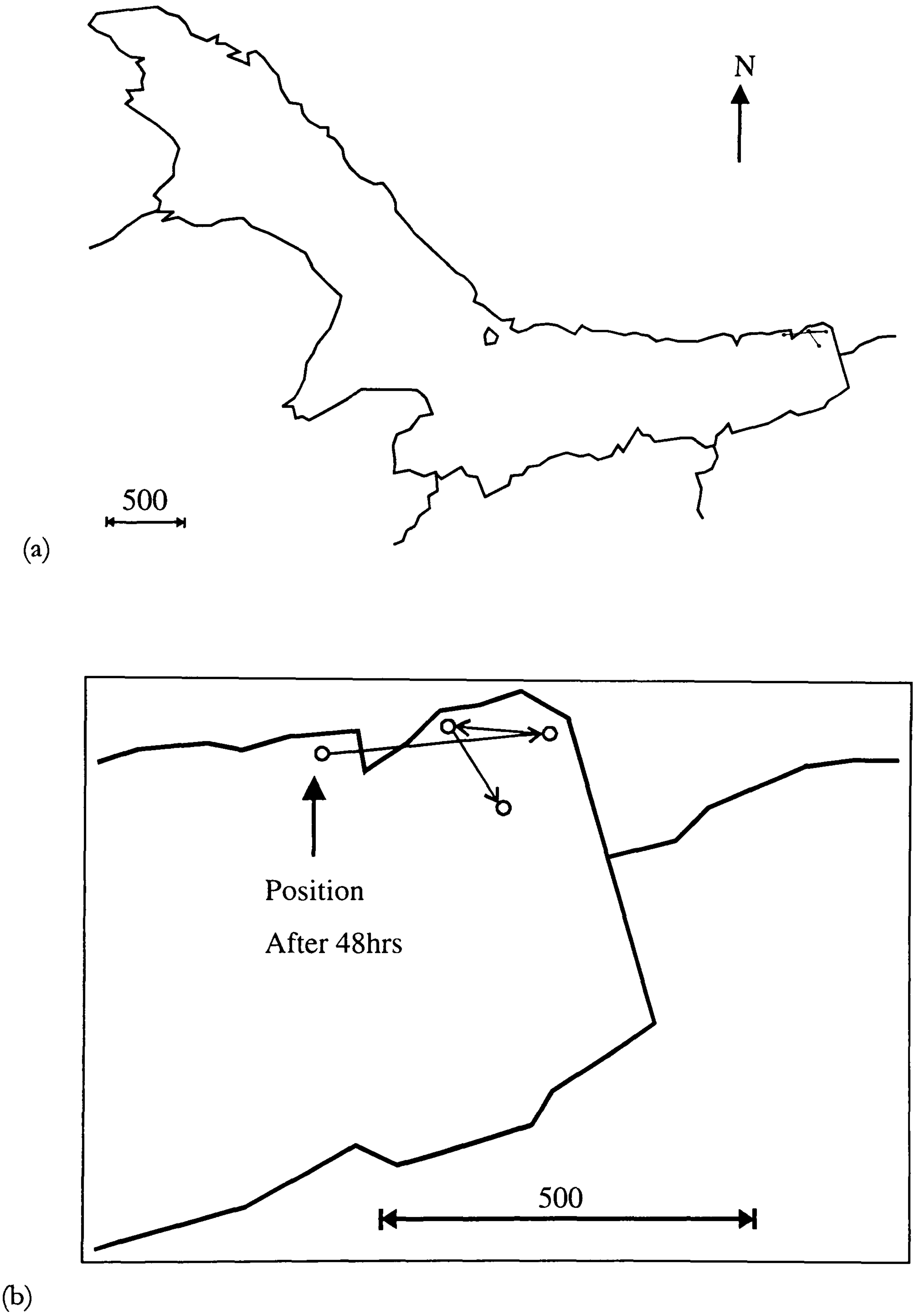
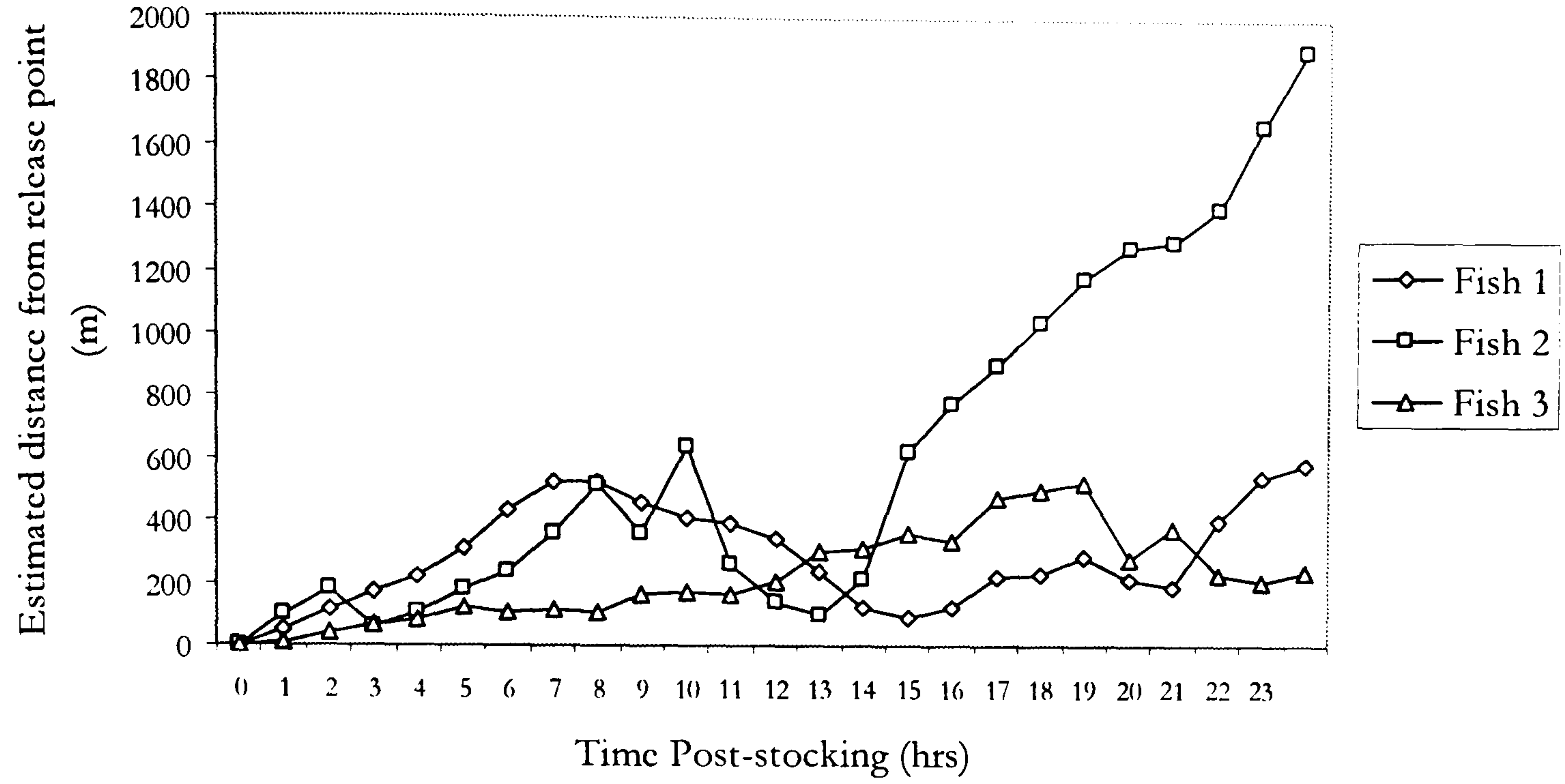
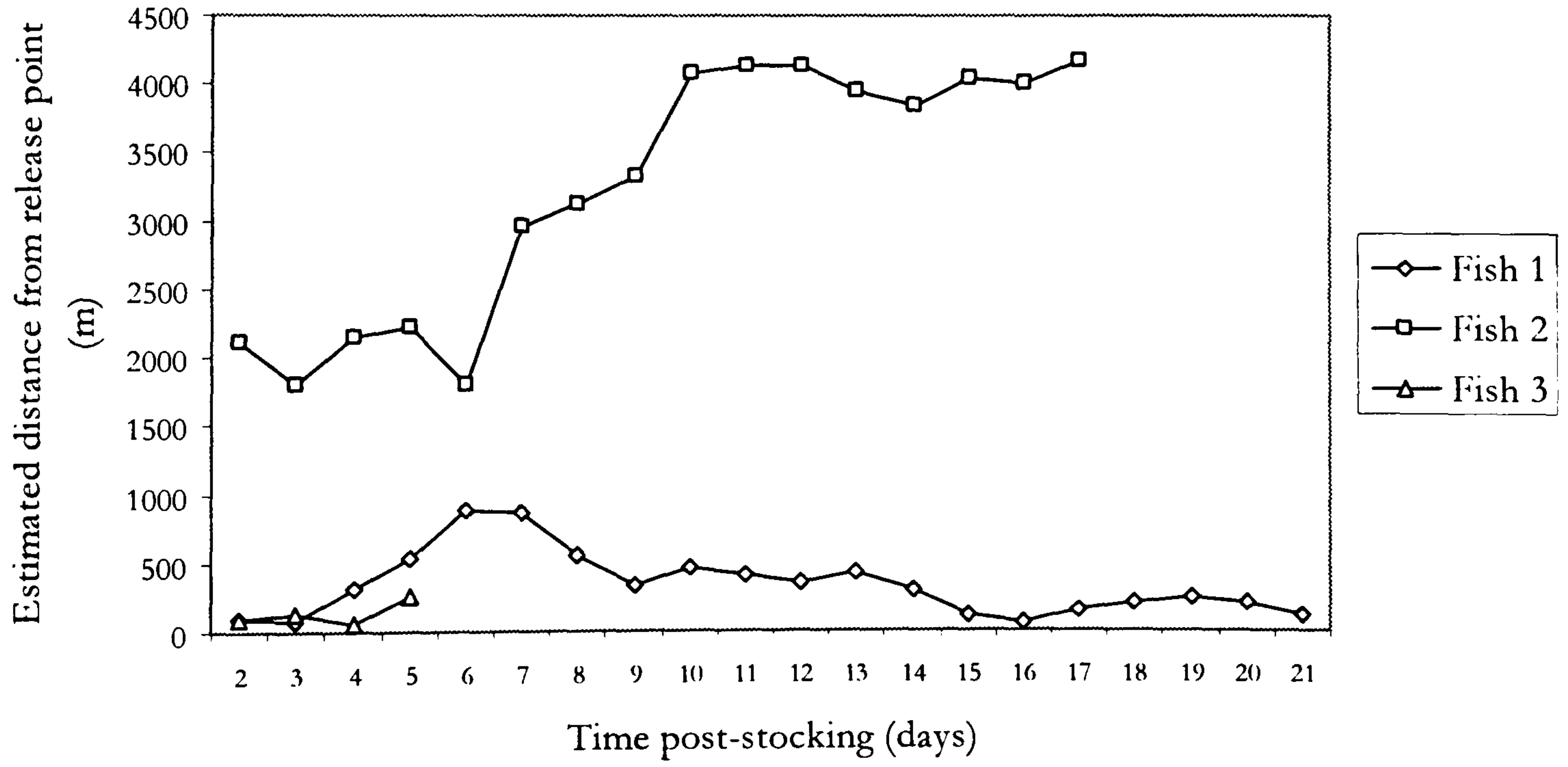


Figure 6.10 – The movement of a single radiotagged hatchery-reared brown trout (Fish 3) over a 4 day period in Carron Valley Reservoir between 18th and 21st August 1999. (a) movement of Fish 3 in relation to Carron Valley Reservoir. (b) detailed daily movement of Fish 3. (o) shows the recorded daily positions.



(a)



(b)

Figure 6.11 - Estimated distance of three radiotagged hatchery-reared brown trout from a single release point (a) over the initial 24hrs following release, and (b)over the observed daily locations until the radiotransmitter signal was lost.

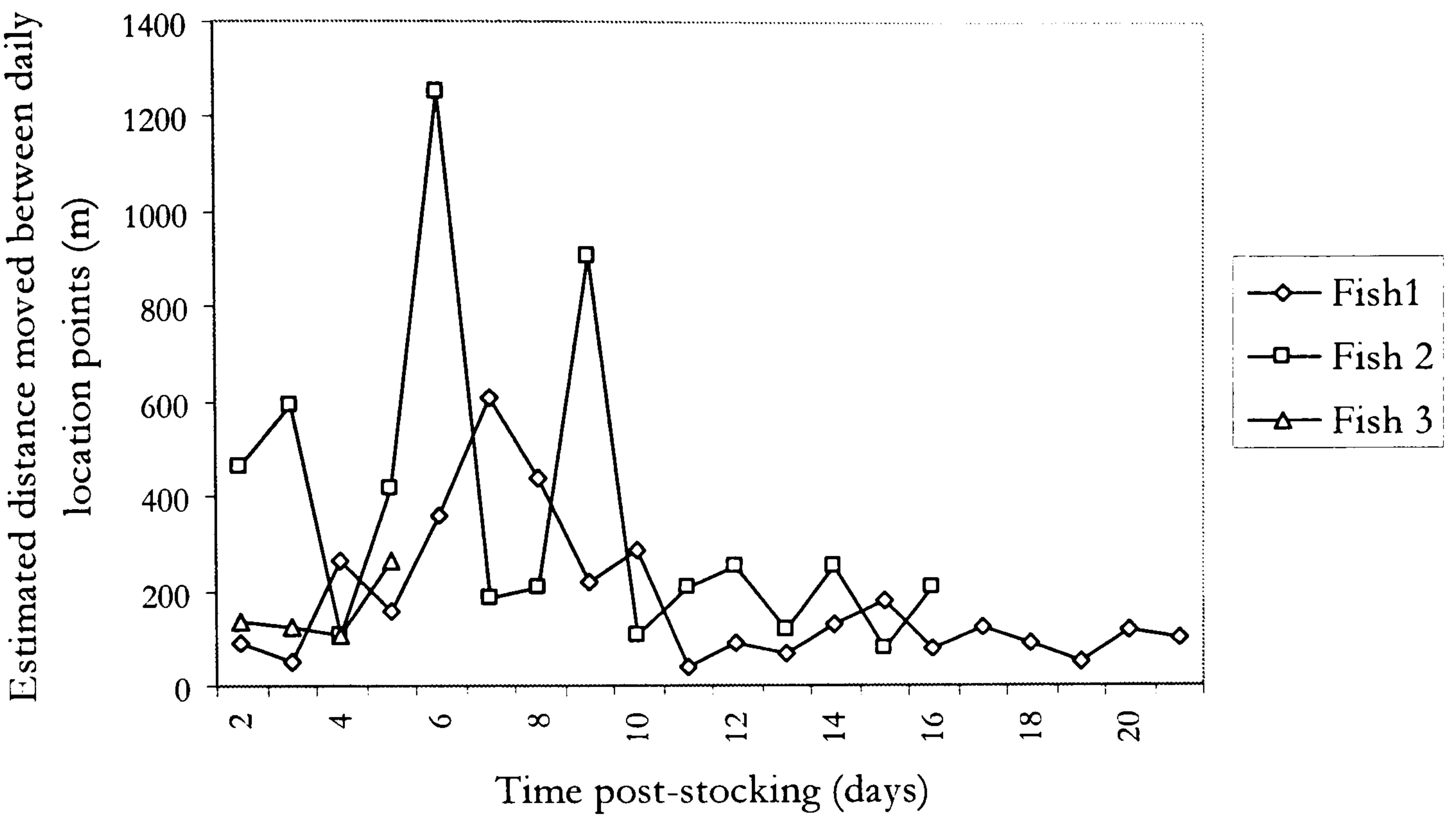


Figure 6.12 - Estimated distance moved between identified daily locations of three radiotagged hatchery-reared brown trout stocked into Carron Valley Reservoir on the 18th August 1999.

pattern away from and then back towards the release site (Figure 6.8) before occupying a relatively confined area between 52-429m linearly distant (Figure 6.11(b)). Unfortunately Fish 3 was lost after only 5 days, but during this period was observed to move back towards the release site before migrating away (Figure 6.10).

6.3 Discussion

6.4.1 Dispersal

In this study, the 'spot' planted hatchery-reared brown trout dispersed quickly from their respective release sites in Carron Valley Reservoir, with no significant difference between the estimated migration distance and the time of recapture after stocking being observed. However, 53% of the tagged hatchery-reared brown trout were reported captured within 1000m and 72% were reported recaptured within 1500m of their respective release sites. These results suggest that whilst the majority of the 'spot' planted, tagged hatchery-reared brown trout disperse quickly, they do so over a relatively small area. These observations support those of Vehanen *et al.* (1998) who found that a large proportion of the 'spot' planted tagged hatchery-reared brown trout released into Lake Oulujarvi, Finland were recaptured in the vicinity of their respective stocking sites, and that there were no differences between the distances migrated and recapture time. L'Abee-Lund and Langeland (1995) also demonstrated that hatchery-reared brown trout dispersed from a release site within 3 weeks of stocking in a Norwegian lake, whilst Thorpe (1974) observed the majority of stocked brown trout released into Loch Leven to remain within 1km of the release site.

Although the majority of the studies on the post-stocking dispersion of hatchery-reared trout have been performed on lotic waters it has been suggested that the post-stocking dispersion of hatchery-reared trout may be influenced by similar factors in both lotic and lentic environments (L'Abee-Lund & Langeland, 1995; Vehanen *et al.*, 1998). Possible influencing factors include the method of fish introduction (Cresswell & Williams, 1982), the time of stocking (Templeton, 1971), the size of the receiving water body (Ratledge & Cornell, 1953; Cresswell & Williams, 1979; Cresswell, 1980), water temperature (Cooper, 1952), the size and physical condition of the trout (Helfrich & Kendall, 1982), social interactions with resident fish (Cresswell & Williams, 1984) and habitat quality (Helfrich & Kendall, 1982).

Between April 1998 and June 2000, a total of 188 (18.8%) of the hatchery-reared tagged brown trout were reported recaptured with adequately identified capture sites. However, only 9.2 and 9.6% of the Visible Implant (VI) tagged brown trout were reported as being recaptured, compared to between 21 and 36% of the 'Floy' style tagged trout. These percentages were similar to those reported in other studies which combined fish tagging and angler survey techniques. Other studies have reported recovery rates of tagged hatchery-reared trout in lotic water bodies ranging from 5 to 17% (Bjornn & Mallet, 1964), 13 to 25% (Moring, 1980) and 1 to 38% (Shetter, 1944).

Cragg-hine (1979) stated that reported captures of tagged fish must be regarded as minimum figures with no account being made for post-stocking mortalities, tag loss and unreported tags within the stocked fish population. Mourning *et al.*, (1994) found no significant differences between the retention rates of Visible Implant (VI) and 'Floy' style tags in hatchery-reared rainbow trout up to 120 days following initial tagging. In the same study Mourning *et al.* (1994) observed higher mortalities in 'Floy' style tagged trout than in Visible Implant (VI) tagged trout. Consequently, it is unlikely that the observed differences in the number of Visible Implant (VI) and 'Floy' style tagged trout reported is due to different tag retention rates over the relatively short study periods used in this experiment. These results suggest that although from a fishery biologists point of view the combined use of Visible Implant tags and adipose fin clips have relatively little effect on the survival, growth and behaviour of hatchery-reared salmonids when compared to 'Floy' style tags (Mourning *et al.*, 1994), they are clearly less easily identified by anglers than 'Floy' style tags.

6.4.2 Accuracy of the angler reported recapture positions

Helfrich and Kendall (1982) stated that the use of angler surveys to determine the post-stocking dispersion patterns of hatchery-reared fish involves unavoidable sociological limitations, of which the most important of which are angler co-operation, angler accuracy and angler effort. This study demonstrated that the accuracy of angler reported positions ranged from 75 to 1763m with a median error in the estimated position of 356.5m when compared to GPS recorded positions. The relative accuracy of angler reported data is often affected by angler experience (i.e. how well the angler knows the environment in which they are fishing)(Cane, 1980), although in this study the estimate of accuracy may also be affected by the inherent variability in the accuracy of handheld GPS systems (approximately ±100m). Cane (1980) concluded that angler surveys could yield accurate and reliable data, but that in order to obtain accurate data high levels of contact and effort are required on the part of the fishery scientist.

6.4.3 Fine scale distribution

It is generally accepted in the ecological literature that lentic dwelling brown trout utilise a variety of habitats dependent on factors including fish size and age, water temperature, inter/intraspecific competition, predator avoidance, season and food availability (Thorpe, 1974; Haraldstad & Jonsson, 1983; L'Abee-Lund & Langeland, 1995). It has been further suggested that the observed localised movement of resident brown trout may be evidence of territorial behaviour and the adoption of defined home ranges within lentic environments (Tytler *et al.*, 1978; James & Kelso, 1995) in similar ways to lotic dwelling salmonids (Symons, 1970; Glova & Field-Dodgson, 1995). Whilst it is clear that hatchery-reared trout are initially at a competitive and ecological disadvantage to resident conspecifics (Ersbak & Haase, 1983), hatchery-reared trout have demonstrated adaptive habitat use in lentic environments when compared to resident conspecifics (L'A'ee-Lund & Langeland, 1995). Consequently, following a period of adaptive learning hatchery-reared brown trout may be expected to occupy localised areas following stocking.

In this study, the three hatchery-reared brown trout were relatively active during the 24hrs following stocking and covered large total distances in a relatively restricted area. This supports the findings of Holliday *et al.*, (1974) who observed increased activity and apparent disorientation in ultrasonically tagged brown trout for 48hrs following release into Loch Leven, Scotland. Schulz and Berg (1992) suggested that following release, trout display random undirected movement. However, in this study the hatchery-reared brown trout were observed to move consistently away from and back towards the release site during the 24hrs following release. Whilst the number of fish tracked in this study was too small to allow any confidence that this observed migration pattern is representative of all stocked trout, it may be possible that initial cyclical movement patterns may occur in response to the ongrowing of the Howietoun brown trout in relatively large earthen ponds.

It has been suggested that possible factors influencing the observed initial high levels of activity following the release of trout include unfamiliarity with a novel environment, competition with resident fish and post-handling stress (Holliday *et al.*, 1974; Tytler *et al.*, 1978; Shulz & Berg, 1992). Holliday *et al.* (1974) further observed that following this initial period of high levels of migration activity, tagged brown trout established a preferred area of residence. Thorpe (1974) observed that the majority of tagged trout remain within 1km of a release point in Loch Leven, Scotland and were recaptured in localised favourable areas. Our observations in this study support these findings, with both Fish 1 and Fish 2 displaying relatively high levels of movement during the first 10 days after release, followed by regular residence within a localised area. However, whilst Fish 1 remained within 1km of the release site, Fish 2 moved approximately 4km before apparently adopting a preferred area. It has been suggested that in novel environments trout adopt preferred areas in response to factors including competition (Tytler *et al.*, 1974), habitat availability (James & Kelso, 1995) and prey abundance (Thorpe, 1974). Tytler *et al.* (1974) further suggested that once trout had adopted a preferred area or home range, whilst individual home ranges may overlap, they may defend some form of refuge or home station within this area.

6.4.4 Summary

In this study it is clear that the majority of the hatchery-reared brown trout distributed quickly over a relatively small area from a release point. This suggests that some combination of 'trickle' and 'scatter' stocking may avoid the rapid overexploitation of the stocked hatchery-reared trout at Carron Valley Reservoir and extend the period of time over which the stocked trout benefit the fishery. However, whilst 'trickle' and 'scatter' stocking may result in an even dispersion of hatchery-reared fish over the entire fishery it may also result in reduced catches due to lower localised population densities of fish (Cresswell & Williams, 1982). As the number of fish caught is often considered a test of fisheries worth by the anglers (Pawson, 1994), this stocking strategy may be less economically beneficial. Consequently it may be necessary to adopt a compromise between the two stocking strategies.

Chapter 7

Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout

7.1 Introduction

Stocking, transfer and introductions of hatchery-reared salmonids are commonly used to enhance recreational or commercial fisheries and to preserve or re-establish threatened populations (Cowx, 1994). The potential divergence of hatchery-reared salmonids from wild fish due to both genetic and environmental factors may have negative ecological consequences for wild populations (Swain & Riddell, 1990; Berejikian *et al.*, 1996). It has also been suggested that hatchery-reared salmonids may have competitive advantages over wild conspecifics that may contribute to the displacement of wild fish (Nickelson *et al.*, 1986). Stream dwelling salmonids seek to acquire territories that provide the best balance of energy gained from the environment and energy required for metabolism, growth and reproduction (Fausch, 1984; Bachman, 1984; Adams & Huntingford, 1996). Competition between conspecific salmonids can be intense (Huntingford & De Leaniz, 1997), consequently additional energy may be required to defend social rank or territory (Fausch, 1984). Individuals vary in their ability to acquire limited resources (Metcalfe *et al.*, 1989) and those individuals which obtain the best territories and highest social status gain greater foraging opportunities and are more likely to survive and reproduce (Fausch, 1984; Metcalfe *et al.*, 1995). However, the exact mechanism through which individuals gain high social status is not completely understood (Adams & Huntingford, 1996).

Hatchery-reared Atlantic salmon (*Salmo salar* L.) fry display greater agonistic activity than wild fry at high population densities, with the reverse being true at low densities (Fenderson *et al.*, 1968). Swain & Riddell (1990) demonstrated that newly emerged domesticated coho salmon (*Oncorhynchus kisutch* Walbaum) fry display greater levels of aggression than wild coho salmon fry when raised under the same environmental conditions. Mesa (1991) found that hatchery-reared cutthroat trout were more aggressive than their wild conspecifics; and he further postulated that excessive expenditure of energy through unnecessary aggression might contribute to poor performance of hatchery fish after stocking. Consequently, the aim of the first experiment in the present study was to determine if hatchery-reared brown trout exhibit relatively higher levels of aggression than simultaneously stocked wild origin fish.

It has been suggested that social dominance in salmonids may be affected by size (Abbot *et al.*, 1985), behavioural fierceness (Huntingford *et al.*, 1990) and prior-residence (Huntingford & De Leaniz, 1997). Levels of aggression have been positively associated with dominance ability in steelhead trout (*Oncorhynchus mykiss* Walbaum) and cutthroat trout (*Oncorhynchus clarki* Richardson) (Mesa, 1991; Berejikian *et al.*, 1996). Several authors have demonstrated the competitive superiority of prior-resident salmonids (Brannas, 1995; Glova & Field-Dodgson, 1995; Huntingford & De Leaniz, 1997). Few studies have considered prior-residence effects in brown trout, although Glova and Field-Dodgson (1995) showed that prior-resident brown trout acquired a greater proportion of optimal territories than chinook salmon (*Oncorhynchus tshawytsca* Walbaum) in an artificial stream environment. Therefore, the aim of the second and final experiment reported here was (1) to examine if established wild brown trout in a semi-natural stream environment will demonstrate a prior-resident competitive advantage over later introductions of trout, (2) to compare the ability of hatchery-reared and wild brown trout to acquire territories, and (3) to determine if hatchery-reared brown trout exhibit relatively higher levels of aggression than simultaneously stocked wild origin fish.

7.2 Materials and methods

7.2.1 Experimental fish

Wild 2+ year class brown trout (fork length range 87-143 mm) were collected on the 2nd June 1998 by direct current electrofishing in the lower reaches of the March Burn, Carron Valley Reservoir, Scotland. The fish were subsequently maintained in an artificial stream environment on an *ad libitum* diet of chironomid larvae at the Glasgow University Field Station, Rowardennan. Hatchery-reared 1+ brown trout were obtained from Howietoun fishery (fork length range 93-133 mm), a domesticated strain extensively used for stocking recreational fisheries in Scotland. The fish were transported to the Glasgow University Field Station on the 24th May 1998 and maintained in stock tanks on commercial pelleted trout food until required.

7.2.2 General laboratory methods

Three experimental replicates of experiments were carried out between July and September 1998 in an artificial stream fluvarium. Water was pumped from Loch Lomond and circulated in the artificial stream by means of a submerged motor. The stream was landscaped to provide a riffle/pool/riffle stream profile of a mixed gravel and cobble substrate. Water depths within the artificial stream ranged from 0.15-0.3m. Light and temperature were ambient for the latitude (56°N), with temperature ranging from 12-15 °C over the experimental period. Flow rates within the artificial stream ranged from 1-35 cms^{-1}, depending on depth. Throughout the experiment fish were fed a continuous (24hr) supply of simulated invertebrate drift using a suspension of rehydrated freeze dried bloodworm at a rate of 5% of the total initial body weight per day; thus the amount of food fed increased proportionally with fish density. The bloodworm suspension was introduced at a depth of 8cm into the centre of the upstream riffle.

Mesh screens at each end of the stream sections prevented individual fish from moving out of the stream section.

Individual fish behaviour was observed five times a day at 2-hour intervals using a focal animal technique (Altmann, 1974). The position of each individual within the stream section, the distance from the point source of feed, the position across the stream width and the position in the water column were all recorded. Each aggressive interaction initiated and received (recorded as nip, chase, charge and fin display (Mesa, 1991)) was recorded for each individual over the 2-minute focal animal sampling period.

Experiment 1 – Aggression and territory acquisition in hatchery-reared and wild brown trout

For each experimental replicate, 10 wild brown trout and 10 hatchery-reared trout were individually measured for fork length (±1mm) and weighed (±0.01g). Each fish was also marked on both lateral surfaces with a unique alcian blue dye tattoo. The fish were simultaneously stocked into the artificial stream resulting in a density of 5 fish/m^2. Following the introduction, the fish were monitored for the next four days using the above methodology. At the end of the experiment all of the fish were removed from the artificial stream section, individually identified, measured and weighed, and their specific growth rate calculated.

Experiment 2 – Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout

For each experimental replicate, 12 wild brown trout were individually measured for fork length (±1mm) and weighed (±0.01g). Each fish was also marked on both lateral surfaces with a unique alcian blue dye tattoo. These fish, subsequently termed prior-residents, were stocked into the artificial stream resulting in a density of 3 fish/m^2, a density similar to that of the March Burn. After 9 days a further six wild brown trout and six hatchery-reared brown trout were measured, weighed, individually marked and simultaneously stocked into the pool area of the artificial stream. Increasing density to 6 fish/m^2, simulating a local significant increase in stocking density common in current commercial stocking practice.

Following the introduction of the second batch of 12 fish, prior-resident and introduced fish were monitored for the next four days using the above methodology. At the end of the experiment, all of the fish were removed from the artificial stream section, individually identified, measured and weighed, and their specific growth rate calculated.

7.2.3 Computational methods

Relative performance between the different fish types was assessed by comparing specific growth rates (*G*) (Nielson & Johnson, 1983), which were calculated as:

$$G = (\ln W_2 - \ln W_1)(t_2 - t_1)^{-1}$$

Where W_1 and W_2 are initial and final weights on days t_1 and t_2, respectively.

Aggression initiated and received, home range size, distance of territory from the point source of feed and specific growth rate were used to assess differences in territory acquisition and aggression between the brown trout groups in both experiments. The distance from the point source of feed was calculated as the distance between the feed tube and each individuals home station (to the nearest 10cm); the home station being defined as the stream position at which an individual was observed on >40% of the total observations. The home range was calculated as the area in which an individual was found on >80% of the total observations. A Kruskal-Wallis (adjusted for ties) revealed no differences in the aggression initiated and received, the home ranges or the home stations between the experimental replicates for the different fish groups in both experiments. Therefore the data from the three replicates in both experiments was pooled for subsequent analysis. The pooled data was tested for normality, and consequently examined using Kruskal-Wallis (adjusted for ties) statistical tests. This study was accepted for publication in the Journal of Fish Biology in October, 1999 (Appendix 4).

7.3 Results

7.3.1 Experiment 1

Aggression initiated and received

Although hatchery-reared fish initiated 58.5% of the total aggression with the wild fish only initiating 41.5% (Figure 7.1), the difference was not significant (Kruskal-Wallis, H=2.80, d.f.=1, p=0.094). There was no significant difference in the number of aggressive acts received by the hatchery-reared and wild fish (Kruskal-Wallis, H=0.256, d.f.=1, p=0.880)(Figure 7.1).

Territory acquisition

To examine differences in territory acquisition between the simultaneously stocked hatchery-reared and wild trout, the mean distance of the home station from the point source of feed (Figure 7.2) and the mean home range (Figure 7.3) were calculated for both fish groups. Wild fish occupied home stations that were significantly closer to the point source of feed than the home stations of the hatchery-reared fish (Kruskal-Wallis, H=4.92, d.f.=1, p= 0.027). However, there was no significant difference in the home range sizes (Kruskal-Wallis, H=0.44, d.f.=1, p=0.809).

Specific growth rates

The wild fish exhibited a higher mean specific growth rate during the three trials than the hatchery-reared fish (Kruskal-Wallis, H=14.33, d.f.=1, p<0.001) (Figure 7.4). Wild fish showed a slight positive mean growth rate during the three trials whilst the hatchery-reared fish showed a negative mean specific growth rate (Figure 7.4).

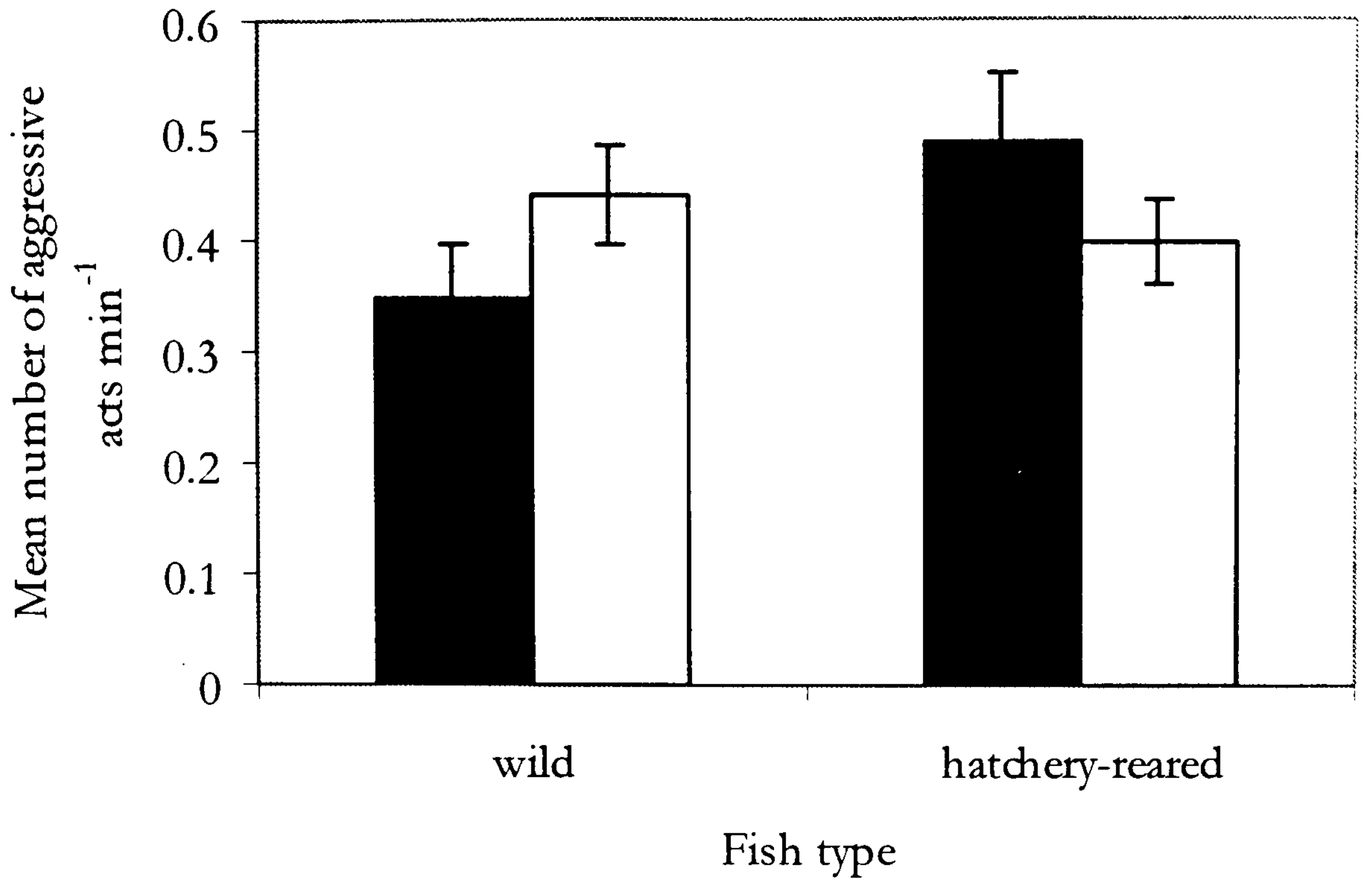


Figure 7.1 – Aggressive behaviour of wild and hatchery-reared brown trout expressed as the mean number (±S.E.) of aggressive acts initiated (■) and the number of aggressive acts received (□).

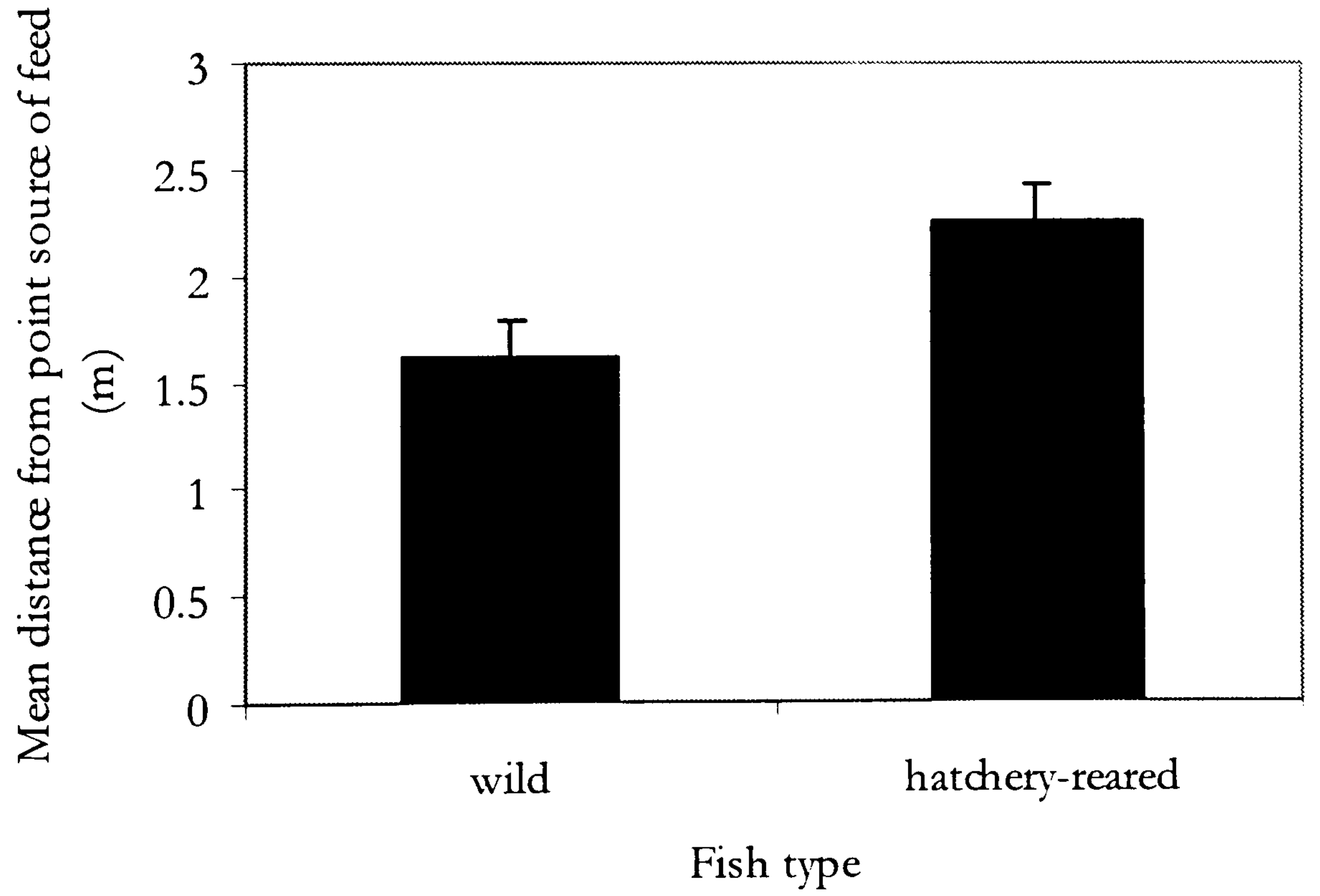


Figure 7.2 – Mean (±S.E.) distance of the home station from the point source of feed of wild and hatchery-reared brown trout.

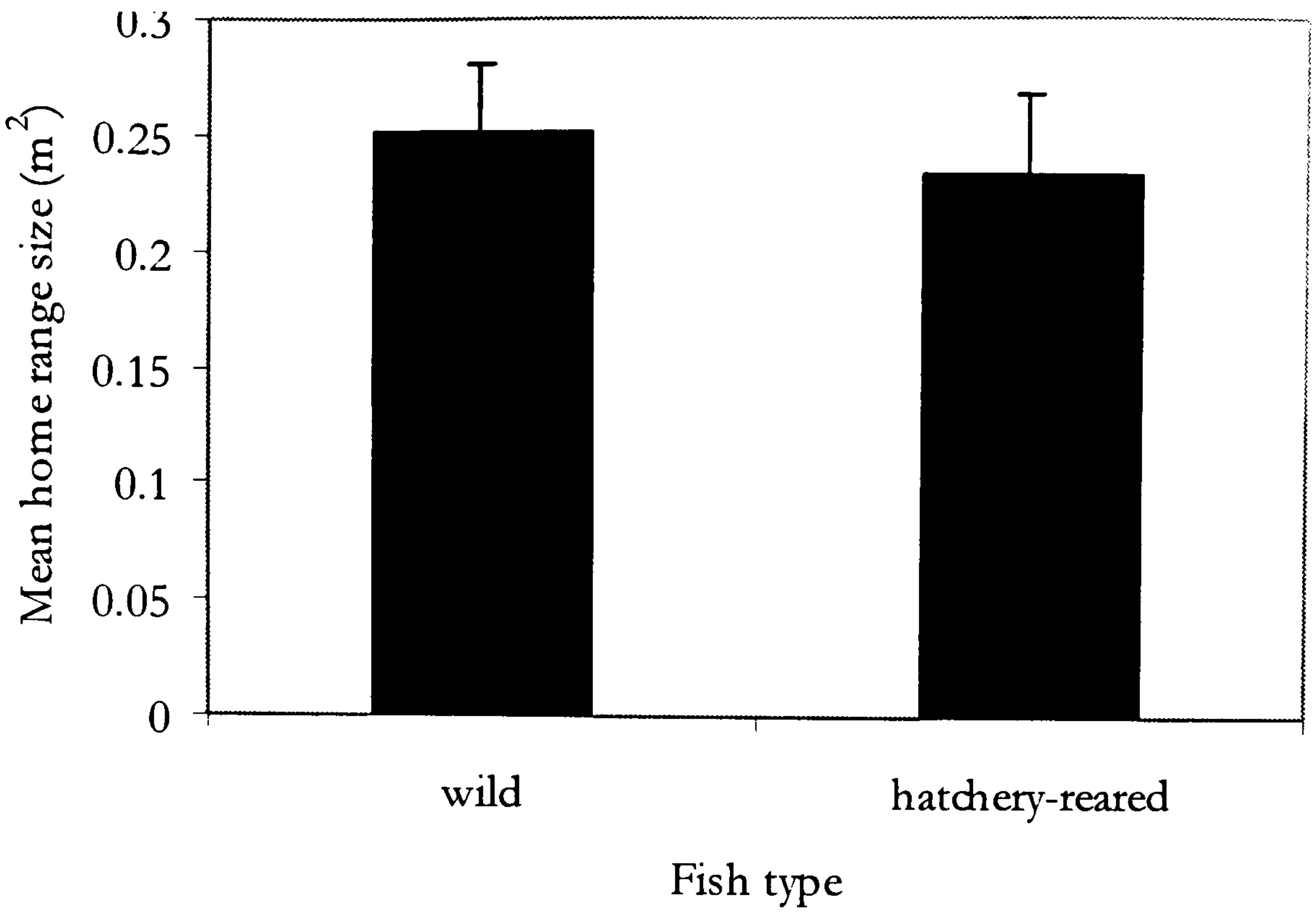


Figure 7.3 – Mean (±S.E.) home range size of wild and hatchery-reared brown trout.

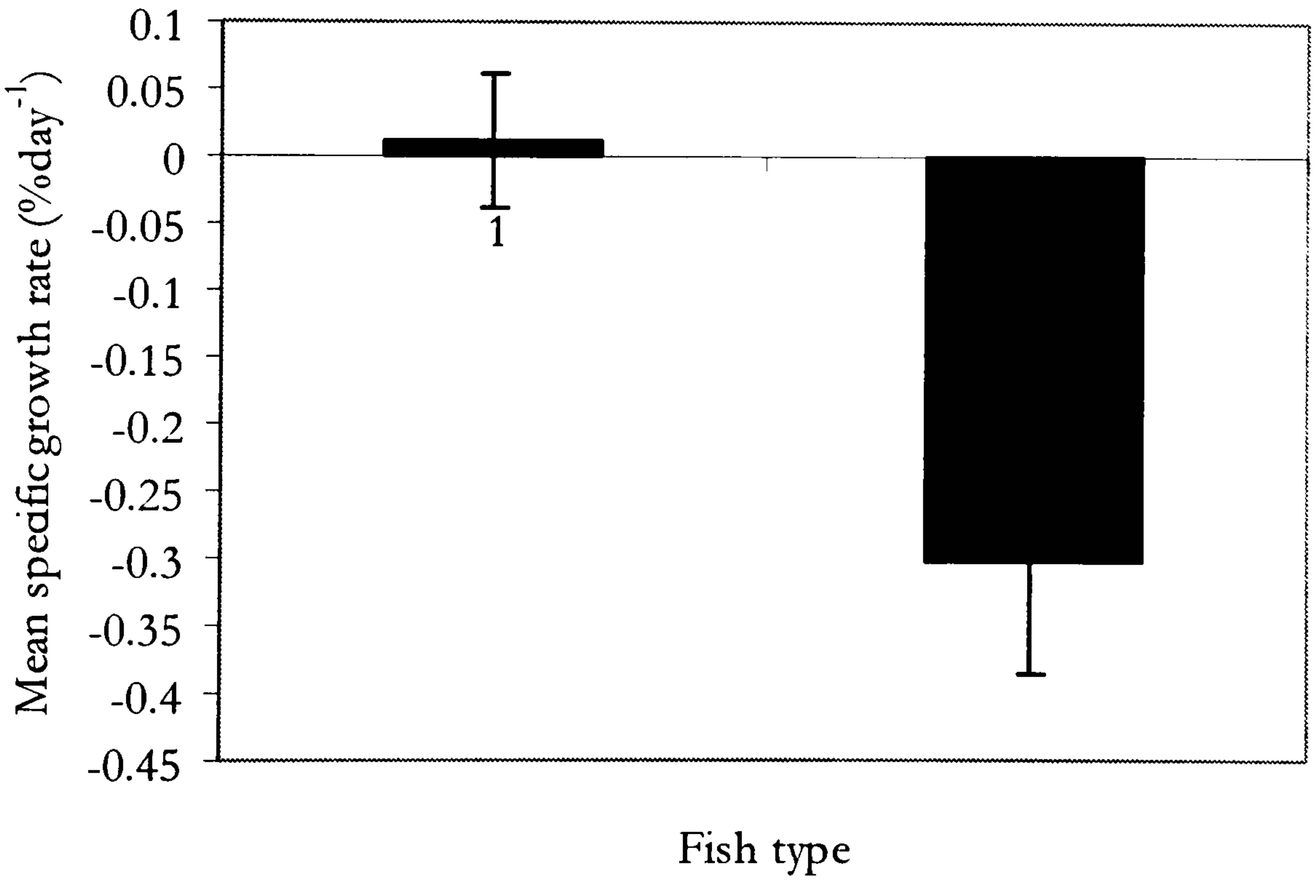


Figure 7.4 – Performance of wild and hatchery-reared brown trout expressed as mean specific growth rates (±S.E.).

7.3.2 Experiment 2

Aggression initiated and received

Figure 7.5 shows the difference in mean aggression initiated and received by the 3 categories of fish (prior-resident wild, introduced wild and introduced hatchery-reared) for the three experimental replicates pooled. Prior-resident wild fish initiated 44%, hatchery-reared 34% and introduced wild fish 22% of the total aggression. There was a significant difference in the number of aggressive acts initiated by each of the 3 groups (Kruskal-Wallis, H = 4.88, d.f. = 2, p = 0.027). Prior-resident wild fish initiated significantly more aggressive acts than later stocked introduced wild or hatchery-reared fish (Kruskal-Wallis, H = 7.08, d.f. = 2, p = 0.029); whilst introduced hatchery-reared fish initiated significantly more aggressive acts than introduced wild fish (Kruskal-Wallis, H = 4.38, d.f. = 1, p = 0.036). There was no significant difference in the number of aggressive acts received by each of the three fish groups (Kruskal-Wallis, H = 3.33, d.f. = 2, p = 0.189).

Territory acquisition

To examine differences in territory acquisition between the three fish groups, the mean distance of the home station from the point source of feed (Figure 7.6) and the mean home range (Figure 7.7) were calculated for each fish group. Mean distances from the point source of feed differed significantly between the three fish types (Kruskal-Wallis, H = 7.12, d.f. = 2, p = 0.028). Prior-resident wild fish occupied home stations that were significantly closer to the point source of feed than both hatchery-reared and introduced wild fish groups (Kruskal-Wallis, H = 7.15, d.f. = 2, p = 0.026). However, introduced hatchery-reared and introduced wild fish occupied similar home stations that were not significantly different distances from the point source of feed (Kruskal-Wallis, H = 0.01, d.f. = 1, p = 0.985). There was no tendency for prior-resident wild fish to maintain

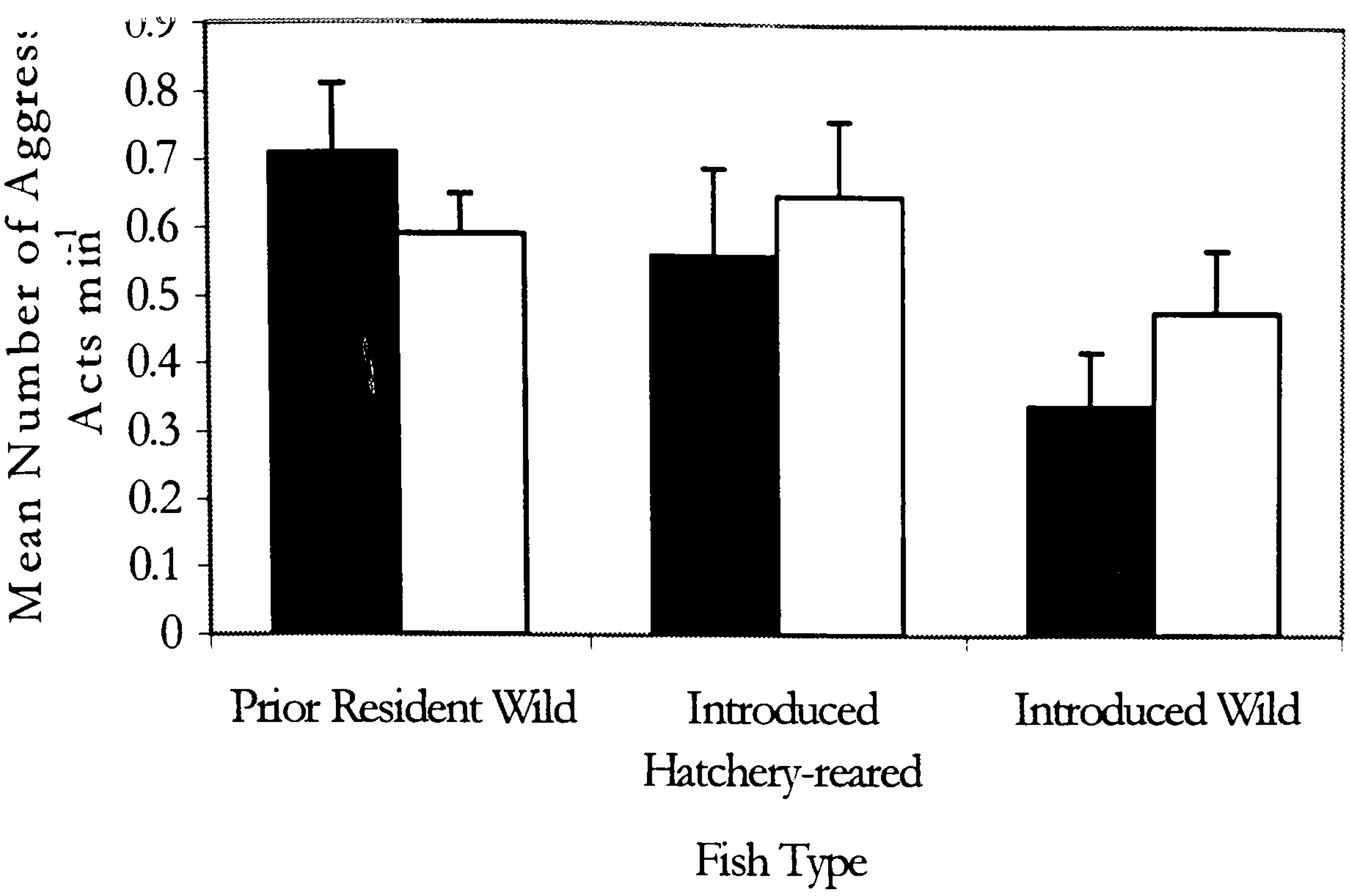


Figure 7.5 – Aggressive behaviour of prior resident wild, introduced wild and introduced hatchery-reared brown trout expressed as the mean number (±S.E.) of aggressive acts initiated (■) and the number of aggressive acts received (□).

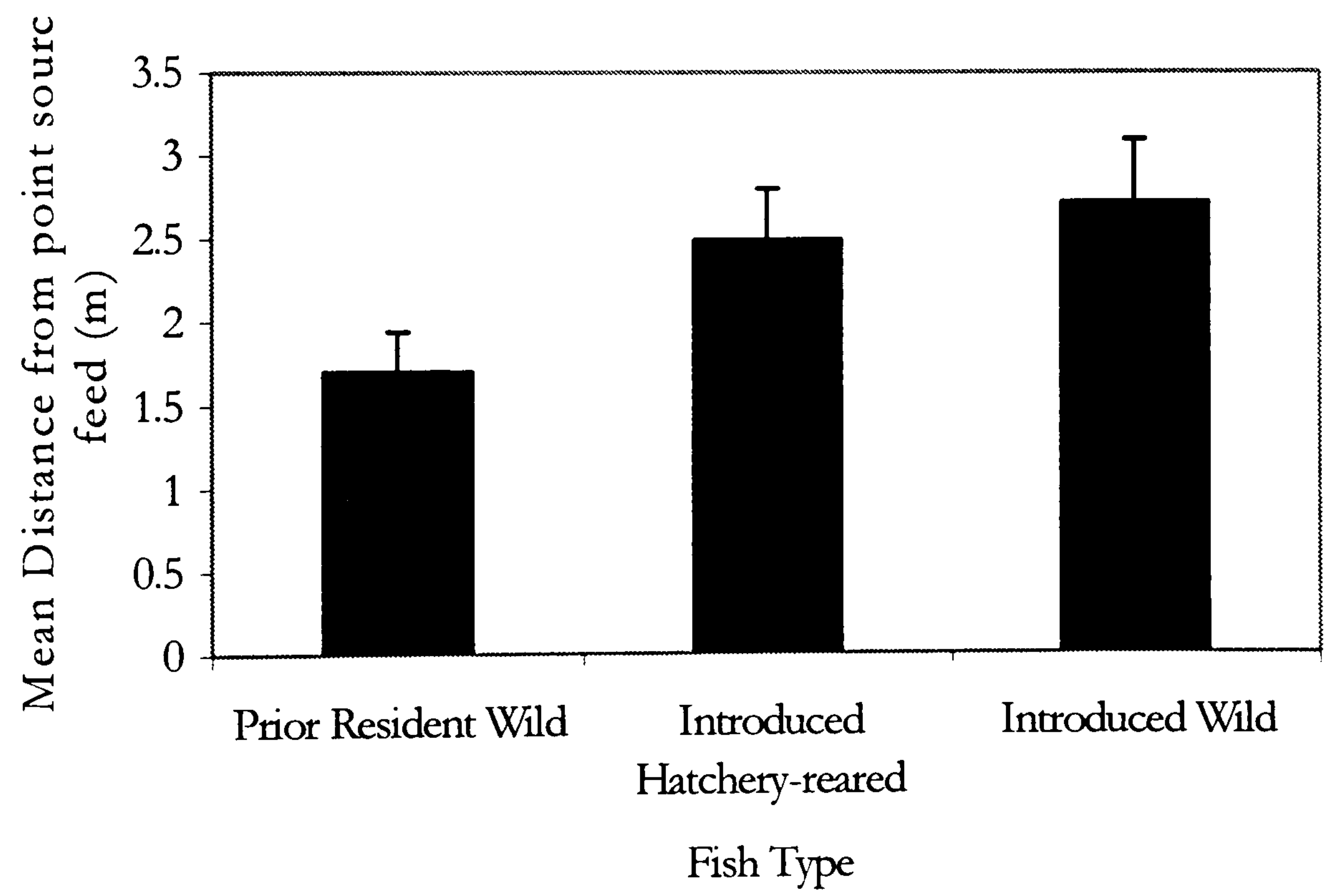


Figure 7.6 – Mean (±S.E.) distance of the home station from the point source of feed of prior resident, introduced wild and introduced hatchery-reared brown trout.

larger home range areas than both categories of introduced fish (Kruskal-Wallis, H = 0.01, d.f. = 2, p = 0.997).

Specific growth rates

Relative performance differences between the three fish types was assessed by comparing the specific growth rates (Figure 7.8). Specific growth rates differed significantly between the three fish types (Kruskal-Wallis, H = 36.41, d.f. = 2, p = 0.001). Prior-resident wild fish were the only group to show a positive mean specific growth rate during the three trials. The specific growth rate of this group was significantly higher than either the introduced hatchery-reared or introduced wild fish (Kruskal-Wallis, H = 29.95, d.f. = 2, p = 0.000). Amongst the introduced fish groups specific growth rates differed significantly (Kruskal-Wallis, H = 10.02, d.f. = 1, p = 0.002). Introduced hatchery-reared fish having a larger negative mean specific growth rate indicating greater weight loss than introduced wild fish.

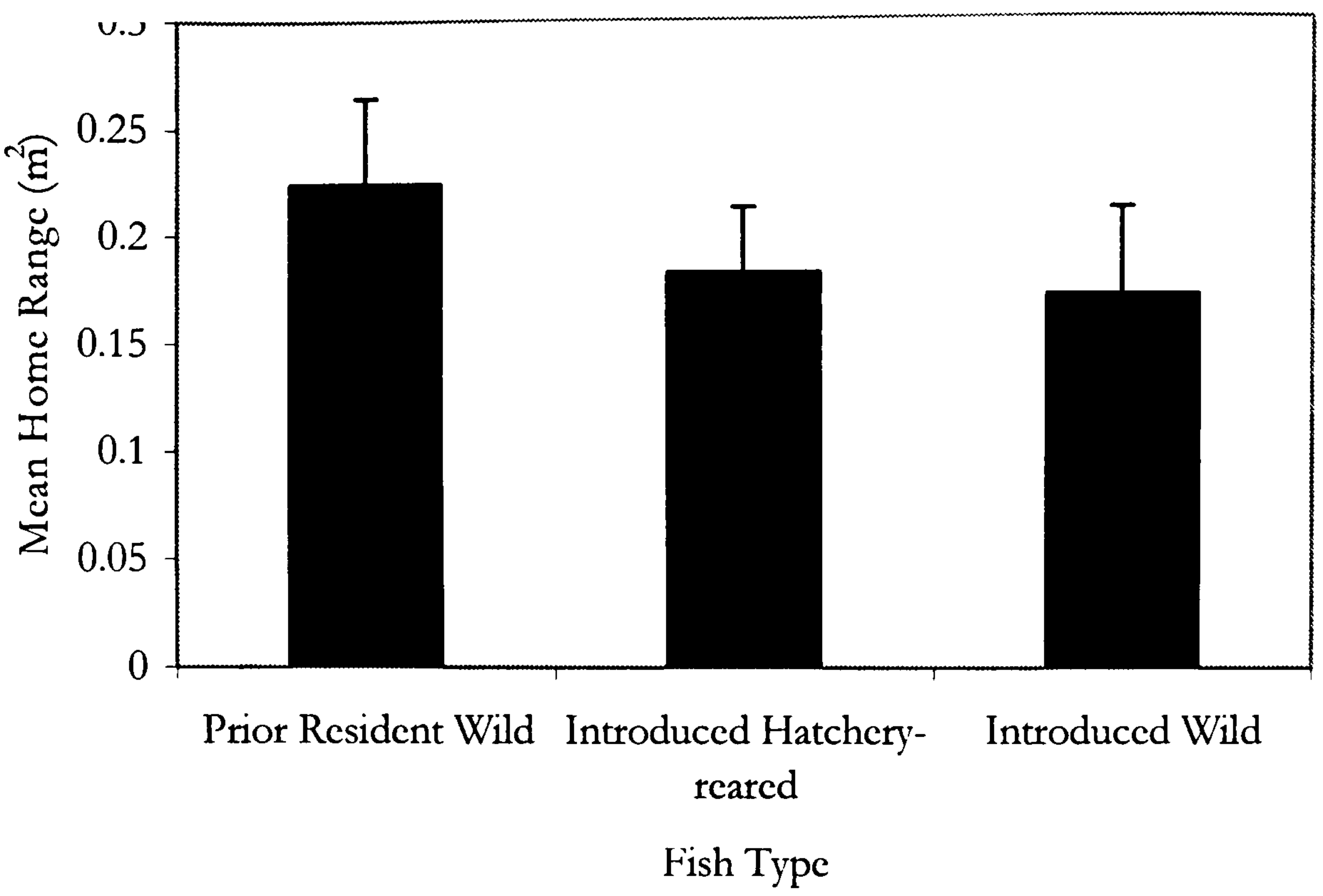


Figure 7.7 – Mean (±S.E.) home range size of prior resident wild, introduced wild and introduced hatchery-reared brown trout.

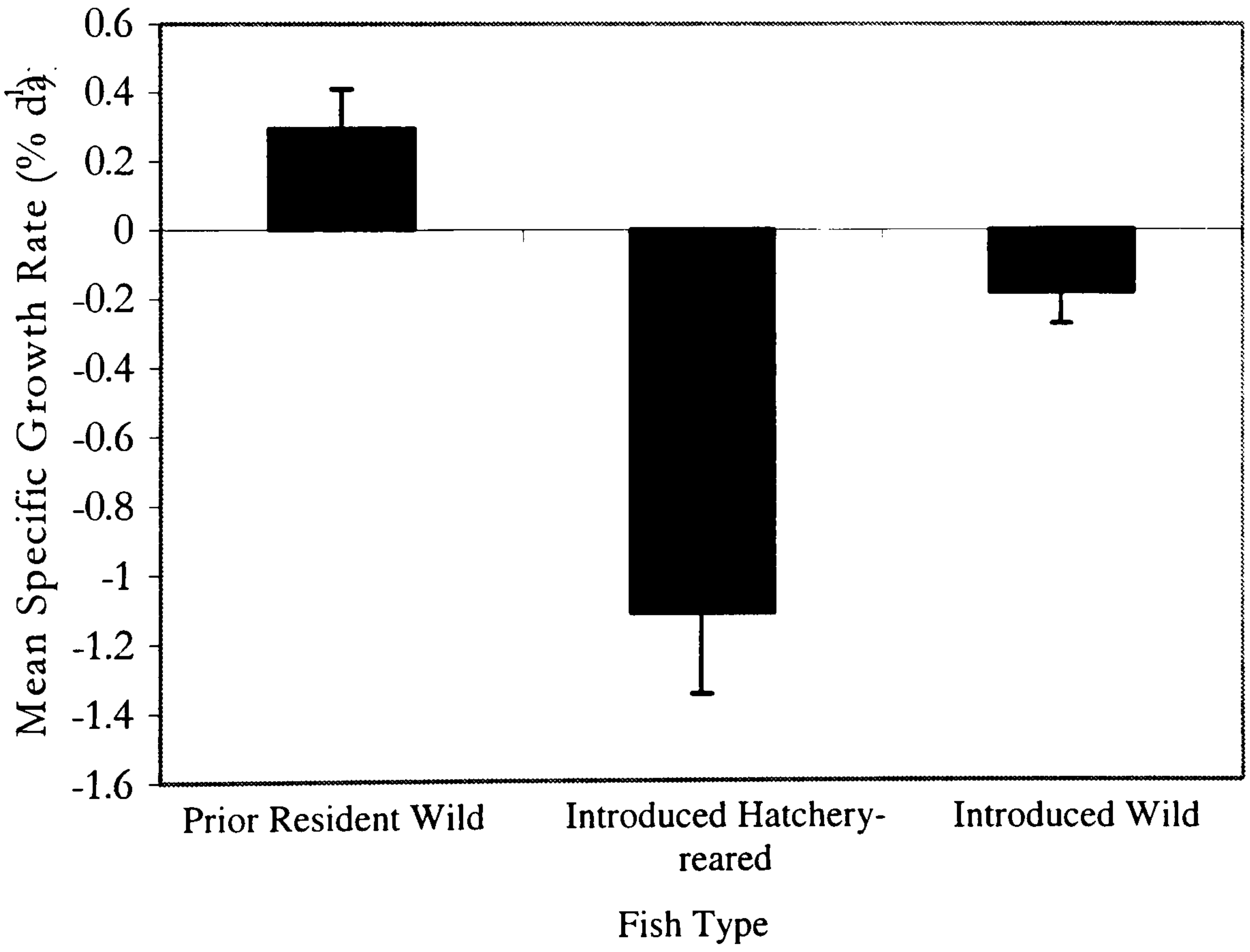


Figure 7.8 – Performance of prior resident wild, introduced wild and introduced hatchery-reared brown trout expressed as mean specific growth rates (±S.E.).

7.4 Discussion

In both experiments, the hatchery-reared fish were observed to initiate more aggressive acts than simultaneously introduced wild conspecifics; although the observed difference was only statistically significant in the second experiment. The hatchery-reared fish also displayed significantly lower mean specific growth rates than simultaneously stocked wild fish in both experiments. This supports the observations of Fenderson *et al.* (1968), Swain and Riddell (1990) and Mesa (1991) who found hatchery-reared salmonids to be more aggressive than wild conspecifics when stocked simultaneously into a variety of environments. The observed higher levels of aggression in the introduced hatchery-reared fish relative to simultaneously stocked introduced wild fish may constitute non-cost effective behaviour and may contribute towards the significantly lower mean specific growth rate. Bachman (1984) suggested that non-cost effective behaviour such as high levels of aggression and poor territory acquisition in hatchery-reared salmonids results in fewer opportunities and less time available for feeding and may consequently result in the poor growth and survival of these fish. The observed relative differences in competitive strategies between the later introduced hatchery-reared and wild fish may be a consequence of the different competitive rearing environments (Huntingford & De Leaniz, 1997). A lack of visual isolation and a need to adopt competitive feeding strategies in hatchery environments may lead to an increase in aggressive feeding behaviour in hatchery-reared salmonids (Wang & White, 1995). In contrast, stream environments produce structured social hierarchies where wild fish develop adaptive flexibility in aggressive behaviour, resulting in reduced levels of aggression; which may constitute an energy conserving advantage (Mesa, 1991). The relatively large decrease in mean specific growth rates observed in the hatchery-reared fish may have also been influenced by a change from high energy commercially-produced diets to relatively less energy dense natural foods (Sosiak, 1982), or an initial period of acclimation to unfamiliar natural food items (Wang & White, 1995).

A general feature of stream salmonids is that dominant fish occupy the most cost-effective territories and initiate a large proportion of a populations' aggressive interactions (Glova & Field-Dodgson, 1995; Symons, 1969). In the second experiment, wild brown trout, stocked into a previously empty habitat demonstrated a competitive advantage, conferred by a brief period of residency, over later introduced conspecifics. These established wild fish initiated more aggressive interactions, maintained home stations closer to a point source of feed and exhibited a higher relative mean specific growth rate than later introductions of hatchery-reared and wild fish. Brannas (1995) and Huntingford and De Leaniz (1997) demonstrated similar effects in newly emergent Atlantic salmon fry showing that early arriving (prior-resident) individuals establish and maintain territories over later arriving individuals. It has been suggested that behavioural differences between hatchery-reared and wild salmonids may be due to genetic and environmentally controlled phenotypic divergence in hatchery-reared populations (Swain & Riddell, 1990; Berejikian *et al.*, 1996). This effect might, in principle, be responsible for the observed competitive advantage of the established wild fish over later introduced hatchery-reared fish. This is considered unlikely since there were significant differences in the initiated aggression rates and home station positions of the established wild fish and the later introduced wild fish. These differences suggest that the initially stocked wild fish are defending and maintaining home stations closer to the limited food resource (point source of feed) through a prior-resident competitive advantage.

Both experiments demonstrated that hatchery-reared fish initiated more aggressive interactions but exhibit relatively poorer growth when compared to simultaneously stocked wild fish. This supports the hypotheses of Bachman (1984) and Mesa (1991) who suggest that non-cost effective behaviour in hatchery-reared salmonids may have important implications on post-stocking survival and consequently existing and future stream stocking programmes. The second experiment demonstrated that established wild brown trout in a semi-natural stream environment do display a prior-resident effect over later introductions of both hatchery-reared and introduced wild conspecifics. This supports other studies which have also demonstrated prior-residence effects over later introductions of hatchery-reared and wild conspecifics in cutthroat trout (Wang & White, 1994), Atlantic salmon (Brannas, 1995) and brown trout (Glova & Field-Dodgson, 1995).

Chapter 8

Prey recognition and short-term changes in the relative feeding efficiency of experienced wild and naïve hatchery-reared brown trout (*Salmo trutta* L.).

8.1 Introduction

Malnutrition has been proposed as a potential source of poor post-stocking performance in hatchery-reared salmonids (Vinyard *et al.*, 1982; Ersbak & Haase, 1983; Bachman, 1984). The change from artificial food to natural feeding is considered to be critical for the successful stocking and subsequent adaptation of hatchery-reared salmonids after release (Ersbak & Haase, 1983; Bachman, 1984; Johnsen & Ugedal, 1989). Hatchery-reared salmonids are confronted by a change from an environment characterized by the homogeneity of feed administration (i.e. temporal, spatial and quality) to the natural environment which is categorised by the spatial and temporal heterogeneity of prey availability and diet quality (Johnsen & Ugedal, 1989). Salmonids are predominantly visual feeders (Stradmeyer & Thorpe, 1987) with wild salmonids selecting prey based on characteristics including size (Wankowski, 1979), colour (Clarke & Sutterlin, 1985), movement (Irvine & Northcote, 1983) and abundance (O'Grady, 1983). Conversely, hatchery-reared salmonids may become visually conditioned to respond to physically, chemically and nutritionally uniform pelleted feeds (Ersbak & Haase, 1983; Stradmeyer & Thorpe, 1987). Consequently, poor prey recognition (Steward & Bjornn, 1990), inefficient foraging (Bachman, 1984), excessive activity and agnostic behaviour (Fenderson *et al.*, 1968; Symons, 1969) and inappropriate behavioural traits inherited through domestication or learned through culture conditions (Ruzzante, 1994) may all contribute to the ability of hatchery-reared salmonids to adapt to natural foods.

Long-term changes in the foraging choices of wild salmonids are influenced by relative abundance and profitability of prey (Paszkowski & Olla, 1985). It has been suggested that hatchery-reared trout can not identify and capture natural prey items following release into natural environments, with some individuals never learning to feed (Ersbak & Haase, 1983; Bachman, 1984). However, several field studies have demonstrated that in the long term both lotic and lentic dwelling hatchery-reared salmonids do adapt to some degree, to natural prey items after a period of several weeks following release into natural environments (O'Grady, 1983; Kelly-Quinn & Bracken, 1989). On a short-term basis, a fish's most recent experience allows the adjustment of feeding behaviour to maximise foraging rewards (Paszowski & Olla, 1985). Several experimental studies performed under controlled laboratory conditions have shown hatchery-reared salmon to recognise and capture unfamiliar natural prey items successfully (Vinyard *et al.*, 1982; Paszkowski & Olla, 1985). Stradmeyer and Thorpe (1987) observed that hatchery-reared juvenile Atlantic salmon (*Salmo salar* L.) immediately recognised novel prey, but with relatively low initial capture success. The feeding success of many fish species has been found to improve with experience (Curio, 1976; Winfield *et al.*, 1983; Colgan *et al.*, 1986; Ibrahim & Huntingford, 1992). Paszkowski and Olla (1985) found that the efficiency of prey capture increased from initially low levels during the first few hours of the first feeding bouts on hatchery-reared coho salmon (*Oncorhynchus kitsutch* Walbaum). Stradmeyer and Thorpe (1987) found prey capture time to decrease with experience over the first 1.5 hours of encountering novel prey.

Foraging behaviour in wild fish may be significantly influenced by predation, with trade offs between predation risks and energetic gains effecting the survival success of fish populations (Dellefors & Johnsson, 1995). Olla and Davis (1989) demonstrated that hatchery-reared coho salmon raised in the presence of predators exhibited more efficient predator avoidance behaviour than hatchery-reared conspecifics raised without predators present. Hatchery-reared salmonids are at their most vulnerable to predation by piscivorous fish, birds and diving mammals immediately after release into natural environments, especially if hatchery-reared fish maintain a conditioned response to feed on surface administered pelleted feeds. In order to survive hatchery-reared salmonids must adapt quickly to natural environments following stocking and consequently the ability to rapidly recognise and adapt to foraging on natural prey items may influence the relative post-stocking success of hatchery-reared salmonids. Studies have been carried out to examine short-term prey recognition and feeding efficiency changes in the first few hours after encountering novel prey in juvenile coho salmon (Pazskowski & Olla, 1985) and juvenile Atlantic salmon (Stradmeyer & Thorpe, 1987). However, few studies have examined the relative differences in short-term feeding efficiency between experienced wild and naïve hatchery-reared brown trout (Pazskowski & Olla, 1985; Stradmeyer & Thorpe, 1987). Consequently, the first aim of the present study was to determine how quickly hatchery-reared trout learn to forage on a novel prey species. Specifically this was tested by examining the number of encounters with non-living chironomid larvae required before any behavioural response (prey recognition) to the prey was observed in naïve hatchery-reared and experienced wild brown trout. The second aim of this study was to examine the relative changes in the short-term feeding efficiency of naïve hatchery-reared and experienced wild brown trout following initial ingestion of non-living chironomid prey.

8.2 Materials and methods

8.2.1 Experimental fish

Wild 2+ year class brown trout (fork length range 80-163mm) were collected on the 3rd May 1999 by direct current electrofishing in the lower reaches of the March Burn, Carron Valley Reservoir, Scotland. The fish were subsequently maintained in an artificial stream environment on an *ad libtum* diet of non-living chironomid larvae to simulate natural invertebrate drift at the Glasgow University's, University Field Station, Loch Lomond. Although the wild trout may have already encountered chironomid larvae in the natural environment, maintaining the experimental wild fish on a diet of non-living chironomid larvae ensured prior experience with this prey type before the initiation of the experiment. Hatchery-reared 2+ brown trout (fork length range 92-181mm) were obtained from a domesticated strain used extensively for stocking recreational fisheries in Scotland, which were reared at the 'Howietoun Fishery' on a commercial pelleted trout food. The fish were transported to the University Field Station on the 27th April 1999 where they were held in stock tanks and fed on a commercial pelleted trout food.

8.2.2 General laboratory methods

In June 1999, a total of 24 wild-caught and 24 hatchery-reared fish were tested for their foraging responses to non-living chironomid larvae (a common prey item in wild populations (O'Grady, 1983; Kelly-Quinn & Bracken, 1989)). Although living prey have been shown to elicit a greater foraging response than non-living prey (Irvine & Northcote, 1983), the non-living chironomid larvae were representative of natural drift prey in terms of size, shape, colour and palatability (Stradmeyer & Thorpe, 1987). The wild-caught trout ranged in fork length from 80-163mm (mean=111.8mm ±3.60 S.E.) and were significantly smaller than the hatchery-reared conspecifics (Kruskal-Wallis, H=4.089, d.f.=1, p=0.043) which ranged is size from 92-181mm (mean=121.2mm ±4.09 S.E.). For each experimental replicate, either a single wild-caught or a hatchery-reared fish was removed from its respective stock area and randomly assigned to a 2m long x 0.3m wide x 0.3m deep, section of an artificial stream. This area was designed to be narrow and shallow enough for the fish to be in visual contact with any drifting prey items passing relatively rapidly through the experimental area. The bottom of the flume was covered with a mixed cobble/gravel substrate, with 5mm square grill mesh screens at each end to prevent fish escaping. Prey items were introduced individually at the upstream end of the experimental section at a depth of 15cm via a 20mm PVC pipe. In each flume section, flow rates ranged from 1-25cms^{-1}, depending on depth. Water was pumped from Loch Lomond and circulated in the artificial stream by means of a submerged motor. Light and temperature were ambient for the latitude (56°N), with temperature ranging from 10-14°C.

Fish were acclimated for a 48hr period during which time no food items were introduced in order to standardise hunger. Individual chironomid larvae, mean length 10mm ± 1mm, were introduced into the stream section at a rate of 1 larvae every 2 minutes, until a total of 20 individual chironomids had been presented. Any uneaten prey items passed through the stream section into a waiting mesh net. All chironomids passing within one body length of the fish were categorised as being visible to the test subject and were included in subsequent analysis. The response of each individual fish to each prey item was scored as in Table 8.1 (Metcalfe *et al.*, 1986).

8.2.3 Computational methods

Prey recognition was assessed as the number of individual prey encounters required before any behavioural response (i.e. any response other than **a** – Table 8.1) to the prey was recorded. The relative short-term changes in feeding efficiency were assessed using a 'Foraging Efficiency Index' (FEI). The Foraging Efficiency Index was calculated as the cumulative total number of successful prey ingestion's per fish (**f** – Table 8.1) as a proportion of the cumulative total number of feeding attempts (**b** + **c** + **d** + **e** – Table 8.1). The foraging efficiency indices for both fish groups, at each prey encounter number, were then combined to produce a mean foraging efficiency index. A Kruskal-Wallis one-way analysis of variance was used to test for differences in the mean number of chironomids encountered prior to a behavioural response being recorded, between the 2 fish types. Regression analysis and a general linear model or F-Test was used to compare the changes in relative mean foraging efficiency of both fish types with increasing numbers of prey encountered.

Score Recorded	Response to non-living chironomid larvae passing within 1 body length of the fish
0	a) No response to the prey item
1	b) Orient towards the prey item but no approach
2	c) Turn back after moving towards prey
3	d) Move towards item but miss
4	e) Ingest prey item but subsequently reject
6	f) Ingest prey item

Table 8.1-Visual scoring system used to assess individual fishes feeding behaviour.

8.3 Results

8.3.1 Number of prey encountered before prey recognition

When feeding on non-living chironomid larvae for the first time, naïve hatchery-reared fish took a significantly longer period of exposure to the prey items than experienced wild-caught fish before any behavioural response was recorded (Kruskal-Wallis, H=36.08, d.f.=1, p<0.001(adjusted for ties))(Figure 8.1). The median number of chironomids encountered before any response to the prey item was recorded was 2.0 for experienced wild-caught fish and 9.5 encounters for naive hatchery-reared fish.

8.3.2 Relative changes in short-term feeding efficiency

The relationship between mean Foraging Efficiency Index and prey encounter number was best described for both hatchery-reared and wild conspecifics by a linear regression(Figure 8.2). Mean Foraging Efficiency Index increased significantly with successive prey encounters in both hatchery-reared and wild origin trout (Figure 8.2)(Regression: hatchery-reared, $F_{2,22}$ = 191.46, P<0.001, R^2 = 0.969; wild-caught, $F_{2,22}$ = 6.83, p = 0.018, R^2 = 0.285). However, the gradient of the regression FEI on prey encounter number was significantly smaller (i.e. closer to 0) for wild caught (gradient = 0.035; t = 2.61, p = 0.018, R^2 = 0.518) than hatchery-reared fish (gradient = 0.372, t = 13.84, p<0.001, R^2 = 0.969)(ANCOVA, $F_{1,37}$=305.96, P<0.001)(Figure 8.2). Indicating that although the foraging efficiency of both trout groups increased over the period of the experiment, the rate of improvement was greater in hatchery-reared than wild trout. Although foraging efficiency index increased fastest in hatchery-reared fish over the duration of the experiment, foraging efficiency in domestic origin trout remained significantly lower than that of wild caught fish at the end of the experiment (F-test; $F_{2,46}$ = 682.2; p< 0.001).

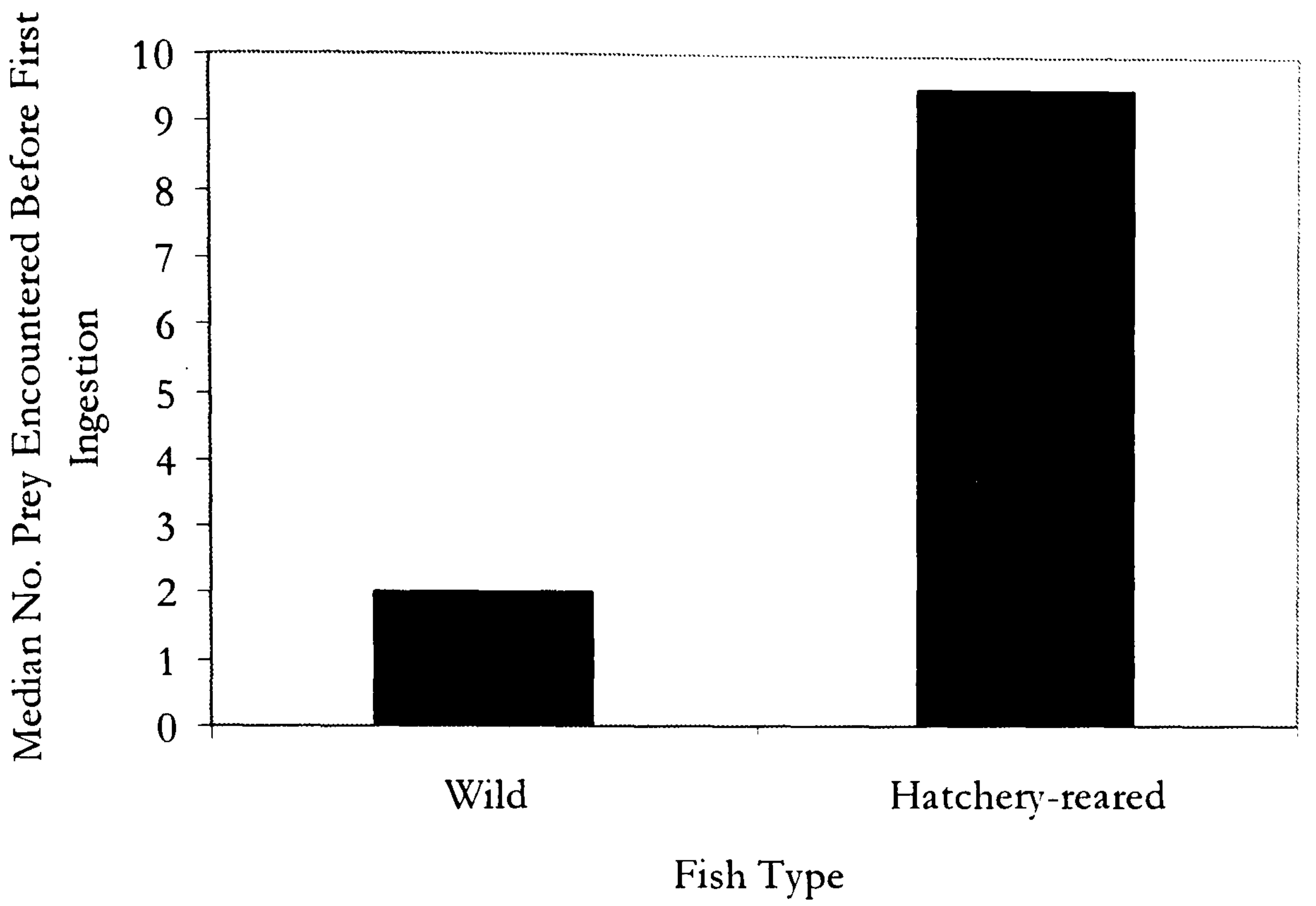


Figure 8.1 - Median number of non-living chironomid larvae encountered before a behavioural response to a prey item was recorded.

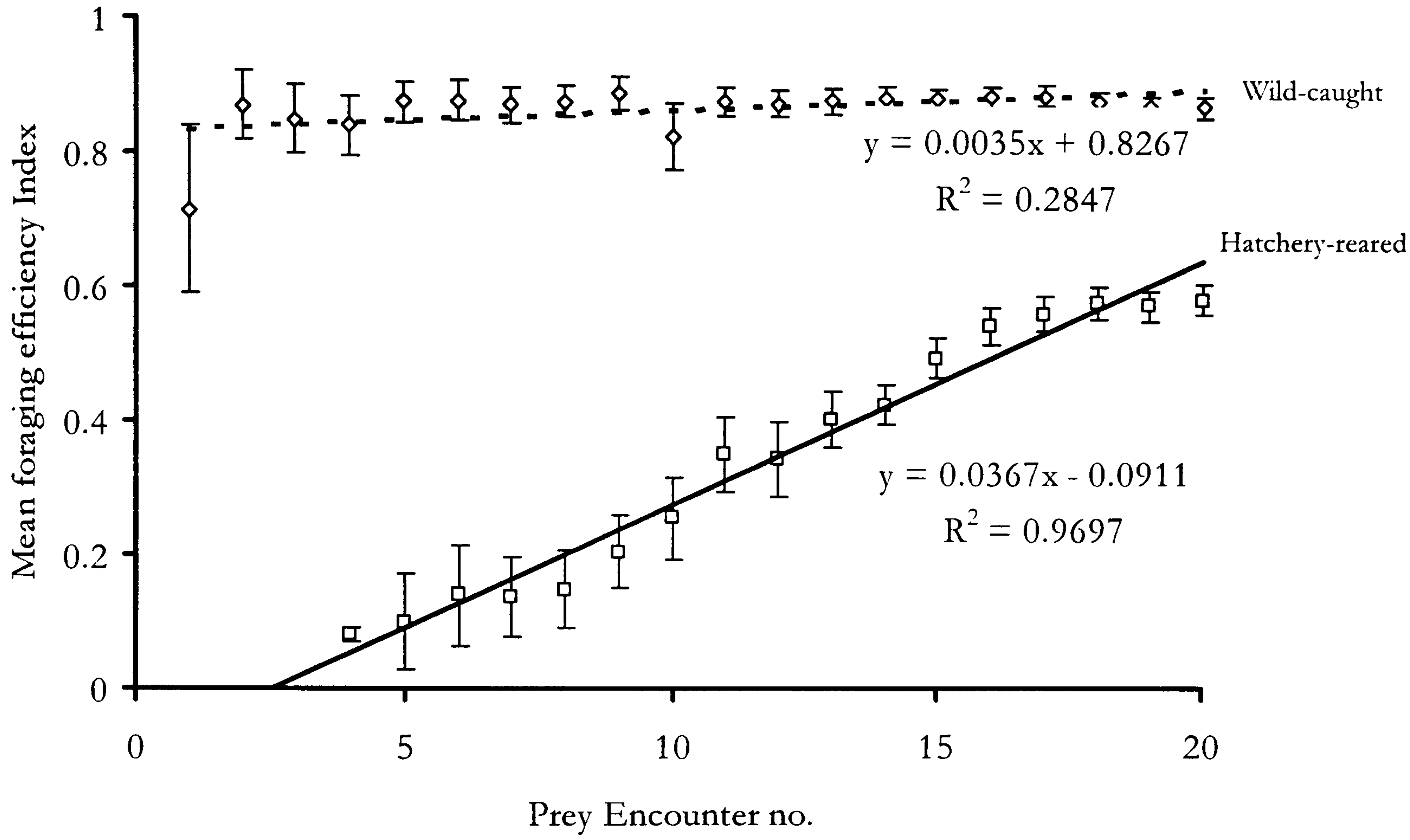


Figure 8.2 – Change in relative foraging efficiency of experienced wild-caught (◊) and naïve hatchery-reared (□) brown trout with increasing numbers of individual non-living chironomid larvae encountered. Linear regression of mean Foraging Efficiency Index of prey encountered.

8.4 Discussion

8.4.1 Number of prey encountered before ingestion

This study shows that on their first exposure to a novel prey item hatchery-reared brown trout took 4.5 times longer to recognise non-living chironomid larvae than experienced wild conspecifics. Although hatchery-reared fish initially failed to identify non-living chironomids as a prey item, the present results indicate that naïve hatchery-reared brown trout may quickly recognise unfamiliar novel prey. Thus after 9.5 exposures on average in this experiment they make feeding attempts, showing that hatchery-reared fish are learning to forage on prey items to which they have never been exposed.

It has been suggested that hatchery-reared fish may lack appropriate search images to recognise natural food (Sosiak *et al.*, 1979) and must consequently learn to recognise and forage efficiently for natural prey (Steward & Bjornn, 1990; Wiley *et al.*, 1993). Ware (1971) found that it took rainbow trout (*Oncorhynchus mykiss* Walbaum) 4 days to readily consume novel prey items; Paszkowski & Olla (1985) found hatchery-reared coho salmon (*Oncorhynchus kisutch* Walbaum) ate *Crangon* (sand shrimp) within forty-five minutes. In contrast Stradmeyer & Thorpe (1987) found naïve Atlantic salmon (*Salmo salar* L.) parr would readily consume unfamiliar prey within 4-6 seconds. Here we have shown that compared with experienced wild origin brown trout, naïve hatchery-reared brown trout require 9.5 encounters on average with a novel prey type in order to recognise its potential as a food source.

8.4.2 Relative changes in short term feeding efficiency

In this study, feeding efficiency improved markedly in hatchery-reared brown trout with increasing numbers of prey encountered. After 5 encounters with non-living chironomid prey items, hatchery-reared fish had only a 9% ingestion success rate (i.e. successful ingestion's following a feeding attempt) compared with a success rate of 83% for wild trout. However, as with prey recognition, feeding efficiency improved, with successive encounters, with foraging efficiency in hatchery-reared trout reaching 56% after 15 prey encounters compared with 88% in wild fish.

It is well documented that foraging efficiency in fishes increases with experience (Ware, 1971; Vinyard *et al.*, 1982; Ibrahim & Huntingford, 1992; Wiley *et al.*, 1993). Godin (1978) demonstrated prey capture rates in pink salmon (*Oncorhyncus gorbuscha* Walbaum) to increase with a fish's increasing experience of the prey item, and Winfield *et al.* (1983) reported an increase in successful prey captures with increasing experience in bream (*Abramis brama* L.). Although in this study, naïve hatchery-reared fish were able eventually to recognise novel prey items and were able to improve feeding efficiency, hatchery-reared fish foraging efficiency levels did not reach comparable levels with wild-caught conspecifics within the twenty, single prey encounters in the relatively simple spatial and competitive environment provided by this experiment. Ersbak & Haase (1983) commented that although hatchery-reared brook trout (*Salvelinus fontinalis* L.) adapted to natural food they were not capable of maximising the available foraging. Thus an apparent ability to adapt to natural foods does not necessarily ensure post-stocking survival, especially if the fish are not able to obtain the necessary caloric reserves to maintain their basal metabolism (Ersbak & Haase, 1983).

The underlying differences between the hatchery-reared and wild caught fish in this study could be the result of genetic variation between the 2 fish types, as the hatchery-reared fish used here have been selected for favourable domesticated rearing characteristics over many generations. Ibrahim and Huntingford (1992) however found significant differences in foraging efficiency in both hatchery-reared and wild caught three spined sticklebacks (*Gasterosteus aculeatus* L.) from the same riverine gene pool suggesting that experience rather than hereditary traits effect foraging efficiency for unfamiliar prey types. The present study supports the theory that previous experience plays a significant role in affecting foraging skills required for survival. Potentially the lag time required to acquire these skills (which are inevitably acquired following introduction to the wild) may account for the observed low survival rate of the stocked fish in some studies, particularly with reference to an increased susceptibility of hatchery-reared trout to predation.

Chapter 9

Synthesis and Summary

9.1 Introduction

Since 1950, the movement of fish from one water body to another has become a relatively large-scale activity (Hickley, 1994); however there has been little systematic examination of both its ecological and economic effectiveness (Welcomme, 1998), particularly how well stocked fish survive in, and respond to, novel environments (Hickley, 1994). The primary aim of this study was to examine the post-stocking temporal changes in the diets and dispersion of hatchery-reared brown trout released into Carron Valley Reservoir in relation to resident conspecifics. Whilst the secondary aim of this study was to directly examine the behavioural and relative feeding responses of hatchery-reared and wild brown trout maintained within an artificial stream environment. In this chapter it is intended to summarise the major findings of the study and discuss their relevance to salmonid fisheries management.

9.2 Post-stocking dietary changes in hatchery-reared brown trout

The change from artificial food to natural feeding is considered to be a critical factor influencing the post-stocking survival of hatchery-reared salmonids following release into natural environments (Ersbak & Haase, 1983; Bachman, 1984; Johnsen & Ugedal, 1989), with malnutrition being proposed as a potential result of poor post-stocking foraging efficiency (Vinyard, 1982; Ersbak & Haase, 1983; Bachman, 1984). Hatchery-reared salmonids may become conditioned to respond to physically, chemically and nutritionally uniform pelleted feeds (Ersbak & Haase, 1983; Stradmeyer & Thorpe, 1987) and consequently poor prey recognition (Steward & Bjornn, 1990) and inefficient foraging (Bachman, 1984) may contribute to the ability of hatchery-reared salmonids to adapt to natural foods. Whilst several studies have suggested that hatchery-reared salmonids have little trouble adapting to natural foods (Stradmeyer & Thorpe, 1987; Johnsen & Ugedal, 1989; L'Abee-Lund *et al.*, 1992). It has been suggested that hatchery-reared salmonids exhibit a period of poor prey recognition and foraging success immediately following release into natural environments (O'Grady, 1983; Kelly-Quinn & Bracken, 1989) potentially resulting in an initial 'look up' behavioural foraging response (O'Grady, 1983), low prey consumption (Ersbak & Haase, 1983; Bachman, 1984; Kelly-Quinn & Bracken, 1989) and an inability to maintain their overall condition. However, few field studies have examined; (1) the post-stocking temporal changes in (a) quantity of prey consumed, (b) prey preferences, (c) foraging habitat use and (d) body condition of hatchery-reared brown trout (Chapter 5); or (2) the relative differences in short-term feeding efficiency between naïve hatchery-reared and experienced wild brown trout (Chapter 8).

In this study the hatchery-reared brown trout were observed to consume significantly lower numbers and weights of prey immediately following release into Carron Valley Reservoir than simultaneously sampled resident brown trout (Chapter 5). It was also observed that, although recently stocked hatchery-reared brown trout did not adapt to natural diets immediately, their relative foraging efficiency increased over the sample period until the diets overlapped considerably with the resident trout diets (Chapter 5). Initially, the hatchery-reared trout appeared to exhibit a preconditioned 'look up' dietary response, only consuming prey that was located on or near the water surface. The dominance of the hatchery-reared trout diets by dipteran pupae indicates that the stocked fish may be unable to locate and exploit cryptic and evasive aquatic prey species as efficiently as the resident trout (Chapter 5), whilst the observed post-stocking decrease in the body condition of the hatchery-reared fish supports this theory. Although in this study naïve hatchery-reared brown trout initially failed to identify non-living chironomids as a prey item (Chapter 8); once identified as a prey item, feeding efficiency was observed to improve with the increasing number of prey encountered indicating increasing foraging efficiency with experience.

This study supports the findings of several studies in which hatchery-reared salmonids were observed to undergo a learning process in choosing food items, with prey recognition and capture rates increasing with experience (Ware, 1971; Godin, 1978; Vinyard *et al.*, 1982; O'Grady, 1983; Johnsen & Ugedal, 1989; L'Abee-Lund & Langeland, 1995). This study further supports the findings of Sosiak *et al.* (1979) and O'Grady (1983) which observed that immediately following release hatchery-reared salmonids appear to favour food items situated on or near the surface, strongly suggesting a 'look up' behavioural feeding response in recently stocked hatchery-reared salmonids.

The aim of stocking hatchery-reared brown trout into Carron Valley Reservoir is to provide a supply of catcheable sized trout which are immediately available for capture by anglers whilst improving the relative yields from stocking. Consequently, an inability to adapt to natural foraging may have profound effects on the post-stocking survival and returns to anglers of hatchery-reared brown trout. The results of this study suggest that most hatchery-reared brown trout can switch to foraging on natural foods, and that feeding efficiency improves with experience. However, the observed inability to maintain their relative body condition may indicate of an inability to maximise the use of all the available forage, maladaptive behavioural traits or that the hatchery-reared trout exceed the maximum sustainable size for Carron Valley Reservoir. The predominance of surface and sub-surface prey in the diets of the hatchery-reared trout immediately after stocking may be evidence of relatively high levels of near-surface foraging habitat utilisation, resulting in an increased susceptibility to predation by piscivorous birds. It appears therefore, that many of the hatchery-reared brown trout currently stocked into Carron Valley Reservoir may not be able to acquire the caloric reserves needed for their basal metabolism and survival.

9.3 Post-stocking dispersion of hatchery-reared brown trout

It is both ecologically and economically important for the success of stocking operations in recreational trout fisheries that hatchery-reared fish disperse rapidly and evenly from their respective stocking sites to exploit all of the available habitats (Helfrich & Kendall, 1982; Jokikokko, 1999). It has been assumed that hatchery-reared salmonids are unable to disperse quickly and evenly into all the available habitats (Helfrich & Kendall, 1982; Jokikokko, 1999); consequently stocking strategies that include the release of large numbers of fish at very few sites may have several potential economic and ecological drawbacks (Pawson, 1982). L'Abee-Lund and Langeland (1995) suggested that, whilst not conclusive, several studies have shown the 'spot' planting of salmonids results in higher overall recapture rates than 'scatter' or 'trickle' planting stocking strategies. Cresswell and Williams (1982) suggested that 'spot' planting results in higher recapture rates due to increased angling effort within the vicinity of these stockings which results in a rapid depletion of the stocked fish population. It has also been suggested that 'spot' planting may result in increased localised competition for limited food and habitat resources and a subsequent increase in susceptibility to predation (Ersbak & Haase, 1983; Bachman, 1984; McKinnell & Lundqvist, 2000). However, despite extensive stocking, the dispersal of catcheable sized, hatchery-reared brown trout into lentic water bodies has not been extensively studied in Scotland.

This study found hatchery-reared brown trout to disperse quickly from their respective release sites, although only over a relatively restricted area (Chapter 6). Individual hatchery-reared brown trout were observed to exhibit relatively high levels of activity immediately following release, during which period they covered relatively large total distances within a relatively restricted area (Chapter 6). However, after an initial period of high levels of migratory activity, this study found individually radiotagged fish to acquire residence within a relatively localised area (Chapter 6).

'Spot' planting is almost invariably used when stocking recreational trout fisheries in preference to the more labour intensive 'scatter' and 'trickle' planting strategies (Cresswell & Williams, 1982). This study suggests that some form of 'scatter'planting is required at Carron Valley Reservoir to avoid the rapid exploitation of stocked fish, to increase the potential survival of the stocked fish by reducing competition for limited resources in a confined area and to reduce the susceptibility of the stocked fish to predation by piscivorous birds.

9.4 Prior-residence, aggression and territory acquisition in hatchery-reared and wild brown trout

It has been suggested that hatchery-reared brown trout adopt different competitive strategies to wild conspecifics (Fenderson *et al.*, 1968; Bachman, 1984; Nickelson *et al.*, 1986; Swain & Riddell, 1990). Several studies have demonstrated the competitive superiority of prior-resident salmonids (Brannas, 1995; Glova & Field-Dodgson, 1995; Huntingford & De Leaniz, 1997), which may significantly effect the ability of hatchery-reared salmonids to obtain access to limited resources such as habitat and food following stocking into water bodies containing existing populations of conspecifics (Bachman, 1984). Hatchery-reared salmonids have also been observed to display higher levels of aggression than wild conspecifics, which may constitute non-cost effective behaviour and have important implications for post-stocking survival. However, few studies have considered the importance of prior-residence effects and levels of aggression on the post-stocking survival of hatchery-reared brown trout.

This study found hatchery-reared brown trout to initiate more aggressive acts and display lower specific growth rates than simultaneously stocked wild conspecifics (Chapter 7). This study also observed wild brown trout to demonstrate a competitive advantage, conferred by a brief period of residency in an artificial stream environment, over later introductions of both hatchery-reared and wild conspecifics (Chapter 7).

This study supports the findings of several studies that have observed hatchery-reared salmonids to display higher levels of aggression than wild conspecifics (Fenderson *et al.*, 1968; Bachman, 1984; Swain & Riddell, 1990; Mesa,, 1991). Bachman (1984) concluded that higher levels of aggression in hatchery-reared brown trout released into the natural environment results in fewer opportunities and less time available for feeding and consequently a reduced potential for survival. This study further supports the findings of Brannas (1995) and Huntingford and De Leaniz (1997) who observed similar competitive advantages through prior-residence in Atlantic salmon fry.

The results of this study support the suggestion that mortality in stocked hatchery-reared salmonids may be associated with their tendency to be excessively aggressive and display non-cost effective behaviour (Fenderson *et al.*, 1968; Ersbak & Haase, 1983; Bachman, 1984). They also support the concept that prior-residence confers a competitive advantage to resident stream dwelling trout populations which may further reduce the potential post-stocking survival of hatchery-reared salmonids, as they may be prevented from occupying territories affording the best access to limited resources.

9.5 Summary and management recommendations

The objectives of any stocking policies adopted at Carron Valley Reservoir are going to be a compromise between conserving and maintaining the resident populations of brown trout and powan and gaining positive economic return from the recreational fishery. Stock enhancement at Carron Valley Reservoir is required due to a combination of the continued impacts of impoundment on the reservoir ecosystem and the overexploitation of the resident brown trout population by recreational anglers. Conflicts will often occur when attempting to implement both conservation and economic fishery management strategies.

This study indicates that the current combination of regular stockings of small numbers of catcheable sized hatchery-reared brown trout, evenly distributed around the reservoir is providing an adequate balance between effective dispersal of the stocked fish whilst still retaining relatively high return rates to the anglers. However, the evidence of the prior-residence component of this study suggests that for long term survival of hatchery-reared brown trout it may be beneficial to scatter the stocks as widely as possible over the area of the reservoir in order to reduce potential competition conflicts for localised limited resources at point stocking sites. The apparent post-stocking dependence of hatchery-reared brown trout on surface and near-surface food items immediately after stocking observed in this study suggests that the stocking of hatchery-reared brown trout into Carron Valley Reservoir should be limited to the early part of the fishing season, when the relative concentrations of surface prey are high.

This study suggests that a key area of further research should be to examine the potential of pre-stocking acclimation to natural environments. Various areas of acclimation could potentially increase post-stocking survival including experience of natural food items, preconditioning to the receiving water and the installation of anti-predator responses through experience. Very few direct observational experiments have been attempted in lentic waters, however further research should also be directed at attempting to examine the behavioural interactions between hatchery-reared and wild brown trout within these environments, particularly with reference to territoriality and prior-residence.

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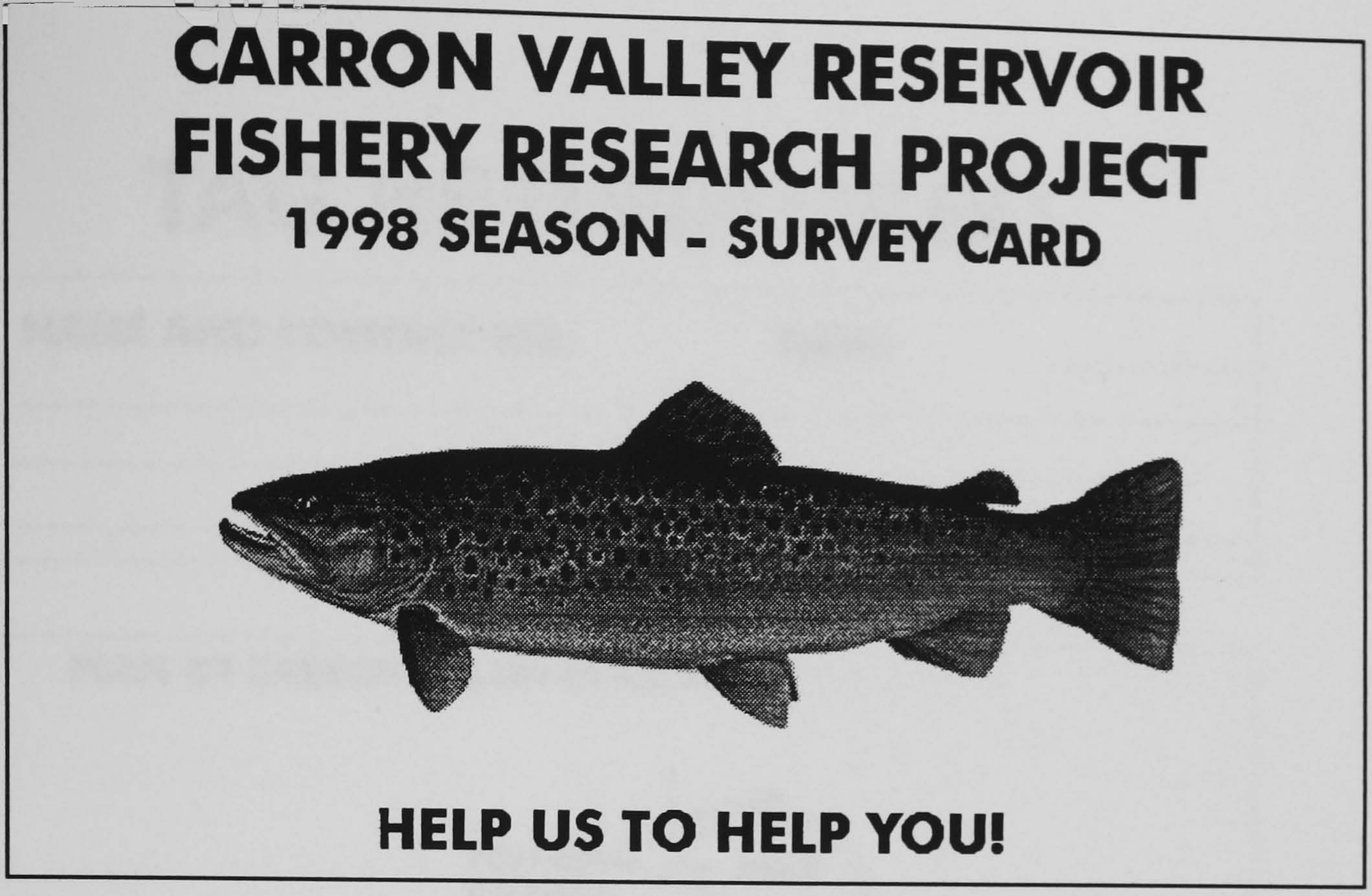
Appendices

Appendix 1

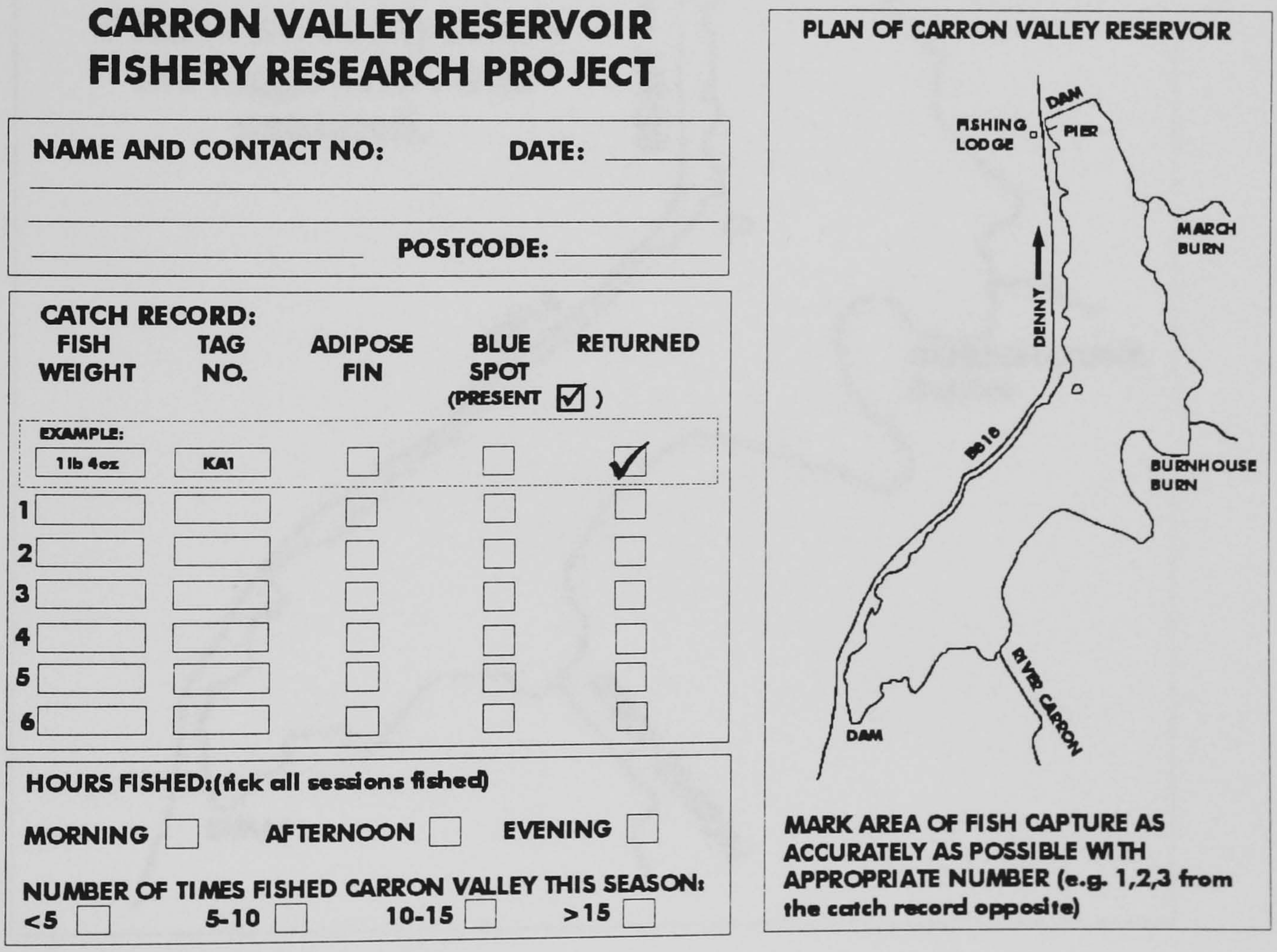
Angler survey cards used to assess the gross post-stocking dispersion of hatchery-reared brown trout at Carron Valley Reservoir during the 1998 (Appendix 1(a)), 1999 (Appendix 1 (b)) and 2000 (Appendix 1 (b)) fishing seasons.



CARRON VALLEY RESERVOIR
FISHERY RESEARCH PROJECT
1998 SEASON - SURVEY CARD

HELP US TO HELP YOU!

Front



CARRON VALLEY RESERVOIR
FISHERY RESEARCH PROJECT

NAME AND CONTACT NO: DATE: ________
____
____
______________ POSTCODE: ________

CATCH RECORD:

	FISH WEIGHT	TAG NO.	ADIPOSE FIN	BLUE SPOT (PRESENT ☑)	RETURNED
EXAMPLE:	1 lb 4oz	KA1	☐	☐	☑
1			☐	☐	☐
2			☐	☐	☐
3			☐	☐	☐
4			☐	☐	☐
5			☐	☐	☐
6			☐	☐	☐

HOURS FISHED:(tick all sessions fished)

MORNING ☐ AFTERNOON ☐ EVENING ☐

NUMBER OF TIMES FISHED CARRON VALLEY THIS SEASON:
<5 ☐ 5-10 ☐ 10-15 ☐ >15 ☐

PLAN OF CARRON VALLEY RESERVOIR

MARK AREA OF FISH CAPTURE AS ACCURATELY AS POSSIBLE WITH APPROPRIATE NUMBER (e.g. 1,2,3 from the catch record opposite)

Back

Appendix 1 (a) – Double sided A5 survey card design for assessing angler catch returns with particular reference to assessing the post-stocking dispersion of hatchery-reared brown trout during the 1998 fishing season.

TAG RETURN CARD

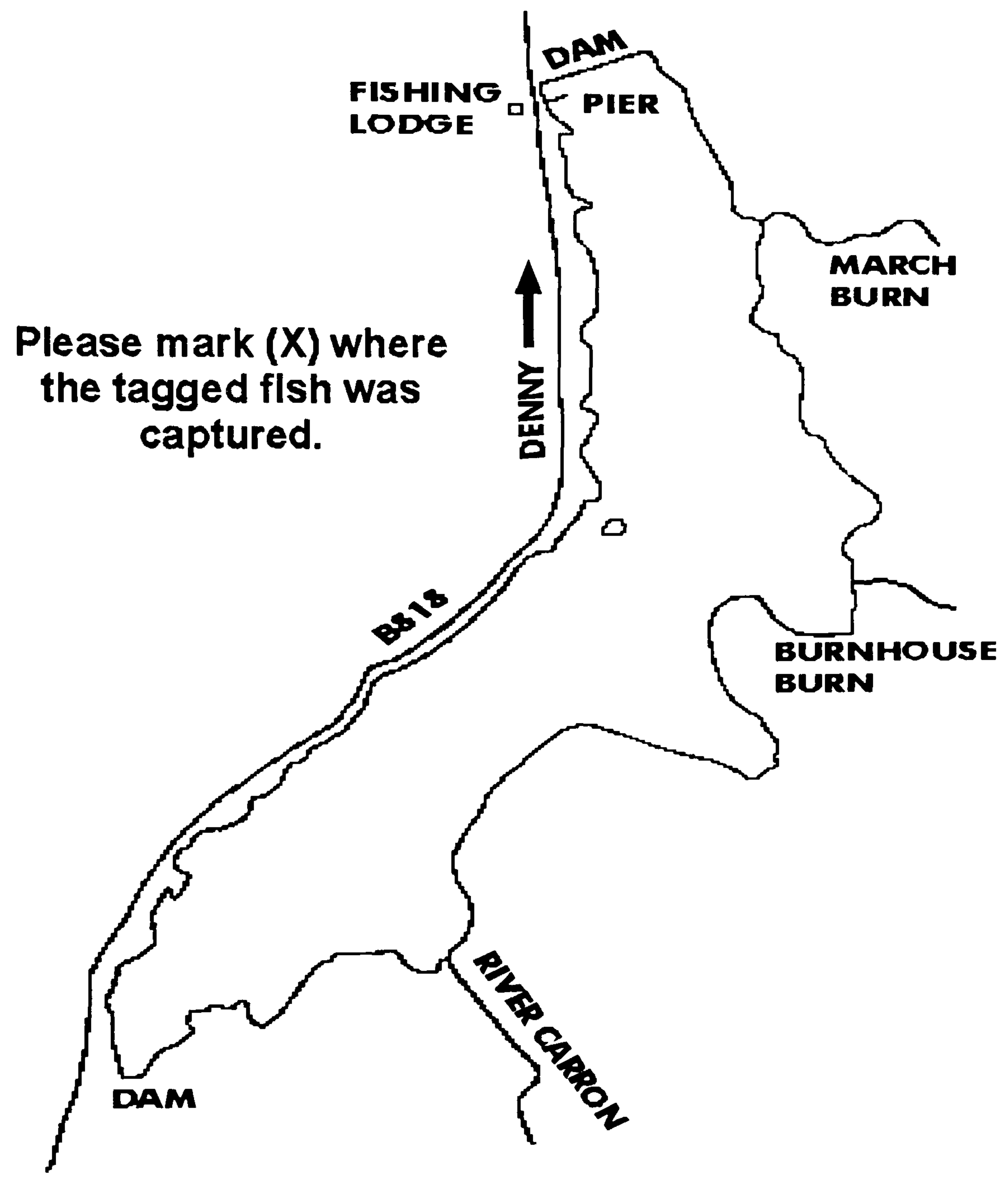
NAME AND CONTACT NO: **DATE:** ____________

____

____

________________________ **POSTCODE:** ____________

PLAN OF CARRON VALLEY RESERVOIR



Please mark (X) where the tagged fish was captured.

Thank You

Appendix 1 (b) - Simplified single sided A5 survey card, designed specifically to assess the post-stocking dispersion of "Floy' style tagged hatchery-reared brown trout during the 1999 and 2000 fishing seasons.

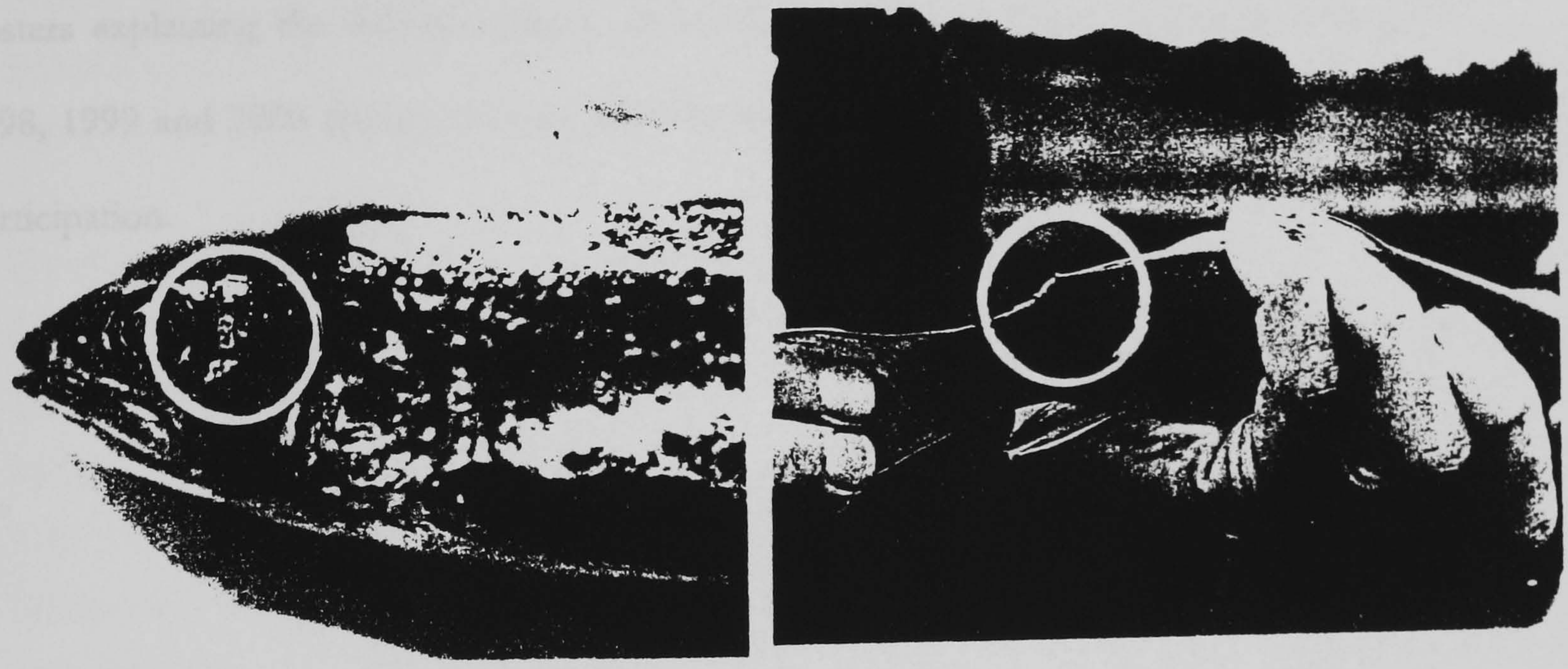
Appendix 2

Poster placed at strategic points around the Carron Valley Reservoir fishery and within the fishery boats to aid angler recognition of the VI tagged and panjetted hatchery-reared brown trout released into Carron Valley reservoir during the 1998 fishing season

WHAT AM I LOOKING FOR?

Carron Valley Reservoir contains many wild brown trout but in order to maintain the fishery some stocking is necessary. Only premium quality brown trout are used so telling the difference between the wild and stocked fish can be difficult. This season the stocked fish have been tagged in two ways to make them visible to you. Here is a quick rundown of the three brown trout groups we are interested in:

1. Tagged Research Fish
These fish will have had their adipose fin removed and a visible tag implanted behind their left eye.



2. Existing Stocked Fish
These fish will display a blue spot on their underbelly.

3. Unmarked fish
All the remaining fish without the above marks are either wild or long-term stocked fish.

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Appendix 3

Posters explaining the fishery research undertaken at Carron Valley Reservoir during the 1998, 1999 and 2000 fishing seasons, and the incentive scheme initiated to increase angler participation.

CARRON VALLEY RESERVOIR FISHERY RESEARCH PROJECT

Dear Angler,

This season we are running a project to examine the distribution patterns and returns to anglers of our stocked and wild brown trout. In order to do this we need your help.

Every angler will be issued a survey card before fishing. Please fill this in as completely as possible and return it to a member of staff at the end of your trip. This information is intended to increase our understanding of the fishery and allow us keep on improving the quality of the fishing. So please, help us to help you.

As an added bonus, every Carron Valley survey card returned will be entered into a prize draw at the end of the season. Feel free to ask the members of staff if you have any questions about the study, and keep an eye out for our resident fishery scientists (Dr. Colin Bean and Mr. James Deverill).

Many Thanks for your Help and Support

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PLEASE HELP US TO HELP YOU !

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CARRON VALLEY RESERVOIR PRIZE DRAW

Every Carron Valley fishery survey card returned this season will be entered into our prize draw. This season's prizes include:

- Six presentation bottles of Glenmorangie 10 year old, single malt whisky.
- A Scientific Anglers 'Windmaster' WF8 flyline
- A free days fishing on Carron Valley Reservoir next season

So please fill in your card and return it to a member of staff (ensuring we have your name and contact address).

PLEASE HELP US TO HELP YOU

Carron Valley Fishery Research Project supported by:

GLENMORANGIE

LEEDA

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UNIVERSITY OF STIRLING

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Appendix 4

Deverill, J.I., Adams, C.E. & Bean, C.W. (1999). Prior-residence, aggression and territory acquisition in hatchery-reared and wild brown trout. *Journal of Fish Biology* **55**, 868-875.

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Prior residence, aggression and territory acquisition in hatchery-reared and wild brown trout

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In an artificial stream environment, established wild brown trout initiated 44% of the mean aggressive acts whilst hatchery-reared trout initiated 34% and introduced wild trout initiated 22%. Established wild fish maintained home stations closer to a point source of feed than did both hatchery-reared and introduced wild conspecifics. Established wild fish were the only group to show a positive mean specific growth rate during the trials. Introduced wild fish showed a slightly negative mean specific growth rate, whilst introduced hatchery-reared fish exhibited a considerable negative mean specific growth rate. These results suggest that established wild brown trout in a semi-natural stream environment display a prior-resident effect over late introductions of hatchery-reared and wild conspecifics. Introduced hatchery-reared fish were more aggressive and exhibited a lower mean specific growth rate than simultaneously stocked wild fish, suggesting that excessive expenditure of energy for unnecessary aggression may contribute to the poor survival of hatchery-reared fish after they are stocked into streams.

Key words: behaviour; dominance; salmonid; *Salmo trutta* L.

INTRODUCTION

Stocking, transfer and introductions of hatchery-reared salmonids are used commonly to enhance recreational or commercial fisheries and to preserve or re-establish threatened populations (Cowx, 1994). The potential divergence of hatchery-reared salmonids from wild fish due to both genetic and environmental factors may have negative ecological consequences for wild populations (Swain & Riddell, 1990; Berejikian *et al.*, 1996). It has been suggested also that hatchery-reared salmonids may have competitive advantages over wild conspecifics that may contribute to the displacement of wild fish (Nickelson *et al.*, 1986). Stream dwelling salmonids seek to acquire territories that provide the best balance of energy gained from the environment and energy required for metabolism, growth and reproduction (Bachman, 1984; Fausch, 1984; Adams & Huntingford, 1996). Competition between conspecific salmonids can be intense (Huntingford & De Leaniz, 1997), consequently additional energy may be required to defend social rank or territory (Fausch, 1984). Individuals vary in their ability to acquire limited resources (Metcalfe *et al.*, 1989) and those individuals which obtain the best territories and highest social status gain greater foraging opportunities and are more likely to survive and reproduce

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(Fausch, 1984; Metcalfe *et al.*, 1995). However, the exact mechanism through which individuals gain high social status is not completely understood (Adams & Huntingford, 1996).

It has been suggested that social dominance in salmonids may be affected by size (Abbot *et al.*, 1985), behavioural fierceness (Huntingford *et al.*, 1990) and prior residence (Huntingford & De Leaniz, 1997). Levels of aggression have been associated positively with dominance ability in steelhead trout *Oncorhynchus mykiss* (Walbaum) and cutthroat trout *Oncorhynchus clarki* (Richardson) (Mesa, 1991; Berejikian *et al.*, 1996). Several authors have demonstrated the competitive superiority of prior-resident salmonids (Brannas, 1995; Glova & Field-Dodgson, 1995; Huntingford & De Leaniz, 1997). Few studies have considered prior-residence effects in brown trout *Salmo trutta* L., although Glova & Field-Dodgson (1995) showed that prior-resident brown trout acquired a greater proportion of optimal territories than did chinook salmon *Oncorhynchus tshawytscha* (Walbaum) in an artificial stream environment. Therefore, the first aim of this study was to examine if established wild brown trout in a semi-natural stream environment will demonstrate a prior-resident competitive advantage over later introductions of both hatchery-reared and wild brown trout.

Hatchery-reared Atlantic salmon *Salmo salar* L., fry display greater agonistic activity than wild fry at high population densities, with the reverse being true at low densities (Fenderson *et al.*, 1968). Swain & Riddell (1990) demonstrated that newly emerged domesticated coho salmon *Oncorhynchus kisutch* (Walbaum) fry display greater levels of aggression than wild coho salmon fry when raised under the same environmental conditions. Mesa (1991) found that hatchery-reared cutthroat trout were more aggressive than their wild conspecifics; and he further postulated that excessive expenditure of energy through unnecessary aggression might contribute to poor performance of hatchery fish after stocking. Consequently, the second aim of the present study was to determine if hatchery-reared brown trout exhibit relatively higher levels of aggression than simultaneously stocked wild origin fish.

MATERIALS AND METHODS

A total of 70 wild 2+ year class brown trout were collected on 2 June 1998 by direct current electrofishing in the lower reaches of the March Burn, Carron Valley Reservoir, Scotland. The fish were maintained subsequently in an artificial stream environment on an *ad libitum* diet of bloodworm at the Glasgow University Field Station, Rowardennan. Hatchery-reared 2+ brown trout were obtained from a domesticated strain used extensively for stocking recreational fisheries in Scotland. The fish were transported to the Glasgow University Field Station on 24 May 1998 and maintained in stock tanks on commercial pelleted trout food until required.

Three experimental replicates were caried out between July and September 1998 in an artificial stream fluvarium. Water was pumped from Loch Lomond and circulated in the artificial stream by means of a submerged motor. The stream was landscaped to provide a riffle/pool/riffle stream profile of a mixed gravel and cobble substrate. Water depths within the artificial stream ranged from 0·15 to 0·3 m. Light and temperature were ambient for 56° N, with temperature ranging from 12 to 15° C over the experimental period. Flow rates within the artificial stream ranged from 1 to 35 cm s^{-1}, depending on depth. Throughout the experiment fish were fed a continuous (24 h) supply of simulated invertebrate drift using a suspension of rehydrated freeze-dried bloodworm at a rate of 5% of the total initial trout body weight per day; thus the amount fed increased proportionally with fish density. The bloodworm suspension was introduced at a depth of 8 cm into the centre of the upstream riffle. Mesh screens at each end of the stream section prevented individual fish from moving out of the stream section.

For each experimental replicate, 12 wild brown trout (length range 87–143 mm) were measured individually for fork length (± 1 mm) and weighed (± 0·01 g). Each fish was also marked on both lateral surfaces with a unique alcian blue dye tattoo. These fish, subsequently termed prior residents, were stocked into the artificial stream resulting in a density of 3 fish m^{-2}, a density similar to that of the March Burn. After 9 days a further six wild brown trout (length range 85–122 mm) and six hatchery-reared brown trout (length range 93–133 mm) were measured, weighed, marked individually and stocked simultaneously into the pool area of the artificial stream. Increasing density to 6 fish m^{-2}, simulating a local significant increase in stocking density common in current commercial stocking practice.

Following the introduction of the second batch of 12 fish, prior-resident and introduced fish were monitored for the next 4 days. On each monitoring day, all fish were observed five times at 2-h intervals using a focal animal technique (Altmann, 1974). The position of each individual within the stream section, the distance from the point source of feed, the position across the stream width and the position in the water column were all recorded. Each aggressive interaction initiated and received [recorded as nip, chase, charge and fin display (Mesa, 1991)] was recorded for each individual over the 2-min focal animal sampling period. At the end of the experiment all fish were removed from the artificial stream section, identified individually, measured and weighed, and their specific growth rate (G) calculated as:

$$G=(\ln W_2-\ln W_1)(t_2-t_1)^{-1}$$

where W_1 and W_2 are initial and final weights on days t_1 and t_2, respectively.

Aggression initiated and received, home range size, distance from the point source of feed and specific growth rate were used to assess differences in territory acquisition and aggression between the three brown trout groups (prior-resident wild, introduced wild and introduced hatchery-reared). The distance from the point source of feed was calculated as the distance between the feed tube and each individual's home station (to the nearest 10 cm); the home station was defined as the stream position at which an individual was present on >40% of the total observations. The home range was calculated as the area in which an individual was found on >80% of the total observations. A Kruskal–Wallis one-way analysis of variance revealed no differences in the aggression initiated and received, the home ranges or the home stations between the experimental replicates for prior-resident wild fish, introduced wild fish or introduced hatchery-reared fish; therefore the data from the three replicates were pooled for subsequent analysis. The pooled data were tested for normality, and consequently examined using a Kruskal–Wallis one-way analysis of variance (adjusted for ties).

RESULTS

Prior-resident wild fish initiated 44%, hatchery-reared 34% and introduced wild fish 22% of the total aggression (Fig. 1). There was a significant difference in the number of aggressive acts initiated by each of the three groups (Kruskal–Wallis, $H=4{\cdot}88$, d.f.$=2$, $P=0{\cdot}027$). Prior-resident wild fish initiated significantly more aggressive acts than did later stocked introduced wild or hatchery-reared fish (Kruskal–Wallis, $H=7{\cdot}08$, d.f.$=2$, $P=0{\cdot}029$); whilst introduced hatchery-reared fish initiated significantly more aggressive acts than did introduced wild fish (Kruskal–Wallis, $H=4{\cdot}38$, d.f.$=1$, $P=0{\cdot}036$). There was no significant difference in the number of aggressive acts received by each of the three fish groups (Kruskal–Wallis, $H=3{\cdot}33$, d.f.$=2$, $P=0{\cdot}189$).

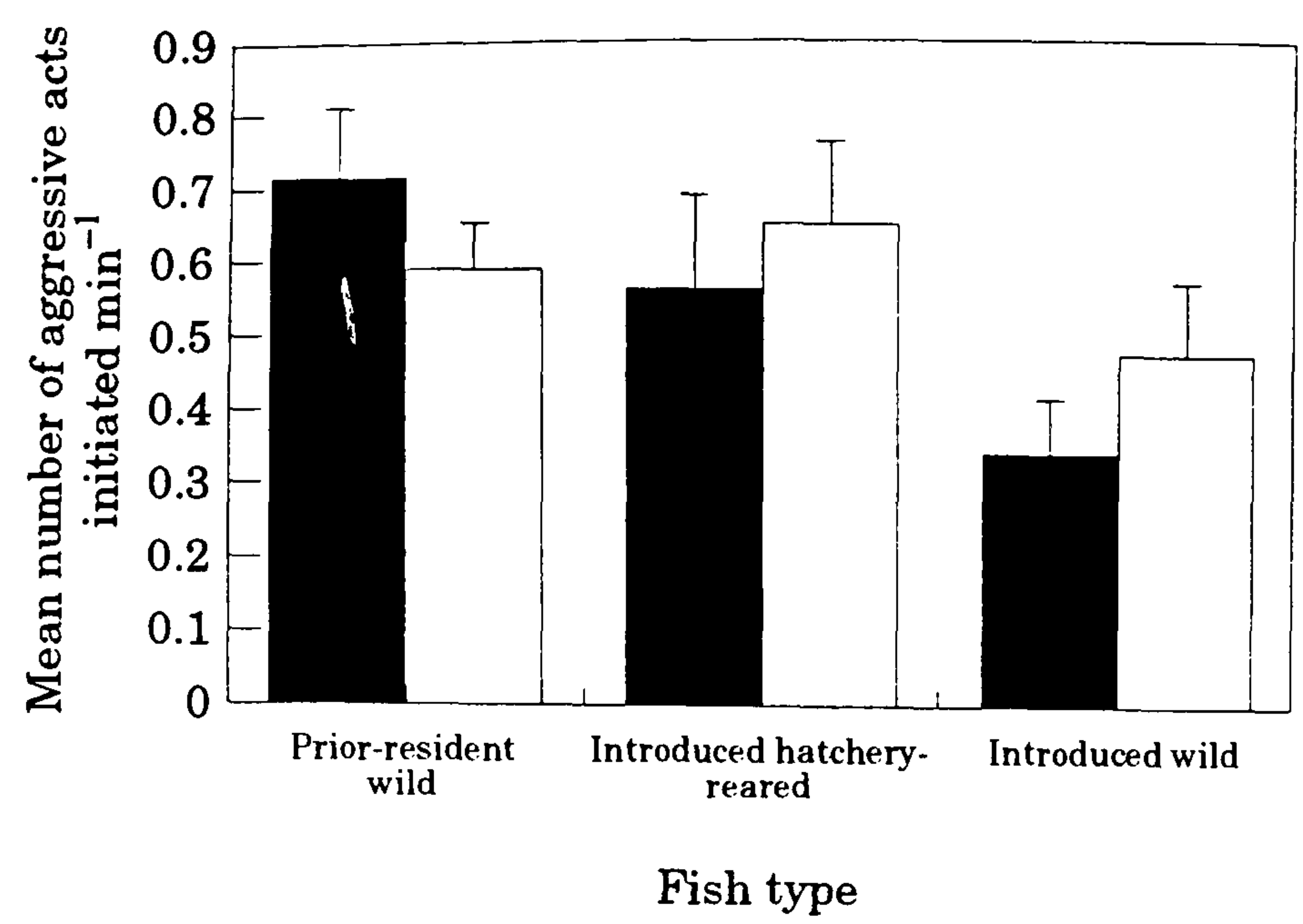

FIG. 1. Aggressive behaviour of prior-resident wild, introduced wild and introduced hatchery-reared brown trout expressed as the mean number (± S.E.) of aggressive acts initiated (■) and the number of aggressive acts received (□).

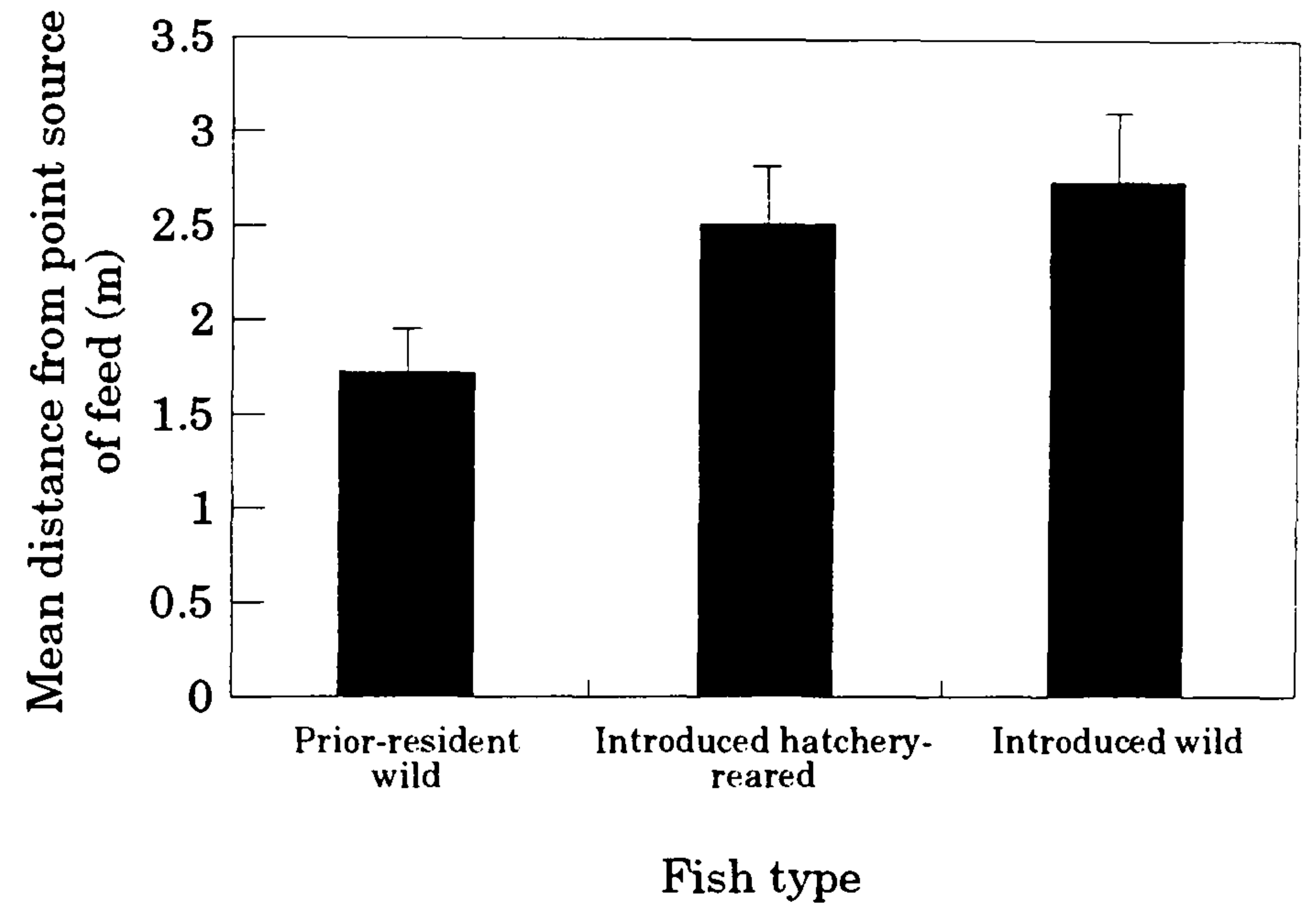

FIG. 2. Mean ± S.E. distance of the home station from the point source of feed of prior-resident, introduced wild and introduced hatchery-reared brown trout.

To examine differences in territory acquisition between the three fish groups, the mean distance of the home station from the point source of feed (Fig. 2) and the mean home range (Fig. 3) were calculated for each fish group. Mean distances from the point source of feed differed significantly between the three fish types (Kruskal–Wallis, H=7·12, d.f.=2, P=0·028). Prior-resident wild fish occupied home stations that were significantly closer to the point source of feed than were both hatchery-reared and introduced wild fish groups (Kruskal–Wallis, H=7·15, d.f.=2, P=0·026). However, introduced hatchery-reared and introduced wild fish occupied similar home stations that were at not significantly different distances from the point source of feed (Kruskal–Wallis, H=0·01, d.f.=1, P=0·985). Although, there was an apparent tendency for prior-resident wild fish to maintain larger home range areas than did both categories of

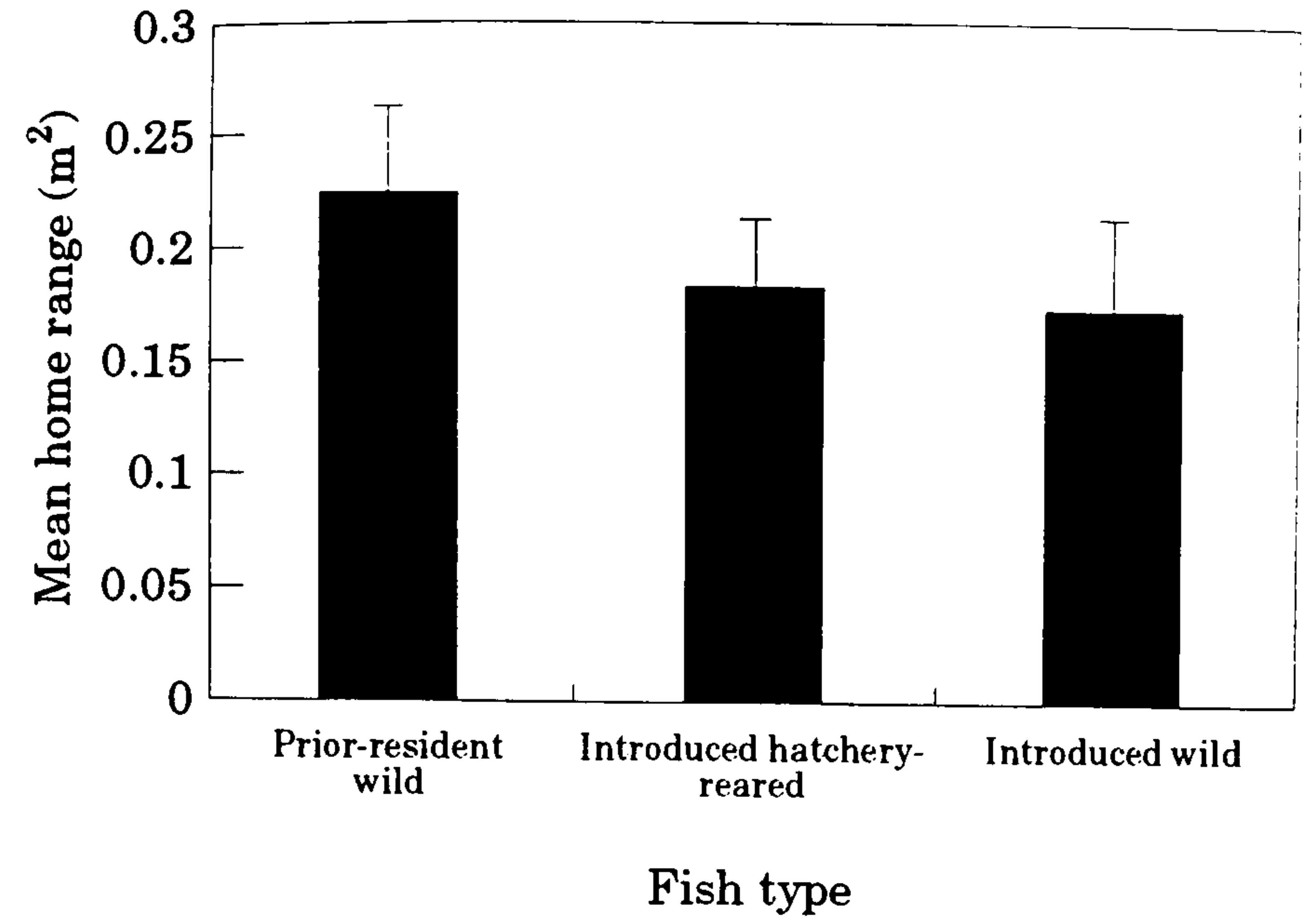

FIG. 3. Mean ± S.E. home range size of prior-resident wild, introduced wild and introduced hatchery-reared brown trout.

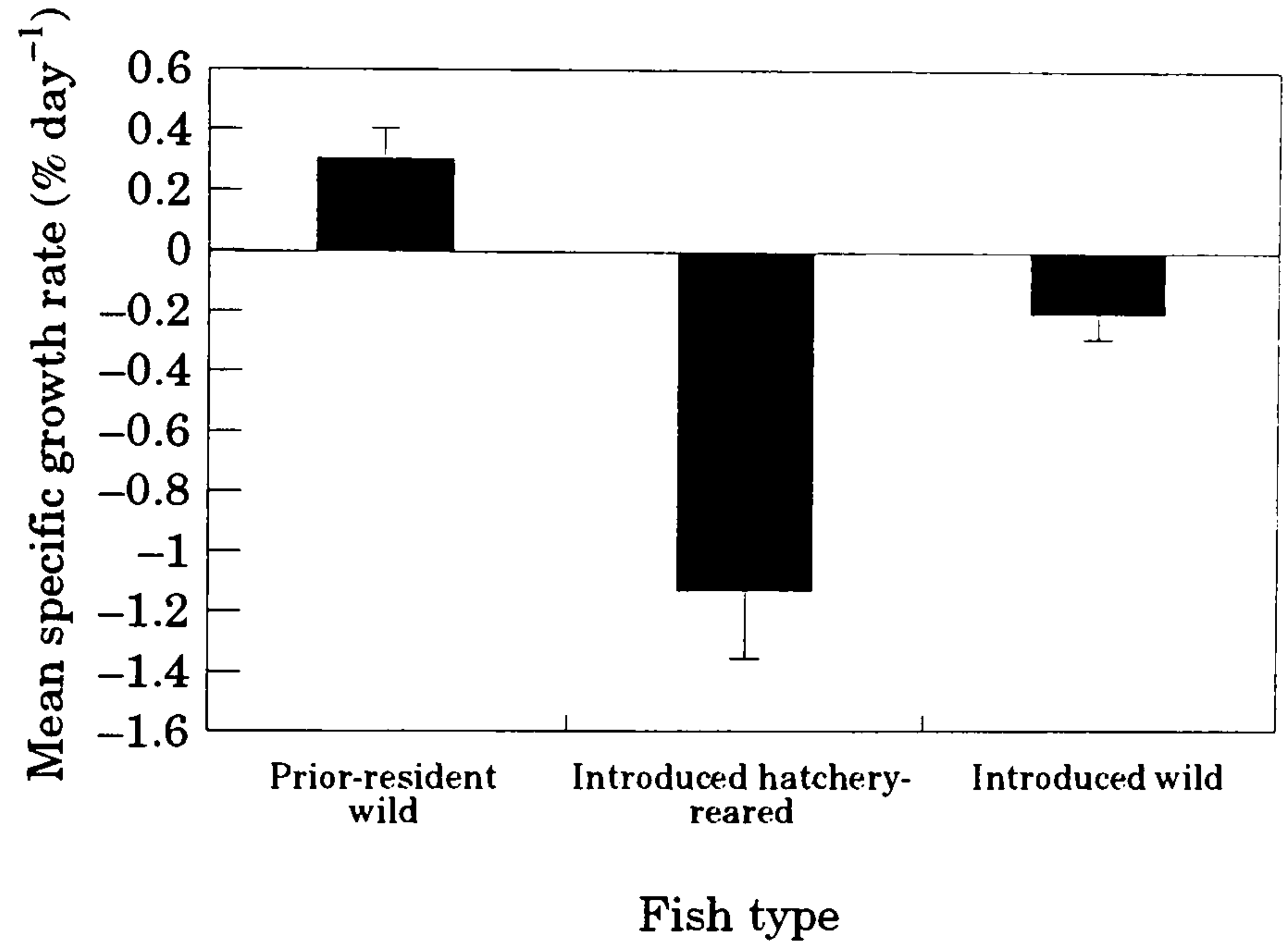

FIG. 4. Performance of prior-resident wild, introduced wild and introduced hatchery-reared brown trout expressed as mean specific growth rates+S.E..

introduced fish, this difference was not significant (Kruskal–Wallis, $H=0·01$, d.f.=2, $P=0·997$).

Relative performance differences between the three fish types was assessed by comparing the specific growth rates (Fig. 4). Specific growth rates differed significantly between the three fish types (Kruskal–Wallis, $H=36·41$, d.f.=2, $P=0·001$). Prior-resident wild fish were the only group to show a positive mean specific growth rate during the three trials. The specific growth rate of this group was significantly higher than those of either the introduced hatchery-reared or introduced wild fish (Kruskal–Wallis, $H=29·95$, d.f.=2, $P=0·000$). Amongst the introduced fish groups specific growth rates differed significantly (Kruskal–Wallis, $H=10·02$, d.f.=1, $P=0·002$), introduced hatchery-reared fish having a larger negative mean specific growth rate indicating greater weight loss than had introduced wild fish.

DISCUSSION

A general feature of stream salmonids is that dominant fish occupy the most cost-effective territories and initiate a large proportion of a population's aggressive interactions (Symons, 1970; Glova & Field-Dodgson, 1995). In this study, wild brown trout, stocked into a previously empty habitat, demonstrated a competitive advantage, conferred by a brief period of residency, over later introduced conspecifics. These established wild fish initiated more aggressive interactions, maintained home stations closer to a point source of feed and exhibited a higher relative mean specific growth rate than did later introductions of hatchery-reared and wild fish. Brannas (1995) and Huntingford & De Leaniz (1997) demonstrated similar effects in newly emergent Atlantic salmon fry showing that early arriving (prior-resident) individuals establish and maintain territories over later arriving individuals.

It has been suggested that behavioural differences between hatchery-reared and wild salmonids may be due to genetic and morphological divergence in hatchery-reared populations (Swain & Riddell, 1990; Berejikian *et al.*, 1996). This effect might, in principle, be responsible for the observed competitive advantage of the established wild fish over later introduced hatchery-reared fish. This is considered unlikely since there were significant differences in the initiated aggression rates and home station positions of the established wild fish and the later introduced wild fish. These differences suggest that the initially stocked wild fish are defending and maintaining home stations closer to the limited food resource (point source of feed) through a prior-resident competitive advantage.

In this experiment, hatchery-reared fish initiated significantly more aggressive acts and displayed a lower mean specific growth rate than did simultaneously stocked wild fish. This supports the observations of Fenderson *et al.* (1968), Swain & Riddell (1990) and Mesa (1991), who found hatchery-reared salmonids to be more aggressive than wild conspecifics when stocked simultaneously into a variety of environments. The observed higher levels of aggression in the introduced hatchery-reared fish relative to simultaneously stocked introduced wild fish may constitute non-cost-effective behaviour and may contribute towards the significantly lower mean specific growth rate. Bachman (1984) suggested that non-cost-effective behaviour such as high levels of aggression and poor territory acquisition in hatchery-reared salmonids results in fewer opportunities and less time available for feeding and may result consequently in the poor growth and survival of these fish. The observed relative differences in competitive strategies between the later introduced hatchery-reared and wild fish may be a consequence of the different competitive rearing environments (Huntingford & De Leaniz, 1997). A lack of visual isolation and a need to adopt scramble feeding strategies in hatchery environments may lead to an increase in aggressive feeding behaviour in hatchery-reared salmonids (Wang & White, 1994). In contrast, stream environments produce structured social hierarchies where wild fish develop adaptive flexibility in aggressive behaviour, resulting in reduced levels of aggression; which may constitute an energy conserving advantage (Mesa, 1991). The relatively large decrease in mean specific growth rate observed in the later introduced hatchery-reared fish may have been influenced also by a change from high energy commercially-produced diets to relatively less energy-dense natural foods (Sosiak, 1982), or by an initial period of acclimation to unfamiliar natural food items (Wang & White, 1994).

This direct behavioural study has demonstrated that established wild brown trout in a semi-natural stream environment do display a prior-resident effect over later introductions of both hatchery-reared and introduced wild conspecifics. This supports other studies which have also demonstrated prior-residence effects over later introductions of hatchery-reared and wild conspecifics in cutthroat trout (Wang & White, 1994), Atlantic salmon (Brännäs, 1995) and brown trout (Glova & Field-Dodgson, 1995). It was also demonstrated that hatchery-reared fish initiated more aggressive interactions but exhibited relatively poorer growth than did simultaneously stocked wild fish. This supports the hypotheses of Bachman (1984) and Mesa (1991) who suggested that non-cost-effective behaviour in hatchery-reared salmonids may have important implications on post-stocking survival and consequently existing and future stream stocking programmes.

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