



BSc. HONOURS DEGREE

IN

Biosciences

Trophic Status and Ontogeny: An Analysis of Brown Trout (*Salmo trutta*, L.1758)
Growth and Diet in Wester Ross, Scotland

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DECLARATION

I, Sara Mamo, hereby declare that "*Trophic status and Ontogeny: An Analysis of Brown trout (Salmo trutta, L.1758) growth and diet in Wester Ross, Scotland*" is my own work and was carried out in accordance with the regulation of Middlesex University. Furthermore, all the sources I have used or quoted have been acknowledged by means of complete references.

Sara Mamo

Abstract

A very common practice in studies on fish feeding is to determine the diet of the species by an analysis of stomach contents. The diet and growth of brown trout, *Salmo trutta* was undertaken by the methods of numerical, stomach analysis and scale-reading.

The diet composition of 23 0+ brown trout (*Salmo trutta* L. 1758) captured in June 2010 in Loch Coire na h-Airigh and Loch Feur, Wester Ross, Scotland was examined. All 23 trout stomachs contained food although fullness varied between individuals. Each age class of fish consumed significantly different prey taxa. Total of 563 different and similar aquatic and terrestrial invertebrates were found in the stomachs of the fish sampled, but diet was mainly composed by aquatic invertebrates. The most consumed prey items were caddis larvae. Although this study did not set out to examine parasite loads, 5 trout were found to contain intestinal parasitic worms.

Diet analysis shows that older trout eat much the kind of animals as younger fish but take a greater variety of bottom living organisms, both larvae and adult. On the whole, stomach analysis indicated that older trout feed more surface food of aquatic origin and small trout have also eaten surface food of aquatic origin. Trout are generally considered as opportunists or generalists but trout can only select food from what is available. In some trout stomach, vegetables, such as grass have found as trout whose stomach is not full is likely to attempt to feed if it sees an object with the visual characteristics of a food animal causing random feeding. There was considerable dietary overlap between the trout fish which implies that they compete with each other. In each trout size class, the prey item size class of highest frequency was 5-10mm, the second most frequent in every size class were the <5mm prey and >10mm were the least frequent prey item.

Scale analyses combined with back-calculation showed that trout growth was slow compared with other populations examined in the literature. Potential influences, including: nutrient availability, intraspecific competition, prey size, temperature, genetic adaptation, spawning, prey handling time, size of the loch and parasite are discussed. Growth analysis shows that there was diet overlap between each size class. Most of the overlap lies between 120mm and 140mm, with <120mm being the greatest area for this. Overlap decrease as the fish gets bigger.

Keywords: gut content, scale analysis, brown trout, salmotrutta

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CHAPTER I: INTRODUCTION

1.1. Salmonids

The salmonids may be considered a phylogenetically primitive group as they lack the high degree of specialization evident in higher teleost groups, for example, the percomorph fishes (Moyle and Cech 1988). The salmonids may also be considered as a relatively plastic group and within a species; a number of distinct genetic races or stocks may be evident. As a result, nomenclature has been somewhat problematic and a number of name changes have been made in the past few decades. Recently, native North America trout of the genus *Salmo* were included with the Pacific salmon and the once familiar scientific name *Salmo gairdneri* for rainbow trout is now only of historical interest (Pennell and Barton 1996, Stearley and Smith 1993). Salmonids seem to be able to adapt rapidly to local conditions by choosing the life strategy which is the most advantageous (Hogasen 1998).

Salmonids are generally considered as opportunists or generalists (Hynes, 1970, Hunt & Jones, 1972) since they are unselective on prey. However, the predatory activity of the brown trout (*Salmo trutta* L.1758) cannot be considered simply proportional to the environmental density of the prey, as shown by Ware (1972) for rainbow trout. Since the diet of fish often changes with body size (Elliott 1967, Werner & Gilliam 1984) and in salmonids older fish shift their preferences towards larger prey (Fochetti *et al.*, 2008).

The brown trout which distributed naturally across Europe was introduced successfully into at least 24 countries outside Europe over a span of less than 90 years (1852-1938) and status of brown trout changed from that of a European species to that of a global species (its plasticity of form and behaviour that it is able to adapt to so many different areas.) (Elliot 1994). This species is exploited whenever it is distributed and as renewable resource it has importance for sport and commercial fishing and aquaculture at the international level (Bagliniere and Maisse 1999, Arslan 2007).

Brown trout is a species of great interest because it is prized by anglers and has high economic value. The study of its feeding habits is one of the basic ways of understanding its biology. The analysis of its diet, apart from indicating its trophic requirements, provides with indirect information about how it feeds, its possible interaction with other species (competition, predation), and also the manner in which it occupies its habitat (Smith *et al.*,

1993). In addition, a study of its diet gives information about the amount of energy consumed by brown trout (Elliott 1994) and when food becomes a limiting factor, aiding in stock management (Oscoz *et al.*, 2005).

The brown trout is a highly successful, polytypic species exhibiting a range of quantitatively complex life cycles (Elliott 1994). These can be simplified into four typical strategies. In the first and simplest, the trout remain in their natal stream for life, growing slowly and achieving only small size. The second involves migration of 1 + or 2 + parr from the natal stream to the parent river and the mature adults do not return until they are ready to spawn (García De Jalón 1985). The third and fourth life cycles are exhibited by trout that migrate as smolts to a lake or to the estuary or sea. The first year of life is a period of rapid growth for the trout. Consequent associated changes in diet due to an increase in gape size and the ability to handle larger prey, and improved locomotory skills increasing potential for migration, account for considerable ontogenetic change early on in the trout life cycle (Grey 2001).

1.2. Trout diet and feeding

Trout are carnivorous. Most of the animals it eats are aquatic; a few are terrestrial. The aquatic invertebrates on its food list are usually insects, molluscs and crustaceans. The insects may be either aquatic for the whole of their lives, as are water boatmen (Corixidae) and beetle (Coleoptera), or only in their nymphal or larval and pupal stages - the adult hatching (emerging) from the nymph or the pupa to become a terrestrial insect- as are the mayflies (Ephemeroptera), stoneflies (Plecoptera), alder-flies (Neuroptera), dragonflies (Odonata) and two-winged flies (Diptera) (Elliott 1994). Trout feed on all stages of all these insects. The aquatic molluscus eaten are snail (Gastropoda) and the small pea mussels (Lamellibranchiata). The remaining aquatic invertebrates which the trout eats are worms including bristle worm (Oligochaeta), flatworms (Turbellaria) and leeches (Hirudinea). Vertebrates found in the food are mainly fish, sometimes frogs and newts and their tadpoles. The terrestrial organisms found in trout stomach are mostly insects and include many kinds of Diptera, some aphids and tree bugs (Hemiptera), and some land beetles (García De Jalón 1985). Animals such as earthworms, slugs, woodlice, spiders and even mammals (mice) are eaten by trout in time of high water, particularly when rivers are in flood.. Weed fragments, moss capsules, etc., found in trout's stomachs are probably taken while catching animals. Trout from a Welsh lake, however, have been recorded as containing semi-digested water plants (Frost & Brown 1967). The stomach of one caught in River Brathay was full of *Nostoc*,

a round gelatinous alga-perhaps the fish had mistaken it for a mollusc, which *Nostoc* closely resembles in appearance (Tippets & Moyle 1978).

As trout grows older, it tends to become more of a food seeker, probably because it spends more time in pools and quiet waters, but the habit of feeding on what is brought by the current, either in mid-water or on the surface, persists throughout its life (Elliott 1994). Older trout eat more surface food of aquatic origin, such as caddis flies, blackflies, mayflies and etc. A trout whose stomach is not full is likely to attempt to feed if it sees an object with the visual characteristics of a food animal (Frost & Brown 1967). The artificial wet fly is sometimes intended to resemble in shape and size an organism on which trout are feeding but by working his flies, the angler increases resemblance by giving them the movement which is so important in stimulating the trout to feed. The dry fly usually has a much closer resemblance to the natural food animal than the wet fly and the angler does not usually give it movements so this implies that visual characteristics are important in the trout's recognition of this food. Some food animals, such as the freshwater limpet attached to its stone, seem to show little or no movement and must be recognised by some other attribute. It seems that sometimes trout will only feed when they see objects conforming to a detailed and specific visual pattern while at other times they will chase any object, regardless of its shape, provided that it is moving (Frost & Brown 1967, Tippets & Moyle 1978).

Adult of aquatic insects are eaten at the surface of the water at certain times of year. Trout living in lakes seem to feed less on this type of food than do those in rivers, probably because there are greater numbers of these insects per unit area in rivers than in lake (Elliott 1967). Moreover a river's flow tends to concentrate this food, which may be dispersed widely over a lake. If there is a very heavy hatch, as during the emergency of the mayfly *Ephemera* on a lake, the numbers may be sufficient to form local concentrations which certainly attract the trout. In rivers aquatic insects are more varied in species and more numerous than in lakes, so the season for surface feeding is longer because the time of emergence of the various species may cover many months. There will thus nearly always be some fly on the water to encourage surface feeding. Surface feeding on terrestrial insects varies greatly from water to water. It seems to be least frequent in waters where there is a relatively rich bottom fauna, such as Blagdon Lake (Frost & Brown 1967). When floods in rivers or the filling up of reservoirs make terrestrial animal such as earthworms, slugs and caterpillars available, these are eaten avidly by the trout regardless of the poverty or abundance of the aquatic fauna. The diet of trout in lakes may include planktonic crustaceans, water fleas, particularly the cladocerans *Daphnia* and (*Bosimina*, and occasionally a few copepods such as *Cyclops*

and *Diaptomus*. Zooplankton has been recorded from trout in many British lakes, in Norway, and elsewhere (Elliott 1970, 1997).

According to Frost & Brown (1967), trout in Windermere eat minnows when they are spawning in May in the lake and the inflowing River Brathay; they also feed heavily on elvers when these run up the River Leven into the lake. The gorges themselves in char egg in November but do not attack the spawning fish. Trout eat fish only when they have reached a certain size, but this size varies from place to place. Thus in Windermere, trout less than 12 inches long seldom eat fish, but fish usually form a large part of the diet of larger trout. Large trout are often accused of cannibalism (Montori 2006). There is no doubt that trout do sometimes eat trout; but the word cannibal is often used to describe eating fish of any species, so the extent of this habit is often overestimated (Montori 2006).

1.3. Food supply and growth of trout

The seasonal cycles in the growth of wild trout have sometimes been attributed to the different amounts of food either present or eaten during the different seasons. These cycles also occur, however, in hatchery ponds where there is no shortage of food. There appear to be no lack of food in nature either. Low temperature seems to have little effect on the feeding of trout (Björnsson *et al.*, 2001). They will take a lure when the water temperature is 4°C and have been found with full stomachs when the temperature has not exceeded 3°C (Gadomski and Caddell 1991). Since digestion is slower at low temperature, the frequency with which fish refill their stomach is likely to be less in winter. Even though there is plenty of food available, digestion, assimilation and growth are all slower because the water is colder in winter than in summer (Frost & Brown 1967).

Trout grow better in hard water than in soft water. The growth of trout differs as between river and lake, between reaches of any one river and between hard and soft waters and it is common practice to attribute these differences to the quantity and quality of food animals present (Degerman 2000). Considering the food supply in the different waters, especially the main source of the trout's food, the bottom fauna, in the hope that some generalisations may emerge about the part played by food supply in determination rates of growth (Elliott 1994). Trout which spend all their lives in running water seldom grow as fast as those living in lakes with similar geological surroundings or water chemistry: the lake trout spend only one, two or at most three years in streams before moving into still water (Gomoiu, 2004). The obvious examples of this according to Frost & Brown (1967) in the Lake District are the trout in Raise Beck and in Three Dubs Tarn while in Wales there is the same contrast

between trout in Llyn Tegid and the nearby River Rhydwen. Trout grow remarkably well in man-made lakes when these are newly filled. This growth is certainly related to the unusual food supply (which includes terrestrial animals such as earth-worms). It seems likely that a lake usually produces less bottom fauna per unit area than a river and therefore less trout food (Degerman 2000).

Topographically, a lake can be divided into the littoral zone down to about six feet, the sublittoral zone, from six to forty feet deep, and the profundal zone below this. In most lakes where trout are found, the littoral zone has a stony substratum, though it may be sandy; the sublittoral is usually muddy, but may be gritty and sandy near its upper limit; the profundal zone has a muddy bottom. Reliable data on the actual numbers of animals per unit area in these zones and on different types of substratum are difficult to find and many studies allow only to obtain an idea of the relative proportions of the different kinds of animals. According to Frost & Brown (1967), investigation of stomach contents (Gut content analysis has been a standard technique to investigate diet and trophic relationships in fish species (Hyslop 1980) shows that most of the food comes from the shallow littoral and sub littoral zone; these produce the greatest number and weight of invertebrate animals and these animals are those most available to the feeding trout. Thus the store of food in a lake will depend largely on the amount of shallow water. A lake with a large area of shallow water, especially if this stony rather than muddy, will produce more trout food than a lake with only a narrow littoral zone (Elliott & Jenkins 1972). The shallow area is also the place where rooted plants and mosses grow and these provide another substratum supporting invertebrate animals and making this area even more productive for trout food (Degerman 2000).

1.4. Age and growth determination

The age of fish can be told by analysing its scale (Martinson 2000). The scales of a fish are its most obvious external feature. They form protective armour. Embedded in a thick and tough layer of dermis, with the outer parts of the scales overlapping those underneath, they form an effective protection against injury (Musk 2006). The free edges of the scales are covered by thin, almost transparent layer of outer skin (epidermis). This provides some protection against fungal spores, bacteria or larval parasites which might lodge under the scales. The outer skin also contains cell which produce mucus, or slime, conspicuous feature of fishes. It has several functions, it lubricates the body as fish swim and also lubricates scales as they slide over each other when a swimming fish flexes its body. Swimming makes demands on the size and shape of scales. Generally they are relatively small and rounded, the fastest swimming fish often having the smallest scales. Scales at the front of a fish's

body are usually the largest as this is the part of the body which flexes least when the fish is swimming (Frost & Brown 1967, Schneider *et al.*, 2000).

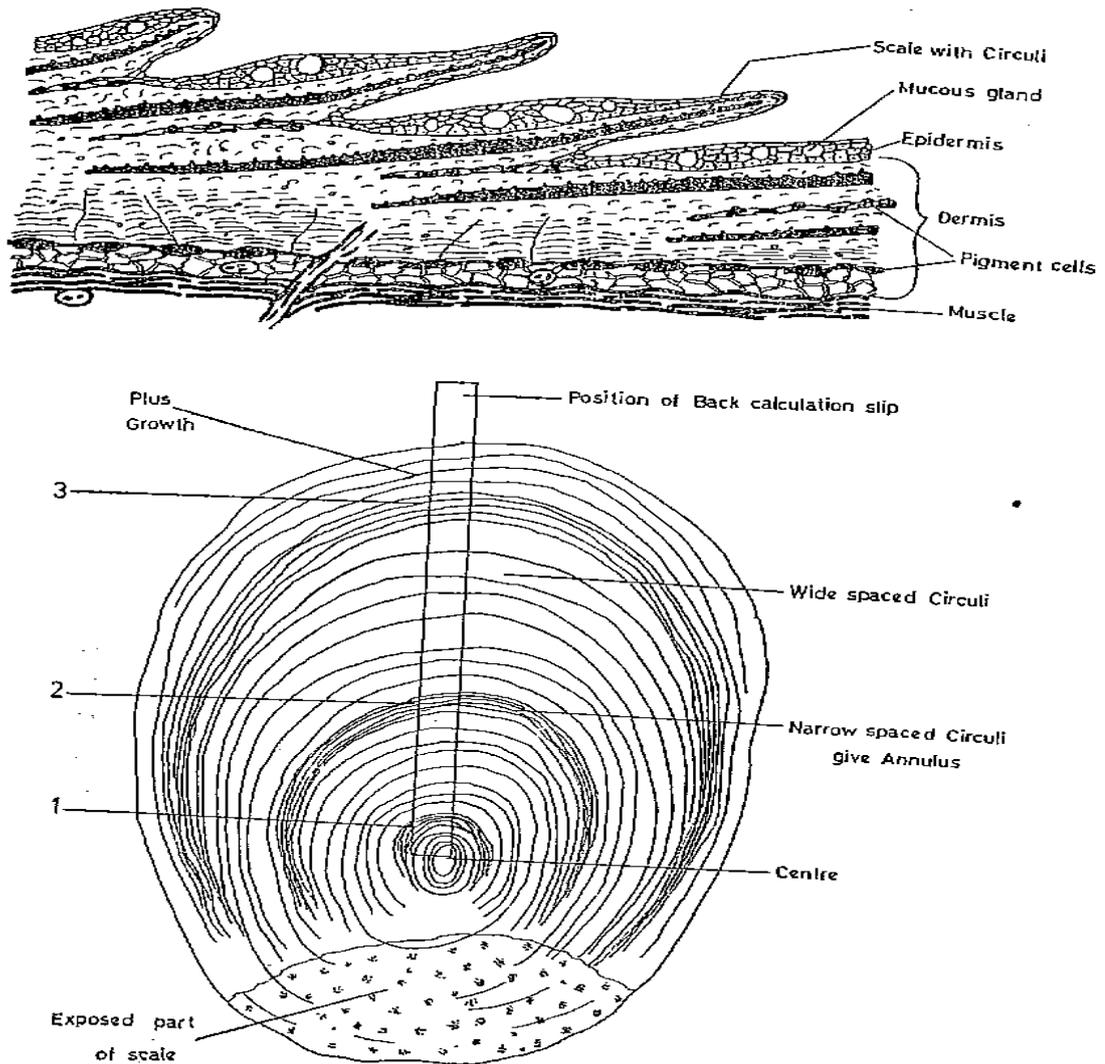


Fig 1. Above, section through the skin of a trout showing scales in pockets of the dermis. Below, diagram of a scale. The circuli are widely spaced in summer, narrowly spaced in winter, the latter giving the winter band, usually called annulus. Diagram from Frost & Brown (1967).

Fish scales are of great practical use to a fisheries biologist for the record the life history of the fish (Schneider *et al.*, 2000). Just as a tree trunk, when cut in cross section, reveals tree rings, varying in width the growing conditions of each year; so a fish scale a ring or Annulus representing each year of the fish's life (Sire and Akimenko, 2004).

Thus the age of brown trout can be told by counting the winter bands, each year of growth being represented by the zone or band of the narrowly separated circuli laid down in the winter (Schneider *et al.*, 2000). The increase in length each year made by the fish is found by measuring the width of each summer plus winter band (the annual growth) and

using the measurements for calculating the length of the fish at the end of each winter. The circuli are therefore the fundamental units on which the scale method of determining age and growth is based. In Windermere, K.R. Allen found that the percentage of fish with wide circuli at the edge of the scale rose in February, was greatest in May and June (in one year July-August), began to fall in July to August and was lowest in January (Lotze 2007).

The trout is naked when hatched. Scale papillae appear when the fry is about 2.6 to 3.0cm long and the scales themselves appear when the fish is about 3.5cm so that by 4.1-4.5cm there may be one to three circuli on each of them (Schneider 2000). The scales show first along the lateral line of the fish, then spread dorsally and ventrally above and below, the region posterior to the dorsal fin being the first to be so colonised. In spite of this, scales used for age determination are usually taken from the area just in front of the dorsal fin. The circuli stand up as dark hills alternating with light valleys when seen by transmitted light. They may extend wholly round the scale, but the majority end at the junction of the anterior and posterior parts of the scale, some circuli do not extend so far but are cut off at the shoulder. The circuli are widely or narrowly spaced and normally a group of the one type is succeeded by a group of the other (Sire and Akimenko 2004).

It is possible, however, to use the scale to determine not only the age (in year) but also the growth made by the fish during each year of its life, trout's history (Elliott 1997, Kingsford and Atkinson 1994). This determination, often referred to as back calculation, means that the growth of the scale is correlated with the growth in length of the body and thus the amount of scale growth made by the end of the first, second, etc. winter band is interpreted in terms of length attained by the fish at the end of its first, second, etc. winter (Cheung *et al.*, 2007, Frost & Brown 1967). This use of the scale for calculating the amount of growth in length made each year by the fish is based on the assumption that the scales, once acquired, are present throughout life and that their numbers remain constant, and that the increase in size of the scale is proportional to the increase in size of the fish (Schneider *et al.*, 2000, Ericksen 1999). Calculating from the scale of the annual length attained by the fish can be obtained than is found by using the scale for age determination only. It is therefore a most useful tool (Ericksen 1997). The scales of some spawning trout look as though they have been worn down at the margin. This is usually termed erosion, a term which suggests that the wearing away is the result of the some mechanical agency. As this is not the case, Crichton's term absorption is preferable. This absorption of the scale is definitely associated with spawning of the fish, and varies considerably in its extent (Frost & Brown 1967). It begins at the posterior end and often only affects this part, but many extend any distance from here to the apex of the scale. Sometimes the surface of the scale is also absorbed. After spawning,

renewed growth forms the spawning mark which looks like a scar or a blur on the scale surface (Frost & Brown 1967).

Scale of salmon and sea trout typically show spawning marks but those of brown trout do so very unusually (Judy 1961). Frost & Brown (1967) points out that scales from the large quick-growing trout of Lough Derg may show considerable absorption but those from the small slow-growing fish of nearby Lough Atorick show none; in the River Liffey the scale of the trout, whether quickly or slowly growing, show no absorption at all. Thus although the presence of a spawning is positive evidence of sexual maturity, the absence of the mark is no proof that trout is a maiden fish. There are certain difficulties in using scales for age and growth determinations (Ericksen 1999). If a trout loses some scales for any reason, they are replaced, but the replacement scale has a centre of scar tissue and the normal circuli appear round this. The extent of the central scar depends on the size of the fish when the new scale grew. Only perfect scales give a full recorded (Ericksen 1999).

1.5. *Plasticity and Genetic control of fish growth*

The growth of most fish is indeterminate. Sexually mature individuals do not have a characteristic adult size. This is in contrast to animals with a determinate growth pattern exemplified by many insects, birds and mammals. Given suitable environmental conditions, most fish continue to grow throughout life, although the rate of growth does tend to decline with age. Beverton (1992) has argued that it is better to describe the growth pattern of fish as asymptotic in contrast to those vertebrates whose growth stops abruptly when sexual maturity is reached. Some mammals such as whales, show asymptotic growth.

Major characteristic of fish growth is its flexibility. The same species may show different patterns of growth in different environments, with sexual maturity being reached at different sizes or at different ages. The weights of five years old brook trout from lakes in the Canadian Rocky Mountains ranged from 65g in Temple Lake to 1751g in Lake Patricia (Donald *et al.*, 1980). These differences were correlated with the density of amphipods, a major food item. Within a population, fish born in different years can show different growth patterns. In Windermere, UK, perch born in 1959 grew more slowly and had a smaller asymptotic size than perch in 1968 (Craig 1987). The analysis of the genetic of growth in fish is made difficult by the flexibility of their growth patterns and the sensitivity of growth to myriad environmental influences, including social interactions (Purdom 1993). Heritability gives an estimate of the contribution of genetic factors, relative to environmental factors, to the variation shown by a phenotypic trait (such as growth) in a population at a given time. In its narrow sense, heritability is the proportion of the total variance in the trait that is due to

additive genetic variance (Falconer 1989). It quantifies the extent to which phenotypes are determined by genes transmitted from the parents. It takes values from 0 (no genetic contribution) to 1 (no environmental contribution). Heritability for body weight is low in juvenile Atlantic salmon and rainbow trout.

1.6. *Predation and competition*

Predation and competition pose important effects on fish community structure, at least in certain system (Steele 1997). To maintain the equilibrium and dynamic of any ecosystem, both predation and competition play vital role and these two events interact in complex ways in fish communities and thereby produce novel community dynamics (Steele 1997). These interactions arise mainly in the ways. Firstly, the mere presence of predators can greatly affect habitat use by prey species. Secondly, both growth rates and predation on a species vary with body size and therefore change during ontogeny. Thirdly, the above factors interact to cause ontogenetic niche shifts in most fish species and such shifts can even change the sign of the interaction between two species. Predation can dramatically influence aquatic communities, both directly and indirectly. By removing prey, predators directly alter community specie (Cooke and Philipp 2009). The study of fish food webs is thus essential for the ecosystem approach to fisheries (Banaru *et al.*, 2009).

1.7. *Aims and objectives*

The aim of this study is:-

- To determine Loch Coire na h-Airigh and Loch Feur brown trout diet by analysis of stomach contents.
- To analyse the possible changes in diet between the different age classes of individuals of brown trout in Loch Coire na h-Airigh and Loch Feur.
- To evaluate the extent of dietary overlap and similarity in prey selection that occurs between size class and loch.
- To use scale back-calculation methods to determine the age, life history and rate of growth of the trout from which they were taken.
- To compare data from this study with past studies and thus place its findings in a wider context.

CHAPTER II: Materials and Methods

2.1. Study area

The study lochs were Loch Coire na h-Airigh and Loch Feur located at NG 804 784 in Wester Ross in North-West Scottish Highlands; a geologically unique and ancient landscape of hills and lochs. There are hundreds of remote lochs in the hills that support populations of wild brown trout and they are one of keystone species within the aquatic systems of Wester Ross. (Cunningham 2007).



<http://getamap.ordnancesurvey.co.uk/getamap/frames.htm> (NG8078).

Map 1. Map indicating the location of sampling sites, Loch Coire na h-Airigh and Loch Feur in the North-West of Scotland, Wester Ross.



Fig 1. Loch Coire na h-Airigh in Wester Ross, where 21 brown trout collected. Photograph by Dr. Steve Kett, in 2010.

2.2. Fish diet analysis (gut contents)

Trout specimens were provided by Wester Ross Fisheries Trust and were examined as part of the Loch Maree Wild Trout Project.

Total length (fork length to nearest mm) and fresh weight of the individual specimens were measured. Trout stomachs were removed and placed in 70% ethanol and refrigerated at 4°C. All food items in the stomachs were identified under a dissection microscope to the most lowest taxonomic level feasible, i.e., genera, whenever possible (Fischer and Bianchi 1984; Lin 1992). Where identities prey was uncertain they were listed as 'unidentified'. Total number and frequency of occurrence of each prey item were recorded

and all were measured to the nearest mm. Proportions of diet items were calculated expressed as a percentage of frequency of occurrence (F) (Hyslop 1980).

$$a_{xy} = \frac{2 * \sum_{i=1}^s X_i * Y_i}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2}$$

Equation 1: Diet overlap coefficient calculation

Where X_i and Y_i are proportions of food items i in fish X and Y

A diet overlap coefficient was used to calculate similarity of diet composition of every trout with every other trout in the sample (equation 1). Mean overlap between different size classes was used as an overall measure of competition for resources.

2.3. Age analysis via Scale reading

A total of 23 brown trout were collected, 21 from Loch Coire na h-Airigh (LCA) and 2 from Loch Feur (LFE) on 17 of July 2010.. Scales were taken from the trout's un-dissected shoulder behind the dorsal fin and above the lateral line. Scales were soaked in water for one minute and were rubbed gently between two sheets of damp tissue paper to remove residual epidermis. Soaked scales were put onto a slide, a few drops of water were added and a cover-slip used to keep them moist and flat. Each scale was examined under a binocular dissecting microscope with an eyepiece graticule and feature of circuli, annulus, plus growth, and visible scale were found. Trout age was established by counting scale rings or annuli. Replacement scales were recognized by the fuzzy, semi-opaque texture of the scale centre and rejected because they are useless for full age determination.

2.4. Back calculation

Back-calculations were carried out using a linear regression model (equation 2) developed by Fraser-Lee (1920), which assumes that first length is directly proportional to scale radius (Dahl 1909).

$$L_i = c + (L_c - c) * (S_i / S_c)$$

Equation 2: The Fraser-Lee Back-calculation model

Where, i = age at the time of annulus formation,
 c = length of fish at the onset of scale formation,
 L_T = fish length at capture,
 L_i = fish length at time of annulus formation
 S_T = scale radius at capture, and
 S_i = scale radius at time of annulus formation

Scales were measured from the focus to the first annulus (S_a), first to second annulus (S_b), second to third annulus (S_c), third to fourth annulus (S_d) and so on and then from the last annulus to the edge (S_e) (the so-called 'plus growth') (*Table 1*). Annuli were interpreted to give an ideal of the fish's age, its growth rate and whether and how often it has spawned.

CHAPTER III: Result

3. Description

Scale annulus data give estimates of trout length at each of its 'birthdays' (Table 1, 2, 3). All trout stomachs contained food although fullness varied between individuals. Total of 563 different and similar aquatic and terrestrial prey items were found (*Appendix 1*). Although this study did not set examine parasite loads, 5 trout were found to contain intestinal parasitic worms.

Table 1. Using trout scale annuli to back-calculate lengths at each year of its life using the Fraser lee Equation.

| Scale radius at <i>i</i> th yr → | Si 0+ | Si 1+ | Si 2+ | Si 3+ | Si 4+ | Si 5+ | Sc | |
|--|------------|-------|-------|-------|-------|-------|----|-------------|
| Fish | Frklgth mm | 0+ | 1+ | 2+ | 3+ | 4+ | 5+ | Total width |
| LFE 23 | 105 | 10 | 10 | 5 | | | | 25 |
| LCA 14 | 115 | 5 | 10 | 5 | | | | 20 |
| LCA 9 | 118 | 10 | 15 | 5 | | | | 30 |
| LCA 21 | 118 | 9 | 9 | 4 | | | | 22 |
| LFE 22 | 130 | 10 | 15 | 5 | | | | 30 |
| LCA 3 | 120 | 10 | 15 | 5 | 5 | | | 35 |
| LCA 10 | 124 | 10 | 12 | 12 | 6 | | | 40 |
| LCA 6 | 125 | 10 | 10 | 10 | 3 | | | 33 |
| LCA 12 | 125 | 7 | 9 | 8 | 2 | | | 26 |
| LCA 1 | 130 | 10 | 10 | 10 | 6 | | | 36 |
| LCA 5 | 130 | 9 | 10 | 8 | 3 | | | 30 |
| LCA 19 | 130 | 7 | 6 | 7 | 5 | | | 25 |
| LCA 17 | 134 | 10 | 9 | 7 | 4 | | | 30 |
| LCA 20 | 134 | 7 | 8 | 8 | 2 | | | 25 |
| LCA 8 | 135 | 12 | 8 | 6 | 4 | | | 30 |
| LCA 7 | 137 | 10 | 10 | 8 | 2 | | | 30 |
| LCA 11 | 140 | 9 | 11 | 7 | 3 | | | 30 |
| LCA 16 | 150 | 8 | 10 | 5 | 3 | | | 26 |
| LCA 13 | 129 | 10 | 12 | 5 | 5 | 3 | | 35 |
| LCA 18 | 159 | 10 | 8 | 7 | 5 | 3 | | 33 |
| LCA 4 | 165 | 7 | 8 | 8 | 7 | 3 | | 33 |
| LCA 2 | 180 | 15 | 10 | 5 | 5 | 5 | | 40 |
| LCA 15 | 249 | 10 | 10 | 8 | 7 | 4 | 3 | 42 |
| | | | | | | | | |
| Length @ 1st scale = | 35 | 'Sc' | | 19 | | | | |

Table 2. Cumulative scale annulus radius widths scale radius at *i*th year

| | | Cumulative scale annulus radius widths | | | | | | |
|----------------------------------|------------|--|-------|-------|-------|-------|-------|-------------|
| Scale radius at <i>i</i> th yr → | | Si 0+ | Si 1+ | Si 2+ | Si 3+ | Si 4+ | Si 5+ | Sc |
| Fish | Frklgth mm | 0+ | 1+ | 2+ | 3+ | 4+ | 5+ | Total width |
| LFE 23 | 105 | 10 | 20 | 25 | | | | 25 |
| LCA 14 | 115 | 5 | 15 | 20 | | | | 20 |
| LCA 9 | 118 | 10 | 25 | 30 | | | | 30 |
| LCA 21 | 118 | 9 | 18 | 22 | | | | 22 |
| LFE 22 | 130 | 10 | 25 | 30 | | | | 30 |
| LCA 3 | 120 | 10 | 25 | 30 | 35 | | | 35 |
| LCA 10 | 124 | 10 | 22 | 34 | 40 | | | 40 |
| LCA 6 | 125 | 10 | 20 | 30 | 33 | | | 33 |
| LCA 12 | 125 | 7 | 16 | 24 | 26 | | | 26 |
| LCA 1 | 130 | 10 | 20 | 30 | 36 | | | 36 |
| LCA 5 | 130 | 9 | 19 | 27 | 30 | | | 30 |
| LCA 19 | 130 | 7 | 13 | 20 | 25 | | | 25 |
| LCA 17 | 134 | 10 | 19 | 26 | 30 | | | 30 |
| LCA 20 | 134 | 7 | 15 | 23 | 25 | | | 25 |
| LCA 8 | 135 | 12 | 20 | 26 | 30 | | | 30 |
| LCA 7 | 137 | 10 | 20 | 28 | 30 | | | 30 |
| LCA 11 | 140 | 9 | 20 | 27 | 30 | | | 30 |
| LCA 16 | 150 | 8 | 18 | 23 | 26 | | | 26 |
| LCA 13 | 129 | 10 | 22 | 27 | 32 | 35 | | 35 |
| LCA 18 | 159 | 10 | 18 | 25 | 30 | 33 | | 33 |
| LCA 4 | 165 | 7 | 15 | 23 | 30 | 33 | | 33 |
| LCA 2 | 180 | 15 | 25 | 30 | 35 | 40 | | 40 |
| LCA 15 | 249 | 10 | 20 | 28 | 35 | 39 | 42 | 42 |
| First scale length (mm) = | | 35 | 'Sc' | | | | | |

Table 3. Trout at *i*th year

| Li 0+ | Li 1+ | Li 2+ | Li 3+ | Li 4+ | Li 5+ | Age (+) |
|--------|---------|---------|----------|-------|-------|---------|
| 63.000 | 91.000 | 105.000 | | | | 2 |
| 55.000 | 95.000 | 115.000 | | | | 2 |
| 62.667 | 104.167 | 118.000 | 2+ trout | | | 2 |
| 68.955 | 102.909 | 118.000 | | | | 2 |
| 66.667 | 114.167 | 130.000 | | | | 2 |
| 59.286 | 95.714 | 107.857 | 120.000 | | | 3 |
| 57.250 | 83.950 | 110.650 | 124.000 | | | 3 |
| 62.273 | 89.545 | 116.818 | 125.000 | | | 3 |
| 59.231 | 90.385 | 118.077 | 125.000 | | | 3 |

| | | | | | | | |
|----------|----------|----------|----------|----------|----------|-----------|---|
| 61.389 | 87.778 | 114.167 | 130.000 | | | | 3 |
| 63.500 | 95.167 | 120.500 | 130.000 | | | | 3 |
| 61.600 | 84.400 | 111.000 | 130.000 | 3+ trout | | | 3 |
| 68.000 | 97.700 | 120.800 | 134.000 | | | | 3 |
| 62.720 | 94.400 | 126.080 | 134.000 | | | | 3 |
| 75.000 | 101.667 | 121.667 | 135.000 | | | | 3 |
| 69.000 | 103.000 | 130.200 | 137.000 | | | | 3 |
| 66.500 | 105.000 | 129.500 | 140.000 | | | | 3 |
| 70.385 | 114.615 | 136.731 | 150.000 | | | | 3 |
| 61.857 | 94.086 | 107.514 | 120.943 | 129.000 | | | 4 |
| 72.576 | 102.636 | 128.939 | 147.727 | 159.000 | 4+ trout | | 4 |
| 62.576 | 94.091 | 125.606 | 153.182 | 165.000 | | | 4 |
| 89.375 | 125.625 | 143.750 | 161.875 | 180.000 | | | 4 |
| 85.952 | 136.905 | 177.667 | 213.333 | 233.714 | 249.000 | | 5 |
| 0 | 1 | 2 | 3 | 4 | 5 | Yr | |

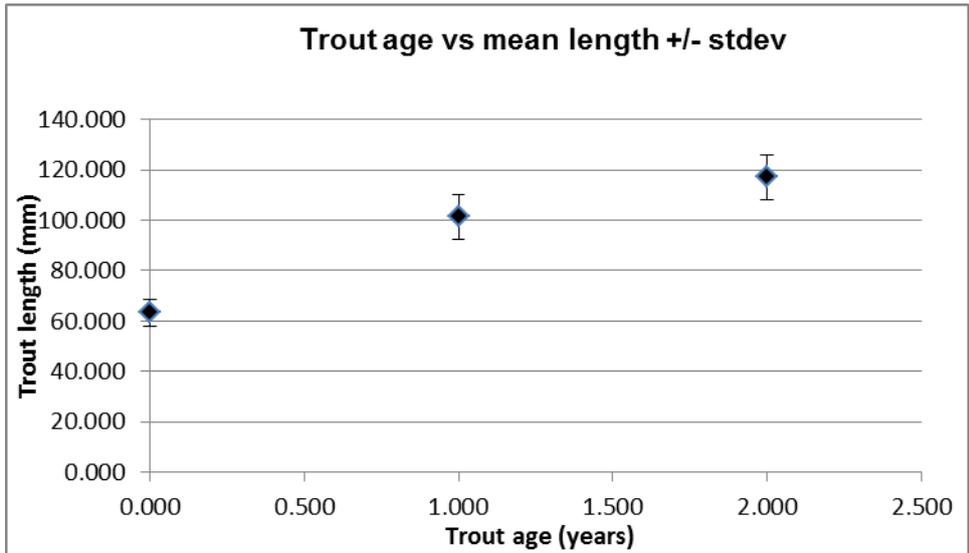
Table 3. shows the length (in mm) of brown trout that grown at each year by using the Fraser Lee Equation.

Table 4. Trout gut contents by taxon and length (mm)

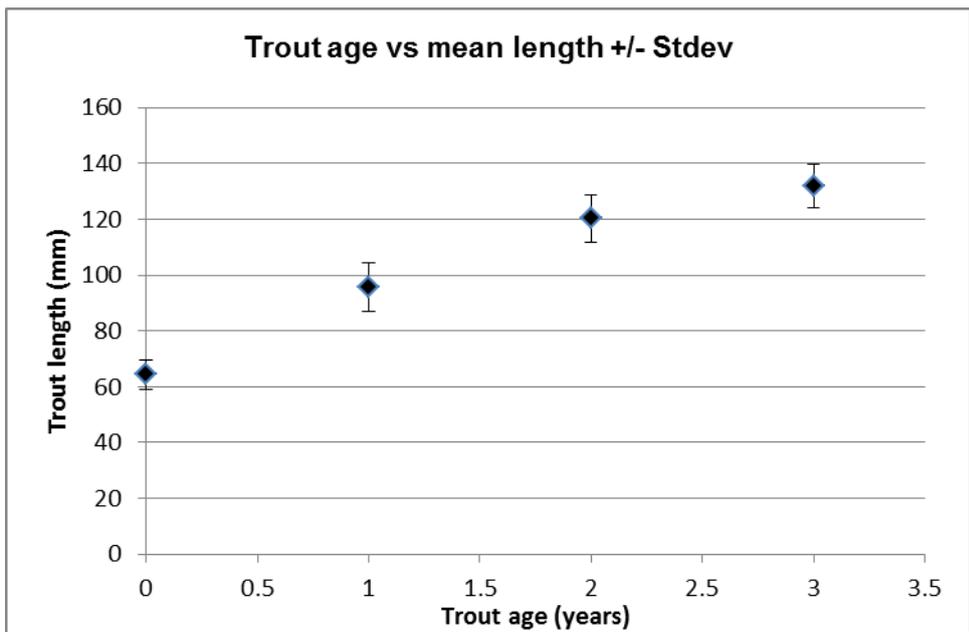
| <i>Diet item <5mm</i> | <i>Diet item 5-10mm</i> | <i>Diet item 10+mm</i> |
|--------------------------|-------------------------|------------------------|
| caddis case | Odonata nymph | Odonata nymph |
| caddis larva | Ephemeroptera | Ephemeroptera |
| caseless caddis larva | caddis case | alderfly |
| Crane fly larva | caddis pupa | stonefly |
| blackfly pupa | caddis larva | caddis case |
| Beetle | caseless caddis larva | caddis pupa |
| F/W mite | Ceratopogonid larva | caddis larva |
| Ostracod | Chironomid larva | caddis fly |
| Cyclopoid copepod | Culicoides larva | caseless caddis larva |
| UnID'd arthropod | dipteran fly | Ceratopogonid larva |
| Pea mussel | meniscus midge | Chironomid pupa |
| F/W limpet | pupa | dipteran fly |
| | Hemiptera | Worm |
| | water scorpion | |
| | Snail | |

*UnID arthropod: - Unidentified arthropod, F/W mite: - fresh water mite

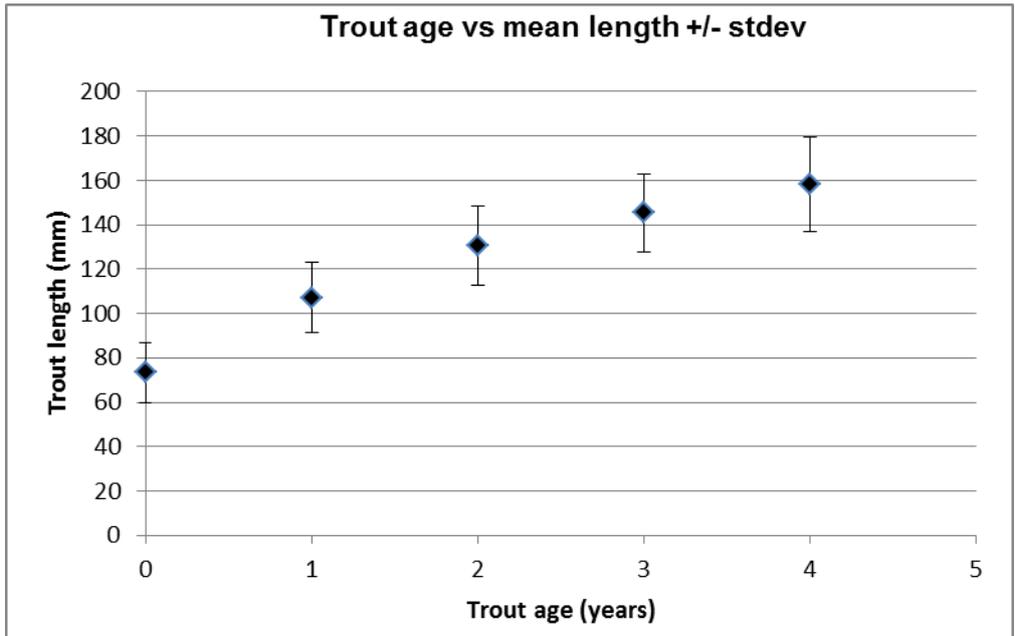
Table 4 shows lists of prey items and their length classes found in trout stomachs from, Loch Coire na h-Airigh and Loch Feur, It shows that trout feed on a variety of animals, and that those eaten mostly belong to the invertebrate bottom fauna.



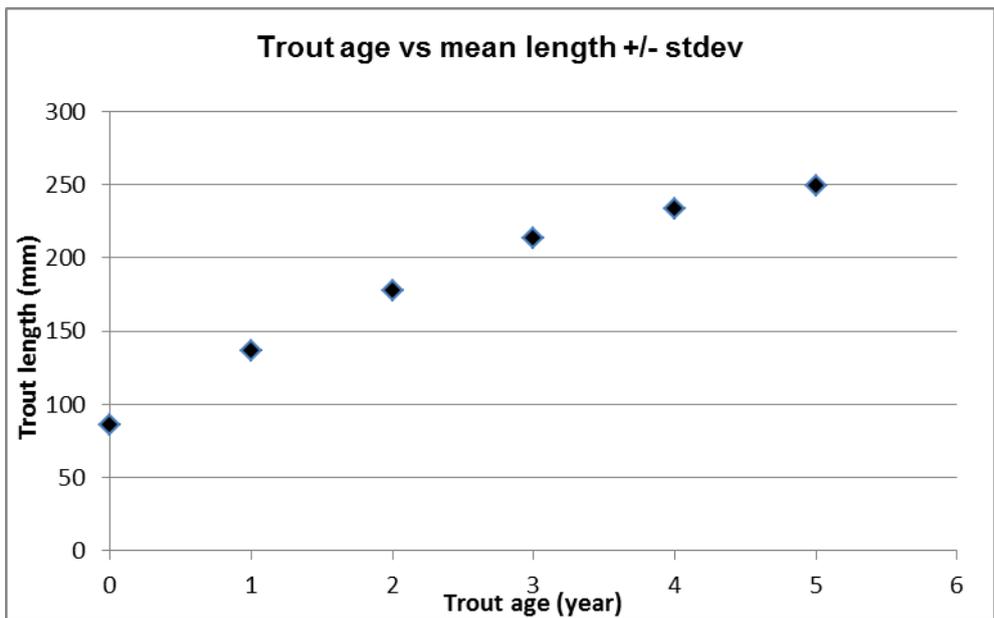
Graph 1. Trout length (mm) vs trout age (yrs) Standard error bar shows the sample mean +/- one standard deviation of 2+ years. There were 5 trout at this age group.



Graph 2. Trout length (mm) vs trout age (yrs) Standard error bar shows the sample mean +/- one standard deviation of 3+ years. There were 13 trout at this age group.



Graph 3. Trout length (mm) vs trout age (yrs) Standard error bar shows the sample mean +/- one standard deviation of 4+ years. There were 4 trout at this age group.



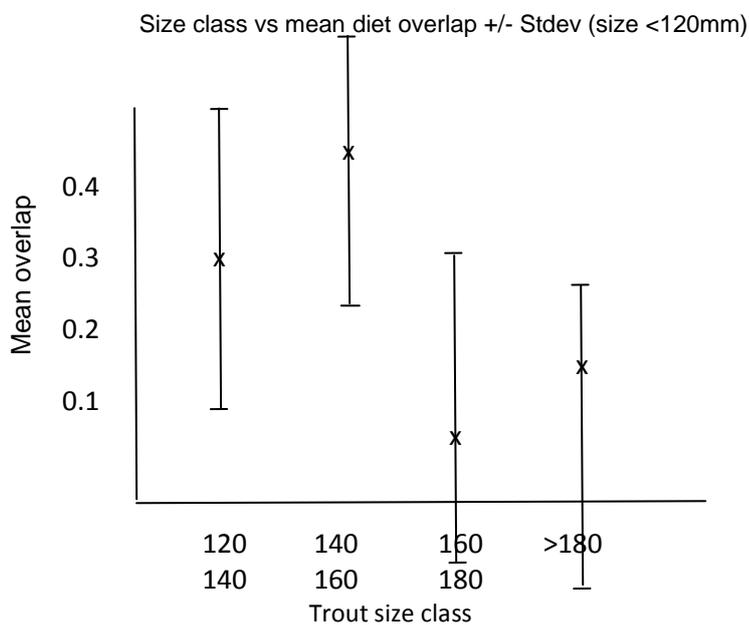
Graph 4. Trout length (mm) vs trout age (yrs) Standard error bar shows the sample mean +/- one standard deviation of 5+ years. There was only 1 trout at this age group.

Graph 1, 2, 3, 4, are showing that the relationship between brown trout age and length. As trout age their length increases but at a diminishing rate.

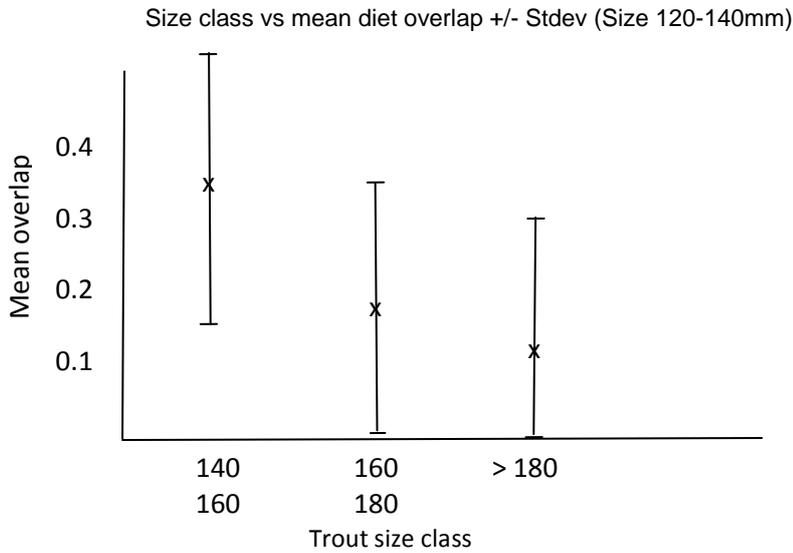
Table 5. Diet Overlap within each size class

| Size class 1 | Size class 2 | Mean diet overlap | Stdev |
|--------------|--------------|-------------------|---------|
| <120 | 120<140 | 0.2991 | 0.21224 |
| <120 | 140<160 | 0.4167 | 0.20106 |
| <120 | 160-180 | 0.0948 | 0.16936 |
| <120 | >180 | 0.1334 | 0.09307 |
| 120-140 | 140<160 | 0.3347 | 0.21694 |
| 120<140 | 160-180 | 0.1932 | 0.18896 |
| 120<140 | >180 | 0.1418 | 0.18164 |
| 140<160 | 160-180 | 0.1334 | 0.11705 |
| 140<160 | >180 | 0.0641 | 0.06155 |
| 160-180 | >180 | 0.0000 | 0 |

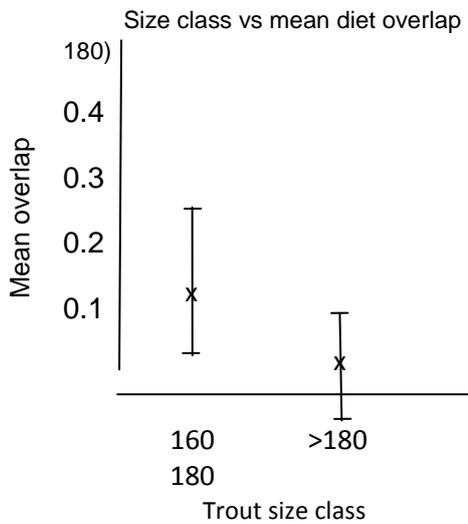
Table 6. Shows diet overlap of brown trout which overlap decreases with size. Diet overlap decreases as size classes more and more dissimilar.



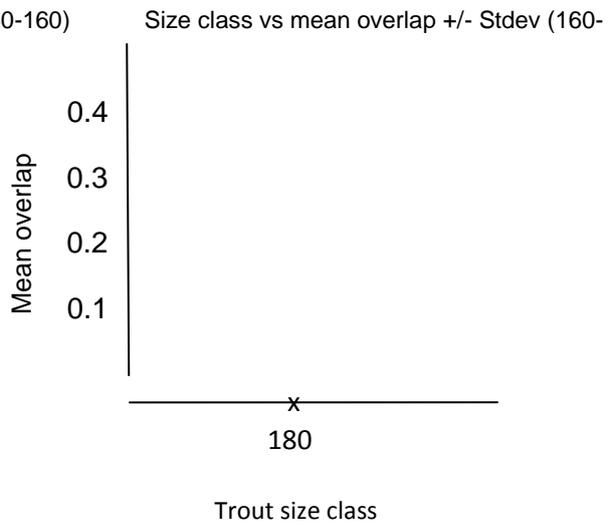
Graph 9. Diet Overlap by age within <120mm.



Graph 10. Diet Overlap by age within 120-140mm.

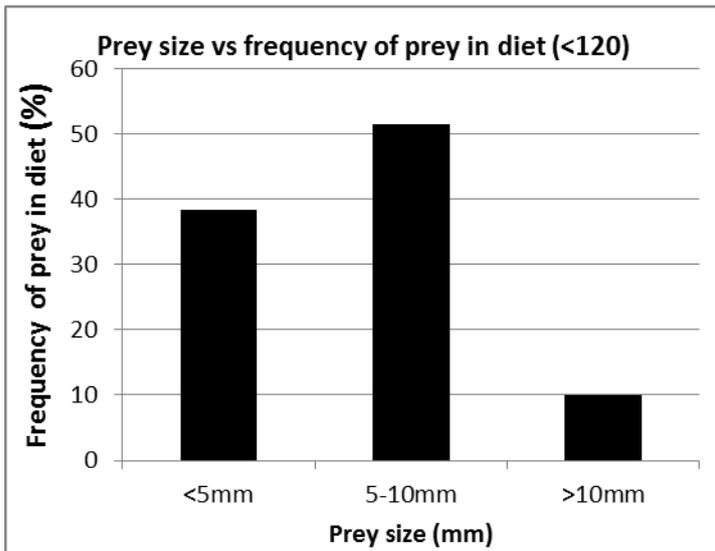


Graph 11. Diet Overlap by age within 140-160mm.

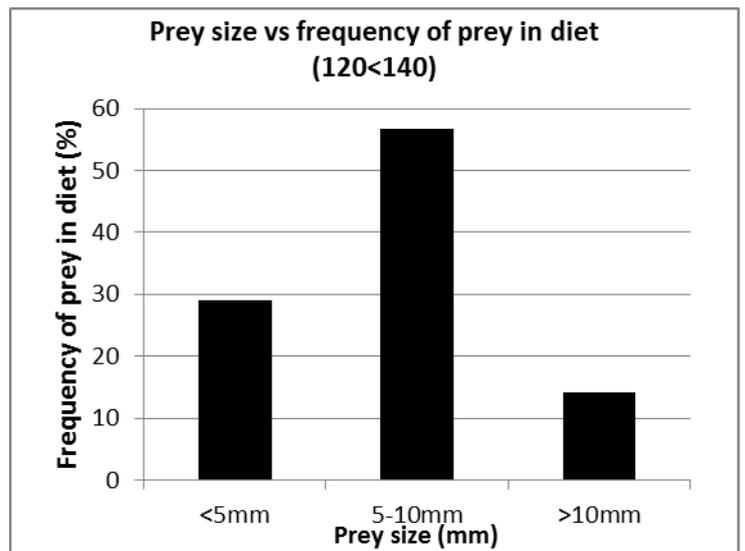


Graph 12. Diet Overlap by age within 160-180mm.

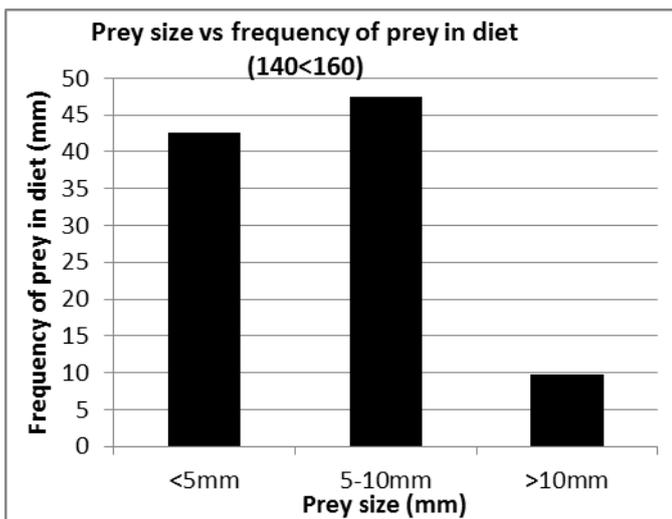
Graph 9, 10, 11, 12 are estimated graph and shows Diet Overlap. Overlap decrease as brown trout gets bigger, overlap lies between 120mm and 140mm, with <120mm being the greatest area for this.



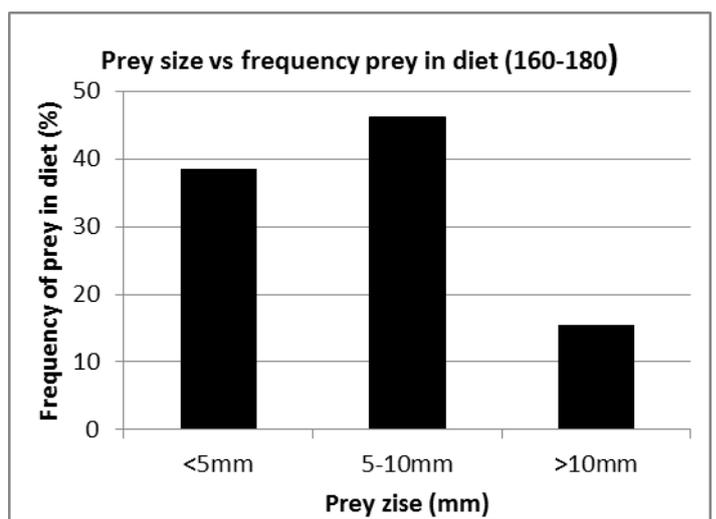
Graph 6. Prey length frequency in (120<140) trout.



Graph 5. Prey length frequency in (<120) trout.



Graph 7. Prey length frequency in (140<160) trout.



Graph 8. Prey length frequency in (160-180) trout.

Graph 5, 6, 7 and 8 shows that in each trout size class, the prey item size class of greatest frequency was 5-10mm. The next most frequent, again in every class, were the <5mm prey items. Prey item of >10mm were least frequent.

CHAPTER IV: Discussion

The main objective of this study was to examine diet of brown trout and analyse scales for age and growth in Loch Coire na h-Airigh and Loch Feur in Wester Ross to estimate the potential for trophic interactions within and between trout size classes within the two Lochs. From Loch Coire na h-Airigh and Loch Feur 21 trout were collected, ranging from 115 to 249mm and 2+ to 5+ years old. From Loch Feur, only 2 trout were collected, of 105 and 130mm both of which were 2+ years old. In comparison to the literature, brown trout from this study showed slow growth (*Table 6*). In other waters trout show more steady growth to large size (c Jonnson *et al.*, 1999). Some of the large trout caught in the Dundonnell lochs grew steadily to 500mm or more; some were found to contain newts as prey items. In Loch Maree, growth of some trout to a large size also seems to be relatively steady. Cunningham (2007) indicates that most lochs in Wester Ross are oligotrophic and trout generally grow more slowly, unless they are present at low densities or the feeding is especially rich (e.g. lochs with farm salmon smolt cages). Geographic location and associated environmental conditions, such as water temperature, which is the determining factor of feeding capacity, seasonality (date and time of capture), stomach fullness, disease, and parasite loads, can affect the growth (Andrew 1997). Cunningham (2007) also ascribes such relatively slow growth to the action of several factors:

- Nutrient availability
- Intraspecific competition
- Diet item or prey size
- Prey handling time
- Size of the loch
- Temperature
- Environmental adaptation
- Spawning
- Parasite

Scale reading for age analysis also shows that most of the scales were closed at the edge of the scale; this indicates a slowing down in the growth which produced the formation of narrow-spaced circuli. In some cases, these will signify that the fish was captured before the start of the next growing season and the closing, therefore, signifies the beginning of a winter band (Shearer 1992).

Table 6. Average length at age and growth relationship for brown trout from different sites.

| Author (s) | Study area | Mean Length (mm) of trout | | | | | |
|--------------------------|---|---------------------------|-----|-----|-----|-----|-----|
| | | 0+ | 1+ | 2+ | 3+ | 4+ | 5+ |
| Present study | Loch coire na h-Airigh and Loch Feur (Scotland) | 62 | 100 | 118 | 130 | 160 | 250 |
| Campbell, 1971 | Loch Lanish, (Scotland) | 87 | 212 | 361 | 431 | 502 | 571 |
| | L.Carn a Chuillin, (Scotland) | 45 | 130 | 258 | 344 | 400 | 490 |
| (Campbell 1979) | Loch Ness (Scotland) | - | 101 | 160 | 200 | 260 | 279 |
| Lobon-Cervia et al, 1986 | River Ucero, (Spain) | - | 110 | 201 | 278 | 342 | 395 |
| Swales, 1986 | Upland Reservoir, (England) | 68 | 101 | 204 | 275 | 306 | 367 |
| Swales, 1986 | Llyn Alaw (Scotland) | - | 102 | 250 | 360 | 480 | 570 |
| Swales, 1986 | Loch Leven (Scotland) | - | 60 | 150 | 270 | 350 | 400 |
| Swales, 1986 | Windermere (Scotland) | - | 95 | 140 | 202 | 360 | 395 |
| Hesthagen et al., 1999 | Sub-Alpine Reservoir, (Norway) | - | 107 | 137 | 185 | 216 | 281 |
| Tabak et al., 2001 | East Black Sea streams (Turkey) | 116 | 146 | 202 | 277 | 362 | 401 |
| Grey, 2001 | Loch ness (Scotland) | - | 90 | 170 | 200 | 300 | 305 |

Table 5. Shows the average length at age and growth of brown trout from different sites and habitats. Regarding the same age classes, fish from the present study are smaller in size than those from the other Loch in the same age. In some sites brown trout grow faster and become slower at certain age at contrary, trout grow slower and in certain age they grow faster.

4.1. Factors influences limiting the growth of brown trout

4.1.1. Intraspecific Competition

Intraspecific competition for food resources and habitat within fish may result in reduced growth, survival and reproductive potential of native fishes (Britton et al., 2011a). Arnott & Elwood (2009) demonstrate that during competition, fish move to improve food intake and growth, to reduce vulnerability to predation risks that vary with fish size and environmental conditions, to seek shelter during high flows and avoid stranding as flows decrease, and to avoid competition with dominant fish. On the current study, Diet Overlap graph 9,10,11,12 indicates that there was competition for food between the trout. High competition levels were

recorded when the trout were young, about <120mm which affected its growth as graph 1,2,3,4 shows, trout were growing slowly compare to other literature (e.g. Grey 2001, Arslan 2007). Competitive effects occur when behavioural interactions cause an unequal distribution of a resource that is directly or indirectly related to growth, survival or recruitment (Wootton, 1998). For example; fishes may alter their diets, and have lower growth rates, in the presence of competing species. Persson & Greenberg (1990) demonstrated that roach had a negative impact on the growth of juvenile perch, with individual growth rates of perch decreasing with increasing roach density, which was related to competition for food resources. In the absence of roach, perch fed mainly upon planktonic cladocerans, whereas in the presence of roach they consumed copepods and macro-invertebrates. Similarly, Amundsen & Gabler (2008) found empirical evidence for food limitation and competition between juvenile Atlantic salmon and Alpine bullhead, resulting in reduced food acquisition and growth rates in Atlantic salmon. Similar interactions have been observed between brown trout and Atlantic salmon, brown trout and Arctic charr, brown trout with brown trout, Atlantic salmon with Atlantic salmon, roach and dace and roach and bream (Nunn *et. al* 2011). Similarly, on the current study, brown trout competed with brown trout which caused slow growth and small size according to the result observed.

4.1.2. Nutrient availability

Fish interacts with habitat by feeding and excreting (Oldham *et al.*, 1997). Several studies have concluded that food availability limits growth of salmonids (Boss and John 2002). Diet quality and quantity is the factor driving fish growth. It may be more appropriate to recognise that fishes have a genetically determined target for body size (perhaps, composition) and that they are capable of recognizing whether the target is achieved or achievable given current environmental and nutritional circumstances. Fish will seek to eat a sufficient amount of an appropriately balanced diet to allow them to achieve their target or preferred performances unless limited by constraint or overridden by an externally managed intervention (Elliott and Hurley 1998). The constraints can be related to dietary factors (nutrient composition, physical characteristics and anti-nutritional factors). For example, on this study, (Graph 5,6,7,8) shows, trout diet was overlapped on each size class and age which all trout, small and large size feed the same kind of prey. It implies that the availability of nutrient/food in the loch was low therefore, these might affected the size and growth of trout. For example, (Table 6), on the present site, the length of trout at age of 2 was 118mm and on another site, Loch Lanish, (Scotland), trout size was 360mm at the same age. Very Different growth showed between the two lochs, the slow growth showed on this study might

be because of the limited factors that have been listed at the above but availability of nutrient/food is the main factor because as Cunningham (2007) stated, in Wester Ross waters, the availability of food is a particularly important factor determining the growth and size of trout.

Furthermore, Boss and John (2002) studied that lack of food limits cutthroat trout growth in small, coastal streams. Solendal (2010) discussed that shortage of food results in reduced growth both in the adult pelagic plankton feeders and their predators. In addition the reproduction is markedly affected by the food supply.

According to Cunningham (2007), the level of nutrients could be decrease with association of grazing. Land use affects the productivity of lochs. Biological productivity in Wester Ross is limited primarily according to the availability of phosphate [PO₄]. Phosphate sources include leaching from soil and basic bedrock and via trophic pathways from animals (birds, amphibians and other fish). Thus, all these factors could limit the growth and size of brown trout on the present study.

4.1.3 Prey size

In general, the average size of food items in the diet increased with increasing body size of the fish. Because of the energetic advantage of feeding on larger prey, salmonoids grow larger when large preys are available (Mittelbach and Persson 1998). Moreover, the slow growth of salmonoids that often occurs because of a lack of suitable prey sufficiently larger to sustain further growth so, on this study, trout showed slow growth this might be because of the prey size were too small to the size of trout . For example, diet overlap (Graph 5), shows that size class <120mm, prey item size class of greatest frequency was 5-10mm (51%). The next most frequent, again in every class, were <5mm (39%) prey items. Prey item of >10mm (10%) were least frequent. This shows that there might be no enough larger or key prey in the loch as they feed only 10% of >10mm prey item thus; this could be the factor that limited trout growth. The result also indicated that trout prefer larger prey as their size increases so they consumed 51% of 5-10mm prey (size class <120mm) item, in fact, trout select food but can only select from what is available. Therefore, there might be more of 5-10mm prey item than other prey item size. Post and McQueen (1994) stated that, trout consume a wide variety of prey but will grow best when key or preferred prey is consumed over other prey. Furthermore, survival of young fish is often regulated by the availability of certain key prey.

4.1.4. *The size of the Loch and burn*

As fish grow they require more space. If nests and eggs are concentrated in a small part of a stream, hatchlings and fry may be too crowded together in some areas when in other areas there is vacant habitat (Elliott and Hurley 1998).

There is burn between the two lochs, Loch Coire na h-Airigh and Loch Feur (*Map 1*). Small burns do not generally have much deep water, which limits the size of fish they can hold, so although these are the areas where much of the trout spawning in the catchment takes place, the young fish have to leave as they get larger (The Tweed Foundation *no date*) so, on this study the trout size were small (Table 3) compared to other studies (Table 6). Young trout drop downstream at all ages and sizes because as fish grow they need more food and space (Elliott and Hurley 1998). A burn generally supports more small trout than large as it has more shallow water than deep so, on the present study, the large trout might migrate to the sea and might become sea trout because as the fish grow, the number of available territories decreases, forcing unsuccessful fish out (The Tweed Foundation *no date*) therefore, more overlaps at small size (*Table 5 and Graph 9, 10, 11 and 12*) which means more food and shelter competition.

4.1.5. *Handling time*

The handling time is usually dependent on the size of the prey (eg. Turesson *et al.*, 2002). Most fishes are visual grabbers, who attack each prey individually according to which size of prey they prefer. Fish and prey size are the predominant influences on the time spent by the fish on each prey item with handling time inversely proportional to fish size (gap width) for a given size prey. This is the basis for diet expansion as a fish grows. The time devoted to handling individual prey items is also influenced by motivational processes, with handling time increasing as station is approached (Woltensohn 2004). According to Wootton *et al.*, (1984), the handling time is determined by the ratio of prey thickness to fish mouth size. Mouth size is, in turn, related to fish length. On the current study, prey item size might be bigger than trout mouth size thus; trout could find it difficult and takes time to swallow which could cause slow growth. For example, Graph 5,6,7,8 shows trout consumed prey item of >10mm were least frequent this could be because trout mouth size smaller than prey size or as mentioned at the above, there were not enough prey item >10mm in the loch (*Appendix 1*).

4.1.6. *Spawning*

Being too big to safely access spawning habitat is another reason why smaller trout which mature at little more than 150mm may be particularly abundant in such lochs they have simply become adapted to their local environment. For example, in this study the average length of 3+ yr was 130mm (Table 3 and 5) and in another study, L.Carn a Chuillin, (Scotland) (Campbell, 1971), the average length was 344mm this might be because the trout on the current site adapted to the loch. Only one trout have reached 5yr+ (249mm) (Table 3) and there were few numbers of large trout than smalls. According to Cunningham (2007), trout were observed spawning in small streams entering three of the larger lochs in the Gairloch Hills (Loch a Mhuilinn, Loch Airigh Mhic Craidh and Loch Airigh a Phuill). At two of the spawning sites, there was evidence of otter predation of spawning fish. Therefore, in this study larger trout could be eaten by otters easily because the spawning streams were all very shallow and there might be very limited spawning gravels in area, large trout would have been less able to move freely from pool to pool than the small trout. Crawford (1996) noted that larger trout were unable to enter the spawning stream flowing into one of her local waters. Within Wester Ross, the occurrence of a few large trout in some lochans with no apparent spawning habitat is sometimes thought to be a result of helping hands (Cunningham 2007).

4.1.7. Temperature

Trout and salmon are able to grow faster when water temperatures are high (up to about 15 °C) than when water temperatures are low survival (Gadomski and Caddell 1991). Because fish are cold blooded, their basal metabolic rate and the maximum rate at which they are able to grow are limited by water temperature. So, the slow growth shows on the current study might be because the water temperature was low. Cunningham (2007) stated that juvenile salmon in high altitude streams at northern latitudes were assumed to be slower growing than those in lowland rivers primarily because of differences in water temperature. Within Wester Ross, some of the fastest fast growing brown trout reaching 350mm aged only 4+ were found in small unnamed shallow lochans near Dundonnell (D2) at 380m and near Gairloch (G1) at 290m. It is possible that summer water temperatures in these shallow lochs were high compared to some of the deeper lochs at lower altitudes. However, evidence that temperature is the major factor limiting growth and production of trout in Wester Ross is lacking. (Cunningham 2007).

Fish generally show temperature optima for growth and survival (Gadomski and Caddell 1991). These may change with age and size, as juveniles of many species prefer

warmer temperatures than adults do. Early life stages may also have different optimal temperatures, which may reflect temporal and spatial field distributions. Further, the combined effects of size and temperature on growth have been described for several fish species.

4.1.8. *Parasitic infection*

Parasitic tapeworms are often found in trout. However, the high abundance of tapeworms and nematodes in trout in Lochan nam Breac near Gairloch led to the suggestion that parasitic infection might be a cause of mortality of trout in this loch, by making infected fish more vulnerable to predation by birds (Cunningham 2007). The two study lochs are located very close to Lochan nam Breac and may be subject to the same parasitic influences five individuals were found to contain intestinal worms. High parasite loads can negatively influence growth rates (Barber *et al.*, 2007) although in this case the presence of parasites could not be shown to have any growth effect.

4.1.9. *Environmental adaptation*

The two lochs are relatively small and are not very deep and also there is burn between the two loch (Map 1) which supports more small trout than large as it has more shallow water than deep, as mentioned at the above, shallow water limits the size of fish they can hold therefore, brown trout might be adapted to their environment (loch) and this could be the factor that slow growth and small size resulted on both sites (Graph 1, 2, 3, 4 and Table 6). As the environmental conditions changes, such as feeding opportunities, water temperature, it allows the fish to respond adaptively with consequences for characters such as growth and developmental rates, reproduction and survival (Stearns 1992). This means that fish with similar genetic constitution raised in different environments can vary but on this study, there were no real measure of genetic diversity to compare with any values elsewhere. Thus, environmental conditions could have significant impact on fish growth and size on the present study.

4.2. *Diet items and dominant prey*

The wide diversity of food types exploited by the fish in Loch Coir na h-Airigh and Loch Feur evidenced that these fish are representatives of all consumer trophic levels. However, at the community level, it was possible to conclude that the most of the energy supporting the fish fauna was derived from insects since individual species widely consumed both food

resources. Crowder & Cooper (1982) suggested that because of high capture rates when prey is plentiful, the feeding niche breadth of a predator will be narrowest when food in a particular site is abundant, this could decrease diet overlap. Although the fish species included more than one kind of food in its diet, the highest dominance by a single food item suggests their abundance in the environment, besides may indicate food active selection.

The majority of prey items in trout stomachs were fully intact and easily identified. The diet of Loch Coire na h-Airgh and Loch Feur trout consisted mainly of aquatic invertebrates, with a portion being terrestrial flying insect larval and pupa stage was the most life stage of aquatic invertebrate found in the trout stomachs, whereas the typical life stage for the terrestrial forms was the winged adult (see *Appendix 1*). The diversity of diet items found within the 23 trout was medium compared to other studies (James 1997) but compared to the area, trout diet was not bad and also it was only one day angling. The most common diet items found in trout stomachs were aquatic invertebrates of caddis larvae, caseless caddis larvae, caddis pupa, caddis case, Culicoides larva and Snail. The most terrestrial diet items were dipteran fly, Beetle and unidentified arthropod. Smaller fish were consuming small size (0+mm) (*Appendix 1 and graph 5, 6, 7, and 8*) caddis larvae and pupa at greater frequency than large fish. Blackfly pupa was found more in smaller trout than large. Snails were found in the stomach of both size classes at high frequency but more common in smaller trout. Other invertebrate diet items that were found in the trout stomachs occurred substantially less often than the other diet groups mentioned previously. It is noteworthy that more terrestrial flying insects (dipteran fly) occurred in the larger fish compared to small fish.

Diet analysis revealed several important things about Loch Coire na h-Airgh and Loch Feur brown trout. First brown trout population consumes a wide variety of invertebrates' prey (*Table 4, Appendix 1*). Both small and large trout are able to consume many of the same invertebrate prey in the loch. This allowed both small and large size trout to consume whatever was available. On this study, small size prey was eaten in greater numbers, for example, (*Appendix 2*), the proportion of item in diet, caddis case at length of 0+mm was 0.452 and caseless caddis larvae at length of 0+mm were 0.333. The large size preys were eaten in fewer numbers for example; the highest proportion of item in diet, caddis larvae 10+mm was 0.154. The large caddis larvae *Dicosmoecus* species was the prey that larger trout were eating. High consumption of *Dicosmoecus* species by trout has also been recorded in the McCloud River (Tippetts and Moyle 1978). Frequent consumption of *Dicosmoecus* species is probably due to the large size of the caddis fly, their abundance during spring and summer and the ease with which they are captured (Glowacki 2003). It seems that smaller fish are not able to swallow them because of the limited size of their

oesophagus or chew them up because of their protective case (Glowacki 2003). Since *Dicosmoecus* sp. seem to be the prey most favoured by larger trout in the Loch Coire na h-Airgh and Loch Feur and then the slow in growth rate and in length at age seen in trout scale samples could be related to decreased availability of caddis larvae.

Based on stomach analysis, of 23 brown trout, caddis larvae were found in almost all trout in both size class and said to be the dominant prey (see *Appendix 1*). The reason caddis larvae were frequently eaten because according to Frost & Brown (1967), caddis larvae with hard, strong cases can be easily seen by trout and it could also associated with seasonal changes, i.e. during certain periods caddis larvae are common but when they have undergone pupation and flown as adults' availability of their aquatic larvae is reduced. However, Allen (1994) gives arithmetical values for forage ratios for salmon parr in the River Eden which would probably also apply to trout. Allen's forage ratios show that the primary factor determining what the trout will eat is probably the availability, accessibility and mobility, prey abundance, prey energy content, prey size selection and seasonal changes (Stergiou and Fourtouni 1991) of food species. An autopsy of such a trout might show that ninety per cent of its contents are *Baetis* and only ten per cent *Simulium* and that it was evidently not feeding at random but was selecting the dun and not the blackfly (Allen 1938).

Similar studies conducted by Frost & Brown (1967) in the River Liffey, at Ballysmuttan, aquatic insect larvae are the main food throughout the year. There are few molluscs and no large crustaceans so the permanent bottom fauna contributes little to the diet. At Straffan, further down-stream, the diet is similar, but there are differences in the degree to which particular insect groups are exploited thus stonefly nymphs are more frequently eaten at Ballysmuttan. These differences can be associated with the relative abundance of the different insects in the fauna at the two places. As mentioned previously, trout select food but can only select from what is available. Another study shown in Windermere, changes in the type of food eaten correspond closely to seasonal changes in the bottom fauna. For example, in summer, from May to July, the larval caddis is a characteristics food and it has probably reached its largest size then. Similarly, in current study, the 23 fishes were collected in summer time, June which, as Frost & Brown (1967) stated, bottom fauna were dominated by caddis larvae (*Appendix 1*) therefore, this might be because caddis larvae were the dominant prey on the present study. The seasonal diet shows clearly the importance of abundance, as well as availability, in determining the kind of organism the trout eats (Frost & Brown 1967).

4.3. *Diet Overlap by age within brown trout*

There was substantial Diet Overlap between the trout of different size classes Table 5 and graph 9,10,11 and 12 shows, most of the overlap lies between 120mm and 140mm, with <120mm being the greatest area for this. The highest overlap size class <120 was 0.4167; size class 120-140 was 0.3347; size class of 140-160 was 0.1334 and the highest overlap size class 160-180 was 0.0000. Overlap decrease as the fish gets bigger this could be because as Heg *et al.*, (2005) stated, salmonid species of a similar size in a similar habitat will overlap broadly in the size and composition of their diet. In addition, in this study, the numbers of large size trout fish were small therefore, less overlap. It might be there was high competition with food when the fishes were young and so small fishes might die or eaten by larger fishes, therefore, very few big fish left. According to Arnott (2009), body size is commonly used as a proxy and is one of the most obvious indicators of fight outcomes because strength is related to size; in intraspecific contests, the larger animal tends to dominate.

Individuals are mainly aggressive against same sized competitors and may ignore smaller and larger sized competitors (Sakai & Kohda 1997, Heg *et al.*, 2005). In one fish species, concepts associated with Hutchinson's rule have been applied (Buston 2002) and non-random distribution in body size ratio is documented. Other examples of size regularity will be from individually territorial fish that share the same home ranges among different sized conspecifics (Sakai & Kohda 1997), where similar sized fish defend territories against each other but accept different sized fish inside their territories, leading to substantial overlap between the territories of dissimilar sized individuals.

4.4. *Diet overlap*

There was considerable dietary overlap between the trout of different size classes which implies that they compete with each other. Graphs 5, 6, 7, 8, for trout show the same kind of prey have been eaten by all size of trout. In each trout size class, the prey item size class of highest frequency was 5-10mm which mostly eaten by the size class of 120<140mm trout which is 57% (*Graph 6*). The second most frequent in every size class were the <5mm prey. >10mm were the least frequent prey item. Therefore, older trout eat much the same kinds of animals as younger fish but take a greater variety of bottom living organisms, both larvae and adult.

Early ontogenetic stages (small size classes) highly depend on insects and zooplankton prey, while the older ontogenetic stages (larger size classes) switch their diets towards larger

macro-invertebrates (Mérona & Mérona 2004). So the frequency of diet overlap on each size class of 160-180mm (*Graph 8*) was towards to the largest prey, which is 17%, also frequency of diet overlap on size class of 160-180 was less comparing to other size class. This suggested that there might be less food competition on larger size classes. Percentage frequency of occurrence provides information on the proportion of fish stomachs containing a particular prey item irrespective of amount. It is, in fact, not a quantity of food but of fish qualified by their diet content (Cailliet 1977). It does not describe the diet of an individual fish, but shows how uniformly the whole group of fish selects a particular prey item without actually indicating the importance of the selected prey item in respect to other prey. From this point of view, the percentage frequency of occurrence provides some information on population-wide food habits.

Allen (1994) discussed selection in the feeding behaviour of salmon parr and found that it was apparent when stomachs contained many food animals but when there were only a few animals in the stomach, there had been random feeding. Fish feeding vigorously tend to select; those that have just begun to feed or are feeding slowly feed at random. When two kinds of fly are equally numerous on the water and a trout choose only one or the other, it must be responding to the highly specific visual stimulus (Frost & Brown 1967). When no animal is particularly abundant, the stimulus need to start feeding is likely to be much less specific and the trout will then take any animals which are available more or less at random. The relationship between the trout's diet and the animals in its environment, can say that the trout is an unspecialised carnivore which feeds mainly by sight. It eats a greater proportion of those animals which are easily captured and noticeable than those which are concealed or difficult to obtain. Tippets & Moyle (1978) states that at times, however, the fish may feed exclusively on one species even though others are equally available therefore, may be because of this reason, the diet of trout overlapped extensively (*Graph 5,6,7,8*). Since they are similar sized species and eat the same food they probably compete directly throughout their lives which might also this reason that the growth of trout showed very slow (*Graphs 1-4*). When the selected animals for example, are blackfly larvae, the trout concentrates not on a transitory source of food but on one which is relatively permanent. The value of selection may be that the trout uses its energy more economically by repeating the same movement many times to snap up larvae instead of changing its feeding movements for different kinds of animals. The full stomachs of trout so feeding testify to the efficiency of this method (Mérona & Mérona, 2004).

CHAPTER V: Conclusion

Gut contents of 23 brown trout were analysed using dissection microscope and their age was identified using scale reading technique. The various food items found in the gut of brown trout in the present study indicate that these species are carnivorous. One major disadvantage of the technique is that it provides a mere snapshot of a diet that may vary substantially over differing temporal scales with regard to ontogeny.

In comparison to the literature, brown trout from this study had a slow growth but relatively to the area, trout growth was not bad. On this study, numbers of factors that have been mentioned on the discussion part may change growth rates during the life of a trout. For example; intraspecific competition is one of growth limiting factors. It typically leads to decreased rates of resource intake per individual, and thus to decreased rates of individual growth or development. Trout diet was overlapped mainly at young age and most of the trout feed the same kind of prey item because of lack of enough nutrient availability which is the main growth limiting factor in Wester Ross waters. According to present study, trout from same loch/body of water have different growth patterns and reach different sizes over a defined period of time so, the result supports to conclude that trout have indeterminate growth. In addition, size by age and diet overlaps could also slow trout growth on current study however; it is premature to conclude that these size and diet overlaps have reduced the growth of trout.

Therefore, to improve the size and growth according to this study, effective management and conservation of brown trout requires recognition and conservation of genetic diversity within and among populations. One of the main arguments for the preservation of such genetic diversity is that it is essential for populations and species to be able to respond to both short-term and long-term environmental challenges.

Reference

- Allen KR (1938). Some observations on the biology of the trout (*Salmo trutta*) in Windemere. *The Journal of Animal Ecology*, 7 (2): 333-349.
- Allen KR (1994). A personal retrospect of the history of fisheries modelling. *In: Population dynamics for fisheries management. Australian Society for Fish Biology Workshop Proceedings, Perth, 24-25 August 1993*. Government Printing Service, Canberra.
- Amundsen, P.A. & Gabler, H.M. (2008). Food consumption and growth of Atlantic salmon *Salmo salar* parr in sub-arctic rivers: empirical support for food limitation and competition. *Journal of Fish Biology*, 73, 250-261.
- Andrew D. Bartels (1997). Growth of Selected Fishes in Navigation Pool 8 of the Upper Mississippi River: A Test of the Flood-Pulse Concept. U.S. *Geological Survey, Environmental Management Technical Centre*. University of Wisconsin-La Crosse.
- Arnott G, Elwood RW (2009). Assessment of fighting ability in animal contests. *Animal Behaviour* 77: 991–1004.
- Arslan Murat, Ayhan Yildirim, Serdar Bektafi, Ali atasever. Growth and Mortality of the Brown Trout (*Salmo trutta*) (2007). Population from Upper Aksu Stream, Northeastern Anatolia, Turkey. *Turk J Zool* :31: 337-346.
- Banaru Daniela, Mireille Harmelin-Vivien (2009). *Feeding behaviour of Black Sea bottom fishes*.
- Bagliniere, J.C. and Maisse, G. (1999). Biology and Ecology of the Brown and Sea Trout. *Springer-Praxis Series in Aquaculture and Fisheries*, Heidelberg.
- Barber Iain, Hazel A. Wright, Stephen A. Arnott & Robert J.Wootton (2007). Growth and energetics in the stickleback–*Schistocephalus* host–parasite system: a review of experimental infection studies.

- Banaru, D., Harmelin-Vivien, M., Gomoiu, M.-T., Onciu, T.-M., (2007). Influence of the Danube River inputs on C and N stable isotope ratios of the Romanian coastal waters and sediment (*Black Sea*). *Mar. Pollut. Bull.* 54, 1385–1394.
- Beverton, R.J.H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *Fish Biol.* 41 (suppl. B): 137–160.
- Björnsson, B., Steinarsson, A. and Oddgeirsson, M. (2001). Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). *ICES Journal of Marine Science* 58, 29-38.
- Boss Shelly M. and John S. Richardson (2002). Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams.
- Britton, J.R., Cucherousset, J., Grey, J. & Gozlan, R.E. (2011a). Determining the strength of exploitative competition from an introduced fish: roles of density, biomass and body size. *Ecology of Freshwater Fish*, 20, 74-79.
- Cailliet GM (1977). Several approaches to the feeding ecology of fishes. In: Sirnenstad CA, Lipovsky SJ (eds) Gutshop 76 Fish food habit studies. *Proec 1st Pacif Northwest Tech Workshop*. Washington Sea Grant Publication, Seattle, p. 1-13.
- Campbell, R.N. (1971). The growth of brown trout *Salmo trutta* L. in northern Scottish lochs with special reference to the improvement of fisheries. *Journal of Fish Biology* 3: 1–28.
- Campbell, R.N. (1979). Ferox trout *Salmo trutta*L., and charr, *Salvelinus alpinus* (L.) in Scottish lochs. *Journal of Fish Biology* 14: 1–29.
- Caroline Gisele Novakowski, Norma Segatti Hahn, Rosemara Fugi (2008). Diet seasonality and food overlap of the fish assemblage in a pantanal pond. *Neotrop ichthyol.* Vol.6 no.4 Porto Alegre.
- Cheung, C.H.Y., P.M. Chaillé, D.J. Randall c, J.S. Gray d, D.W.T. Au (2007). The use of scale increment as a means of indicating fish growth and growth impairment. *Aquaculture* 266, 102–111.
- Cooke Steven J. & Philipp David P. (2009). Centrarchid Fishes. *Diversity, Biology and Conservation*. Published by Blackwell Ltd.

Craig P. Paukert (1987). Spawning Substrate Preferences of Yellow Perch along a Sand–Cobble Shoreline.

Crowder, L. B., and Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, 63: 1802-1813.

Cunningham Peter (2007), Wester Ross Fisheries Trust. *Wester Ross Wild Trout Project. Report for Year 2006 - 2007.*

Degerman, E., I. Naslund & B. Sers (2000). Stream habitat use and diet of juvenile (0+) brown and grayling in sympatry. *Ecol. Freshwater. Fish*, 9: 191-201.

Donald, D. B. & R. S. Anderson (1980). Correlations between Brook Trout Growth and Environmental, Variables for mountain lakes in Alberta. *Transactions of the American Fisheries Society* Volume 109, Issue 6. P. 675-680 .

Elliott J.M (1967). The food of trout (*Salmotrutta*) in a Dartmoor stream. *Journal of Applied Ecology*, 4: 60-71.

Elliott, J. M., (1970). Diet changes in invertebrate drift and the food of trout *Salmo trutta* L. – *J. Fish Biol.* 2: 161–165.

Elliott GV & Jenkins TM (1972). Winter food of trout in three high elevation Sierra Nevada lakes. *California fish and games*, 58: 2213-2237.

Elliott, J.M. (1994). Quantitative ecology and the brown trout. *Oxford series in ecology and evolution*, p. 286.

Elliott, J. M., (1997). Stomach contents of adult sea trout caught in six English rivers. *J. Fish Biol.* 50: 1129–1132.

Elliott, J.M., and Hurley, M.A. (1998). Population regulation in adult, but not juvenile, resident trout (*Salmo trutta*) in a Lake District stream. *J. Anim. Ecol.* 67: 280–286.

Ericksen Randolph P. (1997). Estimation of aging accuracy and precision, growth and sustained yield of costal cutthroat trout in southeast Alaska. Master thesis, University of Alaska, Fairbank, Alaska.

Erickson Randolph P. (1999). Scale Aging Manual for Coastal Cutthroat Trout from Southeast Alaska. *Alaska Department of Fish and Game*.

Falconer DS (1989). Introduction to quantitative genetics. *Longman*, London.

Fischer, W. and G. Bianchi. 1984. FAO species identification sheets for fishery purposes: *Western Indian Ocean (Fishing Area) 51*. Vol. I–V. FAO, Rome.

Fochetti Romolo, Roberto Argano & José Manuel Tierno de Figueroa (2008). Feeding ecology of various age-classes of brown trout in River Nera, Central Italy.

Forseth, T., Hurley, M.A., Jensen, A.J., Elliott, J.M., (2001). Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshw. Biol.* 46, 173–186.

Fraser, C.McL. (1916). Growth of the spring salmon. Trans. 2nd meet. *Pac. Fish. Soc.* 29-35.

Frost W.E & M.E. Brown (1967). *The Trout*. Printed in Great Britain. Collins clear- Type press. London & Glasgow.

Gadomski , D.M., Caddell (1991). Effects of Temperature on Early-life-history Stages of California Halibut *Paralichthys californicus* Fishery Bulletin, U.S. 89, 567-576 (1991).

García DE Jalón, D. (1985). Efectos de la regulación de caudales en las poblaciones de Salmónidos fluviales. *I Simposio Internacional de Estudio, Conservación y Utilización Racional de Áreas de Pesca de Salmónidos, Pamplona*: 106-110.

Geldiay, R. and Balık, S. (1996). Türkiye Tatlısu Balıkları, Ege Üniversitesi Basımevi, İzmir.

Glowacki, S.C. (2003). A comparison of growth rates of wild rainbow trout (*Oncorhynchus mykiss*) in the upper Sacramento River before and after the Cantara Spill of 1991. *M.S. Thesis, Humboldt State University, Arcata, California*. P. 84

Gomoiu, M.-T. (2004). Introduction to Topic 2.1 part Black sea: ecological changes in the Black sea. In: Magni, P., et al., (Eds.). *The Southern and Eastern Mediterranean Sea and the Black Sea: New Challenges for Marine Biodiversity Research and Monitoring: Summary of Discussions*, pp. 22–27.

Grey J. (2001). Ontogeny and dietary specialization in brown trout (*Salmo trutta*) from Loch Ness Scotland, examined using stable isotopes of carbon and nitrogen. *Ecology of Freshwater Fisher*. 10: 168-176.

Gresswell, R. E., and J. D. Varley. (1988). Effects of a century of human influence on the cutthroat trout of Yellowstone Lake. *American Fisheries Society Symposium* 4:45-52.

Heg D. Bender N, Hamilton IM (2005). Strategic growth decision in helper cich-lids. *proc R Soc Londo* 271:s505-S508.

Hesthagen, T., Fløystad, L., Hegge, O., Staurnes, M. and Skurdal, J. (1999). Comparative life-history characteristics of native and hatchery-reared brown trout, (*Salmo trutta*), in a sub-Alpine reservoir. *Fisheries Management and Ecology* 6: 47-61.

Hogasen Helga Rachel (1998). Physiological Changes Associated with the Diadromous Migration of Salmonids. Published by The National Research Council of Canada.

Hunt, P. C., and Jones, J. W. (1972). The brown trout in Llyn Alaw, Anglesey, North Wales. *J. Fish Biol.* 4, 333-352

Hynes HBN (1970). *The ecology of running waters*. Liverpool University Press, Liverpool.

Hyslop, E.J. 1980. Stomach content analysis: A review of methods and their application. *J. Fish Biol.* 17:411-422.

James Brenda Ben (1997). The Feeding Ecology and Conservation of Juvenile Bull Trout, *Salvelinus confluentus*, in an Eastern Cascade stream.

Jonsson, T. F. Næsje, B. Jonsson, R. Saksgård, O. T. Sandlund (1999) The influence of piscivory on life history traits of brown trout. *Journal of Fish Biology* 55 (6), 1129–1141.

Judy Mayo H. (1961). Validity of Age Determination from Scales of Marked American Shad. *Fishery Research Biologist Bureau of Commercial Fisheries*. Published by the US. Fish and Wildlife Service.

Lee, R.M. (1920). A review of the methods of age and growth determination in fishers by means of scales. *Fishery Invest., Lond., ser., vol. 4 NO 2*.

Lin, H.S. (1992). *Coral reefs of Malaysia*. Tropical Press Sdn. Bhd.

Lobon-Cervia, J., Montañés, C.M. and Sostoa, A. (1986). Reproductive ecology and growth of a population of brown trout (*Salmo trutta* L.) in an aquifer-fed stream of Castile (Spain). *Hydrobiologia* 135: 81-94.

Mark, W. And Hofer, R. (1987). Diet spectra and resource partitioning in the larvae and juveniles of cyprinids from a sub-alpine lake. *Oecologia* 71: 388-396.

Martinson, E.C., M.M. Masuda, and J.H. Helle (2000). Back-calculated fish lengths, percentages of scale growth and scale measurements for two scale measurement methods used studies of salmon growth. *N.Pac. Anadr. Fish COmm. Bull. No. 2*: 331-336.

Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management* 40:775-788.

Mittelbach, G.G., and Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* 55: 1454–1465.

Montori Albert, J. Manuel Tierno De Figueroa and Xavier Santos (2006). *The diet of the brown trout salmo trutta* L. During the Reproductive Period: Size-related and Sexual Effect.

Mérona, B. de and J. Rankin-de-Mérona, (2004). Food resource partitioning in a fish community of the central Amazon floodplain. *Neotrop. Ichthyol.* 2(2):75-84.

Mumtaz. E. ~irasinll, Terje ~srgense (1999). *An evaluation of the precision of diet description* Vol. 182: 243-252.

Musk R.S., Britton J.R., Axford S.N. 2006. The effect of subjective fish scale ageing on growth and recruitment analyses: a case study from the UK. *Acta Ichthyol. Piscat.* 36 (1): 81.84.

Nunn, A.D., Tewson, L.H., Taylor, M.J. & Cowx, I.G. (2011). The role of food availability during critical life-stages in determination of the survival and growth of underyearling coarse fish. *Environment Agency Science Project No. SC060048*. EA, Bristol.

Oscoz, J, P. M. Leunda, F. Campos, M. C. Escala and R. Miranda (2005). *Diet of 0+ brown trout (Salmotrutta* L.1758) from the river Erro (Navarra, north of Spain).

Pennell William and Bruce A. Barton (1996). Principle of *Salmonid* Culture Developments in *aquaculture and fisheries science*, volume 29.

Peter B. Moyle, Joseph J. Cech (1988). *An Introduction to Ichthyology*. 2nd edition. Publisher Prentice Hall PTR. p. 495-547.

Persson, L. & Greenberg, L.A. (1990). Juvenile competitive bottlenecks: The perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. *Ecology*, 71, 44-56.

Pinkas, L., M.S. Oliphant and I.L.K. Iverson. (1971). Food habits of albacore, bluefin tuna and bonito in Californian waters. *California Fish Game*, 152:1-105.

Post, J.R. & McQueen, D.J. (1994). Variability in first-year growth of yellow perch (*Perca flavescens*): predictions from a simple model, observations, and an experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2501–2512

Purdom, C.E. (1993). Variation in fish. In: *Sea Fisheries Research* (ed. F.R. Harden Jones) *Elek Science*: London, pp. 347–355.

Schneider, J.C., Laarman, P.W., Gowing, H.(2000). Age and growth methods and state averages. In: Schneider, J.C. (Ed.), *Manual of Fisheries Survey Methods II: With Periodic Updates. Fisheries Special Report. Michigan Department of Natural Resources*, Ann Arbor. vol. 25.

Slaney, P.A., and Ward, B.R. (1993). Experimental fertilization of nutrient deficient streams in British Columbia. *Edited by G. Shooner and S. Asselin. (FQSA). Collection Salmo salar No. 1.* pp. 128–141.

Sire, J.Y., Akimenko, M.A., (2004). Scale development in fish: a review, with description of sonic hedgehog (shh) expression in the zebrafish (*Danio rerio*). *Int. J. Dev. Biol.* 48, 233–247.

Shearer W. M. (1992). Atlantic salmon scale reading guidelines. *Ice cooperative research report NO. 188*.

Smith, I. P., N. B. Metclfe, F. A. Huntingford & S. Kadri (1993). Daily and seasonal patterns in the feeding behaviour of Atlantic salmon (*Salmo salar* L.) in a sea cage. *Aquaculture*, 117: 165-178.

Solendal Per (2010). The University of Sydney Volunteer program. Volunteers on *Ocean Enrichment Project Effect of food increasing fish*.

Steele Mark A. (1997). The relative importance of predation and competition in two reef fishes. *Department of Biological Sciences, University of California, Santa Barbara, CA 93106, USA*.

Stearley , R. F. and Smith, G. R. (1993). Physiology of the Pacific trout and calmons (*incorporhynchus*) and genera of the family Salmonidae. *Trans. Am. Fish. Soc.* 122, 1-33.

Stearns, Stephen C. (1992). *The evolution of Life Histories*. Oxford: oxford University Press.

Stergiou, K. I. & Fournouni, H. (1991). Food habits, ontogenetic diet shift and selectivity in *Zeus faber Linnaeus, 1758*. *Journal of Fish Biology* 39, 589–603.

Swales S. (1986). Population dynamics, production and angling catch of brown trout, *Salmo trutta*, in a mature upland reservoir in mid- Wales. *Environ. Biol. Fish.* 16:279-293.

Tabak, Aksungur, M., Zengin, M., Yılmaz, C., Aksungur, N., Alkan, A., Zengin, B. and Mısır, S. (2001). Karadeniz Alabalı (*Salmo trutta labrax Pallas, 1811*)'nın Biyoekolojik Özelliklerinin Tespiti ve Kültüre Alınabilirliğinin Araştırılması. Proje sonuc raporu. Su Ürünleri Merkez Araştırma Enstitüsü, Trabzon.

The Tweed Foundation (no date). A tweed foundation paper. *Sea-trout & Brown-trout Salmo trutta trutta & Salmo trutta fario*.

Tippets WE & Moyle PB (1978). Epibenthic feeding by rainbow trout in the McCloud River, California. *Journal of Animal Ecology*, 47: 549-559.

Turesson, H., A. Persson, C Bronmark. (2002). Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. *Ecology of Freshwater Fish*. Vol 11. Pg 223-233.

Ursin, E. (1979). Principles of growth in fishes. *Symp. Zool. Soc. London*. 44: 63–87.

Vanderploeg HA & Scavia D (1979a). Two electivity indices for feeding with special reference to zooplankton grazing. *Journal of the Fisheries Research Board of Canada*, 36: 362-365.

Von Cramon-Taubadel, S., Ling, E. N., Cotter, D., and Wilkins, N. P. (2005). Determination of body-shape variation in Irish hatchery-reared and wild Atlantic salmon. *Journal of Fish Biology*, 66: 1471-1482.

Ware, D. M. (1972). Predation by rainbow trout (*salmo gairdneri*): The influence of hunger, prey density, and prey size. *J. Fish. Res. Board Can.* 29, 1193-1201.

Werner EE & Gilliam JF (1984). The ontogenic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematic*, 15: 1042-1052.

Wootton R.J. A functional Biology of Sticklebacks (1984) THE University of College of Wales, Aberystwyth, Library of Congress Cataloguing in Publication Data.

Wootton Robert J. (1998). *Ecology of Teleost Fishes*. 2nd edition. Published by Kluwer Academic Publishers.

Woltensohn Sarah and Lloyd Maggie (2004). *Hand book of laboratory animal management and welfare*. First edition, Blackwell Publishing Company.

<http://getamap.ordnancesurvey.co.uk/getamap/frames.htm>

Appendix 1. Food item in length (mm)

| Food Item | Trout | | | | | | | | | | | | | | | | | | | | | | | | TOTAL |
|---------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|----------|----------|-----------|------------|-------|
| | LFE 23 | LCA 14 | LCA 9 | LCA 21 | LCA 3 | LCA 10 | LCA 6 | LCA 12 | LCA 13 | LCA 1 | LCA 5 | LCA 19 | LFE 22 | LCA 17 | LCA 20 | LCA 8 | LCA 7 | LCA 11 | LCA 16 | LCA 18 | LCA 4 | LCA 2 | LCA 15 | | |
| Odonata nymph 5+ | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | |
| Odonata nymph 10+ | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 13 | |
| Ephemeroptera 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | |
| Ephemeroptera 5+ | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | |
| alderfly 10+ | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | |
| stonefly 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | |
| caddis case 0+ | 0 | 14 | 3 | 1 | 7 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 4 | 0 | 2 | 0 | 4 | 0 | 5 | 0 | 0 | 0 | 50 | |
| caddis case 5+ | 0 | 3 | 0 | 2 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 17 | |
| caddis case 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 7 | |
| caddis pupa 5+ | 0 | 0 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 23 | |
| caddis pupa 10+ | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 5 | |
| caddis larva 0+ | 6 | 0 | 5 | 9 | 1 | 1 | 0 | 4 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 36 | |
| caddis larva 5+ | 0 | 0 | 0 | 2 | 0 | 5 | 0 | 5 | 0 | 0 | 5 | 1 | 3 | 0 | 2 | 10 | 0 | 2 | 0 | 0 | 2 | 2 | 0 | 39 | |
| caddis larva 10+ | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | |
| caddis fly | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | |
| caseless caddis larva 0+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 4 | |
| caseless caddis larva 5+ | 1 | 0 | 0 | 3 | 0 | 1 | 3 | 12 | 4 | 0 | 1 | 2 | 0 | 4 | 4 | 4 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 43 | |
| caseless caddis larva 10+ | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | |
| Ceratopogonid larva 5+ | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | |
| Ceratopogonid larva 10+ | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | |
| Chironomid larva 5+ | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 8 | |
| Chironomid pupa 10+ | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | |
| Crane fly larva <5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | |
| Culicoides larva 5+ | 6 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 5 | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 5 | 1 | 0 | 0 | 0 | 0 | 25 | |
| dipteran fly 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | |
| dipteran fly 5+ | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 8 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 18 | |
| blackfly pupa <5 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | |
| meniscus midge pupa 5+ | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | |
| beetle <5 | 3 | 0 | 8 | 3 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 6 | 0 | 2 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 31 | |
| Hemiptera 5+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | |
| water scorpion 5+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | |
| F/W mite <5 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 4 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 18 | |
| Ostracod <5 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | |
| Cyclopoid copepod <5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | |
| UnID'd arthropod | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 5 | 0 | 0 | 1 | 0 | 15 | |
| Pea mussel | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 12 | |
| Snail | 2 | 7 | 2 | 31 | 5 | 0 | 6 | 1 | 15 | 3 | 8 | 0 | 0 | 0 | 5 | 6 | 3 | 0 | 7 | 3 | 0 | 0 | 1 | 105 | |
| F/W limpet <5 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | |
| Worm | 1 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 26 | |
| TOTAL | 26 | 31 | 52 | 60 | 30 | 13 | 18 | 24 | 27 | 35 | 25 | 12 | 9 | 25 | 17 | 48 | 13 | 20 | 16 | 25 | 6 | 7 | 24 | 563 | |

Appendix 2. Proportion of item in diet

| Proportion of item in diet | LFE 23 | LCA 14 | LCA 9 | LCA 21 | LCA 3 | LCA 10 | LCA 6 | LCA 12 | LCA 13 | LCA 1 | LCA 5 | LCA 19 | LFE 22 | LCA 17 | LCA 20 | LCA 8 | LCA 7 | LCA 11 | LCA 16 | LCA 18 | LCA 4 | LCA 2 | LCA 15 |
|----------------------------|--------|--------|-------|--------|-------|--------|-------|--------|--------|-------|-------|--------|--------|--------|--------|-------|-------|--------|--------|--------|-------|-------|--------|
| Odonata nymph 5+ | 0 | 0 | 0.019 | 0 | 0 | 0 | 0 | 0 | 0.037 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.042 |
| Odonata nymph 10+ | 0 | 0.032 | 0 | 0 | 0 | 0 | 0.167 | 0 | 0.185 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.077 | 0 | 0 | 0.08 | 0 | 0.143 | 0 |
| Ephemeroptera 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.029 | 0 | 0 | 0.111 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.083 |
| Ephemeroptera 5+ | 0.038 | 0 | 0 | 0.017 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.083 |
| alderfly 10+ | 0.038 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.021 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| stonefly 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0.056 | 0 | 0.037 | 0 | 0.04 | 0 | 0.111 | 0 | 0 | 0 | 0.077 | 0 | 0 | 0 | 0 | 0 | 0.042 |
| caddis case 0+ | 0 | 0.452 | 0.058 | 0.017 | 0.233 | 0 | 0 | 0 | 0 | 0.286 | 0 | 0 | 0 | 0.16 | 0 | 0.042 | 0 | 0.2 | 0 | 0.2 | 0 | 0 | 0 |
| caddis case 5+ | 0 | 0.097 | 0 | 0.033 | 0.067 | 0.077 | 0.111 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.059 | 0.021 | 0.077 | 0.2 | 0 | 0 | 0 | 0 | 0 |
| caddis case 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.037 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.12 | 0 | 0 | 0.125 |
| caddis pupa 5+ | 0 | 0 | 0.327 | 0 | 0 | 0 | 0 | 0 | 0 | 0.029 | 0 | 0 | 0.111 | 0 | 0 | 0.021 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0.286 |
| caddis pupa 10+ | 0 | 0 | 0 | 0.05 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0.143 |
| caddis larva 0+ | 0.231 | 0 | 0.096 | 0.15 | 0.033 | 0.077 | 0 | 0.167 | 0 | 0.029 | 0.08 | 0 | 0 | 0.04 | 0 | 0.063 | 0 | 0 | 0.063 | 0.08 | 0 | 0 | 0 |
| caddis larva 5+ | 0 | 0 | 0 | 0.033 | 0 | 0.385 | 0 | 0.208 | 0 | 0 | 0.2 | 0.083 | 0.333 | 0 | 0.118 | 0.208 | 0 | 0.1 | 0 | 0 | 0.333 | 0.286 | 0 |
| caddis larva 10+ | 0 | 0 | 0 | 0 | 0 | 0.154 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0.08 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| caddis fly | 0 | 0 | 0 | 0.033 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| caseless caddis larva 0+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.042 | 0 | 0.029 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.333 | 0 |
| caseless caddis larva 5+ | 0.038 | 0 | 0 | 0.05 | 0 | 0.077 | 0.167 | 0.5 | 0.148 | 0 | 0.04 | 0.167 | 0 | 0.16 | 0.235 | 0.083 | 0.077 | 0 | 0.063 | 0.08 | 0 | 0 | 0 |
| caseless caddis larva 10+ | 0 | 0 | 0 | 0 | 0 | 0.154 | 0.056 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ceratopogonid larva 5+ | 0 | 0 | 0.019 | 0 | 0.067 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.077 | 0.05 | 0 | 0 | 0 | 0 | 0 |
| Ceratopogonid larva 10+ | 0 | 0 | 0.038 | 0 | 0 | 0 | 0 | 0 | 0 | 0.143 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chironomid larva 5+ | 0 | 0.032 | 0 | 0 | 0.067 | 0 | 0 | 0 | 0 | 0 | 0.12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.083 |
| Chironomid pupa 10+ | 0.038 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.042 |
| Crane fly larva <5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.059 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Culicoides larva 5+ | 0.231 | 0 | 0.019 | 0.017 | 0 | 0 | 0.056 | 0 | 0 | 0.143 | 0 | 0.167 | 0.111 | 0 | 0.059 | 0 | 0.077 | 0.25 | 0.063 | 0 | 0 | 0 | 0 |
| dipteran fly 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.021 | 0 | 0 | 0 | 0 | 0 | 0 | 0.042 |
| dipteran fly 5+ | 0.077 | 0 | 0 | 0.017 | 0.033 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0 | 0 | 0 | 0.059 | 0.167 | 0.154 | 0 | 0 | 0.08 | 0 | 0 | 0 |
| blackfly pupa <5 | 0.038 | 0 | 0 | 0 | 0 | 0.077 | 0 | 0 | 0 | 0 | 0 | 0.083 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| meniscus midge pupa 5+ | 0 | 0.032 | 0 | 0 | 0.033 | 0 | 0 | 0 | 0 | 0.029 | 0 | 0 | 0 | 0 | 0.059 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| beetle <5 | 0.115 | 0 | 0.154 | 0.05 | 0.133 | 0 | 0.056 | 0 | 0 | 0 | 0 | 0.083 | 0 | 0.24 | 0 | 0.042 | 0 | 0.05 | 0 | 0.08 | 0 | 0 | 0 |
| Hemiptera 5+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.083 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| water scorpion 5+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.029 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| F/W mite <5 | 0 | 0.032 | 0.038 | 0 | 0.033 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.32 | 0 | 0.083 | 0 | 0.1 | 0 | 0 | 0 | 0 | 0 |
| Ostracod <5 | 0 | 0.032 | 0 | 0 | 0.067 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.063 | 0 | 0 | 0 | 0 |
| Cyclopoid copepod <5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.154 | 0 | 0 | 0.04 | 0 | 0 | 0 |
| UnID'd arthropod | 0 | 0 | 0.038 | 0.017 | 0.033 | 0 | 0 | 0 | 0 | 0.029 | 0 | 0 | 0.111 | 0 | 0 | 0.042 | 0 | 0.05 | 0.313 | 0 | 0 | 0.143 | 0 |
| Pea mussel | 0.038 | 0.065 | 0 | 0 | 0 | 0 | 0 | 0.042 | 0 | 0.114 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.04 | 0.333 | 0 | 0 |
| Snail | 0.077 | 0.226 | 0.038 | 0.517 | 0.167 | 0 | 0.333 | 0.042 | 0.556 | 0.086 | 0.32 | 0 | 0 | 0 | 0.294 | 0.125 | 0.231 | 0 | 0.438 | 0.12 | 0 | 0 | 0.042 |
| F/W limpet <5 | 0 | 0 | 0.038 | 0 | 0.033 | 0 | 0 | 0 | 0 | 0.029 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Worm | 0.038 | 0 | 0.115 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.333 | 0.111 | 0 | 0.059 | 0.063 | 0 | 0 | 0 | 0 | 0 | 0 | 0.417 |

Appendix 3. Coefficient of diet overlap sorted by trout size class

| | Trout | LFE 23 | LCA 14 | LCA 9 | LCA 21 | LCA 3 | LCA 10 | LCA 6 | LCA 12 | LCA 13 | LCA 1 | LCA 5 | LCA 19 | LFE 22 | LCA 17 | LCA 20 | LCA 8 | LCA 7 | LCA 11 | LCA 16 | LCA 18 | LCA 4 | LCA 2 | LCA 15 | |
|-----------------------------|--------|--------|--------|-------|--------|-------|--------|-------|--------|--------|-------|-------|--------|--------|--------|--------|-------|-------|--------|--------|--------|-------|-------|--------|--------|
| | LFE 23 | | 0.096 | 0.337 | 0.396 | 0.289 | 0.131 | 0.308 | 0.267 | 0.19 | 0.347 | 0.311 | 0.419 | 0.183 | 0.239 | 0.327 | 0.373 | 0.362 | 0.407 | 0.291 | 0.383 | 0.054 | 0 | 0.133 | LFE 23 |
| | LCA 14 | | | 0.164 | 0.443 | 0.783 | 0.03 | 0.393 | 0.04 | 0.409 | 0.741 | 0.351 | 0 | 0 | 0.335 | 0.329 | 0.266 | 0.303 | 0.509 | 0.349 | 0.644 | 0.071 | 0.019 | 0.049 | LCA 14 |
| | LCA 9 | | | | 0.188 | 0.337 | 0.039 | 0.126 | 0.072 | 0.083 | 0.269 | 0.127 | 0.303 | 0.317 | 0.324 | 0.113 | 0.274 | 0.079 | 0.184 | 0.154 | 0.362 | 0 | 0.508 | 0.263 | LCA 9 |
| | LCA 21 | | | | | 0.493 | 0.118 | 0.762 | 0.25 | 0.878 | 0.249 | 0.79 | 0.073 | 0.061 | 0.11 | 0.718 | 0.441 | 0.592 | 0.088 | 0.807 | 0.434 | 0.035 | 0.072 | 0.088 | LCA 21 |
| Coefficient of diet overlap | LCA 3 | | | | | | 0.045 | 0.446 | 0.055 | 0.375 | 0.619 | 0.446 | 0.07 | 0.024 | 0.473 | 0.378 | 0.411 | 0.413 | 0.509 | 0.418 | 0.714 | 0 | 0.027 | 0.073 | LCA 3 |
| Sorted by trout size class | LCA 10 | | | | | | | 0.146 | 0.482 | 0.039 | 0.012 | 0.469 | 0.248 | 0.634 | 0.126 | 0.343 | 0.556 | 0.067 | 0.277 | 0.037 | 0.075 | 0.464 | 0.496 | 0 | LCA 10 |
| | LCA 6 | | | | | | | | 0.376 | 0.867 | 0.214 | 0.632 | 0.216 | 0.066 | 0.195 | 0.8 | 0.392 | 0.731 | 0.215 | 0.644 | 0.476 | 0 | 0.115 | 0.079 | LCA 6 |
| | LCA 12 | | | | | | | | | 0.28 | 0.06 | 0.359 | 0.387 | 0.271 | 0.318 | 0.614 | 0.456 | 0.208 | 0.084 | 0.19 | 0.277 | 0.295 | 0.216 | 0.006 | LCA 12 |
| | LCA 13 | | | | | | | | | | 0.184 | 0.682 | 0.088 | 0.015 | 0.081 | 0.727 | 0.338 | 0.62 | 0 | 0.749 | 0.411 | 0 | 0.089 | 0.105 | LCA 13 |
| | LCA 1 | | | | | | | | | | | 0.219 | 0.138 | 0.152 | 0.254 | 0.217 | 0.198 | 0.216 | 0.59 | 0.252 | 0.588 | 0.197 | 0.066 | 0.032 | LCA 1 |
| | LCA 5 | | | | | | | | | | | | 0.127 | 0.396 | 0.065 | 0.738 | 0.667 | 0.555 | 0.116 | 0.616 | 0.375 | 0.315 | 0.287 | 0.127 | LCA 5 |
| | LCA 19 | | | | | | | | | | | | | 0.439 | 0.226 | 0.423 | 0.359 | 0.155 | 0.297 | 0.083 | 0.133 | 0.105 | 0.114 | 0.672 | LCA 19 |
| | LFE 22 | | | | | | | | | | | | | | 0 | 0.289 | 0.554 | 0.106 | 0.375 | 0.17 | 0.03 | 0.429 | 0.697 | 0.298 | LFE 22 |
| | LCA 17 | | | | | | | | | | | | | | | 0.19 | 0.354 | 0.069 | 0.391 | 0.048 | 0.412 | 0 | 0 | 0 | LCA 17 |
| | LCA 20 | | | | | | | | | | | | | | | | 0.655 | 0.666 | 0.221 | 0.611 | 0.415 | 0.154 | 0.168 | 0.186 | LCA 20 |
| | LCA 8 | | | | | | | | | | | | | | | | | 0.497 | 0.321 | 0.366 | 0.472 | 0.309 | 0.42 | 0.192 | LCA 8 |
| | LCA 7 | | | | | | | | | | | | | | | | | | 0.251 | 0.502 | 0.481 | 0 | 0.061 | 0.072 | LCA 7 |
| | LCA 11 | | | | | | | | | | | | | | | | | | | 0.132 | 0.317 | 0.132 | 0.181 | 0 | LCA 11 |
| | LCA 16 | | | | | | | | | | | | | | | | | | | | 0.303 | 0 | 0.169 | 0.07 | LCA 16 |
| | LCA 18 | | | | | | | | | | | | | | | | | | | | | 0.061 | 0.172 | 0.123 | LCA 18 |
| | LCA 4 | | | | | | | | | | | | | | | | | | | | | | 0.341 | 0 | LCA 4 |
| | LCA 2 | | | | | | | | | | | | | | | | | | | | | | | 0 | LCA 2 |